

***Alosa alosa* and *Alosa fallax* spp. Literature Review and Bibliography**

R&D Technical Report W1-014/TR

M. W. Aprahamian
C. D. Aprahamian
J. L. Baglinière
R. Sabatié
P. Alexandrino

Research Contractors
Environment Agency
UMR INRA-ENSA
ENSAR
University of Porto



University of Porto

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The aim of this report is to provide fish biologists and fisheries managers with an overview of the biology, status and conservation options for *Alosa alosa* and *Alosa fallax* species.

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Aprahamian, M. W.⁽¹⁾, Aprahamian, C. D.⁽¹⁾, Baglinière, J. L.⁽²⁾, Sabatié, M. R.^(2,3), Alexandrino, P.⁽⁴⁾,

- (1) The Environment Agency P.O Box 12, Fairclough House, Knutsford Road, Warrington WA 4 1HG, UK.
- (2) UMR INRA-ENSA Ecobiologie et Qualité des Hydrosystèmes Continentaux, 65 rue de Saint-Brieuc, 35042 Rennes Cedex, France
- (3) Laboratoire d'Halieutique, ENSAR, 65 rue de Saint-Brieuc, 35042 Rennes Cedex, France.
- (4) Animal Genetics and Conservation Unit, Faculdade de Ciências, Universidade do Porto, Campus Agrário de Vairão, R. Monte Castro 4480 Vila do Conde, Portugal.

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ALOSA ALOSA; *ALOSA FALLAX FALLAX*; *ALOSA FALLAX RHODANENSIS*; *ALOSA FALLAX NILOTICA*; *ALOSA FALLAX ALGERIENSIS*; *ALOSA FALLAX LACUSTRIS*; *ALOSA FALLAX KILLARNENSIS*; NOMENCLATURE; TAXONOMY; MORPHOLOGY; DISTRIBUTION; HYBRIDIZATION; REPRODUCTION; SPAWNING; ONTOGENY; GROWTH; DIET; DISEASE; PARASITE; INTER- & INTRA-SPECIFIC INTERACTIONS; HOMING; MIGRATION; SEX RATIO; AGE STRUCTURE; RECRUITMENT; MORTALITY; POPULATION DYNAMICS; EXPLOITATION; FISHING EQUIPMENT; FISHING AREA, FISHING SEASONS; CATCHES; HABITAT PROTECTION AND MANAGEMENT; CONSERVATION STATUS; FISH PASS; CULTURE.

PREFACE

This review is for those who have and will work on *Alosa*, to the commercial fisherman and recreational anglers who make their living or obtain pleasure and relaxation from their capture. It is also for the many people we have worked with us over the years, without whose help little would have been achieved and to the many who have freely contributed information and knowledge in the true spirit of collaboration, we hope we have not abused their generosity.

We acknowledge that there still exists mistakes in this draft, especially in the references. We have supplied as much detail as we can but appreciate that in many instances it is incomplete. For this and other errors we apologise, we will, however, endeavour to correct these over time and maintain the review up to date and to help us achieve this we welcome any feedback. In the future we hope the review will be made available on the Internet.



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EXECUTIVE SUMMARY

The review is divided into seven sections:

- Identity: nomenclature, taxonomy and morphology.
- Distribution: European and North African distribution, factors affecting abundance and hybridization
- Bionomic and Life history: reproduction, spawning, ontogeny, growth, diet, disease, parasite, inter- & intra-specific interactions, homing & migration.
- Population (spawning stock): sex ratio, age structure, recruitment, mortality, and population dynamics.
- Exploitation: fishing equipment, area, seasons and catches and the influence of climate on the population.
- Protection and Management: conservation status, protection and management of *Alosa* habitat and fish pass design.
- Enhancement: Culture: collection of spawn and eggs, rearing of larval and juvenile stages.

The review focuses on the European and North African literature with the exception of the section dealing with culture. The section on culture relies on material mainly from North America. Though European alosoids have been cultured the majority of the work was carried out during the second half of the eighteenth and the first half of the nineteenth century. It was therefore considered appropriate to provide a summary of the latest findings in order to take on board some of the more recent advances in culture techniques.

The bibliography contains *c.* 1500 references relating to *Alosa alosa* and *Alosa fallax* spp., it can also be provided in an electronic version. The electronic version (Endnote) incorporates reference abstracts and notes on their contents, together with key words to aid searches.

The shads belong to the subdivision Clupeomorpha. The clupeomorphs are characterised by having ducts running anteriorly from the swim bladder into the skull and sharp bony scutes along their ventral surface. The number of gill rakers on the first gill arch and geographical location have both been used to identify species and subspecies. In the Eastern Atlantic and Mediterranean four species of *Alosa* have been recognised; *Alosa alosa* (Linnaeus, 1758), *Alosa fallax* (Lacépède, 1803), *Alosa macedonica* (Vinciguerra, 1921) and *Alosa caspia* (Eichwald, 1838). No subspecies have been reported for *A. alosa* or for *A. macedonica*, while for *A. fallax* six subspecies have been reported:

Alosa fallax fallax (Lacépède, 1803)
Alosa fallax rhodanensis (Roule, 1924).
Alosa fallax nilotica (Geoffroy Saint-Hilaire, 1808)
Alosa fallax algeriensis (Regan, 1916)
Alosa fallax lacustris (Fatio, 1890)
Alosa fallax killarnensis (Regan, 1916)

It is acknowledged that considerable confusion remains over the systematics of *Alosa fallax* spp. and this ultimately will need to be addressed, especially as there is a move away from subspecies. It has been argued that the following should be reclassified: *Alosa fallax algeriensis* as *Alosa algeriensis*, *Alosa fallax killarnensis* as *Alosa killarnensis* and *Alosa fallax lacustris* as *Alosa agone* (Scopoli, 1786). It has also been suggested that, until explicit data were available the three subspecies *Alosa fallax fallax*, *Alosa fallax nilotica* and *Alosa fallax rhodanensis* should be classified as *Alosa fallax*. This reclassification was on the basis of differences in morphology, habit, life history, and ontogeny. However, for this literature review it is proposed to adopt the classification of Hoestlandt (1991) and Quignard & Douchement (1991e).

Alosa alosa and *Alosa fallax* have been reported from as far North as Iceland at the northern most limit of their range, to Morocco in the south and as far east as Scandinavia and the Baltic Sea. *Alosa alosa* have been reported only from the western part of the Mediterranean, while *Alosa fallax* are encountered through out the Mediterranean. *Alosa fallax rhodanensis* is distributed along the northern coast of the western Mediterranean Sea ranging from Spain to southern Italy while *Alosa fallax nilotica* is distributed around the eastern Mediterranean with its range extending southward down to the River Nile. *Alosa fallax algeriensis* is found along the North African coast from the Rif Peninsula to Tunisia. The landlocked, *Alosa fallax lacustris*, is present in Italy, Sardinia and Montenegro. In Southwest Ireland, a landlocked population of *A. fallax*, (*Alosa fallax killarnensis*) exists in Lough Leane its isolation possibly due to local tectonic changes.

There has been a considerable decline in abundance of *Alosa* spp. throughout their geographic range. It is for this reason that the species have been included in Appendix III of the Bern Convention and into Annexes II and V of the EC Habitats Directive. The main reason for this decline has been the construction of dams preventing access to their spawning grounds. In some river systems this has resulted in the extinction of one and / or both species of *Alosa* and in some cases to hybridization. The prevalence of hybridization appears related to the presence of obstructions to the free passage of migrants upstream resulting in the use of communal areas for spawning. The effect of barriers may have been exacerbated by overfishing as fish congregate and become easier to capture below obstructions. Pollution (poor water quality), especially in the lower reaches and estuaries has also been identified as a threat for anadromous populations and also for some of the landlocked population such as *Alosa fallax lacustris* in Lake Maggiore. Habitat destruction has also been implicated for their decline. This can occur as part of a reengineering scheme to improve navigation and for flood defence purposes, or as a consequence of gravel extraction effectively impacting on the species spawning habitat.

Anadromous alosine mature between 2 and 9 years old with females maturing mainly between 4 and 6 years and males a year earlier. The landlocked populations mature on the whole a year earlier than the anadromous forms. Anadromous *Alosa alosa* has a semelparous life history, while the landlocked form are iteroparous. Except for the most southerly populations in the Sebou and Loukos *Alosa fallax* spp. are multiple spawners. A maximum of seven spawnings has been recorded for *Alosa fallax fallax* and *Alosa fallax nilotica*. The oldest anadromous *Alosa alosa* recorded is 8 years for females and 7 years for males, for *Alosa fallax* spp the maximum age reported is 12 for females and 10 for males. For landlocked populations their longevity is lower 5 for *Alosa alosa* and 4 to

5 for *Alosa fallax* spp. For anadromous *Alosa fallax* a latitudinal cline exists with fish at the northern limit of their range living longer, between 7 and 12 years compared to those at the southern limit where longevity of 5 or 6 years appears normal. The fact that the fish live longer further north and that there is little difference in the age at which fish mature would suggest that the proportion of repeat spawners in the population should increase with latitude.

For *Alosa alosa* absolute fecundity ranges from 50,000 to 636,000 eggs and relative fecundity from 60,000 to 236,000 eggs/kg while for *Alosa fallax fallax* absolute fecundity ranges from 25,942 to 675,000 eggs and relative fecundity from 42,540 to 302,358 eggs/kg. For *Alosa fallax nilotica* the relative fecundity is lower at approximately 80,000 eggs/kg and is less than that of its landlocked conspecific of between 200,000 and 300,000 eggs/kg. The absolute fecundity of the landlocked populations is lower than that of the anadromous forms reflecting in part their smaller size.

The timing of the spawning migration of adults into fresh water occurs along a latitudinal gradient from south to north, and takes place from December to August, mainly during the day. Water temperature, is the most important environmental factor moderating migratory behavior. The freshwater phase of the spawning migration generally take place when temperature ranges from 12 to 20° C, at temperatures below 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. River discharge also has an influence, notably by halting the migration during strong spates.

Spawning takes place in fresh water during the night. During the day the fish shelter in groups along the shore or on the bed of the river. At dusk the fish move on to the spawning shoals. During the night the fish come up to the surface. The males and females, half submerged and along side each other swim in a circular motion violently thrashing the surface of the water with their caudal fin, releasing sperm and eggs into the water column.

For *Alosa alosa*, *Alosa fallax fallax*, *Alosa fallax rhodanensis* and certain populations of *Alosa fallax nilotica* spawning takes place in the main river and major tributaries of the catchment. The fish deposit their eggs onto a substrate which can vary from sand (20µ to 2mm) to pebbles (20 to 200 mm), in water of depth 0.5 to 3.0m and where the current ranges from 0.5 to 2.0ms⁻¹. For *Alosa fallax lacustis* spawning takes place near the shore of the lake. Eggs (1.7 – 4.5mm) successfully develop between 15°C and 25°C. Incubation takes 65 to 240h depending on temperature. Larvae measure between 4 and 12mm at hatching. After hatching the larvae of the anadromous forms migrate transversely into areas of lower current velocity where the juvenile stages can be found from mid-May until mid-September. For *Alosa fallax fallax* temperature preferences for larvae between 7.7 and 15.2 mm were in the range 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+) avoid areas of low dissolved oxygen (<4 mgL⁻¹), the majority being caught in water of between 4 and 5 mgO₂L⁻¹. Seaward emigration occurs in shoals in the surface layers of the water column, taking place in the autumn and winter of their first year of life. Their emigration occurring earlier in southern rivers. The juvenile migration is modulated by water temperature and river discharge. Their residence time in the estuary is poorly

understood. Most young of the year reach the sea at the beginning of winter at lengths ranging from 45 to over 120 mm TL and weighing 2 to 20 g.

The adults do not feed while on their spawning migration in fresh water. During the freshwater phase of the spawning migration there was a gradual loss of condition ($\text{weight} \cdot 100 / \text{length}^3$) during the period. The weight loss associated with the migration and spawning has ranged from 30 to 59% being generally higher for females than for males. In the River Douro and in the Gironde-Garonne-Dordogne system the amount of protein and lipid in the muscle decreased as *Alosa alosa* migrate from the estuary into fresh water for spawning. The protein content of female fish declined in the River Douro stock, while in the Gironde-Garonne-Dordogne a slight increase was reported. The decline in lipid and protein content in the muscle and liver relates in part to the energetic costs of migration and to the remobilization of the lipid and protein, associated with maturation of the gonads. The lipid and protein content of the ovary and testis increased as spawning is approached.

Juvenile alosinae consume mainly insect larvae in fresh water and zooplankton in the estuary. At sea Mysidacea and fish dominate the diet of *Alosa fallax* spp., while for *Alosa alosa* euphausiids and zooplankton were consumed most frequently. Landlocked populations predominantly consume plankton particularly cladocerans and copepods.

Growth of *Alosa alosa* was fastest in the River Douro followed by those from the rivers Mondego, Loire, Lima and Sebou. On those systems where studies had been carried out over a number of years significant temporal differences were evident, particularly on the Loire, Gironde-Garonne-Dordogne and Adour. For *Alosa fallax fallax* the fastest growing populations were in the Mondego followed by the Nyamunas and Lima rivers. Little difference in growth exists between other populations from the Sebou, at the southern limit of their range to the Severn towards their northern limit. In the Tiber growth of *Alosa fallax rhodanensis* in the first year was faster than in French populations, though not for those which had migrated into the Vaccarès lagoon. However, in older age groups growth was faster in French stocks. French stocks were heavier than those from the Tiber when fish of the same age were compared. For *Alosa fallax nilotica* of a given age the River Po population is smaller at ages one and two compared with populations from the Balkans, though for fish three years and older there is little difference in length at age. The maximum size would appear to be greater in the Balkan populations, with males reaching at least 508 to 543 mm and females 546 to 560 mm, compared with 454 and 477 mm for males and females from the Po river. Females were heavier than males with a maximum weight of 2.4 kg compared to 1.9 kg for males. For the land locked *Alosa fallax* spp. their growth in the first year is faster than in the anadromous forms.

Protein, meristic and morphometric differences indicate separate populations of *Alosa* exist and that in order to maintain these differences homing must take place to their natal river. Protein differences indicated that of the eleven populations of *Alosa fallax* studied three groups are apparent. 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.

At sea *Alosa alosa* and *Alosa fallax* are coastal in their habit and are clumped in aggregations around the major catchments for reproduction. *A. alosa* has been reported from depths ranging from 10 to 150m up to *c.* 300m and *A. fallax* from 10 to 110m with a preference for water of 10 to 20m deep. In the Adriatic, *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. In relation to water temperature, *A. alosa* in Moroccan coastal waters were found to be closely associated with water in the temperature range of 14 to 18°C.

The *Alosa alosa* population in the Gironde-Garonne-Dordogne system is regulated through density dependent processes while *Alosa fallax*, towards the northern limit of their range, is controlled through density independent factors specifically temperature. However, there is little information on their population dynamics.

The most important commercial species in Europe is the allis shad. 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 developed in France and in Britain for the twaite shad. Various types of fishing gear are used by the commercial fisheries, the two commonest being the stop net and trammel net. From 1978 to 1998, approximate total landings ranged from 355 to 1,198 tonnes in the current distribution area. About 94% of the total landings are in France and 89% from the Gironde-Garonne-Dordogne system alone. Indeed, catches in this system range from 338 to 1007 tonnes and are very high compared to other rivers. Catches in the River Loire are low, often not exceeding 10 tonnes and declining sharply to about 1 tonne in the years 1995 and 1996. Average catches in the Adour River were approximately 19 tonnes between 1985-1999.

The main conservation options available for the protection and enhancement of *Alosa* populations are reviewed. These include the construction of fish passes to ensure unhindered access to their spawning grounds. Similarly there should not be a water quality barrier preventing access to their spawning areas and no siltation of their spawning grounds. In addition their incorporation into the EC Habitats Directive places an obligation of members of the European Union to assess numbers and exploitation of the populations and to designate Special Areas for Conservation (SAC) / Sites of Community Interest (SCI) to safeguard populations

There have been a number of studies carried out during the second half of the eighteenth – first half of the nineteenth century, which were concerned with the artificial propagation of European alosines. Since then there has been little published information on their culture. In recent years there have been great advances in the techniques used in the artificial culture of *Alosa*, especially in the USA, and this information forms the basis of the summary for alosine culture in this review.

1. IDENTITY

1.1 Nomenclature

1.1.1 Valid name

The valid scientific name for the:

- Allis shad is *Alosa alosa* (Linnaeus, 1758),
- Eastern Atlantic anadromous twaite shad is *Alosa fallax fallax* (Lacépède, 1803),
Western Mediterranean twaite shad is *Alosa fallax rhodanensis* (Roule, 1924) [Roule 1924a],
- Eastern Mediterranean twaite shad is *Alosa fallax nilotica* (Geoffroy Saint-Hilaire, 1808),
- Algerian twaite shad is *Alosa fallax algeriensis* (Regan, 1916),
Agone is *Alosa fallax lacustris* (Fatio, 1890),
- Killarney shad is *Alosa fallax killarnensis* (Regan, 1916),

but see also section 1.2.2 (Taxonomic status)

1.1.2 FAO Code

| | | |
|--|---|-------------------|
| <i>Alosa alosa</i> (Linnaeus, 1758) | - | 1210501104 |
| <i>Alosa fallax fallax</i> (Lacépède, 1803) | - | 1210501105 |
| <i>Alosa fallax rhodanensis</i> (Roule, 1924) | - | 1210501105 |
| <i>Alosa fallax nilotica</i> (Geoffroy Saint-Hilaire, 1808) | - | 1210501105 |
| <i>Alosa fallax algeriensis</i> (Regan, 1916) | - | 1210501105 |
| <i>Alosa fallax lacustris</i> (Fatio, 1890) | - | 1210501105 |
| <i>Alosa fallax killarnensis</i> (Regan, 1916) | - | 1210501105 |

1.1.3 Synonyms

- **Generic** (Svetovidov, 1952; Hoestlandt, 1991; Eschmeyer, 1998)

Alosa Linck, 1790: 6(3) 35; Cuvier, 1829:319

Pomolobus Rafinesque, 1820: 2(3), 170

Alausa Valenciennes, 1847: 20, 389

Alausella Gill, 1861: 36, Suppl.54

Clupeonella (non Kessler) Berg, 1913a: 2 (3)

Caspialosa Berg, 1915: 4(6), 4

Paralosa Roule, 1925: 73

Specific (Svetovidov, 1952; Whitehead, 1985; Quignard & Douchement, 1991a; Kartas, 1991; Kottelat, 1997; Eschmeyer, 1998).

Alosa alosa (Linnaeus, 1758)

Alosa alosa (Linnaeus, 1758): Regan, 1916 (8) 18:8; Lozano Rey, 1935, 5:38 fig. 9a, pl. 1.1; Fowler, 1936: 169, fig. 67; Poll, 1947, 138, fig. 91; Berg, 1948: 145; Svetovidov, 1952: 312, pl. 25, fig.1; Albuquerque, 1954-56: 218, fig. 119, 120a; Svetovidov, 1963: 351, pl. 25, fig.1; Wheeler, 1969a: 127, fig.49; Svetovidov, 1973: 105; Wheeler, 1978a: 70, fig.; Whitehead, 1984: 269, fig.; Poll *et al.*, 1984:41; Whitehead, 1985: 194; Wheeler, 1985: 24-25; Whitehead, 1990: 208; Kottelat, 1997: 37.

Clupea alosa Linnaeus, 1758:318;

Alosa communis Yarrell, 1836, 4: 136.

Alausa vulgaris Valenenciennes, 1847, 20: 391 pl.604.

Alosa rusa Mauduyt, 1849: 49.

Alosa cuvieri Malm, 1877:**154 or 654.**

Alosa vulgaris Moreau, 1881, 3:456.

Clupea alosa Day, 1880-4, 2, 234, pl.CXL; Hoek, 1899: 156; Joubin & Le Danois,

1924, 1:15; Kyle & Ehrenbaum, 1927, XII:13; Schnakenbeck, 1931;

Andersson, 1942: 254; Soljan, 1948: 248.

Clupea alosa var.B. *alosa* Smitt, 1895:985, fig. 249b.

Alosa fallax fallax (Lacépède, 1803)

Alosa fallax fallax (Lacépède, 1803): Berg, 1948: 144; Svetovidov, 1952: 310, figs 51, pl. 24 fig. 2; Poll *et al.*, 1984: 41; Whitehead, 1985: 199; Whitehead, 1990: 209; Quignard & Douchement, 1991b: 225, fig. 57; Kottelat, 1997: 38.

Alosa ficta Duhamel du Monceau, 1772:320.

Alosa fallax Lacépède, 1803: 5: 424, 452.

Clupea rufa Lacépède, 1803: 452

Clupea finta Cuvier, 1829, 2:320; Hoek, 1899: 156; Joubin & le Danois, 1924, 1:17; Kyle & Ehrenbaum, 1927, I:12; Schnakenbeck, 1931:120; Andersson, 1942:254, pl.67.

Alosa finta Moreau, 1881, 3:456; Day, 1880-4,2:236, pl.CXLI; Regan, 1916, (8),18:6.

Clupea alosa var. *A.finta* Smitt, 1895:984, fig248,249a, pl.XLIII(fig.2).

Paralosa fallax Roule, 1925: 78.

Alosa fallax Lozano Rey, 1935, 5:42, fig. 2; Poll, 1947: 141, fig. 92; Albuquerque,

1954-56: 219, fig. 119, 120B; Wheeler, 1969a: 128, fig. 50; Wheeler, 1978a: 68, fig..

Alosa fallax rhodanensis (Roule, 1924).

Alosa fallax rhodanensis (Roule, 1924): Svetovidov, 1973: 108; Quignard & Kartas, 1977, 350:1253; Whitehead & Bauchot, 1985: 36; Whitehead, 1985: 199; Quignard & Douchement, 1991c: 274; Kottelat, 1997:38.

Paralosa (nilotica) rhodanensis Roule, 1925: 80, pl. 16 (fig. 82-88)
Alosa finta Barbieri, 1907a, 9: 127; D'Ancona, 1927a, 38:191.
Alosa finta nilotica: Regan, 1916, 18:10.
Alosa (Paralosa) morpha rhodanensis De Buen, 1930, 5:182.
Alosa fallax Cottiglia, 1963a, 18:34; Cottiglia, 1968, 7:78.
Alosa fallax nilotica Bini, 1970, II: 53, fig.; Tortonese, 1970: 102, fig. 43;
Svetovidov, 1973, I: 107.

Bianco (2002) suggested reclassifying *Alosa fallax rhodanensis* as *Alosa agone* (Scopoli, 1786), see section 1.2.2.

Alosa fallax nilotica (Geoffroy Saint-Hilaire, 1808)

Alosa fallax nilotica (Geoffroy Saint-Hilaire, 1808): Berg, 1932: 91; Berg, 1948: 145; Svetovidov, 1952: 309, fig.51, pl. XXIV, fig. 1; Bini, 1970:, 2:53, fig; Tortonese, 1970, 10: 102, fig. 41-42; Whitehead, 1984, 1:272. Whitehead, 1985: 199; Bianco, 1988: 148; Quignard & Douchement, 1991d: 265; Kottelat, 1997: 38.

Clupea nilotica E. Geoffroy Saint-Hilaire 1808: pl.10.
Clupea finta Boulenger, 1909:154, fig. 123.
Alosa finta Moreau, 1881, 3:456; Soljan, 1948: 247; 1975:631.
Alosa finta nilotica Regan, 1916: 10.

Bianco (2002) suggested that *Alosa agone* (Scopoli, 1786), be recognised as the valid scientific name for *Alosa fallax nilotica*, see section 1.2.2

Alosa fallax algeriensis (Regan, 1916)

Alosa fallax algeriensis (Regan, 1916): Quignard & Kartas, 1977, 501: 1253; Kartas, 1981: 77; Kartas, 1991, 213.

Alosa finta algeriensis Regan 1916, 18: 10.
Alosa fallax bolivari Lozano-Rey, 1929, 15: 660, pl. 30, fig. 3.
Alosa fallax morpha algeriensis De Buen, 1930, 5: 182.

It is possible that *Alosa africana* (Regan, 1916) is a simultaneous synonym for *Alosa fallax algeriensis* (Kottelat, 1997), though Furnestin & Vincent (1958) considered *Alosa africana* to be a hybrid between *Alosa alosa* and *Alosa fallax*.

Kottelat (1997) suggested reclassifying *Alosa fallax algeriensis* (Regan, 1916) as a separate species and proposed *Alosa algeriensis* Regan, 1916 as the valid scientific name. However, Bianco (2002) suggested that the subspecies be classified as *Alosa agone* (Scopoli, 1786), see section 1.2.2.

***Alosa fallax lacustris* (Fatio, 1890)**

Alosa fallax lacustris (Fatio, 1890): Ferrero, 1951:24; Dottrens, 1952:23; Bini, 1970, II:48, 53; Tortonese, 1970, X: 105-106.

Ciprinus [sic] *agone* Scopoli, 1786:71

Clupea Alosa major Pollini, 1816:21

Clupea Alosa minor Pollini, 1816:21

Clupea Alosa parvula Pollini, 1816:21

Alosa Finta var. *lacustris* Fatio, 1890: 51

Alosa lacustris forma *ceresio-verbana* Barbieri, 1907a: 140, pl.1, fig.3

Alosa lacustris forma *lariana* Barbieri, 1907a: 140, pl.1, fig.3.

Alosa lacustris forma *benacensis* Barbieri, 1907a: 140, pl.1, fig.3.

Alosa finta gracilis Regan, 1916: 10.

Kottelat (1997) suggested reclassifying *Alosa fallax lacustris* (Fatio, 1890) as a separate species and recommended *Alosa agone* (Scopoli, 1786) as the valid scientific name. Furnestin & Vincent (1958) considered that *A. fallax* var. *lacustri* could be a hybrid between *A. alosa* and *A. fallax*.

***Alosa fallax killarnensis* (Regan, 1916)**

Alosa fallax killarnensis (Regan, 1916): Trewavas, 1938,(150):110-111; Gibson,1956,12:109; Wheeler,1969a:129; Maitland, 1979:241; Whitehead, 1985: 199.

Kottelat (1997) suggested reclassifying *Alosa fallax killarnensis* (Regan, 1916) as a separate species and proposed *Alosa killarnensis* Regan, 1916 as the valid scientific name.

Alosa finta killarnensis Regan 1916, 18(103):9; Went, 1953, 11(1):10.

1.2 Taxonomy

1.2.1 Affinities

The shads belong to the subdivision Clupeomorpha. The clupeomorphs are characterised by having ducts running anteriorly from the swim bladder into the skull (see section 1.3.2.7) and sharp boney scutes along their ventral surface.

1.2.1.1 Suprageneric (Nelson, 1994).

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata (Craniata)
Superclass: Gnathostomata
Grade: Teleostomi
Class: Actinopterygii
Subclass: Neopterygii

Division: Teleostei
Subdivision: Clupeomorpha
Order: Clupeiformes
Suborder: Clupeoidei
Family: Clupeidae
Subfamily: Alosinae
Genus: *Alosa* Linck

1.2.1.2 Generic (Eschmeyer, 1998)

Alosa Linck, 1790: 6(3) 35; Cuvier, 1829:319

- **Diagnosis** (Svetovidov, 1952; Hoestlandt, 1991; Whitehead, 1985)

The body is tapered at either end, slightly compressed laterally, with the mature fish reaching a maximum length in the region of 830 mm (L_t). The mouth is terminal and the upper jaw bears a prominent median notch on the premaxillae in which the median symphysis of the lower jaw rests (Figure 1.1). The eyelids are well developed and cover much of the anterior and posterior part of the eye (Figure 1.1). The body is covered by cycloid scales, which form a line of scutes that runs along the entire ventral surface. There are elongated scales (alae) present at the base of the caudal fin (Figure 1.1). One or more black spots are present on the side of the body behind the operculum. The opercular bone bears distinct radial striations: canals with pored sensory organs. The number of gill rakers on the first gill arch ranges from 30 to 180, and the number of vertebrae from 43 to 59. Pelvic fins have one unbranched and eight to nine branched (i 8-9) fin rays. The bifurcating ducts of the swim bladder end in two vesicles within bullae of the prootic and pterotic bones, the prootic bulla being the larger of the two.

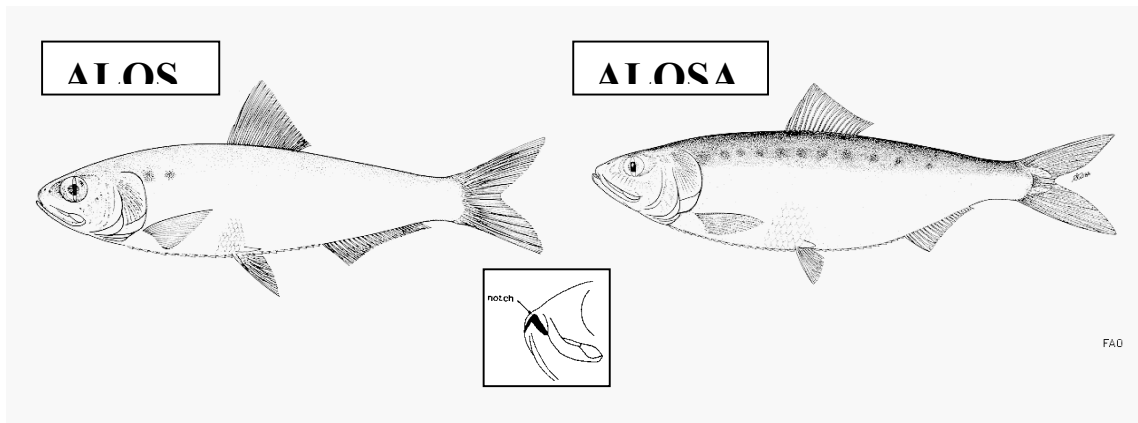


Figure 1.1: *Alosa alosa* and *Alosa fallax*; reproduced with permission of FAO (www.fishbase.org). Insert, showing the distinct notch into which the symphysis of the lower jaw fits (Whitehead, 1985).

1.2.1.3 Specific

The number of gill rakers on the first gill arch and geographical location have both been used to identify species and sub-species (Quignard & Kartas, 1977). In the Eastern Atlantic and Mediterranean four species of *Alosa* have been recognised; *Alosa alosa*

(Linnaeus, 1758), *Alosa fallax* (Lacépède, 1803), *Alosa macedonica* (Vinciguerra, 1921) and *Alosa caspia* (Eichwald, 1838) (Whitehead, 1985; Hoestlandt, 1991). No subspecies have been reported for *A. alosa* or for *A. macedonica*, while for *A. fallax* Quignard & Douchement (1991e) reported six subspecies:

- Alosa fallax fallax* (Lacépède, 1803)
- Alosa fallax rhodanensis* (Roule, 1924).
- Alosa fallax nilotica* (Geoffroy Saint-Hilaire, 1808)
- Alosa fallax algeriensis* (Regan, 1916)
- Alosa fallax lacustris* (Fatio, 1890)
- Alosa fallax killarnensis* (Regan, 1916)

For *A. caspia*, one subspecies, *Alosa caspia vistonica* Economidis & Sinis, 1986 has been reported from Lake Vistonis in Greece.

- Specific diagnosis

Key to adult alosoids from the Eastern Atlantic and Mediterranean (Hoestlandt, 1991).

1. Upper jaw with a median notch; the symphysis of the lower jaw rests in the notch. The last two fin rays on the anal fin are the same length as the others.....2
2. Teeth present on the palatines. Lakes Volvi or Vistonis, Greece.....3
Teeth absent on palatines. Watersheds of the North and Baltic Seas, the Atlantic Ocean and the Mediterranean.....4
3. Poorly developed teeth on the vomer and palatines. Lake Vistonis, Greece *Alosa caspia vistonica* Economidis & Sinis, 1986.
Well developed teeth on the vomer and palatines. Lake Volvi, Greece
.....*Alosa macedonica* (Vinciguerra, 1921).
4. Not less than 85 gill rakers on the first gill arch, gill rakers longer than branchial filaments..... *Alosa alosa* (Linnaeus, 1758)
Not more than 80 gill rakers on the first gill arch, gill rakers approximately the same length as the branchial filaments.....5
5. Between 40 and 60 gill rakers on first gill arch, North Africa
.....*Alosa fallax algeriensis* (Regan, 1916)
Between 38 and 72 gill rakers on first gill arch, lakes of Italy and Sardinia
.....*Alosa fallax lacustris* (Fatio, 1890)
Between 43 and 53 gill rakers on first gill arch, Lough Leane, Ireland.....
.....*Alosa fallax killarnensis* (Regan, 1916)
Between 30 and 49 gill rakers on first gill arch, North West Mediterranean
.....*Alosa fallax rhodanensis* (Roule, 1924)
Between 28 and 40 gill rakers on first gill arch, Adriatic and Eastern Mediterranean.....
.....*Alosa fallax nilotica* (Geoffroy Saint-Hilaire, 1808)
Between 28 and 60 gill rakers on first gill arch, Atlantic Ocean.....
.....*Alosa fallax fallax* (Lacépède, 1803)

1.2.2 Taxonomic status

Kottelat (1997) critically reviewed the systematics of European freshwater fishes and concluded that some of the subspecies identified by Quignard & Douchement (1991e) should be classified as species. This was on the basis of differences in morphology, habit, life history and ontogeny. Kottelat (1997) suggested that the following should be reclassified: *Alosa fallax algeriensis* (Regan, 1916), *Alosa fallax killarnensis* (Regan, 1916), *Alosa fallax lacustris* (Fatio, 1890) and *Alosa caspia vistonica* Economidis & Sinis, 1986 (see section 1.1.3). More recently, Bianco (2002) suggested reclassifying *Alosa fallax algeriensis*, *Alosa fallax lacustris*, *Alosa fallax nilotica* and *Alosa fallax rhodanensis* as *Alosa agone* (Scopoli, 1786), effectively only one taxon being recognised in the Mediterranean area.

It is recognised that the status of various alosoids remains uncertain. As such, for the purpose of this synopsis, it is proposed to follow the classification set out by Hoestlandt (1991) and by Quignard & Douchement (1991e), with the exception that the landlocked populations of Sardinia are classified as *Alosa fallax lacustris* as suggested by Cottiglia (1963b, 1968, 1969 (1970)).

The taxonomic status is further complicated by the occurrence of hybrids mainly between *Alosa alosa* and *Alosa fallax fallax*, which appear to be fertile (Alexandrino & Boisneau, 2000). The taxonomic problem of hybrids has been discussed in detail by Sabatié *et al.* (2000), but see also section 2.3.

1.2.3 Subspecies

See sections 1.2.1.3 and 1.2.2.

1.2.3.1 Standard, common names and vernacular names

A list of the standard and more commonly used names is presented in Table 1.1. Details of vernacular names used can be found in Farran (1946) for Ireland, Maitland & Cambell (1992) for Britain, Taverny (1991a) for France, Tortonese (1970) for Italy and at <http://www.fishbase.org>.

Table 1.1: Standard, common and vernacular names of European alosoids

| Country | <i>Alosa alosa</i> | <i>Alosa fallax fallax</i> | <i>Alosa fallax rhodanensis</i> | <i>Alosa fallax nilotica</i> | <i>Alosa fallax algeriensis</i> | <i>Alosa fallax lacustris</i> | <i>Alosa fallax killarnensis</i> |
|----------------|-------------------------|----------------------------|---------------------------------|------------------------------|--|-------------------------------|----------------------------------|
| Norway | Majfisk | Stamsillen | | | | | |
| Sweden | Majfisken | Staksillen | | | | | |
| Finland | Pilkkusilli | Täpläsilli | | | | | |
| Russia | Aloza, Maiskaya ryba | Atlanticheskaya finta | | Sredizemnom-orskaya finta | | | |
| Lithuania | | Perpele | | | | | |
| Poland | Aloza | Savetha, Parposz | | | | | |
| Germany | Maifisch | Finte | | | | | |
| Denmark | Majsild | Stavsild | | | | | |
| Netherlands | Groote meivisch, Elft. | Meivisch, Fint | | | | | |
| Luxembourg | Péchon de mai | Péchon de mai | | | | | |
| Belgium | Abèye, Alôie | Abèye, Alôie | | | | | |
| United Kingdom | Allis shad | Twaite shad | | | | | |
| Ireland | Allis shad | Twaite shad | | | | | Goureen |
| France | Alose vraie | Alose feinte | Alose feinte du Rhône | | | | |
| Spain | Sábalo común | Saboga | Saboga | | | | |
| Portugal | Sável | Savelha, Fint | | | | | |
| Morocco | Chebel | Chbouk, Ouarsa | | | | | |
| Algeria | | | | | Chbouka | | |
| Tunisia | | | | | Chbouka | | |
| Sardinia | | | Cheppie | | | Agoni | |
| Italy | | | Alosa, Cheppia | Alosa, Cheppia | | Agone | |
| Yugoslavia | | | | Lojka, Kubla, Cepa | | | |
| Albania | | | | Lloca, Kubla | | Kubla ligenore | |
| Greece | | | | Sardelomana | | | |
| Turkey | | | | Tirsi baligi | | | |
| Egypt | | | | | Renget El Sabawgha – sardine, Sardeena, Sarboura | | |

1.3 Morphology

1.3.1 External morphology

Alosa alosa (Linnaeus, 1758) (Wheeler, 1969a; Quignard & Douchement, 1991a; Alexandrino, 1996a).

Gill rakers on first gill arch number 80 to 155, with between 55 and 110 on the lower part of first gill arch (ceratobranchial). Each gill raker is densely covered with lateral spines (Figure 1.2). Total vertebrae number 53 to 58. Number of finrays; anal iii-iv 18-24; dorsal iv-vi 13-18; pelvic i 8-9 (10); pectoral i 13-16. The number of pre-pelvic and post pelvic ventral scutes range from 19 to 25 and 13 to 17, respectively, with the total ranging from 33 to 40 scutes. The number of longitudinal scales along the midline varies between 60 and 90 and the number of transverse scale rows between 20 and 26. The length of the head (tip of snout to hind border of gill cover / operculae) as a percentage of total length ranges from 16.27 to 22.31 % (mean values), snout length ranges from 3.73 to 4.57%, and post-orbital distance ranges from 9.55 to 12.89%. The mean pre-dorsal distance varies between 37.21 and 41.63 %, pre-pelvic between 38.56 and 43.79%, and pre-anal from 57.29 to 66.18 % of total length. Maximum size reported 830 mm (L_t), by Sabatié (1993), see also section on growth (3.4.3). The back is deep blue in colour with the flanks golden-silvery (Wheeler, 1978), usually with one dark spot posterior to the gill cover, sometimes absent, occasionally more.

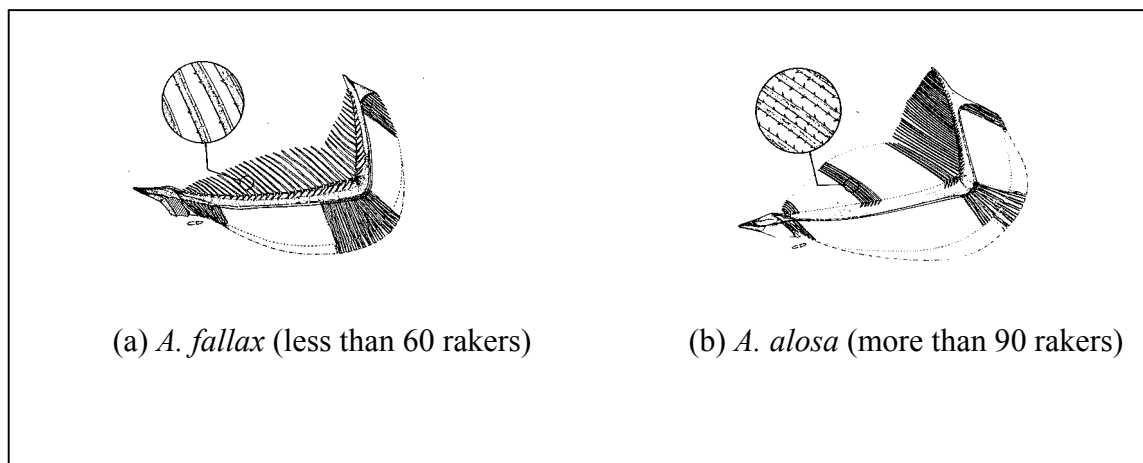


Figure 1.2: First gill arch appearance and approximate number of gill rakers for (a) *A. fallax* and (b) *A. alosa*; from Quignard & Douchement (1991a&b).

Alosa fallax fallax (Lacépède, 1803) (Svetovidov, 1952; Wheeler, 1969; Quignard & Douchement, 1991b; O'Maoileidigh, *et al.*, 1988; Alexandrino, 1996a).

The number of gill rakers on the first gill arch range from 35 to 60, with between 24 and 32 on the lower part of the arch. The gill rakers have few lateral spines and are approximately the same length as the gill filaments (Figure 1.2). The total number of vertebrae varies from 49 to 59. Number of finrays; anal iii-iv 16-22; dorsal iv-vi 12-16;

pelvic i 8 and between 15 to 17 finrays (total) in the pectoral fins. The number of pre-pelvic and post pelvic ventral scutes range from 18 to 23 and 12 to 18, respectively, with the total ranging from 32 to 41 scutes. The number of longitudinal scales along the midline varies between 54 and 71 and the number of transverse scale rows between 16 and 20. A summary of morphometric characteristics is presented in Table 1.2.

Table 1.2: Summary of some morphometric characteristics of *Alosa fallax fallax* (Douchement, 1981; O'Maoileidigh, *et al.*, 1988; Alexandrino, 1996a; Doherty & McCarthy, 2002).

| Morphometric characteristic | Percent of total length | Morphometric characteristic | Percent of total length |
|-----------------------------|--|-----------------------------|--|
| Length of snout | 3.20- 4.56 ¹ | Length of pelvic fin | 8.73 ¹ -8.95 ¹ |
| Post-orbital length | 9.45-12.03 ¹ | Standard length | 79.95 ¹ -81.38 ¹ |
| Head length | 16.61 ¹ -19.87 ¹ | Fork Length | 86.11 ¹ |
| Head width @ eyes | 5.43 ¹ | Height of caudal peduncle | 6.46 ¹ -6.67 ¹ |
| Head width @ nostrils | 4.41 ¹ | Width of caudal peduncle | 3.34 ¹ |
| Gape | 7.77 ¹ | Body depth @ pectoral | 19.78 ¹ |
| Eye diameter | 3.19 ¹ | Pre-pelvic length | 38.04 ¹ -40.43 |
| Base of dorsal fin | 11.27 ¹ -12.18 ¹ | Pre-pectoral length | 16.86-18.69 ¹ |
| Base of anal fin | 12.32 ¹ -13.30 ¹ | Pre-dorsal length | 36.92 ¹ -39.25 ¹ |
| Length of pectoral fin | 12.65 ¹ -13.47 ¹ | Pre-anal length | 57.19 ¹ -60.85 ¹ |

¹Relationship with total length based on mean values.

Interorbital distance varies from 18.5 to 24.2%, with a mean of 20.9%, of the head length. The diameter of the eye ranges from 15.2 to 21.2%, with a mean of 18.5%, of head length. Maximum size attained is estimated to be 568 mm (L_t), from the Nyamunas river, Lithuania (Manyukas, 1989) [see Section 3.4.3]. The back is deep blue in colour with silvery flanks. There is usually a row of dark blotches posterior to the gill cover, sometimes more than one row, and occasionally just a single blotch behind the operculum.

Alosa fallax rhodanensis (Roule, 1924) (Douchement, 1981; Quignard & Douchement, 1991c; Le Corre *et al.*, 1997).

Gill rakers on the first gill arch number 30 to 49, with between 19 and 31 on the lower part of first gill arch. Total number of vertebrae 54 to 59. Number of finrays; anal iii-iv 17-21; dorsal iii-iv 13-16; pelvic i 8-9 and pectoral i 13-15. The number of pre-pelvic and post pelvic ventral scutes range from 15 to 24 and 10 to 17, respectively, with the total ranging from 30 to 40 scutes. The number of longitudinal scales along the midline varies between 54-64 and the number of transverse scale rows between 16 and 20. The length of the head (tip of snout to hind border of gill cover / operculae) as a percentage of total length is 19.46% (mean values). The mean pre-dorsal distance varied between 38.24 and 39.09%, pre-pelvic between 39.83 and 39.87% and pre-anal from 59.38 to 59.66% of total length. The maximum size reported is 676 mm (L_t) [see section 3.4.3].

Alosa fallax nilotica (Geoffroy Saint-Hilaire, 1808) (Vukovic, 1961a; Vitali *et al.*, 1983; Serventi, *et al.*, 1990; Quignard & Douchement, 1991d).

The number of gill rakers on first gill arch varies between 28 and 42, with between 17 and 26 on the lower part of the first gill arch. Total number of vertebrae 47 to 60. Number of finrays; anal i-ii 20-22; dorsal ii-iii 16-17; pelvic (total) 9-10 and pectoral (total) 15-18. The number of pre-pelvic and post pelvic ventral scutes range from 19 to 24 and 13 to 20, respectively, with the total ranging from 32 to 39 scutes. The number of longitudinal scales along the midline varied between 55 and 65 and the number of transverse scale rows between 16 and 20. The maximum size reported is 560 mm (L_t) [see section 3.4.3].

[The morphometric and meristic characteristics of the landlocked population of *Alosa* in Lake Skadar have been described by Vukovic (1961a) and Rakaj & Crivelli (2001). It has been assumed, mainly from their size that the majority of the sample reported by Vukovic (1961a) consisted of the anadromous *Alosa fallax nilotica*. The sample described by Rakaj & Crivelli (2001) was confined to the non-migratory species, which the authors classified as *Alosa agone* after Kottelat (1997) and which for the purpose of this synopsis has been referred to as *Alosa fallax lacustris*.]

Alosa fallax algeriensis (Regan, 1916) (Kartas, **1981**, 1991)

There are between 40 and 60 gill rakers on the first gill arch with 25 to 38 on the lower portion of the arch. The total number of vertebrae ranges from 53 to 57. Total number of finrays; anal 20 to 25; dorsal 18 to 22 and pelvic 9. The number of pre and post-ventral scutes range from 19 to 23 and 13 to 16, respectively, with the total varying from 33 to 39. Head length and pre-dorsal distance as a percentage of **total** length vary between 19.82 and 20.35% and 38.45 and 38.65% (based on mean values), respectively.

Alosa fallax lacustris (Fatio, 1890) (Barbieri, 1907b; **Florin, 1949**; Ferrero, 1951; Cottiglia, 1963b, 1969 (1970); Quignard & Douchement, 1991f).

There are between 38 and 72 gill rakers on the first gill arch with 21 to 59 on the lower portion of the arch. The total number of vertebrae is 59. Total number of finrays; anal i-ii 17-23; dorsal ii-iii 13-18 and pectoral (total) 14 to 18. The number of pre and post-ventral scutes range from 23 to 24 and 13 to 17, respectively, with the total varying from 36 to 41. The number of longitudinal scales along the midline varies between 50 and 70 and the number of transverse scale rows between 17 and 20. Head length and pre-dorsal distance as a percentage of fork length vary between 21.1 and 24.4% and 41.8 and 47.2%, respectively. Maximum size reported is in the region of 500 mm (L_t) [see section 3.4.3].

The morphometric characteristics of landlocked *Alosa fallax lacustris* from Lake Skadar, Yugoslavia are presented in Table 1.3. The maximum size reported is 330 mm and 340 g (Rakaj & Crivelli, 2001).

Table 1.3: Morphometric characteristics (Mean \pm SE) of landlocked *Alosa fallax lacustris* from Lake Skadar, Yugoslavia, n = 27 (Rakaj & Crivelli, 2001).

| Morphometric characteristic | Percent of standard length | Morphometric characteristic | Percent of standard length |
|-----------------------------|----------------------------|-----------------------------|----------------------------|
| Eye diameter | 5.5 \pm 0.12 | Pre-dorsal length | 49.2 \pm 0.06 |
| Head length | 24.4 \pm 0.15 | Pre-ventral length | 49.0 \pm 0.31 |
| Greatest body depth | 26.6 \pm 0.31 | Snout-Anal distance | 72.5 \pm 0.33 |
| Smallest body depth | 8.60 \pm 0.12 | Eye diam./Head length | 22.5 \pm 0.44 |

Alosa fallax killarnensis (Regan, 1916) (Regan, 1916; Trewavas, 1938; O'Maoileidigh, *et al.*, 1988).

There are between 43 and 53 gill rakers on the first gill arch with 29 to 37 on the lower portion of the arch. The total number of vertebrae ranges from 53 to 57. Total number of finrays; anal 19-24; dorsal 17-21; pectoral 15-17 and pelvic 8-9. The number of pre and post-ventral scutes range from 21 to 22 and 15 to 16, respectively. Total number of vertebrae range from 53 to 57 with a mean (\pm 95%CI) of 55.38 \pm 0.17. The number of longitudinal scales along the midline varies between 55 and 60 and the number of transverse scale rows between 16 and 20. A summary of morphometric characteristics are presented in Table 1.4.

Table 1.4 Morphometric characteristics of *Alosa fallax killarnensis* from Lough Leane, Ireland (O'Maoileidigh, *et al.*, 1988). Relationship with total length is based on mean values.

| Morphometric characteristic | Percent of total length | Morphometric characteristic | Percent of total length |
|-----------------------------|-------------------------|-----------------------------|-------------------------|
| Length of snout | 3.8 | Standard length | 80.3 |
| Post-orbital length | 10.3 | Fork Length | 85.6 |
| Head length | 19.7 | Width of caudal peduncle | 6.9 |
| Base of dorsal fin | 12.1 | Pre-pelvic length | 37.6 |
| Base of anal fin | 11.5 | Pre-pectoral length | 17.6 |
| Length of pectoral fin | 13.8 | Pre-dorsal length | 37.3 |
| Length of pelvic fin | 9.5 | Pre-anal length | 58.7 |

Maximum length (total) attained is in the region of 240 mm. There is usually at least one row of dark blotches posterior to the gill cover.

1.3.1.1 Meristic and morphometric variation

The number of gill rakers on the first gill arch effectively separates the two species (Sabatié *et al.*, 2000), with fish of intermediate number of gillrakers indicating hybrids. Douchement (1981) and Quignard & Douchement (1991a) report *Alosa alosa* from the rivers Aude and Rhône (France) with mean gill raker counts of *c.* 70. This number is similar to that reported by Boisneau *et al.*, (1992) and Sabatié (1993) for hybrids from the rivers Loire (France) and Sebou (Morocco), respectively (Figures 1.3 & 1.4). This may indicate that these groups of fish are hybrids between *Alosa alosa* and *Alosa fallax rhodanensis*. The discriminatory ability of other meristic (number of anal and dorsal fin rays, pre and post-pelvic scutes and vertebrae) or morphometric (index of head, pre-dorsal, pre-pectoral and pre-anal length) characters to separate *A. alosa* from *A. fallax* is low (Sabatié *et al.*, 2000). However, significant differences between the two species in meristic characters, other than the number of gill rakers, and morphometric characters do exist within certain river systems and these have been summarised by Sabatié *et al.* (2000).

Significant differences have been reported between cohorts and between the sexes (Sabatié *et al.*, 2000), details of the latter are presented in section 3.1.1 (sexual differentiation / dimorphism). Differences between year classes were observed for *A. alosa* from the Loire (Boisneau, 1990) and for *A. fallax* from the Sebou (Sabatié, 1993). This was not the case for *A. fallax* from the Loire (Boisneau, 1990) nor for *A. fallax rhodanensis* age 1 from the rivers Aude and Rhône (Douchement, 1981). Sabatié *et al.* (2000) concluded that as the variability was low and not systematic, the combining of samples was justified.

Sabatié (1993) examined the difference between juvenile ($L_t = 35-120$ mm) and adults from the River Sebou. Juvenile *A. alosa* and *A. fallax* had significantly more dorsal and anal fin rays and post pelvic scutes. Douchement (1981) found no significant difference in the meristic characteristics of immature *A. alosa* and *A. fallax* ($L_t = 150-220$ mm) and adults from the River Adour.

The variation in certain morphometric indices and meristic characteristics are summarised in Tables 1.5 – 1.9. Where possible the morphometric indices are presented in terms of percentage total length; for the Sardinian populations of *Alosa fallax* (Cottiglia, 1963 a&b; 1969) the indices are in relation to fork length. Significant differences in meristic characteristics and morphometric indices between populations have been reported by Douchement (1981), Sabatié (1993), Alexandrino (1996a) and by Sabatié *et al.* (2000).

Certain of the meristic characteristics vary with size (Sabatié, 1993), most notably the number of gill rakers on the first gill arch (Tables 1.10 & 1.11).

A number of landlocked populations of *Alosa fallax*, in particular those from Italy and Sardinia, have a greater number of gill rakers on the first gill arch compared with their anadromous conspecifics (Tables 1.6 & 1.9). A similar pattern is also evident in the Irish populations of *Alosa fallax*. The number of gill rakers on the lower half of the first gill arch is $32.2 (\pm 0.14)$ for the lacustrine population in Lough Leane compared with $25.5 (\pm 0.12)$ for the anadromous *A. fallax* from the River Barrow (O'Maoileidigh *et al.*, 1988).

The Mediterranean populations of *A. fallax* from North Africa tend towards the higher end of the range in terms of the number of gill rakers (Table 1.6 & Figure 1.4), while those from the Adriatic are at the lower end, and populations from Southern France intermediate. The Tirso population (Sardinia), though tentatively classified as *Alosa fallax rhodanensis* (Quignard & Douchement, 1991c) would appear to be closer to *Alosa fallax algeriensis* in terms of the number of gill rakers (Figure 1.4).

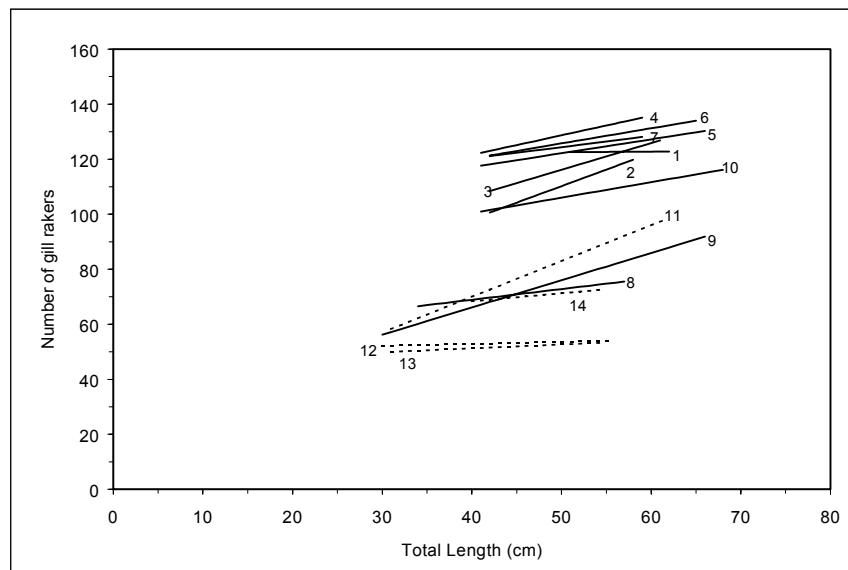


Figure 1.3:

Figure 1.3: The relationship between number of gill rakers on the first gill arch and total length for *Alosa alosa* (1-10, solid line) and *Alosa alosa* x *Alosa fallax* hybrids (11-14, dotted line). 1 = Rhine (Hoek, 1899); 2 = Aulne (Véron, 1999); 3 = Vilaine (Véron, 1999); 4 & 11 = Loire (Douchement, 1981); 5 = Charente (Véron 1999); 6 = Garonne (Douchement, 1981); 7 = Adour (Douchement, 1981); 8 & 12 = Aude (Douchement, 1981); 9 & 13 = Rhône (Douchement, 1981); 10 & 14 = Sebou (Sabatié, 1993).

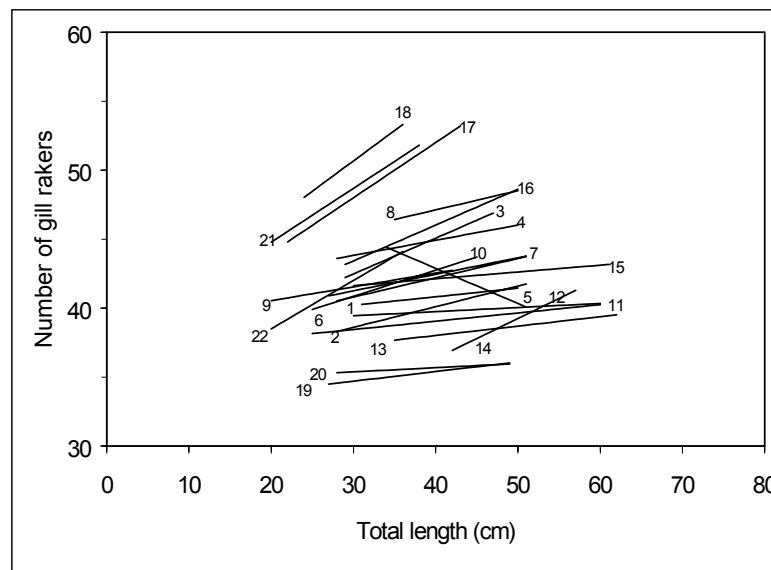


Figure 1.4:

Figure 1.4 The relationship between number of gill rakers on the first gill arch and total length for *Alosa fallax*;

Anadromous populations: *A. fallax fallax*: 1 = Rhine (Hoek, 1899); 2 = Hass (1965); 3 = Severn (Aprahamian, 1982); 4 = Loire (Douchement, 1981); 5 = Charente (Véron, 1999); 6 = Garonne (Quignard & Kartas, 1977); 7 = Garonne (Douchement, 1981); 8 = Adour (Douchement, 1981); 9 = Loukos (Sabatié, 1993); 10 = Sebou (Sabatié, 1993); *A. fallax rhodanensis*: 11 = Rhône (Quignard & Kartas, 1977); 12 = Rhône (Douchement, 1981); 13 = Rhône (Le Corre, *et al.*, 1997); 14 = Aude (Quignard & Douchement, 1991c); 15 = Aude (Douchement, 1981); 16 = Tirso (Quignard & Douchement, 1991c); *A. fallax algeriensis*: 17 = Miliane (Quignard & Kartas, 1977); 18 = Oubeira (Quignard & Kartas, 1977);

Landlocked populations: *A. fallax nilotica*: 19 = Bacin (Vukovic, 1961a); 20 = Skadar (Vukovic, 1961a); *A. fallax algeriensis*: 21 = Ischkeul (Quignard & Kartas, 1977); *A. fallax*: 22 = Sidi Mohamed Ben Abdullah (Sabatié, 1993).

Table 1.5: Mean (SE) morphometric indices (percentage total length) and meristic characteristics of various populations of *Alosa alosa*.

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|--|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|-----------------|-----------------|------------------|-------------------|-----------------|
| Rhine, Germany (Hoek, 1899) | | | | | | | | 122.67 (1.63) | 17.33 (0.10) | 23.11 (0.15) | 20.77 (2.75) | 16.54 (0.10) | 55.37 (0.11) |
| Aulne, France (Véron, 1999) | | | | | | | | 112.00 (3.04) | 19.20 (0.13) | 24.20 (0.32) | 21.10 (0.31) | 14.47 (0.22) | |
| Vilaine, France (Véron, 1999) | | | | | | | | 119.00 (3.23) | 18.60 (0.16) | 22.90 (0.35) | 20.20 (0.28) | 14.80 (0.11) | |
| Loire, France (Douchement, 1981) | | | 19.42 (0.04) | 38.14 (0.06) | | 38.77 (0.08) | 58.05 (0.11) | 129.30 (0.62) | 19.95 (0.06) | 24.40 (0.08) | 21.35 (0.06) | 14.93 (0.05) | 55.84 (0.06) |
| Loire, France ¹ (Mennesson-Boisneau & Boisneau, 1990) | | | 18.97 (0.03) | 37.68 (0.06) | | 38.65 (0.05) | 58.59 (0.07) | 122.10 (0.39) | 17.90 (0.02) | 21.60 (0.03) | 21.20 (0.02) | 14.10 (0.03) | 55.7 (0.04) |
| Charente, France (Veron, 1999) | | | | | | | | 125.00 (1.32) | 18.70 (0.11) | 23.50 (0.16) | 21.40 (0.11) | 14.20 (0.09) | |
| Garonne, France (Douchement, 1981) | | | 19.37 (0.04) | 38.27 (0.09) | | 38.56 (0.08) | 58.17 (0.13) | 127.49 (0.52) | 19.22 (0.06) | 24.34 (0.09) | 21.13 (0.05) | 14.36 (0.06) | 55.90 (0.06) |
| Adour, France (Douchement, 1981) | | | 19.32 (0.05) | 38.52 (0.08) | | 38.87 (0.08) | 58.52 (0.10) | 123.85 (0.41) | 20.16 (0.05) | 24.88 (0.07) | 21.77 (0.05) | 15.28 (0.04) | 56.17 (0.04) |
| Lima, Portugal (Alexandrino, 1996a) | 4.10 (0.09) | 10.18 (0.10) | 17.15 (0.15) | 37.21 (0.22) | 17.52 (0.16) | 38.98 (0.40) | 59.56 (0.33) | 126.02 (1.77) | 19.14 (0.11) | 25.02 (0.17) | 22.15 (0.15) | 13.92 (0.18) | |
| Douro, Portugal (Eiras, 1980) | | | | | | | | 125.66 | 19.38 (0.06) | 23.20 (0.06) | 22.61 (0.08) | 14.78 (0.05) | |
| Mondego, Portugal (Alexandrino, 1996a) | 3.73 (0.15) | 9.55 (0.19) | 16.27 (0.30) | 37.25 (0.18) | 16.32 (0.33) | 38.56 (1.10) | 57.29 (1.12) | 126.07 (2.96) | 18.50 (0.34) | 24.47 (0.35) | 22.80 (0.18) | 14.00 (0.29) | |
| Aude, France (Douchement, 1981) | | | | | | | | 72.30 (1.19) | 20.19 (0.05) | 23.74 (0.08) | 22.14 (0.05) | 15.61 (0.05) | 56.71 (0.05) |
| Rhône, France (Douchement, 1981) | | | | | | | | 69.85 (2.71) | 20.39 (0.11) | 23.69 (0.12) | 22.10 (0.08) | 15.88 (0.07) | 57.75 (0.06) |
| Sebou, Morocco (Sabatié, 1993) | | | 18.00 (0.03) | 36.86 (0.05) | 17.22 (0.06) | 37.02 (0.09) | 58.81 (0.12) | 109.90 (0.39) | 19.25 (0.04) | 23.68 (0.06) | 21.26 (0.97) | 14.54 (0.07) | 55.48 (0.16) |

¹ Fork length (mm) converted to total length using $L_t = 1.1325 L_f + 2.6556$ (Douchement, 1981)

Table 1.6: Mean (SE) morphometric indices (percentage total length) and meristic characteristics of various populations of *Alosa fallax fallax*.

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|---|-------------------|--------------------|--------------------|--------------------|-----------------|--------------------|--------------------|-----------------|-----------------|-----------------|------------------|-------------------|-----------------|
| Rhine, Germany (Hoek, 1899) | | | | | | | | 40.67 (0.63) | 17.11 (0.07) | 21.26 (0.11) | 20.48 (0.08) | 16.30 (0.09) | 54.85 (0.08) |
| Barrow, Ireland (O'Maoileidigh <i>et al.</i> , 1988, O'Maoileidigh, 1990) | 3.20 | 10.66 | 19.20 | 36.81 | 17.70 | 37.43 | 57.84 | 40.53 (0.27) | 19.25 (0.10) | 22.14 (0.12) | | | 55.87 (0.12) |
| Barrow, Ireland (Doherty & McCarthy, 2002) | 3.31 ² | 12.03 ² | 19.88 ² | 39.25 ² | | 39.58 ² | 60.85 ² | 42.10 (0.20) | 17.80 (0.10) | 20.60 (0.10) | | | |
| Loire, France Douchement, 1981) | | | 19.46 (0.05) | 38.46 (0.09) | | 40.02 (0.10) | 59.75 (0.26) | 44.96 (0.14) | 19.20 (0.06) | 21.56 (0.07) | 21.45 (0.06) | 15.58 (0.05) | 56.30 (0.07) |
| Loire, France ¹ (Menesson-Boisneau & Boisneau, 1990) | | | 19.10 (0.13) | 38.19 (0.20) | | 39.25 (0.20) | 60.28 (0.29) | 48.50 (0.66) | 17.6 (0.09) | 20.10 (0.13) | 20.80 (0.09) | 17.30 (0.12) | 55.1 (0.18) |
| Charente, France (Veron, 1999) | | | | | | | | 42.00 (0.78) | 19.10 (0.10) | 20.70 (0.21) | 20.30 (0.17) | 14.80 (0.09) | |
| Garonne, France (Quignard & Kartas, 1977) | | | | | | | | | 18.65 (0.06) | 21.41 (0.10) | 20.30 (0.08) | 15.04 (0.08) | 56.01 (0.13) |
| Garonne, France (Douchement, 1981) | | | 19.34 (0.06) | 38.40 (0.10) | | 40.43 (0.09) | 60.56 (0.12) | 42.44 (0.10) | 18.82 (0.05) | 21.51 (0.07) | 20.61 (0.06) | 14.98 (0.05) | 55.90 (0.09) |
| Adour, France Douchement, 1981) | | | 19.08 (0.07) | 39.15 (0.09) | | 40.39 (0.14) | 60.09 (0.05) | 47.51 (0.36) | 19.18 (0.08) | 22.54 (0.10) | 21.28 (0.10) | 15.03 (0.10) | 56.48 (0.08) |
| Lima, Portugal (Alexandrino, 1996a) | 4.19 (0.12) | 9.74 (0.15) | 16.95 (0.23) | 36.92 (0.41) | 17.56 (0.25) | 38.04 (0.39) | 57.19 (1.09) | 52.63 (1.35) | 18.16 (0.12) | 21.78 (0.22) | 21.64 (0.18) | 14.67 (0.25) | |
| Douro, Portugal (Eiras, 1980) | | | | | | | | 42.17 (0.22) | 17.66 (0.06) | 20.95 (0.18) | 21.35 (0.08) | 14.70 (0.12) | 54.93 (0.20) |
| Mondego, Portugal (Alexandrino, 1996a) | 4.56 (0.17) | 10.68 (0.10) | 18.31 (0.24) | 38.17 (0.18) | 18.69 (0.20) | 39.00 (0.14) | 59.39 (0.18) | 46.41 (0.46) | 18.53 (0.10) | 21.19 (0.15) | 22.12 (0.13) | 14.96 (0.10) | |
| Tejo, Portugal (Alexandrino, 1996a) | 4.28 (0.09) | 10.22 (0.05) | 18.10 (0.12) | 38.42 (0.12) | 18.03 (0.13) | 39.42 (0.11) | 60.25 (0.23) | 41.32 (0.27) | 18.54 (0.07) | 22.31 (0.12) | 22.45 (0.10) | 14.80 (0.12) | |
| Guadiana, Portugal (Eiras, 1980) | | | | | | | | 41.66 (0.14) | 16.52 (0.08) | 20.48 (0.12) | 21.42 (0.08) | 13.84 (0.15) | 54.73 (0.13) |
| Guadiana, Portugal (Alexandrino, 1996a) | 3.47 (0.09) | 9.45 (0.15) | 16.61 (0.26) | 37.53 (0.39) | 16.86 (0.26) | 38.23 (0.31) | 60.19 (0.46) | 41.91 (0.20) | 18.81 (0.09) | 21.42 (0.16) | 21.36 (0.13) | 14.17 (0.13) | |
| Loukos, Morocco (Sabatié, 1993) | | | 18.75 (0.08) | 36.62 (0.10) | 18.14 (0.21) | | 58.58 (0.19) | 41.97 (0.25) | 19.18 (0.10) | 21.18 (0.14) | 20.54 (0.13) | | 55.61 (0.17) |
| Sebou, Morocco (Sabatié, 1993) | | | 18.92 (0.04) | 34.91 (0.07) | 17.57 (0.11) | 37.30 (0.11) | 57.87 (0.13) | 41.77 (0.11) | 18.00 (0.05) | 21.05 (0.06) | 21.23 (0.06) | 13.72 (0.13) | 53.74 (0.11) |

¹Fork length (mm) converted to total length using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981). ²Based on mean values.

Table 1.7: Mean (SE) morphometric indices (percentage total length) and meristic characteristics of various anadromous populations of *Alosa fallax rhodanensis*, *A. fallax nilotica* and *A. fallax algeriensis*, values in italics represent morphometric indices as percentage of fork length (M = male; F = female).

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|--|--------------|--------------|-------------------------|-----------------|-------------------------|-----------------|-----------------|-----------------|------------------|------------------|------------------|-------------------|-----------------|
| <i>Alosa fallax rhodanensis</i> | | | | | | | | | | | | | |
| Aude, France (Quignard & Kartas, 1977) | | | | | | | | | 19.24 (0.11) | 22.46 (0.13) | 20.73 (0.10) | 15.71 (0.11) | 57.16 (0.08) |
| Aude, France Douchement, 1981) | | | 19.46 (0.11) | 39.09 (0.11) | | 39.87 (0.10) | 59.38 (0.12) | 42.32 (0.15) | 19.92 (0.05) | 23.23 (0.07) | 21.88 (0.06) | 15.65 (0.05) | 56.79 (0.06) |
| Rhône, France (Quignard & Kartas, 1977) | | | | | | | | | 19.31 (0.06) | 22.30 (0.08) | 20.59 (0.07) | 15.55 (0.08) | 57.20 (0.07) |
| Rhône, France (Douchement, 1981) | | | 19.46 (0.09) | 38.24 (0.09) | | 39.83 (0.10) | 59.66 (0.14) | 39.85 (0.12) | 19.95 (0.07) | 23.06 (0.10) | 21.92 (0.06) | 15.61 (0.06) | 56.82 (0.07) |
| Rhône, France (Le Corre, <i>et al.</i> , 1996) | | | 22.1 (M) 21.4 (F) | 42.1 | 22.6 (M) 21.9 (F) | 45.3 | 68.3 | | | | | | |
| Rhône, France (Le Corre, <i>et al.</i> , 1997) | | | | | | | | 38.38 (0.12) | 18.92 (0.04) | 21.91 (0.06) | 20.97 (0.05) | 15.12 (0.05) | |
| Coghinas, Sardinia (Cottiglia, 1969 (1970)) | | | 22.33 (0.33) | 44.00 (0.36) | | 44.84 (0.30) | | 44.66 (0.79) | 18.50 (0.56) | 21.50 (0.22) | | 14.50 (0.22) | |
| Tirso, Sardinia (Cottiglia, 1963a) | | | 22.60 (0.35) | 43.96 (0.89) | | 45.94 (0.81) | | 46.68 (0.81) | 18.00 (0.22) | 22.00 (0.38) | | 14.18 (0.24) | |
| <i>Alosa fallax nilotica</i> | | | | | | | | | | | | | |
| Po, Italy ¹ (Serventi, <i>et al.</i> , 1990) | | | | | | | | | 19.00 (15-21) | 21.00 (18-25) | 22.00 (19-24) | 15.00 (13-20) | |
| Neretva, Yugoslavia (Vukovic, 1961a) | | | | | | | | 35.17 (0.14) | 19.25 (0.07) | 22.56 (0.10) | | | 56.91 (0.12) |
| Nile, Egypt (Boulenger, 1907) | | | | | | | | | 19.14 (0.46) | 22.43 (0.43) | 20.14 (0.26) | 14.14 (0.34) | |

Table 1.7: (cont)

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|---|--------------|--------------|-----------------|-----------------|--------------|------------|----------|-----------------|-----------------|-----------------|------------------|-------------------|-----------------|
| <i>Alosa fallax algeriensis</i> | | | | | | | | | | | | | |
| Miliane & Medjerdah, Tunisia (Kartas, 1981) | | | 19.82 (0.01) | 38.47 (0.02) | | | | 48.55 (0.08) | 19.18 (0.03) | 22.59 (0.04) | 21.10 (0.04) | 14.50 (0.03) | 54.96 (0.03) |
| Oubeira, Algeria (Kartas, 1991) | | | 20.35 (0.08) | 38.45 (0.14) | | | | 50.91 (0.56) | 19.13 (0.10) | 22.60 (0.13) | 21.23 (0.13) | 14.39 (0.10) | 55.38 (0.09) |

¹Mode and range

Table 1.8 Mean (SE) morphometric indices (percentage total length) and meristic characteristics of various populations of hybrids of *Alosa alosa* x *Alosa fallax*.

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|--|--------------|--------------|-----------------|-----------------|--------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|-------------------|-----------------|
| Hybrids of <i>Alosa alosa</i> x <i>Alosa fallax fallax</i> | | | | | | | | | | | | | |
| Loire, France (Douchement, 1981) | | | | | | | | | 19.79 (0.10) | 23.27 (0.17) | 21.29 (0.11) | 15.46 (0.13) | 56.26 (0.10) |
| Loire, France ¹ (Mennesson-Boisneau & Boisneau, 1990) | | | 19.29 (0.10) | 37.78 (0.17) | | 39.01 (0.17) | 59.36 (0.22) | 75.90 (0.79) | 17.80 (0.07) | 21.10 (0.07) | 21.10 (0.10) | 14.10 (0.08) | 55.10 (0.17) |
| Sebou, Morocco (Sabatié, 1993) | | | 18.92 (0.08) | 35.54 (0.15) | | | | 70.68 (0.70) | 18.95 (0.10) | 22.74 (0.12) | 21.96 (0.14) | 13.75 (0.34) | 56.04 (0.15) |
| Hybrids of <i>Alosa alosa</i> x <i>Alosa fallax rhodanensis</i> | | | | | | | | | | | | | |
| Aude, France (Douchement, 1981) | | | | | | | | | 19.92 (0.05) | 23.23 (0.07) | 21.88 (0.06) | 15.65 (0.05) | 56.79 (0.06) |
| Rhône, France (Douchement, 1981) | | | | | | | | | 19.95 (0.07) | 23.06 (0.10) | 21.92 (0.06) | 15.61 (0.06) | 56.82 (0.07) |

¹Fork length (mm) converted to total length using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981)

Table 1.9: Mean (SE) morphometric indices (percentage total length) and meristic characteristics of various landlocked populations of *Alosa alosa* and *Alosa fallax*, values in italics represent morphometric indices as percentage of fork length.

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|--|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|-----------------|-----------------|------------------|-------------------|-----------------|
| <i>Alosa alosa</i> | | | | | | | | | | | | | |
| Castelo de Bode, Portugal (Eiras, 1981a) | | | | | | | | 122.40 (4.45) | 19.72 (0.09) | 22.22 (0.16) | 20.97 (0.13) | 13.66 (0.12) | 56.40 (0.18) |
| Castelo de Bode, Portugal (Alexandrino, 1996a) | 4.57 (0.09) | 12.89 (0.11) | 22.31 (0.23) | 41.63 (0.42) | 21.87 (0.20) | 43.79 (0.43) | 66.18 (0.54) | 142.42 (1.47) | 19.75 (0.12) | 24.42 (0.17) | 22.25 (0.25) | 14.50 (0.15) | |
| El Kansera, Morocco (Sabatié, 1993). | | | 19.81 (0.23) | 35.92 (0.34) | | | 58.91 (0.43) | 78.89 (2.83) | 19.44 (0.40) | 22.88 (0.42) | 21.66 (0.19) | | |
| <i>Alosa fallax</i> | | | | | | | | | | | | | |
| L. Sidi Mohamed Ben Abdallah, Morocco (Sabatié, 1993) | | | 19.90 (0.13) | 33.90 (2.00) | 17.40 (0.16) | 36.40 (0.19) | 61.90 (0.38) | 38.44 (0.73) | 17.88 (0.23) | 21.83 (0.17) | 21.16 (0.19) | | 54.38 (0.49) |
| <i>Alosa fallax nilotica</i> | | | | | | | | | | | | | |
| L. Scutari, Yugoslavia (Vukovic, 1961a) | | | | | | | | 35.81 (0.19) | 18.87 (0.03) | 21.38 (0.06) | | | 57.20 (0.05) |
| L. Scutari, Yugoslavia (Rakaj & Crivelli, 2001) | | | | | | | | | 16.90 (0.17) | 20.30 (0.21) | | | |
| L. Bacin, Yugoslavia (Vukovic, 1961a) | | | | | | | | 35.06 (0.14) | 18.67 (0.04) | 22.12 (0.09) | | | 56.75 (0.11) |
| <i>Alosa fallax algeriensis</i> | | | | | | | | | | | | | |
| L. Ichkeul, Tunisia (Kartas, 1981) | | | 20.16 (0.03) | 38.65 (0.08) | | | | 47.03 (0.01) | 19.53 (0.06) | 22.73 (0.08) | 20.96 (0.07) | 14.64 (0.08) | 55.28 (0.05) |
| <i>Alosa fallax killarnensis</i> | | | | | | | | | | | | | |
| L. Leane, Ireland (O'Maoileidigh <i>et al.</i> , 1988) | 3.78 | 10.26 | 19.67 | 37.27 | 17.62 | 37.58 | 58.68 | | 19.08 (0.07) | 21.60 (0.10) | | | 55.38 (0.08) |

Table 1.9: (cont)

| River (Reference) | Snout length | Post orbital | Head length | Pre dorsal | Pre pectoral | Pre pelvic | Pre Anal | Gill rakers | Dorsal finrays | Anal finrays | Prepelvic scutes | Postpelvic scutes | Vertebrae |
|--|--------------|--------------|------------------------|------------------------|--------------|------------------------|----------|-----------------|--------------------|--------------------|------------------|-------------------|-----------|
| <i>Alosa fallax lacustris</i> | | | | | | | | | | | | | |
| L. Omodeo, Sardinia (Cottiglia, 1963b) | | | 22.76 (0.33) | 42.76 (0.44) | | 44.96 (0.41) | | 47.90 (1.08) | 17.76 (0.27) | 21.64 (0.24) | | 14.22 (0.29) | |
| L. Medio-Flumendosa, Sardinia (Cottiglia, 1969 (1970)) | | | 21.97 (0.10) | 42.83 (0.19) | | 43.90 (0.18) | | 43.88 (0.26) | 18.45 (0.08) | 22.01 (0.10) | | 14.17 (0.09) | |
| L. Maggiore, Italy (Barbieri, 1907a) | | | 23.16 (0.11) | 45.01 (0.16) | | | | 48.83 (0.61) | 18.14 (0.26) | 21.29 (0.19) | | 15.86 (0.26) | |
| L. Maggiore, Italy (Ferrero, 1951) | | | 22.10 (0.50) | 44.70 (1.12) | | 47.50 (1.48) | | 46.60 | 16 ¹ | 19-20 ¹ | | | |
| L. Lugano, Italy (Barbieri, 1907a) | | | 22.63 (0.13) | 43.90 (0.31) | | | | 44.38 (1.18) | 18.23 (0.28) | 21.08 (0.14) | | 16.23 (0.12) | |
| L. Como, Italy (Barbieri, 1907a) | | | 23.50 (0.14) | 45.57 (0.29) | | | | 52.83 (0.62) | 18.65 (0.17) | 21.22 (0.22) | | 15.13 (0.11) | |
| L. Como, Italy (Ferrero, 1951) | | | 22.00 (0.85) | 44.50 (0.56) | | 46.30 (0.99) | | 54.10 | 15-18 ¹ | 17-23 ¹ | | | |
| L. Garda, Italy (Barbieri, 1907a) | | | 22.11 (0.10) | 44.45 (0.27) | | | | 64.50 (0.83) | 18.85 (0.15) | 20.90 (0.14) | | 15.50 (0.20) | |
| L. Garda, Italy (Ferrero, 1951) | | | 21.90 (0.65) | 44.70 (0.82) | | 47.00 (0.95) | | 61.70 | 15-16 ¹ | 19-20 ¹ | | | |
| L. Garda, Italy (Oppi & Novello, 1989) | | | | | | | | 60.33 (0.25) | | | | | |
| L. Iseo, Italy (Ferrero, 1951) | | | 21.80 (1.13) | 45.20 (0.76) | | 47.20 (0.92) | | 59.60 | 15-16 ¹ | 19-20 ¹ | | | |
| L. Bracciano, Italy (Ferrero, 1951) | | | 22.00 (0.62) | 44.40 (0.92) | | 46.70 (0.37) | | 58.90 | 15-16 ¹ | 18-23 ¹ | | | |
| L. Bolsena, Italy (Ferrero, 1951) | | | 18.00 (0.43) | 45.60 (0.75) | | 47.00 (0.76) | | 56.00 | 15-16 ¹ | 18-23 ¹ | | | |

¹ Range

Table 1.10: Coefficients of the least square regression relating the number of gillrakers on the first gill arch of adult *Alosa* (Br) to total length (L_t) in cm; Br = a.L_t + b.

| Species / River, Country | a | b | r ² | n | Reference |
|--|-------|--------|----------------|-----|--------------------------------|
| <i>Alosa alosa</i> - Anadromous | | | | | |
| Rhine, Germany | 0.02 | 121.69 | 0.01 | 12 | Hoek (1899) |
| Aulne, France | 1.20 | 50.09 | 0.21 | 20 | Veron (1999) |
| Vilaine, France | 0.97 | 67.77 | 0.17 | 10 | Veron (1999) |
| Loire, France | 0.71 | 93.19 | 0.11 | 114 | Douchement (1981) |
| Charente, France | 0.51 | 96.92 | 0.05 | 60 | Veron (1999) |
| Garonne, France | 0.55 | 98.24 | 0.18 | 107 | Douchement (1981) |
| Adour, France | 0.41 | 103.89 | 0.07 | 138 | Douchement (1981) |
| Aude, France | 0.39 | 53.30 | 0.66 | 12 | Douchement (1981) |
| Rhône, France | 0.99 | 26.50 | 0.55 | 20 | Douchement (1981) |
| Sebou, Morocco | 0.56 | 77.82 | 0.18 | 303 | Sabatié (1993) |
| <i>Alosa fallax fallax</i> – Anadromous | | | | | |
| Elbe, Germany | 0.15 | 34.10 | 0.37 | 67 | Hass (1965) ² |
| Rhine, Germany | 0.06 | 38.33 | 0.06 | 15 | Hoek (1899) |
| Severn, UK | 0.26 | 34.67 | 0.12 | 189 | Aprahamian (1982) |
| Loire, France | 0.11 | 40.52 | 0.12 | 140 | Douchement (1981) |
| Charente, France | -0.26 | 53.08 | 0.04 | 29 | Veron (1999) |
| Garonne, France | 0.14 | 36.60 | 0.37 | 118 | Quignard & Kartas (1977) |
| Garonne, France | 0.12 | 37.65 | 0.15 | 231 | Douchement (1981) |
| Adour, France | 0.14 | 41.52 | 0.64 | 39 | Douchement (1981) |
| Loukos, Morocco | 0.10 | 38.54 | 0.10 | 59 | Sabatié (1993) |
| Sebou, Morocco | 0.19 | 35.15 | 0.17 | 318 | Sabatié (1993) |
| <i>Alosa alosa</i> x <i>Alosa fallax</i> Hybrids – Anadromous | | | | | |
| Loire, France | 1.30 | 17.91 | 0.31 | 48 | Douchement (1981) |
| Aude, France | 0.07 | 50.09 | 0.02 | 31 | Douchement (1981) |
| Rhône, France | 0.14 | 45.64 | 0.07 | 44 | Douchement (1981) |
| Sebou, Morocco | 0.29 | 56.74 | 0.06 | 47 | Sabatié (1993) |
| <i>Alosa fallax rhodanensis</i> – Anadromous | | | | | |
| Rhône, France | 0.06 | 36.65 | 0.41 | 147 | Quignard & Kartas (1977) |
| Rhône, France | 0.03 | 38.56 | <0.01 | 380 | Douchement (1981) |
| Rhône, France ¹ | 0.07 | 35.30 | ca. 0.03 | 346 | Le Corre <i>et al.</i> (1997a) |
| Aude, France | 0.29 | 24.75 | 0.59 | 48 | Quignard & Douchement (1991c) |
| Aude, France | 0.05 | 40.15 | 0.01 | 388 | Douchement (1981) |
| Tirso, Sardinia | 0.26 | 35.62 | 0.61 | 50 | Cottiglia (1963a) ³ |
| <i>Alosa fallax algeriensis</i> – Anadromous | | | | | |
| Miliane, Tunisia | 0.40 | 36.00 | 0.94 | 179 | Quignard & Kartas (1977) |
| Oubeira, Tunisia | 0.44 | 37.47 | 0.72 | 11 | Quignard & Kartas (1977) |
| <i>Alosa fallax</i> – Lacustrine | | | | | |
| L. Sidi Mohamed Ben Abdullah, Morocco | 0.35 | 31.50 | 0.74 | 18 | Sabatié (1993) |
| <i>Alosa fallax algeriensis</i> – Lacustrine | | | | | |
| Ishkeul, Tunisia | 0.39 | 36.98 | 0.77 | 95 | Quignard & Kartas (1977) |
| <i>Alosa fallax lacustris</i> – Lacustrine | | | | | |
| Bacin, Yugoslavia | 0.07 | 32.60 | 0.88 | | Vukovic (1961a) ⁴ |
| Skadar, Yugoslavia | 0.03 | 34.48 | 0.69 | | Vukovic (1961a) ⁴ |

¹Fork length converted to total length using $L_t = 1.0315 L_f + 41.76$ [(adapted from, Douchement (1981)], ²Cited by Quignard & Douchement (1991b), ³Cited by Quignard & Douchement (1991c), ⁴Cited by Quignard & Douchement (1991d).

Table 1.11: Coefficients of the least square regression ($Br = a.L_t + b$) relating the number of gillrakers on the first gill arch of juvenile anadromous *Alosa* (Br) to total length (L_t) in centimetres.

| Species / River, Country | a | b | r ² | n | Reference |
|-----------------------------------|----------------------|-------|----------------|-----|---------------------------|
| <i>Alosa alosa</i> | | | | | |
| Aulne, France | 1.58 | 45.60 | 0.34 | 23 | Veron (1999) |
| Adour, France | 2.11 | 47.73 | 0.53 | 68 | Douchement (1981) |
| Aude, France | 0.98 | 36.69 | 0.32 | 151 | Douchement (1981) |
| Rhône, France | 0.95 | 37.85 | 0.14 | 61 | Douchement (1981) |
| Sebou, Morocco | 0.21 | 32.31 | 0.42 | 42 | Sabatié (1993) |
| <i>Alosa fallax fallax</i> | | | | | |
| Elbe, Germany | 0.50 | 26.50 | 0.90 | 10 | Hass (1965) ² |
| Severn, UK ¹ | 0.90 | 20.70 | c. 0.88 | 72 | Claridge & Gardner (1978) |
| Adour, France | 0.39 | 35.85 | 0.53 | 23 | Douchement (1981) |
| Sebou, Morocco | - 505.9/ L_t | 38.70 | 0.22 | 335 | Sabatié (1993) |

1 Adult & juvenile stages combined, standard length converted to total length.

2 Cited by Quignard & Douchement (1991b)

For *Alosa fallax*, a latitudinal cline would appear to exist for anadromous populations along the Atlantic seaboard. Populations north of and including the River Mondego (Portugal) have a greater number of gill rakers (42.00-52.63) compared with more southern populations (41.32-41.97), with the exception of the population from the river Rhine (Germany) and the study by O'Maoileidigh (1990) on the Barrow (Ireland) which have 40.67 and 40.53 gill rakers, respectively (Table 1.6). The gill raker number of adult *A. fallax* from the Severn, England, (Mean \pm SE = 43.61 \pm 0.35 [Claridge & Gardner, 1978]; 44.51 \pm 0.23 [Aprahamian, 1982]) follows the latitudinal pattern. Similarly, though there is only one population of *Alosa alosa* south of the River Mondego, the population in the Sebou (Morocco) has a significantly lower number of gill rakers than more northern populations.

1.3.1.2 Scale

The scales of various members of the genus *Alosa* (Figure 1.5) are similar in structure (Hass, 1965; Berg & Grimaldi, 1967; Cassou-Leins & Cassou-Leins, 1981; Douchement, 1981; Eiras, 1981; Aprahamian, 1982; Baglinière & Le Louarne, 1987; Quignard & Douchement, 1991a&b; Mennesson-Boisneau & Baglinière, 1992; Sabatié, 1993; Le Corre *et al.*, 1997). The scales are cycloid and polygonal in shape. The anterior part of the scale can become modified after spawning by the erosion and/or absorption of scale material. The anterior portion of the scale displays a number of distinctive marks:

Annuli - Lines on the surface of the scale, following the contours of the periphery through both the anterior and posterior portions of the scale. They are usually indicated by attenuation or slight waviness of the transverse grooves and striae.

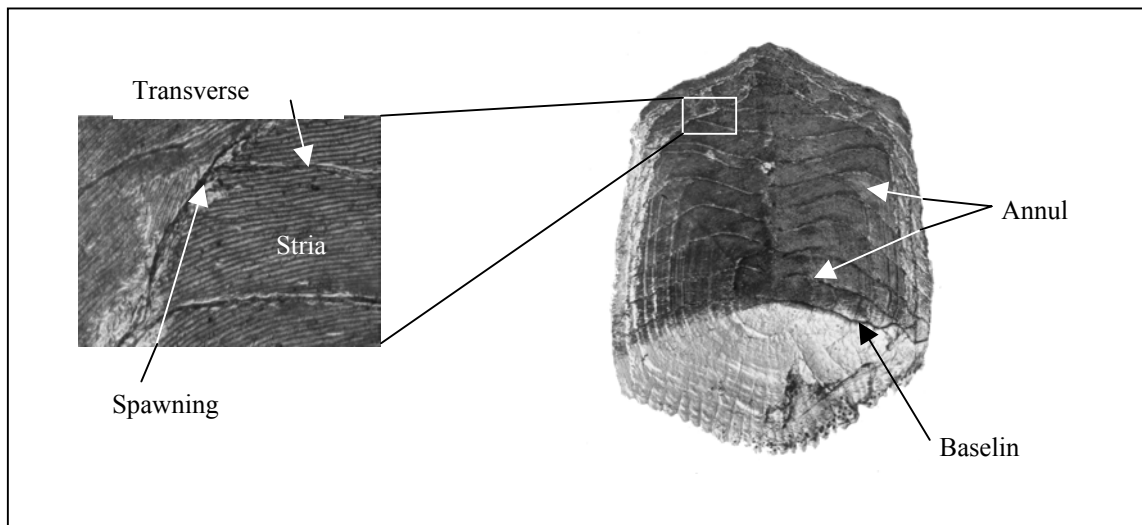


Figure 1.5: Scale from *Alosa fallax fallax*

Spawning mark - Formed during the pre-reproductive period by lateral absorption and/or erosion of the scale followed by rapid regenerative scale growth, leaving a characteristic scar.

Transverse grooves - Characteristic grooves running laterally across the surface of the anterior portion of the scale. The grooves are generally not continuous and may sometimes branch forming two lines.

Stria - Fine ridges covering the anterior portion of the scale; they lie very close together and run laterally across the scale.

Baseline - Taken as that line separating the anterior portion of the scale from the posterior portion.

Supernumary marks / false annuli - They are similar in appearance to true annuli, but are not present on all the scales from an individual. They rarely run around the whole scale and are less accentuated compared to true annuli. In certain populations (e.g. Sebou, Morocco) false annuli form close to the centre and are associated with spates during their first year of life (Baglinière *et al.* 2001; Sabatié & Baglinière, 2001).

For details of the use of scales for age determination see section 4.4.1 and Baglinière *et al.* (2001).

1.3.1.3 Relationship between girth and length

The relationship between girth (mm) and fork length (mm) for *Alosa fallax fallax*, caught in the Severn Estuary at the start of the freshwater phase of their spawning

migration, can be described by the least square regression (95% CI in brackets) [Arahamian, unpubl.]:

$$\text{Girth} = -45.05 (\pm 33.78) + 0.771 (\pm 0.093) L_f \quad n = 71; r^2 = 0.81.$$

1.3.1.4 Relationship between various length measurements

To enable comparison with other studies, equations to convert different length measurements are presented in Table 1.12. Throughout this synopsis where there has been a requirement to convert one length measurement to another, the relationships described by Douchement (1981) have been used.

Table 1.12: Parameters for the regression of $y = ax + b$, all measurements in mm (LS = least square regression, GM = geometric mean regression).

| River | Sex | y | x | a | b | n | r ² | Reg. | Reference |
|---|-------|-----------------|-----------------|--------|---------|-----|----------------|------|----------------------------|
| Alosa alosa | | | | | | | | | |
| Various France | M & F | L _f | L _t | 0.8824 | -2.0989 | 344 | 0.999 | LS | Douchement (1981) |
| | | L _t | L _f | 1.1325 | 2.6556 | 344 | 0.999 | LS | |
| | | L _{st} | L _t | 0.8371 | -6.0969 | 315 | 0.995 | LS | |
| | | L _t | L _{st} | 1.1882 | 9.4799 | 315 | 0.995 | LS | |
| | | L _f | L _t | 0.8974 | -6.6877 | 137 | 0.987 | LS | Véron (1999) |
| G-G-D1 France | M | L _t | L _f | 1.0087 | 5.4460 | | 0.910 | LS | Martin-Vandembulcke (1999) |
| | F | L _t | L _f | 0.9155 | 10.7110 | | 0.880 | LS | |
| Adour France | M | L _t | L _{st} | 1.1090 | 14.6050 | | | LS | Prouzet et al. (1994a) |
| | | L _t | L _f | 1.1000 | 2.2640 | | | LS | |
| | F | L _t | L _{st} | 1.1290 | 3.9490 | | | LS | |
| | | L _t | L _f | 1.0970 | 2.7500 | | | LS | |
| Sebou Morocco | Juv. | L _{st} | L _t | 0.8025 | 1.4977 | 42 | 0.984 | LS | Sabatié (1993) |
| | M | L _{st} | L _t | 0.8581 | -0.5021 | 280 | 0.964 | LS | |
| | F | L _{st} | L _t | 0.8962 | -2.6529 | 226 | 0.947 | LS | |
| Alosa fallax fallax | | | | | | | | | |
| Severn England | M & F | L _t | L _f | 1.1446 | 4.4816 | 197 | 0.978 | GM | Arahamian (1982) |
| | | L _{st} | L _f | 0.9702 | -9.2629 | 197 | 0.842 | GM | |
| Various France | M & F | L _f | L _t | 0.8907 | -4.5426 | 34 | 0.992 | LS | Véron (1999) |
| Sebou Morocco | Juv | L _{st} | L _t | 0.8212 | -0.1786 | 345 | 0.979 | LS | Sabatié (1993) |
| | M | L _{st} | L _t | 0.8511 | -0.4854 | 170 | 0.956 | LS | |
| | F | L _{st} | L _t | 0.8752 | -1.3544 | 149 | 0.949 | LS | |
| Alosa fallax rhodanensis | | | | | | | | | |
| Rhône France | Juv | L _t | L _f | 1.1343 | -0.0808 | 174 | 0.999 | LS | Crivelli & Poizat (2001) |
| Alosa fallax fallax & Alosa fallax rhodanensis | | | | | | | | | |
| Various France | M & F | L _f | L _t | 0.8849 | -2.0954 | 791 | 0.997 | LS | Douchement (1981) |
| | | L _t | L _f | 1.1264 | 3.5260 | 791 | 0.997 | LS | |
| | | L _{st} | L _t | 0.8390 | -4.4002 | 748 | 0.998 | LS | |
| | | L _t | L _{st} | 1.1896 | 5.9359 | 748 | 0.998 | LS | |

1 Gironde-Garonne-Dordogne system

1.3.1.5 Effect of preservation

Taverny & Elie (2001) examined the effect of freezing on length and weight measurements; the following relationships (Table 1.13) were obtained.

Table 1.13: Parameters for the regression of $y = ax + b$, length is in millimetres and weight in grams (Taverny & Elie, 2001).

| Species | Y | X | a | b | n | r^2 | Range |
|---------------------|-----------------------|------------------------|-------|--------|----|-------|------------------|
| <i>Alosa alosa</i> | $L_{t \text{ fresh}}$ | $L_{t \text{ frozen}}$ | 1.007 | 3.206 | 16 | 0.993 | 214 – 540 mm |
| | $W_{t \text{ fresh}}$ | $W_{t \text{ frozen}}$ | 1.016 | -2.825 | 16 | 0.999 | 87.2 – 1,670.0 g |
| <i>Alosa fallax</i> | $L_{t \text{ fresh}}$ | $L_{t \text{ frozen}}$ | 0.992 | 8.944 | 21 | 0.997 | 276 – 445 mm |
| | $W_{t \text{ fresh}}$ | $W_{t \text{ frozen}}$ | 1.023 | -0.978 | 21 | 0.999 | 184.2 – 692.4 g |

1.3.2 Internal Morphology

1.3.2.1 Vertebral column

Bertin (1958) described the arrangement of bones around the vertebrae (Figure 1.6). There are three series of bones; the epineural bones associated with the neural arch, the epicentral (adpleural) bones connected with the epapophyses, and the epipleural bones, which are associated with the hemal arch and ribs.

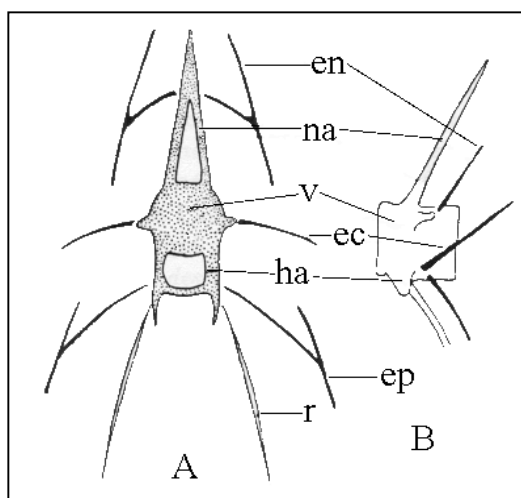


Figure 1.6: Skeletal features of *Alosa alosa*, axial view. *en* epineural bone; *ep* epipleural bone; *ha* hemal arch; *na* neural arch; *r* rib; *v* vertebra; *ec* epicentral bone; *ea* epapophyses. Reproduced from Bertin (1958).

1.3.2.2 Skull

The characteristics of the skull of *Alosa alosa* and *Alosa fallax* (Figure 1.7 & 1.8) have been described by Matthews (1887), Ridewood (1904) and Svetovidov (1964). The description of the skull is taken directly from Svetovidov (1963). *The vomer and the anterior part of the parasphenoid are almost straight. The anterior part of the parasphenoid is rounded in its middle dorsal surface, while the wings of the parasphenoid protrude ventrally underneath the myodome. The ventral edges of the*

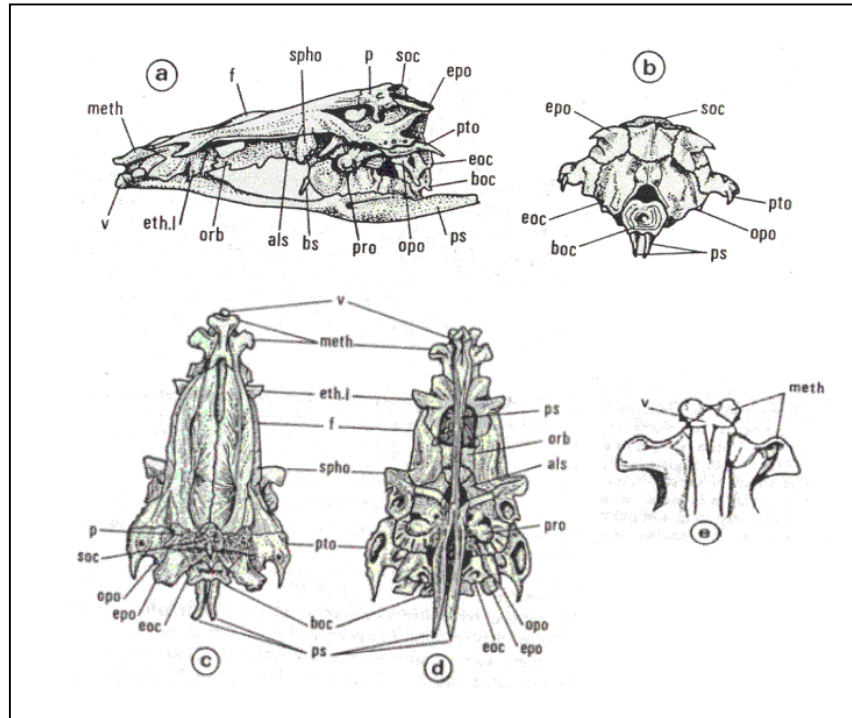


Figure 1.7: The skull of the allis shad *Alosa alosa*

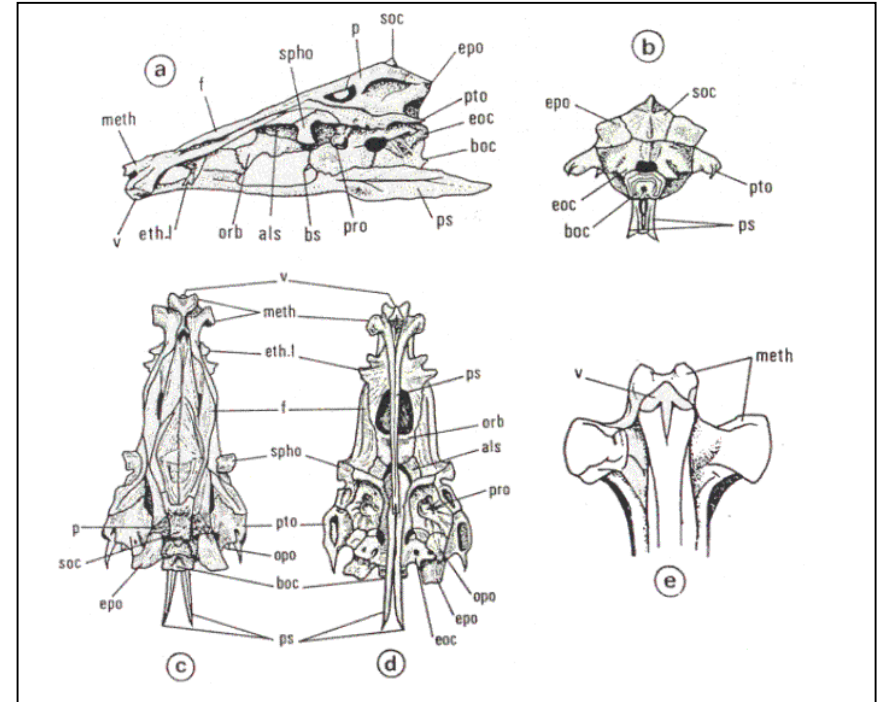


Figure: 1.8 The skull of the twaite shad *Alosa fallax fallax*

a lateral view; *b* posterior view; *c* dorsal view; *d* ventral view; *e* anteroventral view.

als alisphenoid; *boc* basioccipital; *bs* basisphenoid; *eoc* exoccipital (lateral occipital); *epo* epiotic; *eth. l* lateral ethmoidal; *f* frontal; *meth* mesethmoid; *opo* opisthotic; *orb* orbitosphenoid; *p* parietal; *pro* prootic; *ps* parasphenoid; *pto* pterotic; *soc* supraoccipital; *spho* sphenotic; *v* vomer, from Svetovidov (1964).

wings of the parasphenoid are either straight or slightly bent and are pointed at the tips. The descending process of the basisphenoid is long, frequently almost reaching the parasphenoid. The posterior edges of the supraoccipital and each epiotic on the upper part of the skull extend laterally, forming a right angle. The pterotic terminates posteriorly in a small spine. The anterior end of each sphenotic extends laterally, and may occasionally be directed anteriorly or posteriorly. They are rounded at their tips or bear a small, posteriorly directed hook-like appendage. The transverse extensions of the lateral ethmoids protrude from underneath the anterior end of the frontal bones, varying considerably in form and direction. The anterior extensions of the mesethmoid are directed laterally and somewhat anteriorly. They are straight and somewhat rounded at the tips.

The post temporal region is large and slender with two long limbs attached to the epiotic and opisthotic bones and there is a short limb that carries the sensory canal which touches the back of the supratemporal. The supratemporal is elongated horizontally; its sensory canal divides, with one branch going upward to the parietal and the other going forward into to the squamosal. The orbital ring is incomplete (Figure 1.9). Both the maxilla and premaxilla bear a row of between 20 and 30 minute teeth along the lower edge (Figure 1.10). The highest point of the mandible lies over the back half of the ramus. The hyomandibular articulates with the cranium by two distinct heads. The symplectic is rather small, abruptly terminated and is not enclosed by the quadrate. The palatine is short and has a distinct cartilaginous head for articulation with the prefrontal, not touching the premaxilla (Ridewood, 1904). No teeth are present on the palatine nor on the pterygoid bones. There are seven branchiostegal rays; five attached to the ceratohyal and two to the outer face of the epihyal.

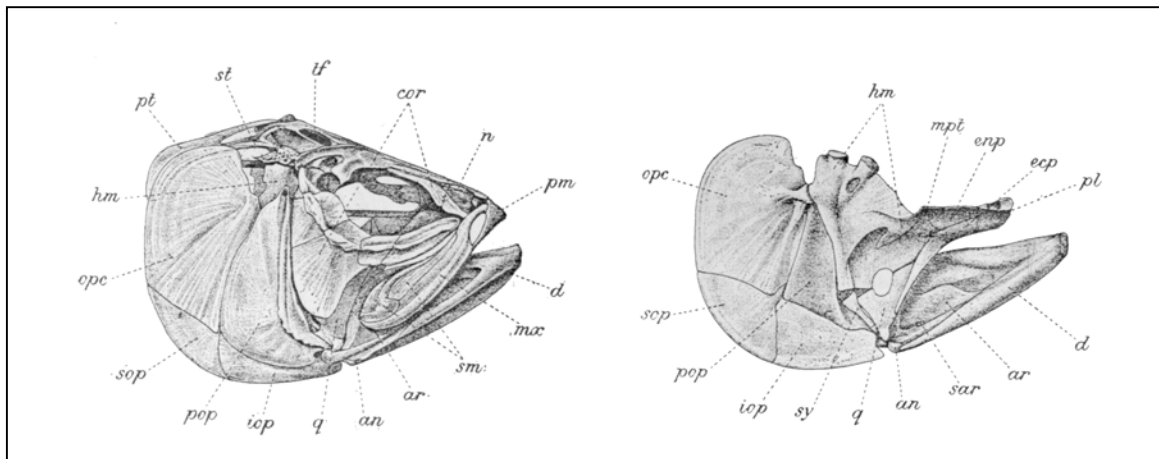


Figure 1.9: Head of *Alosa fallax*; an angular; ar articular; cor circumorbital bones; d dentary; ecp ectopterygoid; enp entopterygoid; hm hyomandibular; iop interopercular; mpt metapterygoid; mx maxilla; n nasal; ope opercular; pl palatine; pm premaxilla; i preopercular; pt post-temporal; sar sesamoidarticular; sm surmaxilla; sop subopercular; st supratemporal; sy symplectic; tf temporal foramen; from Ridewood (1904).

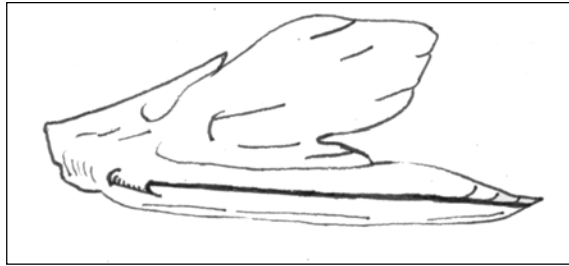


Figure 1.10: The lateral view of the left dentary of *Alosa fallax*, redrawn from Svetovidov (1964).

1.3.2.3 Otolith sagitta

The otolith of *Alosa alosa* has been described by Chaine (1938), and that of *Alosa fallax* by Jenkins (1902), Frost (1925), Chaine (1938) and Bauzá Rullán (1958). The otoliths of *A. alosa* and *A. fallax* (Figure 1.11 a&b) are similar except that, in *A. fallax*, the superior crest is more developed, the anti-rostrum protrudes further, the inferior crest is lower and not as sharp, the post caudal groove runs at an angle from the cauda to the posterior edge of the otolith, and the ventral groove is not as well defined.

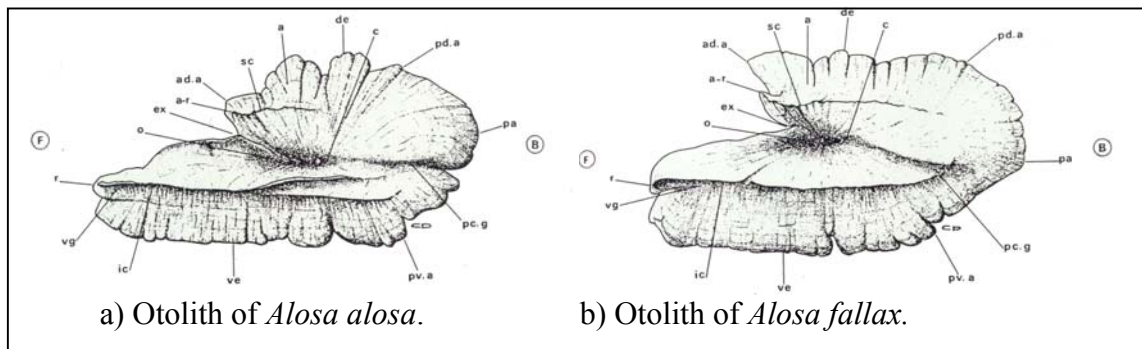


Figure 1.11: Otolith (Sagitta) of a) *Alosa alosa* and b) *Alosa fallax*. a area; ada anterodorsal angle; ar antirostrum; B back; c cauda; de dorsal edge; es excisura; F front; ic inferior crest; O ostium; pa posterior angle; pcg postcaudal groove; pda posteroventral angle; r rostrum; sc superior crest; ve ventral edge; vg ventral groove; from Quignard & Douchement (1991a&b).

1.3.2.4 Stomach

The anatomy of the stomach of alosoids has been described by Harder (1975). It is a Y shaped organ (Figure 1.12) consisting of two parts; a terminal blind sac or gastric caecum which is thin walled and used for storage, and a pyloric region where the muscle wall is much thicker, enabling food items to be crushed. In most cases, the food items found in the terminal blind sac have been used to describe the diet as the contents could be more accurately identified and quantified, little digestion having taken place.

The number of pyloric caeca has been reported for one specimen of *Alosa alosa* as 88 (Svetovidov, 1963) and for two specimens of *A. fallax fallax* as 74 (Svetovidov, 1963) and 96 (Fatio, 1890).

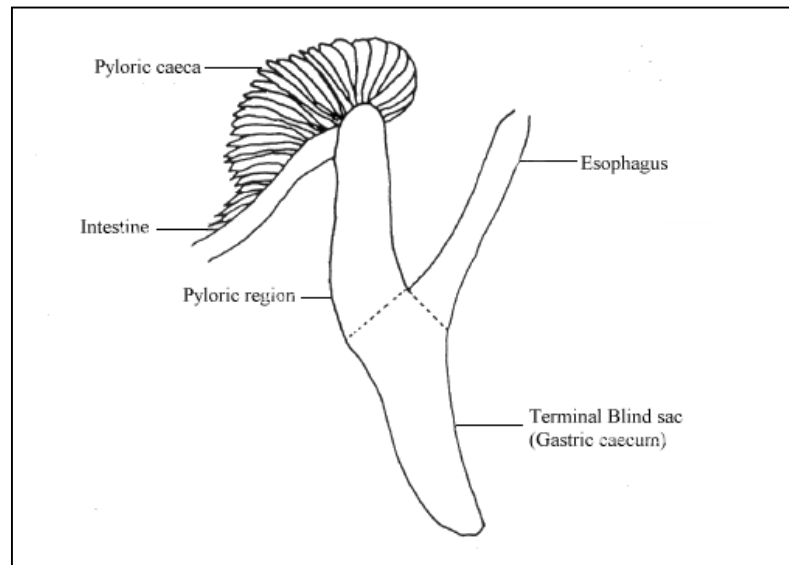


Figure 1.12: Stomach of a typical alosoid.

1.3.2.5 Endocrine system

- Pituitary gland

The pituitary gland has been described by Eiras (1981) for *Alosa alosa* and by Pavlović & Pantić (1975) for *A. fallax nilotica*. The pituitary gland (Figure 1.13) consists of four regions; the pars distalis rostralis (PDR), the pars distalis proximalis (PDP), the pars intermedia (PI) and the neurointermedial lobe (NIL).

The pars distalis rostralis contains both prolactin (PLH) and adrenocorticotrophic (ACTH) cells. The prolactin cells are tall and columnar and form the outer layer of the cavity wall. The ACTH cells are situated in the caudal part of the PDR closely associated with the projections of the neurophyophysis. The gonadotropic (GTH), somatotrophic (STH) and thyrotrophic (TSH) cells are situated in the pars distalis proximalis. The GTH cells are present mainly in the ventral part of the PDP while the STH occupy the dorsocranial part. The latter cells are tall and columnar in shape and situated in the form of a palisade. The TSH cells are present mainly in the dorsal region of the PDP and also in the pars intermedia during spawning. The pars intermedia contains two types of cell, those which stain positively with alcian blue-PAS-orange G(PAS+), and melanostimulating (MSH) cells. The latter cells are distributed mainly around the periphery of the PI.

The volume of the various regions changes during the sexual cycle, with a significant ($P < 0.01$) increase in the size of all three regions as the fish commence the freshwater phase of their spawning migration in April (see Section 3.4.4).

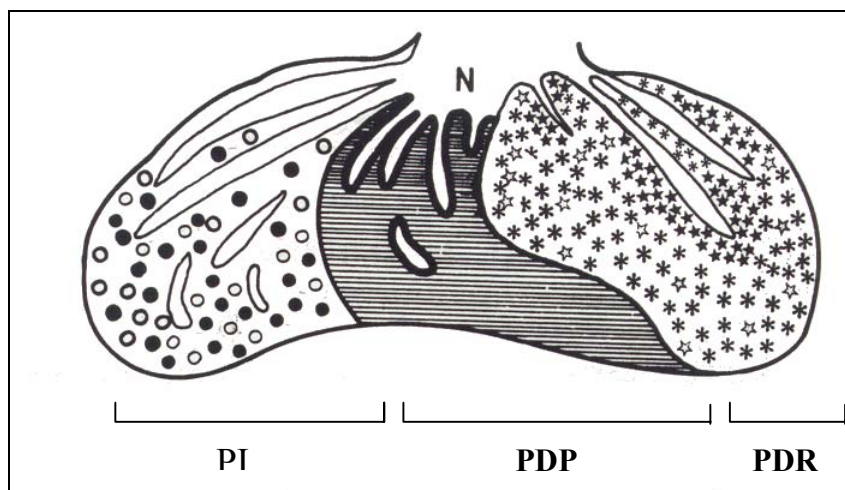


Figure 1.13: The pituitary gland of *Alosa alosa*; Pars distalis rostralis (PDR), Pars distalis proximalae (PDP), Pars intermedia (PI), Neurophyophysis (N), PAS+ (O), Melanostimulating (●), somatic (—), gonadotrophic (≡), prolactin (*), adrenocorticotrophic (☆) and thyrotropic (☆) cells. Reproduced from Eiras (1981b).

1.3.2.6 Thyroid

The thyroid consists of a series of follicle cells situated along the floor of the pharynx between the first and second gill arch (Lahaye, 1959).

1.3.2.7 Muscle

Greer-Walker & Pull (1975) reported that the muscle of a single specimen of *Alosa fallax* measuring 65cm in length (and thus more likely to be *Alosa alosa*) consisted of 21.5% red muscle and 78.5 % white muscle. The section was taken one third of the fish length from the tail and at the position along the fish where there is maximal flexure. The mean diameter of the red and white muscle was 15.9 μm and 39.1 μm , respectively.

1.3.2.8 Swimbladder

The swimbladder of *Alosa fallax* (Figure 1.14) lies at an angle of 90° to the axis of the body (Whitehead & Blaxter, 1989). The anterior end of the swimbladder leads straight into the bifurcating ducts (pre-coelomic ducts), no anterior duct being present. The ducts penetrate the skull and open up inside “bullae” (bony capsules) in the prootic and pterotic bones. The pneumatic duct runs from the posterior end of the blind sac of the stomach to the swimbladder, where it joins it approximately two thirds along its length. The swimbladder ends in a blind sac; no anal pore is present. The lack of an anal pore has also been reported for *Alosa alosa* (De Beaufort, 1909).

The gas-filled bullae are used for sound reception. Gregory (1999) reported that *A. fallax* were sensitive to sound transmitted at 200 K Hz but not at 420 K Hz.

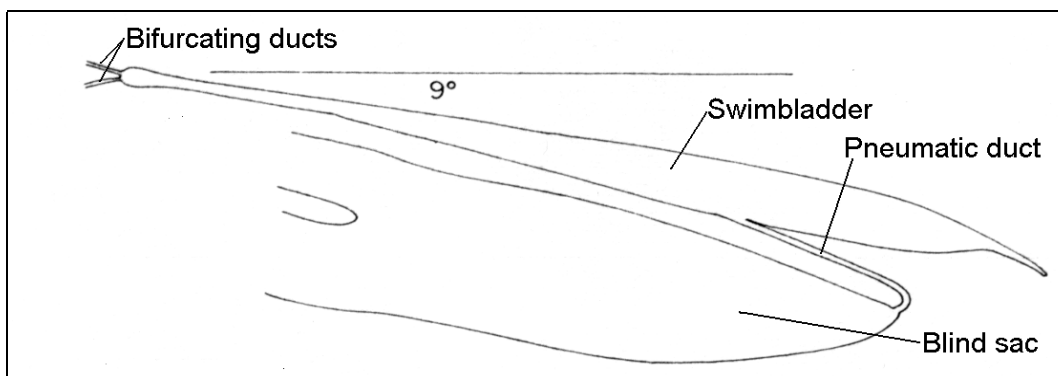


Figure 1.14: General shape of the swimbladder of *Alosa fallax* (Whitehead & Blaxter, 1989).

1.3.2.9 Gonads

The gonads are paired structures in the dorsal lining of the body cavity. In *Alosa* the eggs are released into the external environment via the oviducts, which are continuous with the ovary, forming a closed system. *Alosa* have a lobular testis covered by a membrane, which for *Alosa alosa* varies in thickness from 10.3 μ to 21.1 μ (Eiras, 1981b). The dimensions of the different cell types and their nucleus are shown in Table 1.14.

Table 1.14: Area and diameter of the different cell types and their nucleus in the testis of *Alosa alosa* from the River Douro, Portugal (Eiras, 1981b).

| Cell Type | Cell | | Nucleus | |
|-------------------------|------------------|--------------------|------------------|--------------------|
| | Area (μ^2) | Diameter (μ) | Area (μ^2) | Diameter (μ) |
| Spermatogonia | 39.25 \pm 1.65 | | 18.45 \pm 0.99 | |
| Primary spermatocytes | 17.55 \pm 0.76 | 4.70 \pm 0.11 | 9.01 \pm 0.41 | 3.36 \pm 0.09 |
| Secondary spermatocytes | 11.46 \pm 1.05 | 3.87 \pm 0.17 | 5.16 \pm 0.49 | 2.51 \pm 0.12 |
| Spermatids | | | 2.44 \pm 0.05 | 1.80 \pm 0.09 |
| Spermatozoa | | | 1.05 \pm 0.04 | 1.17 \pm 0.03 |

The histology and maturation of the ovaries is described in the section dealing with the development of the gonads and spawn (Section 3.1.6).

Taverny (1991a) reported that for mature *Alosa alosa* the left-hand ovary was significantly ($P < 0.05$) heavier than the right-hand ovary, for *A. fallax* there was no significant difference in weight between the two ovaries.

1.3.2.10 Liver

The weight of the liver of *Alosa alosa* in relation to that of the soma (mean \pm 95%CI) ranged from 3.25 ± 1.24 % to 2.19 ± 1.11 % for females and 2.34 ± 2.48 % to 1.50 ± 0.39 % for males (Sabatié, 1993). For *Alosa fallax fallax* the index varied from 1.86% (± 1.75) to 2.67 (± 1.07) (Sabatié, 1993). For both species the difference was not significant ($P > 0.05$).

1.3.3 Cytomorphology

The lipid, protein, carbohydrate and water content of adult *Alosa alosa* (Table 1.15) have been described from the River Douro (Portugal) and the Gironde-Garonne-Dordogne system (France) (Eiras, 1981b; Bengen, 1992). The concentration of the various constituents changes during the freshwater phase of their spawning migration (see Section 4.9.2).

Table 1.15: Range in percentage water, protein, lipid and carbohydrate in male and female adult *Alosa alosa* (Eiras, 1981b; Bengen, 1992).

| Organ | Sex | Water | Protein | Lipid | Carbohydrate |
|--------|-----|-----------|-----------|----------|--------------|
| Muscle | M | 67.2-76.6 | 10.1-18.2 | 0.8-10.3 | 1.53-1.83 |
| | F | 66.9-76.1 | 10.5-21.5 | 0.8-11.3 | 1.35-1.59 |
| Gonad | M | 74.7-78.9 | 11.0-17.6 | 3.2-5.8 | 1.62-2.22 |
| | F | 72.2-75.3 | 14.2-22.1 | 3.9-6.7 | 1.59-1.79 |
| Liver | M | 61.3-75.9 | 5.8-11.2 | 5.1-19.2 | 1.19-1.47 |
| | F | 62.3-76.4 | 4.3-16.9 | 3.4-18.5 | 1.19-1.35 |

The nucleic content of larvae *Alosa fallax fallax* (4.65 – 18.10 mm L_{st}) from the Mira estuary (Portugal) can be described by the equations (Esteves, pers. comm.):

$$\text{DNA } (\mu\text{g larvae}^{-1}) = -11.79 e^{(1.62+0.17 L_{st})} \quad n = 402; r^2 = 0.63$$

$$\text{RNA } (\mu\text{g larvae}^{-1}) = -34.03 e^{(2.63+0.15 L_{st})} \quad n = 402; r^2 = 0.47$$

With L_{st} = standard length in mm.

The concentration of the antioxidant enzymes catalase (E.C.1.11.1.6), glutathion peroxidase (E.C.1.11.1.19) and glutathion S-transferase (E.C.2.5.1.18) in the liver of *Alosa fallax nilotica* caught at sea have been reported by Kolayli *et al.* (1997) (Table 1.16).

Table 1.16: Antioxidant enzyme activity in the liver of *Alosa fallax nilotica* (Kolayli *et al.*, 1997).

| Enzyme | Enzyme activity | | |
|--------------------------|---------------------------|--------------|----------------|
| | B.U ¹ /g w.t.w | U/g w.t.w | U/mg.prot |
| Catalase | 0.53 (0.08) | | 177.20 (26.77) |
| Glutathion peroxidase | | 133.9 (23.6) | 1.53 (0.27) |
| Glutathion S-transferase | | 60.2 (4.1) | 0.69 (0.05) |

¹Bergmeyer unit (one B.U. unit is the amount of catalase which decomposes 1.0 g H₂O₂ in one minute).

- Trace metals

The range in concentration of certain trace elements (Table 1.17) has been determined for pre and post-spawned female *Alosa fallax fallax* from the Severn Estuary, England (Aprahamian, unpubl.), see also section 3.4.4 (metabolism).

Table 1.17: Range in concentration ($\mu\text{g g}^{-1}$) of calcium (Ca), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) in the scales, bone (operculae) liver, muscle and ovary of adult female *Alosa fallax fallax* (n=37) from the Severn Estuary (Aprahamian, unpubl).

| Trace Element | Scale | | Operculae | | Liver | | Muscle | | Ovary | |
|---------------|-------|-------|-----------|-------|-------|--------|--------|--------|-------|--------|
| | Min | Max | Min | Max | Min | Max | Min | Max | Min | Max |
| Ca | 94.4 | 127.6 | 125.4 | 185.1 | 158.8 | 2384.0 | 157.0 | 2680.0 | 104.0 | 3664.0 |
| Cu | 3.8 | 14.1 | 5.6 | 27.8 | 7.0 | 45.1 | 1.80 | 19.7 | 2.7 | 19.1 |
| Fe | 19.2 | 425.0 | 18.4 | 387.0 | 803.0 | 6857.0 | 24.2 | 198.7 | 49.6 | 793.0 |
| Mn | 3.9 | 40.2 | 14.4 | 93.6 | 4.6 | 11.1 | 0.0 | 3.5 | 1.0 | 10.0 |
| Zn | 53.8 | 354.0 | 70.9 | 128.5 | 85.7 | 224.0 | 8.3 | 41.5 | 66.0 | 6030.0 |

The mean (\pm 95% CI) concentrations of iron, copper, zinc and manganese in the muscle of *A. fallax lacustris* from Lake Omodeo (Sardinia) was 8.9 (\pm 1.7), 2.1 (\pm 0.5), 10.4 (\pm 2.3) and 1.6 (\pm 0.5) mg kg⁻¹, respectively (Cottiglia et al., 1982).

Berg (1972) reported the calcium and strontium concentrations in *Alosa fallax lacustris* from Lake Maggiore were 6.58 mgCag⁻¹ and 4.99 $\mu\text{g Srg}^{-1}$ (wet weight), respectively. In the scale and bone the calcium concentrations were similar 377 and 376 mgCag⁻¹ (ash). The dry weight and ash content were 235 and 25 mgg⁻¹, respectively. The proportion of dry weight and ash made up by the scales was 3.4 and 12.3% and by bone 11.5 and 51.3% respectively.

- Heavy metals

The mean (\pm 95% CI) amounts of mercury in the liver, kidney and muscle of *Alosa fallax fallax* were 0.67 \pm 0.08 mg kg⁻¹, 0.50 \pm 0.05 mg kg⁻¹ and 0.22 \pm 0.02 mg kg⁻¹, respectively (Aprahamian *et al.*, unpubl.). Samples were from mature fish collected from the Severn Estuary (England) at the start of the freshwater phase of their spawning migration.

- DNA Adducts

The mean (\pm 95% SE) concentration of DNA adducts in *Alosa fallax nilotica* from the south-eastern Black Sea was 4.0 \pm 0.5 and 4.5 \pm 0.5 adduct per 108 nucleotides in the liver and muscle, respectively (Karakoç *et al.* 1998). This suggests a relatively unpolluted environment.

1.3.4 Protein and genetic variability

Morel (1974) found real 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 & Gioppato, 1997). Though Rizzotti & 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* (Figure 1.15). Alexandrino (1996a) found that 4 out of the 15 protein loci examined in *Alosa* populations from Portugal were polymorphic; haemoglobin (HBA), adenosine deaminase (ADA), mannosephosphate isomerase (MPI) and alcohol dehydrogenase (ADH), (Table 1.18). 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.* (1998) 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).

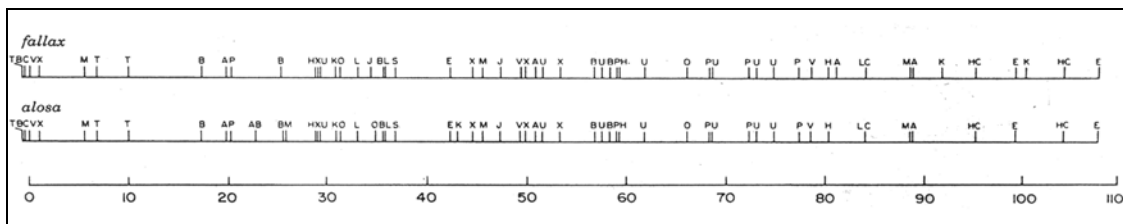


Figure 1.15: Restriction site maps of the mtDNAs of *Alosa alosa* and *Alosa fallax*. The map for each species corresponds to the most common genotype observed for that species. Abbreviated names of restriction sites are as follows: T, *SstII*; P, *PstI*; E, *EcoRI*; L, *Sall*; S, *SstI*; J, *Clal*; C, *EcoRV*; X, *XbaI*; H, *HpaI*; M, *BstEII*; K, *KpnI*; V, *PvuII*; B, *BglI*; A, *ScaI*; U, *StuI*; O, *BclI*. One map unit corresponds to approximately 168 base pairs (Bentzen *et al.*, 1993).

Alexandrino *et al.* (1996) used isoelectric focusing to detect polymorphic variation in haemoglobin and adenosine deaminase, allowing the proteins to be split into subunits. Haemoglobin was split into two subunits (HBA and HBB); no variation was detected at HBB, however, at the HBA zone two codominant alleles were present, HBA*F and HBA*S. HBA*F was nearly totally confined to *Alosa alosa* populations while HBA*S was the most common allele for *Alosa fallax* populations. ADA phenotypes were determined by three codominant alleles; ADA*1F, ADA*1S and ADA*2. ADA*1F and ADA*2 were present at a higher frequency in populations of *Alosa fallax*. Other protein polymorphisms were also detected in both species, *Alosa alosa* and *Alosa fallax*, namely, acid phosphatase (ACP) (Castro *et al.*, 1999), amylase (AMY) and malic enzyme (ME-2) (Alexandrino *et al.*, in preparation; Le Corre, 1999; Veron *et al.*, 2001).

Mitochondrial DNA of both *Alosa alosa* and *A. fallax* (Bentzen *et al.*, 1993) are polymorphic, approximately 18.3 kb in size and have a high degree of similarity (98.8%) (Figure 1.15). 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 mitochondrial DNA (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 recent molecular data (Alexandrino *et al.*, in preparation), based on direct sequencing of 360 bp of cytochrome b mtDNA gene, that reveals two distinct haplotype clades separated by 6 base substitutions (1.3% divergence), (Figure 1. 16).

Table 1.18: 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) and Rhône (R) (Alexandrino, 1996a; Le Corre *et al.*, 1998; Véron *et al.*, 2001).

| Locus | Allele | <i>Alosa alosa</i> | | | | | <i>Alosa fallax</i> | | | | | |
|-------|--------|--------------------|------|------|------|------|---------------------|------|------|------|------|------|
| | | A | C | L | M | CB | C | L | M | T | G | R |
| HBA | HBA*F | 0.85 | 0.77 | 1.00 | 0.97 | 1.00 | 0.00 | 0.12 | 0.15 | 0.02 | 0.00 | 0.01 |
| | HBA*S | 0.15 | 0.23 | 0.00 | 0.03 | 0.00 | 1.00 | 0.88 | 0.85 | 0.98 | 1.00 | 0.99 |
| ADA | ADA*1F | 0.08 | 0.03 | 0.00 | 0.04 | 0.00 | 0.15 | 0.43 | 0.63 | 0.32 | 0.52 | 0.96 |
| | ADA*1S | 0.79 | 0.95 | 0.99 | 0.92 | 1.00 | 0.35 | 0.23 | 0.06 | 0.10 | 0.00 | 0.01 |
| | 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 | MPI*1 | 0.11 | 0.05 | 0.10 | 0.00 | 0.00 | 0.97 | 0.64 | 0.74 | 0.75 | 0.91 | 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 |
| ADH | ADH*1 | 1.00 | 0.96 | 1.00 | 1.00 | 1.00 | 0.71 | 1.00 | 0.71 | 0.18 | 0.50 | 1.00 |
| | ADH*2 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.29 | 0.00 | 0.29 | 0.82 | 0.50 | 0.00 |
| | ADH*3 | | 0.03 | | | | 0.00 | | | | | |

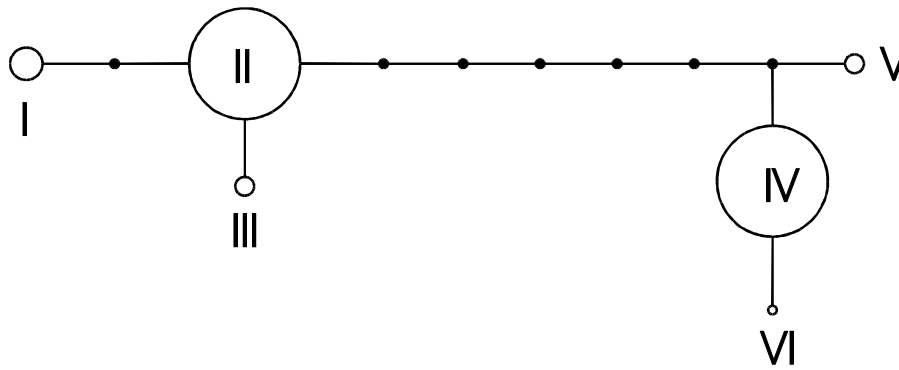


Figure 1.16: Network representing 6 mtDNA haplotypes (360 bp of the 5' -end mtDNA cytochrome b gene) found in 25 *Alosa spp* individuals. Each branch represent a single nucleotide change, solid circles represent missing haplotypes, and size of empty circles reflects the frequency of each haplotype. I, II and III: *Alosa fallax* haplotypes; IV, V and VI: *Alosa alosa* haplotypes (from Alexandrino *et al.*, in preparation).

- Populations and/or stocks

Protein, meristic and morphometric differences indicate separate populations of *Alosa* exist and that in order to maintain these differences homing must take place to their natal river (Alexandrino & Boisneau, 2000; Sabatié *et al.*, 2000).

Protein differences indicated that of the eleven populations of *Alosa fallax* studied (Alexandrino, 1996a; Le Corre *et al.*, 1998; Véron *et al.*, 2001; Alexandrino *et al.*, in preparation; Sabatié, unpubl.) three groups are apparent (Figure 1.17). There is one group comprising *Alosa fallax rhodanensis* from the rivers Rhône, Herault 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 (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. From the six anadromous populations analysed only a slight divergence is observed in *Alosa alosa* from the southern and northernmost populations of Guadiana and Charente respectively (Fig 1.17).

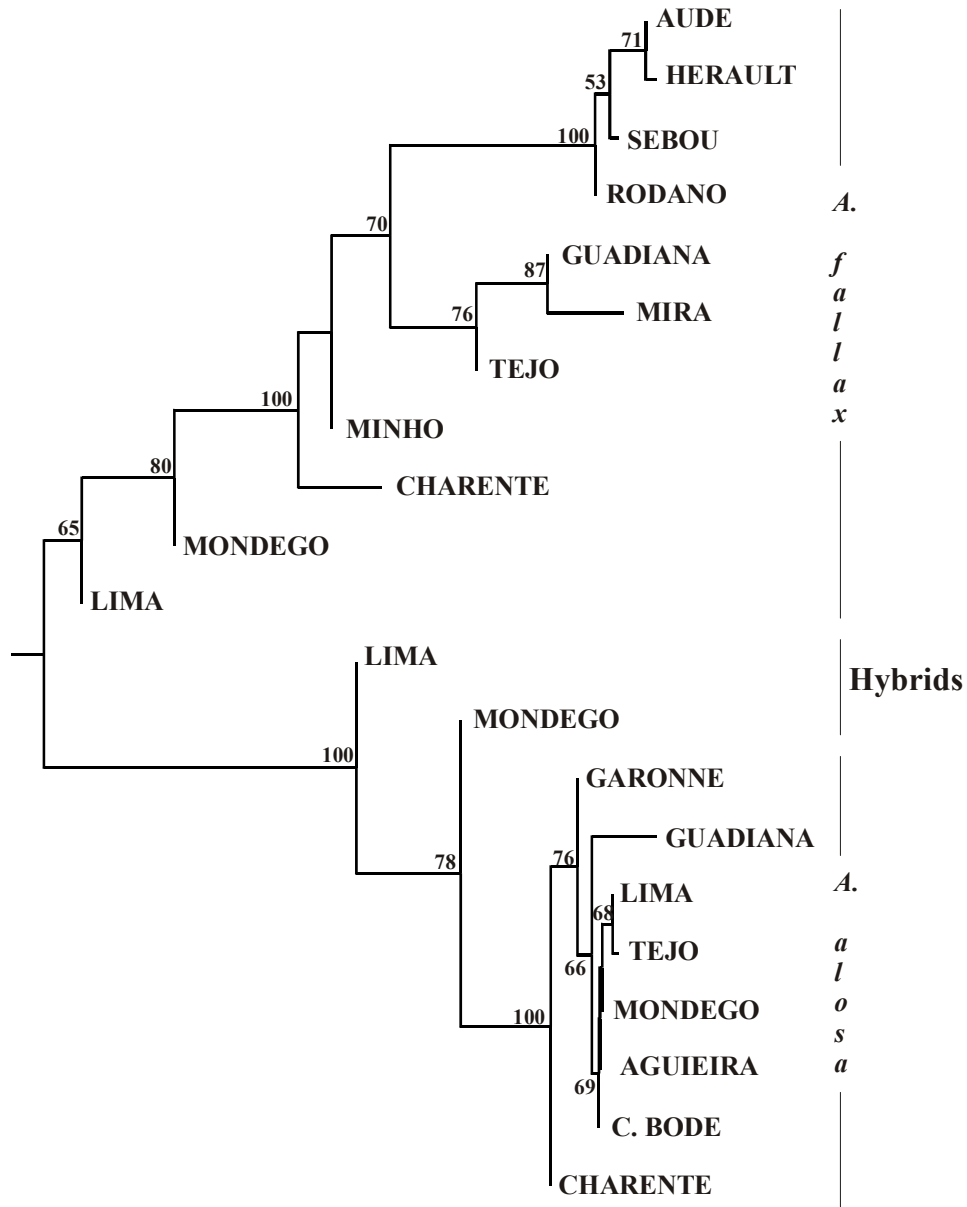


Figure 1.17: Neighbor-Joining tree based on Nei's genetic distances between population samples. Data are based on allelic variance at eight allozyme loci screened (data from Alexandrino, 1996a; Le Corre, 1999; Véron *et al.*, 2001; Alexandrino *et al.*, in preparation). Numbers above nodes represent percent bootstrap values (100 replicates). Aguieira and C. Bode *A. alosa* populations are land-locked populations from Mondego and Tejo basins respectively.

2. DISTRIBUTION

At sea *Alosa alosa* and *Alosa fallax* are coastal in their habit and are clumped in aggregations around the major catchments for reproduction (Quero *et al.*, 1989; Taverny, 1991a). *A. alosa* has been reported from depths ranging from 10 to 150m (Laroche, 1985; Taverny, 1991a) up to *c.* 300m (Roule, 1933; Dottrens, 1952; Lithogoe & Lithogoe, 1971) and *A. fallax* from 10 to 110m with a preference for water of 10 to 20m deep (Taverny, 1991a). Taverny & Elie (2001a) showed that the depth at which both species were caught was significantly positively correlated with their age and size.

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. 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.

2.1 Total Area

The total distribution area is shown in Figure 2.1. It is realised that uncertainty exists with regard to which sub-species of *Alosa fallax* inhabit which rivers draining into the Mediterranean Sea. For the purposes of this review those species of *Alosa fallax* inhabiting the Mediterranean to the West of Italy have been classified as *Alosa fallax rhodanensis*, with the exception of those found around the North African coast which are *Alosa fallax algeriensis*. *Alosa fallax nilotica* has been considered to be confined to that area of the Mediterranean east of the Italian Peninsula.



Figure 2.1: Distribution of *Alosa* spp. in Europe, the Mediterranean and North Africa

2.1.1 *Alosa alosa* and *Alosa fallax fallax*

Alosa alosa and *Alosa fallax* have been reported from Iceland (Saemundsson, 1949) at the northern most limit of their range, to Morocco in the south (Furnestin, 1952; Dollfus, 1955; Blanc *et al.*, 1976; Matallanas *et al.*, 1981) and as far east as Scandinavia (Pethon, 1979) and the Baltic Sea (Manyukas, 1989). *Alosa alosa* have been reported only from the western part of the Mediterranean (Sostoa & Sostoa, 1979; Douchement, 1981), while *Alosa fallax* are encountered through out the Mediterranean.

Both species of *Alosa* have been reported infrequently from around Scandinavia and there have been no reports of a spawning population existing in Norway or Finland. In Sweden *A. alosa* have been caught in the River Dalälven and *A. fallax* from the rivers Lagan and Nissan, though whether a spawning population exists remains uncertain (Nathanson pers. comm). Juvenile *A. fallax* (length 90 to 100 mm) have been found off the Swedish coast around the Skåne peninsula (Nathanson pers. comm.). In the 1930s *Alosa fallax* were considered abundant in the gulfs of Finland and Riga and particularly in the River Narva, Estonia, (Mikelsaar, 1984), which may represent the northern limit for a spawning population. In Estonian waters the species is now only rarely caught (Saat, 2002).

A spawning population of *A. fallax fallax* has been reported from the Nemunas (Nyamunas) River, Lithuania (Manyukas, 1989) [Figure 2.2]. However, since the construction of the Kaunas hydroelectric dam in 1959 and elevated pollution from poorly treated wastewater from paper mills in the lower river the population declined (Maksimov & Toliušis, 1999; Repečka, 1999). *A. fallax fallax* are only occasionally caught in the Curonian Lagoon (Mileriene, 1997; Repečka, 1999) as well as over the Baltic Sea region (Wiktor, 1989; Winkler, 1991) and are now considered very rare. In 1997, however relatively large numbers (160 kg) were caught (Maksimov & Toliušis, 1999). This may reflect a decrease in pollution as a result of the economic



Figure 2.2: Distribution of *Alosa* spp. in Northeast Europe

recession and possibly also the opening of a shipping lane (1984-6) which improved water quality in the lagoon and access to the Nyamunas (Repečka, 1999). In the first half of the 20th century the Nyamunas river did support an important fishery with the average catch for the periods 1930-4; 1935-47; 1948-52 and 1953-57 being 16,100 kg, 28,500 kg, 29,800 kg and 2,200 kg, respectively (Manyukas, 1989), with a peak catch of 50,000 kg in 1948 (Repečka, 1999). After 1960 the fishery ceased.

On the south shore of the Baltic Sea *A. fallax fallax* have been found in the lower reaches of the River Wista (Vistula), Poland (Chmielewski, 1965). They have been reported sporadically in the River Odra (Oder) (Waterstraat, 1986) and from Szczecin Bay into which the Odra drains (Peczalska, 1973) [Figure 2.2]. In the first half of the twentieth century the rivers Elbe, Weser and Ems all supported commercial fisheries for *A. fallax* (Drimmelen, 1951; Nolte, 1976). Wilkens & Köhler (1977) mention that *A. alosa* is now extinct in the River Elbe, however Möller (1989) mentions that allis shad have never been reported from the lower Elbe, but Fric (1859) reports that a few specimens were caught in the 19th century far upstream. Duncker & Ladiges (1960) consider that the conflicting reports may be due to misidentification between the species.

Alosa alosa became extinct in the River Weser at the beginning of the twentieth century, as a result of over-fishing, channelisation and the construction of dams (Busch *et al.*, 1988; 1989). A spawning population of *A. fallax* exists in both the River Elbe (Hass, 1965, 1968; Möller & Dieckwisch, 1991; Thiel *et al.*, 1996a) and the River Weser (Scheffel, 1988, Scheffel & Schirmer, 1991). In the River Elbe, Möller (1989) showed that the abundance of 0+ *A. fallax* in the 1980s was between 3.9 and 9.3 times that of the estimate of Apstein (1895) in 1894. However, the population of *A. fallax* in the River Weser has declined dramatically since the 1950s because of channelisation and an increase in sewage and salt pollution. The increase in salt pollution is related to the expansion of the potash industry, as a result the salinity in the lower Weser is in the region of 1 to 2.5 ‰ (Busch *et al.*, 1988; 1989). *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 & Jager, 2002), suggests that a spawning population may still exist.

In the latter part of the eighteenth century a spawning population of *A. alosa* and *A. fallax* existed in the Rhein (Rhine) (Hoek, 1899; Regan, 1911; Redeke, 1938). A steep decline in numbers of *A. alosa* occurred c.1900 and of *A. fallax* after 1942 (Figure 2.3). The decline of *A. alosa* was due to over fishing, barriers to their migration and destruction of their spawning habitat (de Groot, 1989; Raat, 2001). The most significant factor in the decline of *A. fallax* was the damming of the river (closure of the Haringvliet in 1970) preventing the fish from spawning in the tidal freshwater portion of the river (de Groot, 1989) and the subsequent change in the tidal regime which resulted in an increase in sedimentation (De Nie, 1996). However, *A. fallax* were still spawning at the Biesbosch (where the Meuse meets the Rhine) in 1968 (Boddeke, 1974). Lelek (1976) reported sightings of *A. fallax* in the Rhine and its tributary the River Main, but overall both species now appear to be only rarely encountered (Cazemier, 1988; de Groot, 1990; Bartl & Troschel, 1995; Buijse & Cazemier, 1998). Buijse & Cazemier (1998) concluded that *A. fallax* were unlikely to be successfully breeding in The Netherlands, at present.

At the turn of the nineteenth century both species of shad were present in Belgium (Anonymous, 1901a). Anonymous (1888) reported the presence of a spawning population of

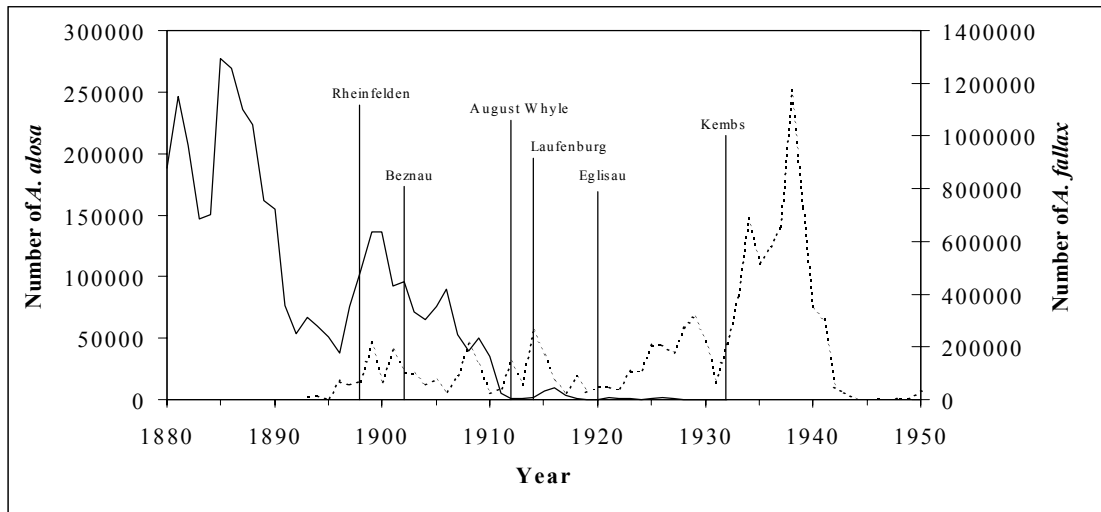


Figure 2.2: The catch of *Alosa alosa* (solid line) between 1880 and 1934, and of *A. fallax* (dotted line) between 1893 and 1950, from the lower Rhine (Data from de Groot, 1989, 1990). Vertical lines show the dates when dams were built.

Alosa alosa and *A. fallax* in the River Meuse (Figure 2.2). However, by 1925 *A. alosa* and by 1950 *A. fallax*, were no longer found in the Walloon part of the rivers Escaut and Meuse (Poll, 1947; Philippart & Vranken, 1981, 1982) as a result of over-exploitation, pollution, habitat destruction and the building of weirs (Philippart *et al.*, 1988). There have been no recent reports of the occurrence of either species in the Flemish lowland rivers (Bervoets *et al.*, 1990).

Alosa alosa and *A. fallax* have been recorded from most areas around the British Isles (Maitland, 1972, 1979; O'Maoileidigh *et al.*, 1988; Potts & Swaby, 1993a; 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 Suir in Ireland (Aprahamian & Aprahamian, 1990) [Figure 2.4].



Figure 2.3: Spawning distribution of *A. fallax* in the UK, 1 = Lough Leane.

A spawning population of *A. alosa* existed in the River Severn until the middle of the nineteenth century. Its decline has been attributed to navigation weirs constructed c. 1842 (Day, 1890). The River Thames supported a spawning population of *A. fallax* up until the middle of the nineteenth century, though its decline appears more attributable to a deterioration in water quality than to the construction of navigation weirs (Aprahamian & Aprahamian, 1990). There is also good evidence to suggest that a population of *Alosa* spp. used to exist in the River Trent (Anon. 1622; Deering, 1751; Anon. 1890).

Along the North French coast a spawning population of both species previously existed in the Seine (Vincent, 1889; Roule 1920a), becoming extinct following the construction of the Poses and Martot dams in 1887 at Rouen (LeClerc, 1941). Spawning populations of *A. fallax fallax* have been reported in the rivers Orne (lower Normandy) and the Brittany rivers Aulne, Blavet and Vilaine (Véron, 1999) [Figure 2.5].

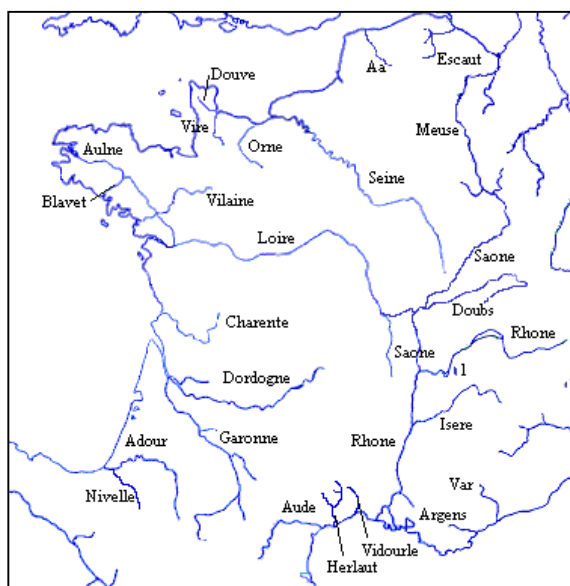


Figure 2.4: Spawning distribution of *Alosa* in France. 1 = Lake Bourget

Of the rivers entering the Atlantic spawning populations of *A. alosa* and *A. fallax* are present in the Loire, Charente, Garonne and Dordogne, Adour and Nivelle (Mennesson-Boisneau & Boisneau, 1990; Taverny, 1991a; Prouzet *et al.*, 1994a; Véron, 1999; Baglinière, 2000) [Figure 2.5]. 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 (see section 6.3).

Along the Atlantic coast of the Iberian Peninsula spawning populations of both species of shad have been reported in the rivers Miño (Minho), Lima, Douro, Vouga, Mondego, Tejo and the Guadiana (Capello, 1880; Regalla, 1888; Nobre, 1932; Ribeiro, 1971; Eiras 1980, 1981b, Alexandrino, 1996a&b; Collares-Pereira *et al.*, 2000; Costa *et al.*, 2001) [Figure 2.6]. However, dam construction on a number of Portuguese rivers has had a dramatic impact on populations (Costa *et al.*, 2001). In the Douro, the Crestuma-Lever dam constructed in 1985 21 km upstream from the river mouth has resulted in the populations of *A. alosa* and *A. fallax* virtually becoming extinct (Alexandrino, 1996b).

While in the rivers Tejo and Miño the populations of *A. alosa* have declined dramatically (Figure 2.7) to the extent that only a residual population now exists in the Tejo (Alexandrino, 1996b). In the Tejo this decline is associated with the construction of the Castelo de Bode and Belver dams in 1951 and 1952 respectively (Costa *et al.*, 2001). Though a Borland fish lift has been installed on the Douro at Crestuma-Lever and on the Tejo at Belver (170 km from the mouth of the Tejo) they do not appear to be effective in passing *Alosa* spp. upstream (Bochechas, 1995). Spawning populations of *A. fallax* exist in the rivers Mira and probably also in the Cavado and the Sado (Alexandrino, 1996b). Lozano Rey (1935, 1947) has reported both species in the River Guadalquivir (Quadalquivir), though recent evidence suggests only a spawning population of *A. fallax* now exists (Doadrio, 1991; Alexandrino, pers. comm.). In Portugal there are two landlocked populations of *A. alosa*; one in the Castelo de Bode reservoir on the River Tejo (Eiras 1981a, 1983) and one in the Aguieira Reservoir on the River Mondego (Collares-Pereira *et al.*, 1999) [Figure 2.6]. These are thought to be the result of the impoundment of the rivers in 1951 and 1981, respectively. In Spain a landlocked population of *A. alosa* exists in the River Guadalquivir (Moron, pers. comm.).



Figure 2.5: Distribution of *Alosa* in Southwest Europe and Northwest Africa. 1 = Aguieira Reservoir, 2 = Castelo de Bode Reservoir, 3 = El Kansera, 4 = Sidi Mohamed Ben Abdallah.

In the Moroccan Oueds draining into the Atlantic Ocean spawning populations of *Alosa fallax* are now only present in the Loukos and Sebou (Sabatié, 1993) [Figure 2.6]. At the start of the 20th century the total annual catch of shad from Moroccan waters (including the Oued Moulouya) was in the region of 1000 t (Watier, 1918). However, the construction of barrages and degradation of the habitat has resulted in a number of

populations becoming extinct. A spawning population of the anadromous form of *Alosa alosa* existed in the Sebou but became extinct following the construction of a barrage at Idriss ler and from pollution derived from the processing of sugar (Figure 2.8) [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.

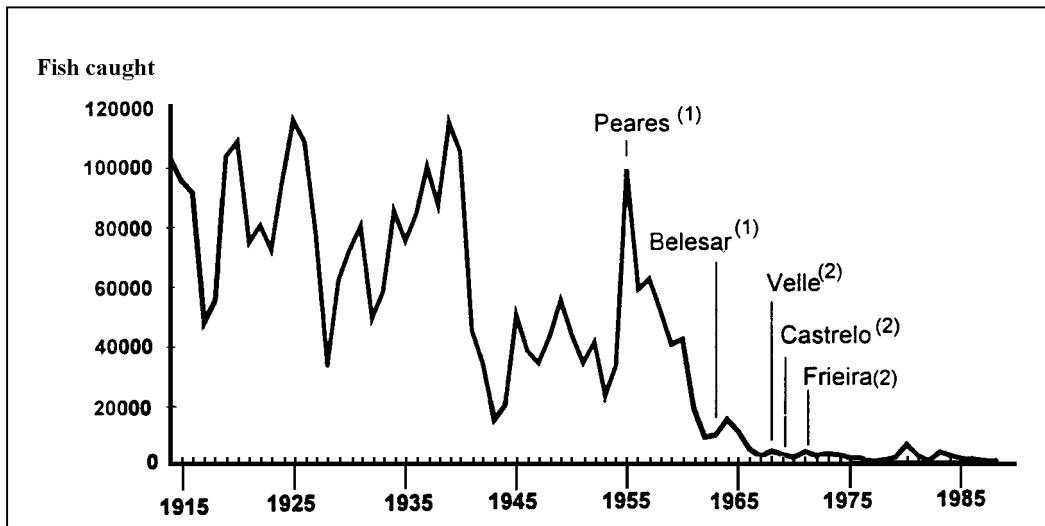


Figure 2.6: The catch of *Alosa alosa* between 1914-1988 from the River Miño, and the dates when barrages were constructed; 1 = Lugo province, 2 = Orense province (Alexandrino, 1996b).

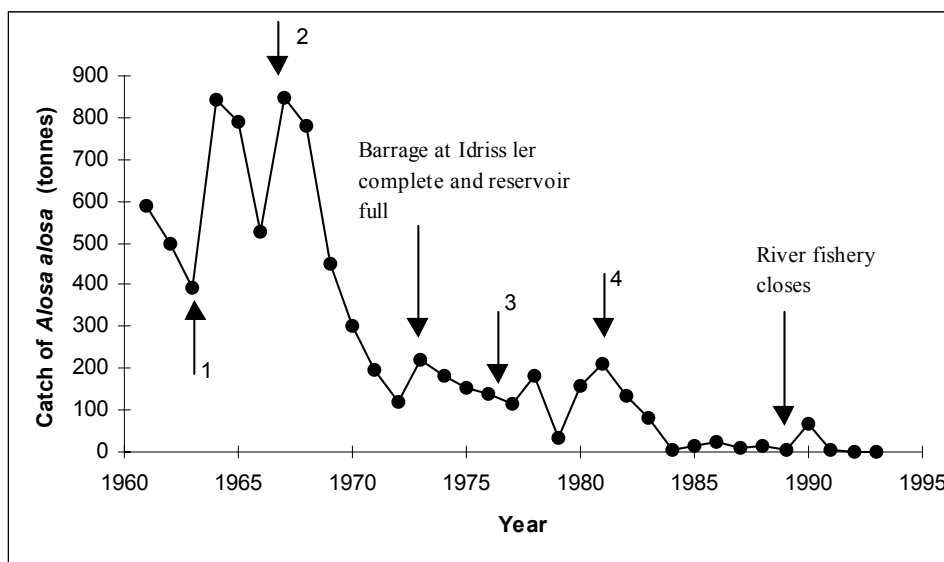


Figure 2.8: The combined marine and river catch of *Alosa alosa* from the Oued Sebou (Morocco) between 1961 and 1993. Numbers refer to when different sugar refineries were constructed (Sabatié, 1993).

The construction of dams has created a number of landlocked populations. Landlocked populations of *Alosa alosa* and *Alosa fallax* have been reported from Lake El Kansera (Furnestin, 1952; Furnestin & Vincent, 1955; Lahaye, 1960a, 1966; Sabatié, 1993) probably resulting from dam completion in 1951. The landlocked population of *A. alosa* is now extinct (Sabatié, 1993). A landlocked population of *A. fallax* also exists in Lake Sidi Mohamed Ben Abdallah (Oued Bou Regreg) which was probably formed after the dam was constructed in 1970 (Sabatié, 1993) [Figure 2.6].

In the Mediterranean, Lozano Rey (1935, 1950) mentions the occurrence of *A. alosa* in the Ebro (Spain). However, the construction of the Ribarroja (1967) and Mequinenza (1964) reservoirs in the lower reaches has meant that they are now confined to the river's delta (Sostoa & Sostoa, 1979; Sostoa & Lobon-Cervia, 1989) [Figure 2.6]. 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 gillrakers suggests that they may have been hybrids (Section 1.3.1.1). The presence of *A. alosa* in the Rhône was also reported by Le Roux (1928) and Rameye *et al.* (1976), but not by Roule (1924b). 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 & Pont, 1995) [Figure 2.5].

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).

2.1.2 *Alosa fallax rhodanensis*

Alosa fallax rhodanensis is distributed along the northern coast of the western Mediterranean Sea ranging from Spain to southern Italy. In Spain it has been reported in the River Ebro (Lozano Rey 1929, 1950; Sostoa & Lobon-Cervia, 1989; Elvira, 1995a) [Figure 2.6] and in France in the rivers Aude, Hérault, Vidourle, Rhône and Argens (Gallois, 1946a, 1947a; Rameye *et al.*, 1976; Douchement, 1981; Changeux & Pont, 1995; Le Corre *et al.*, 1997) [Figure 2.5]. In the past the sub species used to persist in the rivers Gapeau and Siagne (Lebel *et al.*, 2001).

In the River Ebro *A. fallax rhodanensis* are now confined to the river's delta (Sostoa & Sostoa, 1979; Sostoa & Lobon-Cervia, 1989), similarly in the rivers Aude, Hérault, Vidourle, Argens and Tavignano, dams now confine the populations to the lower river (Lebel *et al.*, 2001). The population in the River Ebro may, however, now be extinct (B. Elvira, pers comm. cited by Bianco, 2002). Kiener (1985) reported their presence in the River Var, however, Changeux & Pont (1995) have doubts as to the validity of this report. In the Rhône the original spawning migration was over 600 km (Quignard & Douchement, 1991c) entering several tributaries including the Saône (Roule, 1933; Gallois, 1946a), the Doubs (Ogerien, 1863; Olivier, 1882; Verneaux, 1971) and Lake Bourget (Roule, 1924a; Le Roux, 1928; Leger, 1943) [Figure 2.5]. Their progress has since been restricted by the construction of hydroelectric dams (Figure 2.9).

In 1952 the construction of the Donzère Mondragon dam 150 km from the river's mouth reduced the amount of river available to the shad by 70% and in 1974, the Vallabregges dam reduced it by a further 15% (Keith & Allardi, 1996). This restricted the population to the lower 60km of the river (Rameye *et al.*, 1976; Quignard & Kartas, 1977; Larinier *et al.*, 1978; Petit, 1979; Douchement, 1981; Kiener, 1985). In recent years the construction of two fish passes (Vialle, 1987; Zylberblat *et al.*, 1991) and the use of navigation locks for fish passage has allowed the subspecies to extend its distribution up to the Donzère Mondragon dam and into the lower reaches of the Ardèche (Lebel *et al.*, 2001).

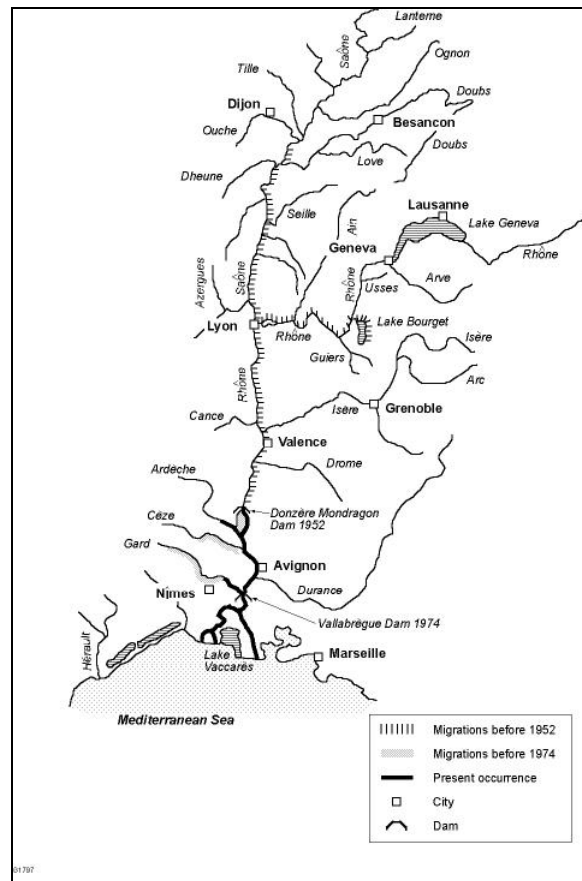


Figure 2.9: The past and present distribution of *Alosa fallax rhodanensis* in the River Rhône, modified from Pattée (1988).

In Corsica *Alosa fallax rhodanensis* has been reported from the rivers Golo and Tavignano (Casabianca *et al.*, 1972-73; Kiener, 1985; Changeux & Pont, 1995; Le Corre *et al.*, 2000), and in Sardinia from the rivers Barca, Cedrino, Coghinas, Flumendosa, Posada, Temo and Tirso (Cottiglia, 1968) [Figure 2.10].

In the past they have been reported from the Italian rivers Arno, Ombrone, Tiber, Volturno and the Sele (Barbieri, 1907a; D'Ancona, 1928a; Berg, 1933; Ferrero, 1951; Bini, 1970; Sammiceli, 1998), but there are no recent records. In the Tiber the fish could migrate to the Paglia River a distance of 210 km from the mouth (D' Ancona, 1927b), a dam near Rome presently blocks their migration.

2.1.3 *Alosa fallax nilotica*

This sub-species is distributed around the eastern Mediterranean (Economidis, 1974) with its range extending southward down to the River Nile (Boulenger, 1907; Ladiges & Vogt, 1965). In Italy they persist in the River Po, (Florin, 1949; Ferrero, 1951; Gandolfi & Le Moli 1977; Vitali & Braghieri, 1981; Vitali *et al.*, 1983; Chiaudani & Marchetti, 1984; Serventi *et al.*, 1990) and in the River Brenta (Rizzotti & Gioppato, 1997) [Figure 2.9]. *Alosa fallax nilotica* have also been reported from the rivers Adige and Veneto (NE Italy) [Gridelli, 1935; Pomini, 1937].



Figure 2.10: Distribution of *Alosa* in Southeast Europe.

1 = Orta, 2 = Maggiori, 3 = Lugano, 4 = Como, 5 = Iseo, 6 = Garda, 7 = Bolsena, 8 = Vico, 9 = Bracciano, 10 = Omodeo, 11 = Flumendosa, 12 = Bacin, 13 = Ichkeul

Alosa fallax nilotica are often found in the Adriatic Sea (Soljan, 1963; Vukovic, 1961a; Nikolaeva, 1966; Bini, 1970; Tortonese 1970) and entering the Croatian rivers Neretva, Drin and Bojona to spawn (Vukovic, 1961a; Vukovic & Ivanovic, 1971; **Kosoric *et al.*, 1989a&b**) [Figures 2.10 & 2.11]. Landlocked populations have also been reported from lakes Skadar (Scutari / Shkodra), Bačin and Sasko in Montenegro and from Lake Ohrid on the border between Croatia and Albania (Tocko & Jovanovic, 1959; Vukovic, 1961a; Vukovic & Ivanovic, 1971; Knezevic *et al.*, 1977, 1986; Pavlović & Pantić, 1975) [Figures 2.10 & 2.11]. In Lake Skadar both the anadromous *Alosa fallax nilotica* and

the non-migratory *Alosa fallax nilotica* exist in sympatry (Rakaj & Crivelli, 2001). The population of the migratory *A. fallax nilotica* in Lake Skadar has declined since the construction of a dam in 1960 on the River Bojana (Figure 2.12), though access to the lake is maintained via a canal (Bianco, pers. comm.).



Figure 2.11: Distribution of *Alosa* in Greece and Southeast Europe.
1 = Scutari, 2 = Ohrid, 3 = Sasko, 4 = Vistonis

In Greece, *A. fallax nilotica* is present in the rivers Evros, Strymon, Pinos, Acheloos and Thyamis and there exists strong evidence that they exist in Loudias, Louros and Arachthos (Economidis, 1974; Bobori *et al.*, 2001) [Figure 2.11]. A population used to exist in the River Nestos however, the construction of a dam near the Bulgarian border and associated change in flow regime has meant that *A. fallax nilotica* no longer migrates into the Nestos (Bobori *et al.*, 2001). The sub species is also caught by trawlers in the Thermaikos Gulf and populations may therefore exist in the rivers Aliakmon, Loudias and Axios (Bobori *et al.*, 2001). Bobori *et al.* (2001) also reported their presence in Lake Vistonis.

Kuru (1980) and Balik (1995) reported this sub-species all along the coasts of Turkey, and Bacescu (1982) [cited by Quignard & Douchement, 1991d] reported them as abundant in the Bosphorus. A spawning population exists in the Yeşilirmak which drains into the Black Sea and have been reported from the Sakarya (Black Sea), Menderes (Aegean Sea) and in the Seyhan and Ceyhan rivers (E. Mediterranean) [Turan & Basusta, 2001; Turan, pers.comm.].

There are no reports of *Alosa fallax nilotica* from the Eastern Mediterranean countries of Syria and Lebanon and they have been only rarely reported from Israel (Golani, pers. comm.). The most southerly population has been reported from the River Nile (Egypt) by Boulenger (1907), though this population may now be extinct as a result of dam construction (Bishai & Khalil, 1997).

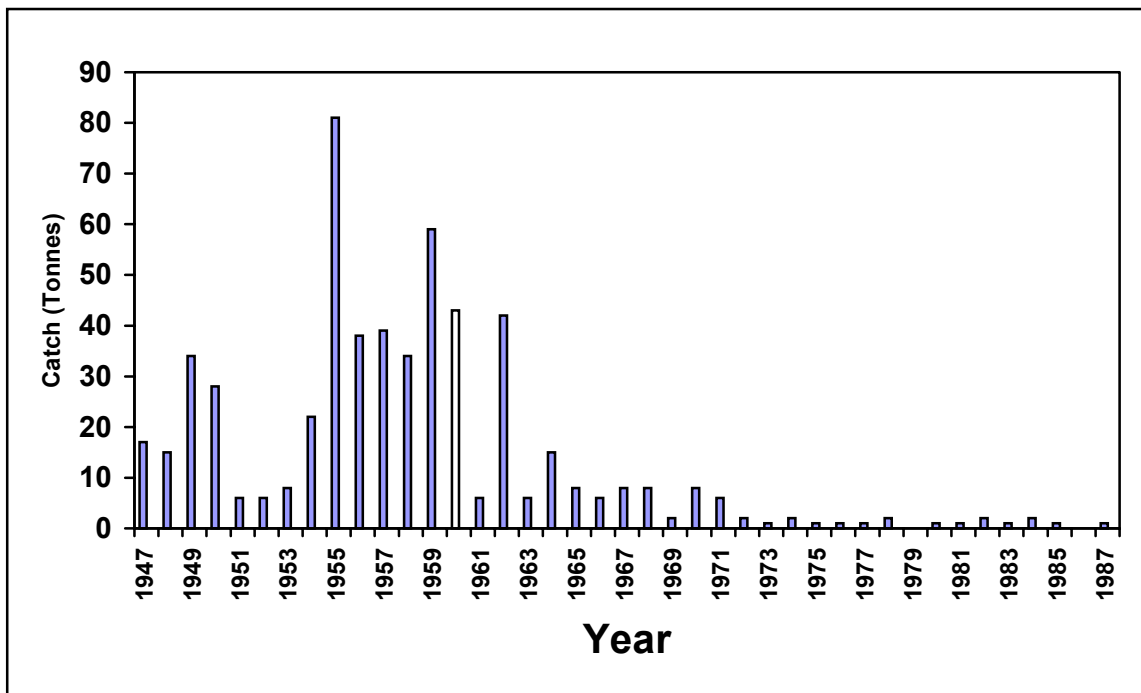


Figure 2.12: Catch of *Alosa fallax nilotica* from Lake Skadar (Montenegro), between 1947 and 1987 (Stein *et al.*, 1981; Maric, 1990), the dam on the River Bojana was constructed in 1960, from Bianco (2002).

2.1.4 *Alosa fallax algeriensis*

Alosa fallax algeriensis is found along the North African coast from the Rif Peninsula (Lozano Rey, 1929) to Tunisia. In Tunisia they have been reported in oueds Miliane and Medjerdah (Quignard & Kartas, 1977; Kartas, 1981) [Figure 2.10] A landlocked population exists in Lake Ichkeul (Kartas, 1981). In Algeria spawning populations exist in the oueds Chelif, Mazafran, Seybouse and Oubeira and in associated lakes (Bounhiol, 1917; Dieuzeide *et al.*, 1959; Quignard & Kartas, 1977) [Figure 2.6].

In Morocco a spawning population of *Alosa fallax* (possibly *Alosa fallax algeriensis*) used to exist in the Oued Moulouya but became extinct in 1953 following the construction of the Mechra-Hommadi dam (Sabatié, 1993) [Figure 2.6].

2.1.5 *Alosa fallax lacustris*

Alosa fallax lacustris is the name given to the subspecies of *Alosa fallax* found in landlocked Italian lakes and which Cottiglia (1963b) gave to those found in Sardinia. They are present in lakes Maggiore, Orta, Lugano, Como, Mergozzo, Iseo and Garda (Vogel, 1903; Barbieri, 1907a; Fatio, 1890; Ferrero, 1951; Berg, 1966a; Giussani & Grimaldi, 1975; Müller, 1990; Müller & Meng, 1992; Luzzana *et al.*, 1996; Bianco, 2002) [Figure 2.10].

In 1921 Pirola (1930) introduced the landlocked form of *A. fallax* from the northern lakes of Como and Garda into the lakes of middle Italy; lakes Bolsena, Vico and Bracciano (Chiappi, 1933a; Gallois, 1946b; Ferrero, 1951; Tortonese, 1970). *Alosa fallax lacustris* are still present in Lake Bracciano (Bianco, 2002) but have disappeared from lakes Bolsena (Taddei *et al.*, 1999) and Vico (P. G. Bianco pers. obs., cited by Bianco, 2002).

In Sardinia, landlocked populations developed in several artificial lakes (Cottiglia, 1963b, 1968; Quignard & Douchement, 1991f) [Figure 2.10]. In the River Tirso landlocked populations developed in lakes Omodeo, Castel Doria, Del Posada and Villanovatulo following completion of a dam in 1922. Similarly following the closure of a dam in 1957 on the River Flumendosa a population subsequently developed in Lake Flumendosa.

2.1.6 *Alosa fallax killarnensis*

In Southwest Ireland, a landlocked population of *A. fallax*, (*A. fallax killarnensis*) exists in Lough Leane (Regan, 1911; Trewavas, 1938; Went, 1946; Gibson, 1956; O'Maoileidigh *et al.*, 1988) [Figure 2.4]. The isolation of this population was possibly due to local tectonic changes (Wheeler, 1977).

2.2 Determination of Distribution Changes

Changes in distribution have arisen mainly as a result of the construction of barriers, pollution, over-fishing and their translocation to new sites, see section 2.1 and Taverny *et al.* (2000a).

2.3 Hybridization

Based on the number of gill rakers, hybrids of *A. alosa* x *A. fallax fallax* have been reported from the Rhine, Germany (Hoek, 1899), the French rivers Loire (Douchement, 1981; Boisneau *et al.*, 1992) and Aude (Douchement, 1981), from the Lima, Portugal (Alexandrino *et al.*, 1996) and from the Sebou, Morocco (Sabatié, 1993). Hybrids of *A. alosa* x *A. fallax rhodanensis* have been observed from the Rhône, France (Douchement, 1981).

These hybrids have been confirmed genetically with morphometric and meristic characteristics intermediate between the two species and appear fertile (Alexandrino & Biosneau, 2000). The prevalence of hybridization appears related to the presence of obstructions to the free passage of migrants upstream resulting in the use of communal areas for spawning (Biosneau *et al.*, 1992).

3. BIONOMIC AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality, sexual differentiation/dimorphism

Alosa alosa and *Alosa fallax* spp. are heterosexual. The inter-sexual differences in morphology have not been well studied. Visually there is little external difference between the sexes except that, once mature, females are on the whole larger than males (see Section 3.4.3) and have an enlarged cloaca.

Alosa alosa

Female *A. alosa* have a higher mean number of scales along the mid-line in the River Loire (Boisneau, 1990), a smaller head length in relation to total length in the Loire and Sebou (Boisneau, 1990; Sabatié, 1993) and a lower mean number of pre-pelvic scutes in the River Sebou (Sabatié, 1993), when compared with males.

Alosa fallax fallax

In the River Loire no significant difference in morphology or meristic characteristics has been found between the sexes (Boisneau, 1990). In the River Sebou female *A. fallax* had a higher number of dorsal and anal fin rays and a greater pre-anal distance in relation to total length than males (Sabatié, 1993).

3.1.2 Maturity

Alosa alosa

The majority of studies have estimated the age at first spawning from catch data that consisted of a number of different cohorts with no correction applied for gear selectivity. The exception is the study of Lambert *et al.* (2001) who estimated the age at maturity for three year-classes of *Alosa alosa* from Gironde-Garonne-Dordogne (France). Anadromous populations of *Alosa alosa* mature at between 3 and 8 years (Table 3.1), with the majority of females maturing at ages 5 and 6 years and males at 4 and 5 years.

On the River Loire (France), Mennesson-Boisneau & Boisneau (1990) reported that female *A. alosa* mature at between 4 and 7 years old and the males a year earlier at 3 to 6 years old. The mean (standard deviation) age at which fish spawn for the first time was 4.9 (\pm 0.6) and 4.3 (\pm 0.7) years for females and males respectively. On the Gironde-Garonne-Dordogne (France) the age at which 50% of the individuals have matured (95% CI) was 4.864 (4.858 - 4.865) years for females and 4.831 (4.819 - 4.831) years for males (Martin-Vandembulcke, 1999).

Landlocked populations of both sexes of *Alosa alosa* in the Castelo do Bode reservoir (River Tejo, Portugal) and in the Agueira reservoir (River Mondego, Portugal) mature at the age of 3 years (Eiras, 1983; Collares-Pereira *et al.*, 1999).

Table 3.1: The percentage of *Alosa alosa* maturing at different ages in different river systems.

| River | Sex | Age (year) | | | | | | No. | Reference |
|--|-----|------------|------|------|------|------|-----|------|---------------------------------|
| | | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Loire (France) | F | | | 63.4 | 33.3 | 3.3 | | 31 | Douchement (1981) |
| | M | | 11.8 | 75.0 | 13.2 | | | 68 | |
| Charente (France) | F | 2.5 | 12.5 | 52.5 | 22.5 | 10.0 | | 40 | Véron <i>et al.</i> (2001) |
| | M | 11.7 | 17.6 | 47.1 | 17.6 | 6.0 | | 17 | |
| Gironde- Garonne- Dordogne (France) | F | 3.5 | 11.5 | 53.1 | 29.5 | 2.4 | | 373 | Taverny (1991a) |
| | M | 3.1 | 13.1 | 74.3 | 9.5 | | | 390 | |
| | F | | | 39.1 | 60.9 | | | 46 | Douchement (1981) |
| | M | | 25.7 | 48.6 | 25.7 | | | 36 | |
| | F | 1.1 | 10.7 | 62.4 | 24.7 | 1.1 | | 956 | Lambert <i>et al.</i> (2001) |
| | M | 1.0 | 19.7 | 67.1 | 11.3 | 1.0 | | 1191 | |
| Adour (France) | F | | 35.3 | 52.9 | | | | 17 | Douchement (1981) |
| | M | 1.4 | 66.7 | 30.5 | 1.4 | | | 72 | |
| Sebou (Morocco) | F | | 2.9 | 25.8 | 52.1 | 17.5 | 1.7 | 240 | Sabatié (1993) |
| | M | 1.1 | 23.9 | 49.3 | 24.6 | 1.1 | | 280 | |

Alosa fallax fallax

Anadromous populations of *Alosa fallax* mature from 2 to 9 years old (Table 3.2) with the majority of females maturing at age 4 and 5 years and the males at 3 and 4 years. Mennesson-Boisneau & Boisneau (1990) reported that female *A. fallax* on the River Loire (France) mature at between 2 and 5 years old and the males at 2 to 4 years old. The mean (standard deviation) at which fish spawn for the first time was 3.55 (± 0.6) and 2.96 (± 0.5) years for females and males respectively. There was no evidence of any latitudinal cline in the mean age at maturity

Alosa fallax rhodanensis

On the Rhône (France) *Alosa fallax rhodanensis* mature at between 2 and 6 years old with the majority of females maturing at age 4 and 5 and the males at ages 3 and 4 (Table 3.3). A similar maturation schedule has been reported from the Aude, Hérault and the Tavignano (Douchement, 1981; Le Corre *et al.*, 2000).

In the rivers Rhône, Aude, Hérault and Tavignano, the mean age at maturation for males was 3.34, 3.60, 3.57 and 3.40 years, respectively, while for females in the Rhône, Aude and Tavignano the mean age was 4.03, 4.80 and 4.28 years, respectively (Le Corre *et al.*, 2000). The data for the rivers Hérault and Tavignano must be interpreted with caution as the sample size was small (≤ 12 individuals).

Table 3.2: Percentage of *Alosa fallax fallax* maturing at different ages from different river systems.

| River | Sex | Age (year) | | | | | | | | Mean ($\pm 95\text{CI}$) | No. | Reference |
|--|----------------|------------|--------------|--------------|-------------|------|-----|-----|-----|----------------------------|----------|--------------------------------|
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | | |
| Wye (Wales) | Female | | | 46.6 | 51.4 | 2.0 | | | | 4.55 (0.09) | 148 | Aprahamian (1982 & unpubl.) |
| | Male | | 17.8 | 79.5 | 2.7 | | | | | 3.85 (0.10) | 73 | |
| Tywi (Wales) | Female | | 3.2 | 61.3 | 32.3 | 3.2 | | | | 4.36 (0.23) | 31 | Aprahamian (unpubl.) |
| | Male | | 10.0 | 40.0 | 50.0 | | | | | 4.50 (0.38) | 10 | |
| Severn (England) | Female | | 2.2 | 33.2 | 48.8 | 14.5 | 1.3 | 0.1 | | 4.80 (0.02) | 5090 | Aprahamian (1982 & unpubl.) |
| | Male | 0.7 | 30.8 | 50.9 | 16.6 | 0.8 | 0.1 | | 0.1 | 3.87 (0.04) | 1527 | |
| Barrow (Ireland) | Female | | 4.7 | 57.2 | 33.3 | 4.8 | | | | 4.38 (0.31) | 21 | O'Maoileidigh (1990) |
| | Male | | 36.8 | 39.5 | 21.1 | 2.6 | | | | 3.90 (0.27) | 38 | |
| (Holland) | Female | | 19.5 | 67.5 | 13.0 | | | | | 3.94 (0.13) | 77 | Aprahamian (1982) |
| | Male | 1.4 | 71.5 | 25.7 | 1.4 | | | | | 3.27 (0.12) | 74 | |
| Loire (France) | Female | | 8.3 | 65.0 | 18.4 | 8.3 | | | | 4.27 (0.20) | 56 | Douchement (1981) |
| | Male | 2.6 | 84.2 | 10.6 | 2.6 | | | | | 3.13 (0.16) | 38 | |
| | Female Male | | | | | | | | | 3.55 (0.20) 2.96 (0.20) | 34 26 | |
| Charente France | Female | | 17.9 | 71.4 | 10.7 | | | | | 3.93 (0.21) | 28 | Véron (unpubl.) |
| | Male | | | 80.0 | 20.0 | | | | | 4.20 (0.56) | 5 | |
| Gironde- Garonne- Dordogne (France) | Female | | 11.1 | 51.1 | 37.8 | | | | | 4.27 (0.20) | 45 | Douchement (1981) |
| | Male | | 75.7 | 18.9 | 5.4 | | | | | 3.30 (0.19) | 37 | |
| | Female Male | | 37.1 45.5 | 51.7 43.2 | 11.2 4.5 | 6.8 | | | | 3.74 (0.14) 3.73 (0.26) | 89 44 | |
| Adour (France) | Female | | | 65.2 | | | | | | 4.35 (0.21) | 23 | Douchement (1981) |
| | Male | | 50.0 | 50.0 | 34.8 | | | | | 3.50 (0.92) | 4 | |
| Sebou (Morocco) | Female | | 5.3 | 40.5 | 35.7 | 18.5 | | | | 4.67 (0.13) | 152 | Sabatié (1993) |
| | Male | 0.6 | 27.3 | 57.5 | 14.6 | | | | | 3.86 (0.09) | 205 | |

Table 3.3: Percentage of *Alosa fallax rhodanensis* maturing at different ages.

| River | Sex | Age (year) | | | | | No. | Reference |
|-------------------|-----|------------|------|------|------|------|------|----------------------------------|
| | | 2 | 3 | 4 | 5 | 6 | | |
| Rhône (France) | F | | 1.6 | 38.7 | 50.0 | 9.7 | 64 | Douchement (1981) |
| | M | | 21.6 | 63.1 | 15.3 | | 109 | |
| | F | 0.2 | 12.6 | 53.0 | 31.3 | 2.9 | 1065 | Le Corre <i>et al.</i> (2000) |
| | M | 3.2 | 43.4 | 45.9 | 7.3 | 0.2 | 705 | |
| Aude (France) | F | | | 20.0 | 45.0 | 35.0 | 38 | Douchement (1981) |
| | M | | 28.0 | 41.3 | 30.7 | | 74 | |
| | F | | | 36.0 | 43.0 | 21.0 | 14 | Le Corre <i>et al.</i> (2000) |
| | M | | 39.0 | 61.0 | | | 25 | |

Alosa alosa x Alosa fallax hybrids

Female and male hybrid *Alosa alosa x Alosa fallax* from the River Loire (France), have both been found to mature at between 3 and 5 years old (Mennesson-Boisneau & Boisneau, 1990). The mean (standard deviation) age at which fish spawn for the first time was 3.89 (± 0.4) and 3.54 (± 0.6) years for females and males respectively. Sabatié (1993) found on the River Sebou (Morocco) that the mean (range) age at which female *A. alosa x A. fallax* hybrids spawn for the first time was at 5 (4 to 6) years old and males at age 4 (4 to 6) years.

Alosa fallax nilotica

Vukovic (1961a) reported that the populations in lakes Skadar (Albania) and Bačina (Croatia) become sexually mature in their second year of life while those from the lower Neretva river (Montenegro) mature from age 2 onwards. The anadromous population of *A. fallax nilotica* in Lake Skadar mature between 3 and 8 years old while the landlocked population in the lake mature between 2 and 5 years old (Rakaj & Crivelli, 2001).

Alosa fallax algeriensis

Kartas (1991) reported that male *Alosa fallax algeriensis* mature at three to four years old and females at age four to five years.

Alosa fallax lacustris

Berg & Grimaldi (1966a) reported that *Alosa fallax lacustris* in Lake Maggiore (Italy), normally reaches maturity at two years of age, at a minimum length (total) of 180 to 190 mm.

Alosa fallax killarnensis

In Lough Leane (Ireland), O'Maoileidigh (1990) reported that *Alosa fallax killarnensis* mature at age 3 and 4 years (Table 3.4).

Table 3.4: Percentage of *Alosa fallax killarnensis* maturing at different ages (O'Maoileidigh, 1990).

| Lake | Sex | Age (year) | | | No. |
|-----------------------|--------|------------|-------|---|-----|
| | | 3 | 4 | 5 | |
| L. Leane (Ireland) | Female | 50.0% | 50.0% | | 18 |
| | Male | 60.0% | 40.0% | | 35 |

3.1.2.1 Variation in age at maturity

The age at first spawning of *Alosa fallax fallax* for a particular year-class has been found to vary (Aprahamian & Lester, 2001). Figure 3.1 shows that the mean age at first spawning for female *A. fallax* ranged from 4.41 to 5.40 years over the 20-year period studied. This was found to be significantly ($P < 0.05$) related to the combined biomass of the 0 to 2 ($r^2 = 0.41$) and 0 to 3 age groups ($r^2 = 0.32$) [Figure 3.2]. The relationship indicates that at low population levels the fish mature early, maturing later with increasing size of the stock up to an asymptote of *c.* 5 years.

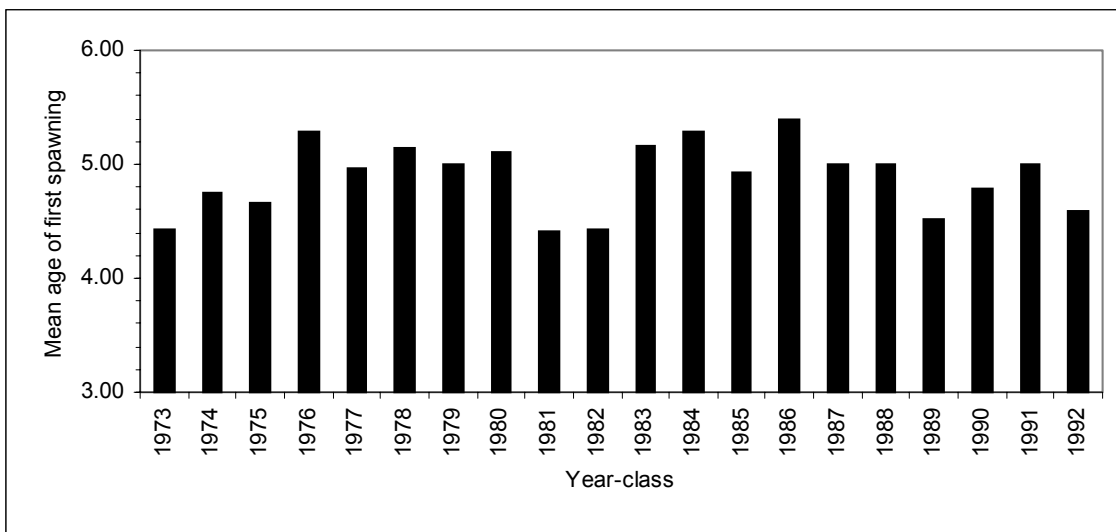


Figure 3.1: The mean age at first spawning for female *Alosa fallax fallax* from the River Severn for the 1973 to 1992 year-classes (Aprahamian & Lester, 2001).

The relationship suggests that the onset of maturity is related to density dependent processes, such as the effect of intra specific competition for food on growth.

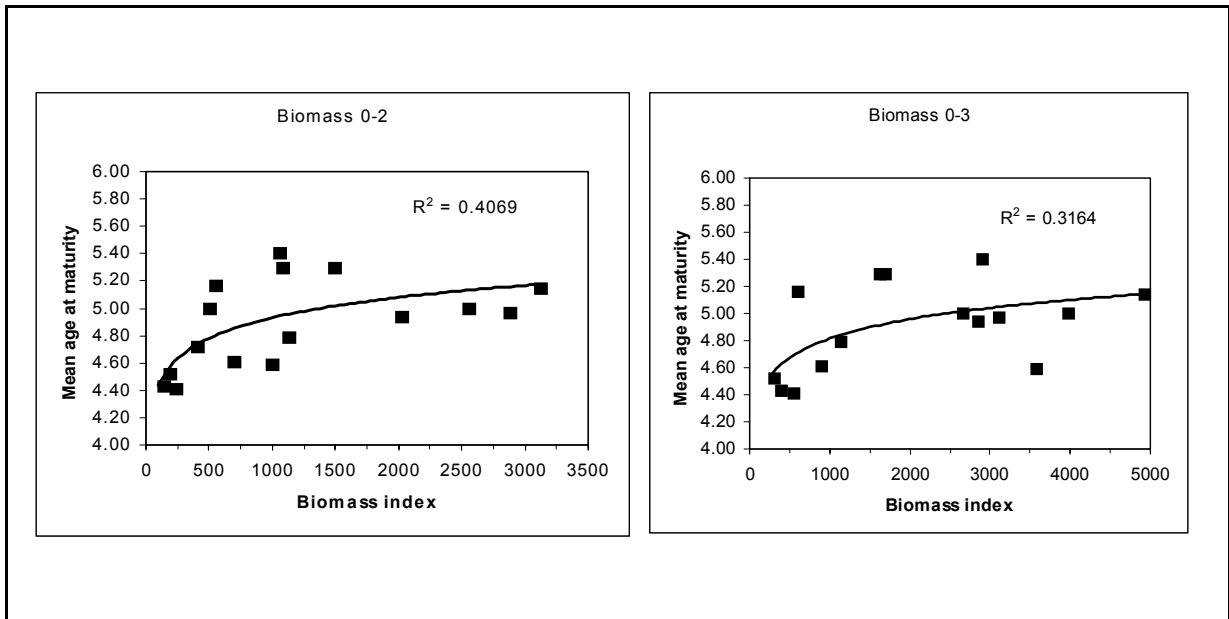


Figure 3.2:The relationship between age at maturity for female *Alosa fallax fallax* and an index of biomass for age groups 0-2 and 0-3 inclusive, only those year-classes where more than 10 fish were sampled have been included (Arahamian & Lester, 2001).

Arahamian (1982) suggested that female *A. fallax* from the River Severn (England) must reach a critical size of approximately 330 mm (L_f), before they enter the adult population. Arahamian & Lester (2001) analysed the growth rates of female *A. fallax* from four cohorts and found that the faster growing fish of a particular cohort matured first (Table 3.5).

Table 3.5. Mean fork length \forall 95%CI (mm) at age of four year-classes of female *Alosa fallax fallax* prior to maturation (Arahamian & Lester, 2001).

| Age at Maturity | Year Class | Age (year) | | | | | | Sample size |
|-----------------|------------|------------------------------|----------------|----------------|----------------|----------------|----------------|-------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | |
| 3 | 1989 | 120 \pm 9.8 | 235 \pm 10 | 314 \pm 9.0 | | | | 11 |
| 4 | 1982 | 76\pm5.0 | 193 \pm 5.9 | 271 \pm 5.5 | 330 \pm 4.5 | | | 30 |
| | 1983 | 92 \pm 4.4 | 188 \pm 5.4 | 267 \pm 6.6 | 321 \pm 6.3 | | | 29 |
| | 1989 | 80 \pm 6.7 | 194 \pm 10.3 | 272 \pm 11.0 | 327 \pm 10.8 | | | 30 |
| 5 | 1982 | 66 \pm 4.2 | 172 \pm 6.1 | 244 \pm 5.6 | 304 \pm 5.6 | 341 \pm 5.5 | | 28 |
| | 1983 | 75 \pm 3.7 | 161 \pm 7.2 | 233 \pm 8.1 | 290 \pm 6.8 | 334 \pm 6.0 | | 30 |
| | 1984 | 77 \pm 4.0 | 149 \pm 8.3 | 224 \pm 8.3 | 285 \pm 7.4 | 332 \pm 5.1 | | 27 |
| | 1989 | 69 \pm 3.9 | 158 \pm 8.4 | 234 \pm 7.4 | 298 \pm 5.1 | 347 \pm 4.6 | | 30 |
| 6 | 1982 | 66 \pm 6.7 | 156 \pm 7.5 | 227 \pm 6.6 | 284 \pm 8.2 | 320 \pm 11.4 | 348 \pm 14.5 | 6 |
| | 1983 | 72 \pm 4.1 | 150 \pm 7.3 | 221 \pm 8.7 | 278 \pm 8.1 | 325 \pm 7.8 | 355 \pm 5.9 | 28 |
| | 1984 | 72 \pm 3.4 | 138 \pm 6.8 | 205 \pm 6.6 | 266 \pm 6.1 | 315 \pm 5.9 | 354 \pm 5.5 | 29 |
| | 1989 | 61 \pm 3.8 | 134 \pm 10.2 | 205 \pm 10.6 | 268 \pm 9.7 | 317 \pm 10.2 | 348 \pm 8.8 | 20 |

This difference in growth rate was evident at an early age with fish of 120 mm at age 1 maturing at age 3; between 76 and 92 mm maturing at age 4; between 66 and 77 mm at age 5 and between 61 and 72 mm at age 6. For fish maturing at ages 5 and 6 years old there was some overlap in the length at age between the two groups until the age of 4 with those maturing at age 5 being on average \exists 285 mm (L_f) compared with those maturing at age 6 years which were $<$ 285 mm.

3.1.3 Number of spawnings

The spawning history of alosoids can be determined from their scales (Section 1.3.1.2) and in theory can be used to characterise populations, for example variation in the proportion of repeat spawners. For such a purpose it is important that sampling is carried out over the same time period in order to take account of variation in year-class strength, and that for each population sampled the gear is equally selective. The selectivity of the gear may mean that the younger fish are under represented in the population and thus the sample may not represent the true spawning structure of the population. For example, $<$ 30% of the *Alosa fallax fallax* sample taken from the River Severn (England) were spawning for the first time (Table 3.6). These data do, however, give an estimate of the number of spawnings a fish may make.

Alosa alosa

Douchement (1981) found no evidence of fish making more than one spawning migration for three French anadromous populations of *Alosa alosa* in the rivers Loire, Garonne and Adour. Similar findings were reported for *A. alosa* by Véron *et al.* (2001) from the Charente (France) and by Sabatié (1993) from the Sebou (Morocco) where the populations have a semelparous life history.

In contrast to the findings of Douchment (1981), Taverny (1991a) reported a higher level of repeat spawning 17.9% and 9.1% for females and males respectively (Table 3.7), while on the Loire 0.8% of males and 1.8% of females have been found to spawn more than once (Mennesson-Boisneau & Boisneau, 1990). A small proportion (20%) of female repeat spawners was also reported in the River Aude (France), though the sample size on which it is based was small, comprising only five fish (Douchement, 1981).

Table 3.7: Percentage of *Alosa alosa* from the Gironde-Garonne-Dordogne (France) spawning one or more times

| Location | Sex | Spawning number | | | No. | Reference |
|-----------------------------------|-----|-----------------|-----------------|-----------------|-----|-----------------|
| | | 1 st | 2 nd | 3 rd | | |
| Gironde-Garonne-Dordogne (France) | F | 82.1 | 17.1 | 0.8 | 480 | Taverny (1991a) |
| | M | 90.9 | 8.9 | 0.2 | 481 | |

The landlocked population of *Alosa alosa* in the Castelo de Bode reservoir (Portugal) has a similar semelparous life history with the fish failing to survive spawning (Eiras, 1983). In contrast Collares-Pereira *et al.* (1999) reported that *A. alosa* from the Aguieira reservoir (River Mondego, Portugal) has an iteroparous life history, with a high

proportion of the fish spawning more than once. The maximum number of spawnings recorded was three.

Alosa fallax fallax

Nearly all anadromous populations have an iteroparous life history with the populations having a high proportion of repeat spawners (Table 3.6), the exception being the Moroccan populations in the Sebou and Loukos which are semelparous (Sabatié, 1993). The maximum number of spawnings recorded has been seven and most have a high proportion of fish spawning two or three times. There is some indication that the number of spawnings, and as such the proportion of repeat spawners increases, with latitude (Mennesson-Boisneau *et al.*, 2000a).

Alosa fallax rhodanensis

On the River Rhône (France) studies on spawning frequency have been carried out by Baglinière *et al.* (1996), Douchement (1981) and by Le Corre *et al.* (1997a), the latter study incorporated the findings of Baglinière *et al.* (1996a). On the Rhône, specimens of *Alosa fallax rhodanensis* have been recorded as having spawned up to five times (Table 3.8). The proportion of repeat spawners in the Rhône population has varied from 13.7% to 62.0% for females and from 11.6% to 40.0% for males (Lebel *et al.* 2000).

Table 3.8: Percentage of *Alosa fallax rhodanensis* from the Rhône (France) spawning one or more times.

| Location | Sex | Spawning number | | | | | | No. | Reference |
|-------------------|-----|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----|----------------------------------|
| | | 1 st | 2 nd | 3 rd | 4 th | 5 th | 6 th | | |
| Aude (France) | F | 62.7 | 30.5 | 1.7 | 1.7 | 3.4 | | 59 | Douchement (1981) |
| | M | 87.9 | 8.8 | 3.3 | | | | 91 | |
| Rhône (France) | F | 42.7 | 29.7 | 19.0 | 7.5 | 0.9 | 0.2 | 436 | LeCorre <i>et al.</i> (1997a) |
| | M | 64.1 | 20.1 | 13.9 | 1.6 | 0.3 | 0.0 | 302 | |
| | F | 74.7 | 14.5 | 9.6 | 1.2 | | | 152 | Douchement |
| | M | 76.8 | 21.1 | 0.7 | 0.7 | 0.7 | | 83 | (1981) |

Alosa fallax nilotica

Vukovic (1961a) reported that *Alosa fallax nilotica* can spawn up to eight times. The spawning history of three populations, were the fish have spawned more than once, is shown in Table 3.9.

Table 3.9: Percentage of fish with more than one spawning mark on their scales, for three populations of *Alosa fallax nilotica* (Vukovic, 1961a).

| Location | Sex | Spawning number | | | | | | |
|---------------|-------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | | 2 nd | 3 rd | 4 th | 5 th | 6 th | 7 th | 8 th |
| Lake Scutari | F & M | 20.19 | 50.98 | 19.60 | 8.04 | 0.39 | 0.58 | 0.19 |
| River Neretva | F & M | 20.65 | 48.41 | 18.25 | 7.14 | 5.55 | | |
| Lake Bačina | F & M | 35.53 | 40.00 | 22.25 | 2.22 | | | |

Table 3.6: Percentage of *Alosa fallax fallax* from a number of populations spawning one or more times

| Location | Sex | Spawning number | | | | | | | | No. | Reference |
|--|--------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------|--|
| | | 1 st | 2 nd | 3 rd | 4 th | 5 th | 6 th | 7 th | 8 th | | |
| River Severn (England) | Female | 29.9 | 27.1 | 22.6 | 13.4 | 5.1 | 1.6 | 0.2 | <0.1 | 4868 | Aprahamian (1982 & unpubl.) |
| | Male | 23.8 | 21.0 | 23.0 | 17.6 | 10.8 | 3.2 | 0.6 | | 1613 | |
| River Wye (Wales) | Female | 56.8 | 34.6 | 3.3 | 2.6 | 2.0 | 0.7 | | | 153 | Aprahamian (1982) |
| | Male | 53.8 | 25.6 | 16.7 | 2.6 | 1.3 | | | | 78 | |
| River Tywi (Wales) | Female | 3.2 | 19.4 | 16.1 | 51.6 | 9.7 | | | | 31 | Aprahamian (unpubl.) |
| | Male | | | 30.0 | 40.0 | 30.0 | | | | 10 | |
| River Barrow (Ireland) | Female | 42.9 | 47.6 | 9.5 | | | | | | 21 | O'Maoileidigh (1990) |
| | Male | 21.1 | 44.7 | 31.6 | | 2.6 | | | | 38 | |
| Loire (France) | Female | 47.4 | 37.5 | 12.3 | 1.4 | 1.4 | | | | 73 | Douchement (1981) |
| | Male | 75.9 | 22.4 | 1.7 | | | | | | 58 | |
| | Female | 70.0 | 21.0 | 9.0 | | | | | | 34 | Menesson-Boisneau & Boisneau (1990) |
| | Male | 54.0 | 38.0 | 8.0 | | | | | | 26 | |
| Charente (France) | Female | 53.5 | 42.9 | 3.6 | | | | | | 28 | Véron <i>et al.</i> (2001) |
| | Male | 60.0 | 40.0 | | | | | | | 5 | |
| Gironde- Garonne- Dordogne (France) | Female | 20.7 | 67.3 | 9.8 | 2.2 | | | | | 92 | Taverny (1991a) |
| | Male | 16.3 | 65.3 | 18.4 | | | | | | 49 | |
| | Female | 36.0 | 44.6 | 15.1 | 3.6 | 0.7 | | | | 139 | Douchement (1981) |
| | Male | 58.2 | 29.1 | 10.9 | 1.8 | | | | | 55 | |
| Adour (France) | Female | | 52.2 | 30.4 | 13.0 | 4.4 | | | | 23 | Douchement (1981) |
| | Male | | 50.0 | 25.0 | 25.0 | | | | | 4 | |
| Loukos (Morocco) | Female | 100 | | | | | | | | 26 | Sabatié (1993) |
| | Male | 100 | | | | | | | | 30 | |
| Sebou (Morocco) | Female | 100 | | | | | | | | 152 | Sabatié (1993) |
| | Male | 100 | | | | | | | | 205 | |

Alosa fallax lacustris

Berg (1966a) observed the development of spawning marks on the scales of *A. fallax lacustris* from Lake Maggiore (Italy). For males maturing at age 2, between 75 and 89% formed a spawning mark following spawning. However, as no fish aged 3 were caught they appear to suffer a high post spawning mortality, and may in fact only spawn once. For females age 2, between 43% and 54% had spawning marks, which increased to 87% for those aged three, indicating that females are multiple spawners.

Alosa fallax killarnensis

O'Maoileidigh (1990), for *Alosa fallax killarnensis*, observed fish with at least two spawning marks on their scales (Table 3.10) indicating that fish can spawn up to three times. There is some indication that males may suffer higher post-spawning mortality than females.

Table 3.10: Percentage of *Alosa fallax killarnensis* from Lough Leane (Ireland) spawning one or more times (O'Maoileidigh, 1990).

| Location | Sex | Spawning number | | | No. |
|--------------------------|-----|-----------------|-----------------|-----------------|-----|
| | | 1 st | 2 nd | 3 rd | |
| Lough Leane (Ireland) | F | 5.6 | 61.1 | 33.3 | 18 |
| | M | 14.3 | 71.4 | 14.3 | 35 |

3.1.4 Mating / Spawning behaviour

Alosa alosa

The spawning activity has been described by Cassou-Leins *et al.* (2000). During the day the fish shelter in groups along the shore or on the bed of the river. At dusk the fish move on to the spawning shoals. During the night the fish come up to the surface. The males and females, half submerged and along side each other swim in a circular motion violently thrashing the surface of the water with their caudal fin, releasing sperm and eggs (Figure 3. 3 & 3.4). The spawning activity lasts between 3 and 10s (Cassou-Leins, 1995) and produces a sound of between 35 and 50 dB at 1m (Cassou-Leins *et al.* 2000). The number of separate spawning activities undertaken by a female was estimated to be between 5 and 7 by Cassou-Leins & Cassou-Leins (1981) and between 10 and 12 by Fatin & Dartiguelongue (1995).

Alosa alosa spawn at night (Couch, 1877; Wheeler, 1978b; Cassou-Leins & Cassou-Leins, 1981; Boisneau *et al.*, 1990; Mennesson-Boisneau & Boisneau, 1990; Fatin & Dartiguelongue, 1995). The time of peak spawning activity was observed by Cassou-Leins & Cassou-Leins (1981) to be between 00:00 and 02:00 (Figure 3.5) and by Boisneau *et al.* (1990) to be from 00:30 to 03:30. Similar findings were also reported by Fatin & Dartiguelongue (1995), who observed little spawning before 01:00 and after 04:00 with the peak of activity between 02:00 and 03:30. In quantitative terms, Cassou-Leins *et al.* (1990) reported that $62.18 \pm 3.20\%$ of the spawning activity took place between 0200h and 0400h.



Figure 3.3: *Alosa alosa* congregating for spawning (from Baglinière & Elie, 2000).



Figure 3.4: The spawning activity (from Baglinière & Elie, 2000).

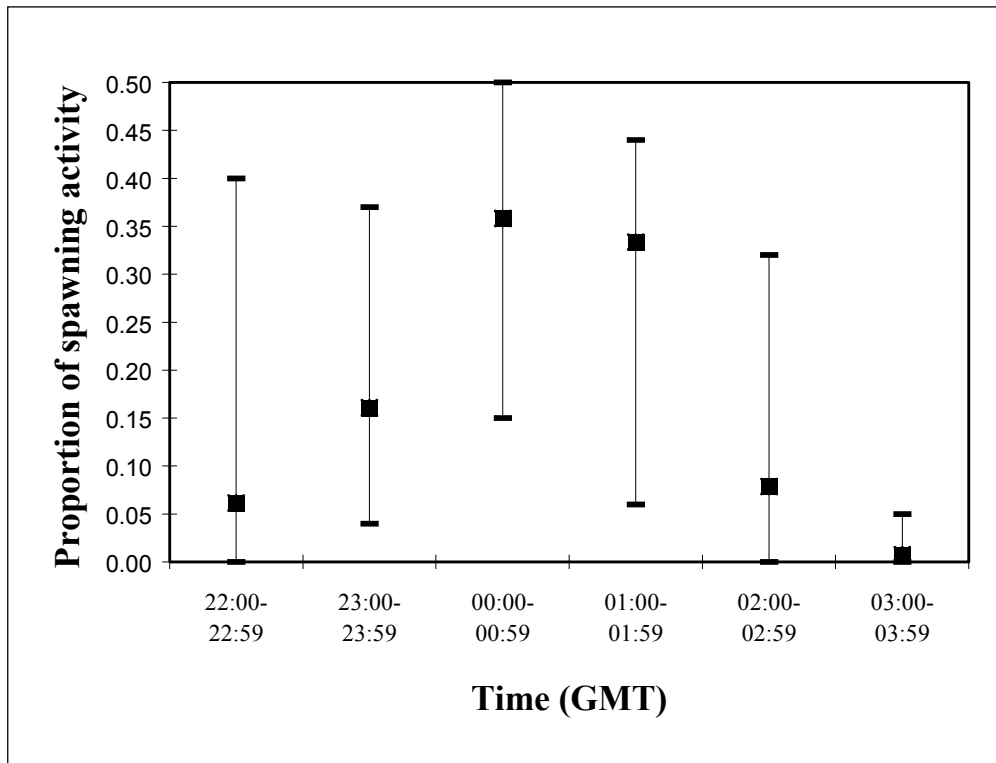


Figure 3.5: Spawning activity of *Alosa alosa* on the Garonne river (France), from Cassou-Leins & Cassou-Leins (1981). Squares represent the mean and dashes the upper and lower limit of the proportion of the spawning activity undertaken each hour between 22:00 and 03:59 (n=8).

Temperature at the onset of spawning has been reported to be in the range of; 15°C to 16°C (Roule, 1922a), 15°C to 18°C (Cassou-Leins & Cassou-Leins, 1981); ≈15°C (Boisneau *et al.*, 1990); 15°C to 25°C (Mohr, 1941); 16°C to 22°C (Phillipart & Vranken, 1982); 17°C to 18°C (Dottrens, 1952); 17°C to 19°C (Duhamel du Monceau, 1772; Roule, 1925), and 18°C (Hoestlandt, 1958). The optimum temperature for spawning was reported by Dottrens (1952) to be 22°C to 24°C. However, Boisneau *et al.* (1990) found that spawning activity was not correlated with temperature but was inversely related to flow, with mean daily flow accounting for 14.8% of the variability in spawning activity.

Cassou-Leins & Carette (1992) observed that spawning activity stopped when flows reached 2.5 ms⁻¹ and during heavy night rain.

Alosa fallax fallax

Alosa fallax spawn during the night (Yarrell cited in Day, 1880-84; Couch, 1877; Jenkins, 1942; Wheeler, 1978b; Aprahamian, 1982). Some authors have narrowed down the actual spawning time to between 22:00 and 02:00 (Breder & Rosen, 1966), between 01:00 and 03:00 (Cassou-Leins & Cassou-Leins, unpubl. [in Cassou-Leins *et al.*, 2000]) and others to between 00:00 and 02:00 (Roule, 1922a, Anon., 1979a).

A commotion can be heard whilst the fish are spawning (Aprahamian, 1982; Edwards & Brooker, 1982; LeClerc, 1941; Yarrell cited in Day 1880-84). This has been described as a swishing noise (Jenkins 1942) and as "rushing about on top of the water in the evenings" by Bracken & Kennedy (1967). It is believed that this surface tail splashing of the water is only done by the males (Edwards & Brooker, 1982), and is less violent in *A. fallax* than in *A. alosa* (Quignard & Douchement, 1991b). The spawning activity is relatively brief lasting *c.* 2 to 3s (Cassou-Leins, 1995).

Temperature appears to play an important role in the onset of spawning. Breder & Rosen (1966) and Spillman (1961) have recorded a range of 18°C to 22°C. Wheeler (1978b) states that a drop below 18°C causes spawning to stop, but temperatures below that mark have been noted; 15°C to 16°C in Northern Europe (Svetovidov 1963), 17°C to 18°C in the Seine (Roule, 1925) and 18°C to 20°C in the Rhine (Redeke, 1939).

Alosa fallax rhodanensis

The spawning activity is relatively short lasting around 2 to 5 s (Cassou-Leins, 1995; Le Corre *et al.*, 1999b) and in most instances (>70%) involves only one partner (Le Corre *et al.*, 1999b; Genoud 1999b, 2001). The fish assemble on the spawning grounds between 2230 and 2300h. Spawning takes place between 2300h and 0300h on the River Rhône, France, (Le Corre *et al.*, 1999b; Roure *et al.*, 1997a) with peak activity being between 2300 and 0200h (Le Corre *et al.*, 1999b; Genoud, 2001). In the Aude spawning occurs between 0000 and 0500h with maximum activity between 0200 and 0400h (Cassou-Leins, 1995). Similar findings, of fish spawning at night, were reported by D'Ancona (1926) from the River Tiber.

In the River Rhône (France) *A. fallax rhodanensis* have been reported to spawn within the temperature range 16°C to 18°C (Roule, 1922a, 1925), 17°C to 19°C (Gallois, 1946a, 1947b), 17°C to 22°C (Genovel, 2001), 18°C to 20°C (Le Corre *et al.*, 1997b; Roure *et al.*, 1997a), 18°C to 24°C (Rameye *et al.*, 1976) and at 20.5°C (Hoestlandt, 1947). Spawning activity was not correlated with flow, lunar cycle or turbidity but was negatively correlated with rain and wind (Le Corre *et al.*, 1999b; Roure *et al.*, 1997a). In the Tiber, spawning takes place once water temperatures are between 22°C and 25°C (D'Ancona, 1926, Svetovidov, 1963).

Alosa fallax nilotica

Relatively little information exists only that spawning takes place once water temperatures are between 18°C and 22°C (Vukovic, 1961a).

Alosa fallax lacustris

Spawning occurs at night between 22:00 and 03:00 in water temperatures ranging from 18.8°C to 19.8°C (Dottrens, 1952).

3.1.4.1 Sex ratio

The sex ratio of three year-classes of *Alosa alosa* from the Gironde-Garonne-Dordogne (France) at maturity was estimated by Lambert *et al.* (2001) to range from 43.2% to 59.1% male. (The sex ratio of the mature population is dealt with in section 4.1).

3.1.4.2 Induction of spawning.

The induction of spawning is discussed in section 7 (Culture).

3.1.5 Fertilisation

Fertilisation is external, eggs and sperm being broadcast into the water column.

3.1.6 Gonad development and fecundity.

3.1.6.1 Coefficient of fecundity

Alosa alosa

The gonad somatic index (gonad weight*100/somatic weight) for females from the Douro (Portugal) increased during the migration period from a mean of 8.40-9.31% to 9.80-10.13% and for males from 4.71-4.84 to 5.19-6.02% (Eiras, 1981b). In the Sebou the index for the males was similar (4.06 to 6.80%) while for females the index (mean \pm 95%CI) at the start of the migration was lower $2.48 \pm 7.88\%$, increasing steadily to $12.66 \pm 5.07\%$ at the end of the period (Sabatié, 1993). In the Loire the index for females varied between 6.0 and 17.8% with a mean of 12.2%, and in the Gironde-Garonne-Dordogne system from 9.1 to 22.5% with a mean of 15.0% (Douchement, 1981). For both male and female fish from the Douro the gonad somatic index was higher for fish on the spawning ground when compared with those in the estuary, by between 0.25 and 1.99% for males and 1.90 to 4.23% for females (Eiras, 1981b).

Alosa fallax fallax

For anadromous populations of *A. fallax fallax* the mean (\pm 95%CI) weight of the ovary as a percentage of somatic weight was 20.6% (\pm 0.87) in the Loire, 27.8% (\pm 1.02) in the Gironde-Garonne-Dordogne system and 24.7% (\pm 1.48) in the Adour (Douchement, 1981). In the Sebou the mean index declined from 16.4% (\pm 4.56) at the start of the migration period to 8.6% (\pm 4.55) at the end (Sabatié, 1993). In the Severn the mean index for female *A. fallax*, over a seven year period varied from 13.8% (\pm 0.48) to 17.3% (\pm 0.77) (Aprahamian, unpubl.). For males from the Severn the gonad somatic index ranged from 8.8 ± 0.5 to 10.3 ± 0.5 over the same period.

Alosa fallax rhodanensis

In the rivers Aude and Rhône (France) the mean gonad-somatic index declined from a pre-spawning level of 15.2% and 16.5% to 3.3% and 1.3% post-reproduction for females and from 6.4% and 7.1% to 1.8% and 0.5% for males, respectively (Douchement, 1981).

Alosa fallax algeriensis

For mature fish, the ovaries constitute 13.80% (mean) with a maximum of 23.83% of somatic weight (Kartas, 1991).

3.1.6.2 Description and development

The biochemical changes associated with the final stages of maturation are reported in the Section 3.5.1 (Adult spawning migration). This section deals with the histology of the gonads and the maturation process.

Alosa alosa

The histology and maturation of the ovaries has been described by Bengen *et al.* (1991), Bengen (1992), Eiras (1981b), Lahaye (1960a, 1961, 1962a&b), Lahaye *et al.* (1963) and by Sabatié (1993). Oocyte development can be classified into six stages; oogenesis, primary oocyte growth, cortical aveolus stage, vitellogenesis, maturation and ovulation (Bromage & Cumaranatunga, 1988). Within the ovary, oocyte development is not synchronous, oocytes passing through a number of the phases simultaneously.

At sea, approximately six months prior to spawning the oocytes range in size from 83 to 166 μ . The primary oocyte contains a distinct yolk nucleus (germinal vesicle), Balbiani body (a complex of cytoplasmic organelles which include mitochondria, multivesicular bodies, endoplasmic reticulum and Golgi elements (Tyler & Sumpter, 1996)), and an acellular vitelline envelope (zona radiata) around the oocyte. Present at the periphery of the nucleus, situated on the nuclear membrane, are numerous nucleoli. At this stage the nucleus represents 45% of the volume of the oocyte (RNP ratio). As the oocyte grows the zona radiata thickens and becomes surrounded by granulosa (follicle) and theca cells (Table 3.11), the latter layers being separated by a basal membrane.

Table 3.11: Change in thickness of the zona radiata and granulosa and theca cells associated with oocyte maturation in *Alosa alosa* (Bengen, 1992).

| Stage of development | Oocyte Diameter (μ) | Zona radiata (μ) | Granulosa layer (μ) | Thecal cells (μ) |
|----------------------|---------------------------|------------------------|---------------------------|------------------------|
| Primary oocyte | < 120 | | | 2 - 2.5 |
| Cortical aveolus | 400 - 900 | 3 - 4 | 3 - 5 | 1 - 2 |
| Vitellogenesis | 900 - 1400 | 12 - 31 | 5 - 7 | 2 - 4 |
| Mature | 1400 - 1800 | 17 - 23 | 15 - 18 | 4 - 7 |

As the oocyte develops, cortical aveoli (15 to 40 μ in diameter) develop within the cell. These structures contain a polysialoglycoprotein (Tyler & Sumpter, 1996). Eventually the cortical aveoli come to fill the entire cytoplasm of the oocyte. During this phase lipid bodies (3 to 10 μ in diameter) appear in the oocyte, coinciding with the appearance of the yolk vesicles (the orange colour being attributable to the carotenoid pigments in the lipid component of the vitellogenin (Tyler & Sumpter, 1996)). During the vitellogenic phase, vitellogenin is sequestered into the cell and accumulates in globules (yolk vesicles), measuring 10 to 35 μ in diameter. The yolk vesicles eventually

completely fill the oocyte, displacing the cortical alveoli towards the periphery. As the oocyte matures the RNP Ratio decreases to 25% and finally stabilises at around 15%. The final stages of maturation are characterised by the fusion of the yolk vesicles, resulting in the formation of a continuous mass of yolk, and the up take of water by the oocyte. The hydration phase results in the eggs becoming translucent and an increase in diameter of approximately 30% from 1200-1500 μ to 1700-1800 μ . Just before ovulation the oocyte becomes separated from the granulosa and thecal cells.

The reported size range of eggs before and after water absorption are shown in Table 3.12. Some of the differences may be associated with stock differences, but may also relate to the stage in the reproductive cycle that the measurements were taken. Lahaye *et al.* (1963) showed that the modal size of eggs increased from 400 μ three to four months before spawning, to 650 μ one month prior to spawning (Figure 3.6).

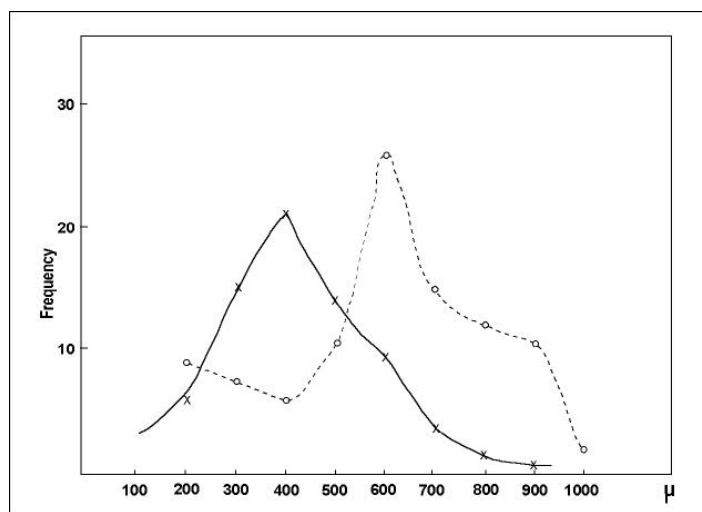


Figure 3.6: Interovarian egg size in *Alosa alosa* three to four months (solid line) and one month (dashed line) prior to spawning (Redrawn from Lahaye *et al.*, 1963).

Bengen *et al.* (1991) also observed a gradual increase in inter-ovarian egg size, from a modal value of 0.6 to 1.0 mm at the start of freshwater phase of their spawning migration in April, to c. 1.4 to 1.8 mm in June and July (Figure 3.7).

Table 3.12: Size of eggs of *Alosa alosa* before and after hydration.

| Size before hydration (mm) | Size after hydration (mm) | Reference |
|---|---------------------------|------------------------------------|
| 0.3-1.4 | | Sabatié (1993) |
| 0.3-1.5 | | Cassou-Leins & Cassou-Leins (1981) |
| 0.99 ± 0.01 ($\bar{x} \pm 95\text{CI}$) | | Taverny (1991a) |
| 1.0 | | Mohr (1941) |
| 1.5 | 4.5 | Duncker & Ladiges (1960) |
| 1.5-1.6 | 4.2-4.6 | Ehrenbaum in Cunningham (1896) |
| 1.5-1.8 | 3.0-3.6 | Roule (1925) |
| 1.8 | 2.5 | Hoestlandt (1958) |
| 2.0 | | Vincent (1894a); Dottrens (1952) |
| | 4.0-5.0 | Maitland (1972) |

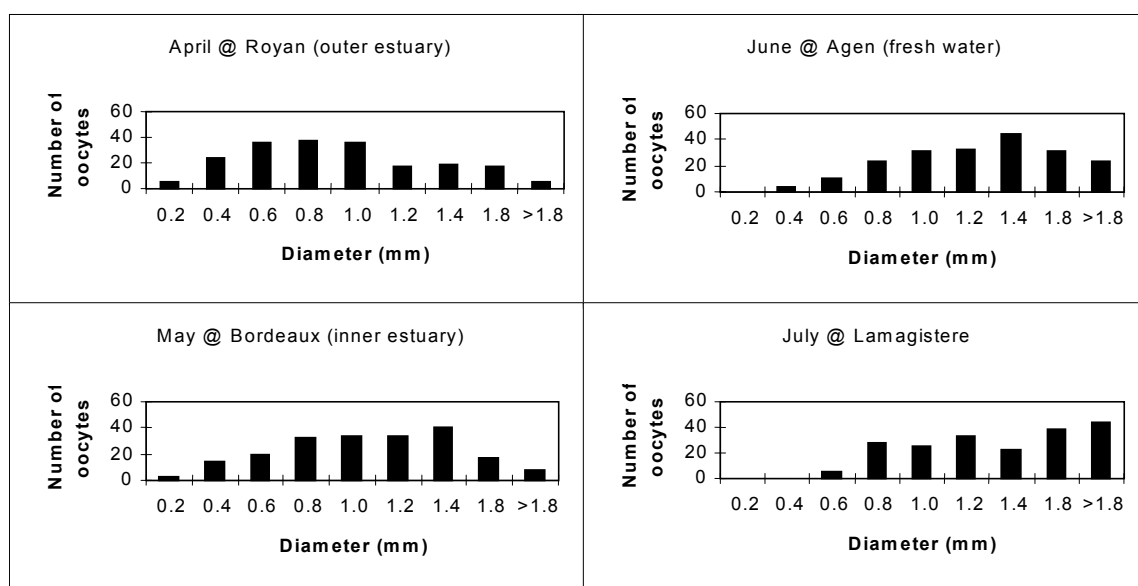


Figure 3.7: The change in oocyte diameter of *Alosa alosa* from the Garonne (France) in relation to maturation, redrawn from Bengen *et al.* (1991)

Part of the difference may also depend on whether fresh or preserved material was studied. If measurements were made on the latter, then a shrinkage of about 7% might be expected (Hiemstra, 1962).

Alosa fallax

The development and growth of the eggs of *Alosa fallax fallax* has been described by Lahaye (1962c), Lahaye *et al.* (1963), Sabatié (1993) and by Pina (2000), and of the sperm by Pina (2000). The structure of the ovary and testis for fish close to spawning

are shown in Figure 3.8 a-c. Eight maturity stages have been described (Table 3.13 a&b). Lahaye (1962c) mentions that the development of the oocytes in *A. fallax* is similar to that described for *A. alosa* with a number of important differences:

1. The cortical alveoli in *A. fallax* are larger ($>30\mu$ compared with $<20\mu$ in an oocyte 600μ in diameter) and the contents more homogenous. In *A. alosa* the cortical alveoli at the periphery are small (10μ) compared with those at the centre.
2. The lipoproteins appear earlier in the developmental process in *A. fallax*, being present in oocytes of 350μ compared with oocytes of 500μ for *A. alosa*.
3. The thickness of the envelope (zona radiata, granulosa and thecal cells) is 25μ in *A. fallax* compared with 35μ for *A. alosa*.

In *Alosa fallax* there exist two populations of developing oocytes; a population of primary oocytes and a population of larger oocytes from which the current batch of eggs develop (Aprahamian, 1982; Sabatié, 1993; Pina, 2000). In pre-spawning *Alosa fallax*

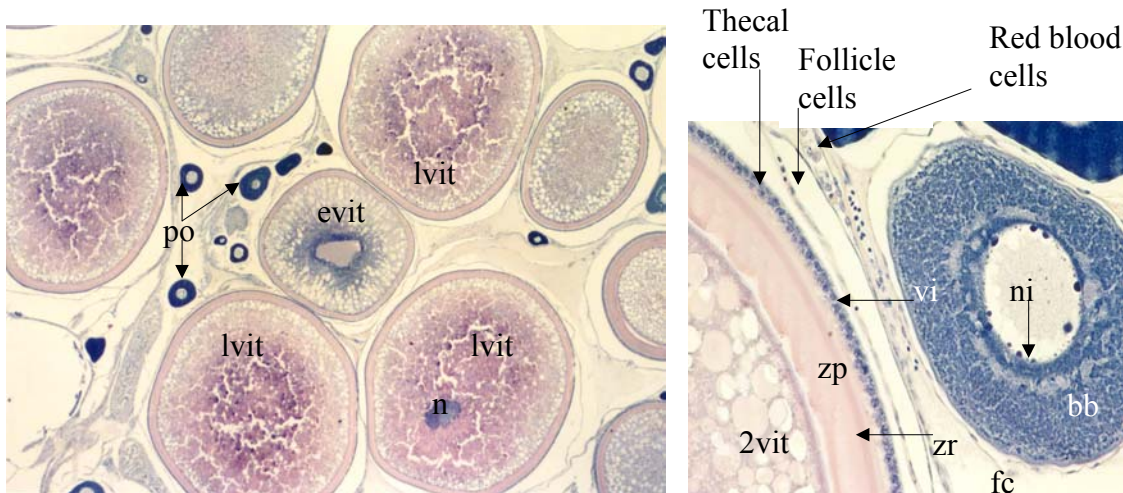


Figure 3.8a: Late vitellogenic female *Alosa fallax* ovary, showing numerous late vitellogenic oocytes (lvit) and early-mid stage vitellogenic oocyte (evit), interspersed with several primary oocytes (po). Nucleus (n), Mayer's Haematoxylin & Eosin x40.

Figure 3.8b: Transverse section through a secondary oocyte and a primary oocyte to illustrate the formation and development of the “egg shell” or chorion. The primary (balbiani body stage) oocyte (bb) is surrounded by a single layer of follicle cells (fc), whereas the more advanced (secondary) vitellogenic oocyte (2vit) is surrounded by a chorion composed of; zona pellucida (zp), zona radiata (zr), villi (vi), thecal cells (te) and follicle cells (fc), Nucleoli can be clearly seen on the periphery of the nucleus of the primary oocyte, Mayer's Haematoxylin & Eosin x400.

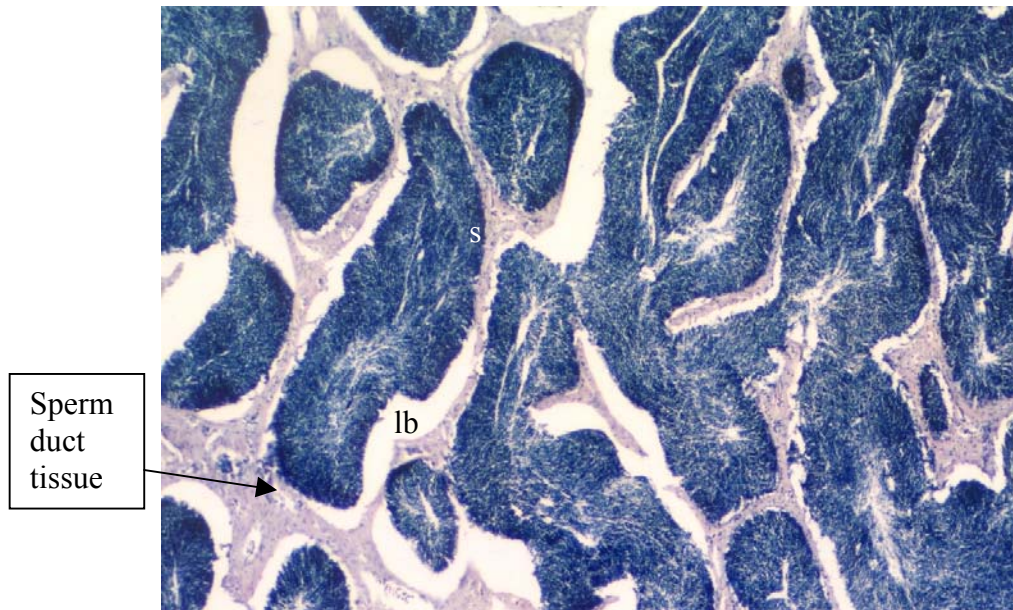
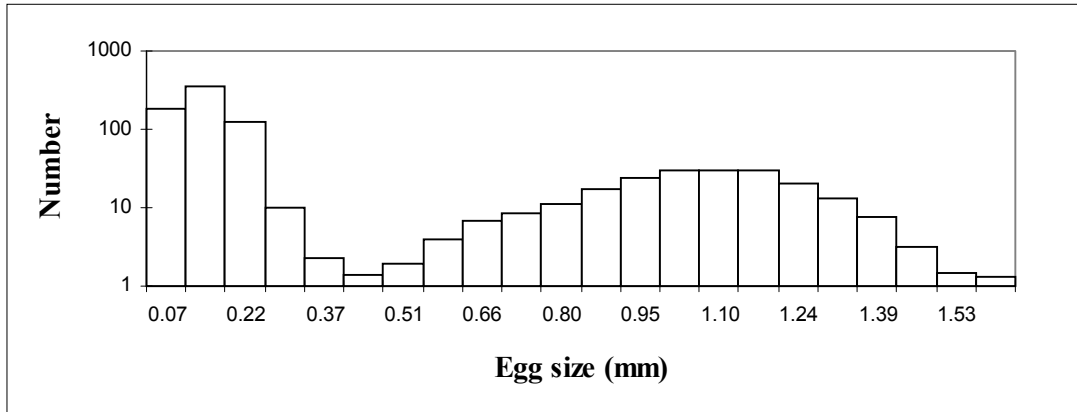


Figure 3.8c: Transverse sections through the testes of *Alosa fallax*, illustrating normal testicular organisation during the later stages of the reproductive cycle (stage IV-V). Histologically, the testes of shad are of a lobular type, in which the connective tissues divide stroma into a complex network of tightly packed lobules, each comprised of numerous cysts Fully mature shad testes at spermiation showing enlargement of the lobules (lb) and loss of cysts. Spermatozoa (s), Mayer's Haematoxylin & Eosin x100.

the larger size group of oocytes contained yolk and were shed during spawning (Figure 3.9) [Aprahamian, 1982]. Eggs in the smaller size group were white and irregularly shaped. The size which effectively separates the two populations of eggs was 0.44 mm in the Severn (Aprahamian, 1982), 0.20 mm in the Mira (Pina, 2000) and 0.166 mm in the Sebou (Sabatié, 1993).

The reported size range of eggs before and after water absorption is shown in Table 3.14. For fish close to spawning, Sabatié (1993) observed three modes of egg size at 0.90, 1.41 and 2.08 mm, indicating that *A. fallax* are asynchronous ovulators, eggs ripening progressively with spawning taking place in batches.

A)



B)

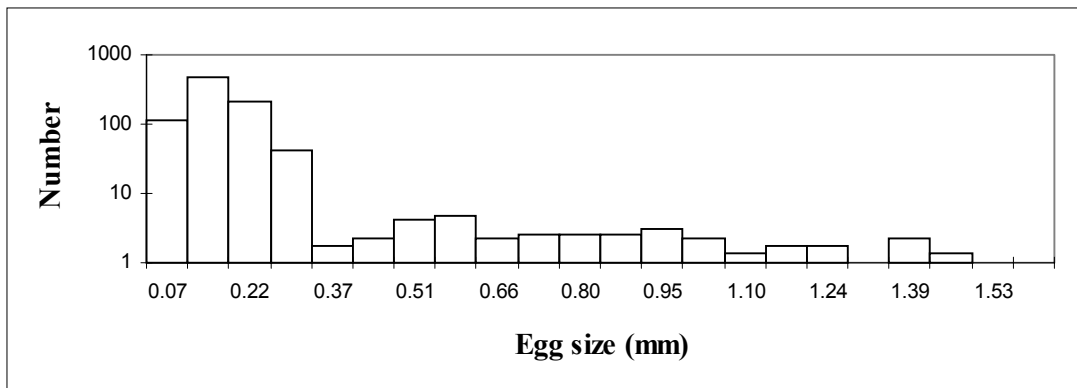


Figure 3.9: A&B. Interovarian egg size in prespawning (A) and postspawning (B) *Alosa fallax fallax* from the R. Severn (England) (Aprahamian, 1982).

Table 3.13a: – Macroscopic characteristics and histological description of the maturity stages of the ovary of *Alosa fallax fallax* (Pina, 2000).

| Maturity stage | Macroscopic description | Histological description |
|---------------------------------|---|--|
| I. Immature/ II. Resting (*) | Small thread-like ovary, pinkish in colour, no oocytes visible | Well spaced ovigerous fold, orientated towards the centre of the ovary, containing both oogonia and chromatin nucleolus and early perinucleolus stage; oogonia generally occur in nests. Oocyte size 0.01-0.04 mm (I); 0.01-0.06 mm (II) |
| III. Early development | Ovaries one-third of ventral cavity, yellowish in colour, opaque oocytes visible through the tunica | Oogonia still present, ovigerous folds fill cavity, late perinucleolus and cortical alveoli oocytes present Oocyte size 0.04-0.64 mm |
| IV. Maturing | Ovaries two-thirds of ventral cavity, yellowish in colour, opaque and translucent oocytes visible, increasing vascularization | Cortical alveoli and yolk granule oocytes predominate; late perinucleolus and vitellogenic oocytes can also be observed. Oocyte size 0.03-1.106 mm |
| V. Ripe | Ovaries highly vascularized occupy most of ventral cavity, opaque, translucent and dominant hyaline oocytes visible | Oocytes observed in previous stage still present; predominance of GVM stage oocytes. Oocyte size 0.03-1.052 mm. |
| VI. Spawning | Ovaries occupying most of ventral cavity, eggs released under slight pressure of the abdomen | Predominance of GVM oocytes and POFs. Oocyte size 0.03-1.211 mm. |
| VII. Partially spent | Ovaries flaccid, deep red in colour, occupying two-third of ventral cavity, with hyaline oocytes visible | Irregular convoluted ovigerous folds, conspicuous spaces in the septa and POFs in the lumen, early perinucleolus and atresia oocytes present. Oocyte size 0.04-1.319 mm. |
| VIII. Spent | Ovaries flaccid and fully empty, a few residual oocytes visible | Ovigerous folds reorganizing, containing atretic follicles and perinucleolus oocytes. Oocyte size 0.04-1.415 mm. |

Table 3.13b: – Macroscopic characteristics and histological description of the maturity stages of the testis of *Alosa fallax fallax* (Pina, 2000).

| Maturity stage | Macroscopic description | Histological description |
|---------------------------------|--|---|
| I. Immature/ II. Resting (*) | Small thread-like testis, transparent and prismatic with triangular section | Primary spermatogonia occupying the germinal epithelium, seminiferous tubules not well evident |
| III. Early development | Flattened and grey testis increasing in length and width, one fourth of body cavity | Seminiferous tubules now evident, interstitial tissues thick, secondary spermatogonia in the tubules and primary spermatocytes in the lumen |
| IV. Maturing | Testis occupying two-thirds of ventral cavity, increasing vascularization | Interstitial tissue and seminiferous tubules still clearly visible, spermatogonia near the tubule wall ; primary spermatocytes, secondary spermatocytes and spermatids closer to the lumen ; some spermatozoa might occur |
| V. Ripe | Testis pinkish very firm texture fill almost entire ventral cavity, with star-like figures clearly visible | Spermatozoa increasing in number, initially occurring in cysts are released in the lumen ; younger stages occur near the tubule wall |
| VI. Spawning | Milt runs from the genital pore on slight pressure, testis turgid and large amounts of milt are produced when they are dissected | Spermatozoa fill the entire seminiferous tubules ; the sperm heads are tightly packed and arranged spirally |
| VII. Partially spent | Testis flacid occupying two-thirds of ventral cavity, milt is often present in the seminiferous duct | Spermatozoa still present in the seminiferous tubules ; tubule walls thicker from the cortex to the medula ; no other germ cell stages present |
| VIII. Spent | Testis very flaccid with dark areas throughout the surface, occupying one-third of ventral cavity | Interstitial tissue unevenly thick ; spermatogonia near the tubule walls and residual spermatozoa in the lumen on empty tubules ; tubules start to reorganize |

* Stage I and Stage II have similar macroscopic and histological characteristics but are distinguished by length at first maturity.

Aprahamian (1982) found a positive correlation between egg size and fish size. The study of fecundity of *Alosa fallax* from the River Severn involved separating the eggs into three size classes; 0.5-0.7 mm, 0.7-1.0 mm and >1.0 mm, and summing the number in each size category to determine the overall fecundity. Figure 3.10 shows that the proportion of eggs >1.0 mm in diameter increased significantly with the size of fish.

Table 3.14: Size of eggs of *Alosa fallax fallax* before and after hydration.

| Size before hydration (mm) | Size after hydration (mm) | River, Country | Reference |
|----------------------------|---------------------------|----------------------------------|-----------------------|
| <0.7-1.8 | | Nyamunas, Lithuania | Manyukas (1989) |
| 0.72 | 1.5 | Elbe, Germany | Jenkins (1902) |
| 0.8-2.3 | | Sebou, Morocco | Sabatié (1993) |
| 1.0 | | Morocco | Lahaye (1962c) |
| 1.01 ± 0.02 ¹ | | Gironde-Dordogne-Garrone, France | Taverny (1991a) |
| | 1.68-2.41 | Mira, Portugal | Esteves (pers. comm.) |
| 1.01 ± 0.03 ¹ | 2.67 ± 0.03 ¹ | Severn & Wye, Britain | Aprahamian (1982) |
| 1.1 ² (0.4-1.6) | | Barrow, Ireland | O'Maoileidigh (1990) |
| 1.2-1.5 | | | Spillman (1961) |
| 1.5 | | Seine, France | Vincent (1894b) |
| 1.5-1.6 | 4.2-4.6 | Elbe, Germany | Ehrenbaum (1894) |
| 1.5-1.8 | 3.0-3.6 | | Roule (1925) |
| 1.6 | | | Mohr (1941) |
| 1.6 | 2.0-3.0 | Rhine, Germany | Redeke (1939) |
| | 3.85 | Elbe, Germany | Hass (1968) |
| | 4.0-5.0 | | Maitland (1972) |
| | 4.5 | | Cunningham (1896) |

¹Mean ± 95% confidence intervals;

²Mode

Alosa fallax rhodanensis

The diameter of eggs of *Alosa fallax rhodanensis* has been reported for relatively few fish. For one female eggs ranged in size from 0.8 to 1.20 mm with a mean size of 1.02 mm (Gallois, 1946a) and of another from 0.8 to 1.85 mm (Hoestlandt (in Gallois, 1946a)). Prior to hydration the eggs have a diameter of 1.7 and 1.85 mm, and following water absorption their diameter increases to 2.4 mm (Hoestlandt, 1947; Hoestlandt (in Gallois, 1946a)). Chiappi (1933a) reported a slightly larger size, with a fertile egg having a mean diameter of 2.9 mm.

Alosa fallax nilotica

Vukovic (1961a) found that fertile eggs of *Alosa fallax nilotica* maintained in an aquarium, ranged in size from 2.9 to 3.1 mm in diameter which compares closely with those eggs collected from the substrate of Lake Bačina of 2.7mm.

Alosa fallax lacustris

The average size of eggs of *Alosa fallax lacustris*, following water absorption, was 2.6 mm from Lake Vico (Chiappi, 1933a), 2.0 mm from Lake Como (Pirola, 1930) and 1.5 mm from lakes Lugano and Maggiore (Fatio, 1890).

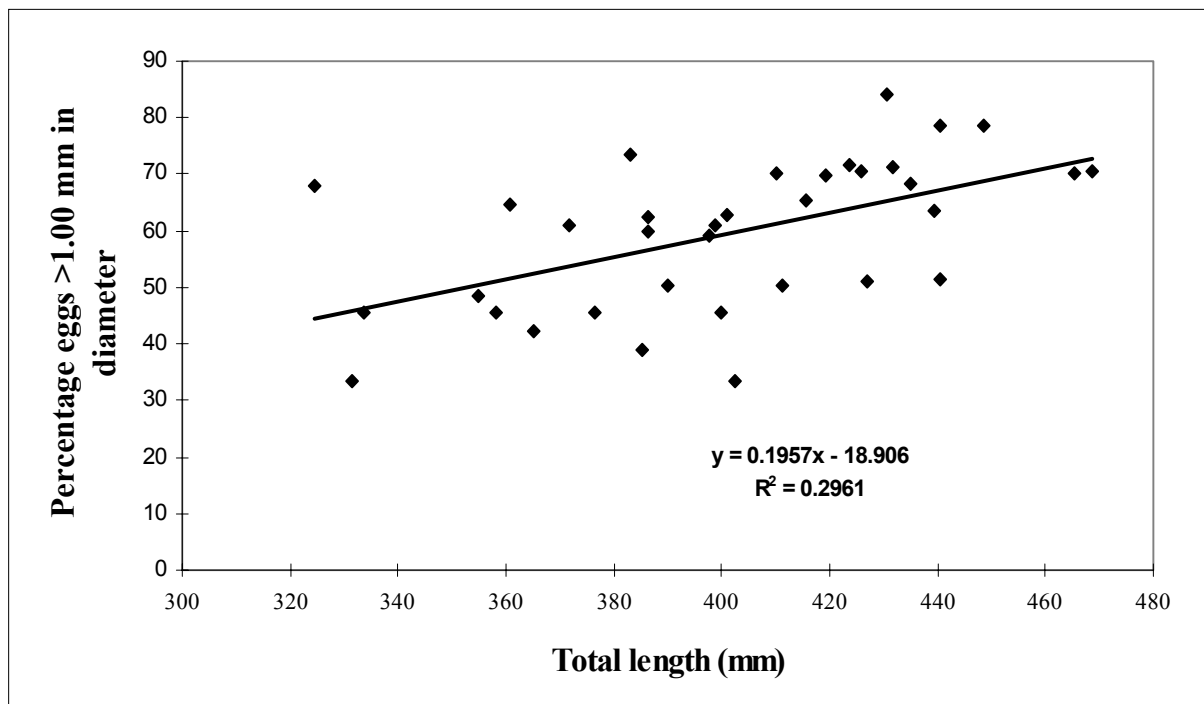


Figure 3.10: The relationship between egg size (percentage of eggs >1.00 mm in diameter) and length (total) of *Alosa fallax fallax* from the River Severn (Aprahamian, 1982).

Alosa fallax killarnensis

The interovarian egg size of *Alosa fallax killarnensis* ranged from 0.3 to 1.33mm in diameter (Figure 3.11). Eggs of <0.5mm were irregularly shaped and pale in colour and represented recruitment eggs for the following year (O'Maoileidigh, 1990). Eggs ranging between 0.5 and 1.33mm, with a modal size of 0.9mm in diameter were orange or yellow in colour and were shed during spawning. Egg size was not correlated with either length or weight.

3.1.6.2 Fecundity and egg size

The comparison and interpretation of some of the data is complicated by the fact that in some of the studies it was not clear whether the estimate of fecundity was based on the total number of eggs (primary oocytes and those going through vitellogenesis) or on just the number of ripe eggs. Except for the study of Sabatié (1993) who provided estimates of both total and absolute fecundity it has been assumed that the authors have estimated absolute fecundity, defined as the number of ripe eggs in the ovaries prior to the next spawning period (Bagenal & Braum, 1978). Similarly in the majority of cases no information was provided on the method used to estimate fecundity. Where the methods have been described the estimates have been based on volume (Cassou-Leins & Cassou-Leins, 1981; Dautrey & Lartigue, 1983; Sabatié, 1993), weight (Eiras, 1981b; Aprahamian, 1982; Pina, 2000) or stereological analysis (Pina, 2000). Pina (2000) compared the histological and gravimetric methods and reported that fecundity estimated using histology was approximately 3 times (2.98 ± 0.30) that based on weight. Sub-sampling to improve the precision of the estimate has been reported in a few studies. Where this has been reported it has ranged from three (Sabatié, 1993) to 12; four from each of three size classes; 0.5-0.7mm, 0.7-1.0mm and >1.0mm (Aprahamian, 1982). In the case of the latter the precision of the method was estimated to be $\pm 6.26\%$ with 95% confidence.

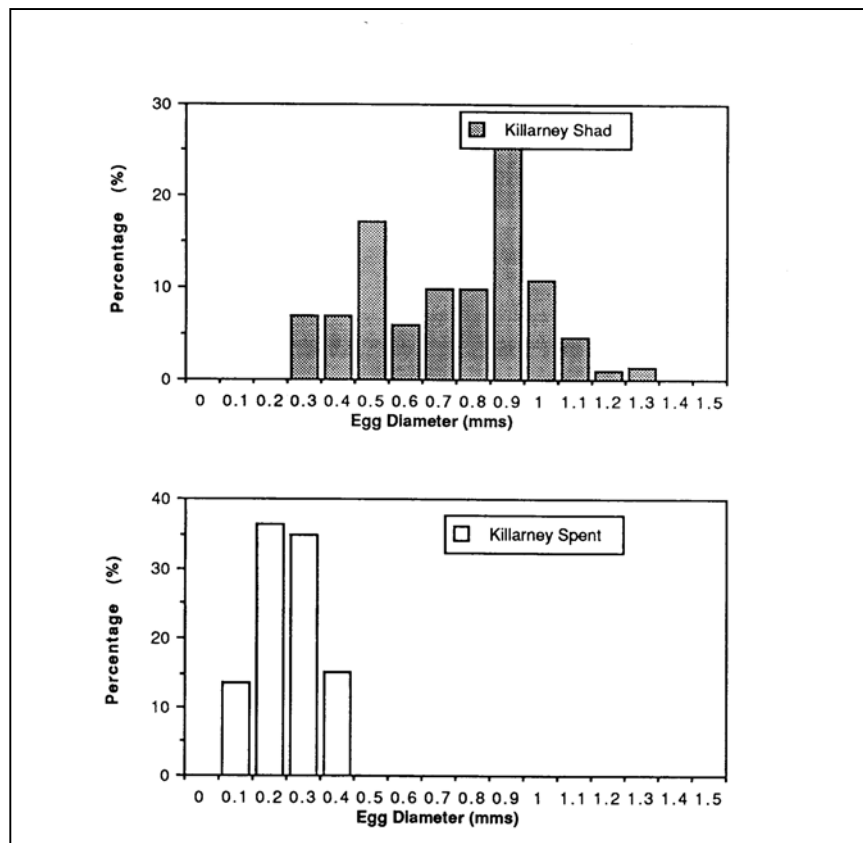


Figure 3.11: Interovarian egg size for pre-spawning and spent *Alosa fallax killarnensis* from Lough Leane, Ireland; for pre-spawning fish only eggs >0.3mm were counted (Reproduced from O'Maoleidigh, 1990).

Alosa alosa

In *Alosa alosa* the absolute fecundity has been reported to range from 50,000 to 636,000 eggs (Hoek, 1888; Fatio, 1890; Vincent, 1894c; Roule, 1925; Dottrens, 1952; Hoestland, 1958; Spillman, 1961; Rameye *et al.*, 1976; Cassou-Leins & Cassou-Leins, 1981; Eiras, 1981b; Philippart & Vranken, 1982; Dautrey & Lartigue, 1983; Sabatié, 1993).

The relative fecundity, defined as the number of eggs per kilogram total weight, has ranged from 60,000 egg kg⁻¹ in the Sebou, Morocco (Sabatié, 1993) to 236,000 egg kg⁻¹ in the Garonne river, France (Cassou-Leins & Cassou-Leins, 1981) [Table 3.15]. There is an indication of an increase in relative fecundity with increasing latitude from *c.* 60,000 in Morocco to *c.* 200,000 in the Loire (Table 3.15).

Table 3.15: The relative fecundity (Mean ± 95CI) of populations of *Alosa alosa*.

| River (Country) | Eggs per kg total weight | No. | Reference |
|-----------------------------------|--|------------------------|--|
| Loire (France) | 233,400 ¹ | 26 | Mennesson-Boisneau, Boisneau & Sabatié (unpubl.) |
| Gironde-Garonne-Dordogne (France) | 125,000 156,600 236,316 ± 17,799 104,325 ± 8,070 | >200 30 25 74 | Hoestland (1958) Dautrey & Lartigue (1983) Cassou-Leins & Cassou-Leins (1981) Taverny (1991a) |
| Douro (Portugal) | 79,910 ± 12,727 | 27 | Eiras (1981b) |
| Sebou (Morocco) | 59,560 ² ± 3,117 76,780 ³ ± 2,807 | 25 | Sabatié (1993) |

¹ Eggs per kg somatic weight; ² Number of oocytes ≥ 166µ; ³ Total number of oocytes.

The relationship between fecundity and size (Table 3.16) has been determined for populations in the Gironde-Garonne-Dordogne system (France), the River Douro (Portugal) and the River Sebou (Morocco). Significant correlations existed between absolute fecundity and length, weight and ovarian weight. In the River Douro the relationship between fecundity and ovarian weight was not examined (Eiras, 1981b).

Table 3.16: The relationship between fecundity and fish size for *Alosa alosa*.

A) Length

| River (Country) | Fecundity - Total Length (cm) | No. | r ² | Reference |
|-----------------------------------|----------------------------------|-----|----------------|-----------------|
| Gironde-Garonne-Dordogne (France) | $F = -2.71.10^5 + 7.97.10^3 L_t$ | 76 | 0.114 | Taverny (1991a) |
| Douro (Portugal) | $F = 3.72.10^{-2} L_t^{3.72}$ | 27 | 0.391 | Eiras (1981b) |
| Sebou (Morocco) | $F = 2.28.10^{-4} L_t^{4.92}$ | 25 | 0.152 | Sabatié (1993) |

B) Weight

| River (Country) | Fecundity - Total weight (g) | No. | r ² | Reference |
|-----------------------------------|----------------------------------|-----|----------------|-----------------|
| Gironde-Garonne-Dordogne (France) | $F = 6.41.10^4 + 59.78 W_t$ | 73 | 0.155 | Taverny (1991a) |
| Douro (Portugal) | $F = -6.52.10^4 + 1.07.10^2 W_t$ | 27 | 0.332 | Eiras (1981b) |
| Sebou (Morocco) | $F = -1.72.10^5 + 1.13.10^2 W_t$ | 25 | 0.237 | Sabatié (1993) |

C) Ovarian weight

| River (Country) | Fecundity - Ovary weight (g) | No. | r ² | Reference |
|-----------------------------------|-----------------------------------|-----|----------------|-----------------|
| Gironde-Garonne-Dordogne (France) | $F = 1.14.10^5 + 2.85.10^2 OW_t$ | 74 | 0.139 | Taverny (1991a) |
| Sebou (Morocco) | $F = -3.79.10^3 + 5.78.10^2 OW_t$ | 25 | 0.195 | Sabatié (1993) |

The relationship between fecundity and age was examined by Taverny (1991a) for *Alosa alosa* from the Gironde-Garonne-Dordogne system (France). A comparison of the fecundity of fish aged between 5 and 6 years indicated that there was no significant difference ($P > 0.05$) in either absolute or relative fecundity between the two age groups.

No information was found on the fecundity of landlocked populations of *Alosa alosa*.

Alosa fallax fallax

The absolute fecundity of *Alosa fallax fallax* has been reported to range from 25,942 to 675,000 eggs (Vincent, 1894b&c; Jenkins, 1902; Bounhiol, 1917; Hass, 1965; Manyukas, 1989; Aprahamian, 1982; Dautrey & Lartigue, 1983; Taverny, 1991a; Sabatié, 1993; Pina, 2000). The relative fecundity for an individual fish has been reported to range from 42,540 to 403,562 egg kg⁻¹ (Vincent, 1894b; Manyukas, 1989; Aprahamian, 1982; Taverny, 1991a; Sabatié, 1993; Pina, 2000). The mean relative fecundity for four anadromous populations of *A. fallax* is shown in Table 3.17.

Table 3.17: The relative fecundity (Mean ± 95CI) of populations of *Alosa fallax fallax*.

| River (Country) | Eggs per kg total weight | No. | Reference |
|-----------------------------------|--|-----|----------------------|
| Severn (England) | 139,479 ± 10,435 | 35 | Aprahamian (unpubl.) |
| Gironde-Garonne-Dordogne (France) | 147,378 ± 19,272 | 35 | Taverny (1991a) |
| Mira (Portugal) | 403,562 ¹ ± 55,162 142,848 ² ± 26,225 | 14 | Pina (2000) |
| Sebou (Morocco) | 86,700 ³ ± 3,206 103,270 ⁴ ± 5,881 | 31 | Sabatié (1993) |

¹ Stereological estimate; ² Gravimetric estimate (number of oocytes ≥ 200µ);

³ Number of oocytes ≥ 166µ; ⁴ Total number of oocytes.

The population of *A. fallax fallax* showing the greatest fecundity was from the Guadiana River where the number of eggs ranged from 101,878 to 673,533, followed by the River Mira (110,669 - 445,051) (Pina, 2000) and the Nyamunas River (83,900 – 362,700) (Manyukas, 1989). However, direct comparisons are difficult as the estimate of fecundity for the Portuguese population was through stereological analysis and the estimate is approximately three times greater than that based on weight (Pina, 2000).

A significant relationship between fecundity and size (Table 3.18) has been determined for a number of populations. The relationships for the Nyamunas River which drains into the Kurshskiy Bay (Manyukas, 1989) and the River Elbe (Hass, 1965) have been derived from mean values. In the latter case data was only available for the relationship between fecundity and total length. All the studies, except that of Taverny (1991a) found a significant relationship between fecundity and length and with the exception of Manyukas (1989) all observed a significant relationship between total weight and ovarian weight.

Table 3.18: The relationship between fecundity and fish size for *Alosa fallax fallax*.

A) Length

| River (Country) | Fecundity - Total Length (cm) | No. | r ² | Reference |
|----------------------|--|-----|----------------|--------------------------------|
| Severn (England) | $F = 1.31L_t^{3.00}$ | 35 | 0.506 | Aprahamian (1982) ¹ |
| Nyamunas (Lithuania) | $F = - 4.28 \cdot 10^5 + 1.3 \cdot 10^4 L_t$ | 26 | | Manyukas (1989) ² |
| Elbe (Germany) | $F = 1.25 \cdot 10^{-2} L_t^{4.22}$ | 19 | | Hass (1965) |
| Mira (Portugal) | $F = 2.04 \cdot 10^2 L_t^{-1.93}$ | 47 | 0.295 | Pina (2000) |
| Guadiana (Portugal) | $F = 1.55 \cdot 10^2 L_t^{2.05}$ | 38 | 0.213 | Pina (2000) |
| Sebou (Morocco) | $F = 1.72 \cdot 10^{-5} L_t^{5.97}$ | 31 | 0.388 | Sabatié (1993) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.13 L_f + 0.353$ (Douchement, 1981).

² Calculated from mean values; standard length (L_s) converted to total length (L_t) using $L_t = 1.19 L_s + 0.594$ (Douchement, 1981).

B) Weight

| River (Country) | Fecundity - Total weight (g) | No. | r ² | Reference |
|-----------------------------------|--|-----|----------------|-------------------|
| Severn (England) | $F = 1.82 \cdot 10^2 W_t^{0.96}$ | 35 | 0.620 | Aprahamian (1982) |
| Gironde-Garonne-Dordogne (France) | $F = 1.25 \cdot 10^2 W_t^{0.98}$ | 35 | 0.268 | Taverny (1991a) |
| Mira (Portugal) | $F = 9.77 \cdot 10^2 W_t^{0.87}$ | 47 | 0.490 | Pina (2000) |
| Guadiana (Portugal) | $F = 4.79 \cdot 10^2 W_t^{0.99}$ | 38 | 0.405 | Pina (2000) |
| Sebou (Morocco) | $F = -3.34 \cdot 10^4 + 1.44 \cdot 10^2 W_t$ | 31 | 0.494 | Sabatié (1993) |

C) Ovarian weight

| River (Country) | Fecundity - Ovary weight (g) | No. | r ² | Reference |
|-----------------------------------|---|-----|----------------|-------------------|
| Severn (England) | $F = 6.61 \cdot 10^3 OW_t^{0.59}$ | 35 | 0.580 | Aprahamian (1982) |
| Gironde-Garonne-Dordogne (France) | $F = 3.30 \cdot 10^3 OW_t^{0.66}$ | 35 | 0.535 | Taverny (1991a) |
| Mira (Portugal) | $F = 2.19 \cdot 10^4 OW_t^{0.25}$ | 47 | 0.542 | Pina (2000) |
| Guadiana (Portugal) | $F = 1.91 \cdot 10^4 OW_t^{0.27}$ | 38 | 0.345 | Pina (2000) |
| Sebou (Morocco) | $F = -1.62 \cdot 10^4 + 1.10 \cdot 10^3 OW_t$ | 31 | 0.494 | Sabatié (1993) |

D) Age

| River (Country) | Fecundity - Age (year) | No. | r ² | Reference |
|----------------------|--------------------------------|-----|----------------|------------------------------|
| Severn (England) | $F = 3.55 \cdot 10^4 A^{0.52}$ | 35 | 0.098 | Aprahamian (1982) |
| Nyamunas (Lithuania) | $F = 3.02 \cdot 10^4 A^{1.04}$ | 26 | | Manyukas (1989) ³ |

³ Calculated from mean values.

Information on age was only available for the populations in the River Severn and the Nyamunas River, both of which showed a significant relationship between fecundity and age. However, for fish from the Gironde-Garonne-Dordogne river system, the inclusion of age in a multiple regression relating fecundity to length (total) and weight (total) did not significantly improve the relationship (Taverny, 1991a).

There are few studies relating fecundity to spawning history. On the Elbe Jenkins (1902) observed that those fish spawning for a second time had a higher fecundity than those spawning for the first time. Similarly on the Severn Aprahamian (unpubl.) found a significant correlation ($P < 0.05$) between fecundity and number of spawnings ($r^2 = 0.114$).

Aprahamian (1982) examined the effect of using more than one independent variable to estimate fecundity for fish from the River Severn. Of the four variables tested, total weight and age accounted for a significant proportion of the variability (61.9% and

13.1% respectively). The inclusion of total length and spawning history did not significantly improve the relationship.

The relationship between fecundity and length for the various populations of *A. alosa* and *A. fallax fallax* is presented in Figure 3.12. The Gironde-Garonne-Dordogne *A. alosa* population appears the most fecund when compared to those from the Douro and Sebou. The latter populations showed a very similar fecundity to size relationship.

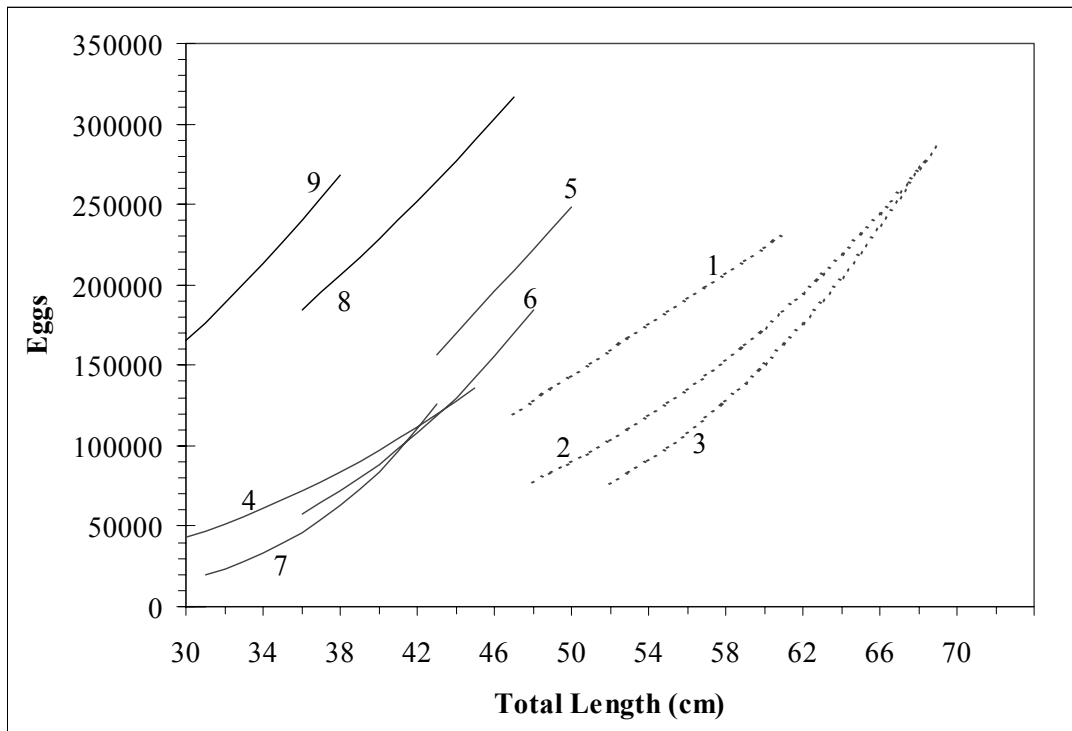


Figure 3.12: A comparison of the relationship between fecundity and length for a number of populations of *Alosa alosa* (dashed line) and *Alosa fallax fallax* (solid line). 1= Gironde-Garonne-Dordogne (France), Taverny (1991a); 2 = Douro (Portugal), Eiras (1981b); 3 & 7 = Sebou (Morocco), Sabatié (1993); 4 = Severn (England), Aprahamian (1982); 5 = Nyamunas (Lithuania), Manyukas (1989); 6 = Elbe (Germany), Hass (1965); 8 = Mira (Portugal), Pina (2000); 9 = Guadiana (Portugal), Pina (2000).

The population of *A. fallax fallax* showing the greatest fecundity for a fish of a given size was from the River Guadiana followed by the River Mira and Nyamunas River. The relationship for the other three populations in the Severn, Elbe and Sebou, was very similar. Direct comparisons are difficult as the estimate of fecundity for the Portuguese populations was through stereological analysis and the estimate is approximately three times greater than that based on weight (Pina, 2000).

Alosa fallax rhodanensis

Gallois, Hoestlandt and Germand (Gallois, 1946a) estimated the fecundity of three specimens of *Alosa fallax rhodanensis* ranging in size (L_t) from 400 to 430 mm to be between 114,000 and 175,000 eggs. The mean estimated relative fecundity was estimated by Le Corre and Sabatié (unpubl.) to be 109,149 egg kg^{-1} somatic weight ($n=9$), and by Cassou-Leins & Panisello (unpubl.) to be 100,000 egg kg^{-1} total weight.

Alosa fallax nilotica

Vukovic (1961a) estimated the absolute fecundity of three Yugoslavian populations of *Alosa fallax nilotica* to be between 25,624 and 336,592 eggs (Table 3.19). There was no significant correlation between the number of eggs per gram of ovary and weight of the fish. The relative fecundity of the landlocked population of *Alosa fallax nilotica* in Lake Skadar (Albania) was between 200,000 and 300,000 egg kg^{-1} (Rakaj & Crivelli, 2001).

Table 3.19: The absolute and relative fecundity of *Alosa fallax nilotica* (Vukovic, 1961a).

| Weight Group (g) | Absolute Fecundity | | | Relative Fecundity (egg g^{-1}) | | |
|------------------|--------------------|------------|---------------|------------------------------------|------------|---------------|
| | Lake Scutari | Lake Bacin | River Neretva | Lake Scutari | Lake Bacin | River Neretva |
| 0-250 | 30,123 | 25,624 | | 831 | 789 | |
| 251-500 | | 26,001 | 46,716 | | 729 | 916 |
| 501-750 | 103,919 | 51,528 | 64,320 | 863 | 683 | 800 |
| 751-1000 | 105,585 | 56,525 | 74,533 | 830 | 595 | 752 |
| 1001-1500 | 164,537 | 109,441 | 141,372 | 932 | 735 | 816 |
| 1501-2000 | 219,320 | 197,959 | 229,646 | 746 | 858 | 740 |
| 2001-2500 | 336,592 | | 238,901 | 872 | | 821 |

Alosa fallax algeriensis

The absolute fecundity has been reported to range from 50,000 to 269,000 eggs (Bounhiol, 1917; Kartas, 1991) with a mean relative fecundity of 200,000 egg kg^{-1} (Kartas, 1991). The relationship between fecundity and size is presented in Table 3.20.

Table 3.20: The relationship between fecundity (F) and total length (L_t), weight (W_t) and ovary weight (OW_t) for *Alosa fallax algeriensis* (Kartas, 1981).

| Relationship | No. | r^2 |
|-------------------------------------|-----|-------|
| $F = 9.60 \cdot 10^{-4} L_t^{3.51}$ | 64 | 0.423 |
| $F = 0.21 \cdot 10^2 W_t^{0.992}$ | 64 | 0.410 |
| $F = 3.02 \cdot OW_t^{0.84}$ | 64 | 0.846 |

In relation to age, Bounhiol (1917) reported that fish aged three years old produced between 50,000 and 60,000 eggs, increasing to 150,000 by the age of five.

Alosa fallax lacustris

The absolute fecundity has been reported to range from 15,000 to 20,000 eggs (Tortonese, 1970).

Alosa fallax killarnensis

In Lough Leane (Ireland), O'Maoileidigh (1990) examined the fecundity of *Alosa fallax killarnensis*. The absolute fecundity ranged from 10,700 to 30,560 eggs and relative fecundity (eggs per 100g total weight) from 7,605 to 22,741 with a mean \pm 95% confidence limits of $14,934 \pm 2,830$ eggs (n=11). There was no significant correlation between fecundity and age ($r^2=0.284$), total weight ($r^2=0.005$) and length (fork) ($r^2=0.148$).

3.1.6.3 Resorbition of spawn

Berg (1966b) mentions that under unfavourable conditions females of *Alosa fallax lacustris* may resorb their eggs.

3.1.7 Spawning grounds

Alosa alosa

Alosa alosa spawn in fresh water. Spawning takes place in the main river and major tributaries of the catchment, the width of the sites range from 15 m in the River Aulne (Véron, pers. comm.) to 200 m in the River Loire (Boisneau *et al.*, 1990). The fish deposit their eggs onto a substrate which can vary from sand (20 μ to 2mm) to pebbles (20 to 200 mm), in water of depth 0.5 to 3.0m and where the current ranges from 0.5 to 2.0ms⁻¹ (Roule, 1923; Ellison, 1935; LeClerc, 1941; Mohr, 1941; Dottrens, 1952; Hoestlandt, 1958; Anon. 1979a; Cassou-Leins & Cassou-Leins, 1981; Dautrey & Lartigue, 1983; Boisneau *et al.*, 1990; Fatin & Dartiguelongue, 1995; Belaud *et al.*, 2001).

On the River Garonne (France) the substrate of the spawning grounds was dominated by pebbles of mean size 70 to 80 mm and with a range of 30 to 160 mm (Cassou-Leins & Cassou-Leins, 1981). On the River Dordogne, Fatin & Dartiguelongue (1995) reported that the majority of the spawning took place over a substrate composed mostly of pebbles ranging in size from 20 to 200 mm. Similarly on the River Adour, Boigontier (1987) reported a mean (range) in particle size of 70 (30 – 80) mm and 50 (20 –130) mm. In contrast, on the River Loire (France), Boisneau *et al.* (1990) reported that the spawning site consisted mainly of sand followed by gravel (2 to 20 mm).

Alosa fallax fallax

Alosa fallax fallax spawn in both the tidal and non-tidal river. Spawning has been reported in the tidal freshwater section of estuaries (Hass, 1968; Taverny, 1991a; Thiel

et al., 1996a), as well as in the river (Ehrenbaum, 1894; Meek, 1916; Mohr, 1941; Hoestlandt, 1958; Maitland, 1972; Aprahamian, 1982).

The spawning habitat of twaite shad in the rivers Wye, Usk, Tywi and Teme (UK) comprises a fast-flowing shallow area of unconsolidated gravel/pebble and/or cobble substrate (Caswell & Aprahamian, 2001). The mean size of the substrate at one site on the River Garonne was 70 mm with a range of between 30 and 120 mm (Cassou-Leins & Cassou-Leins, 1981). The River Habitat Survey (Raven *et al.*, 1997) flow types ‘smooth flow’, ‘rippled flow’ and ‘unbroken standing waves’ were significantly ($P < 0.05$) associated with the presence or absence of shad eggs. The presence of eggs was significantly associated with the higher energy flow types ‘rippled flow’ and ‘unbroken standing waves’, and the absence of eggs was significantly associated with the lower energy flow type ‘smooth flow’ (Caswell & Aprahamian, 2001). Similar findings were also reported by Bracken & Kennedy (1967), Philippart & Vranken (1982) and Wheeler (1969a). In tidal waters of the River Dordogne, *Alosa fallax* spawned over substrate ranging in size from 20 to 100 mm at one site and between 2 and 20 mm at another (Taverny, 1991a), while in the River Garonne (France), eggs were reported deposited over mud (Anon. 1979a).

The fish accumulate in pools during the day, moving out onto the shallow / riffle areas to spawn during the night. The depth of water at spawning can range from $>0.15\text{m}$ (Figure 3.13) to 1.20m (Caswell & Aprahamian, 2001). The fact that egg density was found to decline with increasing depth suggests that, in these particular rivers *A. fallax* prefer to deposit their eggs in the shallow areas where the water depth is $<0.45\text{m}$ (Figure 3.14).

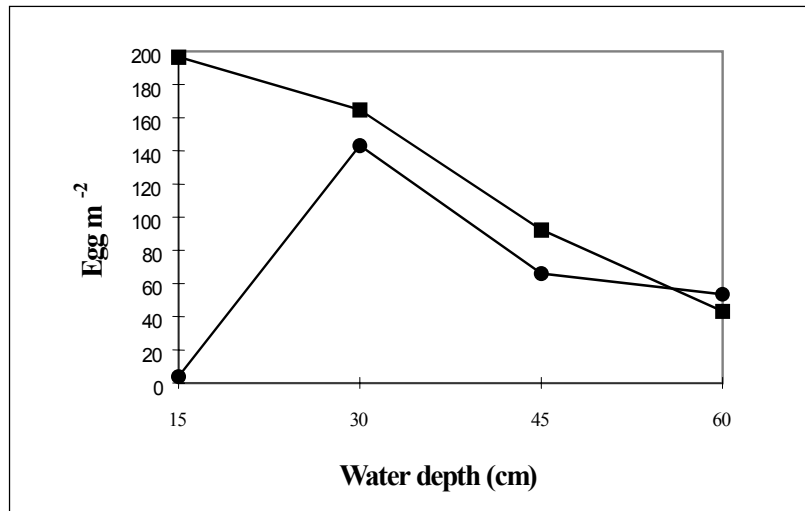


Figure 3.13 Mean density of eggs of *A. fallax* at two sites on the River Wye (Wales); Monmouth (■) and Courtfield (●) from Aprahamian (1981).

On the River Elbe (Germany), Hass (1968) and Thiel *et al.* (1996a) reported *Alosa fallax* spawning in the upper reaches of the estuary where the salinity was in the region of 0.3‰ . The current stirs up the eggs and there is a general increase in egg density with water depth (Figure 3.14).

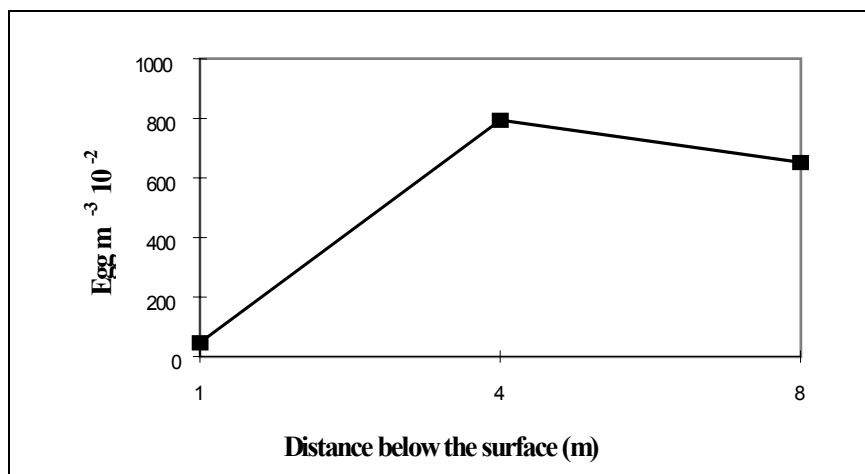


Figure 3.14 Mean density of eggs of *A. fallax* in relation to water depth in the estuary of the River Elbe (Germany) from Thiel *et al.* (1996a).

Alosa fallax rhodanensis

In the River Rhône (France) *A. fallax rhodanensis* spawn in fresh water at a depth ranging from 0.8 to 2.0 m (Cassou-Leins & Panisello, unpubl. [in Cassou-Leins *et al.*, 2000]) over a sandy-muddy substrate (Gallois, 1946a), and/or over a clean gravel substrate (Rameye *et al.*, 1976), where the current velocity is between 0.5 and 2.0 ms⁻¹ (Genoud, 1997; Moulin, 1997; Genoud, 1999b). At spawning sites the size of the substrate ranges from 10 to 400mm (Mazens, 1997; Roure *et al.*, 1997a) and the median particule size at these locations from 11 to 84.4 mm (Genoud, 1997; Mazens, 1997; Roure *et al.*, 1997a). In the River Aude (France), Cassou-Leins (1995) observed fish spawning over cobbles ranging in size from 50 to 150 mm with a median size of 90 mm. If, however, the (gravel) substrate is covered by mud the eggs are likely to be asphyxiated (Rameye *et al.*, 1976).

Alosa fallax nilotica

Vukovic (1961a) and Ivanovic (1977) report that *Alosa fallax nilotica* spawn over a sandy-muddy substrate in water depths ranging from 1 to 6m.

Alosa fallax lacustris

Alosa fallax lacustris spawn near the shore of the lake (Dottrens, 1952; Tortonese, 1970).

3.2 Preadult Phase

3.2.1 Ontogeny

Alosa alosa

Hatching takes place, depending on temperature, between 240 h and 65 h following fertilisation (Table 3.21), and is well described by the equation:

$$H = -220.98 \text{Log}_e T + 770.6 \quad r^2 = 0.84$$

Where: H = hatching time in hours; T = temperature in degrees centigrade.

Table 3.21: Incubation time for eggs of *Alosa alosa* in relation to temperature.

| Temperature (°C) | Incubation time (hours) | Reference |
|------------------|-------------------------|---|
| 12 | 240 | Hoek (1888) |
| 14 | 160 | Hoek (1888) |
| 18 | 168 | Cassou-Leins & Cassou-Leins (1981) |
| 19 | 96 | Pouchet & Bietrix (1889a); Ehrenbaum (1936) |
| 20 | 126 | Cassou-Leins & Cassou-Leins (1981) |
| 20-21 | 80 | Hoestlandt (1958) |
| 22 | 96 | Cassou-Leins & Cassou-Leins (1981) |
| 23 | 84 | Cassou-Leins & Cassou-Leins (1981) |
| 24-25 | 65 | Hoestlandt (1958) |

Hoestlandt (1958) mentions that at temperatures below 16°C the larvae die in the eggs. At temperatures below 18°C the larvae are not in good condition and have difficulty in emerging from the egg (Cassou-Leins & Cassou-Leins, 1981). The upper survival limit would appear to be *c.* 26°C, with all eggs dying at a temperature $\geq 26.3^\circ\text{C}$ (Cassou-Leins & Cassou-Leins, 1990).

At hatching the larvae measure between 7 and 12 mm (L_t) [Vincent, 1894b; Hoestlandt, 1958; Wheeler, 1969a; Cassou-Leins & Cassou-Leins, 1981; Veron *et al.*, 2003]. The larvae are transparent with few chromatophores, a well-developed yolk sac and large pigmented eyes. The gill arches bear short gill filaments and are clearly visible, as are the otoliths and the auditory vesicle - the caudal fin contains primary rays (Pouchet & Bietrix, 1889a; Cassou-Leins & Cassou-Leins, 1981; Quignard & Douchement, 1991a). The change in certain morphometric characteristics through development are shown in Table 3.22, scales first appear in the lateral anteroventral part at a L_{st} of 20-25 mm, in the caudal part at a length of 25-27 mm and in the anterodorsal part at 25-31mm (Bergot *et al.*, unpublished).

Table 3.22: Ontogenetic change in certain morphometric characteristics of *Alosa alosa*, measured as a percentage of standard length (Mean \pm SD) [Bergot *et al.*, unpublished].

| Life stage | L _{st} (mm) | Snout length (%) | Eye Diam. (%) | Predorsal length (%) | Preal length (%) | Caudal fin length (%) | Body height (%) |
|--------------|----------------------|------------------|---------------|----------------------|------------------|-----------------------|-----------------|
| Larvae | 8.8 \pm 0.2 | 2.5 \pm 0.3 | 4.8 \pm 0.4 | 59.0 \pm 2.3 | 81.7 \pm 0.8 | 3.4 \pm 0.8 | 10.9 \pm 0.8 |
| | 15.0 \pm 0.5 | 3.4 \pm 0.9 | 6.3 \pm 0.5 | 57.9 \pm 2.1 | 80.6 \pm 0.7 | 9.4 \pm 1.1 | 12.8 \pm 1.4 |
| Pre-juvenile | 16.8 \pm 0.4 | 3.3 \pm 0.9 | 7.0 \pm 0.6 | 56.1 \pm 1.1 | 78.7 \pm 1.1 | 12.2 \pm 1.6 | 14.4 \pm 1.0 |
| | 20.5 \pm 0.1 | 5.6 \pm 0.7 | 7.9 \pm 0.2 | 52.3 \pm 1.0 | 73.7 \pm 0.4 | 15.2 \pm 1.4 | 15.7 \pm 0.9 |
| Juvenile | 23.0 \pm 0.5 | 5.3 \pm 0.4 | 9.0 \pm 0.8 | 49.0 \pm 1.8 | 70.8 \pm 0.7 | 16.7 \pm 1.3 | 18.9 \pm 1.6 |
| | 40.8 \pm 0.9 | 5.8 \pm 0.7 | 8.6 \pm 0.7 | 44.8 \pm 2.0 | 69.9 \pm 0.6 | 20.0 \pm 1.4 | 25.6 \pm 0.8 |

Alosa fallax fallax

Vincent (1894b) reported that eggs could successfully develop between 15 and 25°C. Incubation takes 72 to 120 h at 16.4°C (Ehrenbaum, 1894) and 96 to 120 h at 19°C (Pouchet & Bietrix, 1889b; Vincent, 1894b; Mohr, 1941; Wheeler, 1969a).

No pigmentation is present on the embryo or yolk sac, though in the latter stages of development the eye capsules become heavily pigmented (Aprahamian, 1982). At hatching larvae measure between 4 and 9 mm (total length) (Vincent, 1894b; Ehrenbaum, 1894, 1936; Redeke, 1939; Mohr, 1941; Aprahamian, 1982). At hatching the yolk sac is slightly oval, with a number of oil droplets scattered through it, and there is a very slight pigmentation of the ventral and posterior regions of the yolk sac as well as the ventral region of the larvae (Aprahamian, 1982).

Morphometric indices (mean \pm 95% CI, in relation to total length) for newly hatched larvae are; standard length 0.968 \pm 0.0032; snout to anus 0.788 \pm 0.0069; yolk sac 0.217 \pm 0.012; snout to back of head 0.125 \pm 0.0056; snout to back of eye 0.072 \pm 0.0037 and eye diameter 0.050 \pm 0.0025 (Aprahamian, 1982).

Ehrenbaum (1894) and Mohr (1941) have described the juvenile stages (Figure 3.15) and have been reported by Quignard & Douchement (1991b) in quotes, as follows:

“ The 8-9 mm stage – 6 days old:

- The yolk sac is being resorbed;
- The gill arches are visible, not covered completely by the very tiny operculum;
- The unpaired fins are not distinguishable in the primordial finfold. The rays of the caudal fin are beginning to appear.
- The pectoral fins are rather large and already have fleshy bases;
- Star-shaped chromatophores are distributed on the ventral sides of the gut, yolk sac and body, even beyond the anus which is situated in a very posterior position on the body;
- The head is relatively short and blunt, with large dark eyes.

The 13-15 mm stage – 15 to 20 days old:

- The place of the fully resorbed yolk sac is taken by a rather elongated liver which bears a small gall bladder;
- The swim bladder is hardly distinguishable;
- The operculum is still rather small, and a large part of the gills is still uncovered;
- Otoliths, one large and one small are visible within the auditory organ;
- The dorsal fin, with 10-12 rays, is already well developed. Though difficult to see, the rays of the primordial anal fin are growing. The pelvic fins are present as skin folds only and, like the dorsal fin, very posteriorly situated. The pectoral fins have shown no change.

The 16-20 mm stage:

- The fish has already assumed its typical shape;
- The swim bladder is visible, dorsal to the gut and anterior to the base of the dorsal fin;
- The dorsal and anal fin rays can be counted;
- Although it is externally symmetrical, a heterocercal development of the caudal fin is apparent;
- It is possible to count the vertebrae;
- Teeth are evident on the upper and lower jaws.”

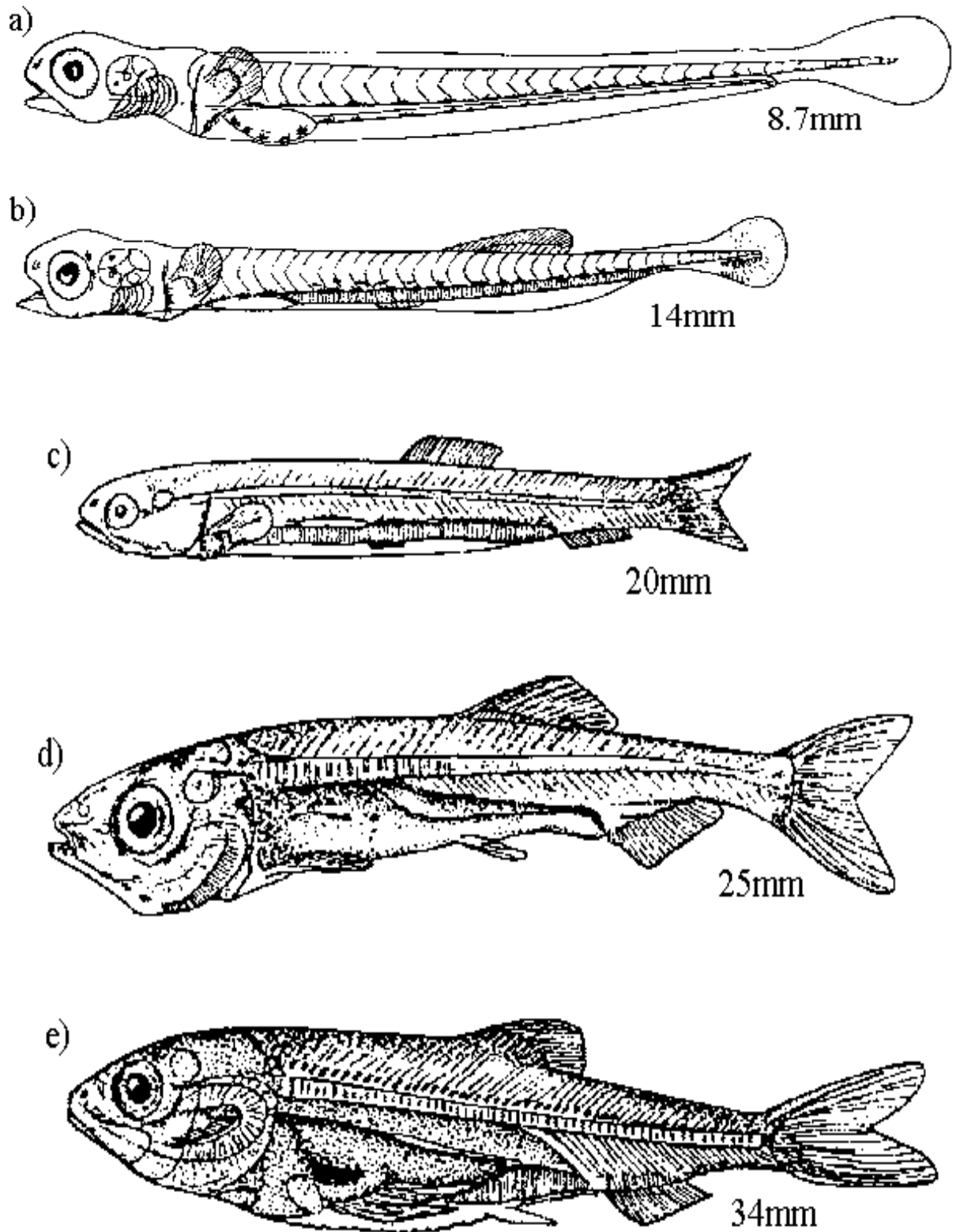


Figure 3.15: Diagrams of twaite shad from Quignard and Douchement (1991b) from the figures of Ehrenbaum (1894) and Mohr (1941); (a) pro-larva six days after hatching, (b) and (c) post-larvae, (d) transitional larva, (e) juvenile.

The level of pigmentation appears dependent on location; those from heavily turbid waters of the Severn Estuary, England had little or no pigmentation compared with those from the relatively clear freshwater reaches of the River Wye, Wales which were heavily pigmented (Aprahamian, 1982).

The migration anteriorly of the dorsal and anal fins occurs at a fork length of between 25 to 28 mm as the larvae transform into a fully metamorphosed juvenile (Aprahamian, 1982). Scales completely cover the body once the juveniles have reached a total length of 30 to 32 mm (Mohr, 1941).

Alosa fallax rhodanensis

Hoestlandt (1947) reported that the eggs do not hatch at temperatures less than 18°C. Hatching takes 96 h at 18 to 20°C (Chiappi, 1933a) and 80 h at 20.5 to 23.5°C (Hoestlandt, 1947). At hatching the larvae measure 7mm (Chiappi, 1933a; Hoestlandt, 1947). Larval development has been described by Chiappi (1933a) (Figure 3.16 a-c).

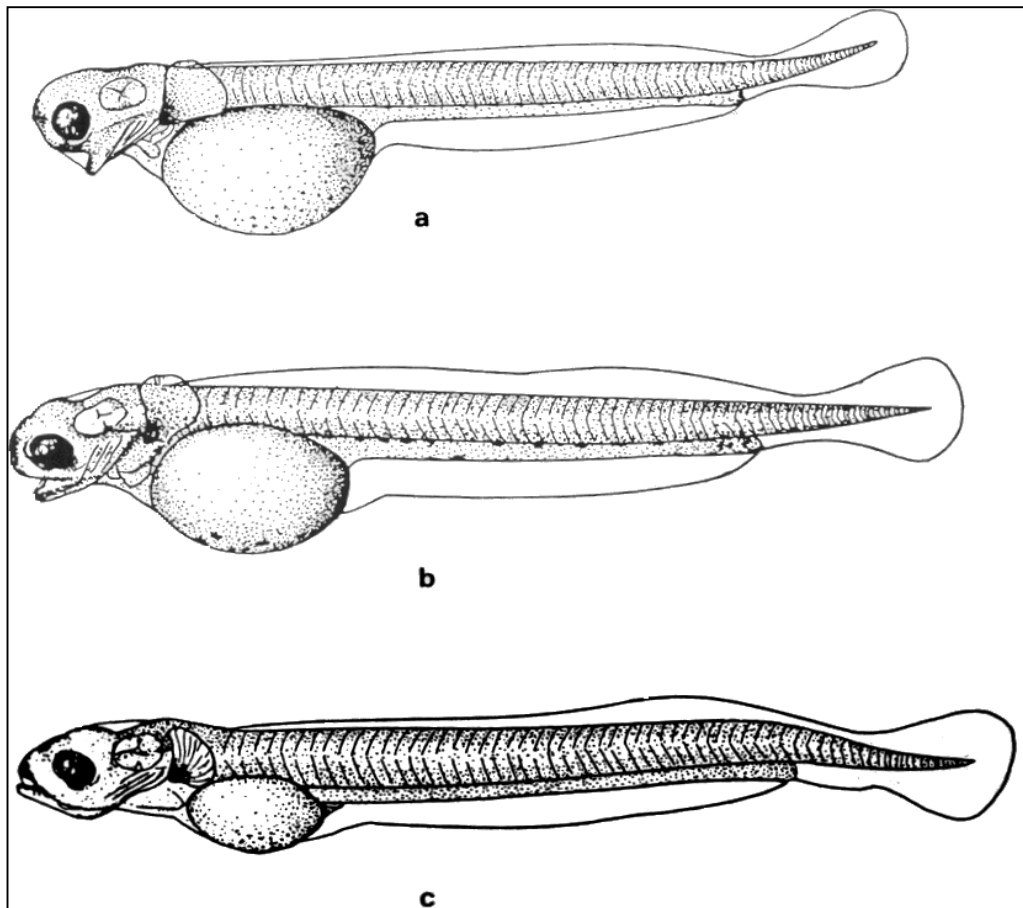


Figure 3.16: Immature stages of *Alosa fallax rhodanensis*, from Quignard & Douchement (1991c) from the figures of Chiappi (1933a). (a) newly hatched larva of 7mm; (b) 7.8mm larva, four to five days after hatching; (c) six days after hatching.

At hatching the larvae have a well-developed yolk sac. Chromatophores are present on the yolk sac and on the dorsal and ventral surface of the gut, and absent from the post-anal area. The pectoral fins are approximately twice the diameter of the eye. Hoestlandt (1947) reported that the yolk sac becomes completely absorbed 24h after hatching, however Chiappi (1933a) observed that the yolk sac, though partly resorbed, was still present six days after hatching.

Alosa fallax lacustris

The time from fertilisation to hatching takes *c.* 115 h at 17 to 20°C (A. Negri, pers. comm. in Luzzana *et al.*, 1996) and 75 to 96 h at 20 to 24°C (Pirola, 1930; Chiappi, 1933a) and could be described by the equation:

$$\text{Hatching time (hours)} = 1800 / \text{Temperature (}^{\circ}\text{C)} \quad (\text{Pirola, 1930}).$$

The larvae are 6.5 to 7.0 mm in length at hatching (Pirola, 1930; Chiappi, 1933a). The yolk sac on newly hatched larvae is small (Figure 3.17a) and is fully absorbed by the time the larvae have reached 7 to 8 mm (Figure 3.15b). At hatching the pectoral fins are small and are approximately equal in length to that of the radius of the eye. Chromatophores are most abundant on the dorsal surface but are also present on ventral surface, the head, and the post-anal region (Chiappi, 1933a).

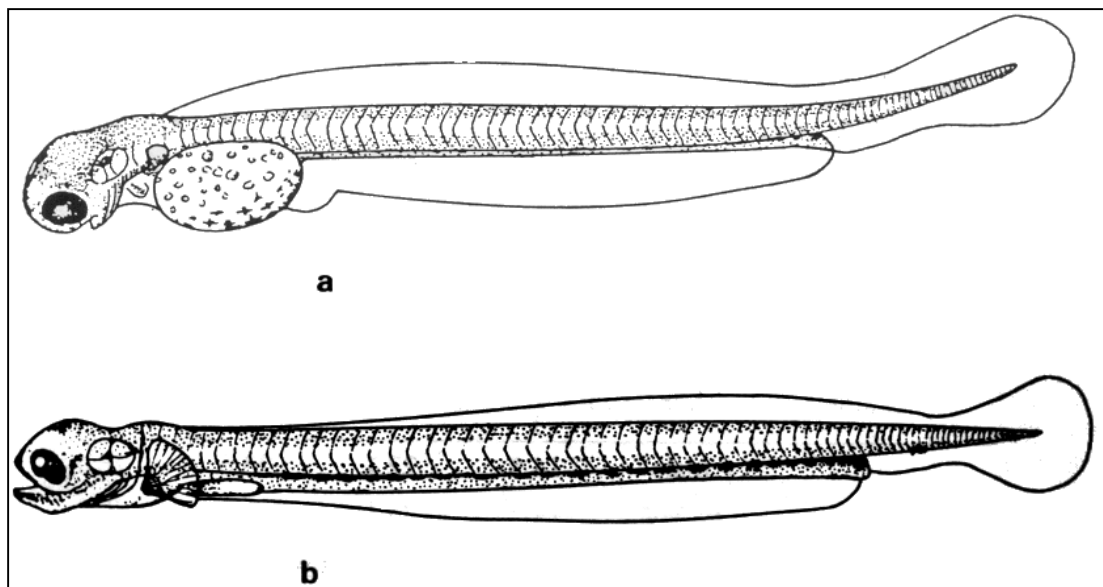


Figure 3.17: Juvenile stages of *Alosa fallax lacustris*, according to Chiappi (1933a). (a) just hatched, length 6.5mm; (b) four days after hatching, length 7mm.

3.2.2 Larval and juvenile (age 0) phase

Alosa alosa

Laboratory studies (Veron *et al.*, 2003) indicate that prolarvae swim actively to the surface on hatching. During the first 48 hours the prolarvae would swim to the surface, then sink passively towards the bottom before returning again to the surface. After this phase and until day 19 the larvae showed a preference for the top 50mm of the water column. After this the proportion at the surface decreased as larvae started to use a greater proportion of the water column, there was also an increase in larvae drifting downstream.

In the wild the larvae, after hatching, migrate transversely into areas of lower current velocity where the juvenile stages can be found from mid-May until mid September (Cassou-Leins *et al.*, 1988a).

Alosa fallax fallax

In the Elbe estuary twaite shad spawn along the southern shore of the main channel over a distance of *c.*12 km (Dieckwisch, 1987). The larvae ($L_t = 7.7-23.8$ mm) on the other hand were more abundant in the side-channels, which because of their slower currents compared to the main channel, were considered to be better nursery and feeding areas (Gerkens & 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 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 mgL⁻¹), the majority being caught in water of between 4 and 5 mgO₂L⁻¹ (Möller & Scholz, 1991).

3.3 Adult Phase

The adult phase starts when the fish reach sexual maturity (see section 3.1.2 Maturity).

3.3.1 Longevity

Alosa alosa

The maximum age observed for females of anadromous populations of *Alosa alosa* is 8 years and for males 7 years (Sabatié, 1993; Prouzet *et al.*, 1994a). Differences existed between populations, but it is unclear whether they reflect actual population differences or sampling effects. In the Adour and Sebou the maximum age recorded for females was 8 years (Sabatié, 1993; Prouzet *et al.*, 1994a), in the Loire, Gironde-Garonne-Dordogne, Lima and Mondego 7 years was the oldest observed (Anon. 1979a; Mennesson-Biosneau & Boisneau, 1990; Alexandrino, 1996b) while in the Aude, Rhône, Douro and Loukos the greatest age recorded was 6 years (Douchement, 1981; Eiras, 1981b; Sabatié, 1993). The maximum age for males was the same as for females in the Gironde-Garonne-Dordogne, Lima and Douro (Anon. 1979a; Eiras, 1981b; Alexandrino, 1996b). It was one year younger in the Loire, Adour and Loukos

(Mennesson-Boisneau & Boisneau, 1990; Sabatié, 1993; Prouzet *et al.*, 1994a) and 2 years younger in the Sebou (Sabatié, 1993).

The maximum age recorded for landlocked populations was 5 years in the Aguieira reservoir on the Mondego (Collares-Pereira *et al.*, 1999) and in El Kansera on the Sebou (Furnestin, 1952). In the Aguieira reservoir the maximum age reported was 5 years for females and 4 years for males (Collares-Pereira *et al.*, 1999) while for both sexes in Castelo do Bode reservoir on the Tejo the oldest fish were aged 4 years (Alexandrino, 1996b).

Alosa fallax fallax

The oldest fish (female) recorded were 12 years of age taken from the Severn (Mennesson-Boisneau, *et al.* 2000a). Females up to the age of 9 years have been reported from the Nyamunas, from Holland and the Wye (Manyukas, 1989; Aprahamian, 1982 & unpubl.) and up to 8 years old from the Elbe, Tywi and Adour (Hass, 1965; Aprahamian, unpubl.). The oldest female recorded in the Barrow was 7 years (O'Maoileidigh, 1990), while in the Loire, Gironde-Garonne-Dordogne, Guadiana and Sebou age 6 was the maximum (Anon. 1979a; Douchement, 1981; Sabatié, 1993; Alexandrino, 1996). Females of age 5 were the oldest reported fish from the Seine, Lima, Mondego, Tejo and Loukos (Roule, 1922a; Sabatié, 1993; Alexandrino, 1996b).

The oldest male fish recorded was 10 years old from the Severn (Aprahamian, unpubl.). Males of 9 years old were reported from Holland (Aprahamian, 1982) and fish of up to 8 years old from the Elbe, Wye, Tywi and Barrow (Hass, 1965; O'Maoileidigh, 1990; Aprahamian, unpubl.) and up to 7 years old on the Nyamunas (Manyukas, 1989). In the Loire, Gironde-Garonne-Dordogne, Adour, Lima, Mondego, Guadiana, Loukos and Sebou males aged 5 years were the oldest recorded (Douchement, 1981; Sabatié, 1993; Alexandrino, 1996b), while in the Tejo fish aged 4 years is the maximum (Alexandrino, 1996b).

A latitudinal cline exists with fish at the northern limit of their range living longer, between 7 and 12 years compared to those at the southern limit where longevity of 5 or 6 years appears normal (Figure 3.18). The fact that the fish live longer further north and that there is little difference in the age at which fish mature (Table 3.2) would suggest that the proportion of repeat spawners in the population should increase with latitude.

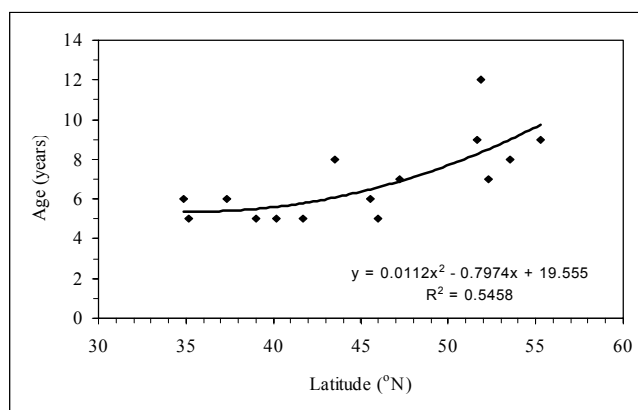


Figure 3.18: Longevity of various populations of female *Alosa fallax fallax* in relation to latitude; see Table 3.47 for sources of data.

Alosa fallax rhodanensis

The maximum age of female *Alosa fallax rhodanensis* recorded was age 9 years in the Tiber (D'Ancona, 1927c) while in the Rhône and Aude the oldest fish was 8 years old (Douchement, 1981; Le Corre *et al.*, 1997a). The longevity for males is 8 years in the Rhône and Tiber (D'Ancona, 1927c; Le Corre *et al.*, 1997a) and 5 years in the Aude (Douchement, 1981).

Alosa fallax nilotica

The oldest fish recorded for both sexes was 10 years old from the Neretva (Vukovic, 1961a). Female *Alosa fallax nilotica* from the lakes Skadar and Bačín had a maximum age of 10 and 9 years respectively and the males a year younger (Vukovic, 1961a). In the Po (Italy) the maximum age for both sexes was 7 years (Serventi *et al.* 1990).

Alosa fallax algeriensis

In the Miliane and Medjerah the oldest fish recorded was 9 years, for both sexes, while in Lake Ichkeul the maximum age recorded for males and females was 7 years (Kartas, 1981). In the Mazafran, Bounhiol (1917) reported the oldest fish for both sexes was aged 5 years.

Alosa fallax lacustris

For the populations in lakes Garda and Maggiore the maximum age of both sexes is 4 years (Berg & Grimaldi, 1966a; Oppi & Novello, 1989). Bianco (2002) reported longevity of up to 5 – 6 years for *Alosa fallax lacustris* from Italian fresh waters.

Alosa fallax killarnensis

In Lough Leane the oldest fish reported was aged 5 years for females and 4 for males (O'Maoileidigh, 1990).

3.3.2 Hardiness

No information was found relating to hardiness.

3.3.3 Competition

Alosa fallax lacustris

Berg & Grimaldi (1966b) studied the relationship between *Alosa fallax lacustris* and *Coregonus macrophthalmus* Nusslin in Lake Maggiore (Italy). Any competition between the two species was small and relates mainly to the lack of overlap in the food spectrum in spring and autumn, when food is more limiting than in summer. *Alosa fallax lacustris* prey on copepods as opposed to cladocerans, which are consumed by the coregonids. Any interaction is further limited by the fact that the species are spatially segregated. During the winter the coregonids live nearer the shore and in summer occupy the cooler deeper waters of the lake, whereas *A. fallax lacustris* remain in open

water all year round, preferring the warmer surface layers during the summer. In addition at temperatures lower than 14°C *Alosa fallax lacustris* feed less than *C. macrophthalmus*. *Alburnus alburnus alborello* (bleak), which are present in the lake also feed on copepods, the larger cladocerans, and on algae, insects and the smaller cladocerans (Giussani & Grimaldi, 1975).

Similar findings have been reported for the sympatric populations of alosoids, coregonids and *A. alburnus alborello* in Lake Garda, and for *A. fallax lacustris* and *A. alburnus alborello* in Lake Lugano (Giussani & Grimaldi, 1975). In Lake Como the diet of *A. fallax lacustris*, *Coregonus* spp. and *A. alburnus alborello* was dominated by the larger cladoceran species (Giussani & Grimaldi, 1975).

3.3.4 Predators

Alosa alosa

Le Clerc (1941) reported that yearling *Alosa alosa* in the River Maine, France were preyed upon by *Alburnus alburnus*.

Alosa fallax fallax

On the River Wye, Wales Gough (pers. comm.) [cited by Edwards & Brooker, 1982] found that *Esox lucius* L. had been feeding on adult *Alosa fallax*. Otters (*Lutra lutra*) have also been found to predate on adult *Alosa fallax fallax* in fresh water.

In the Sado estuary (Portugal) *Alosa fallax* form an important prey item of the bottlenose dolphin (*Tyrsiops truncatus*) [Dos Santos & Lacerda, 1987].

3.3.5 Parasites and disease.

3.3.5.1 Parasites

Alosa alosa and *Alosa fallax*

The species of parasite recorded from *Alosa alosa* and the various subspecies of *Alosa fallax* are presented in Table 3.23a-f. Most of those parasites reported from anadromous *Alosa* populations in the western Atlantic, have been reported from both *A. alosa* and *A. fallax*. Exceptions are *Pomphorhynchus laevis* and *Caligus elongatus* which have been found in *A. fallax* from the River Severn, England (Aprahamian, 1985), and *Mazocraes harengi* which have only been reported from *A. alosa* in southern England (Baylis & Jones, 1933), and *M. vilelai* from the River Tego, Portugal (Tendeiro & Valdez, 1955).

Table 3.23: Parasites recorded from *Alosa alosa*, *A. fallax fallax*, *A. fallax nilotica*, *A. fallax rhodanensis*, *A. fallax algeriensis* and *A. fallax lacustris*.

a) Anadromous populations of *Alosa alosa*

| Family | Site of infection | Species | Location of record and reference |
|------------------|-------------------|---|---|
| Copepoda | Gills | <i>Clavellisa emarginata</i> (Krøyer, 1837) | North Sea (Boxshall, 1974) Gironde-Garonne-Dordogne, France (Taverny, 1991a) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | Body | <i>Lernaeeniscus encrasicoli</i> (Turton, 1807) | Not Recorded (Markevich, 1956; Kabata, 1979) |
| Cestoda | Pyloric caeca | <i>Scolex pleuronectis</i> (Rudolphi, 1802) syn. <i>Scolex polymorphus</i> | Holland (Willemse, 1968) |
| | | <i>Eubothrium fragile</i> (Rudolphi, 1802) | Rhine, Switzerland (Fatio, 1890) Europe (Yamaguti, 1959) Not Recorded (Protasova, 1977) |
| | Intestine | <i>Eubothrium fragile</i> (Rudolphi, 1802) | Baltic, North & Irish sea (Joyeux & Baer, (1936) |
| Monogenea | Gills | <i>Mazocraes alosae</i> (Herman, 1782) syn. <i>Octobothrium lanceolatu</i> (Euckart, 1828) | Severn, Wye, Plymouth, Britain (Finlayson, 1981) Rhine, Switzerland (Fatio, 1890) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Not Recorded (van Beneden, 1858; Sproston, 1946; Yamaguti, 1968) |
| | | <i>Mazocraes harengi</i> (Beneden & Hesse, 1863) | Plymouth, England (Yamaguti, 1963) |
| | | <i>Mazocraes vilelai</i> (Tendeiro & Valdez, 1955) | Tejo, Portugal (Tendeiro & Valdez, 1955) |

| | | | |
|-----------------------------|--------------------------------------|--|--|
| Digenea | Intestine | <i>Hemiurus appendiculateus</i> (Rudolphi, 1802) | Griande-Garonne-Dordogne, France (Taverny, 1991a) Rhine, Switzerland (Fatio, 1890) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Europe (Yamaguti, 1971); Not Recorded (Dawes, 1947) |
| | | <i>Pronoprymna venticosa</i> (Rudolphi, 1819) | Belgian Coast, Rhine at Basle and Celtic Sea (Bray & Gibson, 1980) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | | <i>Pronopyge ocreata</i> (Rudolphi, 1802) | Rhine, Switzerland (Fatio, 1890) |
| | Stomach | <i>Hemiurus appendiculateus</i> (Rudolphi, 1802) | Rhine, Switzerland (Fatio, 1890) |
| | Eye | <i>Diplostomum gasterostei</i> Williams | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | | <i>Diplostomum spathaceum</i> Rudolphi | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| Nematoda | Intestine and stomach | <i>Hysterthylacium aduncum</i> (Rudolphi, 1802) syn. <i>Thynnascaris aduncum</i> syn. <i>Contraeaecum aduncum</i> | North Sea (Punt, 1941) Baltic (Markowski, 1937) Rhine, Switzerland (Fatio, 1890) Griande-Garonne-Dordogne, France (Taverny, 1991a) Tejo, Portugal (Almaça, 1988a) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Not Recorded (Yamaguti, 1961) |
| | | <i>Hysterthylacium osculatum</i> | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | | <i>Agamonema capsularia</i> (Rudolphi, 1802) | Rhine, Switzerland (Fatio, 1890) |
| Acantho- cephala | Intestine | <i>Rhadinorhynchus lintoni</i> (Cable & Lindroth, 1963) syn. <i>Echinorhynchus subulatus</i> (Zeder, 1800) | Rhine, Switzerland (Fatio, 1890) |
| | | <i>Echinorhynchus alosae</i> (Hermann, 1782) | Rhine, Switzerland (Dujardin, 1845) |
| | | <i>Pomphorhynchus tereticollis</i> (Rudolphi, 1809) | Not Recorded (Golvan, 1969) |

b) *Alosa fallax fallax*

| Family | Site of infection | Species | Location of record and reference |
|------------------|-----------------------------|--|---|
| Copepoda | Gill arches & pseudobranch | <i>Clavellisa emarginata</i> (Krøyer, 1837) | Severn, England (Aprahamian, 1985) Gironde-Garonne-Dordogne, France (Taverny, 1991a) Rhine, Germany (Hoek, 1899; Redeke, 1939) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Not recorded (Fatio, 1890; Brian, 1906; Scott & Scott, 1913; Mohr, 1941; Kabata, 1979; Fryer, 1982) |
| | Skin | <i>Caligus elongatus</i> (Nordmann, 1833) | Severn, England (Aprahamian, 1985) |
| Cestoda | Pyloric caeca/ intestine | <i>Scolex pleuronectis</i> (Muller, 1788) syn. <i>Scolex polymorphus</i> (Rudolphi, 1810) | Holland (Willemse, 1968) |
| | Intestine | <i>Eubothrium fragile</i> (Rudolphi, 1802) | Severn, England (Kennedy, 1978; Kennedy, 1981; Andersen & Kennedy, 1983; Aprahamian, 1985) North & Irish seas (Joyeux & Baer, 1936); Baltic Sea (Nybelin, 1922; Joyeux & Baer, 1936) Rhine, Germany (Hoek, 1899); Holland (Willemse, 1968) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Not recorded (Mohr, 1941; Protasova, 1977) |
| Monogenea | Gills | <i>Mazocraes alosae</i> (Hermann, 1782) syn. <i>Octobothrium lanceolatum</i> | Severn, Wye, Britain (Finlayson, 1981; Aprahamian, 1985) Plymouth, England (Sproston, 1946; Finlayson, 1981) Gironde, Garonne, Dordogne, France (Taverny, 1991a) Rhine, Germany (Hoek, 1899; Redeke, 1939) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Not recorded (Mohr, 1941; Yamaguti, 1968) |

| | | | |
|-----------------------|-----------------------|---|--|
| Digenea | Intestine | <i>Hemiurus appendiculatus</i> (Rudolphi 1802) | Severn, England (Aprahamian, 1985) Gironde, Garonne, Dordogne, France (Taverny, 1991a) Rhine, Germany (Hoek, 1899; Redeke, 1939) Holland (Willemse, 1968) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) Atlantic coast of Africa & Portugese coast (Rodrigues <i>et al.</i> , 1972) Not recorded (Mohr, 1941) |
| | | <i>Pronopyge ocreata</i> (Rudolphi 1802) | Not recorded (Dawes, 1947) |
| | | <i>Pronoprymna ventricosa</i> (Rudolphi 1819) | Severn, England (Aprahamian, 1985) NE. Atlantic, Severn, Scarborough, England (Bray & Gibson, 1980) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| Nematoda | Eye | <i>Diplostomum gasterostei</i> Williams | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | | <i>Diplostomum spathaceum</i> Rudolphi | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | Stomach and Intestine | <i>Hysterthylacium aduncum</i> (Rudolphi 1802) syn. <i>Contracaecum aduncum</i> syn. <i>Thynnascaris aduncum</i> | North Sea, (Punt, 1941) Fjords near Bergen & Tromso, Norway (Berland, 1961) Baltic Sea (Markowski, 1937) NE Atlantic, N. Europe seas (Petter & Cabaret, 1995) Severn, England (Aprahamian, 1985) Gironde-Garonne-Dordogne, France (Taverny, 1991a) Rhine, Germany (Hoek, 1899; Redeke, 1939) Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| | | <i>Hysterthylacium osculatum</i> | Waterford Estuary, Ireland (Doherty & McCarthy, 2002) |
| Acanthocephala | Intestine | <i>Rhadinorhynchus lintoni</i> (Cable & Linderoth, 1963) | Sebou, Morocco (Golvan, 1969) |
| | | <i>Pomphorynchus laevis</i> (Muller, 1776) | Severn, England (Aprahamian, 1985) |

c) *Alosa fallax nilotica*

| Family | Site of infection | Species | Location of record and reference |
|-----------------------|----------------------------|---|--|
| Copepoda | Gill arches & pseudobranch | <i>Clavellisa emarginata</i> (Krøyer, 1837) | Black Sea (Markevich, 1952) Not recorded (Tortonese, 1970) |
| | Skin | <i>Caligus minimus</i> (Otto, 1848) | Not recorded (Tortonese, 1970) |
| | Eyes | <i>Pseudoeucanthus alosea</i> (Brian, 1906) | Not recorded (Tortonese, 1970) |
| Digenea | Stomach Intestine | <i>Hemiurus appendiculateus</i> (Rudolphi, 1802) | Adriatic Sea (Nikolaeva, 1966) L.Skadar, Montenegro (Kazic & Cankovic, 1969; Ubelaker <i>et al.</i> , 1981) |
| | | <i>Hemiurus lühei</i> (Rudolphi, 1802) syn. <i>Hemiurus ocreatus</i> (Looss, 1879) | Split, Adriatic Sea (Sey, 1968) |
| | | <i>Orientophorus petrowi</i> (Layman, 1930) | L.Skadar, Montenegro (Kazic & Cankovic, 1969; Ubelaker <i>et al.</i> , 1981) |
| | Intestine | <i>Pronopyge ocreata</i> (Rudolphi, 1802) | Trieste, Italy (Yamaguti, 1971) |
| | | <i>Distoma catervarium</i> (Loss, 1896) | Egypt (Yamaguti, 1971) |
| Cestoda | Intestine | <i>Eubothrium crassum</i> (Bloch, 1779) | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) |
| | | <i>Ligula intestinalis</i> (Linnaeus, 1758) | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) |
| | | <i>Proteocephalus</i> (Weinland, 1858) spp. | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) |
| Nematoda | Stomach & intestine | <i>Hysterothylacium aduncum</i> (Rudolphi 1802) | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) Split, Adriatic Sea (Sey, 1970) |
| | | <i>Rhabdochona</i> sp. | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) |
| | | <i>Contracaecum clavatum</i> (Rudolphi, 1809) | Split, Adriatic Sea (Sey, 1970) |
| | | <i>Goezia ascaroides</i> (Goeze, 1782) | Montenegro (Moravec & Ergens, 1971) |
| | | <i>Raphidascaris acus</i> (Bloch, 1779) | Montenegro (Moravec & Ergens, 1971) |
| Acanthocephala | Intestine | <i>Pomphoryncus bosniacus</i> (Kiskaraj & Cankovic, 1968) | L.Skadar, Montenegro (Ubelaker <i>et al.</i> , 1981) |

d) *Alosa fallax rhodanensis*

| Family | Site of infection | Species | Location of record and reference |
|-----------------|---------------------|---|---|
| Nematoda | Stomach & intestine | <i>Hysterothylacium aduncum</i> (Rudolphi 1802) | Western Mediterranean (Petter & Maillard, 1987) |

e) *Alosa fallax algeriensis*

| Family | Site of infection | Species | Location of record and reference |
|-----------------|----------------------------|--|---|
| Copepoda | Gill arches & pseudobranch | <i>Ergasilus nanus</i> (Van Beneden, 1871) | Lake Ischkaul, Tunisia (Raibaut <i>et al.</i> , 1971) |

f) *Alosa fallax lacustris*

| Family | Site of infection | Species | Location of record and reference |
|----------------|-------------------|--|---|
| Cestoda | Intestine | <i>Proteocephalus agonis</i> (Barbieri, 1909) Syn. <i>Ichthyotaenia agonis</i> | Lake Maggiore , Italy (Pecorini, 1959) |
| | | <i>Proteocephalus longicollis</i> (Zeder, 1800) Syn. <i>Ichthyotaenia longicollis</i> | Lake Maggiore , Italy (Pecorini, 1959) |

In terms of distribution, *Eubothrium fragile* would appear to have a limited distribution compared with that of its host. It has only been reported from *Alosa* in England (Kennedy, 1978 & 1981; Anderson & Kennedy, 1983), Ireland (Doherty & McCarthy, 2002), Holland (Willemse, 1968), Germany (Redeke, 1939) and the Baltic North and Irish seas (Nybelin, 1922; Joyeux & Baer, 1936), but not from populations south of the Bay of Biscay.

Older fish are more heavily infected than juveniles (Claridge & Gardner, 1978; Quignard & Douchement, 1991b), and this is certainly the case for *Mazocraes alosae* (Finlayson, 1981; Aprahamian, 1985) and *Eubothrium fragile* (Kennedy, 1981), where infection is only evident in the adult population.

- Spatial or temporal differences

Spawning migration into fresh water has been reported to have effects on parasites, by a number of authors (Kennedy, 1981; Aprahamian, 1985; Taverny, 1991a). For *A. fallax* migration into fresh water does not appear to affect the relative density or the prevalence of *Eubothrium fragile*, *Hemiurus appendiculatus* and *Pomphorhynchus laevis*. However, for *Clavellisa emarginata* and *Hysterothylacium* (syn. *Thynnascaris*) *aduncum*, prevalence and relative density were both found to have declined in fresh water when compared with pre-spawning fish in the estuary or at sea (Table 3.24 & 3.25). In contrast for *A. alosa* there was a decline of 58.5% in the prevalence of *H. appendiculatus* and an increase of nearly 40% for *H. aduncum* for fish from the Gironde-Dordogne-Garrone system (Table 3.25).

Table 3.24: Prevalence and relative density of parasites from the branchial chamber and alimentary tract of adult *Alosa fallax fallax* taken in the Severn estuary and fresh water (Aprahamian, 1985).

| Parasite | Estuary | | | Fresh water | | |
|--|----------------|------------------|-----|----------------|------------------|----|
| | Prevalence (%) | Relative density | N | Prevalence (%) | Relative density | N |
| <i>Mazocraes alosae</i> | 77.7 | 13.4 | 112 | 78.9 | 4.5 | 57 |
| <i>Clavellisa emarginata</i> | 30.4 | 2.5 | 112 | 12.3 | 1.2 | 57 |
| <i>Thynnascaris aduncum</i> ¹ | 64.3 | 13.2 | 42 | 11.4 | 0.3 | 35 |
| <i>Hemiurus appendiculatus</i> | 88.1 | 5.2 | 42 | 77.1 | 5.8 | 35 |
| <i>Pronoprymna ventricosa</i> | 95.0 | * | 20 | 100 | * | 11 |
| <i>Pomphorhynchus laevis</i> | 10.0 | 0.3 | 20 | 9.1 | 0.3 | 11 |
| <i>Eubothrium fragile</i> | 54.5 | 1.1 | 33 | 69.6 | 1.0 | 23 |

¹ *Hysterothylacium aduncum* (Rudolphi 1802); * Numerous, relative density not determined.

Both *A. alosa* and *A. fallax* appear to become infected with *Hemiurus appendiculatus* and *Hysterothylacium aduncum* during the marine phase of their life history (Table 3.25).

The prevalence of infection of *H. aduncum* for both juvenile and adult *A. fallax* caught at sea (Table 3.25b) and from fish caught at the start of their spawning migration (Table 3.24) was c. 60%. This is approximately twice that reported by Hillman (2002) of

25.7% (n=35) for adult twaite shad caught at sea around the South West Coast of England between January and April.

Table 3.25: The prevalence of infection of a) *Hemiurus appendiculateus* and b) *Hysterothylacium aduncum* in *Alosa alosa* and *A. fallax* in relation to life stage and location, sample size in brackets (Taverny, 1991a).

a) *Hemiurus appendiculateus*

| Life stage | Location | <i>Alosa alosa</i> | <i>Alosa fallax</i> |
|----------------------|-------------|--------------------|---------------------|
| Juvenile (age 2 & 3) | Estuary | 53.6% (28) | 53.8% (39) |
| Juvenile & Adult | Sea | 87.0% (171) | 94.5% (174) |
| Adult | Fresh water | 28.5% (35) | 91.0% (21) |

b) *Hysterothylacium aduncum*

| Life stage | Location | <i>Alosa alosa</i> | <i>Alosa fallax</i> |
|----------------------|-------------|--------------------|---------------------|
| Juvenile (age 2 & 3) | Estuary | 3.57% (28) | 0.0% (39) |
| Juvenile & Adult | Sea | 55.5% (171) | 61.0% (174) |
| Adult | Fresh water | 94.5% (35) | 32.0% (21) |

- Inter- and intra-specific differences

In the marine environment, Taverny (1991a) reported the existence of a higher relative density of *Hemiurus appendiculateus* in *Alosa fallax* than in *Alosa alosa* (90.9 individuals per fish in *A. fallax* compared with 40.9 for *Alosa alosa*). In contrast, Doherty & McCarthy (2002) found a greater prevalence and abundance of *H. appendiculateus* in *A. alosa* compared with *A. fallax*.

Alosa fallax contained a higher relative density and prevalence of *P. ventricosa* and the eye parasites (*D. gasterostei* and *D. spathaceum*) compared with *A. alosa* and *E. fragile* were only reported from *A. fallax* (Doherty & McCarthy, 2002). Taverny (1991a) observed little difference in the densities of *Hysterothylacium aduncum* between species: 16.6 individuals per fish for *A. fallax* and 11.2 for *A. alosa*.

An assessment of the relative density of *Hysterothylacium aduncum* and *Hemiurus appendiculateus* in *A. fallax* from the Bay of Biscay (Taverny, 1991a) and Severn Estuary (Aprahamian, 1985) indicated that the relative densities of *Hysterothylacium aduncum* were similar: 16.6 individuals per fish (Bay of Biscay) compared with 13.2 (Severn Estuary). However, the relative density of *Hemiurus appendiculateus* was substantially higher in the marine environment; 90.9 compared with 5.2 individuals per fish in the Severn Estuary. This may reflect differences in the infection rate and/or abundance of prey organisms, or alternatively it may relate to the fact that the population on the Severn was not actively feeding, having commenced the freshwater phase of their spawning migration.

A comparison between *A. fallax* caught in fresh water on their spawning migration indicated a higher intensity and prevalence of *M. alosae* and *H. aduncum* in fish from

the River Barrow when compared with those from the River Severn (Table 3.26). The levels for *C. emarginata* were similar while the prevalence of *H. appendiculatus* was higher in the Severn (Table 3.26).

Table 3.26: Prevalence and relative density of parasites from adult *A. fallax* from freshwater reaches of the River Barrow (Doherty & McCarthy, 2002) and the River Severn (Aprahamian, 1985).

| Parasite | Barrow (Ireland) | | | Severn (England) | | |
|----------------------------------|------------------|------------------|----|-------------------|------------------|----|
| | Prevalence (%) | Relative density | N | Prevalence (%) | Relative density | N |
| <i>Mazocraes alosae</i> | 100.0 | 43.4 | 60 | 78.9 | 4.5 | 57 |
| <i>Clavellisa emarginata</i> | 25.0 | 2.6 | 60 | 12.3 | 1.2 | 57 |
| <i>Diplostomum gasterostei</i> | 21.7 | 1.3 | 60 | Eyes not examined | | |
| <i>Diplostomum spathaceum</i> | 90.0 | 10.5 | 60 | | | |
| <i>Hysterthylacium aduncum</i> | 81.7 | 36.9 | 60 | 11.4 | 0.3 | 35 |
| <i>Hysterthylacium osculatum</i> | 63.3 | 7.6 | 60 | Not detected | | 35 |
| <i>Hemiurus appendiculatus</i> | 25.0 | 5.6 | 60 | 77.1 | 5.8 | 35 |
| <i>Pronoprymna ventricosa</i> | 100.0 | 353.1 | 60 | 100.0 | Not counted | 11 |
| <i>Pomphorhynchus laevis</i> | Not detected | | 60 | 9.1 | 0.3 | 11 |
| <i>Eubothrium fragile</i> | 58.3 | 1.1 | 60 | 69.6 | 1.0 | 23 |

More than 80% of juvenile (age 0+) *A. alosa* living in the estuary of the Sebou (Morocco) had Hemiurid spp. present in their stomachs (Sabatié, 1993). This is higher than that reported by Taverny (1991a) for juvenile *A. alosa* in the Gironde estuary (Table 3.25A), and by Doherty & McCarthy (2002) from the Waterford estuary (Ireland) of 41.7% for *A. alosa* (L_t 386-504 mm).

The spawning of *A. fallax* and the presence of *M. alosae* have been shown to be closely synchronised (Bychowsky, 1957). Table 3.27 shows the relative density and prevalence of *M. alosae* in relation to various life stages of *A. fallax* from the Severn Estuary, England (Aprahamian, 1985). Fish spawning for the first time were relatively lightly infected in contrast to the repeat spawners, who had a 100% infection and a significantly heavier burden (Figure 3.19). This may explain the higher prevalence and level of infection reported by Doherty & McCarthy (2002) for fish from the River Barrow compared to that observed by Aprahamian (1985) in the Severn (Table 3.26).

Table 3.27: The relative density and prevalence of *M. alosae* between juvenile (age 0 + & 1+) *A. fallax*, adult *A. fallax* on their first spawning migration, and from repeat spawners (Finlayson, 1981; Aprahamian, 1985).

| Life stage | Relative Density (range) | Prevalence (%) |
|----------------------|--------------------------|----------------|
| Juvenile (age 0+&1+) | 0.0 (0-0) | 0.0 |
| First time spawners | 1.5 (0-18) | 54.5 |
| Repeat spawners | 24.8 (2-83) | 100 |

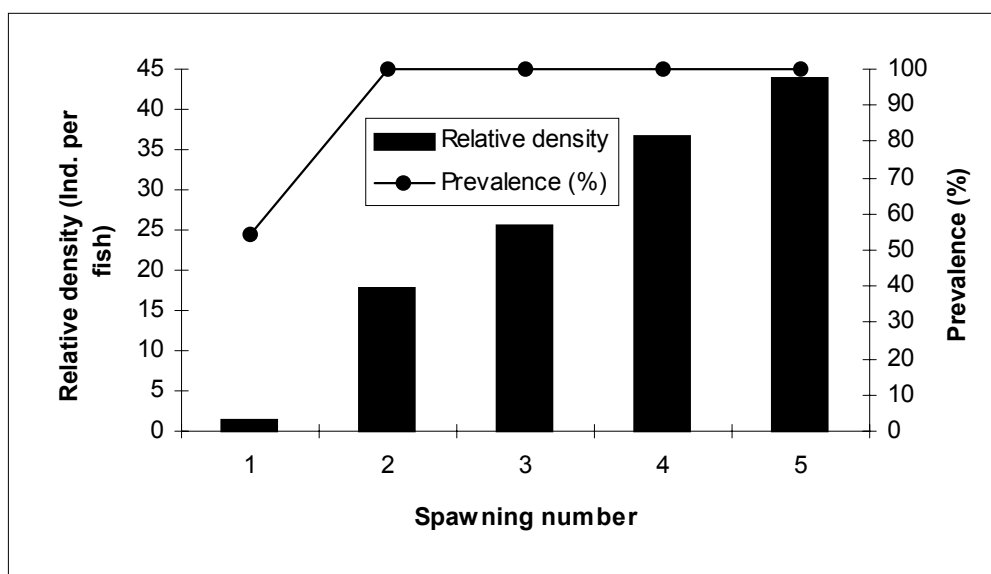


Figure 3.19: The relative density of *Mazocraes alosae* found in samples of *Alosa fallax fallax* from the Severn estuary in relation to the number of previous spawnings of individual fish (from Aprahamian, 1985).

3.3.5.1 Disease

Alosa fallax lacustris

Vogel (1903) reported the occurrence of the bacterium *Colibacillosis alosa fintae* in specimens of *Alosa fallax lacustris* in Lake Lugano (Italy). Fish that were infected with the bacterium did not feed or try to escape when handled. They had also lost their sense of balance, and the rear portion of the body was paralysed. The body organs, anus and cloaca were inflamed and small tumour-like thickenings were present on the gills and fins. Infected fish had a higher respiration rate (90 to 96 times min^{-1}) than healthy fish (28 to 36 times min^{-1}).

3.4 Nutrition and Growth

3.4.1 Feeding

3.4.1.1 Food intake

Alosa fallax fallax

The daily ration of 0+ *A. fallax* in the Elbe estuary decreased with fish size from 45% of their body weight (wet) per day in May to a minima of 1.3% in December for 0+ fish (Oesmann & Thiel, 2001). The daily ration for 1+ fish was lower at between 5 and 6 % day^{-1} , part of the difference may be related to size but also to the lower temperatures prevalent in 1993 (Figure 3.20).

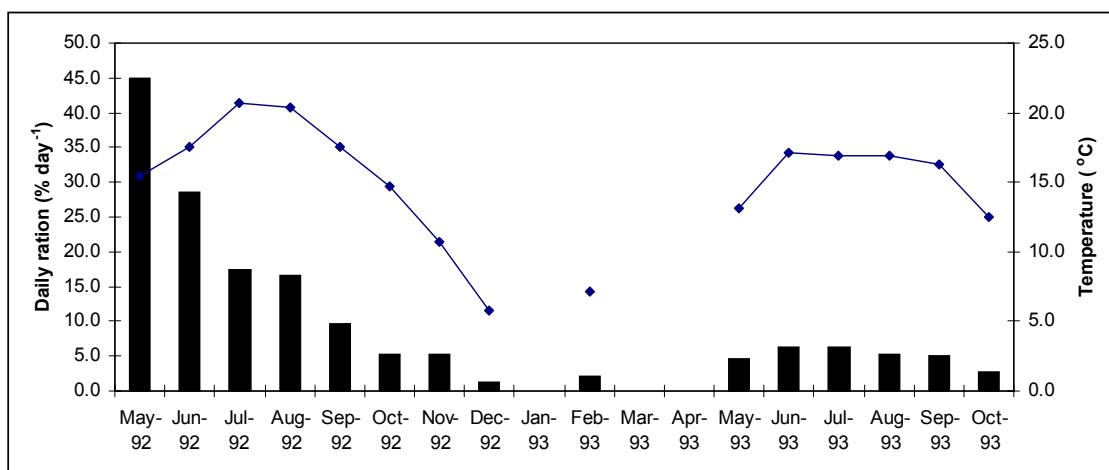


Figure 3.20: Winberg's (1956) daily ration and mean water temperature of the 1992 year class of *A. fallax* from the Elbe Estuary (Reproduced from Oesmann & Thiel, 2001).

3.4.2 Food

3.4.2.1 Diet of larvae

Alosa fallax fallax

In the freshwater reaches of the River Wye (Wales) the diet of the larvae (mean L_f 22.2 \pm 0.4 mm) was dominated by Uniramia, particularly the orders Ephemeroptera and Diptera. The Diptera, specifically the families Chironomidae (pupae and larvae) and Simuliidae (larvae), accounted for more than 80% (by number) of all the food items recorded (Aprahamian, 1989).

In relation to time of day, Esteves (pers. comm.) reported no diurnal pattern in feeding activity for larvae (4.65 – 18.10 mm L_{st}) from the Mira estuary, Portugal.

3.4.2.2 Diet of juveniles

Alosa alosa

In fresh water, the diet of the juvenile anadromous *Alosa alosa* (32 to 112mm L_t) consisted mainly of insects from the Order Ephemeroptera, Trichoptera, Diptera (in particular Chironomidae, both adult and larval stages) and Hemiptera (specifically Corixidae) (Wheeler, 1969a; Cassou-Leins & Cassou-Leins, 1981; Dautrey & Lartigue, 1983; Sabatié, 1993).

Cassou-Leins & Cassou-Leins (1981) observed that in the River Garonne (France), the main feeding activity occurred between 1000 and 2200 h. Diet was dominated by Diptera between 1000 and 1800 h and by Ephemeroptera between 2200 and 1000 h (Figure 3.21).

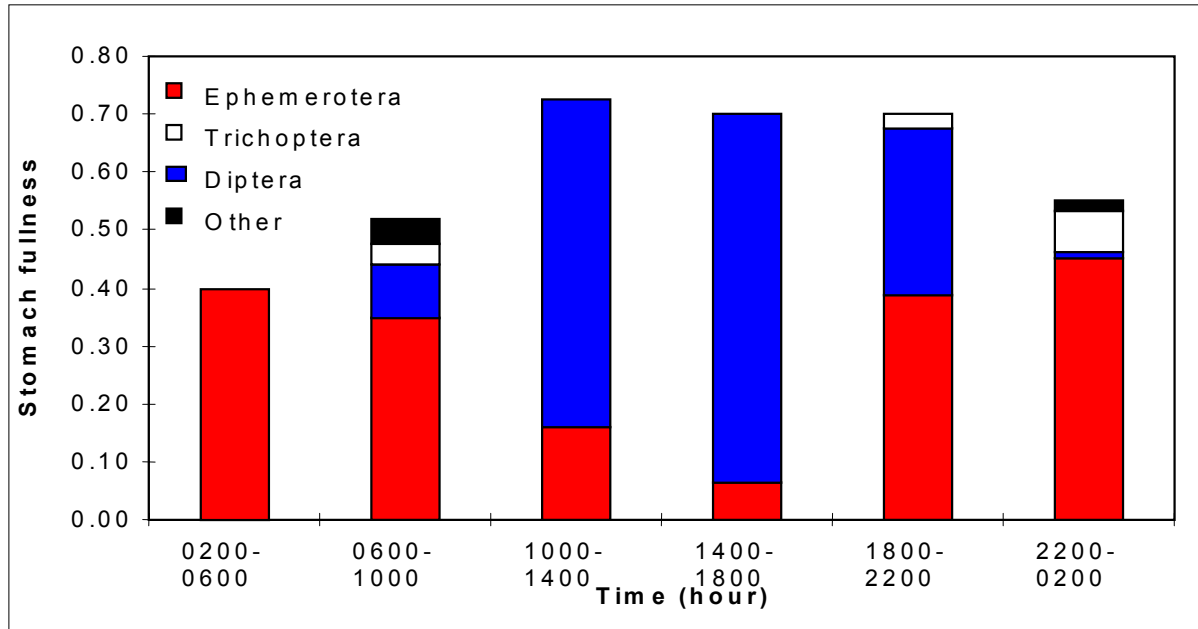


Figure 3.21: Diet of juvenile *Alosa alosa* from the River Garonne (France) in relation to time of day (Cassou-Leins & Cassou-Leins, 1981).

In relation to size, Cassou-Leins & Cassou-Leins (1981) reported that *A. alosa*, less than 40mm in length, fed equally on Ephemeroptera and Diptera, while those greater than 40mm fed primarily on Ephemeroptera and secondarily on Diptera. Trichoptera were only consumed by fish larger than 40mm. In the Sebou (Morocco), Sabatié (1993) found that only those alosids over 60mm in length fed on adult insects, specifically from the Order Hymenoptera.

Juvenile *Alosa alosa* (ranging in total length from 50 to 115mm) caught in estuarine waters fed mainly on crustaceans, particularly those from the orders Isopoda, Amphipoda and Mysidacea, and from the Class Copepoda (Anon., 1979a (in Taverny, 1991a); Sabatié, 1993). Ehrenbaum (1936) and Mohr (1941) also reported that juvenile *A. alosa* included the larvae of *Clupea harengus* in their diet.

A detailed description of the diet of immature (>0+) *Alosa alosa* at sea (Table 3.28) has been reported by Taverny (1991a) and is similar to that reported by Poll (1947), Bracken & Kennedy (1967), Wheeler (1969a), Quero (1984) and Maitland & Lyle (1991c).

In the Bay of Biscay euphausiids were the preferred prey item through out the year followed by copepods, the other prey items were consumed infrequently, fish became

more important in the diet during the summer and autumn months (Taverny & Elie, 2001b).

Table 3.28: Stomach contents of *Alosa alosa* (181-538 mm L_t) from the Bay of Biscay, France (Taverny, 1991a).

| Phylum | Class | Order | Species |
|-----------|---------------|----------------------------|---|
| Algae | Rhodophyceae | | <i>Rhodymenia palmata</i> |
| | Chlorophyceae | | <i>Ulva lactuca</i> |
| Crustacea | Malacostraca | Calanoidea | <i>Calunus helgolandicus</i> <i>Calunus</i> spp. <i>Aetideus armatus</i> <i>Candacia armata</i> <i>Diaxis pigmaea</i> |
| | | Mysidacea | <i>Gastrossacus</i> spp. <i>Mysis</i> spp. <i>Sphaeroma rugicauda</i> or <i>S. monodi</i> <i>Nyctiphanes couchi</i> |
| | | Isopoda | |
| | | Euphausiacea Gammaridae | |
| Mollusca | Bivalvia | Mytiloidea | <i>Mytilus</i> spp. (veliger stage) |
| | Cephalopoda | Sepioidea | <i>Sepiola atlantica</i> |
| Chordata | Osteichthyes | Clupeiformes | <i>Sprattus sprattus</i> <i>Engraulis encrasicolus</i> |

In brackish water close to estuaries, *A. alosa* fed mainly on Crustacea; Calanoidea (*Eurytemora affinis* Pope), Mysidacea (*Neomysis vulgaris* Thomps) and Amphipoda (*Corophium grossipes* L.) [Ehrenbaum, 1936; Mohr, 1941]. In the Waterford estuary (Ireland), the diet of *Alosa alosa* measuring between 386 and 504 mm (L_t) consisted of the marine mysid *Pranus neglectus* (G.O.Sars) and the fish species *Merlangus merlangus* (L.), *Sprattus sprattus* and *Osmerus eperlanus* L., and a small quantity of the shrimp *Crangon allmani* Kinahan (Doherty & McCarthy, 2002).

Alosa fallax fallax

In fresh water the diet of juvenile (age 0+) *Alosa fallax fallax* has been reported from the River Wye, Wales (Aprahamian, 1989) and from the River Sebou, Morocco (Sabatié, 1993). In both systems diet was dominated by Uniramia, particularly the orders Ephemeroptera, Diptera and Trichoptera. The main groups of Diptera found were Chironomidae (all life stages), and, in the Wye, the larval stage of Simuliidae. In the Sebou the juveniles were also found to consume fish larvae, Decapoda (*Atyaephira desmarestii*) and adult insects from the Order Hymenoptera. Planktonic Crustacea (Copepoda and Cladocera) were not found to be a significant food source in the freshwater reaches of either river system. For those fish ranging in size from 35 to 115 mm (L_t) there was no significant change in diet with size (Sabatié, 1993).

In the Severn estuary, the diet of the 0+ age group was dominated by the Crustacea Harpacticoida (mainly *Tachidius discipes* and a few *Microarthridion*) and Mysidacea

(*Neomysis integer*), followed by Gammaridae and Calanoidea (*Eurytemora affinis*) [Aprahamian, 1989]. The smaller members of the zooplankton (Copepoda; Harpacticoida and Calanoidea, and Cladocera; Daphnidae and Chydoridae) were more prominent in the diet during July and August than in September and October. In the autumn months the larger Crustacea members of the zooplankton; Mysidacea (*N. integer*), Amphipoda (*Gammarus zaddachi*, *G. salinus* and *Corophium volutator*) and Isopoda (*Eurydice pulchra*) together with fish species predominated. This may be a function of size (the mean size of juvenile *A. fallax* in July and August being 32.5 ± 1.2 mm (L_f) compared with 50.2 ± 2.5 mm in September and October), or it may reflect variation in the abundance of prey organisms.

In the Elbe estuary the diet in July was similarly dominated by copepods in terms of number (83%), but in terms of biomass fish dominated the diet (46%), followed by insects (32%), mysids (15%), plants (4%) and copepods (2%) [Oesmann & Thiel, 2001]. In August mysids (*N. integer*, *Mesopodopsis slabberi*) dominated the diet in terms of both number and biomass, followed by fish (*Sprattus sprattus*, *Osmerus eperlanus*, *Pomatoschistus* spp.) with a significant relationship between diet and fish size. The proportion of fish and *N. integer* in the diet increased and of *M. slabberi* and copepods decreased with fish size. *A. fallax* showed a preference for *M. slabberi* and *S. sprattus* larvae, cladocerns were consumed according to their availability and *O. eperlanus*, *Pomatoschistus* spp, *C. crangon*, *N. integer* and copepods were negatively selected (Figure 3.22).

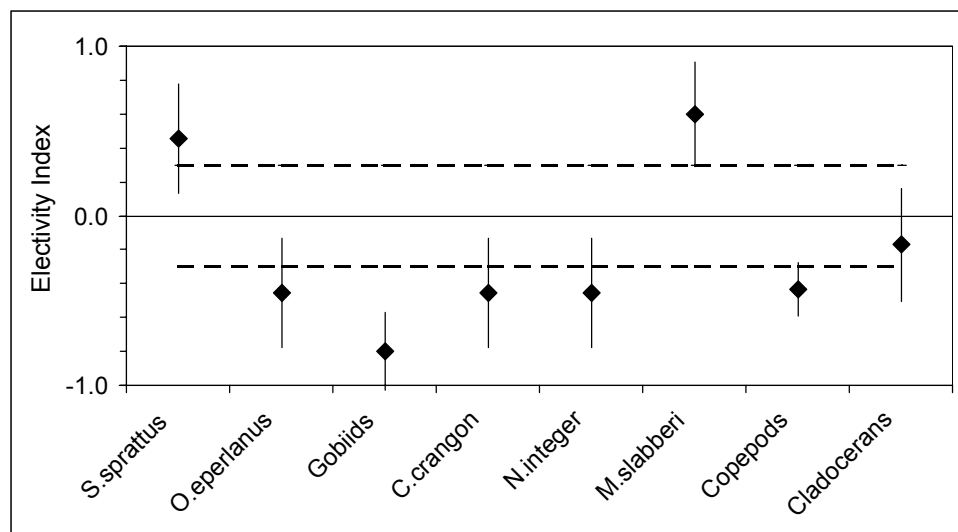


Figure 3.22: Daily mean of Ivlev's (1961) electivity index with regard to the main food items in the stomachs of age 0+ *A. fallax* from the Elbe Estuary between July 8th –9th 1993. Bars: confidence limits; broken lines: levels of significance according to Lazzaro (1987) [Reproduced from Oesmann & Thiel, 2001].

In the estuary of the Sebou, juvenile fish (55 to 105 mm (L_t)) fed primarily on Crustacea, (Amphipoda, Mysidacea, Isopoda and Decapoda (*Palaemon longirostris garciadii* and *P. varians*)) and consumed few of the smaller crustacean members of the zooplankton (Copepoda) (Sabatié, 1993). Also consumed, though infrequently, were Uniramia, (Diptera (adult Chironomidae), Hymenoptera) and fish.

Sabatié (1993) found that fish between 60 and 80 mm in length fed primarily on Isopoda (Gnathidae) and secondarily on Decapoda (Palaemonidae), while those between 80 and 100 mm fed almost exclusively on Palaemonidae. In the Gironde estuary (France) Uniramia were a much more important component of the diet in juvenile fish between 50 and 100 mm (total length) than in fish between 30 and 50 mm. In the smaller size range the diet consisted mainly of Uniramia and Crustacea (Mysidacea) and allochthonous plant material (Anon., 1979a in Taverny, 1991a).

The diet of fish (age 1) in the Elbe estuary was dominated by copepod eggs and copepodids, 96% and 4% in terms of number, respectively; copepods dominated the biomass (49%), followed by detritus (26%), mysids (10%) and plant material (10%) [Oesmann & Thiel, 2001]. In the outer Severn Estuary in May their diet was dominated by Gammaridae followed by Calanoidea (Arahamian, 1989). However, during June and August the fish fed mainly on Mysidacea (*Neomysis integr*) followed by Gammaridae and fish (*Sprattus sprattus* and members of the Gobiidae).

At sea immature fish, between 50 and 130 mm in length possessed a similar diet of Mysidacea, Copepoda and 0+ Clupeidae and Gobiidae (Svetovidov, 1963; Wheeler, 1969a).

- Diurnal and tidal effects

Diurnal and tidal effects on diet have been reported by Oesmann & Thiel (2001) and Arahamian (1988), respectively. In the Elbe Estuary fish dominated the diet during the day, their importance declining during the night (Figure 3.23). During dusk and dawn mysids became more important. At night insects dominated the diet with copepods (*Eurytemora affinis*) increasing in significance towards the end of the night / early morning (Oesmann & Thiel, 2001). The diurnal change in composition may reflect a change in feeding behaviour from particulate feeding during the day on the larger food items (fish and mysids) to filter feeding on insects and copepods during the night.

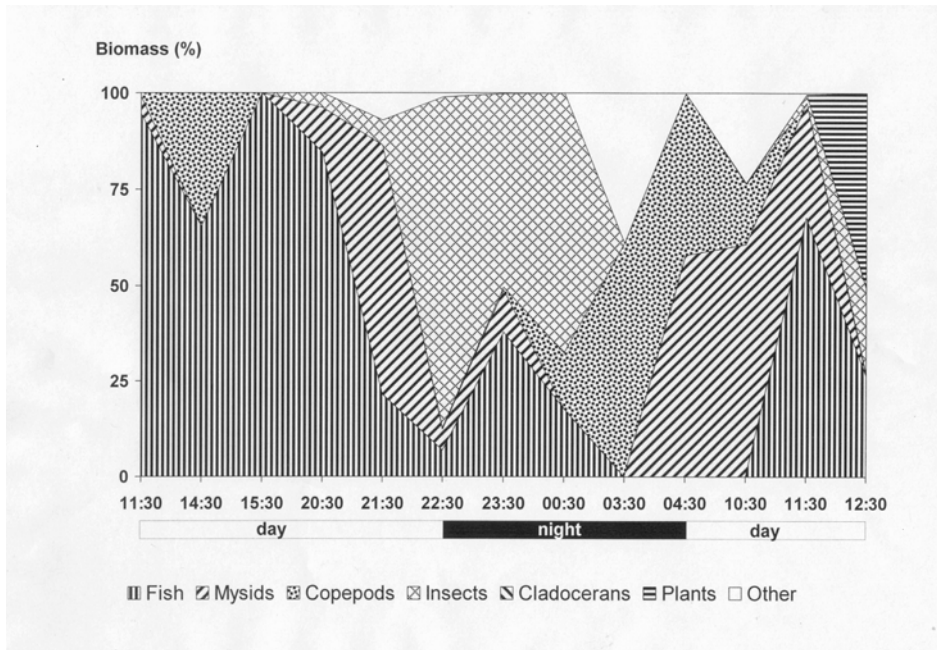


Figure 3.23: Diet (% biomass) of age 0 *A. fallax* shad in the Elbe Estuary during a 24 h period between 8th and 9th July 1993 (Oesmann & Thiel, 2001).

The influence of tidal height on the diet of juvenile (0+) *A. fallax fallax* in the Severn Estuary is shown in Figure 3.24. On spring tides the diet was almost equally dominated by Harpacticoidea copepods and Mysidacea, while under neap tides the Mysidacea were absent from the diet which was dominated by Harpacticoidea copepods (Aprahamian, 1988).

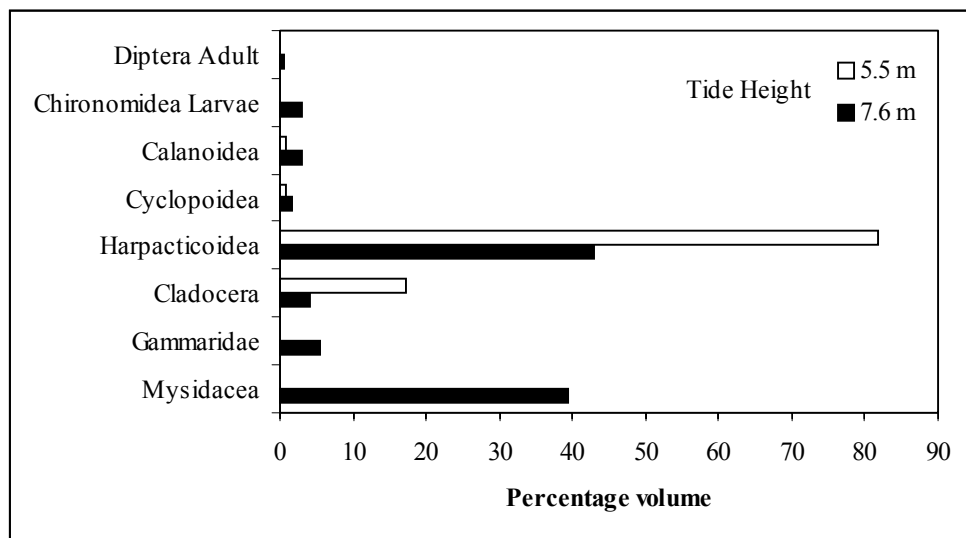


Figure 3.24: The diet of juvenile (0+) *Alosa fallax fallax* from the Severn Estuary (England) in relation to tidal height (Aprahamian, 1988).

- **Size effects**

The influence of size can be seen from Figure 3.25. The diet of one year old fish (L_f 96.6 ± 2.73 mm) from the Severn Estuary (England) was dominated by Mysidacea, and did not include smaller members of plankton. In contrast the Copepoda and Cladocera constituted *c.*50%, in terms of volume, of the diet of the 0+ age-class (L_f 32.5 ± 1.2 mm).

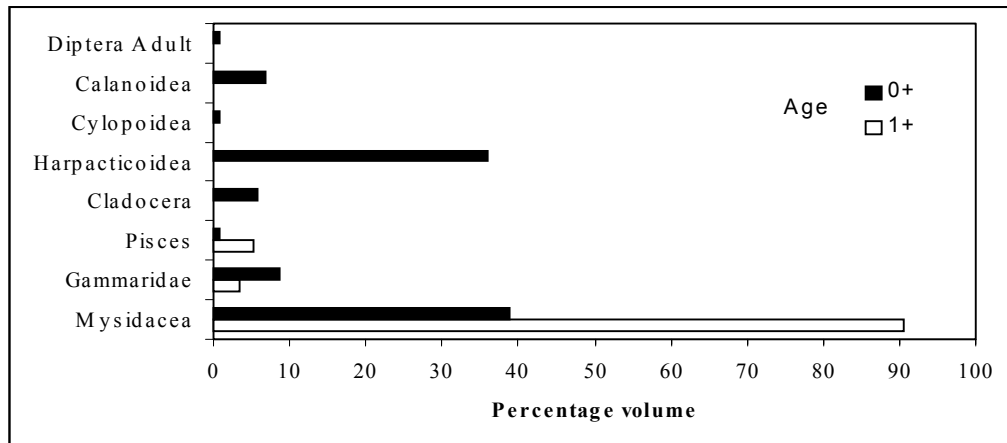


Figure 3.25: The diet of *Alosa fallax fallax* age 0+ (July and August) and 1+ (June to August) from the Severn Estuary, England (Aprahamian, 1989). [Only includes those food items that constituted >1% by volume.]

Alosa fallax rhodanensis

In the River Tiber, Italy, juveniles (40 to 90 mm) in length fed on Crustacea, which included Arthropoda and Uniramia (D'Ancona, 1928a). In the Rhône, Genoud (1999a) reported the diet from two fish (99&106 mm L_t). The fish consumed Simuliidae adults, Ephemeroptera and fish larvae.

Alosa fallax nilotica

Vukovic (1961a) described the diet of 0+ fish from Lake Skadar and 1+ fish from Lake Baćin (Table 3.29). The diet of those aged 0+ consisted of Crustacea (Branchiopoda and Copepoda), Uniramia (Diptera) and Rotifera, as well as plant material, particularly Algae from the phylums Euglenophyta, Chrysophyta, Chlorophyta and Bacillariophyta. In contrast the 1+ *A. fallax nilotica* fed mainly on Crustacea and Rotifera and Algae from the Phylum Dinophyta. This difference may reflect the larger fish size or it may be that the other species of algae were not present in Lake Baćin.

Table 3.29: Diet of 0+ *A. fallax nilotica* from Lake Skadar and 1+ *A. fallax nilotica* from Lake Bačin (Vukovic, 1961a).

| Phylum | Class | Order | Species consumed by 0+ <i>A. fallax nilotica</i> from Lake Skadar | Species consumed by 1+ <i>A. fallax nilotica</i> from Lake Bačin |
|-------------------------------------|------------------------------|------------------------------|---|--|
| Cyanophyta (Blue-green Algae) | | | <i>Microcystis flos aqua</i> <i>M.aeruginosa</i> | |
| Euglenophyta (Green Algae) | | | <i>Euglena</i> spp. | |
| Chrysophyta (Golden-brown Algae) | | | <i>Dinobryon</i> spp. | |
| Chlorophyta (Green Algae) | | | <i>Oocystis solitaria</i> <i>Scenedesmus</i> spp. <i>Pediastrum</i> spp. <i>Mougeotia</i> spp. <i>Spirogyra</i> spp. | |
| Bacillariophyta (Diatoms) | | | <i>Amphora ovalis</i> <i>Pleurosigma</i> spp. <i>Nitschia</i> spp. | |
| Dinophyta (Dinoflagellates) | | | | <i>Ceratium hirundinella</i> |
| Rotifera | | | <i>Asplanchna priodnta</i> <i>Polyarthra trigla</i> <i>Tetramastix opoliensis</i> <i>Notholca longispina</i> | <i>Asplanchna priodnta</i> <i>Brachionus falcatus</i> |
| Crustacea | Branchiopoda Copepoda | Cladocera Cyclopoidea | <i>Daphnia longispina</i> <i>D.cuclata</i> <i>Leptodora kindti</i> <i>Sida cristalina</i> <i>Cyclops</i> spp. <i>Mesocyclops leukarti</i> <i>Eudiaptomus gracilis</i> | <i>Daphnia longispina</i> <i>Diaphanasoma brachyurum</i> <i>Bosmina longirostris</i> <i>Moina</i> spp. <i>Cyclops</i> spp. <i>Canthocamptus staphylinus</i> |
| Uniramia (Insects) | Pterygota | Diptera | Chironomidae (larvae) | |

3.4.2.3 Diet of adults

Alosa alosa

The diet of adult *A. alosa* at sea was similar to that for immature fish.

During the freshwater phase of their spawning migration, adult *A. alosa* do not feed (Eiras, 1981b). In those fish examined, the stomach usually contained a whitish or greenish fluid (Quignard & Douchement, 1991a).

- Landlocked *Alosa alosa*

The diet of the landlocked population of *Alosa alosa* in the Castelo de Bode reservoir (Portugal), was found to consist of Copepoda: *Copidodiaptomus* spp., *Cyclops* spp. and *Acanthocyclops* spp. (Eiras, 1981a). Similar findings were reported by Correia *et al.* (2001) where calanoid copepods (*Dussartius baeticus*) and cladocerans (Family Daphniidae) were preferentially consumed with cyclopoid copepods (*Acanthocyclops* spp.) being of secondary importance. Ostracods, insects and algae were consumed very infrequently.

In Aguieira reservoir (Portugal) cladocerans (Family Daphniidae) and cyclopoid copepods (*Acanthocyclops* spp.) occurred most frequently in the diet of both juvenile and adult *A. alosa* (Correia *et al.*, 2001). Calanoid copepods (*Copidodiaptomus numedicus*) and ostracods are consumed less frequently and insects only rarely. For the adults, calanoid copepods were more important during the autumn and winter months and ostracods during the summer months, but the diet was still dominated by cladocerans and cyclopoid copepods.

Alosa fallax fallax

Pre-spawning adult fish, on their spawning migration into fresh water were not found to be feeding actively (Bracken & Kennedy, 1967; Claridge & Gardner, 1978; Aprahamian, 1989; Doherty & McCarthy, 2002). Where fish had been feeding the total volume of food per feeding fish was low, less than 0.1% that of post-spawning fish (Aprahamian, 1989).

In fresh water, the stomach of those fish that had fed contained plastic, allochthonous plant material and emergent adult Trichoptera, suggesting that the fish had been feeding on relatively large particles in the drift or at the water surface (Bracken & Kennedy, 1967; Aprahamian, 1989).

The diet of post-spawning adult *A. fallax* in the Severn Estuary, England was dominated by Mysidacea (*Neomysis integer*) followed by Gammaridae (*Gammarus zaddachi*) and Crangonidae (*Crangon crangon*), and the occasional fish species (*Platichthys flesus*, *Sprattus sprattus* and Gobiidae) (Aprahamian, 1989). Similarly in the Waterford Estuary (Ireland), Doherty & McCarthy (2002) reported adult *A. fallax* to be feeding almost exclusively on the marine mysid *Praunus neglectus*.

In contrast, in the Tagus Estuary, Portugal, fish species dominated the diet. The main species were *Sardina pilchardus*, *Engraulis encrasicolus*, *Pomatoschistus minutus*, *Pomatoschistus microps* and *Atherina boyeri* (Assis *et al.*, 1992a). Food items which were considered of secondary importance were Mysidacea (*Neomysis integer*), Crangonidae (*Crangon crangon* and *Palaemon* spp.), Isopoda (Gnathiidae, Sphaeromatidae, Idoteidae, Cirolanidae and Limnoriidae) and Uniramia (Diptera, Coleoptera and Lepidoptera). The occasional specimens of Annelida (*Neris diversicolor*), Mollusca: Gastropoda (*Hydrobia ulvae*) and Cephalopoda (*Sepia officinalis*) were also found.

The diet of adult fish in the marine environment consisted of small fish and Crustacea, mainly Mysidacea, Isopoda and Euphausiacea (Murie, 1903; Redeke, 1939; Colette in Mohr, 1941; Rae & Wilson, 1952, 1956a & b, 1961; Rae & Lamont, 1961, 1962a; Svetovidov, 1963; Bracken & Kennedy, 1967; Wheeler, 1969a; Minchin, 1977; Taverny, 1991a).

In the Bay of Biscay, the preferred diet of *Alosa fallax* was fish, in particular *Engraulis encrasicolus* and *Sprattus sprattus*, but also including *Trisopterus luscus* and *Merlangius merlangius merlangus* followed by Euphausiacea (Taverny, 1991a; Taverny & Elie, 2001b). Peak feeding activity from April to December occurred between 4 and 8 hours after sunrise (Taverny & Elie, 2001b). Small fish dominated the diet throughout the year, while Euphausiacea were only a major component during the winter and spring months. Prey size, in particular that of *Engraulis encrasicolus*, increased with the size of *A. fallax* and could be explained by the equation (Taverny, 1991a):

$$Lt_{Ee} = 0.1788 Lt_{Af} + 10.4611 \quad (n = 61; r^2 = 0.25; P < 0.001)$$

Where: Lt_{Ee} = Total length (mm) of *Engraulis encrasicolus*;
 Lt_{Af} = Total length (mm) of *Alosa fallax*.

Similar findings were reported for *A. fallax* caught off the South West coast of England between January and April where their diet was dominated by *Sprattus sprattus* (Hillman, 2002). In contrast, fish caught during the autumn in Cardigan Bay (West Wales) were found to be feeding almost entirely on Mysidacea (*Schistomysis spiritus*), with fish, mainly 0+ Clupeiformes, being of lesser importance (Aprahamian, 1989).

Alosa fallax rhodanensis

Adult fish did not feed on their spawning migration into the River Tiber (D'Ancona, 1928a).

From the Mediterranean Sea around the mouth of the River Tiber, D'Ancona (1928a) found that adult fish, less than 200 mm in length, fed on Crustacea: Amphipoda (*Gammarus pungenis*) and Decapoda (*Palaemonidae* spp.); small fish of the family Engraulidae and Mugilidae, and the larval stages of Uniramia. The diet of those fish less than 200mm in length was similar, and consisted of Crustacea: Amphipoda (*G. pungenis*), Decapoda (larval stages) and Isopoda (*Zenobiana prismatica*, *Idotea basteri*); and small fish of the families Engraulidae, Clupeidae (*Sardina pilchardus*) and Gobiidae.

Alosa fallax nilotica

A significant portion of the sexually mature fish in the Lower Neretva River and in Lake Baćin fed during the spawning period (April to May), with the percentage of stomachs which contained food ranging from 9.1 to 50.0%, and 20.0 and 72.3%, for the Lower Neretva River and Lake Baćin respectively (Vukovic, 1961a). In contrast in Lake Skadar the majority of the fish had empty stomachs, with less than 9.5% of the fish feeding. After spawning all fish commenced feeding.

In fresh water, the diet included fish (Table 3.30); Crustacea: Amphipoda and Decapoda; and Uniramia larvae, specifically of the Order Diptera (Vukovic, 1961a).

Table 3.30: Species of fish consumed by *A. fallax nilotica* from the River Neretva and from lakes Bačin and Skadar (Vukovic, 1961a).

| Family | R. Neretva | Lake Bačin | Lake Skadar |
|-------------|---|---|---|
| Cyprinidae | <i>Alburnus albidus</i> <i>alborella</i> <i>Chondrostoma kneri</i> <i>Leuciscus svallize</i> | <i>Alburnus albidus</i> <i>alborella</i> <i>Chondrostoma kneri</i> <i>Leuciscus</i> spp. | <i>Alburnus scoranza</i> <i>Chondrostoma kneri</i> <i>Scardinius crytrophthalmus</i> <i>scardafa</i> |
| Mugilidae | <i>Mugil</i> spp. | <i>Mugil</i> spp. | |
| Gobiidae | <i>Pomatoschistus microps</i> <i>Gobius</i> spp. | <i>Gobius panizzai</i> <i>Gobius</i> spp. | |
| Poeciliidae | <i>Gambusia</i> spp. | <i>Gambusia</i> spp. | |

The marine diet of *A. fallax nilotica* has been reported by Canestrini (1885), Zompolas (1939) and Morovic (1959). During the winter months fish feed on the sea bottom at depths of 160m, on fish (*Cepola rubescens*, *Gobius* spp., *Brachyochirus pellucidus*, *Smaris vulgaris*, *S. alcedo*, *Box boops*, *Trisopterus capelanus*, *Mullus barbatus*) and Crustacea; Decapoda (*Leander* spp., *Penaeus* spp.) and Mysidacea (*Gastrosaccus normani*, *Anhialina agilis*) [Morovic, 1959]. During the summer months fish feed close to the surface on *Sprattus sprattus*, *Sardina pilchardus*, *Engraulis encrasicolus* and *Atherina* spp. (Canestrini, 1885; Morovic, 1959).

Zompolas (1939) reported similar findings for *Alosa fallax* from both the East and West coasts of Italy and therefore the samples were likely to have contained both *A.fallax rhodanensis* and *A.fallax nilotica*. The diet was found to consist mainly of fish (*Engraulis encrasicolus*, *Sardina pilchardus*, *Cepola rubescens*, *Aphia meridionalis*) and Crustacea; Decapoda (*Leander xiphias*, *Crangon spinosus*, *Pasiphae norvegica*), Mysidacea (*Mysis oculata*) and Ampipoda (*Gammarus pulex*, *G.rhipidiophorus*, *G.duebeni*, *Sextonia longirostris*, *Hyperoche kroyeri*). The fish were also found to have consumed Uniramia larvae (Chironomidae) and Algae. Those fish which were about to enter fresh water for spawning were not found to be feeding actively.

Alosa fallax algeriensis

The adults do not feed during their upstream migration (Kartas, 1981). At sea and while in the estuary, the shad consume small fish (*Engraulis*, *Sardina* and *Sardinella*) and small benthic crustaceans, mainly isopods and amphipods (Dieuzeide *et al.*, 1959; Kartas, 1981).

Alosa fallax lacustris

The diet of *A. fallax lacustris* has been described, for fish greater than 150mm (total length), from the lakes Maggiore, Como, Garda, Iseo and Lugano, (Italy/Switzerland)

by Guccini (1904a&b), Malfer (1907), Barbieri (1908a), Ferrero, (1951), Berg & Grimaldi, (1966b), Grimaldi (1966), Guissani & Grimaldi (1975) and Oppi & Novello (1989). *A. fallax lacustris* were found to predominantly consume plankton, particularly Cladocera and Copepoda, whilst those fish over 300mm (total length) from Lake Maggiore also preyed on fish. The adult fish in Lake Maggiore did not feed during their spawning period in July (Quignard & Douchement, 1991f).

In Lake Maggiore the main species consumed were Cladocera: *Daphnia hyalina*, *Bythotrephes longimanus*, *Leptodora kindti*, *Sida cristallina* and *Diaphanosoma brachyurum*, and Copepoda: *Cyclopidae* spp., *Diaptomidae* spp. and *Heterocope saliens* (Berg & Grimaldi, 1966b; Grimaldi, 1966). In the winter months diet was dominated by Copepoda, the shad then switching to prey on *D. hyalina* during the spring when production was reaching a maximum. At the end of the summer, once production of Cladocera (*D. hyalina* and *B. longimanus*) began to decline, the shad returned to feeding on Copepoda.

Influence of eutrophication on the diet of *A. fallax lacustris* from Lake Lugano has been discussed by Guissani & Grimaldi (1975). The Copepoda were a more significant food source during the spring and summer months in Lake Lugano than the larger Cladocera (*Daphnia hyalina*, *Bythotrephes longimanus*, *Leptodora kindti*), in contrast to the situation in the less productive lakes Maggiore, Como, and Garda.

In Medio Flumendosa Lake, Sardinia, Cottiglia (1969(70)) reported that the adults fed almost exclusively on plankton except during their reproductive period (March to May) when they fed on benthic Decapoda and Uniramia larvae. In Lake Omodeo (Sardinia) their diet consisted entirely of cladocerans and copepods (Cottiglia *et al.*, 1982).

Alosa fallax killarnensis

Very little information exists on the diet of *A. fallax killarnensis*. A sample of fish (L_f 170 to 224mm) were found to contain almost entirely plankton (Table 3.31), specifically Cladocera (*Daphnia longispina*) and Copepoda (Trewavas, 1938; O'Maoileidigh, 1990).

Table 3.31: The stomach contents of 32 *Alosa fallax killarnensis* from Lough Leane (Ireland) caught during June (O'Maoileidigh, 1990).

| Food category | Occurrence (%) | Number (%) |
|---|----------------|------------|
| Crustacea | | |
| Copepoda | 82.1 | 4.76 |
| Branchiopoda -cladocera (<i>Daphnia longispina</i>) | 100.0 | 93.20 |
| Branchiura | 14.3 | 0.02 |
| Uniramia | | |
| Diptera (pupae) | 14.3 | 0.03 |
| Chironomidae (pupae) | 35.7 | 0.06 |
| Ceratopogonidae (pupae) | 7.1 | <0.01 |
| Arachnida | | |
| Hydracarina | 25.0 | 0.03 |
| Osteichthyes | | |
| Clupeiformes | | |
| <i>Alosa</i> (scales) | 17.8 | 0.02 |

The fact that all Uniramia found in the stomach were pupating suggests that they were migrating up through the water column.

3.4.3 Growth rate

The description of growth concentrates mainly on growth in length, as weight varies with nutritional condition and reproductive state. For the mature population weight at age data is presented, where possible, for pre-spawned fish. The effect of spawning on condition and on the relationship between length and weight is discussed in Section 3.5 (Adult spawning migration).

Length has been reported in terms of total length, fork length and standard length. Total length has been adopted as the standard measurement and data was converted using the relationships reported in Douchement (1981).

- Estimation of age

Age has been estimated using both scales and otoliths and their structure has been described in Section 3.1.4, see also Baglinière *et al.* (2001). Scales on the whole are more difficult to interpret than otoliths (Mennesson-Boisneau & Boisneau, 1990) for the following reasons:

- The variability in scale morphology is large when compared to otoliths. However, using scales from the optimum part of the body (above the mid-line and in line with the dorsal fin) can reduce this.
- The intensity of the annulus differs on scales on the same fish and between fish.
- The loss of scale material associated with spawning, can in some cases eliminate the annulus or spawning mark from the previous year.

Mennesson-Boisneau & Boisneau (1990) compared estimates of age from both scales and otoliths and found for both *A. alosa* and *A. fallax fallax* the level of agreement between both methods to be greater than 90%. However, for hybrids (*A. alosa* x *A. fallax*) the level of agreement was lower (77% for females and 81.1% for males). Similarly for *A. fallax fallax*, O'Maoileidigh (1990) reported excellent agreement between the two methods up to age four, however, for fish older than 4 years it was considered more accurate to estimate age from otoliths because of the difficulties created by loss of scale material associated with spawning.

The level of precision was greater for age estimated from otoliths, as compared with estimates from scales (Mennesson-Boisneau & Boisneau, 1990). For otoliths, mean percentage error for both species was less than 1% (upper 95% confidence interval) compared with less than 2% from scales from *A. alosa* and less than 4% for *A. fallax fallax*.

- Reconstruction of growth history

For the anadromous populations in particular, where it has not been possible to sample all the age groups, the only approach to estimating length for the younger age groups is by backcalculation. The method depends on the annual nature of the annulus, and that the relationship between the size of the fish and its scale/otolith is directly proportional. Both scales (Berg & Grimaldi, 1966a; Douchement, 1981; Aprahamian, 1982; O'Maoileidigh, 1990; Sabatié, 1993) and otoliths (Taverny, 1991a; Gordo, 2002) have been used to reconstruct growth history.

On their spawning migration into fresh water, *Alosa* erode and /or absorb scale material that later regenerates and forms a characteristic scar or spawning mark (Section 3.1.4). Such loss of scale material could effectively bias the results. This was examined by Aprahamian (1982), who found that though the scale radius (measured at the apex) for a given size of fish was smaller for fish that had previously spawned, this difference was not significant ($P > 0.05$).

The length at age from both scales and otoliths was compared by Taverny (1991a). The backcalculated length at age 1 was significantly greater ($p < 0.05$) when estimated from otoliths than from scales, by 116% and 125% for *A. alosa* and *A. fallax fallax* respectively.

Comparison between length at age backcalculated from scales and that observed directly has been undertaken by Aprahamian (1982), Douchement (1981) and Sabatié (1993). Aprahamian (1982) reported no significant difference in the mean length of fish caught in one year with the mean (backcalculated) length of fish, from the same year-class, caught at a later date ($P > 0.05$). In contrast Sabatié (1993) found that in the majority of cases the actual length observed was significantly greater ($P < 0.05$) than that backcalculated. Similarly Douchement (1981) reported that the actual length was greater than the backcalculated length. The difference was greatest for the one year old age group by factor of between 2.19 and 2.10, while for fish two years and older the difference was between 1.19 and 0.99 that of the backcalculated value. Except for the one-year-olds, part of this difference may relate to the fact that the lengths of different year-classes were being compared.

Alosa alosa

For anadromous populations spawning takes place between May and July (Section 4.9.2) and at hatching the larvae measure between 7 and 12 mm (total length) [Vincent, 1894b; Le Clerc, 1941]. Samples of juvenile *A. alosa* from the Rhine (Germany) and from the Loire (France), taken in July approximately two months after spawning, ranged in length (total) from 30 to 69 mm (Hoek, 1899) and from 35 to 50 mm (Le Clerc, 1941), respectively. After three months the juveniles ranged from 30 to 97 mm in the Rhine and between 60 to 75 mm in the Loire. Juveniles sampled on the spawning grounds in the Garonne (France), during July, measured (mean \pm 95% confidence intervals) 18.4 ± 0.38 mm (total length) [Cassou-Leins *et al.*, 1988a]. Their growth until emigration in October is shown in Table 3.32.

In then Loire juveniles caught on their downstream migration in August had reached a total length of between 50 and 83 mm, by September they ranged from 66 to 111 mm, by October from 57 to 124 mm and in November from 72 to 105 mm (Luquet, 1990). In the Gironde, after approximately 4 to 6 months, at the time of their seaward migration (October to December) the young range in size from 27 to 117 mm with mean length (\pm 95% confidence intervals) of 63.0 ± 0.6 mm (Anon., 1979a; Taverny, 1991a). Other studies have reported similar growth rates with fish reaching, by the autumn of their first year: 40 to 140 mm in the Rhine (Hoek, 1899); 80 to 110 mm in the Seine (Vincent, 1894b); 80 to 120 mm from Schleswig-Holstein (probably the Elbe) [Dunker & Ladiges, 1960; Ladiges & Vogt, 1965]; 150 mm in the Dordogne (Hoestlandt, 1958), 82 to 135 mm in the Lima (Alexandrino, 1996b) and 65 to 115 mm in the Sebou (Sabatié, 1993).

Table 3.32: Mean total length (\pm SD) in mm of juvenile (0+) *Alosa alosa* from the Gironde-Garonne-Dordogne system (France), data from Cassou-Leins *et al.* (1988a) and Taverny (1991a). Samples from different years have been combined.

| Location Year | Agen (Garonne) 1986 | Bergerac (Dordogne) 1988 | Inner Estuary 1985 & 1986 | Outer Estuary 1985 & 1988 |
|------------------|------------------------|--------------------------------|------------------------------|------------------------------|
| Month | | | | |
| July | 18.4 ± 2.2 | 40.0 ± 4.4 | | |
| August | 37.6 ± 7.5 | 50.2 ± 6.7 | 77.9 ± 7.4 | |
| September | 57.7 ± 8.3 | 52.7 ± 5.9 | 72.2 ± 9.7 | 86.4 ± 9.2 |
| October | | | 73.5 ± 9.6 | 78.7 ± 10.3 |

Little growth occurs over winter with fish in the Garonne measuring 68 mm by the following March, 81 mm by May and 91mm (80 to 120 mm) by July, when the fish are just over one year old (Anon. 1979a). Hoek (1899) reported similar findings for *A. alosa* from the Rhine (Table 3.33).

Table 3.33: Range in total length (mm) of *A. alosa* from the River Rhine (Hoek, 1899) and Gironde (Cassou-Leins *et al.*, 1988a and Taverny, 1991a).

| Month | Total length (mm) | |
|-----------|-------------------|---------|
| | Rhine | Gironde |
| July | 30 – 69 | |
| August | 30 – 97 | |
| September | 50 – 129 | 64-100 |
| October | 40 – 140 | 58-105 |
| November | 71 – 100 | 52-109 |
| December | No samples | 52-112 |
| January | | 61-112 |
| February | | 64-115 |
| March | | 61-118 |
| April | 90 – 160 | 67-94 |
| May | 93 – 160 | |
| June | 96 – 194 | |
| July | 100 – 187 | |

For male and female *Alosa alosa* the length and weight at age for a number of populations is shown in Tables 3.34 & 3.35 and Tables 3.36& 3.37, respectively. The population in the River Douro represented the fastest growing population (Eiras, 1981b), followed by those from the rivers Mondego, Loire, Lima and Sebou (Alexandrino, 1996b; Mennesson-Boisneau & Boisneau, 1990; Sabatié, 1993; Gordo, 2002). On those systems where studies had been carried out over a number of years significant temporal differences were evident, particularly on the Loire, Gironde-Garonne-Dordogne and Adour.

The parameters for the von Bertalanffy growth model (von Bertalanffy, 1957) have been recalculated using data from Tables 3.34 & 3.36, and are presented in Table 3.38 for both male and female *A. alosa*. There was a significant correlation between the growth coefficient (K) and L4 for both male ($r^2 = 0.72$) and female ($r^2 = 0.79$) *A. alosa*. Though differences in the parameters existed between the sexes and populations the growth performance index (Pauly, 1979) varied little with a mean ($\pm 95\%$ CI) of 3.19 (± 0.03) and a coefficient of variation of 2.0%.

The seasonality of growth of *A. alosa* from Gironde-Garonne-Dordogne can be expressed by the equation (Taverny, 1991a):

$$L_t = L_\infty \{1 - \exp[-K(t-t_0) - (KC/2\pi (\sin(2\pi (t-t_s))))]\}$$

where: $L_\infty = 702.5(M), 745.0(F)$; $K = 0.4655(M), 0.6996(F)$;

$t_0 = -0.4512(M), -0.3375(F)$; $t_s = 0.3126(M), 0.6527(F)$ and $C = 1(M\&F)$.

The maximum length recorded for *A. alosa* was for a female fish of 830 mm from the rivers Mondego (Gordo, 2002) and Sebou, the details of the latter were reported to, but not corroborated by Sabatié (1993).

For male *A. alosa* the maximum size differed between river systems and ranged from 670 mm in the Douro (Eiras, 1981b) and Sebou (Sabatié, 1993) to 530 mm in the Adour (Douchement, 1981). Weight ranged from 3275 to 1350g (Table 3.39). For females the maximum length ranged from 680 to 740mm and weight from 3550 to 4430g, except in the Rhine and Adour (Table 3.39). In the case of the latter two rivers the sample size was small. Comparable findings were reported by **Ehrenbaum (1894, 1936), Roule (1925, 1929)**, Poll (1947), **Dottrens (1952)**, Dunker & Ladiges (1960), **Ladiges & Vogt (1965)** and Castelnaud (1978).

The relationship between length and weight for fish caught during the freshwater phase of their spawning migration are presented in Tables 3.40 & 3.41, and for juvenile fish in Table 3.42. For those populations where a reasonable number of fish were sampled, the allometric growth parameter (b) for males ranged from 2.55 to 3.27 and for females from 2.61 to 3.52. Significant temporal differences were evident from Gironde-Garonne-Dordogne populations (Taverny, 1991a) with values over a three year study ranging from 2.85 to 3.27 for males and 2.61 to 3.52 for females. For juvenile (age 0+) *Alosa alosa* from the Gironde-Garonne-Dordogne and the Sebou the exponent varied from 2.78 to 3.03 (Sabatié, 1993; Taverny, 1991a).

Growth of the landlocked populations in their first year of life is greater than that in the anadromous populations, with fish capable of reaching 315 mm (Table 3.43). Subsequently growth slows, and their length at age becomes comparable with anadromous populations. The maximum length attained by landlocked populations is less than that of anadromous populations, with *A. alosa* from the Aguieira Reservoir (River Mondego, Portugal) reaching a maximum of *c.* 630 mm (male) and *c.* 590 mm (female) [Gordo, 2002]. The von Bertalanffy parameters are shown in Table 3.44 for Aguieira and El Kansera, the parameters for the latter were calculated using the middle value of the range in length for each age group quoted by Furnestin (1952). For the landlocked populations L4 was less and K was towards the upper end of the values observed in migratory populations. The highest value of the Brody growth coefficient was for the El Kansera population.

Table 3.34: Total length and standard deviation (mm) of anadromous male *Alosa alosa*.

| River Country | Actual / Backcalculated | Age (year) | | | | | | | | Reference |
|--|-----------------------------|-----------------|-----------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|---|--|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Aulne France | Actual | | | | 460.6 (25.3) | 462.5 (38.8) | | | | Véron (1999) |
| Loire France | Backcalculated | 89.6 (13.9) | 225.9 (28.6) | 333.8 (35.6) | 430.5 (36.1) | 493.2 (28.5) | 521.1 (23.4) | | | Douchement (1981) |
| | Actual ¹ | | | 427.0 (27.8) | 478.8 (30.6) | 532.2 (27.9) | 578.8 (24.2) | | | Menesson-Boisneau & Boisneau (1990) |
| Charente France | Actual | | | 467.5 (81.3) | 506.7 (43.7) | 546.9 (28.9) | 523.3 (37.5) | 560.0 | | Véron (1999) |
| Gironde – Garonne – Dordogne France | Backcalculated ¹ | 93.2 (4.7) | 222.4 (8.0) | 348.1 (16.0) | 455.7 (14.8) | 499.8 (11.4) | 527.0 (13.7) | 556.4 (20.5) | | Anon. (1979a) |
| | Backcalculated ² | 97.5 (8.7) | 217.1 (9.1) | 317.8 (12.2) | 418.7 (22.1) | 488.4 (19.3) | 531.1 (12.3) | | | Cassou-Leins & Cassou-Leins (1981) |
| | Backcalculated | 74.9 (15.0) | 204.3 (28.5) | 335.2 (36.5) | 436.1 (31.8) | 496.7 (26.0) | 526.1 (24.4) | | | Douchement (1981) |
| | Backcalculated ² | 98.2 (14.5) | 237.8 (35.2) | 404.4 (37.7) | 493.2 (34.2) | 555.3 (29.4) | 586.3 (31.6) | | | Dautrey & Lartigue (1983) |
| | Backcalculated | 90.4 (12.5) | 183.8 (26.2) | 307.2 (39.4) | 419.9 (34.3) | 511.9 (29.8) | 540.1 (29.8) | | | Taverny (1991a) |
| Adour France | Backcalculated | 89.2 (19.4) | 242.2 (34.1) | 373.9 (40.9) | 460.6 (29.4) | 491.4 (19.0) | | | | Douchement (1981) |
| | Actual ¹ | | | | 488.0 (23.5) | 510.6 (27.8) | 539.5 (20.5) | 567.9 (32.2) | | Prouzet <i>et al.</i> (1994a) |
| Aude France | Backcalculated ³ | 109.3 (18.0) | 221.5 (8.6) | 320.8 (14.1) | | | | | | Douchement (1981) |
| Rhône France | Backcalculated ³ | 101.7 (13.9) | 226.2 (19.8) | 318.5 (16.7) | 412.3 (25.8) | 454.0 (22.9) | 490.0 | | | Douchement (1981) |
| Lima Portugal | Actual | | | 421.0 (54.4) ⁴ | 469.8 (16.4) ⁴ | 550.2 (11.7) ⁴ | 589.2 (17.2) ⁴ | 655.5 (54.4) ⁴ | | Alexandrino (1996b) |
| Douro Portugal | Actual | | | 440 - 510 | 500 - 575 | 576 - 620 | 610 | | | Eiras (1981b) |

Table 3.34: (cont.) Total length and standard deviation (mm) of anadromous male *Alosa alosa*.

| River Country | Actual / Backcalculated | Age (year) | | | | | | | | Reference |
|------------------|--|-----------------|-----------------|-----------------|-----------------|-----------------|------------------------------|---|---|-----------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Mondego Portugal | Backcalculated | 223.0 (31.6) | 341.5 (26.0) | 436.0 (19.1) | 504.0 (11.8) | 560.2 | | | | Gordo (2002) |
| Loukos Morocco | Actual ³ | | 216.0 (11.0) | | 487.0 (67.0) | 576.0 (7.0) | | | | Sabatié (1993) |
| Sebou Morocco | Backcalculated (⁵ Actual) | 133.6 (34.1) | 309.7 (61.6) | 434.7 (47.2) | 501.2 (40.5) | 547.0 (46.2) | 582.1 ⁵ (48.2) | | | Sabatié (1993) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1325 L_f + 2.6556$ (Douchement, 1981).

² Standard length (L_{st}) converted to total length using $L_t = 1.1882 L_{st} + 9.4799$ (Douchement, 1981).

³ Total sample ≤ 10 .

⁴ 95% Confidence intervals.

Table 3.35: Mean weight (standard deviation) in relation to age for anadromous male *Alosa alosa*.

| River Country | Age (year) | | | | | | | Reference |
|-----------------|------------|------------|------------|------------|------------|------------|---|--------------------------------------|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Loire, France | | 653 (187) | 979 (247) | 1310 (254) | 1658 (265) | | | Mennesson-Boisneau & Boisneau (1990) |
| Adour, France | | | 1099 (30) | 1352 (18) | 1657 (27) | 2114 (133) | | Prouzet <i>et al.</i> (1994a) |
| Loukos, Morocco | 84 (139) | | 995 (64) | 1950 (175) | | | | Sabatié (1993) |
| Sebou, Morocco | | 1407 (128) | 1619 (324) | 1948 (406) | 2225 (513) | 1703 (285) | | Sabatié (1993) |

Table 3.36: Total length and standard deviation (mm) of anadromous female *Alosa alosa*.

| River Country | Actual / Backcalculated | Age (year) | | | | | | | | Reference |
|---|-----------------------------|-----------------|-----------------|-----------------|-----------------|------------------------------|------------------------------|------------------------------|----------------|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Aulne France | Actual | | | 545.0 | 556.7 (10.4) | 560.0 (21.2) | 540.0 | | | Véron (1999) |
| Loire France | Backcalculated | 94.1 (16.1) | 224.6 (25.5) | 350.7 (34.3) | 455.5 (40.3) | 528.0 (39.3) | 538.4 (24.3) | | | Douchement (1981) |
| | Actual ¹ | | | | 519.8 (28.3) | 574.3 (24.5) | 614.7 (22.3) | 649.1 (19.3) | | Mennesson-Boisneau & Boisneau (1990) |
| Charente France | Actual | | | 530.0 | 558.0 (26.8) | 572.4 (44.0) | 580.0 (48.5) | 552.5 (36.6) | | Véron (1999) |
| Gironde – Garonne – Dordogne France | Backcalculated ¹ | 78.5 (4.7) | 202.0 (10.3) | 318.6 (13.7) | 437.5 (19.4) | 522.5 (23.9) | 559.8 (17.1) | 575.5 (31.9) | | Anon. (1979a) |
| | Backcalculated ² | 95.3 (9.1) | 247.6 (28.0) | 380.3 (52.3) | 482.3 (48.4) | 547.3 (32.4) | 580.6 (9.4) | 598.1 (5.1) | | Cassou-Leins & Cassou- Leins (1981) |
| | Backcalculated | 73.1 (10.8) | 198.6 (23.6) | 326.7 (34.7) | 444.5 (33.1) | 530.0 (32.5) | 573.2 (25.1) | | | Douchement (1981) |
| | Backcalculated ² | 97.0 (19.0) | 220.2 (43.4) | 384.8 (41.1) | 510.4 (37.2) | 595.8 (40.0) | 625.3 (43.7) | 646.9 | | Dautrey & Lartigue (1983) |
| | Backcalculated | 101.0 (16.9) | 205.9 (35.5) | 329.9 (44.3) | 438.6 (41.5) | 530.5 (40.2) | 571.5 (23.4) | 601.0 | | Taverny (1991a) |
| Adour France | Backcalculated | 72.2 (12.0) | 208.0 (29.6) | 339.3 (39.6) | 454.0 (50.9) | 521.9 (38.6) | 554.7 (31.6) | | | Douchement (1981) |
| | Actual ¹ | | | | 529.3 | 548.5 (23.3) | 590.2 (22.8) | 610.2 (20.8) | 622.7 (4.0) | Prouzet <i>et al.</i> (1994a) |
| Aude France | Backcalculated ³ | 107.7 (13.3) | 231.9 (25.1) | 340.9 (21.5) | 433.8 (27.5) | 489.7 (27.1) | 536.1 (34.1) | | | Douchement (1981) |
| Rhône France | Backcalculated ³ | 101.1 (10.7) | 266.4 | 363.7 | 415.0 | 476.5 | 520.0 | | | Douchement (1981) |
| Lima Portugal | Actual | | | | | 585.9 (16.0) ⁴ | 643.4 (11.3) ⁴ | 666.0 (18.2) ⁴ | | Alexandrino (1996b) |
| Douro Portugal | Actual | | | 500 – 580 | 570 - 630 | 610 – 690 | 690 - 730 | | | Eiras (1981b) |
| Mondego Portugal | Actual | | | | | 625.5 (34.4) ⁴ | 635.0 (42.2) ⁴ | 680.0 (84.3) ⁴ | | Alexandrino (1996b) |

Table 3.36: (cont.) Total length and standard deviation (mm) of anadromous female *Alosa alosa*.

| River Country | Actual / Backcalculated | Age (year) | | | | | | | | Reference |
|---------------------|--|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------------------|-----------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Mondego Portugal | Backcalculated | 155.9 (52.0) | 319.8 (35.7) | 443.9 (37.9) | 548.6 (29.6) | 642.8 (27.9) | 733.7 (14.0) | 782.4 | | Gordo (2002) |
| Loukos Morocco | Actual ³ | | 270 | | 463.0 (42.0) | | 605.0 | | | Sabatié (1993) |
| Sebou Morocco | Backcalculated (⁵ Actual) | 119.4 (9.9) | 322.5 (47.0) | 437.5 (42.6) | 528.8 (34.9) | 587.8 (33.3) | 619.1 (22.7) | 633.0 (26.3) | 666.7 ⁵ (9.3) | Sabatié (1993) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1325 L_f + 2.6556$ (Douchement, 1981).

² Standard length (L_{st}) converted to total length using $L_t = 1.1882 L_{st} + 9.4799$ (Douchement, 1981).

³ Total sample ≤ 10 .

⁴ 95% Confidence intervals.

Table 3.37: Mean weight (standard deviation) in relation to age for anadromous female *Alosa alosa*.

| River Country | Age (year) | | | | | | | Reference |
|--|------------|---|------------|------------|------------|------------|------------|---|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Loire, France | | | 1307 (312) | 1716 (345) | 2174 (363) | 2665 (489) | | Mennesson-Boisneau & Boisneau (1990) |
| Gironde – Garonne Dordogne, France | | | | 1880 (344) | 2172 (323) | 2565 (230) | | Taverny (1991a) |
| Adour, France | | | 1285 | 1701 (27) | 2266 (24) | 2599 (54) | 3050 (50) | Prouzet <i>et al.</i> (1994a) |
| Loukos, Morocco | 152 | | 852 (72) | | 2005 | | | Sabatié (1993) |
| Sebou, Morocco | | | 2171 (377) | 2872 (494) | 3162 (343) | 3368 (398) | 3580 (202) | Sabatié (1993) |

Table 3.38: von Bertalanffy growth parameters for male and female anadromous *Alosa alosa*, 95% confidence intervals in brackets.

| River Country | Male | | | Female | | | Reference |
|--|---------------|----------------|--------|---------------|----------------|-------|---------------------------------------|
| | K | L_{∞} | T_0 | K | L_{∞} | T_0 | |
| Loire, France | 0.288 (0.105) | 663.9 (110.7) | 0.502 | 0.277 (0.099) | 701.4 (118.4) | 0.496 | Douchement (1981) |
| Gironde – Garonne – Dordogne France | 0.280 (0.035) | 683.7 (41.1) | 0.489 | 0.332 (0.057) | 658.2 (33.5) | 0.628 | Anon. (1979a) |
| | 0.184 (0.044) | 825.9 (114.4) | 0.327 | 0.383 (0.064) | 656.7 (26.6) | 0.597 | Cassou-Leins & Cassou-Leins (1981) |
| | 0.279 (0.100) | 688.5 (119.5) | 0.600 | 0.173 (0.080) | 954.1 (277.5) | 0.550 | Douchement (1981) |
| | 0.315 (0.109) | 727.7 (113.7) | 0.550 | 0.213 (0.113) | 939.0 (291.6) | 0.508 | Dautrey & Lartigue(1983) |
| | 0.124 (0.096) | 1108.9 (603.4) | 0.337 | 0.150 (0.105) | 1006.0 (443.4) | 0.312 | Taverny (1991a) |
| Adour, France | 0.404 (0.163) | 596.7 (93.6) | 0.608 | 0.236 (0.104) | 783.3 (190.1) | 0.597 | Douchement (1981) |
| Mondego, Portugal | 0.259 (0.105) | 746.2 (110.6) | -0.372 | 0.184 (0.041) | 1058.9 (99.2) | 0.706 | Gordo (2002) |
| Sebou , Morocco | 0.450 (0.205) | 632.3 (95.0) | 0.474 | 0.402 (0.061) | 699.6 (21.3) | 0.534 | Sabatié (1993) |

Table 3.39: Maximum length (total) and weight of anadromous *A. alosa* recorded from a number of river systems.

| River (Country) | Male | | Female | | Reference |
|---------------------------------------|-----------|-----------|-----------|-----------|---|
| | L_{max} | W_{max} | L_{max} | W_{max} | |
| Rhine (Germany) | 590 | 3000 | 624 | 3000 | Hoek (1899) |
| Loire (France) | 560 | 2180 | 630 | 2470 | Douchement (1981) |
| | 643 | 2487 | 687 | 3800 | Mennesson-Boisneau & Boisneau (1990) |
| Gironde-Garonne- Dordogne (France) | 613 | 2600 | 681 | 3240 | Anon. (1979a) |
| | 517 | | 591 | 2520 | Cassou-Leins & Cassou-Leins (1981) |
| | 565 | 1890 | 650 | 3020 | Douchement (1981) |
| | 659 | | 710 | | Dautrey & Lartigue(1983) |
| | 597 | 2775 | 650 | 3550 | Taverny (1991a) |

Table 3.39: (cont) Maximum length (total) and weight of anadromous *A.alosa* recorded from a number of river systems.

| | | | | | |
|--------------------|-----|------|------------|------|-------------------------------------|
| Adour (France) | 530 | 1350 | 595 | 1980 | Douchement (1981) |
| Lima (Portugal) | 666 | 3215 | 733 | 4400 | Alexandrino (1996b) |
| Douro (Portugal) | 670 | 3200 | 740 | 4430 | Eiras (1981b) |
| Mondego (Portugal) | 614 | 2287 | 680 830 | 3571 | Alexandrino (1996b) Gordo (2002) |
| Sebou (Morocco) | 670 | 3275 | 720 | 4525 | Sabatié (1993) |

Table 3.40: Parameters for the equation weight (g) = aLength^b (mm) for male *Alosa alosa*, (Imm. = immature).

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|-------------------------------------|------------|---------------------|---|---------------|--------|----------------|-------------------------|----------------|---|
| Rhine (Germany) | Adult | L _t (mm) | 2.716.10 ⁻⁸ | 3.965 | 8 | 0.91 | 499-590 | 1290-3000 | Hoek (1899) |
| Loire (France) | Adult | L _f (mm) | 5.507.10 ⁻³ | 3.114 | 1172 | 0.66 | 349-643 | 174-2487 | Mennesson-Boisneau & Boisneau (1990) Douchement (1981) |
| | | L _t (mm) | 1.679.10 ⁻⁵ | 2.924 | 89 | 0.82 | 440-570 | 830-2180 | |
| Gironde – Garonne – Dordogne France | Adult | L _t (mm) | 7.510.10 ⁻⁵ | 3.045 | 51 | 0.90 | 420-560 | 740-1890 | Douchement (1981) Taverny (1991a) |
| | | | 1.801.10 ⁻⁶ – 2.574.10 ⁻⁵ | 2.853 – 3.271 | 83-152 | 0.61-0.87 | 383-597 | 580-2775 | |
| Adour France | Adult | L _t (mm) | 1.662.10 ⁻⁴ | 2.551 | 120 | 0.66 | 420-530 | 750-1570 | Douchement (1981) Douchement (1981) |
| | Imm. | | 1.774.10 ⁻⁵ | 2.868 | 31 | 0.95 | 150-300 | 35-216 | |
| Aude France | Imm. | L _t (mm) | 3.119.10 ⁻⁶ | 3.189 | 79 | 0.97 | 150-380 | 34-480 | Douchement (1981) |

Table 3.40: (cont) Parameters for the equation weight (g) = aLength^b (mm) for male *Alosa alosa*, (Imm. = immature).

| | | | | | | | | | |
|---------------------|-----------------------------|----------------------|------------------------|-------|-----|------|----------|-----------|------------------------|
| Rhône France | Imm. | L _t (mm) | 4.963.10 ⁻⁶ | 3.104 | 23 | 0.97 | 150-340 | 28-345 | Douchement (1981) |
| Lima Portugal | Adult | L _t (cm) | 0.011 | 2.981 | 86 | 0.96 | 400-666 | 668-3215 | Alexandrino (1996b) |
| Douro Portugal | Adult | L _t (mm) | 1.778.10 ⁻⁵ | 2.903 | 69 | 0.84 | 480-670 | 1100-3200 | Eiras (1981b) |
| Mondego Portugal | Adult | L _t (cm) | 0.018 | 2.854 | 9 | 0.93 | 535-614 | 1553-2287 | Alexandrino (1996b) |
| | Juv & Adult | L _t (mm) | 3.6. 10 ⁻³ | 3.249 | 37 | 0.99 | 80-c.680 | | |
| Loukos Morocco | Juv & Adult ¹ | L _t (mm) | 2.536.10 ⁻⁶ | 3.216 | 17 | 0.73 | 210-585 | 75-2125 | Sabatié (1993) |
| Sebou Morocco | Adult | L _t (mm) | 2.071.10 ⁻⁶ | 3.259 | 482 | 0.93 | 445-670 | 850-3275 | Sabatié (1993) |

¹ Male & Female combined

Table 3.41: Parameters for the equation weight (g) = aLength^b (mm) for female *Alosa alosa*, (Imm. = immature)

| River Country | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|--------------------------------------|-------------|---------------------|--|------------------|---------------|-------------------|-------------------------|----------------|---|
| Rhine, Germany | Adult | L _t (mm) | 1.172.10 ⁻⁶ | 3.374 | 16 | 0.85 | 467-625 | 1050-3000 | Hoek (1899) |
| Loire, France | Adult | L _f (mm) | 7.298.10 ⁻³ | 3.019 | 1054 | 0.65 | 423-687 | 500-3800 | Mennesson-Boisneau & Boisneau (1990) Douchement (1981) |
| | | L _t (mm) | 2.769.10 ⁻⁵ | 2.852 | 26 | 0.75 | 500-630 | 1450-2470 | |
| Gironde – Garonne – Dordogne, France | Adult | L _t (mm) | 4.656.10 ⁻⁷ | 3.497 | 58 79 -188 | 0.78 0.62-0.71 | 500-650 | 1130-3020 | Douchement (1981) Taverny (1991a) |
| | | | 3.958.10 ⁻⁷ – 1.227.10 ⁻⁴ | 2.610 – 3.518 | | | 436-650 | 1150-3550 | |
| Adour France | Adult | L _t (mm) | 1.867.10 ⁻⁵ | 2.915 | 21 | 0.61 | 500-590 | 1350-2460 | Douchement (1981) Douchement (1981) |
| | Imm. | L _t (mm) | 9.302.10 ⁻⁶ | 2.868 | 31 | 0.95 | 150-300 | 35-216 | |
| Aude France | Imm. | L _t (mm) | 5.518.10 ⁻⁶ | 3.088 | 71 | 0.85 | 150-380 | 34-480 | Douchement (1981) |
| Rhône France | Imm. | L _t (mm) | 2.592.10 ⁻⁶ | 3.221 | 24 | 0.98 | 150-340 | 28-345 | Douchement (1981) |
| Lima Portugal | Adult | L _t (cm) | 0.036 | 2.717 | 71 | 0.71 | 480-733 | 1237-4400 | Alexandrino (1996b) |
| Douro Portugal | Adult | L _t (mm) | 1.193.10 ⁻⁵ | 2.970 | 91 | 0.89 | 540-730 | 1530-4430 | Eiras (1981b) |
| Mondego Portugal | Adult | L _t (cm) | 0.158 | 2.333 | 11 | 0.53 | 583-680 | 1984-3571 | Alexandrino (1996b) Gordo (2002) |
| | Juv & Adult | L _t (mm) | 4.2. 10 ⁻³ | 3.201 | 40 | 0.99 | 80-830 | | |
| Sebou Morocco | Adult | L _t (mm) | 8.206.10 ⁻⁷ | 3.411 | 317 | 0.72 | 490-720 | 1250-4525 | Sabatié (1993) |

Table 3.42: Parameters for the equation weight (g) = aLength^b (mm) for juvenile *Alosa alosa*.

| River Country | Life stage | Length | a | b | n | R ² | Range (length) mm | Range (weight) g | Reference |
|--------------------------------------|------------|---------------------|--|---------------|---------|----------------|-------------------|------------------|-----------------|
| Gironde - Garonne - Dordogne, France | 0+ | L _t (mm) | 6.511.10 ⁻⁶ – 2.02.10 ⁻⁵ | 2.777 – 3.031 | 179-806 | 0.86-0.96 | 27-117 | 0.1-11.3 | Taverny (1991a) |
| Sebou, Morocco | 0+ | L _t (mm) | 8.308.10 ⁻⁶ | 3.008 | 47 | 0.96 | 5.5-11.5 | 1.4-12.1 | Sabatié (1993) |

Table 3.43 Range in total length (mm) or mean (SD or 95% confidence intervals) of landlocked male and female *Alosa alosa*.

| Waterbody, River Country | Sex | Age (Year) | | | | | | Reference |
|--------------------------------|----------------------|---------------------------|---------------------------|---------------------------|--|---|--------------|---------------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | |
| Aguieira, Mondego, Portugal | M | 298 | 375 | 430 | 567 | 502 | | Collares-Pereira <i>et al.</i> (1999) |
| | F | 315 | 404 | 453 | 500 | | | |
| | M | 236.7 (36.3) ¹ | 345.2 (32.7) ¹ | 430.0 (28.0) ¹ | 484.8 (24.8) | 536.2 (31.4) | 563.8 | Gordo (2002) |
| | F | 237.5 (36.6) ¹ | 353.6 (37.7) ¹ | 431.2 (26.4) ¹ | 1 486.1 (28.6) 1 | 1 539.8 (26.3) 1 | | |
| Castelo do Bode, Tejo Portugal | M | <274 | 268 – 413 | 407 – 491 | | | | Eiras (1983) |
| | F | <313 | 299 – 450 | 446 – 498 | | | | |
| | M F | | | 320.0 (74.7) ² | 420.7 (12.8) ² 400.3 (18.7) ² | | | Alexandrino (1996b) |
| El Kansera, Sebou Morocco | M&F | 180 – 270 | 310 – 360 | 350 – 400 | 400 – 450 | >450 | | Furnestin (1952) |

¹ = SD; ² = 95%CI

Table 3.44: von Bertalanffy growth parameters for male and female landlocked *Alosa alosa*, 95% confidence intervals in brackets.

| Waterbody, River Country | Sex | Growth parameter | | | Reference |
|--------------------------------|-----|------------------|---------------|--------|--|
| | | K | L_{∞} | T_0 | |
| Aguieira, Mondego, Portugal | M | 0.363 (0.009) | 610.1 (4.4) | -0.780 | Collares-Pereira <i>et al.</i> (1999) |
| | F | 0.373 (0.017) | 586.1 (7.6) | -1.077 | |
| | M | 0.279 (0.082) | 660.8 (50.9) | -0.048 | Gordo (2002) |
| | F | 0.291 (0.227) | 672.4 (194.6) | -0.513 | |
| El Kansera, Sebou, Morocco | M&F | 0.543 (0.018) | 467.1 (3.8) | -0.224 | Furnestin (1952) |

Alosa fallax fallax

In the Elbe (Germany), larval *A. fallax fallax* measure 4.25 to 6.0 mm (Ehrenbaum, 1894) while in the Wye (Wales) larvae measured 6.2 to 9.2 mm (Aprahamian, 1982), at hatching. Their growth rate during their first year until their emigration has been reported from the Severn, England (Claridge & Gardner, 1978; Aprahamian, 1988), Elbe, Germany (Ehrenbaum, 1894; Möller, 1988; Oesmann, 1994; Thiel *et al.*, 1996a), Gironde-Garonne-Dordogne, France (Anon., 1979a; Taverny, 1991a) and from the Sebou, Morocco (Sabatié, 1993) [Table 3.45].

Table 3.45: Mean total length (SD) in mm of *Alosa fallax fallax* from the rivers Elbe (Ehrenbaum, 1894; Möller, 1988; Oesmann, 1994), Severn (Aprahamian, 1988), Gironde estuary (Taverny, 1991a) and Sebou (Sabatié, 1993).

| Month | Elbe (Germany) | | | Severn ¹ (England) | Gironde (France) | Sebou (Morocco) |
|-----------|---------------------|------------------|-------------------|----------------------------------|---------------------|--------------------|
| | Ehrenbaum (1894) | Möller (1988) | Oesmann (1994) | | | |
| June | | 46.3 (12.2) | 34.2 (2.7) | | | |
| July | 49.9 (8.5) | 49.0 (9.2) | 48.6 (7.7) | 30.9 (4.2) | 36.5 (5.0) | 64.6 (9.6) |
| August | 57.3 (11.4) | 61.2 (18.5) | 75.6 (12.3) | 44.0 (7.7) | 44.1 (7.0) | 69.7 (6.0) |
| September | 91.6 (12.3) | 72.0 (9.1) | 81.3 (16.1) | 58.9 (11.6) | 54.6 (11.5) | 75.1 (10.8) |
| October | 89.0 (6.3) | 76.0 (9.6) | 94.2 (13.0) | 68.7 (11.3) | 63.4 (10.8) | |
| November | 104.3 (10.7) | 74.5 (9.3) | 104.0 (8.2) | | | 78.8 (10.3) |
| December | | | 101.0 (18.1) | | | 79.2 (10.2) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

Little growth occurs over winter (Anon. 1888; Claridge & Gardner, 1978; Anon. 1979a; Aprahamian, 1988; Taverny, 1991a; Thiel *et al.*, 1996a) [Figure 3.26].

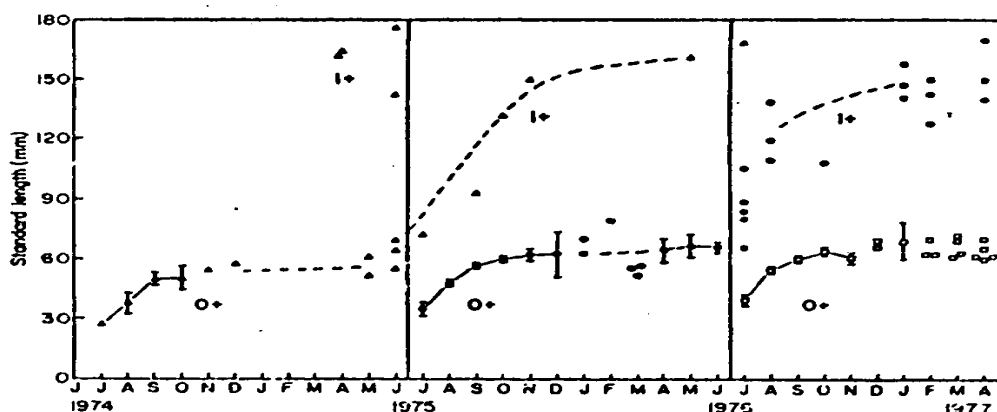


Figure 3.26: The standard length (mean \pm 95% confidence intervals) of 0+ *Alosa fallax fallax* from the Severn Estuary (England) between July 1974 and April 1977 (Reproduced from Claridge & Gardner, 1978).

The growth of juvenile (age 0+) twaite shad from the Elbe during their first 18 months; June until October the following year, could be described using the equation (Thiel *et al.*, 1996a):

$$L_t = L_\infty \{1 - \exp(-K(t-t_0) - [KC/2B (\sin(2\pi (t-t_s)) - \sin(2\pi (t_0 - t_s)))])\}$$

where:

$$L_\infty = 61.29;$$

$$K = 0.2;$$

$$t_0 = 0.336;$$

$$t_s = 0.538$$

$$C = 1.219.$$

The equation accurately described the pattern of growth ($r^2 = 0.994$) and correctly reflected the period of little growth over the winter period.

Length and weight at age data for various populations are shown in Tables 3.46 & 3.47 and 3.48 & 3.49 for *A. fallax fallax*, respectively. The fastest growing populations were in the rivers Nyamunas, Lithuania (Manyukas, 1989) and in the Loire and Charente, France (Mennesson-Boisneau & Boisneau, 1990; Véron, 1999). There was little difference in length at age between the other populations ranging from the Sebou (southern limit of range) to those in the Severn (northern limit of range). However, growth in the first year was higher in fish from the Sebou and in females from the Gironde-Garonne-Dordogne. Except for the Nyamunas and Loire stocks there was little difference in weight at age for the males. Females from the French populations in the rivers Loire and Gironde-Garonne-Dordogne were heavier compared with fish of the same age from other stocks. However, the sample from the Gironde-Garonne-Dordogne was small (Taverny, 1991a).

The values of the exponent reported by Aprahamian (unpubl.) for the 0+ and 1+ populations from the Severn and Wye were higher than values found by other studies (Claridge & Gardner, 1978; Taverny, 1991a; Sabatié, 1993). The findings indicate that fish become heavier for their length, partly reflecting the transformation from larvae to juvenile for the 0+ age group. Fish aged 1+ and where the sample was taken over the entire year it may reflect the improvement in feeding conditions between spring and autumn.

The parameters for the von Bertalanffy growth model have been recalculated using data from Tables 3.46 & 3.48, and are presented in Table 3.50 for both male and female *A. fallax*. No significant correlation ($\alpha = 0.05$) existed between the growth coefficient (K) and L_9 for male ($r^2 = 0.45$) and female ($r^2 = 0.43$) *A. fallax*. Combining the data for the two sexes indicated a significant negative relationship (Figure 3.27). The value of K ranged from 0.265-0.543 year⁻¹ for males and 0.259-0.403 year⁻¹ for females. L_9 varied between 384-531 mm and 467-577 mm for males and females, respectively. Of the various populations, significant differences ($P < 0.05$) were only evident between females from the Gironde-Garonne-Dordogne (Anon. 1979a) and the Severn and Adour (Aprahamian, unpubl.; Douchement, 1981). There was no trend in either parameter

from North to South. The growth performance index (\emptyset') varied little between the sexes and between populations with an overall mean (n=15) of 2.90 (\pm 0.04) and a coefficient of variation of 2.6%.

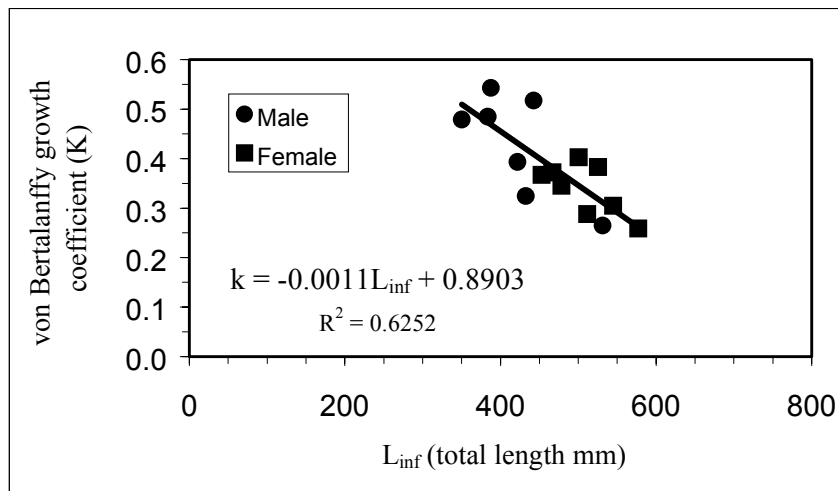


Figure 3.27: Relationship between von Bertalanffy coefficient (K) and the asymptotic length (L_{∞}).

The seasonality of growth of *A. fallax* from the Gironde-Garonne-Dordogne can be expressed by the equation (Taverny, 1991a):

$$L_t = L_{\infty} \{ 1 - \exp[-K(t-t_0) - (KC/2\pi (\sin(2\pi (t-t_s))))] \}$$

where:

$$\begin{aligned} L_{\infty} &= 478.5(\text{M}), 621.0(\text{F}); \\ K &= 0.6551(\text{M}), 0.5286(\text{F}); \\ t_0 &= -0.0948(\text{M}), -0.1593(\text{F}); \\ t_s &= 0.6038(\text{M}), -3.9127(\text{F}); \\ C &= -0.6658(\text{M}), 0.5844(\text{F}). \end{aligned}$$

Females obtain a larger size than males (Table 3.51). Manyukas (1989) reported that the largest specimen from the River Nyamunas (Lithuania) measured 568mm (L_t) and 1520g. For other populations the maximum length obtained ranged from approximately 460 to 520 mm for females and from 430 to 500 mm for males. There was reasonable agreement between L_{max} and L_{∞} for both female and male *A. fallax*, with the exception of the studies by Anon. (1979a) and Taverny (1991a) from the Gironde-Garonne-Dordogne. The maximum weight for females was approximately 1.1 to 1.5kg, and for males was 0.6 to 1.0kg.

For those populations where adequate samples were obtained the allometric growth parameter (b) for males ranged from 2.62-3.38, and for females from 2.49-3.37 (Table 3.52 & 3.53). For juvenile (age 0+) *Alosa fallax* from the Severn, Wye, Gironde-Garonne-Dordogne and Sebou the exponent varied from 2.73-4.36 (Claridge & Gardner, 1978; Taverny, 1991a; Sabatié, 1993; Aprahamian, unpubl.) [Table 3.54]. For the 1+ age group the exponent was 3.82 (Aprahamian, unpubl.) [Table 3.54].

Table 3.46: Total length and standard deviation (mm) of anadromous male *Alosa fallax fallax*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | Reference | |
|-----------------------|--|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------|------------------|------------------|------------------|-----------|--|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | |
| Nyamunas Lithuania | Measured ² | | | 367.0 | 405.0 | 439.6 | 458.6 | 488.3 | | | | | Manyukas (1989) |
| Elbe Germany | Measured | | | 321.5 | 354.4 | 385.2 | 389.5 | 405.7 | 401.8 | | | | Hass (1965) |
| Holland | Measured | | | | | 354.5 (22.2) | 373.9 (15.5) | 386.0 (19.8) | 395.0 | 400.0 | | | Aprahamian (1982 & unpubl.) |
| Severn England | Measured ² | | | 284.4 (22.2) | 341.7 (14.9) | | | | | | | | Claridge & Gardner (1978) |
| | Backcalculated ¹ * Measured | 85.5 (14.8) | 181.9 (35.5) | 270.7 (35.1) | 325.1 (24.1) | 349.8 (23.5) | 365.8 (21.7) | 386.4* (21.0) | 400.7* (17.2) | 407.6* (22.2) | 408.0* (32.8) | | Aprahamian (Unpubl.) |
| Wye Wales | Measured ¹ | | | 317.4 (4.8) | 316.1 (20.1) | 348.4 (20.3) | 348.9 (18.9) | 412.1 | 373.7 | | | | Aprahamian (Unpubl.) |
| Tywi Wales | Measured ¹ | | | | | | 364.8 | 364.2 (12.2) | 381.9 (14.0) | | | | Aprahamian (Unpubl.) |
| Barrow Ireland | Backcalculated ¹ Male & Female | 87.7 | 161.9 | 239.7 | 293.7 | 360.3 | 389.5 | 397.4 | | | | | Bracken & Kennedy (1967) |
| | Backcalculated ¹ | 64.0 (10.4) | 166.5 (23.2) | 265.6 (31.6) | 322.0 (20.2) | 347.8 (38.4) | 350.1 (12.1) | 374.9 | 391.8 | | | | O'Maoileidigh 1990 |
| | Measured Male & Female | | 209.0 | 351.0 | 368.0 | 390.0 | 400.0 | 429.0 | | | | | Doherty & McCarthy (2002) |
| Seine France | Measured ³ | | 223.5 | 292.5 | | | | | | | | | Roule (1922a) |

Table 3.46: (cont) Total length and standard deviation (mm) of anadromous male *Alosa fallax fallax*

| Loire France | Measured ¹ | | | 353.5 (29.4) | 391.8 (40.5) | | | | | | | Mennesson- Boisneau & Boisneau (1990) |
|--|------------------------------|-----------------|------------------------------|------------------------------|------------------------------|------------------------------|---|---|---|---|----|--|
| | Backcalculated | 86.3 (8.7) | 227.5 (20.6) | 319.2 (21.8) | 367.5 (21.8) | 397.5 (10.6) | | | | | | Douchement (1981) |
| Charente France | Measured | | | | 376.0 (29.2) | | | | | | | Véron (1999) |
| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | Reference |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Gironde – Garonne – Dordogne France | Backcalculated ¹ | 66.3 (8.3) | 161.9 (19.6) | 266.8 (17.2) | 317.4 (12.6) | 391.8 (50.2) | | | | | | Anon. (1979a) |
| | Backcalculated | 74.1 (10.1) | 196.0 (22.4) | 292.2 (21.9) | 323.4 (25.8) | 348.1 (29.6) | | | | | | Douchement (1981) |
| | Backcalculated | 76.8 (16.4) | 180.6 (27.3) | 245.8 (28.0) | 285.1 (27.9) | 308.7 | | | | | | Taverny (1991a) |
| Adour France | Backcalculated ³ | 78.1 (5.9) | 191.8 (19.0) | 276.3 (14.8) | 342.2 (12.5) | 407.5 (31.8) | | | | | | Douchement (1981) |
| Lima Portugal | Measured | | 289.0 (37.0) ⁴ | 360.7 (24.2) ⁴ | 391.5 (14.7) ⁴ | 439.4 (24.2) ⁴ | | | | | | Alexandrino (1996b) |
| Mondego Portugal | Measured | | | 372.0 (13.4) ⁴ | 397.5 (9.9) ⁴ | 430.0 (11.6) ⁴ | | | | | | Alexandrino (1996b) |
| Tejo Portugal | Measured | | 293.4 (18.3) ⁴ | 327.0 (13.1) ⁴ | 390.5 (25.0) ⁴ | | | | | | | Alexandrino (1996b) |
| Guadiana Portugal | Measured | | | 322.0 (25.0) ⁴ | 374.5 (5.2) ⁴ | 407.0 (25.0) ⁴ | | | | | | Alexandrino (1996b) |
| Loukos Morocco | Measured | | 224.0 (24.0) | 283.0 (27.0) | 312.0 (16.0) | 333.0 (17.0) | | | | | | Sabatié (1993) |
| Sebou Morocco | Backcalculated * Measured | 100.5 (19.0) | 190.6 (33.3) | 261.1 (27.0) | 304.9 (23.9) | 342.1* (22.3) | | | | | | Sabatié (1993) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

² Standard length (L_{st}) converted to total length using $L_t = 1.1896 L_{st} + 5.9359$ (Douchement, 1981).

³ Total sample ≤ 10 .

⁴ 95% Confidence intervals.

Table 3.47: Mean weight (g) and standard deviation (in brackets) in relation to age for anadromous male *Alosa fallax fallax*.

| River Country | Age (year) | | | | | | | | | | | Reference | |
|----------------------------|------------|--------------|----------------------|----------------------|----------|----------|--------------|--------------|--------------|----------|----|-----------|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | |
| Nyamunas , Lithuania | | | 323 | 552 | 624 | 735 | 890 | | | | | | Manyukas (1989) |
| Severn , England | | 166 | 183 (53) 293 (74) | 290 (62) 355 (70) | 428 (86) | 467 (90) | 537 (110) | 602 (107) | 640 (122) | 608 (90) | | | Claridge & Gardner (1978) Aprahamian (Unpubl.) |
| Wye, Wales | | | 320 (56) | 272 (58) | 380 (84) | 385 (66) | 643 | 478 | | | | | Aprahamian (Unpubl.) |
| Tywi, Wales | | | | | | 360 | 423 (64) | 449 (66) | | | | | Aprahamian (Unpubl.) |
| Seine, France | | 92 | 208 | | | | | | | | | | Roule (1922a) |
| Loire, France | | | 390 (85) | 505 (189) | | | | | | | | | Menesson- Boisneau & Boisneau (1990) |
| Loukos, Morocco | | 231 (260) | 238 (74) | 316 (63) | 361 (76) | | | | | | | | Sabatié (1993) |
| Sebou, Morocco | | 118 | 280 (95) | 329 (46) | 390 (64) | | | | | | | | Sabatié (1993) |

Table 3.48: Total length and standard deviation (mm) of anadromous female *Alosa fallax fallax*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | | Reference |
|-----------------------|--|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------------------|------------------------------|------------------------------|------------------------------|--|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |
| Nyamunas Lithuania | Measured ² | | | 368.2 | 388.2 | 450.3 | 477.6 | 496.6 | 521.6 | 563.2 | | | Manyukas (1989) |
| Elbe Germany | Measured | | | 364.6 | 407.2 | 410.2 | 446.8 | 446.8 | 471.6 | | | | Hass (1965) |
| Holland | Measured | | | | 365.0 | 412.1 (21.8) | 416.4 (27.2) | 453.8 (36.4) | 452.5 (31.8) | 465 | | | Aprahamian (1982 & unpubl.) |
| Severn England | Measured ² | | | | 365.3 (19.8) | 394.9 (18.7) | 410.6 (6.6) | | | | | | Claridge & Gardner (1978) |
| | Backcalculated ¹ ⁴ Measured | 88.6 (15.4) | 189.1 (30.8) | 279.8 (35.6) | 348.0 (28.6) | 385.9 (19.8) | 406.2 (18.4) | 419.4 (20.6) | 434.0 ⁴ (21.3) | 446.6 ⁴ (21.9) | 460.7 ⁴ (21.9) | 479.7 ⁴ (28.4) | Aprahamian (Unpubl.) |
| Wye Wales | Measured ¹ | | | | 357.1 (15.0) | 380.8 (16.0) | 394.3 (16.4) | 416.5 (8.4) | 432.3 | 449.2 (28.3) | | | Aprahamian (Unpubl.) |
| Tywi Wales | Measured ¹ | | | | | | 410.1 (21.9) | 428.5 (24.0) | 409.4 (36.0) | | | | Aprahamian (Unpubl.) |
| Barrow Ireland | Backcalculated ¹ | 60.6 (12.6) | 161.9 (28.3) | 263.4 (36.8) | 330.9 (31.1) | 363.7 (21.7) | 433.5 | 453.8 | | | | | O'Maoileidigh 1990 |
| Seine France | Measured ³ | | | 358.0 | 450.0 | 447.5 | | | | | | | Roule (1922a) |
| Loire France | Measured ¹ | | | 404.1 (21.3) | 450.4 (33.3) | 451.5 (23.2) | | | | | | | Mennesson- Boisneau & Boisneau (1990) |
| | Backcalculated | 90.5 (9.4) | 228.7 (26.8) | 325.7 (28.3) | 388.1 (25.9) | 428.9 (16.2) | 462.8 (15.9) | | | | | | Douchement (1981) |
| Charente France | Measured | | | 418.8 (14.3) | 438.7 (24.9) | 467.7 (39.1) | | | | | | | Véron (1999) |

Table 3.48: (cont) Total length and standard deviation (mm) of anadromous female *Alosa fallax fallax*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | | Reference |
|--|------------------------------|-----------------|-----------------|------------------------------|------------------------------|------------------------------|------------------------------|----------------|----------------|---|----|----|------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |
| Gironde – Garonne – Dordogne France | Backcalculated ¹ | 68.5 (3.5) | 169.9 (9.2) | 264.5 (11.4) | 356.9 (17.1) | 397.4 (13.7) | 428.9 (33.0) | | | | | | Anon. (1979a) |
| | Backcalculated | 67.0 (8.3) | 205.0 (26.7) | 311.7 (27.3) | 372.1 (20.7) | 412.5 (21.1) | | | | | | | Douchement (1981) |
| | Backcalculated | 101.0 (13.8) | 201.7 (30.4) | 284.4 (36.2) | 347.8 (32.2) | 369.3 (18.2) | | | | | | | Taverny (1991a) |
| Adour France | Backcalculated | 83.8 (10.4) | 205.1 (18.3) | 294.2 (17.3) | 361.2 (15.7) | 408.0 (16.8) | 445.0 (16.3) | 468.8 (8.9) | 490.5 (5.0) | | | | Douchement (1981) |
| Lima Portugal | Measured | | | 386.9 (17.2) ⁴ | 412.5 (11.2) ⁴ | 455.5 (15.8) ⁴ | | | | | | | Alexandrino (1996b) |
| Mondego Portugal | Measured | | | | 431.2 (11.2) ⁴ | 468.0 (8.9) ⁴ | | | | | | | Alexandrino (1996b) |
| Tejo Portugal | Measured | | | 365.0 (5.9) ⁴ | 408.6 (8.6) ⁴ | 439.3 (23.9) ⁴ | | | | | | | Alexandrino (1996b) |
| Guadiana Portugal | Measured | | | | 404.7 (20.0) ⁴ | 420.0 (72.0) ⁴ | 465.0 (72.0) ⁴ | | | | | | Alexandrino (1996b) |
| Loukos Morocco | Measured | | 215.0 (10.0) | 275.0 (7.0) | 376.0 (32.0) | 393.0 (15.0) | | | | | | | Sabatié (1993) |
| Sebou Morocco | Backcalculated * Measured | 98.2 (21.0) | 199.7 (33.4) | 292.0 (41.5) | 350.0 (27.3) | 386.4 (20.1) | 406.2* (17.2) | | | | | | Sabatié (1993) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

² Standard length (L_{st}) converted to total length using $L_t = 1.1896 L_{st} + 5.9359$ (Douchement, 1981).

³ Total sample ≤ 10 .

⁴ 95% Confidence intervals

Table 3.49: Mean weight (g) and standard deviation (in brackets) in relation to age for anadromous female *Alosa fallax fallax*.

| River Country | Age (year) | | | | | | | | | | | Reference | |
|--|------------|---------|-----------|-----------|-----------|-----------|-----------|-------------------|-----------|-----------|------------|-----------|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | |
| Nyamunas Lithuania | | | 353 | 448 | 643 | 769 | 810 | 1183 ¹ | 1487 | | | | Manyukas (1989) |
| Severn England | | | 426 (81) | 535 (101) | 596 (102) | 661 (109) | 725 (133) | 834 (159) | 921 (176) | 968 (178) | 1031 (165) | | Claridge & Gardner (1978) Arahamian (Unpubl.) |
| Wye Wales | | | | 446 (58) | 556 (76) | 556 (97) | 635 (81) | 745 | 775 (247) | | | | Arahamian (Unpubl.) |
| Tywi Wales | | | | | | 582 (93) | 568 (85) | 576 (149) | | | | | Arahamian (Unpubl.) |
| Seine France | | | 380 | 565 | 798 | | | | | | | | Roule (1922a) |
| Loire France | | | 647 (144) | 870 (184) | 848 (162) | | | | | | | | Mennesson- Boisneau & Boisneau (1990) |
| Gironde – Garonne – Dordogne France | | | | 696 (78) | 885 (214) | 842 (414) | | | | | | | Taverny (1991a) |
| Loukos Morocco | | 84 (15) | 161 | 551 (170) | 328 (81) | | | | | | | | Sabatié (1993) |
| Sebou Morocco | | | 502 (103) | 548 (116) | 626 (119) | 759 (138) | | | | | | | Sabatié (1993) |

¹Estimated

Table 3.50: von Bertalanffy growth parameters for male and female anadromous *Alosa fallax fallax*, 95% confidence intervals in brackets.

| River Country | Male | | | Female | | | Reference |
|--|---------------|---------------|-------|---------------|---------------|-------|-------------------------|
| | K | L_{∞} | T_0 | K | L_{∞} | T_0 | |
| Severn England | 0.393 (0.083) | 421.7 (20.4) | 0.428 | 0.345 (0.058) | 478.1 (20.2) | 0.413 | Aprahamian (unpubl.) |
| Barrow Ireland | 0.485 (0.128) | 383.8 (28.2) | 0.634 | 0.288 (0.184) | 511.4 (169.4) | 0.570 | O'Maoileidigh (1990) |
| Loire France | 0.517 (0.130) | 442.8 (33.6) | 0.582 | 0.383 (0.103) | 525.5 (50.0) | 0.506 | Douchement (1981) |
| Gironde – Garonne – Dordogne France | 0.265 (0.187) | 531.3 (225.6) | 0.441 | 0.259 (0.005) | 577.1 (5.2) | 0.552 | Anon. (1979a) |
| | 0.543 (0.210) | 387.6 (56.7) | 0.612 | 0.403 (0.152) | 500.4 (82.3) | 0.644 | Douchement (1981) |
| | 0.479 (0.415) | 350.2 (129.3) | 0.484 | 0.367 (0.216) | 453.0 (102.7) | 0.317 | Taverny (1991a) |
| Adour France | | | | 0.305 (0.035) | 544.8 (17.7) | 0.451 | Douchement (1981) |
| Sebou Morocco | 0.324 (0.238) | 432.6 (136.6) | 0.184 | 0.372 (0.154) | 466.6 (63.6) | 0.379 | Sabatié (1993) |

Table 3.51: Maximum length (total) and weight of anadromous *A. fallax fallax* recorded from a number of river systems.

| River (Country) | Male | | Female | | Reference |
|-----------------------------------|------------------|------------------|------------------|------------------|-------------------------------------|
| | L _{max} | W _{max} | L _{max} | W _{max} | |
| Nyamunas (Lithuania) | 508.5 | 930 | 568.0 | 1520 | Manyukas (1989) |
| Rhine (Germany) | 378.0 | 430 | 500.0 | 1350 | Hoek (1899) |
| Severn (England) | 482.8 | 951 | 513.4 | 1448 | Aprahamian (unpubl) |
| Loire (France) | 410.0 | 510 | 500.0 | 940 | Douchement (1981) |
| | 501.0 | 1000 | 523.6 | 1408 | Menesson-Boisneau & Boisneau (1990) |
| Gironde-Garonne-Dordogne (France) | 399.0 | 550 | 489.6 | 1120 | Anon. (1979a) |
| | 380.0 | 340 | 510.0 | 750 | Douchement (1981) |
| | 450.0 | 610 | 519.0 | 1210 | Taverny (1991a) |
| Lima (Portugal) | 468.0 | 1040 | 560.0 | 1920 | Alexandrino (1996b) |
| Mondego (Portugal) | 440.0 | 762 | 486.0 | 1123 | Alexandrino (1996b) |
| Tejo (Portugal) | 418.0 | 612 | 460.0 | 905 | Alexandrino (1996b) |
| Guadiana (Portugal) | 407.0 | 670 | 465.0 | 912 | Alexandrino (1996b) |
| Adour (France) | 430.0 | 660 | 495.0 | 925 | Douchement (1981) |
| Sebou (Morocco) | 430.0 | 620 | 460.0 | 1080 | Sabatié (1993) |

Table 3.52: Parameters for the equation weight (g) = aLength^b (mm) for male *Alosa fallax fallax*.

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|----------------------------------|--------------------|----------------------|--|-------------|---------|----------------|-------------------------|----------------|---|
| Nyamunas, Lithuania | Adult | L _t (mm) | 9.658. 10 ⁻⁷ | 3.327 | | | 342-509 | 274-930 | Manyukas (1989) |
| Rhine, Germany | Adult | L _t (mm) | 9.772. 10 ⁻⁴ | 2.205 | 8 | 0.73 | 316-378 | 280-430 | Hoek (1899) |
| | | L _t (mm) | 2.003. 10 ⁻⁷ | 3.630 | 13 | 0.74 | 330-350 | 283-327 | Jenkins (1902) |
| Severn (England) | Adult ¹ | L _{st} (mm) | 1.014.10 ⁻⁵ | 3.038 | 39 | 0.98 | 288-416 | 183-568 | Claridge & Gardner (1978) Aprahamian (unpubl.) |
| | | L _t (mm) | 9.775.10 ⁻⁶ | 2.992 | 1329 | 0.84 | 259-481 | 143-951 | |
| Wye (Wales) | Adult | L _t (mm) | 2.173.10 ⁻⁶ | 3.237 | 77 | 0.88 | 266-412 | 157-643 | Aprahamian (unpubl.) |
| Barrow (Ireland) | Adult | L _f (cm) | 1.445.10 ⁻² - 4.786.10 ⁻³ | 3.28 – 2.93 | 16 - 17 | 0.76 – 0.83 | 320-423 | | O'Maoileidigh (1990) |
| Loire (France) | Adult | L _t (mm) | 6.168.10 ⁻⁵ | 2.677 | 63 | 0.90 | 270-420 | 225-635 | Douchement (1981) |
| | | L _f (mm) | 1.578.10 ⁻² | 2.696 | 26 | 0.92 | 290-501 | | Menesson-Boisneau & Boisneau (1990) |
| Gironde-Garonne-Dordogne, France | Adult | L _t (mm) | 7.109.10 ⁻⁵ | 2.620 | 66 | 0.81 | 270-380 | 155-430 | Douchement (1981) |
| Lima (Portugal) | Adult | L _t (cm) | 0.003 | 3.319 | 49 | 0.90 | 284-468 | 163-1040 | Alexandrino (1996b) |
| Mondego (Portugal) | Adult | L _t (cm) | 0.011 | 2.912 | 25 | 0.81 | 349-440 | 348-762 | Alexandrino (1996b) |
| Tejo (Portugal) | Adult | L _t (cm) | 0.006 | 3.090 | 21 | 0.88 | 274-418 | 177-612 | Alexandrino (1996b) |
| Guadiana (Portugal) | Adult | L _t (cm) | 0.014 | 2.884 | 25 | 0.55 | 322-407 | 268-670 | Alexandrino (1996b) |
| Loukos (Morocco) | Adult ¹ | L _t (mm) | 2.616.10 ⁻⁶ | 3.377 | 56 | 0.98 | 195-415 | | Sabatié (1993) |
| Sebou (Morocco) | Adult | L _t (mm) | 6.503.10 ⁻⁶ | 3.069 | 271 | 0.86 | 245-390 | 118-500 | Sabatié (1993) |

¹ Male & Female combined

Table 3.53: Parameters for the equation $\text{weight (g)} = a\text{Length}^b \text{ (mm)}$ for female *Alosa fallax fallax*.

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|----------------------------------|------------|---------------------|-----------------------|-------|------|----------------|-------------------------|----------------|--------------------------------------|
| Nyamunas, Lithuania | Adult | L _t (mm) | $5.076 \cdot 10^{-6}$ | 3.060 | | | 354-568 | 325-1535 | Manyukas (1989) |
| Rhine, Germany | Adult | L _t (mm) | $5.395 \cdot 10^{-7}$ | 3.479 | 5 | 0.86 | 396-500 | 630-1350 | Hoek (1899) |
| | | L _t (mm) | $3.095 \cdot 10^{-6}$ | 3.187 | 10 | 0.83 | 380-480 | 503-1041 | Jenkins (1902) |
| Severn, England | Adult | L _t (mm) | $1.147 \cdot 10^{-5}$ | 2.977 | 3784 | 0.76 | 295-530 | 220-1448 | Aprahamian (unpubl.) |
| Wye (Wales) | Adult | L _t (mm) | $2.080 \cdot 10^{-4}$ | 2.486 | 150 | 0.67 | 326-477 | 333-1050 | Aprahamian (unpubl.) |
| Barrow, Ireland | Adult | L _f (cm) | $3.090 \cdot 10^{-3}$ | 3.390 | 19 | 0.85 | 342-456 | | O'Maoileidigh (1990) |
| Loire, France | Adult | L _t (mm) | $1.944 \cdot 10^{-5}$ | 2.892 | 76 | 0.90 | 350-500 | 520-1230 | Douchement (1981) |
| | | L _f (mm) | $4.914 \cdot 10^{-2}$ | 2.286 | 34 | 0.57 | 377-524 | | Mennesson-Boisneau & Boisneau (1990) |
| Gironde-Garonne-Dordogne, France | Adult | L _t (mm) | $3.256 \cdot 10^{-5}$ | 2.787 | 165 | 0.72 | 330-510 | 335-2480 | Douchement (1981) |
| Lima, Portugal | Adult | L _t (cm) | 0.004 | 3.260 | 45 | 0.72 | 342-560 | 388-1920 | Alexandrino (1996b) |
| Mondego, Portugal | Adult | L _t (cm) | 0.030 | 2.670 | 13 | 0.40 | 425-486 | 551-1123 | Alexandrino (1996b) |
| Tejo, Portugal | Adult | L _t (cm) | 0.295 | 2.051 | 78 | 0.71 | 316-460 | 318-905 | Alexandrino (1996b) |
| Guadiana, Portugal | Adult | L _t (cm) | 0.818 | 1.287 | 15 | 0.30 | 306-465 | 531-912 | Alexandrino (1996b) |
| Sebou, Morocco | Adult | L _t (mm) | $1.127 \cdot 10^{-6}$ | 3.374 | 180 | 0.93 | 315-460 | 310-1080 | Sabatié (1993) |

Table 3.54: Parameters for the equation weight (g) = aLength^b (mm) for juvenile (age 0+ and 1+) *Alosa fallax fallax*.

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) mm | Range (weight) g | Reference |
|--------------------------------------|------------|----------------------|--|---------------|----------|----------------|----------------------------|------------------|---------------------------|
| Elbe, Germany | 0+&1+ | L _t (cm) | 1.248.10 ⁻² | 2.755 | 177 | 0.99 | 36-126 | 0.1-13.6 | Oesmann (1994) |
| Severn, England | 0+ | L _{st} (mm) | 4.256.10 ⁻⁵ – 4.786.10 ⁻⁶ | 2.725 – 3.248 | 21- 400 | 0.80 – 0.93 | | | Claridge & Gardner (1978) |
| | 0+ | | 3.330.10 ⁻⁷ | 3.700 | 796 | 0.96 | 24-95 | 0.02-4.7 | Aprahamian (unpubl.) |
| | 1+ | L _t (mm) | 1.327.10 ⁻⁷ | 3.824 | 84 | 0.98 | 57-168 | 0.7-34.8 | Aprahamian (unpubl.) |
| | | L _t (mm) | | | | | | | Aprahamian (unpubl.) |
| Wye, Wales | 0+ | L _t (mm) | 2.237.10 ⁻⁸ | 4.363 | 216 | 0.93 | 24-54 | 0.01-0.7 | Aprahamian (unpubl.) |
| Gironde - Garonne - Dordogne, France | 0+ | L _t (mm) | 7.363.10 ⁻⁶ – 1.986.10 ⁻⁵ | 2.772 - 2.986 | 64 -1189 | 0.96 - 0.98 | 52-118 | 1.0-12.9 | Taverny (1991a) |
| Sebou, Morocco | 0+ | L _t (mm) | 5.419.10 ⁻⁶ | 3.124 | 386 | 0.95 | 35-149 | 0.9-14.6 | Sabatié (1993) |

Alosa fallax rhodanensis

In the Rhône, France, spawning takes place during May and June (Baglinière *et al.*, 2001; Le Corre, pers. comm.). By June – July the juveniles in the main river had reached a modal length (L_t) of 34 mm while that had migrated in to the Vaccarès lagoon were slightly larger with a modal size of 40 mm (Crivelli & Poizat, 2001). The modal length for those in the main river had increased to between 80 and 90 mm by September while those in the Lagoon were significantly ($P < 0.001$) larger at between 120 and 140 mm. For those fish that remained in the Lagoon until January, the fish had reached a mean length of 182.9 ± 24.3 mm and weight of 53.9 ± 22.4 g (Crivelli & Poizat, 2001). In the lagoon the growth rate between July 17th and December 17th was linear and varied from 0.86 and 1.36 mm day⁻¹ between years, once temperatures fell to below 10 to 11°C little growth occurred (Crivelli & Poizat, 2001). In an earlier study, Gallois (1947a) reported that by November the 0+ age group had reached between 57 and 109 mm (L_t) with a mean ($\pm 95\%$ CI) of 68.8 ± 12.0 mm, which is smaller than that reported by Menella & Tabardel (1994), Tabardel *et al.* (1995) and Gendre *et al.* (1997a). These authors reported a range in size from 67 to 197 mm¹ by the autumn of their first year. The mean length of the 0+ juveniles in those years when reasonable numbers were obtained was 98.9 and 91.0 mm¹, for fish caught between September and November.

In the Tiber (Italy) growth in the first year was faster than in French populations, though not for those which had migrated into the Vaccarès lagoon (Crivelli & Poizat, 2001); however in older age groups growth was faster in French stocks (Tables 3.55 & 3.57). French stocks were heavier than those from the Tiber when fish of the same age were compared (Tables 3.56 & 3.58).

The parameters for the von Bertalanffy growth model have been recalculated using data from Tables 3.55 & 3.57, and are presented in Table 3.59 for both male and female *A. fallax rhodanensis*. The value of K ranged from 0.272 to 0.377 year⁻¹ for males and 0.137 to 0.347 year⁻¹ for females. L_∞ varied between 549 to 566 mm and 602 to 801 mm for males and females, respectively. There was no significant difference between the K and L_∞ for the rivers Aude and Rhône ($P > 0.05$). No comparison with the parameters from the Tiber was possible as the latter were based on mean length at age data and no information on variability was available.

The maximum length (total) and weight recorded for *Alosa fallax rhodanensis* from the Rhône was 569 mm¹ and 676 mm¹ and 1627 g and 3010 g for males and females, respectively (Le Corre *et al.*, 1997a). From the Aude, France, Douchement (1981) reported a maximum length of 505 for males and 615 mm for females. For stock from the River Tirso, Sardinia, the maximum length recorded was smaller, 440 mm for females and 402 mm for males (Cottiglia, 1963a). For both sexes from the rivers Aude and Rhône there was reasonable agreement between the maximum length recorded and L_4 .

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

The allometric growth parameter (b) for both adult and immature male *Alosa fallax rhodanensis* ranged from 2.34 to 3.42, and for females from 2.54 to 3.29 (Tables 3.60 & 3.61).

Table 3.55: Total length and standard deviation (mm) of male *Alosa fallax rhodanensis*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | Reference |
|---------------|-----------------------------|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-------|-------|---|--------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| Aude France | Backcalculated | 86.7 (15.7) | 225.0 (29.2) | 330.7 (26.5) | 401.7 (25.1) | 448.0 (18.8) | | | | | Douchement (1981) |
| Rhône France | Backcalculated | 97.0 (12.8) | 237.0 (24.7) | 336.2 (22.5) | 409.9 (18.1) | 448.3 (20.5) | | | | | Douchement (1981) |
| | Measured ¹ | | | 398.9 (32.0) | 422.5 (29.9) | 470.6 (41.7) | 501.2 (34.6) | 543.9 | 532.5 | | Le Corre <i>et al.</i> (1997a) |
| Tiber Italy | Backcalculated ¹ | 143.3 | 230.9 | 305.3 | 366.3 | 414.1 | 448.5 | 469.7 | 477.6 | | D'Ancona (1927c) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

Table 3.56: Mean weight and standard deviation (g) in relation to age for anadromous male *Alosa fallax rhodanensis*.

| River Country | Age (year) | | | | | | | | | Reference |
|---------------|------------|-----|-----------|-----------|-----------|------------|------------|------|--------------------------------|-------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| Aude, France | 17 | 156 | 395 | 659 | 900 | | | | | Douchement (1981) |
| Rhône, France | 19 | 166 | 409 | 667 | 896 | | | | | Douchement (1981) |
| | | | 540 (114) | 620 (142) | 911 (278) | 1033 (277) | 1436 (149) | 1007 | Le Corre <i>et al.</i> (1997a) | |
| Tiber, Italy | 20 | 50 | 140 | 305 | 510 | 645 | 700 | 720 | | D'Ancona (1927c) |

Table 3.57: Total length and standard deviation (mm) of female *Alosa fallax rhodanensis*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | Reference |
|---------------|-----------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-------|--------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| Aude France | Backcalculated | 89.1 (15.2) | 236.0 (29.3) | 338.4 (31.4) | 425.7 (28.5) | 483.0 (21.0) | 535.2 (21.4) | 557.6 (25.2) | 586.3 (16.5) | | Douchement (1981) |
| Rhône France | Backcalculated | 101.0 (11.9) | 238.2 (22.4) | 349.1 (27.7) | 433.4 (27.7) | 485.3 (25.9) | 510.7 (15.6) | 536.1 (25.0) | | | Douchement (1981) |
| | Measured ¹ | | | 445.3 (36.9) | 494.3 (31.7) | 524.4 (31.6) | 557.2 (32.1) | 576.3 (39.4) | 596.4 (34.7) | | Le Corre <i>et al.</i> (1997a) |
| Tiber Italy | Backcalculated ¹ | 149.2 | 227.7 | 299.1 | 362.8 | 420.9 | 471.4 | 518.4 | 551.3 | 572.5 | D'Ancona (1927c) |

¹ Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981).

Table 3.58: Mean weight and standard deviation (g) in relation to age for anadromous female *Alosa fallax rhodanensis*.

| River Country | Age (year) | | | | | | | | | Reference |
|---------------|------------|-----|-----------|------------|-----------|------------|------------|------------|------|--------------------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| Aude, France | 10 | 136 | 418 | 792 | 1190 | 1563 | 1890 | 2161 | | Douchement (1981) |
| Rhône, France | 19 | 190 | 498 | 847 | 1172 | 1443 | 1657 | | | Douchement (1981) |
| | | | 917 (266) | 1128 (276) | 1361(289) | 1642 (307) | 1683 (396) | 2169 (370) | | Le Corre <i>et al.</i> (1997a) |
| Tiber, Italy | 20 | 55 | 130 | 295 | 575 | 885 | 1125 | 1250 | 1300 | D'Ancona (1927c) |

Table 3.59: von Bertalanffy growth parameters for male and female anadromous *Alosa fallax rhodanensis*, 95% confidence intervals in brackets.

| River Country | Male | | | Female | | | Reference |
|------------------|---------------|---------------|--------|---------------|--------------|--------|-------------------|
| | K | L_{∞} | T_0 | K | L_{∞} | T_0 | |
| Aude France | 0.353 (0.144) | 566.0 (103.0) | 0.531 | 0.297 (0.053) | 657.9 (42.0) | 0.511 | Douchement (1981) |
| Rhône France | 0.377 (0.137) | 552.4 (87.1) | 0.490 | 0.347 (0.076) | 601.6 (46.5) | 0.477 | Douchement (1981) |
| Tiber Italy | 0.272 (0.003) | 549.2 (2.4) | -0.077 | 0.137 (0.002) | 800.5 (6.3) | -0.469 | D’Ancona (1927c) |

Table 3.60: Parameters for the equation weight (g) = aLength^b (mm) for male *Alosa fallax rhodanensis*.

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|--------------------|----------------|---------------------|--|------------------|--------|----------------|-------------------------|-------------------|---|
| Aude France | Imm. | L _t (mm) | 3.431.10 ⁻⁶ | 3.158 | 427 | 0.98 | 130-380 | 16-490 | Douchement (1981) |
| | Adult | | 2.176.10 ⁻⁵ | 2.864 | 83 | 0.88 | 330-500 | 385-1365 | Douchement (1981) |
| Rhône France | Juv. | L _f (mm) | 4.420.10 ⁻⁶ | 3.198 | | 0.96 | 60-120 | 2-20 | Tabardel <i>et al.</i> (1995) |
| | Imm. | L _t (mm) | 3.605.10 ⁻⁶ | 3.147 | 146 | 0.97 | 170-380 | 30-525 | Douchement (1981) |
| | Adult | L _t (mm) | 1.317.10 ⁻⁵ | 2.944 | 196 | 0.88 | 330-500 | 365-1290 | Douchement (1981) |
| | Adult | L _f (mm) | 1.000.10 ⁻⁶ – 6.000.10 ⁻⁴ | 2.340 – 3.420 | 79-314 | 0.67-0.92 | 135-500 | 335-1627 | Douchement (1981) Le Corre <i>et al.</i> (1997a) |
| Tiber Italy | Juv & Adult | L _t (mm) | 2.201.10 ⁻⁶ | 3.174 | | | | | D’Ancona (1927c) |

Table 3.61: Parameters for the equation weight (g) = aLength^b (mm) for male *Alosa fallax rhodanensis*.

| River (Country) | Life stage | Length | a | b | n | R ² | Range (L _t) | Range (weight) | Reference |
|-----------------|----------------|---------------------|---|------------------|---------|----------------|-------------------------|----------------|--------------------------------|
| Aude France | Imm. | L _t (mm) | 2.786.10 ⁻⁶ | 3.198 | 429 | 0.98 | 130-380 | 16-490 | Douchement (1981) |
| | Adult | | 1.611.10 ⁻⁶ | 3.294 | 43 | 0.64 | 450-580 | 1000-2060 | Douchement (1981) |
| Rhône France | Imm. | L _t (mm) | 4.615.10 ⁻⁶ | 3.102 | 135 | 0.98 | 170-380 | 30-525 | Douchement (1981) |
| | Adult | L _t (mm) | 7.516.10 ⁻⁶ | 3.051 | 102 | 0.86 | 410-600 | 650-2480 | Douchement (1981) |
| | Adult | L _f (mm) | 1.000.10 ⁻⁴ – 2.000.10 ⁻⁴ | 2.540 – 2.660 | 154-342 | 0.54-0.67 | 335-595 | 110-3010 | Le Corre <i>et al.</i> (1997a) |
| Tiber Italy | Juv & Adult | L _t (mm) | 9.779.10 ⁻⁷ | 3.320 | | | | | D'Ancona (1927c) |

Alosa fallax nilotica

For male and female *A. fallax nilotica*, length and weight at age data are shown in Tables 3.62 & 3.63 and 3.64 & 3.65. For fish of a given age the River Po population is smaller at ages one and two compared with populations from the Balkans, though for fish three years and older there is little difference in length at age (Vukovic, 1961a; Serventi *et al.*, 1990). The maximum size would appear to be greater in the Balkan populations, with males reaching at least 508 to 543 mm and females 546 to 560 mm, compared with 454 and 477 mm for males and females from the Po river. Females were heavier than males with a maximum weight of 2.4 kg compared to 1.9 kg for males.

The value of the von Bertalanffy parameters K and L_{∞} were calculated from the length at age data in Tables 3.62 & 3.64, and ranged from 0.07 to 0.30 year⁻¹ and from 521 to 973 mm for males and between 0.11 and 0.27 year⁻¹ and from 567 to 792 mm for females (Table 3.66). There was no significant difference in K and L_4 between the stocks for either sex ($P > 0.05$). The allometric growth coefficient (b) was based on mean length and weight at age data and ranged from 3.18 to 3.61 for males and 2.72 to 3.46 for females (Table 3.67).

Alosa fallax algeriensis

Growth rate was faster for females than for males in terms of length (Tables 3.68 & 3.70) and weight (Tables 3.69 & 3.71). Significant differences ($P < 0.05$) existed in the von Bertalanffy growth parameters between the sexes and between stocks (Table 3.72), based on mean values. The coefficients for the length - weight regression are shown in Table 3.73.

Alosa fallax lacustris

In Lake Maggiore, Italy, Berg & Grimaldi (1966a) reported that the growth rate of female *Alosa fallax lacustris* was greater than that for males (Table 3.74). Ferrero (1951) reported a range in size of 182 to 268 mm for mature *Alosa fallax lacustris* at age 2 in Lake Maggiore, which was similar to that reported for specimens from Lake Iseo of between 171 and 237 mm. Oppi & Novello (1989) reported a similar growth rate for the Lake Garda population (Table 3.74). For the populations inhabiting the mid-Italian lakes Bracciano and Bolsena, growth rate was greater than that for populations from Northern Italy, with fish reaching 253 mm at age two and 303 mm at age three (Ferrero, 1951).

For the populations inhabiting the lakes of Northern Italy the maximum length of populations was 500 mm (Lake Maggiore) [Berg & Grimaldi, 1966a] and 400 mm (Lake Garda) [Fatio, 1890]. For Sardinian stocks the maximum length reached for males and females in Lake Flumendosa was 396 and 395 mm (L_f) respectively (Cottiglia, 1969) while in Lake Omodeo males reach 256 mm and females 277 mm (L_f) [Cottiglia, 1963b].

Table 3.62: Total length and standard deviation (mm) of male *Alosa fallax nilotica*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | Reference |
|------------------|---|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------------------|-------|--------------------|----------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Po Italy | Backcalculated | 136.8 (25.8) | 228.5 (31.4) | 308.6 (32.1) | 364.0 (28.7) | 405.3 (27.4) | 429.7 (34.1) | 453.5 (75.7) | | | | Serventi <i>et al.</i> (1990) |
| Neretva | Backcalculated ⁴ Measured | 202.8 (14.6) | 268.0 (14.8) | 312.6 (16.5) | 355.8 (18.4) | 396.4 (17.9) | 438.3 (14.1) | 482.5 (15.2) | 512.0 | 521.0 | 543.0 ⁴ | Vukovic (1961a) |
| L.Skadar | Backcalculated | 207.2 (13.4) | 272.3 (16.9) | 322.3 (20.4) | 369.1 (17.3) | 400.5 (18.0) | 441.7 (13.2) | 475.2 (9.0) | 495.0 (5.2) | 520.0 | | Vukovic (1961a) |
| L.Bačin | Backcalculated ⁴ Measured | 200.0 (12.9) | 262.3 (11.9) | 307.9 (17.6) | 343.9 (20.4) | 383.3 (22.3) | 446.6 (7.0) | 480.0 | 508.0 ⁴ (12.2) | | | Vukovic (1961a) |

Table 3.63: Mean weight (g) in relation to age for male *Alosa fallax nilotica*.

| River Country | Age (year) | | | | | | | | | | Reference |
|------------------|------------|-----|-----|-----|-----|------|------|------|------|----|--------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Neretva | | 213 | 466 | 621 | 893 | 1377 | 1569 | 1920 | | | Vukovic (1961a) |
| L.Skadar | 101 | 198 | 275 | 658 | 785 | 1045 | 1198 | 1366 | 1372 | | Vukovic (1961a) |
| L.Bačin | 41 | 144 | 254 | 348 | 552 | 871 | 1200 | 1213 | | | Vukovic (1961a) |

Table 3.64: Total length and standard deviation (mm) of female *Alosa fallax nilotica*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | Reference |
|---------------|---|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|------------------------------|--------------------|-------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Po Italy | Backcalculated | 135.1 (23.6) | 231.7 (37.7) | 310.4 (38.1) | 376.3 (37.4) | 423.1 (33.9) | 457.0 (31.8) | 477.3 (29.0) | | | | Serventi <i>et al.</i> (1990) |
| Neretva | Backcalculated ⁴ Measured | 213.9 (13.8) | 280.4 (14.4) | 331.1 (15.2) | 378.4 (16.4) | 418.4 (17.8) | 459.3 (16.3) | 492.1 (15.3) | 524.0 (22.6) | 552.5 (19.2) | 560.0 ⁴ | Vukovic (1961a) |
| L.Skadar | Backcalculated | 212.9 (14.1) | 283.3 (17.2) | 337.2 (18.6) | 382.9 (18.7) | 422.7 (17.2) | 455.9 (16.0) | 487.8 (13.0) | 516.1 (13.2) | 538.8 (16.9) | 554.0 (14.1) | Vukovic (1961a) |
| L.Bačin | Backcalculated ⁴ Measured | 201.9 (14.5) | 267.8 (19.1) | 319.0 (13.0) | 362.2 (19.0) | 407.2 (18.4) | 445.2 (15.3) | 478.5 (13.5) | 510.0 (13.1) | 546.0 ⁴ (19.3) | | Vukovic (1961a) |

Table 3.65: Mean weight (g) in relation to age for female *Alosa fallax nilotica*.

| River Country | Age (year) | | | | | | | | | | Reference |
|---------------|------------|-----|-----|-----|------|------|------|------|------|------|-----------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Neretva | | | 467 | 759 | 1158 | 1481 | 1663 | 1980 | 2379 | | Vukovic (1961a) |
| L.Skadar | 92 | 208 | 234 | 788 | 972 | 1182 | 1492 | 1496 | 1840 | 1953 | Vukovic (1961a) |
| L.Bačin | 38 | 147 | 284 | 385 | 645 | 995 | 1359 | 1480 | 1701 | | Vukovic (1961a) |

Table 3.66: von Bertalanffy growth parameters for male and female anadromous *Alosa fallax nilotica*, 95% confidence intervals in brackets.

| River Country | Male | | | Female | | | Reference |
|------------------|---------------|---------------|--------|---------------|---------------|--------|-------------------------------|
| | K | L_{∞} | T_0 | K | L_{∞} | T_0 | |
| Po, Italy | 0.296 (0.167) | 521.3 (115.1) | -0.016 | 0.269 (0.130) | 567.0 (104.0) | -0.001 | Serventi <i>et al.</i> (1990) |
| Neretva | 0.073 (0.078) | 972.9 (658.4) | -2.283 | 0.115 (0.047) | 772.1 (152.0) | -1.857 | Vukovic (1961a) |
| L.Skadar | 0.153 (0.047) | 646.3 (76.4) | -1.536 | 0.155 (0.038) | 667.2 (59.6) | -1.503 | Vukovic (1961a) |
| L.Bačín | 0.088 (0.047) | 873.3 (262.8) | -2.024 | 0.106 (0.046) | 792.1 (172.0) | -1.826 | Vukovic (1961a) |

Table 3.67: Parameters for the equation weight (g) = $aLength^b$ (mm) for male and female *Alosa fallax nilotica*, based on mean length and weight at age data.

| River (Country) | Life stage | Length | Male | | Female | | Reference |
|-----------------|-------------|------------|-----------------------|-------|-----------------------|-------|-----------------|
| | | | a | b | a | b | |
| Neretva | Adult | L_t (mm) | $3.327 \cdot 10^{-7}$ | 3.612 | $8.155 \cdot 10^{-5}$ | 2.716 | Vukovic (1961a) |
| L.Skadar | Juv & Adult | L_t (mm) | $3.770 \cdot 10^{-6}$ | 3.181 | $1.224 \cdot 10^{-6}$ | 3.366 | Vukovic (1961a) |
| L.Bačín | Juv & Adult | L_t (mm) | $1.351 \cdot 10^{-6}$ | 3.321 | $6.042 \cdot 10^{-7}$ | 3.460 | Vukovic (1961a) |

Table 3.68: Mean or range in total length (mm) of male *Alosa fallax algeriensis*.

| River Country | Actual / Backcalculated | Age (year) | | | | | | | | | | Reference |
|-----------------------------------|----------------------------|------------|---------|---------|---------|---------|-----|-----|-----|-----|----|--------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| L. Ichkeul Tunisia | | 136 | 216 | 263 | 290 | 306 | 315 | 320 | | | | Kartas (1981) |
| Miliane & Medjerah, Tunisia | | 118 | 203 | 268 | 319 | 358 | 388 | 412 | 430 | 444 | | Kartas (1981) |
| Mazafran, Algeria | | 130 | 180-190 | 250-260 | 270-280 | 290-300 | | | | | | Bounhiol (1917) |

Table 3.69: Mean weight (g) of male *Alosa fallax algeriensis*.

| River Country | Age (year) | | | | | | | | | | Reference |
|--------------------------------------|------------|----|-----|-----|-----|-----|-----|-----|-----|----|---------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| L. Ichkeul, Tunisia | 17 | 84 | 164 | 229 | 274 | 303 | 321 | | | | Kartas (1981) |
| Miliane & Medjerah, Tunisia | 11 | 64 | 156 | 273 | 396 | 512 | 621 | 713 | 790 | | Kartas (1981) |

Table 3.70: Mean or range in total length (mm) of female *Alosa fallax algeriensis*.

| River Country | Measured / Backcalculated | Age (year) | | | | | | | | | | Reference |
|-----------------------------------|------------------------------|------------|---------|---------|---------|---------|-----|-----|-----|-----|----|--------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| L. Ichkeul Tunisia | | 136 | 223 | 279 | 316 | 340 | 355 | 366 | | | | Kartas (1981) |
| Miliane & Medjerah, Tunisia | | 119 | 206 | 276 | 331 | 376 | 411 | 439 | 461 | 479 | | Kartas (1981) |
| Mazafran, Algeria | | 160-170 | 220-230 | 300-320 | 330-350 | 380-400 | | | | | | Bounhiol (1917) |

Table 3.71: Mean weight (g) of female *Alosa fallax algeriensis*.

| River Country | Age (year) | | | | | | | | | | Reference |
|-------------------------------|------------|----|-----|-----|-----|-----|-----|-----|------|----|---------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| L. Ichkeul Tunisia | 17 | 88 | 187 | 282 | 360 | 417 | 458 | | | | Kartas (1981) |
| Miliane & Medjerah Tunisia | 11 | 66 | 170 | 306 | 462 | 617 | 764 | 895 | 1013 | | Kartas (1981) |

Table 3.72: von Bertalanffy growth parameters for male and female anadromous *Alosa fallax algeriensis*, 95% confidence intervals in brackets.

| River Country | Male | | | Female | | | Reference |
|-----------------------------------|---------------|--------------|--------|---------------|--------------|--------|--------------------|
| | K | L_{∞} | T_0 | K | L_{∞} | T_0 | |
| L. Ichkeul Tunisia | 0.543 (0.010) | 327.6 (1.1) | 0.013 | 0.429 (0.007) | 384.6 (1.5) | -0.018 | Kartas (1981) |
| Miliane & Medjerah, Tunisia | 0.257 (0.003) | 492.0 (2.0) | -0.070 | 0.227 (0.003) | 548.8 (2.5) | -0.073 | Kartas (1981) |
| Mazafran, Algeria | 0.385 (0.014) | 344.2 (4.0) | -0.194 | 0.186 (0.010) | 593.8 (15.7) | -0.711 | Bounhiol (1917) |

Table 3.73: Parameters for the equation weight (g) = aLength^b (mm) for male and female *Alosa fallax algeriensis*, based on mean length and weight at age data.

| River (Country) | Life stage | Length | Male | | Female | | Reference |
|----------------------------------|-------------|------------|-----------------------|-------|-----------------------|-------|---------------|
| | | | a | b | a | b | |
| L. Ichkeul Tunisia | Juv & Adult | L_t (mm) | $9.171 \cdot 10^{-7}$ | 3.409 | $1.372 \cdot 10^{-6}$ | 3.325 | Kartas (1991) |
| Miliane & Medjerah Tunisia | Juv & Adult | L_t (mm) | $2.495 \cdot 10^{-6}$ | 3.211 | $2.106 \cdot 10^{-6}$ | 3.239 | Kartas (1991) |
| Oubeira, Algeria | Juv & Adult | L_t (mm) | $1.326 \cdot 10^{-6}$ | 3.327 | $1.326 \cdot 10^{-6}$ | 3.327 | Kartas (1991) |

Table 3.74: Length (total) of male and female *Alosa fallax lacustris* from the Italian lakes Maggiore (Berg & Grimaldi, 1966a) and Garda (Oppi & Novello, 1989).

| Lake | Sex | Age (year) | | | |
|----------|-----|------------|-------|-------|-------|
| | | 1 | 2 | 3 | 4 |
| Maggiore | M | 143.6 | 214.0 | 246.1 | 273.7 |
| | F | 142.6 | 222.7 | 264.8 | 289.4 |
| Garda | M&F | 130 | 225 | 256 | 273 |

Based on mean length at age data (Table 3.74) the von Bertalanffy growth parameters for *Alosa fallax lacustris* are presented in Table 3.75. There was no significant difference in K ($P>0.05$) between the sexes, while L_{∞} for females was significantly greater than that for males ($P<0.05$).

Table 3.75: von Bertalanffy growth parameters for male and female *Alosa fallax lacustris*, 95% confidence intervals in brackets, calculated from the mean length at age data presented in Table 3.74.

| Lake | Sex | von Bertalanffy growth parameters | | |
|----------|-----|-----------------------------------|--------------|--------|
| | | K | L_{∞} | T_0 |
| Maggiore | M | 0.557 (0.027) | 301.5 (3.7) | -0.167 |
| | F | 0.608 (0.024) | 317.2 (3.2) | 0.018 |
| Garda | M&F | 0.987 (0.031) | 279.3 (1.5) | 0.364 |

Alosa fallax killarnensis

Mean length at age for male and female *Alosa fallax killarnensis* is presented in Table 3.76. There is little difference in growth rate between the sexes. The sub-species reach a maximum length of c. 240 mm (Trewavas, 1938; Gibson, 1956; Twomey, 1958; O'Maoileidigh, 1990). There was no significant difference ($P>0.05$) in the von Bertalanffy growth parameters K and L_4 between the sexes (Table 3.77).

Table 3.76: Backcalculated length (total) and standard deviation (mm) of male and female *Alosa fallax killarnensis* from Lough Leane, Ireland (O'Maoileidigh, 1990). [Fork length (L_f) converted to total length (L_t) using $L_t = 1.1264 L_f + 3.5260$ (Douchement, 1981)].

| Sex | Age (year) | | | | |
|-----|-------------|--------------|--------------|--------------|-------|
| | 1 | 2 | 3 | 4 | 5 |
| M | 45.3 (9.9) | 124.2 (13.8) | 186.4 (9.0) | 210.9 (6.8) | |
| F | 50.2 (13.5) | 127.9(16.3) | 191.6 (10.9) | 219.1 (12.4) | 234.1 |

Table 3.77: von Bertalanffy growth parameters for male and female *Alosa fallax killarnensis* from Lough Leane, Ireland, 95% confidence intervals in brackets. Parameters calculated from data presented in Table 3.76.

| Male | | | Female | | |
|---------------|--------------|-------|---------------|--------------|-------|
| K | L_{∞} | T_0 | K | L_{∞} | T_0 |
| 0.533 (0.202) | 255.3 (36.7) | 0.643 | 0.465 (0.261) | 279.2 (69.2) | 0.586 |

The coefficients for the geometric mean regression relating length to weight of pre-spawned *Alosa fallax killarnensis* are presented in Table 3.78 for both males and females.

Table 3.78: Parameters for the equation: weight (g) = aLength^b (cm) for adult pre-spawned male and female *Alosa fallax killarnensis* from Lough Leane, Ireland (O'Maoileidigh, 1990).

| Length (cm) | Male | | Female | |
|-------------|----------------------|------|----------------------|------|
| | a | b | a | b |
| L_f | $2.29 \cdot 10^{-4}$ | 4.43 | $4.79 \cdot 10^{-2}$ | 2.63 |

- Comparison of growth parameters

The relationship between the von Bertalanffy growth coefficient (K) and the asymptotic length for *Alosa alosa* and *Alosa fallax* spp. is shown in Figure 3.28. The population of *Alosa* furthest removed from the overall trend was that of *Alosa fallax lacustris* from Lake Garda.

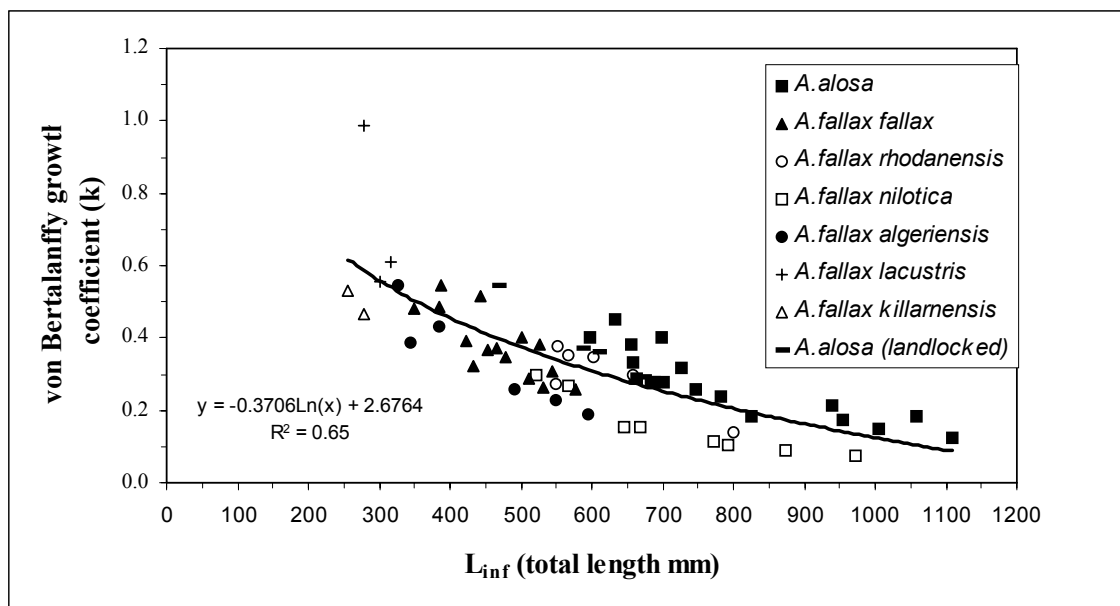


Figure 3.28: Auximetric plot for *Alosa alosa* and *Alosa fallax* spp.

3.4.4 Metabolism

Alosa alosa

During the freshwater phase of the spawning migration there was a gradual loss of condition (weight.100/length³) during the period (Cassou-Leins & Cassou-Leins, 1981). The weight loss associated with the migration and spawning has ranged from 30 to 59% being generally higher for females than for males (Cassou-Leins & Cassou-Leins, 1981; Mennesson-Boisneau & Boisneau, 1990; Pustelnik, unpublished). At the start of the migration the white muscle exhibits the classic structure of alternating white and dark bands, rich in myofibrils and incorporating lipid deposits (Bengen, 1992). However, on the spawning grounds the myofibrils are much less abundant, having become separated, giving a disorganised appearance. The hepatocytes of the liver at the start of the migration are rich in glycogen and lipid. As the fish migrate to their spawning grounds the granular reticulum in the females undergoes further development attaining its maximum by the time the fish have reached the spawning ground. In contrast, no such change was observed in the male. The mitochondria develop a crest, suggesting intense secretory activity, so that by the time the fish have reached the spawning grounds only a few lipid droplets and granules of glycogen remain (Bengen, 1992). Vacuoles appear in the cytoplasm, which has a much more heterogeneous appearance compared with fish from the estuary. Many of the cells have atrophied and their diameter has declined from $4.1\mu \pm 0.15$ to $3.6\mu \pm 0.19$ (Eiras, 1981b).

In the River Douro and in the Gironde-Garonne-Dordogne system (France) the amount of protein and lipid in the muscle decreased (Tables 3.79 & 3.80) as *Alosa alosa* migrate from the estuary into fresh water for spawning (Eiras, 1981b; Bengen, 1992). In both studies the lipid concentration for both sexes in the liver also declined. The protein content of female fish declined in the River Douro stock, while in the Gironde-Garonne-Dordogne Bengen (1992) reported a slight increase.

Table 3.79: The range in mean monthly percentage water, protein, lipid and carbohydrate in the muscle, gonad and liver of *Alosa alosa* from the River Douro, Portugal (Eiras, 1981b), (Est. = estuary; FW = fresh water).

| Organ | Sex | Water | | Protein | | Lipid | | Carbohydrate | |
|--------|----------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| | | Est. | FW | Est. | FW | Est. | FW | Est. | FW |
| Muscle | M | 67.2 – 71.5 | 72.8 – 76.6 | 14.9 – 16.7 | 10.1 – 14.2 | 8.2 – 10.3 | 4.6 – 8.2 | 1.53 – 1.70 | 1.67 – 1.83 |
| | F | 66.9 – 71.3 | 73.3 – 76.1 | 15.6 – 17.1 | 10.5 – 12.7 | 9.0 – 11.3 | 4.3 – 9.5 | 1.35 – 1.49 | 1.49 – 1.59 |
| Gonad | M | 74.7 – 77.8 | 75.2 – 78.9 | 11.0 – 12.2 | 12.0 – 13.7 | 4.5 – 5.8 | 3.2 – 5.0 | 1.62 – 1.8 | 1.69 – 2.22 |
| | F | 72.2 – 74.8 | 72.5 – 75.3 | 13.7 – 15.0 | 14.2 – 16.1 | 5.9 – 6.7 | 4.3 – 6.0 | 1.59 – 1.70 | 1.62 – 1.79 |
| Liver | M | 61.3 – 68.7 | 72.1 – 75.9 | 9.2 – 11.1 | 5.8 – 8.1 | 17.1 – 19.2 | 11.2 – 15.2 | 1.19 – 1.25 | 1.30 – 1.47 |
| | F | 62.3 – 68.4 | 71.4 – 76.4 | 9.7 – 10.2 | 4.3 – 8.2 | 16.5 – 18.5 | 9.7 – 15.1 | 1.19 – 1.24 | 1.30 – 1.35 |

The decline in lipid and protein content in the muscle and liver relates in part to the energetic costs of migration, as the adults do not feed during the freshwater phase of the spawning migration (Section 3.4). It also relates partly to the remobilization of the lipid and protein, associated with maturation of the gonads. The lipid and protein content of the ovary and testis increase as spawning is approached.

Table 3.80: The percentage protein and lipid in the muscle, gonad and liver of *Alosa alosa* obtained from the outer estuary of River Gironde-Garonne-Dordogne (France) in April and from fresh water in July (Bengen, 1992).

| Organ | Sex | Protein | | Lipid | |
|--------|----------|-----------------------|-------------------|-----------------------|-------------------|
| | | Outer estuary (April) | Freshwater (July) | Outer estuary (April) | Freshwater (July) |
| Muscle | M | 18.2 | 12.9 | 9.5 | 0.8 |
| | F | 21.5 | 13.9 | 14.6 | 0.8 |
| Gonad | M | 14.6 | 17.6 | 2.1 | 3.2 |
| | F | 17.1 | 22.1 | 3.9 | 5.2 |
| Liver | M | 11.2 | 9.1 | 15.2 | 5.1 |
| | F | 15.2 | 16.9 | 12.9 | 3.4 |

Lahaye (1966) observed an increase in thyroid activity associated with fish entering fresh water to spawn. For females there was a decrease from 200 to 100 μ in the diameter of the follicle cells while the epithelium increased from 4-5 μ to c. 16 μ . A similar pattern was also observed for the males. For *Alosa alosa* from the River Douro, Portugal (Table 3.81), Eiras (1981b) reported a significant increase in activity of PLH, TSH and GTH cells of the pituitary as the fish migrated from the estuary into fresh water. There was no significant change reported in the area of ACTH ($19.6 \pm 0.7 \mu^2$) and STH ($12.9 \pm 0.8 \mu^2$) cells.

Table 3.81: The mean (SE) area (μ^2) of the adenohipophyseal cells of *Alosa alosa* during the freshwater phase of their spawning migration (Eiras, 1981b).

| Cell type | Estuary | Fresh water |
|--------------|------------|-------------|
| Prolactin | 25.9 (1.1) | 35.5 (1.4) |
| Thyrotropic | 23.2 (1.0) | 24.1 (1.0) |
| Gonadotropic | 15.3 (0.5) | 24.1 (1.2) |

Alosa fallax fallax

In the River Severn (England), where the fish migrate a maximum of 15 km upstream of the limit of tide reversal, the somatic weight loss of female *Alosa fallax* ranged from 6 to 25%, being highest in those migrating earlier in the season (Aprahamian, 1982). In the Oued Sebou, the somatic weight loss for some females (which had migrated 220 km from the sea) ranged from 32 to 37% (Sabatié, 1993). For female *A. fallax* in the Severn, lipid levels in the muscle fell by 59.1% during the spawning migration. The mean (\pm SE) percentage composition of lipid in the muscle and ovaries of pre-spawning fish was 3.66 ± 0.40 % (wet weight) and 4.50 ± 0.08 % respectively. Following

spawning the percentage declined significantly to $1.50 \pm 0.17 \%$ and $2.66 \pm 0.34 \%$ in the muscle and ovaries respectively (Aprahamian, 1982).

The change in the level of calcium, copper, iron, manganese and zinc in the scales, bone (operculae) liver, muscle and ovary of female *Alosa fallax fallax* from the Severn during the freshwater phase of their spawning migration is shown in Table 3.82. Non-parametric analysis (Mann-Whitney test) suggested a significant increase ($P < 0.05$) in the levels of calcium and iron in the liver, muscle and ovary, but only in the muscle and ovary for zinc in spent females. Copper decreased significantly in the liver but was significantly higher in the ovaries while the manganese concentration in the ovaries decreased significantly following spawning.

Table 3.82 The mean (\pm SE) concentration ($\mu\text{g g}^{-1}$) of calcium (Ca), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) in the scales, bone (operculae) liver, muscle and ovary of pre- (n=22) and post (n=15) spawned female *Alosa fallax fallax* from the Severn Estuary (Aprahamian, unpubl).

| Trace Element | Scale | | Operculae | | Liver | | Muscle | | Ovary | |
|---------------|---------------------|---------------------|---------------------|--------------------|----------------------|-----------------------|---------------------|----------------------|----------------------|----------------------|
| | Pre | Post | Pre | Post | Pre | Post | Pre | Post | Pre | Post |
| Ca | 107.0 ± 2.1 | 103.5 ± 1.3 | 155.5 ± 3.5 | 148.3 ± 3.7 | 273.0 ± 15.7 | 1195.0 ± 193.0 | 483.0 ± 78.0 | 768.0 ± 146.0 | 362.0 ± 158.0 | 597.0 ± 48.0 |
| Cu | 7.55 ± 0.46 | 6.34 ± 0.55 | 10.63 ± 1.09 | 8.42 ± 0.59 | 20.96 ± 1.62 | 14.63 ± 1.42 | 6.69 ± 0.95 | 5.24 ± 0.74 | 6.18 ± 0.66 | 8.61 ± 1.00 |
| Fe | 112.0 ± 24.0 | 76.1 ± 8.1 | 73.5 ± 16.6 | 89.6 ± 23.4 | 1246.0 ± 67.0 | 2463.0 ± 439.0 | 59.7 ± 8.9 | 72.6 ± 8.8 | 80.9 ± 6.2 | 330.0 ± 52.0 |
| Mn | 22.55 ± 1.89 | 24.05 ± 2.32 | 38.70 ± 3.60 | 44.7 ± 3.9 | 7.13 ± 0.37 | 6.94 ± 0.38 | 1.41 ± 0.11 | 1.35 ± 0.29 | 5.75 ± 0.34 | 3.96 ± 0.38 |
| Zn | 121.5 ± 17.3 | 89.2 ± 5.9 | 92.9 ± 3.4 | 90.92 ± 2.7 | 120.7 ± 6.6 | 120.8 ± 5.3 | 18.4 ± 1.5 | 24.5 ± 2.1 | 129.0 ± 22.0 | 913.0 ± 493.0 |

Alosa fallax rhodanensis

On the Rhône, somatic weight loss during the fresh water phase of their spawning migration was *c.* 40% for fish, for fish which had migrated 60km upstream to spawn (Rameye *et al.*, 1976). This figure was higher than that of 21.6% for males and 22.7% for females reported by Douchement (1981). A weight loss of *c.* 20% was also reported from the River Aude (Douchement, 1981).

Alosa fallax nilotica

The volume of the various regions of the pituitary (Table 3.83) changed during the sexual cycle, with a significant ($P < 0.01$) increase in the size of all three regions (see Section 1.3.2.5), as the fish commence the freshwater phase of their spawning migration in April.

Hypertrophy was observed in all cell types during their spawning migration (Table 3.84) with a significant increase in volume ($P < 0.01$) as the fish migrated into fresh water and approached spawning.

Table 3.83: The mean (SE) volumes of the hypophyseal regions (PDR = pars distalis rostralis; PDP = pars distalis proximalis; NIL = neurointermedial lobe) of *Alosa fallax nilotica* during different periods of the sexual cycle in μcm^3 (Pavlović & Pantić, 1975).

| Period in sexual cycle | PDR | PDP | NIL |
|-------------------------|------------------|------------------|-----------------|
| Before migration Autumn | 150,360 (6,835) | 50,827 (2,501) | 60,689 (1,909) |
| Before migration March | 180,420 (8,113) | 80,295 (3,146) | 70,689 (2,437) |
| Migration April | 799,392 (18,305) | 209,166 (7,737) | 150,190 (6,022) |
| Spawning April | 787,266 (20,469) | 246,765 (7,912) | 150,961 (5,648) |
| Spawning May | 809,392 (18,702) | 409,166 (10,350) | 149,027 (6,103) |

Table 3.84: The mean (SE) volumes (μm^3) of the adenohypophyseal cells (PLH = prolactin; ACTH = adrenocorticotropic; TSH = thyrotropic; STH = somatotropic; GTH = gonadotropic; PAS+ = stain positive with alcian blue-PAS-orange and MSH = melanostimulating cells) and their nuclei of *Alosa fallax nilotica* during different seasons of the sexual cycle (Pavlović & Pantić, 1975).

| Cell type | Autumn | Before migration - March | Migration - April | Before spawning - April | Spawning season - May |
|-----------|--------------|--------------------------|-------------------|-------------------------|-----------------------|
| PLH | 79.8 (8.2) | 200.2 (16.3) | 654.9 (36.1) | 621.3 (44.2) | 672.1 (45.6) |
| nuclei | 33.2 (4.1) | 37.6 (3.7) | 139.2 (10.0) | 145.2 (8.4) | 142.0 (9.0) |
| ACTH | 60.9 (5.2) | 175.4 (15.5) | 300.0 (24.2) | 150.2 (8.6) | 194.8 (18.4) |
| nuclei | 35.5 (2.2) | 65.7 (5.2) | 86.3 (9.4) | 46.6 (3.9) | 56.2 (6.0) |
| TSH | 175.4 (15.2) | 442.0 (28.7) | 534.6 (30.1) | 300.7 (27.4) | 288.3 (29.1) |
| nuclei | 55.7 (4.0) | 87.0 (6.8) | 78.6 (6.4) | 66.8 (6.0) | 57.8 (6.2) |
| STH | 56.4 (4.1) | 79.1 (6.4) | 112.1 (8.1) | 144.0 (11.7) | 300.7 (20.3) |
| nuclei | 30.7 (2.4) | 38.2 (3.9) | 56.6 (4.2) | 55.7 (4.3) | 76.3 (5.6) |
| GTH | 87.0 (7.1) | 89.1 (7.7) | 175.4 (14.2) | 356.4 (28.4) | 853.3 (60.0) |
| nuclei | 44.5 (3.1) | 45.7 (3.9) | 87.0 (9.8) | 94.5 (13.3) | 124.4 (16.5) |
| PAS + | 114.4 (8.2) | 129.2 (8.7) | 175.7 (11.2) | 154.6 (9.9) | 170.2 (8.7) |
| nuclei | 44.5 (3.1) | 46.6 (3.7) | 66.8 (5.5) | 55.7 (5.0) | 62.8 (4.8) |
| MSH | 55.7 (4.1) | 66.8 (5.2) | 72.0 (7.0) | 69.9 (8.0) | 65.5 (5.9) |
| nuclei | 33.5 (2.6) | 35.0 (2.7) | 35.2 (3.1) | 34.0 (2.2) | 33.8 (2.3) |

Alosa fallax lacustris

The annual cycle in fat content and fatty acid composition has been reported for *Alosa fallax lacustris* by Luzzana *et al.* (1996) from Lake Como, Italy. The lipid content of the liver and muscle in both sexes was higher in October, prior to spawning in June (Table 3.85). The fats stored in the muscle were mobilised to a greater extent in males

Table 3.85: Percentage fatty acid composition of liver/muscle/gonad total lipids of *Alosa fallax lacustris* from Lake Como, Italy (Luzzana *et al.*, 1996); SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid and HUFA = highly unsaturated fatty acid.

| Fatty Acids | Liver | | | | Muscle | | | | Gonad | | | | Pervisceral Fat | | | | | |
|-------------|--------|------|---------|------|--------|------|--------|------|---------|------|------|------|-----------------|------|--------|------|---------|------|
| | August | | October | | June | | August | | October | | June | | June | | August | | October | |
| | M | F | M | F | M | F | M | F | M | F | M | F | M | F | M | F | M | F |
| 14:0 | 3.4 | 4.9 | 4.0 | 3.9 | 2.6 | 2.2 | 4.3 | 4.7 | 5.3 | 5.4 | 3.8 | 4.3 | 1.6 | 2.0 | 4.9 | 5.1 | 5.9 | 5.5 |
| 16:0 | 19.6 | 26.0 | 16.5 | 16.5 | 18.7 | 21.4 | 19.7 | 21.2 | 23.4 | 23.8 | 20.1 | 19.7 | 25.2 | 23.4 | 19.8 | 23.9 | 21.4 | 21.7 |
| 18:0 | 6.5 | 5.0 | 5.9 | 5.8 | 6.0 | 8.5 | 4.4 | 3.7 | 3.9 | 4.0 | 4.2 | 3.4 | 6.4 | 6.4 | 3.3 | 3.9 | 4.1 | 4.2 |
| ΣSFA | 30.6 | 36.7 | 27.2 | 26.9 | 28.5 | 33.5 | 30.0 | 31.0 | 34.5 | 34.8 | 29.5 | 28.9 | 34.5 | 33.2 | 29.6 | 34.4 | 32.6 | 32.4 |
| 16:1ω7 | 2.2 | 3.5 | 2.0 | 2.0 | 2.5 | 2.3 | 3.5 | 4.3 | 3.9 | 4.0 | 4.1 | 5.0 | 0.9 | 2.4 | 3.9 | 4.0 | 3.8 | 4.0 |
| 18:1ω9 | 25.5 | 28.8 | 44.4 | 43.5 | 18.5 | 12.0 | 19.9 | 18.9 | 21.3 | 22.4 | 19.3 | 19.3 | 9.2 | 11.5 | 27.6 | 22.5 | 24.0 | 25.3 |
| 18:1ω7 | 3.3 | 3.6 | 2.0 | 2.0 | 4.2 | 5.8 | 3.9 | 4.2 | 3.4 | 3.7 | 3.8 | 3.8 | 4.3 | 4.0 | 4.2 | 4.6 | 3.7 | 3.8 |
| 20:1ω9 | 1.3 | 2.0 | 3.4 | 3.4 | 0.7 | 0.5 | 1.0 | 1.0 | 1.3 | 1.4 | 1.0 | 0.9 | - | - | 1.3 | 1.0 | 1.2 | 1.4 |
| ΣMUFA | 32.7 | 38.4 | 52.5 | 51.6 | 26.2 | 20.9 | 28.7 | 28.7 | 30.2 | 31.8 | 28.6 | 29.4 | 14.8 | 18.5 | 37.3 | 32.5 | 33.2 | 35.0 |
| 18:2ω6 | 2.4 | 1.9 | 2.1 | 2.5 | 3.0 | 2.2 | 4.8 | 4.8 | 6.6 | 6.6 | 4.5 | 4.8 | 2.2 | 2.2 | 5.1 | 5.1 | 7.5 | 7.3 |
| 18:3ω3 | 2.0 | 1.7 | 1.3 | 1.6 | 2.9 | 2.2 | 4.2 | 5.2 | 4.6 | 4.5 | 3.7 | 4.0 | 1.6 | 2.3 | 4.8 | 5.8 | 5.4 | 5.2 |
| 18:4ω3 | 1.0 | 1.0 | 0.7 | 0.9 | 2.1 | 2.1 | 2.2 | 2.9 | 2.3 | 2.2 | 2.1 | 2.2 | 0.6 | 2.2 | 2.7 | 3.4 | 2.9 | 2.9 |
| 20:4ω6 | 6.5 | 3.9 | 2.5 | 3.1 | 6.2 | 6.3 | 5.3 | 4.6 | 4.6 | 4.5 | 5.0 | 4.6 | 9.5 | 6.3 | 4.2 | 3.5 | 4.0 | 3.5 |
| 20:4ω3 | 1.4 | 0.8 | 0.8 | 0.7 | 1.9 | 2.5 | 1.6 | 1.8 | 1.4 | 1.2 | 1.6 | 1.7 | 1.2 | 2.2 | 1.2 | 1.0 | 1.1 | 1.0 |
| 20:5ω3 | 5.5 | 3.0 | 1.6 | 1.8 | 6.1 | 6.3 | 7.1 | 7.8 | 4.3 | 4.3 | 6.9 | 7.9 | 10.4 | 8.3 | 6.9 | 6.9 | 4.6 | 4.4 |
| 22:4ω6 | 2.4 | 1.0 | 1.2 | 1.0 | 3.2 | 1.5 | 1.0 | 0.8 | 0.7 | 0.7 | 0.6 | 0.5 | 2.2 | 1.8 | 0.6 | 0.9 | 0.6 | 0.5 |
| 22:5ω6 | 1.1 | 0.7 | 0.2 | 1.1 | 1.4 | 1.5 | 1.3 | 1.9 | 1.3 | 1.1 | 1.6 | 1.4 | 1.8 | 1.4 | 0.6 | 0.3 | 1.0 | 0.8 |
| 22:5ω3 | 1.6 | 0.9 | 0.6 | 0.7 | 2.6 | 3.0 | 2.5 | 2.1 | 1.4 | 1.3 | 2.6 | 2.4 | 4.7 | 3.3 | 1.9 | 1.5 | 1.2 | 1.2 |
| 22:6ω3 | 9.8 | 6.7 | 4.4 | 4.5 | 12.8 | 14.9 | 8.0 | 5.8 | 4.5 | 3.7 | 9.6 | 7.6 | 14.9 | 15.2 | 1.9 | 1.6 | 2.7 | 1.5 |

Table 3.85: (cont) Percentage fatty acid composition of liver/muscle/gonad total lipids of *Alosa fallax lacustris* from Lake Como, Italy (Luzzana *et al.*, 1996); SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid and HUFA = highly unsaturated fatty acid.

| | | | | | | | | | | | | | | | | | | |
|----------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| ΣPUF A | 36.8 | 24.9 | 20.2 | 21.5 | 45.3 | 45.6 | 41.3 | 40.0 | 35.2 | 33.4 | 41.8 | 41.7 | 50.7 | 48.2 | 33.1 | 33.2 | 34.2 | 32.7 |
| ω3 | 21.3 | 14.2 | 9.9 | 10.3 | 28.3 | 31.1 | 25.7 | 25.7 | 18.6 | 17.3 | 26.8 | 27.4 | 33.5 | 33.4 | 19.5 | 20.3 | 17.8 | 17.3 |
| ω6 | 13.8 | 8.6 | 8.0 | 8.9 | 15.4 | 13.5 | 13.9 | 12.6 | 14.7 | 14.5 | 12.9 | 12.5 | 16.5 | 13.5 | 11.9 | 11.0 | 14.5 | 13.5 |
| ω3 HUFA | 16.9 | 10.6 | 7.1 | 7.1 | 21.4 | 24.3 | 17.6 | 15.7 | 10.3 | 9.3 | 19.1 | 17.8 | 30.0 | 26.7 | 10.7 | 10.1 | 8.5 | 8.1 |
| ω6 HUFA | 10.0 | 5.6 | 4.9 | 5.2 | 10.8 | 9.3 | 7.6 | 6.1 | 6.7 | 6.3 | 7.2 | 6.4 | 13.5 | 9.5 | 5.5 | 4.8 | 5.6 | 4.8 |
| Total lipids % | 6.9 | 11.6 | 16.3 | 22.1 | 4.7 | 4.7 | 5.1 | 8.4 | 8.5 | 9.9 | 4.4 | 6.9 | 3.3 | 3.7 | | | | |

(declining by 48.2%) than in females, where levels fell by 30.3% between October and June. In October, the lipid content of the liver was higher in females than in males (22.1% and 16.3% respectively), however, by the time spawning was complete (June) the level for both sexes was the same (4.7%). There was no perivisceral fat present in the body cavity at spawning time. The findings suggest that liver and muscle lipids are used for gonadal development and to meet energy requirements when the fish are not feeding, while those of the body cavity are used solely to meet the overwintering needs of the fish.

The development of the gonads and the energy requirements of the fish resulted in a selective reduction of saturated fatty acids (SFA) in the muscle and of mono-unsaturated fatty acid (MUFA) in the liver, and an increase in polyunsaturated fatty acids (PUFA) in both the muscle and liver.

The predominant fatty acid in both the liver and muscle, though not the gonads, was 18:1 ω 9. This suggests that its mobilisation, after feeding stops in October, was for energy purposes as opposed to development of the gonads. Specific muscle and liver ω 3 and ω 6 highly unsaturated fatty acids (HUFA) retention was evident for both sexes and was associated with development of the gonads. The precursors of ω 3 and ω 6 HUFA (18:2 ω 6, 18:3 ω 3 and 18:4 ω 3) were mobilised in particular from the muscle.

3.5 Behaviour

3.5.1 Migration

- Adult spawning migration

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 3.86).

Temperature has long been considered one of the main factors affecting the timing of the freshwater phase of their spawning migration (**Duhamel Du Monceau, 1772; Pennant, 1777**) 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), with 50% of the

migration occurring at temperatures <15.0 to <16.0°C and 90% from temperatures ranging from <17.5 to <20.0°C (Rochard, 2001).

Table 3.86: Timing of the freshwater phase of the spawning migration of *Alosa alosa*.

| 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 | II (I) | IV-V | VI | Lozano Rey (1935) |
| 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 & Cassou-Leins (1981); Rochard (2001) |
| Loire, France | III | IV-V | VI | Mennesson-Boisneau & 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) |

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 (Figure 3.29). 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.

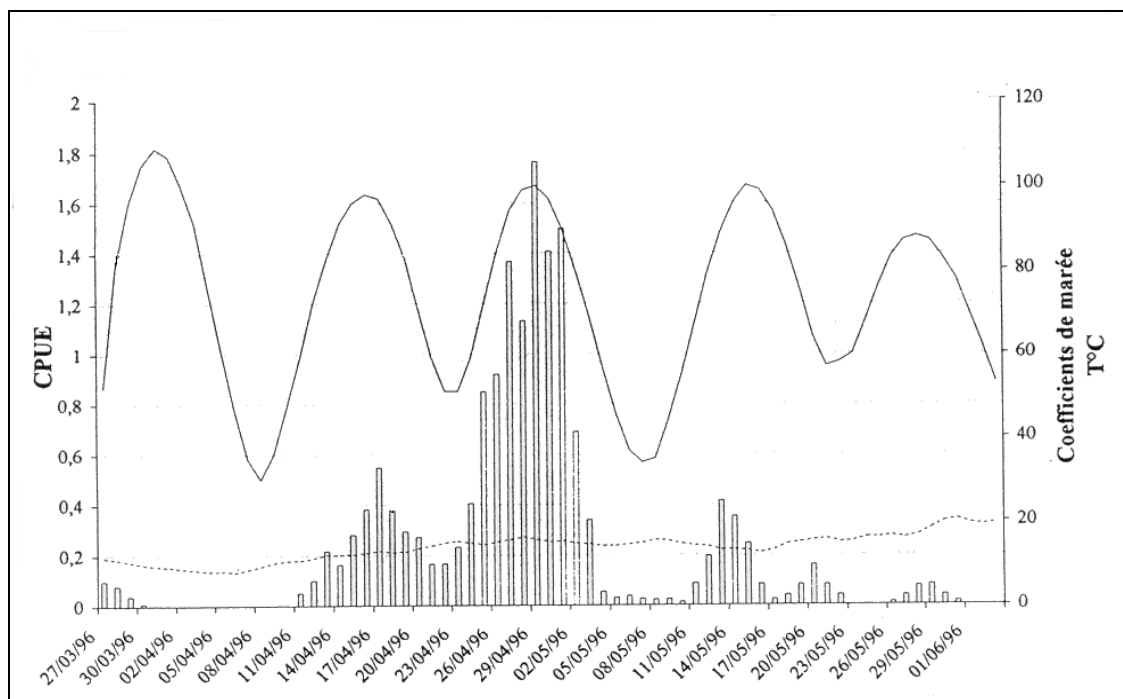


Figure 3.29: The abundance of *Alosa alosa* in the Loire (c.150 km from the ocean) and the relationship with tidal state (11 days prior to capture) and temperature (Mennesson-Boisneau *et al.*, 1999).

In fresh water, Mennesson-Boisneau & Boisneau (1990), Dartiguelongue (1996a&b) and Travade *et al.* (1998) have shown that *Alosa alosa* migrate upriver in several waves (Figure 3.30). 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 (Mennesson-Boisneau & 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 & Lartigue (1983) and Bellariva & 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).

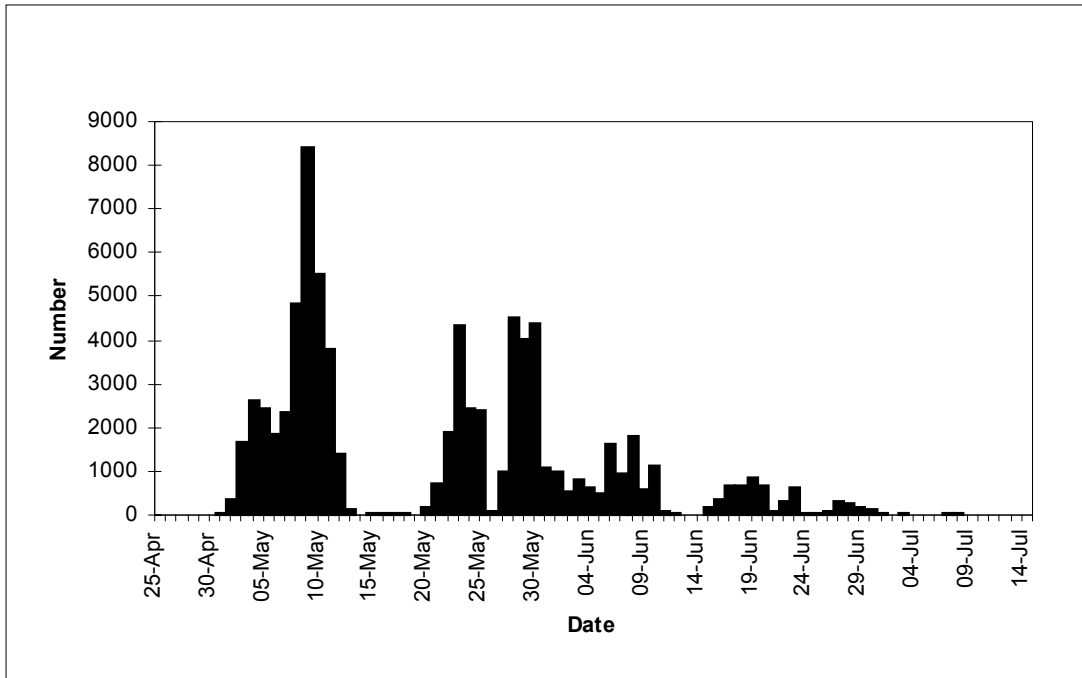


Figure 3.30: The daily count of *Alosa alosa* at Tuiliers fish pass on the River Dordogne, France, in 1995 (Dartiguelongue, 1996a).

In relation to discharge, Dautrey & Lartigue (1983) observed a negative correlation with flow ($r^2 = 0.28-0.29$) though Bellariva & 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 (Figure 3.31); it increased gradually from 0800h, reaching a peak at 1900h after which it declined steadily until 2300h. There was little upstream movement between 0000 and 0700h (Travade *et al.*, 1998).

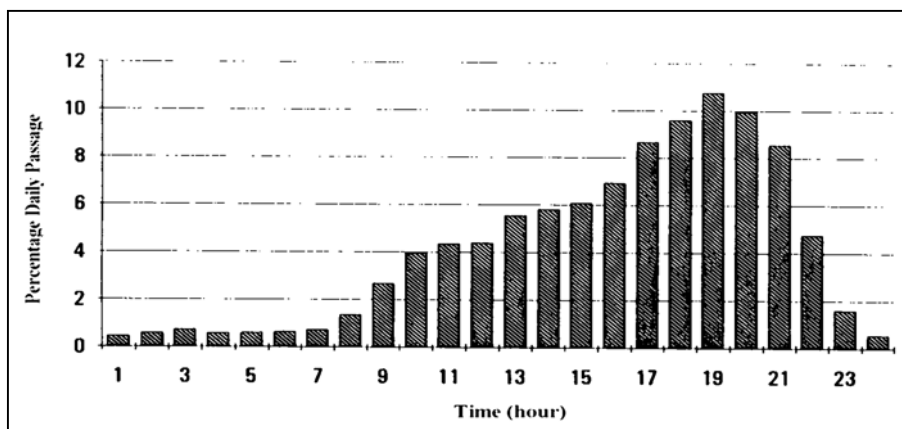


Figure 3.31: The daily pattern of movement of *Alosa alosa* at Tuiliers fish pass on the River Dordogne, France, in 1995 (Reproduced from Travade *et al.*, 1998).

The larger and older males and females were the first to migrate and the condition of the fish deteriorates during the migration period (Dautrey & Lartigue, 1983; Sabatié, 1993). The early part of the migration was characterised by a higher proportion of males (Mennesson-Boisneau & Boisneau, 1990; Sabatié, 1993). However, in the Lima (Portugal) there was no significant difference ($P>0.05$) in the sex ratio during the migration period (Alexandrino, 1996b).

Alosa fallax fallax

Migration into the estuary begins between February (for stocks at the southern limit of their range) and May (for those at the northern limit), and usually extends for three months (Table 3.87). 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 & Gardner, 1978; Aprahamian, 1982, 1988), the Sebou (Sabatié, 1993) and the Loire (Mennesson-Boisneau & Boisneau, 1990). In warmer years migration can commence approximately a month earlier than normal (Mennesson-Boisneau & Boisneau, 1990).

Shad migrate mainly during the day between 0500 and 2000 (Figure 3.32), in the lower half of the water column close to the river bed, where water velocity is lowest (Clabburn, 2002). The fish enter the river in a series of waves (Aprahamian, 1981). There is a higher proportion of males at the start of the migration (Roule, 1922a; Hass, 1965; Claridge & Gardner, 1978; Aprahamian, 1981, 1982; Alexandrino, 1996b). Of the females, the larger fish were the first to migrate and this was also apparent with fish of the same age and spawning history (Aprahamian, 1981; 1982; Sabatié, 1993). Similar findings were reported for males from the Sebou (Sabatié, 1993) but not for the Severn, and for the latter the lack of size differentiation may reflect gear selectivity (Aprahamian, 1982).

Table 3.87: Timing of the freshwater phase of the spawning migration of *Alosa fallax fallax*.

| River, Country | Start | Peak | End | Reference |
|---------------------------|------------|------|----------|--|
| Sebou, Morocco | II (XII-I) | IV | V | Sabatié (1993) |
| Guadiana, Portugal | I | V | VI | Esteves (pers. comm.) |
| Mira, Portugal | II | IV | VI | Esteves (pers. comm.) |
| Tejo, Portugal | II | | VI | Baglinière <i>et al.</i> (2001) |
| Lima, Portugal | III (II) | IV-V | VI | Alexandrino (1996b) |
| Adour, France | | V-VI | | Douchement (1981) |
| Gironde, France | IV (III) | V | VI | Anon. (1979a) |
| Loire, France | V (IV) | V | VII | Mennesson-Boisneau & 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) |
| Barrow-Nore-Suir, Ireland | IV | V | VI | Bracken & Kennedy (1967) |
| Wye, Wales | IV | V | VI | Aprahamian (1982); Gregory (pers. comm.) |
| Severn, England | IV | V | VI | Aprahamian (1981,1982) |

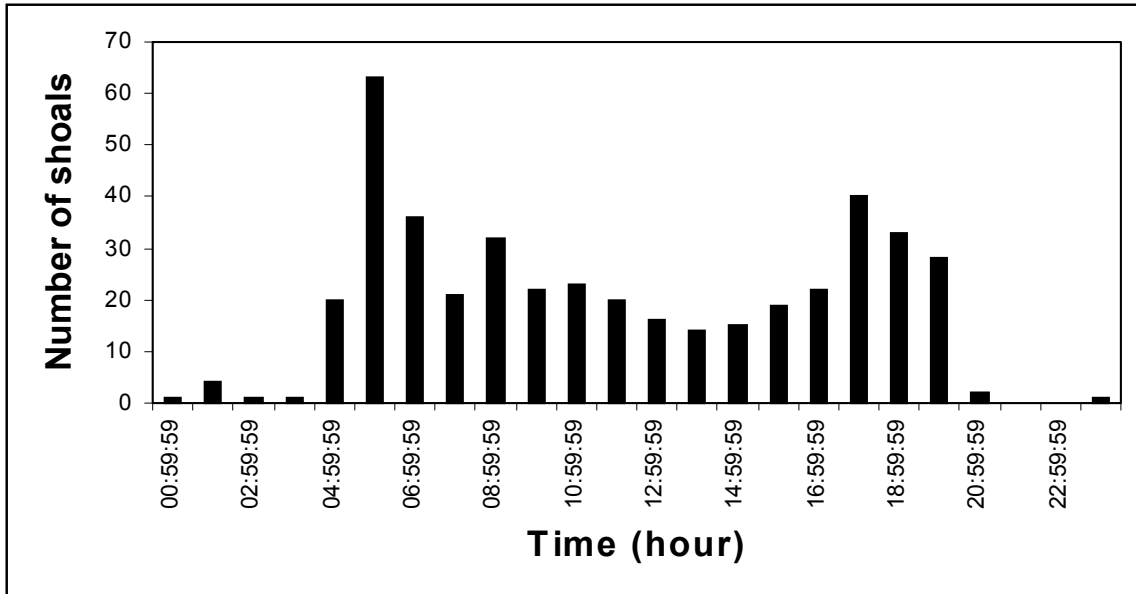


Figure 3.32: The diel movement of *Alosa fallax fallax* shoals in the River Wye, Wales (J. Gregory, pers. comm.).

Fish entering the estuary near the end of the migration period were lighter for a given size both in terms of total weight and somatic weight when compared to those that migrated earlier (Aprahamian, 1982). In some years there was an indication that fish which had spawned previously migrated first, though in other years this was not the case; no trend was apparent.

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

Alosa fallax rhodanensis

On the River Rhône migration takes place between mid-March and the beginning of July, with a peak in April to May (Roule, 1924c; Gallois, 1946a, 1947a; Rameye *et al.*, 1976; Douchement, 1981; Baglinière *et al.*, 1996; Le Corre *et al.*, 1997a; Lebel *et al.*, 1999). The main migration period is similar on the Aude (Douchement, 1981). On the River Tiber the onset of the migration begins during the first half of March (D’Ancona, 1928a) and on the Tirso the migration period extends from February or March until the end of April (Cottiglia, 1963a).

The temperature at the start of the freshwater phase of the migration has been reported to range from about 10°C to 14°C (Gallois (1947a; Rameye *et al.*, 1976; Baglinière *et al.*, 1996). Guillard & Colon (2000) showed that there was a significant positive correlation between the number of fish migrating upstream over a four day period and water temperature ($r^2 = 0.42 - 0.86$), up until the migration reached its peak. No relationship was found with, conductivity, pH or oxygen content of the Rhône, however, with flow the results were inconclusive, with a significant negative relationship in one year and an absence of any relationship in the other year of study. The migration can be delayed due to poor weather conditions, in some cases by up to a

month (Rameye *et al.*, 1976). At flows greater than $2500 \text{ m}^3 \text{ s}^{-1}$, Baglinière *et al.* (1996) observed that upstream migration on the Rhône ceased.

At the start of the migration there is a higher proportion of males which declines during the period of the run (D'Ancona, 1928a; Quignard & Douchement, 1991c; Baglinière *et al.*, 1996). The weight of both male and female fish of a given length was greater at the start of the migration period than that of later migrants (Baglinière *et al.*, 1996).

Alosa fallax nilotica

The onset of the migration into fresh water begins in March or April with a peak in April or May, though the timing of the migration has been shown to vary by approximately one month between years (Vukovic, 1961a; Vitali *et al.*, 1983; Serventi *et al.*, 1990). In the River Evros (Greece) the sub species migrates upriver from the end of March to the end of May and into Lake Vistonis between April and June (Bobori *et al.*, 2001). Temperature at the start of the migration in the River Po ranged from 8 to 12°C and upstream movement of fish was positively correlated with temperature but not with flow (Vitali *et al.*, 1983; Serventi *et al.*, 1990).

In the River Po (Italy) males predominated at the start of the migration (Vitali *et al.*, 1983). In the River Neretva, females dominated throughout the spawning period in particular at the start and at the end where they were *c.* 3 times more abundant than males. For the remaining periods the sex ratio was approximately 1:1 (Vukovic, 1961a).

Alosa fallax algeriensis

The migration period extends from mid-March to the end of May, with the temperature at the start of migration varying between 14 and 17.8°C (Bounhiol, 1917; Kartas, 1991). Males were predominant at the start of the migration (Kartas, 1991).

- Juvenile seaward migration

Alosa alosa

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 & 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). Certainly, Castelnaud *et al.* (2001) reported the 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. Migration from estuary to sea of the 0+ age group commenced 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). 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 & Lithogoe (1971) and Wheeler (1969a)**. 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.

At the time of migration the majority of the 0+ population in the Gironde ranged in size (upper and lower 95% confidence intervals) from 54.5 to 79.6 mm (total length) and the 1+ from 138.2 to 161.2 mm (Taverny, 1991a). In the Rhine, Anon. (1888) reported a size range of between 72 and 143 mm for fish caught in October, the largest may, however, not be young of the year.

Alosa fallax fallax

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

The juveniles can be found through out 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). The 0+ fish migrate seaward during the autumn (Figure 3.33) in the surface layers of the water column (Taverny, 1991a). In the Severn and Elbe the majority have left the estuary by the end of October (Claridge & 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).

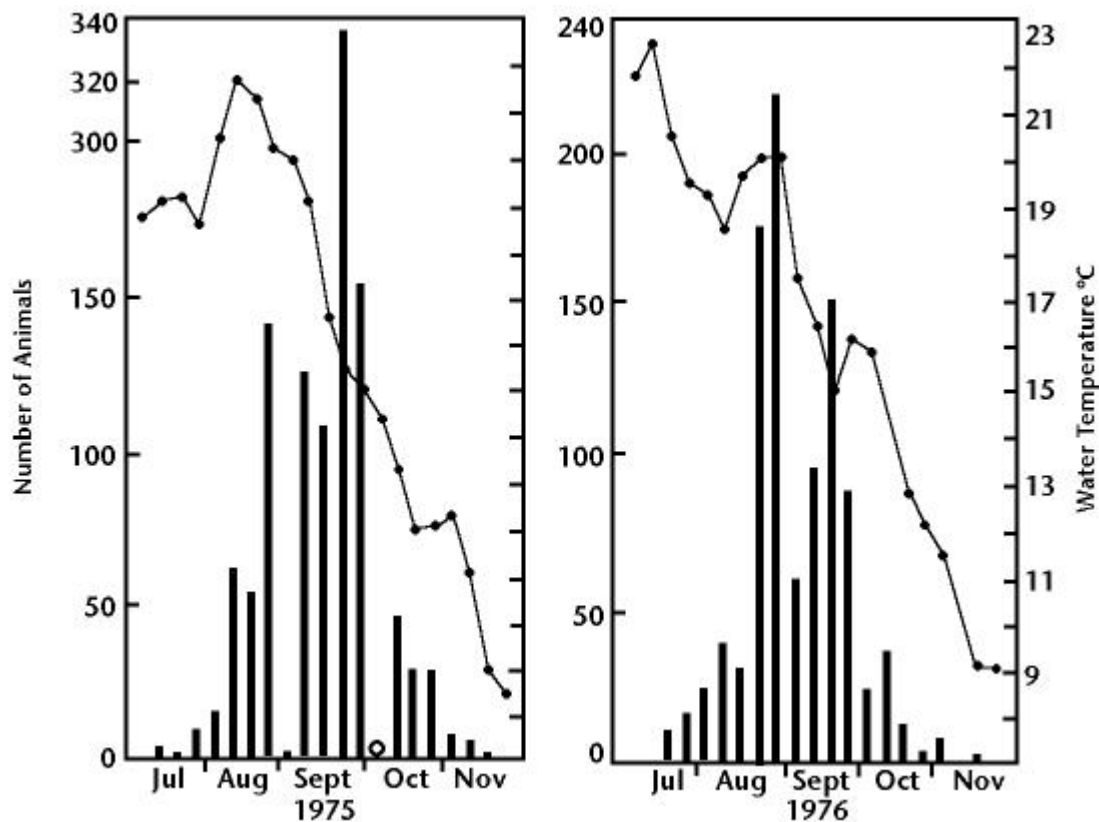


Figure 3.33: The weekly 24-h sample size of 0+ *Alosa fallax* from the Severn Estuary (England) between July and November in 1975 and 1976, and the mean water temperature for the week prior to the collection. ‘o’ indicates that no collection was made, from Claridge & Gardner (1978).

Claridge & 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 & 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 & 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).

The size (L_t) of the 0+ juveniles (upper and lower 95% CI) in the autumn on their seaward migration ranged from 45 to 76mm on the Severn (Arahamian, 1988²; Claridge & Gardner, 1978³), 72 to 118mm on the Elbe (Thiel *et al.*, 1996a) and between 71 and 84mm on the Gironde (Taverny, 1991a). In the Rhine, Anon. (1888) reported a size range of between 54 and 150 mm for fish caught in October-November, the largest may, however, be one year old.

Alosa fallax rhodanensis

In the Rhône, Crivelli & Poizat (2001) found that the juveniles could start their downstream migration between mid June and mid July, approximately 3 to 5 weeks after spawning had ceased. Their seaward migration occurring between the end of August and the end of October at a length (L_t) ranging from 68 to 161mm² (Menella & Tabardel, 1994; Tabardel *et al.*, 1995; Gendre *et al.*, 1997a), with a maximum of 213 mm (Crivelli & Poizat, 2001). In the Aude the main migration period is between July and September (Cassou-Leins, 1995).

Alosa fallax algeriensis

Kartas (1991) reported that in the Tunisian rivers Miliane and Medjerdah the juveniles migrate seaward in September.

- Migration at sea

Alosa alosa

Except for the study by Sabatié (1993) little information exists on their 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 1,200 km. The fish remain in this rich feeding area until they mature when they return to the Sebou to spawn.

¹ Fork length (mm) converted to total length using $L_t = 1.1264L_f + 3.526$ (Douchement, 1981).

² Standard length (mm) converted to total length using $L_t = 1.1896L_{st} + 5.9359$ (Douchement, 1981).

3.5.2 Swimming speed

There is little information about the swimming ability and endurance of *Alosa alosa* and *Alosa fallax*. Litaudon (1985) estimated that the burst swimming speed of *Alosa alosa* ranged from 3.1 ms⁻¹ to 4.7 ms⁻¹ at temperatures of 16 to 17°C. At these temperatures the fish could maintain such speed for approximately 6.5s. The maximum speed was estimated at between 4.1 ms⁻¹ and 6.1ms⁻¹, but could only be sustained for a few seconds. Table 3.88 summarise the swimming capabilities of shad measuring 0.30 to 0.50 m in length (Larinier, 1996).

Table 3.88: Swimming capabilities of shad (0.30 to 0.50 m in length) from Larinier (1996).

| Temperature (°C) | Maximum speed (ms ⁻¹) | Endurance at maximum speed (sec) | Cruising speed (ms ⁻¹) |
|------------------|-----------------------------------|----------------------------------|------------------------------------|
| 10 | 2.75 – 3.30 | 15 – 60 | 0.8 – 1.5 |
| 15 | 3.50 – 4.30 | 10 – 25 | |
| 20 | 4.40 – 5.40 | 5 – 10 | |

Anon (1975) mentions that the swimming speed of *A. fallax rhodanensis*, as measured in a fish ladder which had been fitted with baffles (Lachadenc model), varied between 1.5 and 2.3 ms⁻¹. Anon (1975) and Larinier *et al.* (1978) both report that at current speeds greater than 1.5 ms⁻¹ shad did not enter the fish pass. Gendre (1997a) reported that *A. fallax rhodanensis* could maintain a swimming speed of < 1.4 ms⁻¹ for several hours (cruising or sustained swimming speed), while speeds of between 2 to 2.4 ms⁻¹ could only be maintained for a few minutes, with a maximum (burst) swimming speed of 2.4 to 3.1 ms⁻¹.

4. POPULATION (SPAWNING STOCK)

This section is confined to characterising the adult component of the stock, except section 4.5.1, which deals with production. Interpretation of data is complicated by the fact that in all circumstances, except for the study of Lambert *et al.* (2001), there has been no correction for gear selectivity. In addition, because different methods operate in different locations, comparisons between systems and between species must be made with caution.

4.1 Structure

4.1.1 Sex Ratio

Sex ratio has been taken as the number of males in relation to the number of females (male/female).

Alosa alosa

In the Loire (France) the sex ratio of the population over a six-year period varied from 0.84:1 to 4.5:1. In three of the six years there was no significant difference from a 1:1 ratio, and in the other years there were significantly more males than females ($P < 0.01$) (Mennesson-Boisneau & Boisneau, 1990).

In the Gironde-Garonne-Dordogne (France) system the sex ratio of fish caught in the estuary (Anon., 1979a; Taverny, 1991a) and on the spawning grounds (Cassou-Leins & Cassou-Leins, 1981) showed no significant difference from parity ($P > 0.05$). However, over a three-year period Lambert *et al.* (2001) found the sex ratio to range from 0.76:1 to 1.47:1 and how it varied with age is shown in Table 4.1.

Table 4.1: Range in the annual sex ratio of *A. alosa* from the Gironde-Garonne-Dordogne (Lambert *et al.*, 2001).

| Age | Sex ratio (M / F) | |
|-------|-------------------|--------------|
| | Mean | Range |
| 3 | 6.82 | 4.23 - 10.71 |
| 4 | 2.99 | 1.99 - 3.56 |
| 5 | 1.08 | 0.51 - 1.63 |
| 6 | 0.29 | 0.16 - 0.44 |
| 7 | 0.13 | 0.00 - 0.26 |
| Total | 1.15 | 0.76 - 1.47 |

No significant difference from a 1:1 ratio was reported from the Portuguese rivers Douro (Eiras, 1981b) and Lima (Alexandrino, 1996b). In the Oued Sebou (Morocco), Sabatié (1993) studied the sex ratio in four years between 1978 and 1985 and observed the annual sex ratio to vary from a preponderance of females (0.5:1) to one where males dominated (4.8:1).

Alosa fallax fallax

For samples obtained using rod and line from the rivers Wye (Wales), Severn (England) and Barrow (Ireland), Aprahamian (1982) and O'Maoileidigh (1990) reported no significant difference ($P>0.05$) from a 1:1 sex ratio. Similar findings were reported by Douchement (1981) for *A. fallax* from the Loire, by Anon. (1979a) for the Gironde-Garonne-Dordogne system and by Alexandrino (1996b) for the Lima. In contrast, in the Sebou males were more abundant with the sex ratio varying between years from 1.35:1 to 2.15:1 (Sabatié, 1993), while in the Tejo females predominated (0.36:1) [Alexandrino, 1996b].

Alosa fallax rhodanensis

In the Rhône (France), the sex ratio has been found to vary between years, from parity to a preponderance of females (0.24:1) and then to a dominance of males (4.15:1) (Douchement, 1981; Le Corre *et al.*, 1997a). On the Tiber (Italy), D'Ancona (1928a) reported a dominance of males with a sex ratio of 2.44:1 at the start of the migration period (March-April) to 1.30:1 in May and June.

Alosa fallax nilotica

In the River Neretva the population was dominated by females, while in lakes Bačín and Skadar the sex ratio was close to 1:1 (Vukovic, 1961a).

Alosa fallax killarnensis

Gill net (50.8 to 63.5 mm) samples of *Alosa fallax killarnensis* from Lough Leane (Ireland) showed no significant difference from a 1:1 sex ratio (O' Maoileidigh, 1990).

4.1.2 Age composition

Alosa alosa

The age structure of the spawning population ranges from 3 to 8 years old for both sexes (Tables 4.2 & 4.3). The majority of the catch consisted of females aged 5 or 6 years old and 4 or 5 year old males. Similar findings were reported from the River Lima, Portugal (Alexandrino, 1996b).

Alosa fallax fallax

In the more northerly populations (Severn, England) the spawning stock consists of females mainly aged between 5 and 7 years old and males of 4 to 6 years old, with a maximum age of 12 and 10 years for females and males, respectively (Tables 4.4 & 4.5). At the southern limit (Sebou, Morocco) of their range the spawning population consists of fish aged 3 or 4 years old, with a maximum age of 6 and 5 years for females and males respectively.

Table 4.2: Age structure (mean percent and range) of the spawning population of female *Alosa alosa* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | N | n |
|---|---------------------|----------------------|----------------------|----------------------|---------------------|-------------------|---|---|------|
| | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | |
| Aulne, France (Véron, 1999) | 14.29 | 42.85 | 28.57 | 14.29 | | | | 1 | 7 |
| Loire, France (Douchement, 1981) | | | 64.50 | 32.30 | 3.20 | | | | 31 |
| Loire, France (Mennesson-Boisneau & Boisneau, 1990) | | 28.84 (1.6-60.9) | 49.94 (30.4-79.5) | 17.74 (2.7-50.8) | 3.48 (0.0-12.7) | | | 6 | 1054 |
| Charente, France (Véron, 1999) | 2.50 | 12.50 | 52.50 | 22.50 | 10.00 | | | 1 | 40 |
| Gironde-Garonne-Dordogne, France (Douchement, 1981) | | | 39.10 | 60.90 | | | | | 46 |
| Gironde-Garonne-Dordogne, France (Anon., 1979a) | | | | 25.00 | 45.00 | 30.00 | | 1 | 20 |
| Gironde-Garonne-Dordogne, France (Cassou-Leins & Cassou-Leins, 1981) | | 33.50 (20.0-47.0) | 54.25 (48.5-60.0) | 10.00 (0.0-20.0) | | | | 2 | 98 |
| Gironde-Garonne-Dordogne, France (Martin-Vandembulcke, 1999) | | 4.15 (3.1-5.4) | 66.94 (59.9-78.0) | 27.65 (18.2-36.1) | 1.25 (0.0-3.1) | | | 3 | 585 |
| Gironde-Garonne-Dordogne, France (Lambert <i>et al.</i> , 2001) | 0.74 (0.4-1.2) | 13.42 (11.5-16.7) | 61.34 (53.0-68.4) | 23.91 (17.9-34.4) | 0.60 (0.0-1.0) | | | 3 | 956 |
| Adour, France (Douchement, 1981) | | | 11.80 | 35.30 | 52.90 | | | | 17 |
| Adour, France (Prouzet <i>et al.</i> , 1994a) | | 0.40 | 35.08 | 49.60 | 14.11 | 0.81 | | 5 | 248 |
| Douro, Portugal (Eiras, 1981b) | 23.03 (8.7-46.2) | 17.80 (13.7-20.1) | 41.67 (23.1-60.7) | 16.90 (5.3-35.0) | 0.40 (0.0-1.2) | | | 3 | 270 |
| Sebou, Morocco (Sabatié, 1993) | | 3.19 (0.0-6.5) | 28.53 (11.9-42.9) | 49.60 (38.1-60.0) | 17.43 (6.7-31.3) | 2.26 (0.0-4.8) | | 4 | 240 |

Table 4.3: Age structure (mean percent and range) of the spawning population of male *Alosa alosa* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | N | n |
|---|---------------------|----------------------|----------------------|----------------------|-------------------|------|---|---|------|
| | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | |
| Aulne, France (Véron, 1999) | | 69.23 | 30.77 | | | | | 1 | 13 |
| Loire, France (Douchement, 1981) | 11.80 | 75.00 | 13.20 | | | | | | 68 |
| Loire, France (Mennesson-Boisneau & Boisneau, 1990) | 7.35 (0.0-18.2) | 49.77 (20.2-86.9) | 37.87 (9.9-72.6) | 5.01 (0.0-15.6) | | | | 6 | 1173 |
| Charente, France (Véron, 1999) | 11.76 | 17.65 | 47.06 | 17.65 | 5.88 | | | 1 | 17 |
| Gironde-Garonne-Dordogne, France (Douchement, 1981) | | 25.00 | 50.00 | 25.00 | | | | | 36 |
| Gironde-Garonne-Dordogne, France (Anon., 1979a) | | | 26.00 | 40.00 | 26.00 | 8.00 | | 1 | 35 |
| Gironde-Garonne-Dordogne, France (Cassou-Leins & Cassou-Leins, 1981) | 4.85 (0.0-9.7) | 54.05 (50.0-58.1) | 41.10 (32.2-50.0) | | | | | 2 | 93 |
| Gironde-Garonne-Dordogne, France (Martin-Vandembulcke, 1999) | | 15.61 (8.9-22.0) | 71.23 (64.8-80.9) | 13.05 (3.2-22.8) | 0.11 (0.0-0.3) | | | 3 | 682 |
| Gironde-Garonne-Dordogne, France (Lambert <i>et al.</i> , 2001) | 4.12 (2.9-6.6) | 34.18 (27.8-43.9) | 54.08 (42.6-60.8) | 6.56 (2.3-10.4) | 0.05 (0.0-0.1) | | | 3 | 1191 |
| Adour, France (Douchement, 1981) | 1.40 | 66.70 | 30.50 | 1.40 | | | | | 72 |
| Adour, France (Prouzet <i>et al.</i> , 1994a) | | 12.97 | 62.34 | 21.76 | 2.93 | | | 5 | 239 |
| Douro, Portugal (Eiras, 1981b) | 20.03 (5.0-55.8) | 24.33 (5.0-37.2) | 29.03 (10.0-41.6) | 23.43 (3.3-45.0) | | | | 3 | 239 |
| Sebou, Morocco (Sabatié, 1993) | 0.86 (0.0-2.4) | 22.27 (11.3-37.4) | 48.92 (39.6-54.9) | 27.07 (11.0-49.1) | 0.88 (0.0-3.5) | | | 4 | 240 |

Table 4.4: Age structure (mean percent and range) of the spawning population of female *Alosa fallax fallax* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | | | | N | n |
|--|--------------------|----------------------|---------------------|---------------------|---------------------|---------------------|--------------------|-------------------|-------------------|-------------------|----|------|
| | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | | |
| Severn, England (Arahamian, 1982 & unpubl.) | 0.44 (0.0-5.5) | 11.72 (0.0-67.0) | 23.43 (0.4-78.6) | 25.49 (0.0-74.7) | 20.26 (0.5-61.8) | 11.28 (0.2-42.3) | 6.21 (0.0-42.1) | 1.20 (0.0-5.6) | 0.19 (0.0-1.9) | 0.04 (0.0-0.5) | 17 | 4598 |
| Wye, Wales (Arahamian, 1982) | | 21.28 | 70.21 | 4.26 | 4.26 | | | | | | 1 | 47 |
| Barrow, Ireland (O'Maoleideigh, 1990) | | 18.20 | 59.10 | 13.60 | | 9.1 | | | | | 1 | 22 |
| Holland (Arahamian, 1982) | | 1.29 | 80.54 | 9.09 | 5.19 | 2.60 | 1.29 | | | | 1 | 77 |
| Loire, France (Douchement, 1981) | 5.40 | 30.20 | 41.10 | 21.40 | 1.80 | | | | | | | 56 |
| Charente, France (Véron, 1999) | 17.86 | 71.43 | 10.71 | | | | | | | | 1 | 28 |
| Gironde-Garonne-Dordogne, France (Douchement, 1981) | 6.70 | 26.70 | 66.70 | | | | | | | | | 45 |
| Adour, France (Douchement, 1981) | | | 30.40 | 43.60 | 13.00 | 13.00 | | | | | | 23 |
| Sebou, Morocco (Sabatié, 1993) | 8.81 (2.5-20.0) | 48.19 (33.3-75.0) | 28.42 (0.0-49.0) | 14.58 (5.0-25.0) | | | | | | | 3 | 151 |

Table 4.5: Age structure (mean percent and range) of the spawning population of male *Alosa fallax fallax* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | | | N | n |
|--|-------------------|----------------------|----------------------|----------------------|---------------------|---------------------|--------------------|--------------------|-------------------|----|------|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | |
| Severn, England (Aprahamian, 1982 & unpubl.) | 0.02 (0.0-0.4) | 5.57 (0.0-46.0) | 20.48 (0.5-75.7) | 21.68 (0.0-78.9) | 21.61 (0.0-65.3) | 17.83 (1.0-61.5) | 8.62 (0.0-34.2) | 2.21 (0.0-10.2) | 0.28 (0.0-2.6) | 17 | 1527 |
| Wye, Wales (Aprahamian, 1982) | | | 63.46 | 34.62 | 1.92 | | | | | 1 | 52 |
| Barrow, Ireland (O'Maoleideigh, 1990) | | | 16.20 | 73.00 | 2.70 | 2.70 | 2.70 | 2.79 | | 1 | 37 |
| Holland (Aprahamian, 1982) | | | | 66.22 | 24.32 | 6.76 | 1.35 | 1.35 | | 1 | 74 |
| Loire, France (Douchement, 1981) | 26.00 | 60.50 | 31.60 | 5.30 | | | | | | | 38 |
| Charente, France (Véron, 1999) | | | 100.0 | | | | | | | 1 | 5 |
| Gironde-Garonne- Dordogne, France (Douchement, 1981) | | 51.40 | 29.70 | 16.20 | 2.70 | | | | | | 37 |
| Sebou, Morocco (Sabatié, 1993) | 0.37 (0.0-1.1) | 35.86 (23.8-57.1) | 49.37 (28.6-61.1) | 14.41 (11.1-17.8) | | | | | | 3 | 205 |

The age structure of the Portuguese populations (Table 4.6) is similar to that of the more southern stocks, with the exception of the River Tejo, which appears younger than other populations.

Table 4.6: Age structure of the adult population of *Alosa fallax fallax* from four Portuguese rivers (Alexandrino, 1996b).

| River | Sex | Mean \pm SD | Range | n |
|----------|-----|-----------------|-------|----|
| Lima | M | 3.83 \pm 0.85 | 2-5 | 51 |
| | F | 4.04 \pm 0.70 | 3-5 | 54 |
| Mondego | M | 4.08 \pm 0.76 | 3-5 | 25 |
| | F | 4.62 \pm 0.51 | 4-5 | 13 |
| Tejo | M | 2.77 \pm 0.69 | 2-4 | 22 |
| | F | 3.38 \pm 0.56 | 3-5 | 78 |
| Quadiana | M | 4.00 \pm 0.29 | 3-5 | 25 |
| | F | 4.20 \pm 0.56 | 4-6 | 15 |

Alosa fallax rhodanensis

The age of the spawning population ranges from 3 to 8 years old for both sexes, with the majority being between 5 and 6 years old for females and 4 and 5 years old for males (Tables 4.7 & 4.8). Though both sexes can mature as young as 2 years old (Le Corre *et al.*, 2000). The average age for the upstream migrants in the Rhône was 4.16 years for males and 5.05 for females and in the Aude 4.7 years and 5.7 years for male and females, respectively (Le Corre *et al.*, 2000). In the Hérault and Tavignano the males ranged in age from 4 to 5 and 3 to 6 years and the females 4 to 6 and 5 to 6 years, respectively, though caution must be exercised as sample sizes were small (Le Corre *et al.*, 2000).

Alosa fallax nilotica

The age structure of the anadromous population in the River Neretva ranged from 2 to 10 years old with the majority consisting of fish aged 5 years (Table 4.9). In the River Po (Italy) the maximum age recorded was 7 years old for both sexes (Serventi *et al.*, 1990). The range in the age structure for the landlocked population in Lake Skadar reflects samples taken using two different methods, trawl and seine net (Vukovic, 1961a).

Alosa fallax lacustris

The maximum population age is *c.* 5 years old in Lake Maggiore (Table 4.10) and four in Lake Garda (Oppi & Novello, 1989).

Alosa fallax killarnensis

The majority of the spawning population consisted of fish aged 4 years old (Table 4.10).

Table 4.7: Age structure (mean percent and range) of the spawning population of female *Alosa fallax rhodanensis* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | | N | n |
|--|-------------|-------------------|---------------------|----------------------|----------------------|--------------------|-------------------|---|---|-----|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | |
| Aude, France (Douchement, 1981) | | | 15.80 | 23.70 | 44.70 | 5.30 | 10.50 | | | 38 |
| Rhône, France (Douchement, 1981) | | 4.70 | 29.70 | 46.90 | 10.90 | 6.40 | 1.60 | | | 64 |
| Rhône, France (Le Corre <i>et al.</i> , 1997a) | | 1.82 (0.0-3.5) | 19.22 (6.1-26.7) | 47.27 (46.4-47.7) | 23.47 (14.0-35.5) | 7.40 (4.6-10.7) | 0.82 (0.0-1.3) | | 3 | 436 |

Table 4.8: Age structure (mean percent and range) of the spawning population of male *Alosa fallax rhodanensis* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | | N | n |
|--|-------------|---------------------|----------------------|----------------------|--------------------|-------------------|-------------------|---|---|-----|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | | |
| Aude, France (Douchement, 1981) | | 27.00 | 33.80 | 36.70 | 2.70 | | | | | 74 |
| Rhône, France (Douchement, 1981) | | 15.60 | 62.40 | 21.10 | | | | | | 109 |
| Rhône, France (Le Corre <i>et al.</i> , 1997a) | | 16.33 (7.3-23.4) | 48.31 (36.4-57.5) | 26.30 (19.1-38.2) | 7.49 (2.6-14.5) | 0.96 (0.0-1.8) | 0.61 (0.0-1.8) | | 3 | 302 |

Table 4.9: Age structure (mean percent and range) of the spawning population of female and male *Alosa fallax nilotica* (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | | | | N | n |
|------------------------------|-------------|----------------|----------------|----------------|-----------------|------------|-----------|-----------|-----------|-----------|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | |
| Neretva, (Vukovic, 1961a) | | 0.29 | 2.92 | 9.94 | 51.75 | 16.66 | 9.94 | 4.38 | 3.53 | 0.58 | | |
| Bačin, (Vukovic, 1961a) | 0.39 | 29.13 | 14.17 | 8.66 | 22.83 | 12.99 | 5.11 | 4.72 | 1.96 | | | |
| Skadar (Vukovic, 1961a) | 0.16-5.94 | 6.30- 29.38 | 2.36- 21.49 | 9.21- 11.94 | 26.38- 47.80 | 3.44-19.43 | 3.07-8.11 | 1.75-3.09 | 0.45-0.56 | 0.16-0.45 | | |

Table 4.10: Age structure (mean percent and range) of the spawning land locked populations (N = number of years sampled; n = number of fish aged).

| River | Age (Years) | | | | | | | N | n | |
|--|---------------------|--------------------|--------------------|----------------------|-------------------|----------------------|-------------------|---|---|------|
| | 1 | 2 | 3 | 4 | >4 | 5 | 6 | | | 7 |
| <i>Alosa fallax lacustris</i> (Berg, 1966a) | | | | | | | | | | |
| Lake Maggiore, Italy (sexes combined) | 49.10 (3.3-93.0) | 42.9 (3.0-78.7) | 5.83 (1.0-14.5) | 1.33 (0.4-2.6) | 0.37 (0.1-0.5) | | | | 3 | 1461 |
| <i>Alosa fallax killarnensis</i> (O'Maoleideigh, 1990) | | | | | | | | | | |
| Lough Leane, Ireland Female | | | | 62.50 (50.0-75.0) | | 33.35 (16.7-50.0) | 4.15 (0.0-8.3) | | 2 | 38 |
| Lough Leane, Ireland Male | | | 2.65 (0.0-5.3) | 76.05 (63.2-88.9) | | 21.35 (11.1-31.6) | | | 2 | 56 |

4.2 Abundance and Density

Alosa alosa

Estimates of abundance in terms of the total size of the spawning stock are presented in section 4.5 (Dynamics of the population). Some catch per unit effort data (number of fish caught per net per day) does exist for the Gironde system for the period 1984 to 1999 (Figure 4.1), the mean \pm 95% CI CPUE was 33.3 ± 3.3 and a coefficient of variation of 20.43% (Castelnaud *et al.*, 2001). The data suggests that that the population remained relatively stable up until 1993 and then started to increase which may be related to the provision of fish pass facilities in the Garonne and Dordogne (see section 6.3.5).

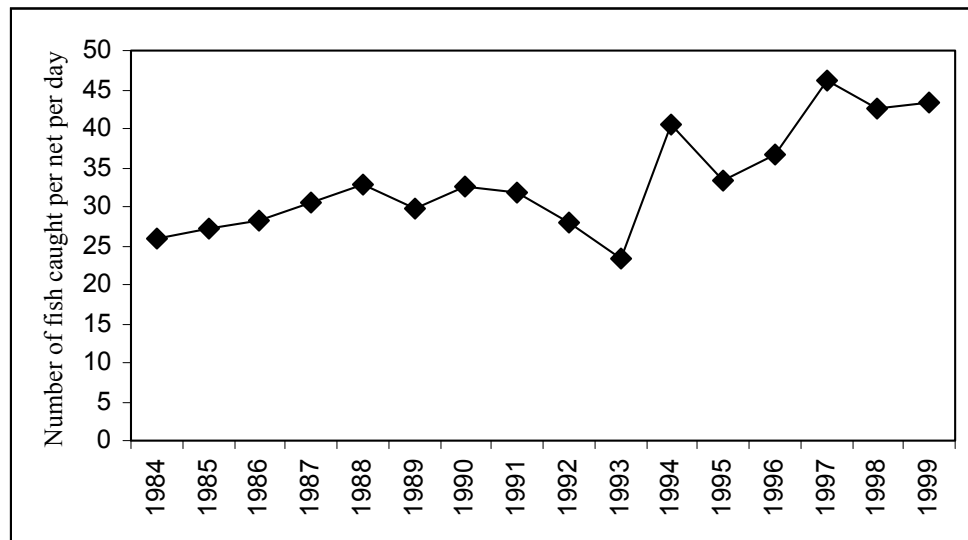


Figure 4.1: Annual variation in the number of *Alosa alosa* caught in the Gironde per net per day between 1984 to 1999 (Castelnaud *et al.*, 2001).

Alosa fallax fallax

Variation in a catch per unit effort estimate of abundance (Arahamian & Arahamian, 2001) of the female portion of the spawning population is shown in Figure 4.2 for *Alosa fallax fallax*, the coefficient of variation for the period was 39.3%.

Abundance (ind ha⁻¹) has been reported for the Elbe, downstream of Hamburg, for the period 1985 and 1986 (Möller, 1988) and from 1989 to 1994 (Thiel *et al.*, 1996a). During the period 1989 to 1994 the abundance of individuals in the spawning stock ranged from 1.75 to 11.72 ind h⁻¹ with a mean (SD) of 6.41 (4.37) ind h⁻¹ and coefficient of variation of 68.3%.

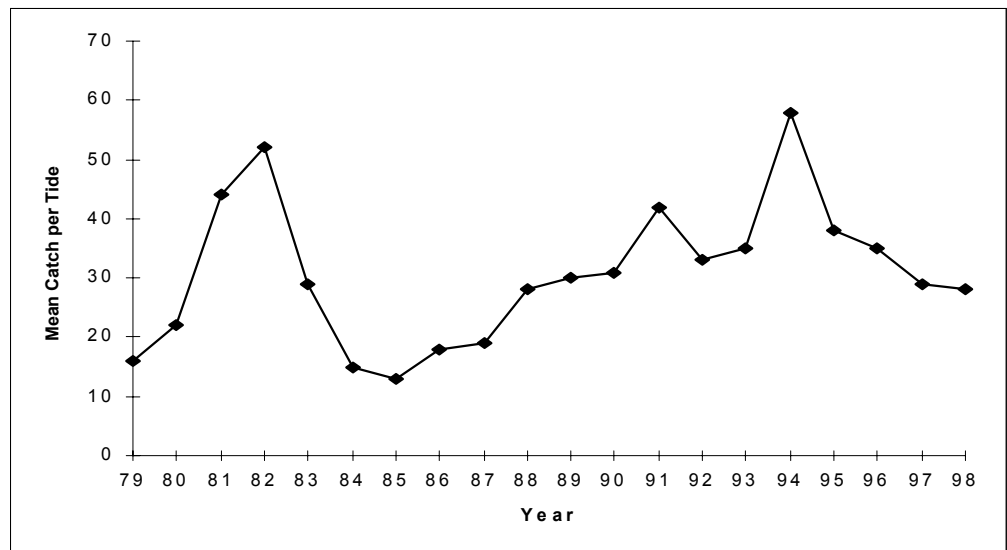


Figure 4.2: The CPUE index of female *Alosa fallax fallax* from the Severn Estuary (England) between 1979 and 1998.

4.3 Natalaty and Recruitment

4.3.1 Recruitment

Alosa alosa

The relationship between stock and recruitment for *Alosa alosa* from the Gironde-Garonne-Dordogne (France) was found to fit a Ricker curve (Figure 4.3) [Martin-Vandembulcke, 1999]:

$$R = aSe^{-bS} \quad r^2 = 0.45$$

where:

R = Number of recruits (0+ juvenile in autumn)

S = Parent stock (weight of female stock in kilograms)

a = 99.191

b = $7.717 \cdot 10^{-6}$

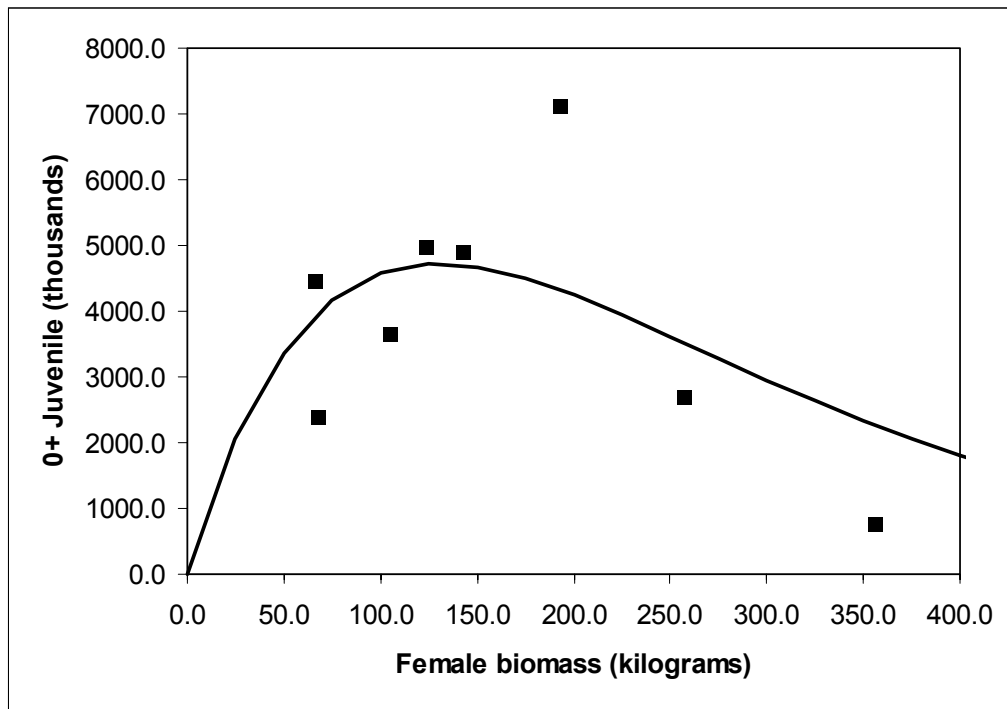


Figure 4.3: The stock recruitment relationship for *Alosa alosa* in the Gironde-Garonne-Dordogne (Martin-Vandembulcke, 1999).

On the Loire (France), Mennesson-Boisneau *et al.* (1999) found recruitment was significantly correlated with flow during the period of upstream migration (March 15th to June 15th), though the relationship is heavily influenced by the flow in one year. The relationship between year-class strength and flow can be described by the equation:

$$YCS = 0.068e^{(0.0016F)}$$

where:

YCS = year-class strength

F = mean flow ($m^3 s^{-1}$) for the period March 15th to June 15th.

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

The coefficient of variation in recruitment for the 1980 to 1992 year-classes was estimated as 124.4%. However, the spawning in 1983 coincided with a 1:100 year flood, which opened up much of the Loire that was usually inaccessible to allis shad for reproduction. If the 1983 year-class was excluded then the coefficient of variation reduced to 55.8%. The level of variation in year-class strength is lower than that from the Gironde-Garonne-Dordogne system of 79.7% for the period 1979 to 1996 (Martin-Vandembulcke, 1999).

Alosa fallax fallax

Drimmelen (1951) observed similar patterns of recruitment in relatively disparate stocks suggesting that large-scale climatic factors might be responsible, particularly flow and temperature.

Variation in recruitment, as measured by the coefficient of variation was estimated for 0+ *Alosa fallax* from the Severn Estuary to be 110.34 % (n = 18; 1981 to 1998) [Henderson & Seaby, 1999]. This compares well with the estimate of 124.45% (n=20; 1972 to 1991) for female *A. fallax* age 6 years old (Aprahamian & Aprahamian, 2001). In the Elbe (Germany), Thiel *et al.* (1996a) observed a coefficient of variation of 118.1% (n=5; 1989 to 1994) for the 0+ age group. Further south in the Gironde (France) the coefficient of variation was lower at 67.0% (n=9; 1979 to 1987) [Taverny *et al.*, 2000b]. However, more recent studies carried out between 1992 and 1999 indicated a higher level of variability with a CV of 113.8% (Taverny, pers. comm.).

Part of this variation can be associated with variation in temperature for example, Holmes & Henderson (1990) reported that good recruitment was associated with warm years. Aprahamian & Aprahamian (2001) found that mean July temperature explained the greatest proportion of the variance (67.1%) in year class strength, followed by August (50.9%) and June (30.9%). Taking the mean temperature for the three month period improved the proportion of variability explained to 77.1% (Figure 4.4)[Aprahamian & Aprahamian, 2001].

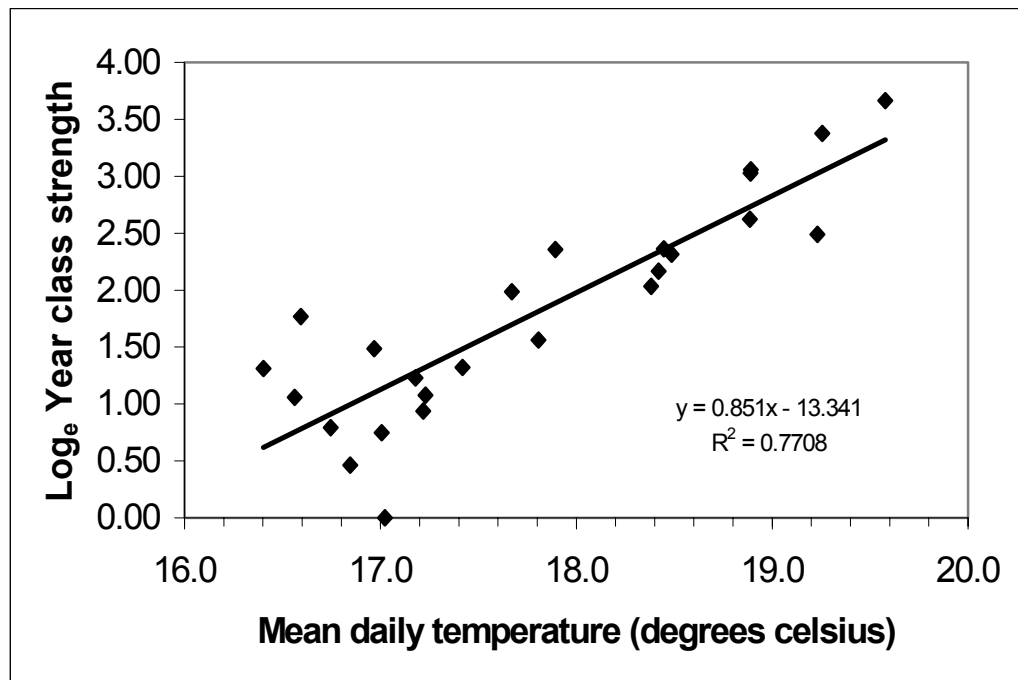


Figure 4.4: The relationship between year class strength of *Alosa fallax fallax* from the Severn Estuary, England between 1972 and 1996 and mean water temperature between June and August inclusive (Aprahamian & Aprahamian, 2001).

River flow was found to be inversely related to year-class strength, though flow and temperature were significantly inversely related ($P < 0.05$) during the summer months (June to August). The greatest proportion of the variability (42.3%) was explained by August flows, followed by July flows (36.8%) and June (27.7%) flows. Flows during the main upstream migration period in May were not significantly correlated ($P > 0.05$) with year-class strength.

4.4 Mortality and Morbidity

4.4.1 Mortality rates

Alosa alosa

The instantaneous rate of natural mortality (95% CI) for *A. alosa* from the Gironde-Garonne-Dordogne system was estimated to be 0.3528 (0.3527-0.3542) for females and 0.3445 (0.3385-0.3445) for males respectively (Martin-Vandembulcke, 1999). This rate effectively represents the mortality rate of immature fish at sea. Estimates of abundance existing for 0+ fish in the autumn and of adult fish from the same cohort when they mature four to seven years later.

Alosa fallax fallax

The mean (\pm S.D.) instantaneous mortality rate for adult *Alosa fallax fallax* from the Severn Estuary was 0.58 (\pm 0.24) for males and 0.49 (\pm 0.13) for females (Aprahamian, 1988). These rates were not significantly different ($P > 0.05$); combining the sexes gave an instantaneous rate of 0.53 (\pm 0.18). The instantaneous mortality rate for adult female *Alosa fallax fallax* from the Severn was similar to that estimated by Aprahamian & Lester (2001) from the number of fish caught at age 6 in year n and the number of 7 year olds caught in year $n+1$ of 0.472.

4.5 Dynamics of the Population

No information exists on the total size of the population. Some estimates of the size of the spawning population are available for the Gironde-Garonne-Dordogne system and Aulne (Véron, unpublished).

Alosa alosa

In the Gironde-Garonne-Dordogne system, Martin-Vandembulcke (1999) estimated the size of the spawning population between 1989 and 1996 to range from *c.* 270,000 to 615,000 individuals with a mean of 481,000 individuals (Figure 4.5).

Levels of exploitation have been calculated for *A. alosa* on the Gironde-Garonne-Dordogne (France) by Martin-Vandembulcke (1999) and by Chanseau *et al.* (unpubl.). Percentage exploitation over the period 1987 to 1998 (excluding 1988) ranged from 47.5% to 87.5% with a mean (\forall 95% CI) of 67.8% (\forall 8.2%). Annual exploitation rates by age and sex is presented in Table 4.11.

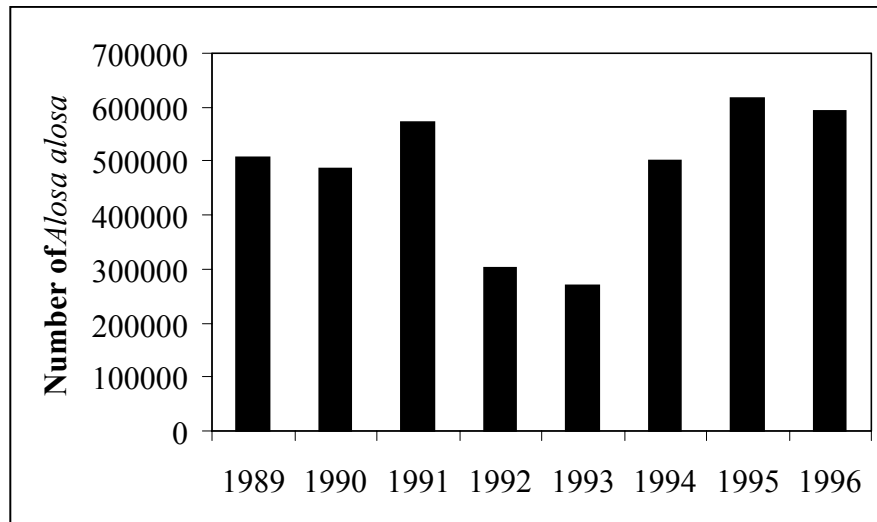


Figure 4.5: Size of the adult population between 1989 and 1996 in the Gironde-Garonne-Dordogne system (Martin-Vandembulcke, 1999).

Table 4.11: Range in the annual level of exploitation of *A. alosa* from the Gironde-Garonne-Dordogne by age and sex (Lambert *et al.*, 2001).

| Sex | Age (years) | | | | |
|--------|-------------|-----------|-----------|-----------|------|
| | 3 | 4 | 5 | 6 | 7 |
| Female | 0.00 | 0.04-0.13 | 0.46-0.54 | 0.39-0.61 | 1.00 |
| Male | 0.00 | 0.14-0.17 | 0.50-0.64 | 0.81-0.92 | 1.00 |

In the River Aulne, Véron (unpublished) estimated the size of the spawning population to be 2,182 individuals in 2000.

4.5.1 Production

Alosa fallax fallax

Thiel (2001) estimated production for fish age 0+ and 1+ in the Elbe estuary to be 759.6 g WW ha⁻¹ yr⁻¹ and 2.0 g WW ha⁻¹ yr⁻¹, respectively.

5. EXPLOITATION

Details of the main fishing methods can be found in Elie *et al.* (2000) and Sabatié *et al.* (2002).

5.1 Fishing Equipment

- Stow nets

Stow nets are bag nets where the opening is held open by a frame and the net is kept stretched by the current. They can be staked out in rows fishing adjacent to each other as in the River Weser (Von Brandt, 1972) or fished pelagically either side of a boat as in the Elbe (Figure 5.1) [Thiel *et al.*, 1995]. In the Elbe the net has an opening of 90m², a mesh at the cod end of 8 mm and at least one non-return valve (Thiel *et al.*, 1995). Eels are the main target species, reflecting the small mesh size, shad being taken as a by-catch.

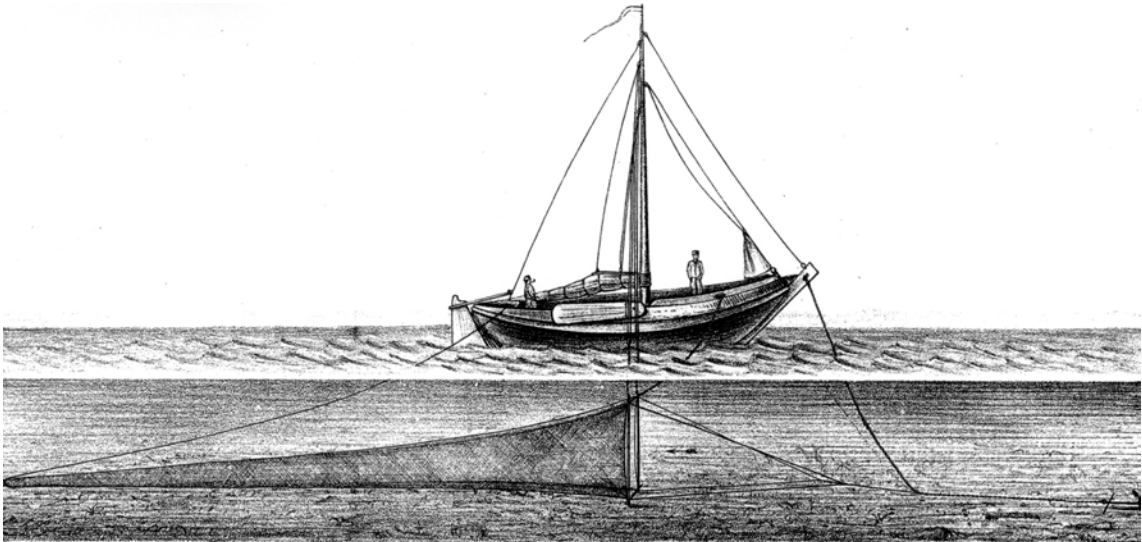


Figure 5.1: A schematic diagram of a stow net being fished (Anon. 1888).

- Putts and Putchers

Putts and putchers are characteristic of the Severn Estuary, England (Figures 5.1 & 5.2). These devices are mainly used for catching salmon and in the case of putts also shrimp. Putts are conical in shape and consist of four parts, the kype, forewheel, butt and bung, they are usually made from closely woven whitethorn or hazel twigs. Putts measure about 2m in diameter at the open end and the whole trap is about 4 m long. Putchers are more coarsely constructed trumpet shaped traps designed solely for taking fish, mainly salmon. Historically they were made from willow or hazel but recently they have been constructed from metal wire. They can vary in size from being round with a diameter of 0.76m at the mouth tapering to 0.07m at the tail, to square being 0.91 x 1.06m at the mouth. Several hundred putchers are supported in a framework on the foreshore, to form a rank or fishing weir, where it will be covered by the tide at high water some of the traps are positioned to fish the ebb tide (more common) and others the flood tide.

The fish swimming with the tide pass through the mouth and become jammed by the head and are soon drowned by the flow of water past the gills.



Figure 5.2: Putts.



Figure 5.3: Putchers.

- “Filet-barrage”

The *filet-barrage* is used on the rivers Loire, Lima and in Morocco, to catch shad as well as salmon and lamprey. In the Loire a net (mesh 110 to 180 mm knot to knot) is installed perpendicular to the bank, held in place by cables and stakes anchored into the bed of the river. A flat-bottomed boat, locally called a *toue*, approximately 9 to 15 m in length supports a fishing net of mesh 40 mm knot to knot (Figure 5.4). The fish are stopped by the larger mesh net, but not gilled. They search along the net until they find the gap, which leads into the smaller mesh net. The fishermen detect when fish are in the net from vibrations felt from thin nylon lines, which run from the base of the net to the fishermen. Once the fish are in the net a counter weight is released and the net raised. The arrangement of the *filet-barrage* in Portugal (River Lima) and Morocco is similar with the exception that in Morocco the large mesh net is set in the form of a “V” with the point facing upstream (Sabatié, 1993). In Morocco the fish are caught in a triangular holding net placed at the end of the “V” while in Portugal the shad are caught downstream of the net using seine nets. In the River Weser shad were caught in fyke nets placed at either end of the net barrier (Schnakenbeck, 1928).

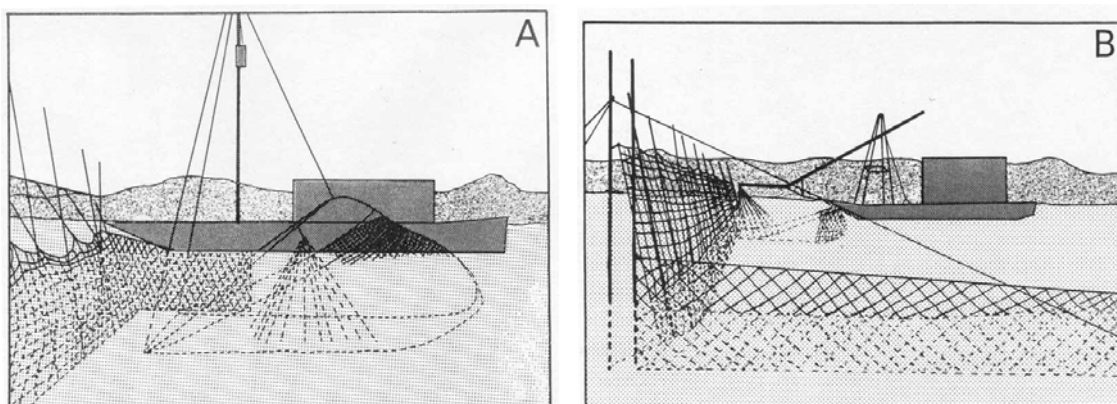


Figure 5.4: A schematic diagram of a *filet-barrage* (A) downstream of Tours and (B) upstream of Tours, from Mennesson-Biosneau & Boisneau (1990).

The *filet-barrage* can be fished either with the net under the boat as is done downstream of Tours on the Loire where the boat is placed adjacent to a bank (Figure 5.4A). Alternatively the net can be fished in front of the boat as is done upstream of Tours, in which case the boat is fished in the middle of the barrage (Figure 5.4B).

There are a number of regulations imposed on the fishery in the Loire;

- no fishing from two hours before sunset to two hours before sunrise,
- no fishing between 1800 h on Saturday and 0600 h on Monday,
- no fishing after June 15th.

- Fishing wheel / "baro" (or "vire-Blanchard" on the lower Rhône)

The "baro" is a stationary fishery which is carefully positioned on a channel or installed on a landing stage, boat or raft which is solidly attached to the river bank (Figure 5.5). The gear consists of two rectangular shaped nets made of regular or metal netting, attached to a horizontal axis and equipped with a funnel positioned towards the interior axis. The "baro" is driven by the current, so that the nets turn like the vanes of a windmill. The immersed rotating nets effectively scoop up fish moving upstream, the fish are then lifted out of the water and slide through the spout into the holding tank.

This automatic fishing gear was used to catch shad, salmon and lamprey. Today it is presently used on the lower Rhône where it is known as "vire-Blanchard" (Rameye *et al.*, 1976). It has almost disappeared from most of the larger rivers; Loire, Garonne and Adour in France and the Tiber in Italy where they were locally known as "giornelli" or "girarelli" (Von Brandt, 1972).



Figure 5.5: Fishing wheel / "baro" (from Baglinière & Elie, 2000).

- The square dip net

This type of fishing gear is mainly used by amateur fishermen on the lower Rhône, downstream of Beaucaire-Vallabrègues where it is known as “Le carrelet” (Figure 5.6) [Rameye *et al.*, 1976]. The fishing gear can be loaded onto a boat or raft or installed on the bank. The net, with a mesh size of between 30-40 mm, is stretched on a metal frame (4m x 4m) and suspended under a pole to which a pulley is attached. Lowered to a depth of two meters, it is regularly raised up by a hand winch. Larger tipping square dip nets are used, either in association with or independent of stop nets, in strong currents.



Figure 5.6: “Le carrelet” (from Baglinière & Elie, 2000).

- "Globe-net" fishing

The "globe-net" is a stationary Mediterranean-type fishing gear found, in the Languedoc region of France. It consists of a large rectangular net with fine mesh (15-20 mm), which is lowered to the bottom across a waterway and regularly lifted by means of complex mechanical devices, operated either by hand or automatically, and which require considerable skill. Several of these fisheries exist on the canals and streams draining into the lower reaches of the Rhône and the Aude Rivers.

- Stopping boats

The stopping boat is characteristic of the Severn and Wye estuaries (Figure 5.7), but few remain today. They are wide-beamed stoutly built boats up to 7m in length with a shallow draft. They are moored at right angles to the tide, attached to a cable and generally fish the ebb tide. A “V” shaped bag net is attached to poles about 6.7m in length and with a gape of 9.75m when open and suspended below the boat. Taut cords (“babbling lines”) run to various parts of the nets so that a fish striking the nets can be easily detected. The whole structure is very finely balanced with a counterweight, which is used to lift the net above the water surface once a fish has been detected.



Figure 5.7: Stopping boats in the Severn Estuary.

During the floods on the Loire River, a barge ("toue") is placed in a counter-current and the dip net, without a stop net, is directed downstream. The migrating fish, which let themselves be carried along by the counter-current in an upstream direction, brush against the nylon lines held by the fisherman who then raises the net.

- Seine nets

Seine nets are used in the Severn Estuary, in the Garonne and Dordogne (Figure 5.8) and in the past in the Elbe. In the Severn the nets measure 160m in length with a depth at the centre of 1.9 m and a mesh size of 50 mm knot to knot. The net is selective catching *A.fallax* in the length (L_f) range ≥ 300 mm.



Figure 5.8: Seine netting for *Alosa alosa* in the lower Garonne (from Baglinière & Elie, 2000).

- Trammel and drift nets

The nets can be either fixed as in the Rhône and Charente or attached to a boat, which drifts for several kilometres with the tide as in the Gironde and in the Bristol Channel. The nets used are either multi or monofilament gill nets or trammel nets. They can vary from 30 to 1000 m long, 2 to 15 m deep and with mesh between 40 to 110 mm dependent on local regulations. The size of the net are adapted to the depths encountered and the types of fish targeted.

In the Gironde-Garonne-Dordogne the mesh of the central sheet of the trammel net ranges from 45 to 60 mm (Rochard, 1985) and the selectivity curve for the net has been reported by Martin (1995). The mesh size used in other river systems is as follows: 55 mm in the Adour (Prouzet *et al.*, 1994c), >60 mm in the Rhône (Changeux & Zylberbat, 1993a), 80 mm in the Tage and 100 mm in other Portuguese rivers (Elie *et al.*, 2000). The mesh of the outer net can vary from 220mm (Rameye *et al.*, 1976) to 400 mm (Rochard & Castelnaud, 1986). In the Bristol Channel a single net of mesh 50 mm is used which catches *A. fallax* >330 mm (L_f).

Experimental netting carried out by Ruchon *et al.* (1994) on th Rhône provides some estimate of gear selectivity for *Alosa fallax rhodanensis*. A Mesh of 40 mm caught *A. fallax rhodanensis* ranging in size from 350 to 600 mm (L_t) while a 60 mm mesh caught fish between 410 and 620 mm. The smaller mesh net caught mostly males (61%) while females predominated (89%) in the 60 mm net. In the Bristol Channel a single net of mesh 50 mm is used which catches *A. fallax* >330mm (L_f).

- Landing net fishing.

This technique uses a large landing net (80 cm in diameter; 40 mm monofilament or braided mesh, depending on local regulations) with a long handle which is operated manually in currents where shad congregate. In the River Wye, Wales, the *Clinching net* was triangular in shape approximately 1.8 m wide at the base, the net measured 1.8 m in length with mesh of between 38 to 50 mm. The net was attached to a handle of between 1.8 and 2.1 m in length.

On the Severn Estuary triangular nets with a mesh of 50 mm called a *Lave net* (Figure 5.9) are used to catch shad but the nets are mainly used for catching salmon. The net is suspended from a collapsible Y shaped frame about 2.5m high and with a gape of about 3m. A lave net can either be fished passively waiting for the fish to swim into the net or actively which depends on the fishermen seeing the wake of a fish and running towards it and scooping it up.

- Angling

Recreational fishing of shad with a rod is widely practised in the British Isles, but is a recent phenomenon in France particularly in the rivers Charente, Garonne and Rhône as well as in a number of the small rivers. Fishermen either use a light fishing rod and small rubber sandeels, or small white or golden coloured 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 as shad have a hard and bony mouth and unless sharp a high percentage of hooked fish will be lost.



Figure 5.9: A fisherman with laval net, from the Severn Estuary.

5.2 Fishing Areas

Today the main fishing area for *Alosa alosa* and *Alosa fallax fallax* is in the Gironde-Garonne-Dordogne system in France and in Lake Garda (Italy) for the landlocked subspecies, *Alosa fallax lacustris* (see section 5.4).

5.3 Fishing Seasons

For the anadromous populations the main fishing season is associated with the commencement of the freshwater phase of their spawning migration (section 3.5.1). The migration / fishing season starting earlier in the year for populations at the southern limit of their range, becoming later with increasing latitude (table 3.85 and 3.86). For example, in France, where there are no restrictions as to when fishing for *Alosa* spp. can occur, the main season for fishing in the Loire is between March 15th and June 15th. While in the Gironde estuary the season is from February 1st to June 30th extending up until July 15th for fishing in the freshwater reaches of the Garonne and Dordogne. In Portugal the legal season for fishing runs from February 1st to June 15th.

5.4 Fishing Operations and Results

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. As a general characteristic, commercial fisheries are not targeted at allis shad as Atlantic salmon, sea trout, eel (glass and adult), river and marine lampreys and twaite shad are caught according to the country, the geographical position and the fisheries regulations. 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*.

Shad are marketed for human consumption, either fresh, frozen or smoked. Shad are a traditional dish in Portugal and Morocco (Baglinière & 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).

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 5.10). 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 when compared to 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).

In France, catches in Loire River are low, do not often exceed 10 t and have decreased to about 1t in 1995 and 1996. Average annual catches in the River Adour are approximately 19 tonnes between 1985 and 1999. Catches at sea catches 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.

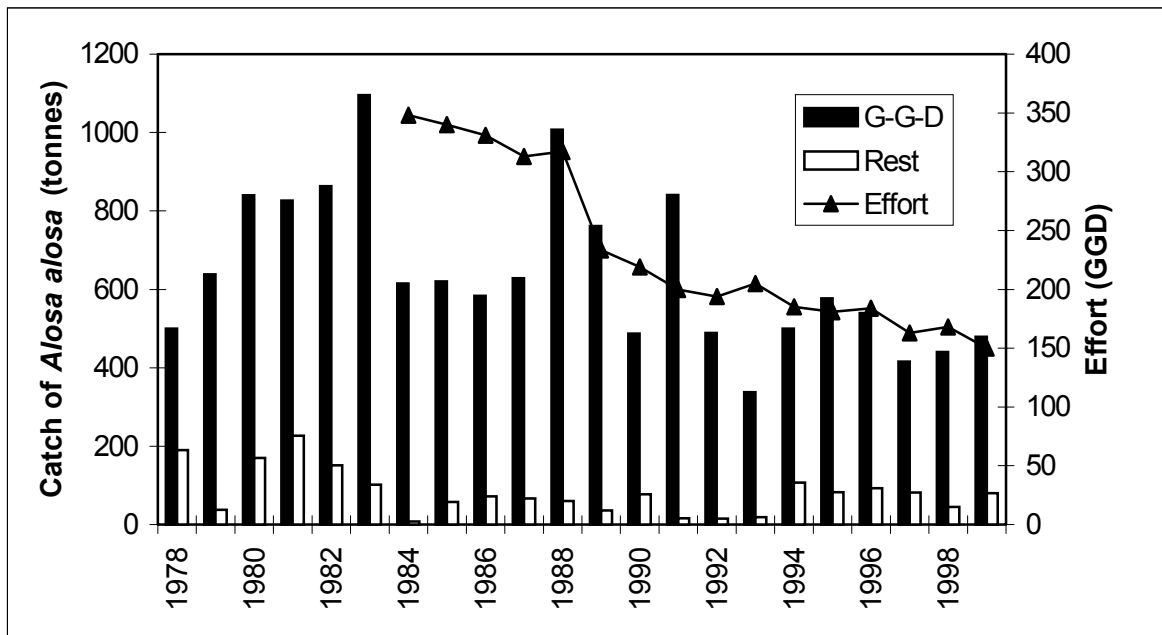


Figure 5.10: Total landings of *Alosa alosa* from 1978 – 1999 and effort data from the Gironde-Garonne-Dordogne system. Solid area indicates catches from the Gironde-Garonne-Dordogne system and clear area represents the combined catches from other river systems and at sea, data from Baglinière *et al.* (2002) and Castelnaud *et al.*, (2001).

In Portugal, the total catch is small and comes mainly from small rivers such as the Lima where the catch was abundant at the beginning of the 1990's, 2 to 10 tonnes annually, but has recently decreased markedly (1998). The fishery ceased operating in 1999. In the Sebou Wadi (Morocco) which was the main and last river to support an 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 (Figure 2.7).

In France, during the 1989-1997 period, shad landings, of which 98% were of *A. alosa*, were 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.*, 2002). In 1997, 280 commercial fishermen were recorded fishing for allis shad; equivalent to 19.8 % of the total number of fishermen (Castelnaud, 2000).

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* (Baglinière *et al.* 2002). In some countries notably 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 increasing with the decline in the population of *Alosa alosa*. Similarly in the North Sea catches between 1910 – 1914 and from 1915 – 1919 averaged 900 and 200 tonne per year, respectively and that in the Baltic Sea were 2,100 and 1,700 tonnes 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 it's *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 to 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 tonnes after which, the catches declined markedly and show a similar trend to that of *Alosa alosa* (Figure 2.8) [Sabatié, 1993].

Currently the best estimates of their importance for various rivers systems is shown in Table 5.1 (Baglinière *et al.* 2001). The major fishery is on the Gironde-Garonne-Dordogne system with an estimated annual catch of between 13 and 15 tonnes per year. Prior to 1989 the annual catch was higher at between 60 and 192 tonnes 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 tonnes per year.

Table 5.1: Annual catch (tonnes) of *Alosa fallax fallax* from various river systems.

| River | Annual catch (tonnes) |
|-----------------------------|--|
| Severn (England) | 5-6 (prior to 1999) - Insignificant after 1999 |
| Loire (France) | 0.6-2 |
| Dordogne & Garonne (France) | 13-15 |
| Lima (Portugal) | 0.5-1.5 |
| Tage (Portugal) | Insignificant |
| Guadiana (Portugal) | Insignificant |
| Sebou (Morocco) | 0.2-0.6 |

Alosa fallax rhodanensis

Prior to the construction of the Donzère Mondragon in 1952 a fishery for *Alosa fallax rhodanensis* existed in the upper Rhône, with an estimated annual catch of 50 kg y⁻¹ in the Rhône and 5 kg y⁻¹ in the Ain (Tripier, 1903 (cited by Bravard, 1985)). Estimates for various sections have been provided for the lower Rhône by Pattée (1988). In the section of river between Lyon and Serrières (58 km) 15,000 shad were caught in 1944, between Serrières and the Ardèche confluence (133 km) 6,010 were caught in 1926 and between the Ardèche confluence and Arles (89 km) 13,000 were captured in 1937. If these are taken as annual averages then this represents a total catch by both legal (professional and amateur fisherman) and illegal (poaching) means of 34,000

individuals. For the whole river upstream of Arles, Gallois (1950) reported a total catch of 53 tonnes for 1927. In the Petit Rhône estuary at the end of the 19th century annual catches ranged from 2,300 kg to 6,400 kg (1890-1895) [Gourret, 1897].

In 1974 the year of the construction of the most downstream barrier at Vallabrègues situated 58 km from the sea 23 t were caught (Rameye, *et al.*, 1976). More recently catches have declined being estimated at 6.3 t in 1988 and 1989 (Changeux & Zylberblat, 1993b) and 8.3 t in 1997 (Lebel *et al.*, 1997). Barral (2001) reported the total average catch in 1997, 1998 and 2000 (in 1999 there was no estimate of the catch taken by amateur fishermen) was 11.3 t yr⁻¹ with 50.2% being taken by recreational (rod and line) anglers, 29.5% by professional and 20.3% by amateur fishermen.

Alosa fallax lacustris

The trend in catch of *Alosa fallax lacustris* in lakes Maggiore and Garda are shown in Figure 5.11. In Lake Garda the annual catch appears to have stabilised at between 150 and 200 tons. In Lake Como, between 1996 and 1999, approximately 30 tons are caught per year, with catches ranging from 19 to 39 tons (Negri, pers. comm. cited by Bianco, pers. comm.).

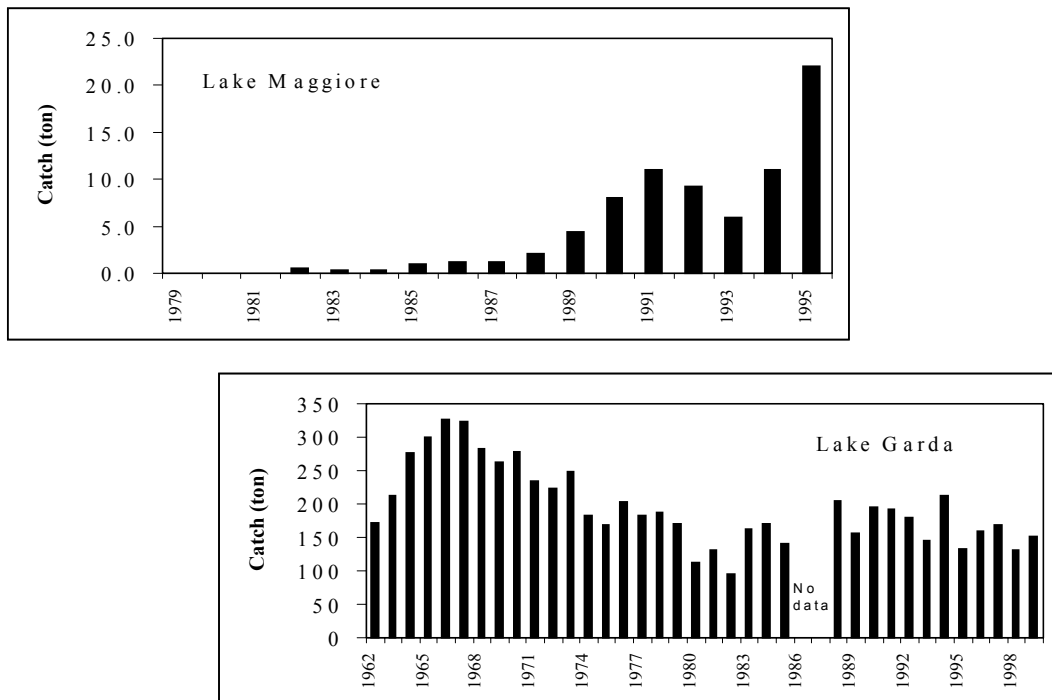


Figure 5.11: Catch of *Alosa fallax lacustris* from lakes Maggiore (Grimaldi, 1997) and Garda (Novello & Oppi, 1985; Confortini, 1998; pers. comm.), from Bianco (2002).

Alosa fallax nilotica

Catches prior to the construction of the dam on the River Bojana in 1960 ranged from 6 to 81 tons per year after which catches declined markedly such that today relatively few are taken (Figure 2.12).

5.5 Climate Influences

The influence of temperature and flow on recruitment is dealt with in section 4.3, Natalaty and recruitment.

Alosa fallax fallax

The possibility that large scale environmental factors may act on quite disparate populations in a similar way was postulated by Drimmelen (1951) who observed similar patterns of recruitment in *Alosa fallax* suggesting that large-scale climatic factors might be responsible, particularly flow and temperature. Certainly a similar pattern of recruitment exists in the Severn and Elbe (Aprahamian & Aprahamian, 2001) with higher recruitment in 1989 and 1990 compared with the period 1991-1994 (Figure 5.12). Alternatively, Thiel *et al.* (1996b) concluded that the lower catches of juvenile *A. fallax* between 1991 and 1993 compared with 1989 and 1990 were the result of a change in spawning area as a consequence of an improvement in water quality in 1991 (see section 6.2.2). It was suggested that the lower abundance of juveniles in the period after 1991 was due to the higher level of power station mortality because the adults had moved 20 km upstream, and thus closer to Stade power station, to spawn.

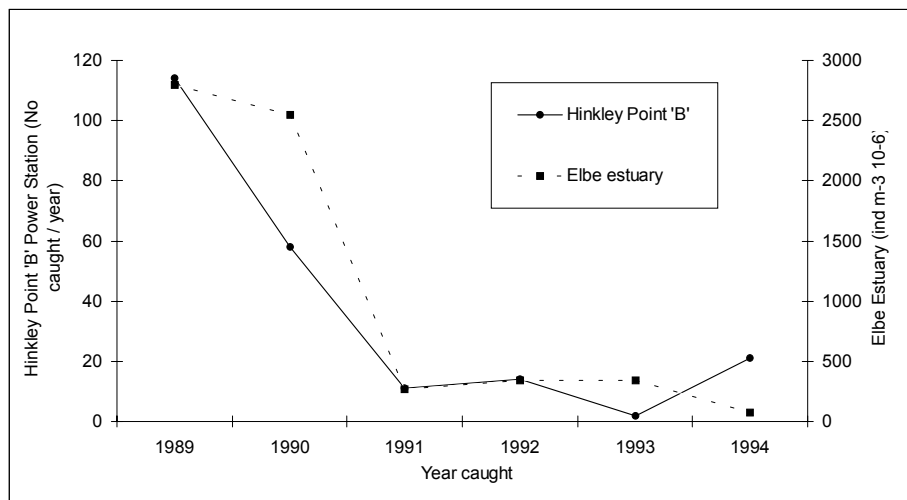


Figure 5.12: The number of juvenile (age 0+) *Alosa fallax* from the Bristol Channel, at Hinkley Point 'B' Power Station and from the Elbe Estuary between 1989 and 1994 (Aprahamian & Aprahamian, 2001).

The summer weather pattern in England is strongly influenced by the position of the north wall of the Gulf Stream (Willis *et al.*, 1995). If large-scale global weather patterns are impacting on the population then any change in its position should manifest itself in

terms of a change in recruitment, with higher recruitment the further north the north wall is positioned. Aprahamian & Aprahamian (2001) suggested there might be (Figure 5.13). The two outliers (1976 and 1989) corresponded to two very hot summers and, if the relationship is true then, it is likely that local meteorological conditions overrode the wider global weather pattern.

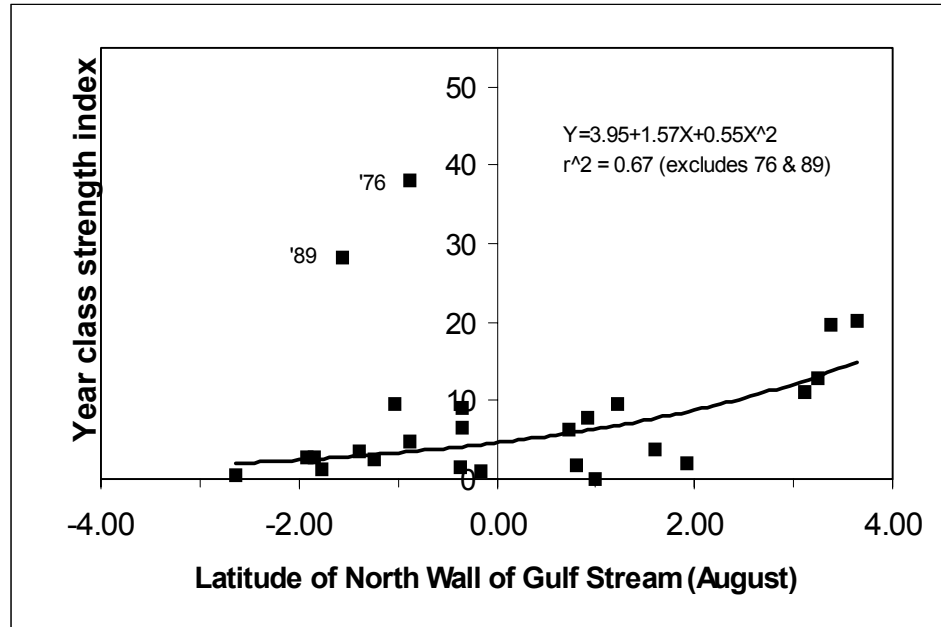


Figure 5.13: The relationship between year-class strength of *Alosa fallax* from the Severn Estuary and the position of the North Wall of the Gulf Stream (First principal component of the position of the North wall of the Gulf Stream), August 1976 and 1989 year-classes marked (Data from A. H. Taylor; <http://www.pml.ac.uk/gulfstream/inetdat.htm>), from Aprahamian & Aprahamian, 2001.

6. PROTECTION AND MANAGEMENT

There has been a considerable decline in abundance of *Alosa* spp. throughout their geographic range (see section 2, Distribution), but also Keith *et al.* (1992) specifically for France. It is for this reason that the species have been included in Appendix III of the Bern Convention (Anon., 1982) and into Annexes II and V of the EC Habitats Directive. The main reason for this decline has been the construction of dams preventing access to their spawning grounds (see section 2). In some river systems this has resulted in the extinction of one and / or both species of *Alosa*. Examples include the loss of *Alosa alosa* from the Severn (Aprahamian & Aprahamian, 1990), *Alosa fallax rhodanensis* from the Tiber (Bianco, 2002) and both species *A. alosa* and *A. fallax* from the Rhine (de Groot, 1989; Raat, 2001). The effect of barriers may have been exacerbated by overfishing as fish congregate and become easier to capture below obstructions. Such a situation may well have developed on the Rhine (see Figure 2.3). Pollution (poor water quality), especially in the lower reaches and estuaries has also been identified as a threat. For example in the Baltic Sea region (Repečka, 1999), Thames (Aprahamian & Aprahamian, 1990), Weser (Busch *et al.*, 1988, 1989) and in the Sebou (Sabatié, 1993) as well as for some of the landlocked population such as *Alosa fallax lacustris* in Lake Maggiore (Grimaldi, 1997). Habitat destruction has also been implicated for their decline. This can occur as part of a reengineering scheme to improve navigation and for flood defence purposes as on the Rhine (de Groot, 1989; Raat, 2001), or as a consequence of gravel extraction effectively impacting on the species spawning habitat (Taverny *et al.*, 2000a).

The conservation options available for the protection and enhancement of *Alosa* populations has been reviewed by Maitland & Lyle (1992, 1993) and by Maitland (1994). Generic guidelines for the protection of endangered species have been described by Costello *et al.* (2002). These include unhindered access to their spawning grounds where this is not possible, their migration being blocked by a physical barrier, then the obstruction must support an effective and efficient fish pass. Similarly there should not be a water quality barrier preventing access to their spawning areas and no siltation of their spawning grounds (see section 3.1.7.1).

6.1 Conservation Status

Populations of *Alosa* have declined throughout their range and in many instances have become extinct, mainly through the construction of barriers, pollution and over fishing (Section 2). The rare and threatened status of *Alosa alosa* and *Alosa fallax* spp. (Table 6.1) is reflected in their occurrence on nationally and internationally based protective legislative schedules. However, in some cases there is some uncertainty over the species actual conservation status. For example in Spain both species were classified as “endangered” by Elvira (1997) while Blanco & Gonzalez (1992) and Elvira (1996) categorised them as “vulnerable”. Similarly for *Alosa fallax* from Germany the species is classified as “vulnerable” by Freyhof (2002) and as “endangered” by Nowak *et al.* (1994).



Figure 6.1: Location of Special Areas of Conservation (SAC) or Sites of Community Interest (SCI) under the EC Habitats Directive, for *Alosa alosa*. Where a number of sites on a particular river have been designated the whole river has been included for clarity. The individual sites are presented in Appendix 1.



Figure 6.2: Location of Special Areas of Conservation (SAC) or Sites of Community Interest (SCI) under the EC Habitats Directive, for *Alosa fallax* spp. Where a number of sites on a particular river have been designated the whole river has been included for clarity. The individual sites are presented in Appendix 2.

Table 6.1: Conservation status of *Alosa alosa* and *Alosa fallax* spp., data from P. Maitland (pers. comm.) unless otherwise stated.

| Conservation status (IUCN, 1990) | <i>Alosa alosa</i> | <i>Alosa fallax fallax</i> | <i>Alosa fallax nilotica</i> |
|--|--|--|---|
| Extinct 'when there is no reasonable doubt that the last individual has died' | Poland ¹¹ Luxembourg Czech Republic ¹ | Luxembourg Netherlands | |
| Critically Endangered 'when it is facing an extremely high risk of extinction in the wild in the immediate future' | Denmark | Denmark | |
| Endangered 'when it is not critically endangered but is facing an extremely high risk of extinction in the wild in the near future' | Germany ⁹ Ireland ² Spain ⁵ Netherlands Belgium ¹³ UK | Lithuania ¹⁰ Poland ¹¹ Spain ⁵ Belgium¹³ | Croatia ⁶ Montenegro ⁶ Albania ⁷ |
| Vulnerable 'when it is not Critically Endangered or Endangered but is facing a high risk of extinction in the wild in the medium-term future' | France ³ Portugal ⁴ | France ³ Portugal ⁴ Ireland ² UK Germany ⁹ | Italy ⁸ |
| Not Evaluated 'when it has not been assessed against the criteria' | Finland | Finland | |
| Absent from red data book or equivalent | Austria Greece Italy | Austria | |
| Data Deficient | Sweden ¹² | Sweden ¹² | |

¹ Lusk (1996); ² Whilde (1993); ³ Keith *et al.* (1992); Keith & Allardi (1996);
⁴ SNPRCN (1991); ⁵ Elvira (1997); ⁶ Mrakovic *et al.* (1995); ⁷ Rakaj & Flloko (1995);
⁸ Bianco (1998); ⁹ Freyhof (2002); ¹⁰ Balevičiene, *et al.* (1992); ¹¹ Skora (1996);
¹² Kullander (2002); ¹³ Vandelannot & Coeck (1998).

Alosa alosa and *Alosa fallax* are both included in Appendix III of the Bern Convention (Anon., 1982) which requires member states to carry out provisions to ensure conservation of flora and fauna and their habitats with particular attention to endangered and vulnerable species, including migratory species. Both species are incorporated into Annexes II and V of the EC Habitats Directive (EC Directive on the conservation of natural habitats and wild flora (92/43/EEC)). This places an obligation of members of the European Union to assess numbers and exploitation of the populations and to designate Special Areas for Conservation (SAC) / Sites of Community Interest (SCI) to safeguard populations (Figures 6.1 & 6.2). The individual sites are listed in Appendix 1 and 2 for *Alosa alosa* and *Alosa fallax* spp. respectively.

6.2 Habitat Protection and Management

6.2.1 Physical habitat

Other than maintaining access to their spawning grounds (see section 6.3) and safe passage for the juveniles on their out-migration (Travade & Larinier, 1992a), the other main habitat features that need to be maintained are:

Deep pools where the adults can congregate prior to spawning (see section 3.1.7.1). Silt free spawning gravels to ensure that the eggs do not suffocate (see section 3.1.7.1).

Areas of reduced current / backwaters as these are the preferred habitat of the juveniles in fresh and estuarine waters (see section 3.2.2).

Particularly sites (sanctuary areas) important for the persistence of the population can 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).

6.2.2 Water quality

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 maximised 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 & 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 & 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 & Scholz (1991) on juvenile *Alosa fallax* suggests a dissolved oxygen level of >4 mgL⁻¹ (section 3.2.2) would protect shad.

6.3 Fish Passes

The construction of physical barriers, preventing the adult fish reaching their spawning grounds, has been one of the main reasons for the decline of *Alosa* populations throughout Europe, see section 2. Differences between upstream and downstream water level of ~1m and especially if the flows are plunging will create a barrier to shad

(Larinier & Travade, 1992a; 2002a). Fish passes designed for salmonids are not altogether suitable for shad because passes are generally characterised by turbulent flow patterns, whereas shad prefer smooth, laminar flow. The swimming capability of shad is summarised in section 3.5.2 and flows in excess of 3.5 to 4 ms⁻¹ will generate difficulties for *Alosa* spp. (Larinier & Travade, 1992a; 2002a).

Fish passes for shad, mainly *Alosa alosa* and *Alosa fallax rhodanensis*, have been described by Larinier *et al.* (1978), Larinier (1983), Vialle (1987), Baril (1988), Larinier & Travade (1992a, 2002a), Travade *et al.* (1992) and Travade *et al.* (1998).

Larinier & Travade (1992a; 2002a) have outlined some of the requirements, which are necessary to ensure effective passage for shad. Shad are a shoaling species, which swim close to the surface and tend to bypass obstructions by swimming rather than leaping. As such, flow should be "streaming" as opposed to "plunging". The species are sensitive to changes in flow direction, therefore unidirectional flow running parallel is required in a shad pass. Where there is a change in flow direction the fish can get trapped in the currents and in some cases the whole shoal may drop back downstream. In addition shad appear sensitive to sudden changes in light intensity, therefore it may be necessary to light particular sections in a fish pass. The entrance to the pass must be situated along the bank and the velocity at the entrance of the pass should be about 2 ms⁻¹.

6.3.1 Pool passes

Pool type passes have been shown to be effective for passing shad, however, there have been few studies on their efficiency. For the Ramier pool pass (R. Garonne, France) the efficiency was estimated at 70% (Dartiguelongue, 1990). This was regarded as high and considered to be the result of favourable hydrological conditions (low flows) making the pass more attractive in that particular year (Larinier & Travade, 1992a). On the Dordogne (France) the annual efficiency of the pool pass at Mauzac varied between 6 and 56%, the variation being largely dependent on flow conditions during the migration period (Larinier & Travade, 2002a).

Pool passes (Figure 6.3) must meet the following requirements:

- Drop between pools should not exceed 0.30m, preferably lower, between 0.20 and 0.25m.
- Flow should be "streaming" as opposed to "plunging".
- Gaps or slots must have a minimum width of 0.45 to 0.50m and must be along the wall. Central gaps must be avoided. There must be no submerged orifices.
- Large recirculation eddies must be avoided.
- Pools must be at least 1.20m deep, have a volume in excess of 12m³ and have a maximum mean power dissipation of 150 watts m⁻³.

6.3.2 Baffled passes

Studies carried out in France indicate that Denil fish passes have not proved suitable for passing shad. This is the case for two passes in France, at Beaucaire on the Rhône and at Bazacle on the Garonne. The pass at Beaucaire has two Denil flights, flat baffles, gradients of 8% and 10% and measures 1.30m wide with an overall length of 40m

(CTGREF, 1981). The pass at Bazacle has three Denil flights, broad arrow-shaped baffles, a gradient of 17% and measures 1.50m wide by 12m long. Poor performance in the Beaucaire pass is attributed to the hydraulic conditions in the fish pass, and in the Bazacle pass poor positioning of the entrance is thought to be the problem. The efficiency (minimum estimate) of the Bazacle fish pass was estimated to range from 6% to 34% with a mean of 18.5% (Larinier & Travade, 2002).

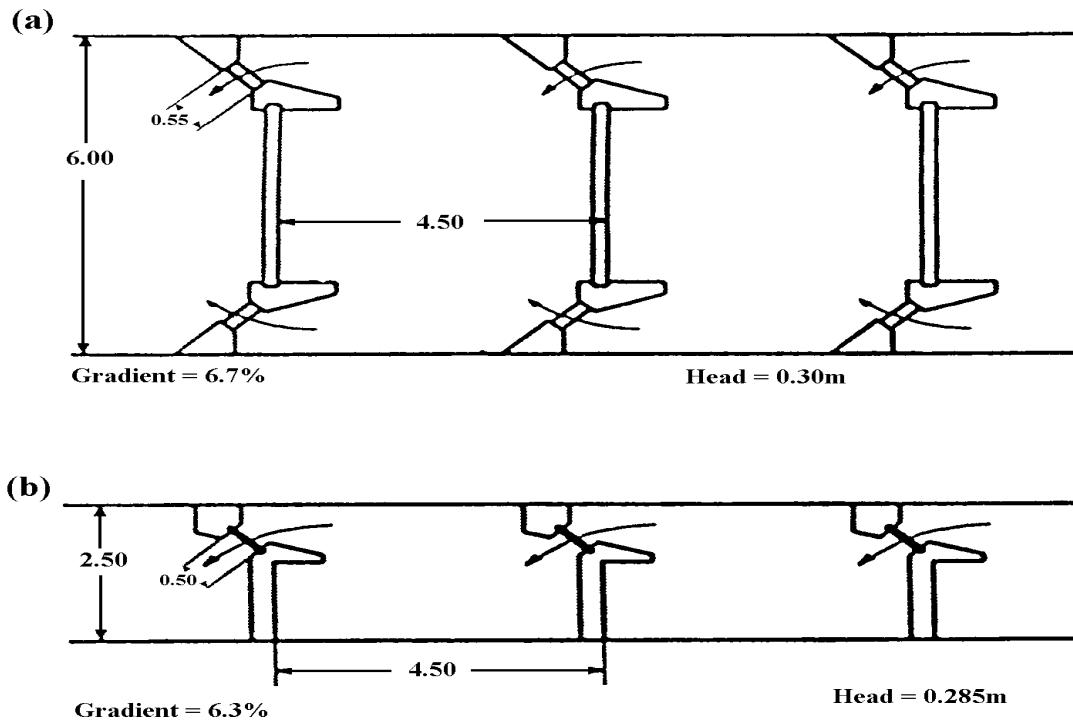


Figure 6.3: Pool fish passes (a) at Bergerac (R. Dordogne, France) and (b) at Ramier (R. Garonne, France), from Larinier & Travade (1992a).

Baril (1988) carried out studies on the River Rhône, France, using a Denil fish pass with broad arrow-shaped baffles (gradient 16%, width 1.80m, length 10m, baffle cross section 0.10 x 0.10m) and found that shad passed at flows of 300 to 750 $\text{l}^{-1}\text{s}^{-1}\text{m}^{-1}$. However, the efficiency of the pass was closely related to the flow pattern at the entrance to the pass.

Chevron type baffled fish ways may be suitable for passing shad over relatively low obstacles (Richard pers. comm., cited by Larinier & Travade, 2002a).

6.3.3 Fish lifts

Fish lifts which have been designed to pass *Alosa* spp. are situated at Golfech on the River Garonne, France (Figure 6.4) and at Tuilières on the River Dordogne, France. Travade & Larinier (2002a) have described the working principle of the fish lift. It involves trapping the fish in a tank, which is then raised and emptied upstream. The

fish are caught and held in a large holding pool fitted with a non-return device. Before the tank is raised the vertical screens on the crowder are shut and moved horizontally, confining the fish to a space just above the tank. The tank, situated in the floor of the holding pool, is then raised and the fish are emptied out into a channel via a chute. After the fish have been released, the trap and crowder return to their original position and the vertical screens on the crowder are re-opened.

Fish lifts must meet the following requirements:

- The lift must be designed to take between 1.5 and 2% of the total run at each operation.
- The large holding pool used to trap the fish must be at least 5m x 2.5m x 1.5m with a minimum water volume of 30 litres per shad.
- The volume of the tank into which the fish are crowded must be ≥ 10 litres per shad.
- The spacing of the bars on the screens must be < 25 mm.
- The auxiliary flow must be fed in upstream of the tank and the velocity at the entrance to the holding pool must be around 1ms^{-1} .
- The width of the channel leading out of the tank and allowing the fish to progress upstream must be $> 1.5\text{m}$ wide.
- The water velocity in the channel leading out of the tank must be $> 0.3\text{ms}^{-1}$.

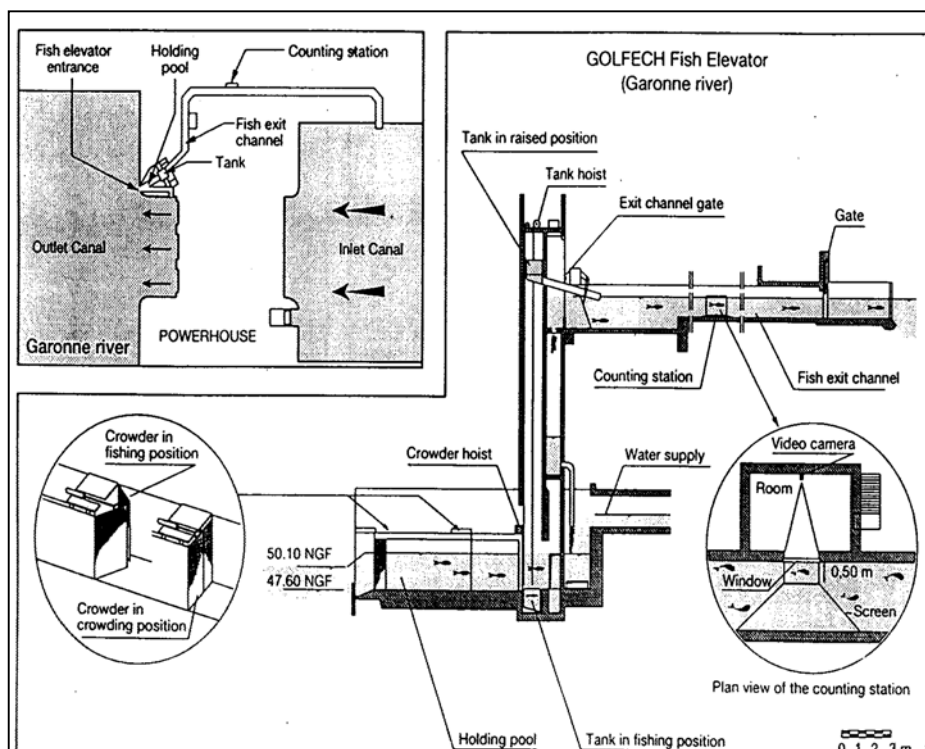


Figure 6.4: The Golfech fish lift on the River Garonne, France (Travade *et al.*, 1998).

A Borland fish lift has been installed at the Crestuma-Lever dam on the Douro and on the Belver dam on the Tejo, both appear to be ineffective for passing *Alosa* spp.

upstream (Bochechas, 1995). This is thought to be due to the location of the entrance in that it can't be easily found by the migrating species and that the attraction flow is small in relation to the competing flow.

6.3.4 Navigation locks

The use of navigation locks to circumvent barriers has been reported by Zylberblat & Menella (1996) for *Alosa fallax rhodanensis* from the Rhône. The main criterion for successful operation was ensuring adequate attraction flow, which was estimated at 10.5% of the conventional low-water flow for 20 minutes. Extending the period to 40 minutes did not significantly increase the number of shad entering the lock.

For locks operated using vertical gates, the recommended exit conditions were with the gates fully opened (down) as opposed too partially opened.

6.3.5 Performance

Comparison between installations is difficult because of differences in counting devices and the number of fish available to migrate (Travade *et al.*, 1998). The number of shad passing two sites on the Garonne (France) has ranged from 14,000 to 106,000 at Golfech and from 1,000 to 21,000 at Le Bazacle (Figure 6.5) [Travade *et al.*, 1998; Larinier pers. comm.]. At three sites on the Dordogne (France) the counts have ranged from 2,000 to 78,000 at Bergerac, from 2,000 to 87,000 at Tuilières and from 100 to 34,000 at Mauzac (Figure 6.5) [Dartiguelongue, 1996; Travade *et al.*, 1998; Larinier, pers. comm.].

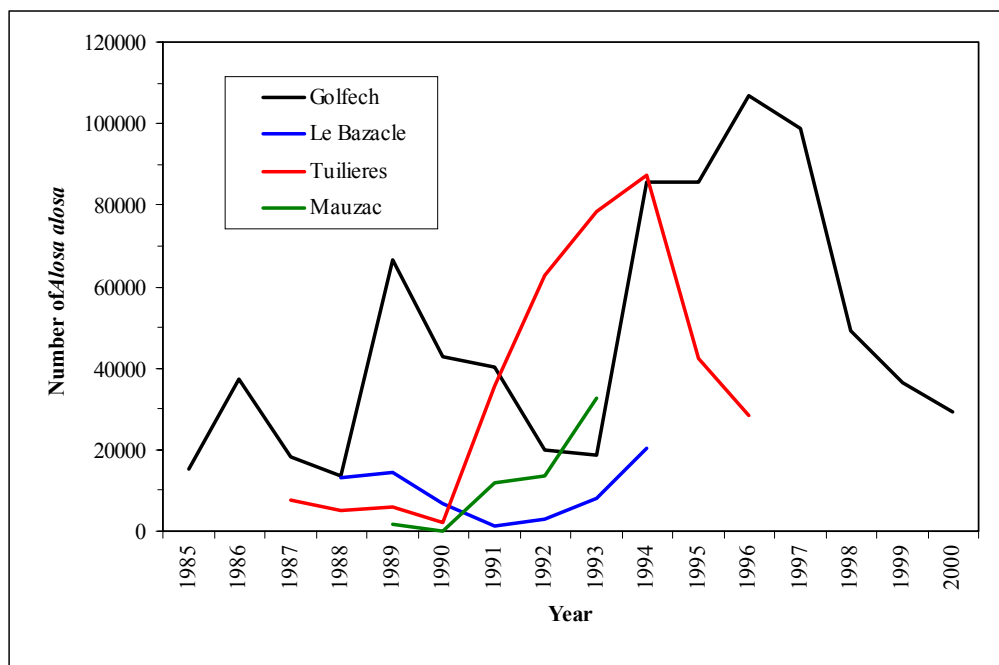


Figure 6.5: The count of shad at four fish passes; Golfech and Bazacle on the River Garonne and Tuilières and Mauzac on the River Dordogne, France.

6.4 Screens

Impingement at water intakes does provide a potential threat. Hadderingh & Jager (2002) estimated that in the region of 54,000 *Alosa fallax*, mainly juveniles were impinged annually by the Eems power station in the Ems Estuary (The Netherlands - Germany). Quantitative estimates also exist for the Blayais power station in the Gironde Estuary (France) where Taverny (1990) estimated that 434,860 *Alosa alosa* and 713,800 *Alosa fallax* were entrained in 1986.

Larinier & Travade (2002b) provide details of the various methods and types of screens that can be used to reduce entrapment at water intakes. Acoustic deterrents offer one of the most promising ways of reducing the level of impingement as *Alosa* spp. are known to be sensitive to a frequency of 200 kHz (Gregory, 1999) [section 1.3.2.7], though some development work will undoubtedly be needed. A frequency of 200 kHz was found to act as a barrier to the upstream migration of *Alosa fallax*, such that the fish would accumulate in shoals downstream of the acoustic beam, once the barrier was removed the adults would continue on their upstream migration (Gregory, 1999).

6.5 Translocation / Transplantation.

Translocation or transportation is the movement of any taxon from one place to another; guidelines for which have been proposed by Williams *et al.* (1988) and by Maitland & Lyle (1992). Hoestlandt (1958) transferred approximately 500,000 eggs of *Alosa alosa* from the Dordogne to the Rhône in 1953. Evidence of whether the transfer was successful is difficult to determine for though *A. alosa* was recorded by LeRoux (1928) in the Rhône it wasn't by Roule (1924), suggesting uncertainty as to whether a population did already exist. By the mid-1970s Rameye *et al.* (1976) considered them to be rare. In the more recent study by Le Corre *et al.* (1997) none were recorded, suggesting that the population may now be extinct.

Persat and Keith (2002) mention that *Alosa fallax* spp. have been introduced into some rivers of the Côte d'Azur in Southern France.

The translocation of *Alosa fallax lacustris* to the lakes of central Italy has been described by Chiappi, 1929, 1933). In 1921 alevins derived from fish from Lake Garda were stocked into Lake Vico, this stocking failed. In June 1922 500,000 fry from stock from Lake Como were introduced into Lake Vico, by 1924 the population had matured and were reproducing naturally. Fry derived stock from Lake Vico were used to populate lakes Bracciano and Bolsena where yields in the three lakes in subsequent years reached 40-50 tons year⁻¹. In 1926-27 the species was introduced into the central Italian lakes; Castel Gandolfo, Piediluco and Albano. By 1930 a total of 16.65 million 0+ *Alosa fallax lacustris* had been introduced over a six year period (1924/5-1929/30) into the lakes of middle Italy (Brunelli, 1926; MAF, 1931; Chiappi, 1933; Bianco, 1998, P. G. Bianco, Department of Zoology, University of Federico II, Naples, Italy, personal communication). At the end of the twentieth century a self-sustaining population still existed in Lake Bracciano but had disappeared from Lake Bolsena (Taddei *et al.*, 1999) and lakes Albano, Castel Gandolfo and Piediluco (P. G. Bianco, pers. comm.) and Lake Vico (P. G. Bianco pers. obs. cited by Bianco, 2002).

7. CULTURE

There were a number of studies carried out during the second half of the eighteenth – first half of the nineteenth century which were concerned with the artificial propagation of European alosines (Eckart, 1877; Pouchet & Bietrix, 1889; Vincent, 1894; Hoek, 1899; Pirola, 1930; Chiappi, 1933; Le Clerc, 1941; Mohr, 1941; Hoestlandt, 1958). Since then there has been little published information on their culture (Ramos, 1977). In recent years there have been great advances in the techniques used in the artificial culture of *Alosa*, especially in the USA, and this information forms the basis of the summary for alosine culture.

7.1 Collection of Spawn

The collection of spawn can either be achieved through the stripping of ripe fish on their spawning grounds, the fish in general being caught using gill nets, or by inducing fish to spawn in captivity. The eggs can be fertilised “dry” with the eggs stripped manually into a bowl and sperm added and mixed for a few minutes. Water is then added to activate the sperm and fertilisation takes place within 30 seconds. The eggs are then rinsed with water to remove excess milt and poured into a container to water harden (*c.* 1hr). Alternatively the eggs can be fertilised “wet” where the eggs and milt are mixed in a small amount of water (Edsall, 1970; Heinrich, 1981).

Eggs can be transported to the hatchery in plastic bags, in oxygen enriched water (dissolved oxygen $>6 \text{ mg l}^{-1}$ (Bradford *et al.*, 1966)), placed in styrofoam cartons. Eggs should be placed in at least an equal volume of water (Wiggins *et al.*, 1984; Howey, 1985).

For fish being transported back to the hatchery rod and line caught fish experience less stress and survive better than those obtained, for example, from a fish lift but did have similar spawning success (Minkkinen *et al.*, 1997). Fish are transported back to the hatchery in water of 5 ppt salinity, with a dissolved oxygen concentration of $>7 \text{ mg l}^{-1}$ (Minkkinen *et al.*, 1999).

For fish being induced, implantation with Gonadotropin-Releasing Hormone analogue (GnRHa) can take place either at site of capture (preferred) or in the hatchery (Minkkinen *et al.*, 1999). Fish are anaesthetised in aerated water containing $0.02 \text{ g NaCl l}^{-1}$ using a concentration of 0.25 ml l^{-1} of 2-phenoxyethanol (Mylonas *et al.*, 1995). Effective doses of hormone are:

- $25\text{-}50 \text{ } \mu\text{g kg}^{-1}$ body weight (Minkkinen *et al.*, 1999)
- $117 (\pm 28) \text{ } \mu\text{g kg}^{-1}$ (Male), $77 (\pm 8) \text{ } \mu\text{g kg}^{-1}$ (Female) (Mylonas *et al.*, 1995).

At the hatchery fish are placed into circular tanks, at a density of 1 to 2.2 fish m^{-3} and maintained in water of between 2 and 3 ppt salinity. The sex ratio in the tanks range from unity to between 1.5 and 4 males for every female (Mylonas *et al.*, 1995; Minkkinen *et al.*, 1997). Spawning takes place in the tank and the eggs are collected using inline, outflow collectors on a daily basis (Mylonas *et al.*, 1995).

7.2 Incubation of Eggs

Eggs can be incubated in 6.5 L hatching jars with about 2.5 L of eggs per jar (Howey, 1985; Wiggins *et al.*, 1985, 1986), which can have a 2.5cm deep layer of gravel at the base of each jar (Howey, 1985). Alternatively a fine mesh metal screen can be used and has the advantage of being easier to clean than gravel (M. Hendricks, pers. comm. Pennsylvania Fish and Boat Commission, 1225 Shiloh Rd., State College, PA 16801, USA.). A flow of 1.2 to 2.0 Lmin⁻¹ was sufficient to keep the eggs rolling and allow dead eggs to accumulate near the surface for easy removal (Howey, 1985). Prophylactic treatments have included:

- Daily treatment of formalin at a concentration of 1667 to 1670 mg l⁻¹ for 17 minutes (Wiggins *et al.*, 1984; Howey, 1985).
- Daily treatment of formalin at a concentration of 1.67 ml l⁻¹ for 10 minutes (Zydlewski & McCormick, 1997).
- Twice daily treatment of formalin (600:1) for 20 minutes (Minkkinen *et al.*, 1999).

Gerstell (1998) suggested that if the eggs were from different sources they should be disinfected by immersion in iodine for a short period of time.

Favourable conditions for incubation are; temperature between 18 and 22°C (see section 4.3), ammonia nitrogen < 0.025 mg l⁻¹ (Wiggins *et al.*, 1984), dissolved oxygen *c.* 9 mg l⁻¹ (Wiggins *et al.*, 1984) and pH > 7.5 (Leach & Houde, 1999). However, lower temperatures (15 to 16°C) are preferred as at these temperatures the risk of fungal problems is reduced (M. Hendricks, pers. comm.).

Once eggs start to hatch, hatching can be synchronised by placing the jars in sunlight and stirring occasionally with a feather (Minkkinen *et al.*, 1999).

7.3 Larval and Juvenile Rearing

At hatching the larvae are transferred to rearing tanks at densities ranging from 50 – *c.* 300 fish per litre (Howey, 1985; Wiggins *et al.*, 1985, 1986). Circular rearing tanks being preferred to rectangular tanks (M. Hendricks, Pers. comm.).

Feeding regimes are as follows:

- Brine shrimp (*Artemia*) nauplii (>2000 nauplii L⁻¹) at 5 min intervals throughout the day (from day 1-42) and Biokyowa fry feed (250-400µ, day 1-48; 700µ day 38-62; 1000µ day 49 onwards; salmon no.2 day 69 onwards), dry food fed at 5% of total mass per day (Zydlewski & McCormick, 1997).
- Brine shrimp nauplii and Ziegler's AP100 (100µ) larval diet fed for 5 seconds at 5 minute intervals for 10-12 hr, during daylight hours (Peterson *et al.*, 1994).
- Brine shrimp nauplii and Ziegler's AP100 (100µ) larval diet fed three times daily (Minkkinen *et al.*, 1999).
- Brine shrimp nauplii (12-24 nauplii fish⁻¹ day⁻¹) fed for 5 seconds at 5 minute intervals for 24hr per day (Wiggins *et al.*, 1985, 1986).

- Brine shrimp nauplii (20-40 nauplii fish⁻¹ day⁻¹) fed at 15 minute intervals for 18 hr day⁻¹ for a minimum of 50 days (Howey, 1985).

Dissolved levels of nitrogen (N₂) need to be kept low as levels of 109% saturation resulted in gas bubble disease (Peterson *et al.*, 1994). Optimum rearing conditions are; dissolved oxygen from 5.6 to 9.1 mg l⁻¹ (Murai *et al.*, 1979; Peterson *et al.*, 1994), pH from 7.2 to 7.5 (Peterson *et al.*, 1994; Leach & Houde, 1999), ammonia < 0.35 mg l⁻¹ (Murai *et al.*, 1979) and temperature 18°C to reduce fungal problems (M. Hendricks, Pers. comm.).

Howey (1985) used a prophylactic treatment of formalin at a concentration of 167 mg l⁻¹ for 1 hour per week to protect the juveniles against *Saprolegnia* and other fungal infections. In order to reduce stress the juveniles were transferred in a 1% salt (NaCl) solution.

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APPENDIX 1. Sites that have been designated as Special Areas for Conservation (SAC) or Sites of Community Interest (SCI) under the Habitats Directive for *Alosa alosa*.

Type: A = Designated SPA (Special Protected Area) not related to other Natura 2000 site; B = Eligible SCI not related to another Natura 2000 site; C = Area of eligible SCI is same as designated SPA; D = SPA touches another Natura 2000 site; E = Eligible touchess another Natura 200 site; F = SPA containing eligible SCI; G = Eligible SCI within designated SPA; H = Designated SPA contains an eligible SCI; I = Eligible SCI contains a designated SPA; J = SPA overlaps an eligible SCI; K = Eligible SCI overlaps a SPA.

Global: A = site originally selected for shad (excellent representative); B = site originally selected for shad (good representative); C = site not primarily for shad (significant representative); D = non-significant shad presence

| Country | Type | Site Code | Site Name | Specimen Number | Specimen | Global |
|-----------------|------|-----------|---|-----------------|------------------------|--------|
| Germany | C | DE0916303 | Ntp s-h Wattenmeer u. Angrenzender Küstenstreifen | 1102 | <i>Alosa alosa</i> | A |
| Denmark | I | DK00CY163 | Ringkøbing fjord og Nymindestrømmen | 1102 | ALOSA ALOSA | A |
| Denmark | K | DK00FX122 | Ålborg Bugt, Randers fjord og Mariager fjord | 1102 | <i>Alosa alosa</i> | C |
| England | | UK0013111 | Plymouth Sound and Estuaries | 1102 | <i>Alosa alosa</i> | C |
| England & Wales | | UK0012642 | River Wye | 1102 | <i>Alosa alosa</i> | C |
| Wales | | UK0013010 | River Tywi | 1102 | <i>Alosa alosa</i> | C |
| Wales | | UK0020020 | Carmarthen Bay and Estuaries | 1102 | <i>Alosa alosa</i> | D |

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|--------|---|-----------|---|------|--------------------|---|
| Wales | | UK0013116 | Pembrokeshire Marine | 1102 | <i>Alosa alosa</i> | C |
| Wales | | Uk0013007 | River Usk | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR2400565 | Vallee de la Loire de Mosnes a Tavers | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR2400528 | Vallee de la Loire de Tavers a Belleville-sur-Loire | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR2600968 | Bec d'Allier | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR2600967 | Vallee de la Loire entre Devay et Digoïn | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR2600966 | Vallee de la Loire entre Imphy et Decize | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR2600964 | Val de Loire de Iguerande a Digoïn | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR4201797 | Le secteur alluvial Rhin - Ried - Bruch | 1102 | <i>Alosa alosa</i> | |
| France | B | FR5200629 | Vallee de la Loire des Ponts-de-Ce a Montsoreau | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR5200630 | Basses vallees Angevines et aval de la riviere Mayenne | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR7200662 | Vallee de la Dronne de Brantome a sa confluence avec l'Isle | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR7300952 | Gorges de l'Aveyron, causses proches et vallee de la Vere | 1102 | <i>Alosa alosa</i> | |
| France | B | FR8201689 | Forets alluviales, riviere et gorges de l'Eygues | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR8301020 | Vallee alluviale de la Loire | 1102 | <i>Alosa alosa</i> | C |

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| France | B | FR9101405 | Le Petit Rhône | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR9101436 | Cours inferieur de l'Aude | 1102 | <i>Alosa alosa</i> | |
| France | B | FR5200622 | Vallee de la Loire de Nantes au Ponts-de-Ce et zones adjacentes | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR9301589 | La basse durance et ses ripisylves, de Cadarache a la confluence du Rhône | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR9301571 | Riviere et gorges du Loup | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR9301590 | Le Rhône, de Donzere-Mondragon a la Mediterranee | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR7200661 | Vallee de l'Isle de Perigueux a sa confluence avec la Dordogne | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR2400548 | La Loire de Candes Saint Martin a Mosnes | 1102 | <i>Alosa alosa</i> | A |
| France | B | FR2400536 | Vallee de la Creuse et affluents | 1102 | <i>Alosa alosa</i> | C |
| France | B | FR7300889 | Vallee de l'Adour | 1102 | <i>Alosa alosa</i> | B |
| France | B | FR7301822 | Garonne, Ariège, Hers, Salat, Pique et Neste | 1102 | <i>Alosa alosa</i> | |
| France | B | FR8201657 | Vallee moyenne de l'Ardeche et ses affluents | 1102 | <i>Alosa alosa</i> | C |
| France | E | FR5400430 | Vallee de la Charente (basse vallée) | 1102 | <i>Alosa alosa</i> | B |
| France | E | FR7200660 | La Dordogne | 1102 | <i>Alosa alosa</i> | A |

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|--------|---|-----------|---|------|--------------------|---|
| France | E | FR7200700 | La Garonne | 1102 | <i>Alosa alosa</i> | A |
| France | E | FR7300898 | Vallee de la Dordogne quercynoise | 1102 | <i>Alosa alosa</i> | B |
| France | E | FR8301016 | Vallee de l'Allier sud | 1102 | <i>Alosa alosa</i> | C |
| France | E | FR8301032 | Zones alluviales de la confluence Dore-Allier | 1102 | <i>Alosa alosa</i> | C |
| France | E | FR8301038 | Val d'Allier pont du chateau/Jumeaux-Alagnon | 1102 | <i>Alosa alosa</i> | C |
| France | E | FR7200668 | La Vezere | 1102 | <i>Alosa alosa</i> | A |
| France | E | FR7200677 | Estuaire de la Gironde | 1102 | <i>Alosa alosa</i> | A |
| France | E | FR7200724 | L'Adour | 1102 | <i>Alosa alosa</i> | A |
| France | E | FR5400469 | Pertuis Charentais | 1102 | <i>Alosa alosa</i> | B |
| France | E | FR5400472 | Vallee de la Charente (moyenne vallée) et Seugne et Coran | 1102 | <i>Alosa alosa</i> | B |
| France | I | FR8301015 | Vallee de l'Allier nord | 1102 | <i>Alosa alosa</i> | |
| France | I | FR9301592 | Delta de Camargue | 1102 | <i>Alosa alosa</i> | B |
| France | K | FR2300121 | Estuaire de la Seine | 1102 | <i>Alosa alosa</i> | A |
| France | K | FR2300122 | Marais Vernier et basse vallee de la Risle | 1102 | <i>Alosa alosa</i> | |
| France | K | FR2500088 | Marais du Cotentin et du Bessin - baie des Veys | 1102 | <i>Alosa alosa</i> | A |
| France | K | FR2600969 | Val d'Allier | 1102 | <i>Alosa alosa</i> | A |

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|----------|---|-----------|---|------|--------------------|---|
| France | K | FR5200621 | Estuaire de la Loire | 1102 | <i>Alosa alosa</i> | C |
| France | K | FR5200659 | Marais Poitevin et baie de l'Aiguillon | 1102 | <i>Alosa alosa</i> | C |
| France | K | FR5300010 | Cote de Trestel a la Baie de Paimpol, estuaires du Jaudy et du Trieux, Archipel de Brehat | 1102 | <i>Alosa alosa</i> | C |
| France | K | FR2400522 | Vallee de la Loire de Neuvy au bec d'Allier | 1102 | <i>Alosa alosa</i> | A |
| France | K | FR2500077 | Baie du Mont Saint-Michel | 1102 | <i>Alosa alosa</i> | B |
| France | K | FR5400446 | Marais Poitevin | 1102 | <i>Alosa alosa</i> | B |
| Portugal | B | PTCON0039 | Serra d'Arga | 1102 | <i>Alosa alosa</i> | B |
| Portugal | E | PTCON0032 | Rio Guadiana/Juromenha | 1102 | <i>Alosa alosa</i> | B |
| Portugal | E | PTCON0020 | Rio Lima | 1102 | <i>Alosa alosa</i> | C |
| Portugal | I | PTCON0013 | Ria Formosa/Castro Marim | 1102 | <i>Alosa alosa</i> | C |
| Portugal | K | PTCON0009 | Estuário do Tejo | 1102 | <i>Alosa alosa</i> | C |
| Portugal | K | PTCON0036 | Guadiana | 1102 | <i>Alosa alosa</i> | B |
| Portugal | K | PTCON0019 | Rio Minho | 1102 | <i>Alosa alosa</i> | B |
| Spain | B | ES5140010 | Ribera de l'Ebre a Flix-Illes de l'Ebre | 1102 | <i>Alosa alosa</i> | B |
| Spain | B | ES1140001 | Sistema fluvial ulla - deza | 1102 | <i>Alosa alosa</i> | B |
| Spain | B | ES1200025 | Río Navia | 1102 | <i>Alosa alosa</i> | C |

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|-------|---|-----------|--|------|--------------------|---|
| Spain | B | ES2200014 | Río Bidasoa | 1102 | <i>Alosa alosa</i> | C |
| Spain | C | ES0000024 | Parque nacional de Doñana | 1102 | <i>Alosa alosa</i> | |
| Spain | C | ES0000051 | Sierra de Aracena y Picos de Aroche | 1102 | <i>Alosa alosa</i> | C |
| Spain | E | ES4310026 | Rio Guadiana Alto - Zujar | 1102 | <i>Alosa alosa</i> | B |
| Spain | E | ES4310027 | Rio Guadiana Internacional | 1102 | <i>Alosa alosa</i> | B |
| Spain | E | ES6150008 | Doñana | 1102 | <i>Alosa alosa</i> | |
| Spain | E | ES6150010 | Andevalo occidental | 1102 | <i>Alosa alosa</i> | C |
| Spain | E | ES6150014 | Marismas y riberas del Tinto | 1102 | <i>Alosa alosa</i> | |
| Spain | E | ES6150018 | Rio Guadiana y ribera de Chanza | 1102 | <i>Alosa alosa</i> | C |
| Spain | E | ES6150019 | Bajo Guadalquivir | 1102 | <i>Alosa alosa</i> | |
| Spain | E | ES6170016 | Valle del rio del Genal | 1102 | <i>Alosa alosa</i> | |
| Spain | E | ES1300011 | Rio Ason | 1102 | <i>Alosa alosa</i> | C |
| Spain | E | ES1140007 | Baixo Miño | 1102 | <i>Alosa alosa</i> | B |
| Spain | E | ES1200023 | Río Eo (asturias) | 1102 | <i>Alosa alosa</i> | B |
| Spain | E | ES2120006 | Aiako Harria | 1102 | <i>Alosa alosa</i> | B |
| Spain | E | ES2120015 | Terrazas y marismas del Bidasoa | 1102 | <i>Alosa alosa</i> | B |
| Spain | G | ES1300007 | Marismas de Santoña , Victoria y Joyel | 1102 | <i>Alosa alosa</i> | C |

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|-------|---|-----------|------------------------|------|--------------------|---|
| Spain | G | ES1200016 | Ría del Eo | 1102 | <i>Alosa alosa</i> | B |
| Spain | I | ES5140013 | Delta de l'Ebre | 1102 | <i>Alosa alosa</i> | C |
| Spain | I | ES1140004 | Complexo ons - o grove | 1102 | <i>Alosa alosa</i> | B |
| Spain | K | ES1120002 | Río Eo | 1102 | <i>Alosa alosa</i> | B |

APPENDIX 2. Sites that have been designated as Special Areas for Conservation (SAC) or Sites of Community Interest (SCI) under the Habitats Directive for *Alosa fallax* spp.

Type: A = Designated SPA (Special Protected Area) not related to other Natura 2000 site; B = Eligible SCI not related to another Natura 2000 site; C = Area of eligible SCI is same as designated SPA; D = SPA touches another Natura 2000 site; E = Eligible touchess another Natura 200 site; F = SPA containing eligible SCI; G = Eligible SCI within designated SPA; H = Designated SPA contains an eligible SCI; I = Eligible SCI contains a designated SPA; J = SPA overlaps an eligible SCI; K = Eligible SCI overlaps a SPA.

Global: A = site originally selected for shad (excellent representative); B = site originally selected for shad (good representative); C = site not primarily for shad (significant representative); D = non-significant shad presence.

| Country | Type | Site Code | Site Name | Specimen Number | Specimen | Global |
|---------|------|-----------|---|-----------------|---------------------|--------|
| Germany | B | DE2526302 | Komplex NSG Heuckenlock Und NSG Schweenssand | 1103 | <i>Alosa fallax</i> | C |
| Germany | B | DE2527303 | Borghorster Elblandschaft | 1103 | <i>Alosa fallax</i> | C |
| Germany | B | DE2627301 | Komplex NSG Zollenspieker Und NSG Kiebitzbrack | 1103 | <i>Alosa fallax</i> | C |
| Germany | C | DE0916303 | NTP S-H Wattenmeer U. Angrenzender Küstenstreifen | 1103 | <i>Alosa fallax</i> | A |
| Germany | C | DE2016301 | Nationalpark Hamburgisches Wattenmeer | 1103 | <i>Alosa fallax</i> | B |
| Germany | E | DE2222301 | Unternelbe Bei Glückstadt | 1103 | <i>Alosa fallax</i> | B |
| Germany | I | DE2424302 | Komplex NSG Neßsand Und LSG Mühlenberger | 1103 | <i>Alosa fallax</i> | A |

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| | | | Loch | | | |
| Germany | K | DE2119301 | Unternelbe | 1103 | <i>Alosa fallax</i> | B |
| Germany | K | DE2323303 | Schleswig-Holsteinisches Elbästuar | 1103 | <i>Alosa fallax</i> | B |
| Denmark | C | DK00EX026 | Dråby Vig | 1103 | <i>Alosa fallax</i> | B |
| Denmark | C | DK00CY040 | Venø, Venø Sund | 1103 | <i>Alosa fallax</i> | A |
| Denmark | G | DK009X182 | Vidå, Rudbøl Sø Og Magisterkogen | 1103 | <i>Alosa fallax</i> | |
| Denmark | I | DK00CX160 | Nissum Fjord | 1103 | <i>Alosa fallax</i> | C |
| Denmark | I | DK00CY163 | Ringkøbing Fjord Og Nymindestrømmen | 1103 | <i>Alosa fallax</i> | C |
| Denmark | I | DK00EY133 | Agger Tange, Nissum Bredning, Skibsted Fjord Og Agerø | 1103 | <i>Alosa fallax</i> | B |
| Denmark | K | DK00FX122 | Ålborg Bugt, Randers Fjord Og Mariager Fjord | 1102 | <i>Alosa alosa</i> | C |
| Denmark | K | DK00AY176 | Vadehavet Med Ribe Å, Tved Å Og Varde Å Vest For Varde | 1103 | <i>Alosa fallax</i> | A |
| Denmark | K | DK00FX122 | Ålborg Bugt, Randers Fjord Og Mariager Fjord | 1103 | <i>Alosa fallax</i> | C |
| Netherlands | C | NL1000021 | Volkerakmeer | 1103 | <i>Alosa fallax</i> | C |
| Netherlands | E | NL1000015 | Haringvliet | 1103 | <i>Alosa fallax</i> | B |
| Netherlands | E | NL4000017 | Voordelta | 1103 | <i>Alosa fallax</i> | B |
| England & | | UK0012642 | River Wye | 1103 | <i>Alosa fallax</i> | |

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| Wales | | | | | | |
| Wales | | UK0013010 | River Tywi | 1103 | <i>Alosa fallax</i> | |
| Wales | | UK0020020 | Carmarthen Bay and Estuaries | 1103 | <i>Alosa fallax</i> | |
| Wales | | UK0013116 | Pembrokeshire Marine | 1103 | <i>Alosa fallax</i> | |
| Wales | | UK0013007 | River Usk | 1103 | <i>Alosa fallax</i> | |
| Eire | B | IE0002137 | Lower River Suir | 1103 | <i>Alosa fallax</i> | B |
| Eire | B | IE0002162 | River Barrow And River Nore | 1103 | <i>Alosa fallax</i> | A |
| Eire | E | IE0000781 | Slaney River Valley | 1103 | <i>Alosa fallax</i> | B |
| Eire | I | IE0002170 | Blackwater River (Cork/Waterford) | 1103 | <i>Alosa fallax</i> | B |
| Eire | K | IE0000365 | Killarney National Park, Macgillicuddy's Reeks And Caragh River Catchment | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR2400565 | Vallee De La Loire De Mosnes A Tavers | 1103 | <i>Alosa fallax</i> | C |
| France | B | FR2400528 | Vallee De La Loire De Tavers A Belleville-Sur-Loire | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR2600966 | Vallee De La Loire Entre Imphy Et Decize | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR2600968 | Bec D'allier | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR4201797 | Le Secteur Alluvial Rhin - Ried - Bruch | 1103 | <i>Alosa fallax</i> | C |
| France | B | FR5200629 | Vallee De La Loire Des Ponts-De-Ce A Montsoreau | 1103 | <i>Alosa fallax</i> | C |

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| France | B | FR5200630 | Basses Vallees Angevines Et Aval De La Riviere Mayenne | 1103 | <i>Alosa fallax</i> | B |
| France | B | FR8201677 | Milieux Alluviaux Du Rhone Aval | 1103 | <i>Alosa fallax</i> | C |
| France | B | FR8201689 | Forets Alluviales, Riviere Et Gorges De L'eygues | 1103 | <i>Alosa fallax</i> | C |
| France | B | FR9101405 | Le Petit Rhone | 1103 | <i>Alosa fallax</i> | B |
| France | B | FR9101436 | Cours Inferieur De L'aude | 1103 | <i>Alosa fallax</i> | |
| France | B | FR9400572 | Mucchiatana | 1103 | <i>Alosa fallax</i> | |
| France | B | FR5200622 | Vallee De La Loire De Nantes Au Ponts-De-Ce Et Zones Adjacentes | 1103 | <i>Alosa fallax</i> | C |
| France | B | FR9301589 | La Basse Durance Et Ses Ripisylves, De Cadarache A La Confluence Du Rhone | 1103 | <i>Alosa fallax</i> | B |
| France | B | FR9301627 | Embouchure De L'argens - Marais De Frejus - Etangs De Villepey | 1103 | <i>Alosa fallax</i> | B |
| France | B | FR9301590 | Le Rhone, De Donzere-Mondragon A La Mediterranee | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR9301608 | Mont Caume - Mont Faron - Foret Domaniale Des Morieres | 1103 | <i>Alosa fallax</i> | B |
| France | B | FR7200661 | Vallee De L'isle De Perigueux A Sa Confluence Avec La Dordogne | 1103 | <i>Alosa fallax</i> | A |
| France | B | FR2400548 | La Loire De Candes Saint Martin A Mosnes | 1103 | <i>Alosa fallax</i> | B |

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| France | E | FR5400432 | Marais De Seudre | 1103 | <i>Alosa fallax</i> | B |
| France | E | FR7200660 | La Dordogne | 1103 | <i>Alosa fallax</i> | B |
| France | E | FR7200700 | La Garonne | 1103 | <i>Alosa fallax</i> | B |
| France | E | FR7200677 | Estuaire De La Gironde | 1103 | <i>Alosa fallax</i> | A |
| France | E | FR7200724 | L'adour | 1103 | <i>Alosa fallax</i> | B |
| France | E | FR5400469 | Pertuis Charentais | 1103 | <i>Alosa fallax</i> | B |
| France | I | FR8201654 | Basse Ardeche Urganienne | 1103 | <i>Alosa fallax</i> | B |
| France | I | FR9101395 | Le Gardon Et Ses Gorges | 1103 | <i>Alosa fallax</i> | B |
| France | I | FR9301592 | Delta De Camargue | 1103 | <i>Alosa fallax</i> | B |
| France | K | FR2300121 | Estuaire De La Seine | 1103 | <i>Alosa fallax</i> | A |
| France | K | FR2300122 | Marais Vernier Et Basse Vallee De La Risle | 1103 | <i>Alosa fallax</i> | B |
| France | K | FR2500088 | Marais Du Cotentin Et Du Bessin - Baie Des Veys | 1103 | <i>Alosa fallax</i> | A |
| France | K | FR5200621 | Estuaire De La Loire | 1103 | <i>Alosa fallax</i> | C |
| France | K | FR5200659 | Marais Poitevin Et Baie De L'aiguillon | 1103 | <i>Alosa fallax</i> | C |
| France | K | FR2400522 | Vallee De La Loire De Neuvy Au Bec D'allier | 1103 | <i>Alosa fallax</i> | A |
| France | K | FR2500077 | Baie Du Mont Saint-Michel | 1103 | <i>Alosa fallax</i> | B |
| France | K | FR5400446 | Marais Poitevin | 1103 | <i>Alosa fallax</i> | B |

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| France | K | FR2600965 | Vallee De La Loire Entre Fourchambault Et Neuvy-Sur-Loire | 1103 | <i>Alosa fallax</i> | A |
| Portugal | B | PTCON0039 | Serra D'arga | 1103 | <i>Alosa fallax</i> | C |
| Portugal | E | PTCON0020 | Rio Lima | 1103 | <i>Alosa fallax</i> | C |
| Portugal | I | PTCON0011 | Estuário Do Sado | 1103 | <i>Alosa fallax</i> | C |
| Portugal | K | PTCON0009 | Estuário Do Tejo | 1103 | <i>Alosa fallax</i> | C |
| Portugal | K | PTCON0036 | Guadiana | 1103 | <i>Alosa fallax</i> | B |
| Portugal | K | PTCON0019 | Rio Minho | 1103 | <i>Alosa fallax</i> | B |
| Spain | B | ES5140010 | Ribera De l'Ebre A Flix-Illes De l'Ebre | 1103 | <i>Alosa fallax</i> | B |
| Spain | B | ES1140001 | Sistema Fluvial Ulla - Deza | 1103 | <i>Alosa fallax</i> | B |
| Spain | C | ES0000024 | Parque Nacional De Doñana | 1103 | <i>Alosa fallax</i> | C |
| Spain | E | ES4310026 | Rio Guadiana Alto - Zujar | 1103 | <i>Alosa fallax</i> | B |
| Spain | E | ES4310027 | Rio Guadiana Internacional | 1103 | <i>Alosa fallax</i> | B |
| Spain | E | ES6150008 | Doñana | 1103 | <i>Alosa fallax</i> | C |
| Spain | E | ES6150014 | Marismas Y Riberas Del Tinto | 1103 | <i>Alosa fallax</i> | |
| Spain | E | ES6150019 | Bajo Guadalquivir | 1103 | <i>Alosa fallax</i> | C |
| Spain | E | ES6170016 | Valle Del Rio Del Genal | 1103 | <i>Alosa fallax</i> | |

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| Spain | E | ES1140007 | Baixo Miño | 1103 | <i>Alosa fallax</i> | B |
| Spain | I | ES5140013 | Delta De l'Ebre | 1103 | <i>Alosa fallax</i> | C |
| Spain | I | ES1140004 | Complexo Ons - O Grove | 1103 | <i>Alosa fallax</i> | B |
| Italy | B | IT1315720 | Fiume Roia | 1103 | <i>Alosa fallax</i> | C |
| Italy | B | IT3210018 | Basso Garda | 1103 | <i>Alosa fallax</i> | B |
| Italy | B | IT3320036 | Anse Del Fiume Stella | 1103 | <i>Alosa fallax</i> | |
| Italy | B | IT6010035 | Fiume Mignone (Basso Corso) | 1103 | <i>Alosa fallax</i> | B |
| Italy | B | IT6040025 | Fiume Garigliano (Tratto Terminale) | 1103 | <i>Alosa fallax</i> | B |
| Italy | B | IT7140107 | Lecceta Litoranea Di Torino Di Sangro E Foce Fiume Sangro | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT2040022 | Lago Di Mezzola E Pian Di Spagna | 1103 | <i>Alosa fallax</i> | C |
| Italy | C | IT3320037 | Laguna Di Marano E Grado | 1103 | <i>Alosa fallax</i> | |
| Italy | C | IT3330005 | Foce Dell' Isonzo - Isola Della Cona | 1103 | <i>Alosa fallax</i> | |
| Italy | C | IT4010001 | Isola De Pinedo | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4010009 | Fiume Po Dalla Foce Del Fiume Trebbia Alla Lanca Di Mezzano | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4020002 | Fiume Taro Da Fornovo Di Taro All'autostrada Del Sole | 1103 | <i>Alosa fallax</i> | A |

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| Italy | C | IT4060003 | Vene Di Bellocchio, Sacca Di Bellocchio, Foce Del Fiume Reno,... | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4060004 | Valle Bertuzzi, Valle Porticino-Cannevie' | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4060005 | Sacca Di Goro, Po Di Goro, Valle Dindona, Foce Del Po Di Volano | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4060008 | Bonifica Del Mezzano | 1103 | <i>Alosa fallax</i> | B |
| Italy | C | IT4060011 | Garzaia Dello Zuccherificio Di Codigoro | 1103 | <i>Alosa fallax</i> | A |
| Italy | C | IT4060013 | Po Da Golena Bianca A Isola Bianca | 1103 | <i>Alosa fallax</i> | A |
| Italy | E | IT1343502 | Parco Della Magra - Vara | 1103 | <i>Alosa fallax</i> | B |
| Italy | E | IT6010020 | Fiume Marta (Alto Corso) | 1103 | <i>Alosa fallax</i> | B |
| Italy | E | IT8010003 | Basso Corso Del Fiume Volturno | 1103 | <i>Alosa fallax</i> | A |
| Italy | E | IT8010007 | Foce Del Fiume Garigliano | 1103 | <i>Alosa fallax</i> | B |
| Italy | E | IT8010008 | Foce Del Fiume Volturno | 1103 | <i>Alosa fallax</i> | A |
| Italy | E | IT8050007 | Basso Corso Del Fiume Bussento | 1103 | <i>Alosa fallax</i> | A |
| Italy | E | IT8050012 | Fiume Alento | 1103 | <i>Alosa fallax</i> | B |
| Italy | E | IT8050015 | Foce Del Fiume Sele | 1103 | <i>Alosa fallax</i> | A |
| Italy | G | IT6010017 | Sistema Fluviale Fiora - Olpeta | 1103 | <i>Alosa fallax</i> | B |
| Greece | B | GR1260002 | Ekvoles Potamou Strymona | 1103 | <i>Alosa fallax</i> | B |

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| Greece | C | GR1110001 | Delta Evrou | 1103 | <i>Alosa fallax</i> | B |
| Greece | C | GR2310001 | Delta Acheloou, Limnothalassa Mesolongiou-Aitolikou, Ekvoles Evinou Kai Nisoi Echinades | 1103 | <i>Alosa fallax</i> | C |
| Greece | I | GR1130009 | Limnes & Limnothalasses Tis Thrakis-Evryteri Periochi | 1103 | <i>Alosa fallax</i> | B |
| Greece | I | GR1150010 | Delta Nestou & Limnothalasses Keramotis-Evryteri Periochi | 1103 | <i>Alosa fallax</i> | B |

