
Anguillidae Jordan and Evermann, 1896

Vernacular name: Eels.

Etymology: Derived from the Latin, *anguis* (snake).

Brief description: It has tiny scales. The mouth is terminal and the lower jaw is slightly protruding. The teeth are small in several rows on the jaws and the palate. The tongue is present, the lips are thick, the frontal bones are twinned and the palato-ptyergoid arch is well developed. The gill slits, small and vertical, are located in front of the base of the pectoral. The lateral line, well developed, is complete. The pectoral fins are well developed and supported by seven to nine rays (more than 11 in juveniles). Dorsal anal fins are united to the caudal fin. The origin of the dorsal fin is located far behind the pectoral fin, but before the anus. The anal fin takes its origin a little behind the anus. The number of vertebrae is 100–119 (Nelson, 2006).

Biogeography: Tropical, subtropical and temperate warm and cold seas, with the exception of the eastern Pacific and southern Atlantic.

Habitat and bioecology: Adults live in fresh and brackish waters (estuaries and lagoons), spawn at sea and their larval stages are marine.

Systematics and phylogeny: Recent studies have shown that Anguillidae have affinities with the “eels” of deep marine waters: Nemichthyidae and Serrivomeridae (Inoe *et al.*, 2010).

Biodiversity: Anguillidae are currently represented in the world by only one genus *Anguilla* (Nelson, 2006).

1.1. *Anguilla* (Schrank, 1798)

Type: Muraena anguilla Linnaeus, 1758 (named by Schrank, 1798, in *Fauna Boica*, 1(2): 304).

Synonyms: None.

Etymology: *Anguilla*, name derived from the Latin *anguis* (snake).

Brief description: See box, “Brief description”.

Biogeography: Species of the genus *Anguilla* are widely distributed in most tropical, subtropical and temperate areas of the world. They are present on all continents, except in Antarctica. The continental distribution of temperate species seems to be related to the subtropical circulation of the oceans, with a majority of species living along the western coasts of the Atlantic, Indian and Pacific oceans, except for *Anguilla anguilla* (Ege, 1939; Watanabe, 2003) (see Figure 1.1).

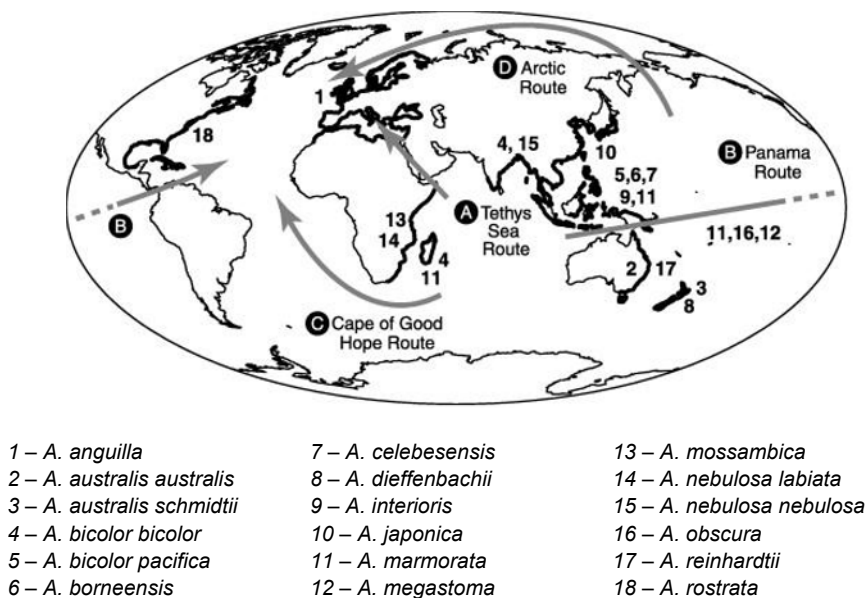


Figure 1.1. Geographical distribution of the genus *Anguilla* (bold lines) and possible dispersal routes of eel ancestors in the Atlantic Ocean (gray arrows). The regions where each species is present are indicated in numbers. The *Anguilla marmorata* (11) is the most widespread species and is found from the western Indian Ocean across the Indonesian archipelago, to southern Japan and all along the islands of the Southeast Pacific (according to Minegishi et al., 2005)

However, eels are absent from the eastern coasts of South America, despite the existence of the hot current of Brazil. On the basis of this geographical distribution, the Atlantic species (*A. anguilla* and *Anguilla rostrata*) are geographically separated from their counterparts in the Pacific and Indian Oceans.

Habitat and bioecology: The genus *Anguilla* occupies a variety of habitats. Because of their euryhalinity, the species of this genus colonize inland waters, including estuaries, lagoons, rivers, lakes and marshes. All these catadromous species spawn in the tropical ocean and their larvae are distributed in fresh and brackish estuarine and lagoonal waters by warm subtropical currents (Schmidt, 1923, 1925; Tesch, 1977; Tsukamoto, 1992). Let us mention the recent discovery regarding ocean residents, which never enter freshwater. Three temperate species *A. anguilla*, *A. rostrata*, and *Anguilla japonica* seem to have a flexible life story (Tsukamoto *et al.*, 1998; Tzeng *et al.*, 1997; Tsukamoto and Arai, 2001; Jessop *et al.*, 2002). By studying the Sr/Ca ratio in otoliths, these authors have highlighted the existence of permanent populations of yellow and silver eels in coastal marine waters. The stay in fresh water and can therefore be optional. Tsukamoto *et al.* (2002) consider that there are two ecophenotypes of eels: one estuarine, the other one, marine. All the species of the genus *Anguilla* are semelparous (they die after one laying).

Biodiversity: The genus *Anguilla* is represented by 18 species in the world (Hastings *et al.*, 2014), 16 Indo-Pacific and two Atlantic ones: the *A. anguilla* (Afro-European eel) and the *A. rostrata* (American eel) (Lecomte-Finiger, 2003). The six Indo-Pacific subspecies listed by Ege (1939) have been considered as invalid by Tsukamoto and Aoyama (1998). However, Minegishi *et al.* (2005) have not taken this revision into account in their work on the phylogeny and the evolution of the genus *Anguilla*. Only the *A. anguilla* lives in the Mediterranean.

Systematics and phylogeny: The results of the studies carried out have not yet made it possible to know the most probable dispersal routes of the genus *Anguilla* nor the most “ancestral” species. On the basis of molecular phylogenetic analyses, Aoyama and Tsukamoto (1997) and Aoyama *et al.* (2001) were the first ones to propose the hypothesis according to which the founding species of Atlantic eels might have moved from its place of origin, Indonesia, and reached the future Atlantic via the Tethys, about 30 million years ago (Figures 1.1 and 1.2, Route A). However, Lin *et al.* (2001) have suggested an opposite dispersal direction based on phylogenetic molecular analyses and the estimation of eel divergence time. They have suggested that the original migration to the Atlantic took place via the Central American “Seaway”, closed for about 3 million years (Isthmus of Panama). This

path is the only one possible since, according to these authors, the origin of the genus *Anguilla* is approximately 20 million years old (Figures 1.1 and 1.2, Route B).

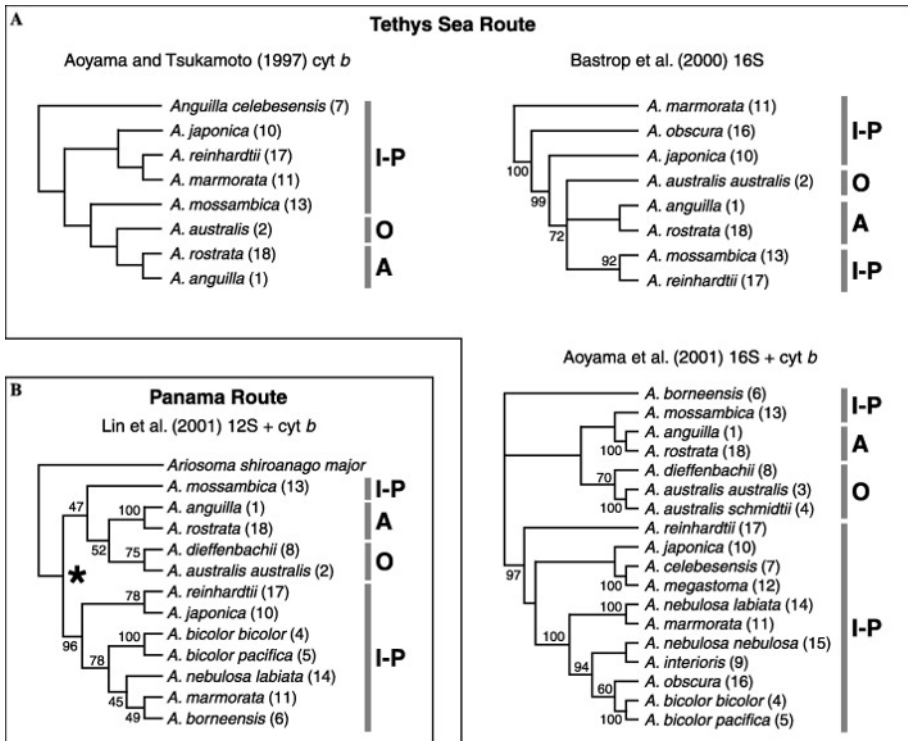


Figure 1.2. Topologies of phylogenetic trees that support two different hypotheses concerning the eel entry route in the Atlantic Ocean. The numbers following the name of each species correspond to those in Figure 1.1. The asterisk on the tree by Lin et al. (2001) shows the first divergence that divides the 12 species into two large cladi. Cyt b: cytochrome b; 12S: 12S ribosomal RNA; 16S: 16S ribosomal RNA, IP: Indo-Pacific; O: Oceanic; A: Atlantic (according to Minegishi et al., 2005)

Although Ege (1939) considered that current eels derive from *A. japonica*, more recent studies (Aoyama et al., 1997) have shown that *A. mossambica* might be their common ancestor. Moreover, this viewpoint has been confirmed by the sequence analysis of the entire mitochondrial genome of 18 eel species and subspecies (Minegishi et al. 2005). These authors have suggested that *A. mossambica* is the species from which three geographical eel cladi (with the exception of *Anguilla borneensis*) originated: Atlantic (two species), Oceania (three species), Indo-Pacific (11 species) (Figure 1.3).

1.1.1. *Anguilla anguilla* (Linnaeus, 1758)



1.1.1.1. *Nomenclature and systematics*

Type: Muraena anguilla, Linnaeus, 1758. Syst. Nat. Edit X: 245 (*Habitat in Europa*). One specimen named by Linnaeus is at the Natural History Museum in London: Linnaeus collection, no. 80.

Synonyms: Thirty-three synonyms, according to Tesch (1991).

*Vernacular names*¹: *Anguilla* (DZ), *hannash* (EG), *anguila* (ES), *anguille* (FR), common eel (GB), *chéli* (GR), *sallura* (IS), *anguilla*, *capitone* (IT), *noune* (MY), *zelifah* (MT), *hancha*, *sannour* (TN), *yilan* (TR).

Etymology: *Anguilla* is the diminutive of the Latin name *Angius*, which means snake.

1.1.1.2. *Description*

1.1.1.2.1. The larvae

– “*Leptocephalic*” stage: The larva, called “leptocephalus”, from *lepto* (thin) and *cephale* (head) is morphoanatomically and chromatically different from later “postmetamorphic” and continental stages (Figure 1.4).

Its length after hatching in the Sargasso Sea from a 1.2 mm diameter egg (Yamamoto *et al.*, 1974) is about 3 mm (Yamamoto and Yamauchi, 1974). Its final size reached on the European continental shelf, after about 1–2.5 years of oceanic migration, is about 70 mm.

Lecomte-Finiger *et al.* (2004) provided an update to the knowledge about this larva. Its body, shaped like a willow or an olive tree leaf, is crystalline or transparent and compressed laterally. The head is proportionally small compared to the rest of the body. The transparency of leptocephalic larvae (Figure 1.5) suggests their anatomy.

¹ Short forms: (DZ) Algeria, (EG) Egypt, (ES) Spain, (FR) France, (GB) Great Britain, (GR) Greece, (IS) Israel, (IT) Italy, (MA) Morocco, (MT) Malta, (TN) Tunisia, (TR) Turkey.

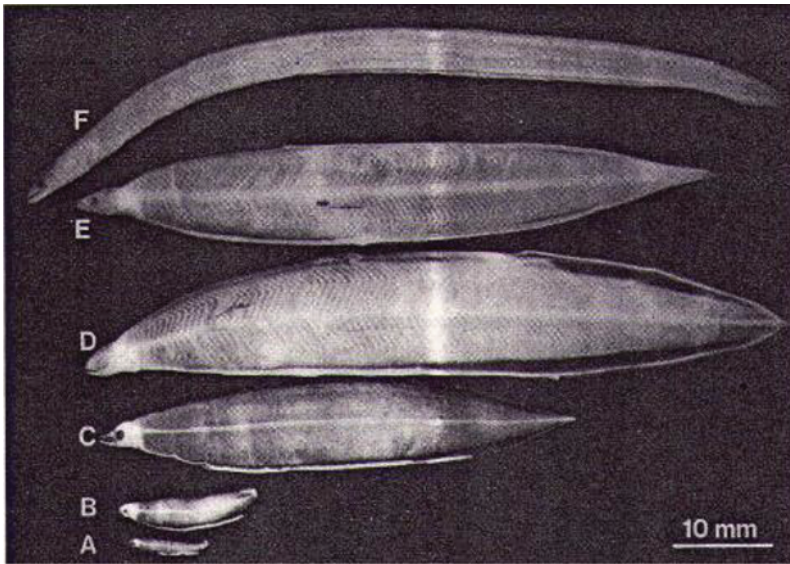


Figure 1.4. *Metamorphosis of the Anguilla anguilla eel. Leptocephalic larvae (A, B, C and D), leptocephalic larvae undergoing metamorphosis (E and F)*

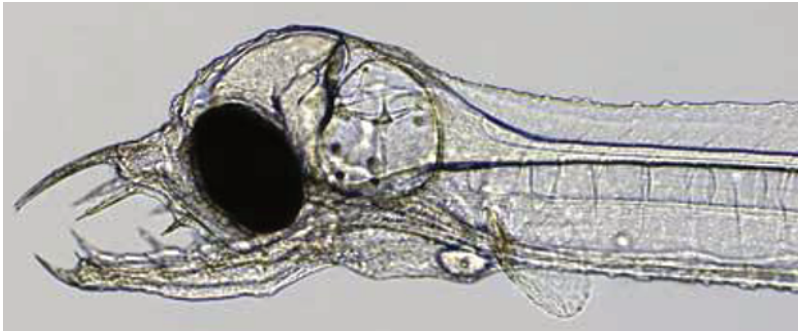


Figure 1.5. *Twelve-day-old Anguilla anguilla larvae ready to feed (photo J. Tomkiewicz, DTU Aqua)*

The musculature consists of myotomes arranged in a V or W stripe. In the axial zone, we can find the spinal cord, the chord and the aortic artery. Leptocephali do not possess either red blood cells or hemoglobin. The heart and the circulatory system, with very thin and transparent walls, are difficult to observe. The olfactory lobes are well developed, as are the optical capsules (Rasquin, 1955). The structure

of the eyes (Pfeiler 1989; Appelbaum and Riehl, 1993) is remarkable in relation to the way of life of these mesopelagic larvae (–600 m), with nyctohemeral rhythms at the surface at night (–30 m). Indeed, the photoreceptor layer of the retina is entirely made up of sticks rich in chrysopsin (Wood *et al.*, 1992), which indicates an essentially nocturnal vision. The dentition is typical and, depending on the size of the planktonophagous larva, it comprises between 3 and 20 long and pointed teeth, projected forward (Bertin, 1951; Appelbaum and Riehl, 1993).

Leptocephali are characterized by a development strategy of their own, called *leptocephalus strategy* (Pfeiler, 1986), different from other teleosts. This strategy consists of a long phase of larval growth or pre-metamorphic phase (phase I), followed by a rapid metamorphosis (phase II) during which the lepharocephalic larva will radically change its shape and acquire the definitive serpentine shape and pigmentation that are characteristic of the larvae species. This metamorphosis begins when the leptocephalic larva reaches the continental shelf and measures 70–80 mm.

– *Elver stage*: The “larva” resulting from the metamorphosis of the leptocephalus is called an elver (or pibale), but some authors describe the larva as elver as soon as the metamorphosis of the leptocephalus begins at sea on the continental shelf (see ontogenesis). The larval stage that we are describing here corresponds to the end of the acquisition of the “anguilliform, serpentine” morph in the course of “metamorphosis” (Struberg’s stage V, 1913; Elie *et al.*, 1982). This “larva” measures an average of 6 cm and weighs between 0.2 and 0.5 g. A staged classification according to pigment development was developed by Strubberg (1913). Many authors worked over this classification, either by simplifying it (Boetius, 1976, Charlon and Blanc, 1982) or by adding a stage (Elie *et al.*, 1982).

Except for pigmentation, the eel at the elver stage has reached its final morphological appearance (juvenile type). With regard to pigmentation, we can observe the presence of a spot of melanophores on the skull, another one at the end of the tail and some rostral pigments.

Subsequently, melanophores develop along the body. In stage VI B, the strongly colored larva loses its transparency; this signals the end of the glass eel stage. At the following stage (stage VII), in addition to the black color, yellow pigments appear, and thus the “eel” stage is reached.

Alongside the chromatic transformations, anatomical changes take place. At the level of the eyes, the cones appear and the retinal pigments change. Chrysopsin is thus replaced by rhodopsin, associated with porphyropsin (Wood *et al.*, 1992).

These changes show the transition to a new way of life. In fact, once pelagics, the larvae will become benthic. The gaseous bladder will appear in the glass eel at the end of its colonization migration from continental waters at the end of the pigmentation process (Hickman, 1981). We can observe the replacement of leptocephalic-type larval teeth by caniniform teeth (Bauchot, 1959). The glass eel stage is accompanied by a prolonged period of fasting, following the “partial or total” obstruction of the digestive tract by three valves (Monein-Lang, 1985) at the VB stage (continental transparent stage). The digestive tract is subsequently remodeled as follows: in addition to the teeth, the gastric glands appear and it becomes functional again through the suppression (stage VI A3) of the three valves that obstructed it (Monein-Langle, 1985). The glass eel becomes a carnivorous eel, with a diet based on benthic preys, and the growth process is resumed.

1.1.1.2.2. *Juveniles and subadults*

Juvenile (yellow, green) and subadult (silver) eels have a very elongated, serpentine, circular-shaped body, which is slightly compressed particularly close to the caudal end.

The tail is rounded. The head is compressed, with a rather elongated snout, which is sometimes wide. The oral cleft extends to almost half of the eye. The mouth is terminal, with a prominent lower jaw. The jaws and the vomer are equipped with a series of teeth.

The eye is round and represents between 1/8th and 1/12th of the length of the head. Its diameter varies throughout its development. It is bigger in the silvery eel than in the yellow eel in relation to the different visual abilities required for freshwater and for marine environments (Pankhurst, 1982a).

The dorsal, caudal and anal fins are fused, forming a very long odd fin. Pelvic fins are absent. The skin is smooth and viscous, rich in mucus cells. This mucus, made up of glycoproteins containing sialic acid, contributes to the protection of the cutaneous barrier. The lateral line is clear. Numerical characters have been provided by different authors:

– Berg *et al.* (1949): vert. 111–119 (normally 114–116), D. 245–275, A. 176–249, C. 7–12, P. 15–21;

– Wheeler (1969): vert. 112–117, D. 245–275, A. 205–235, P. 14–18 rays.

The number of vertebrae enables a specific diagnosis (Boetius, 1980, see Figure 1.6).

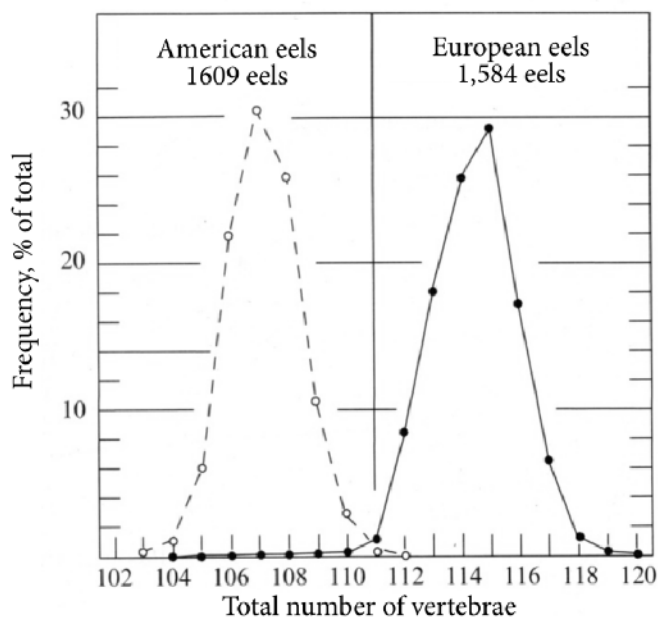


Figure 1.6. Differences in the number of vertebrae between American eels and European eels (according to Boetius, 1980)

– *Yellow eel stage*: When the pigmentation is fully developed, the “yellow eel” stage, also called “green eel”, is reached. The back varies from dark green or brown to black, depending on the habitat. Abnormal colors have been found (Lohnisky, 1982). These anomalies range from almost white eels (Walter, 1910) to mottled or mottled in black individuals. The yellow eel phase, called the “growth phase”, lasts for several years, depending on the sex and the environment.

The black, brownish, greenish or yellowish colors, at the yellow eel stage, are related to the habitat (homochromy). The dark color of the integument and its changes (the chromatic adaptation to the environment) depend on the number and extent of the melanophores (melanophoric index); these pigment cells are under neuro-endocrine control (Fremberg and Olivereau, 1973), namely the pituitary hormone, the melanophore stimulating hormone (MSH), itself dependent on the hypothalamic nervous system: the catecholamines, the MIF-1 (MSH-release inhibiting factor) and/or MRF (MSH-releasing factor). In fresh water, the yellow color depends on the extension of endocrine-induced xanthophores: the prolactin

secretion (PRL) by hypothalamic controlled hypophysis, with the inhibition of prolactin hormonal synthesis in salt water (Olivereau, 1978).

– *Silver eel stage*: The end of the “yellow/green eel” stage is marked by the appearance of a new skin, with a dark green to black back, flanked with silvery reflections and a whitish belly. Due to the presence of guanine and hypoxanthine in the skin, this “silvering” is the visible expression of a second metamorphosis which, linked to physiological and morphological changes, prepares fish for the oceanic reproductive migration toward the Sargasso Sea. Fontaine (1994) was the first to suggest that the simple distinction between “green-yellow eel/silver eel” does not correspond to reality and that it is necessary to subdivide this transformation into several stages.

Feunteun *et al.* (2000) recognized three stages: yellow, silvery, yellow/silver. These stages are based on external variables (skin color, visibility of the lateral line, surface of the eye). In any case, the silver skin of eels at the time of their downstream migration is the most apparent external change, although the use of color for identifying migrating eels has been criticized (Pankhurst and Lythgoe, 1982). An increase in the eye size, the pigmentation of the lateral line and the darkening of the pectoral fins are also commonly used indicators in order to determine the “pre migratory” stage of eels.

However, the sequence of events leading to this stage and the factors that trigger silvering remain unknown. According to Durif *et al.* (2005), it is likely that the production of the growth hormone (GH) at the premigratory stage (stage III of the classification by these same authors) induces an important period of growth and triggers silvering. In migrating eels, the development of the gonads, the production of the gonadotropic hormone (GTH-II) and an increase in the surface of the eyes have been confirmed. Differences between sites involved the regression of the intestine, as well as the length of the pectoral fin. These variables appear to vary with the size of the watershed and the distance from the sea, which may indicate the time when an eel started its migration. The reversibility of silvering was pointed out by Svedäng and Wickström (1997). The latter concluded that silvering is much more flexible than has been predicted. Eels can stop their metamorphosis and start eating again if the chances of a successful migration are compromised.

Coloring: See the chromatic characteristics of the various development stages in section 1.1.1.2, “Description”.

Variations: The European eel shows variations in the width of the head: it is narrow and wide (Figure 1.7) (Torlitz, 1922; Thurow, 1958; Tesch, 1983).

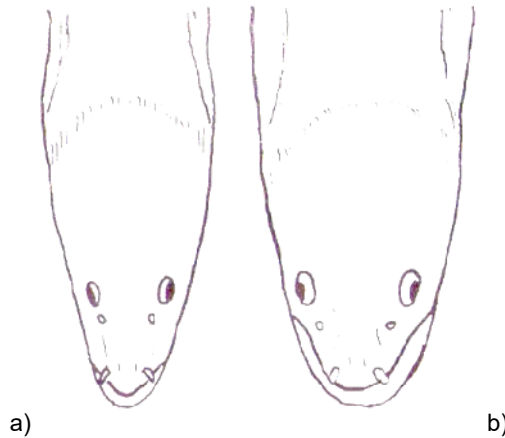


Figure 1.7. a) *Narrow-headed eel*. b) *Broad-headed eel* (according to Tesch, 1983)

These variations probably depend on environmental influences, including the type of available prey (Tesch, 1991; De Meyer *et al.*, 2016). In silver eels, these variations are not so important (Muller, 1975). Cucherouss *et al.* (2011) have shown that, regardless of their size, individuals with a broader head occupy a higher trophic position than fish with a narrower head. The former consume more fish prey than invertebrates and occupy more distant habitats from the river banks than the latter. In addition, individuals with intermediate cephalic morphology display a less favorable condition than fish with extreme cephalic morphologies (broad and narrow), which might indicate the existence of disruptive selection, associated with individual specialization. However, the trophic determinism of cephalic dimorphism in eels is questionable, because “fasting” elvers are also concerned (De Meyer *et al.*, 2015). Let us note that the two forms display a different predisposition toward parasitism in *Anguillicola crassus*, depending on whether they are more or less piscivorous (Pegget *et al.*, 2015).

Yahyaoui (1988) found no correlation between the average number of vertebrae and the size of glass eels from two Mediterranean sites (the mouth of the Moulouya in Morocco and the Bages-Sigean lagoon in France), and a site in the Atlantic (Sebou estuary). Chromatic analyses (pigmentation), morphometrics (height–weight) and meristics (vertebrae) made by this author have confirmed the results of enzymatic polymorphism (Yahyaoui *et al.*, 1983) and revealed a homogeneity between Mediterranean and near-Atlantic populations, arguing in favor of their common Atlantic origin.

Sexual dimorphism: *Anguilla anguilla* is characterized by a clear sexual dimorphism that essentially concerns the size. For example, in two lagoons in the southern Adriatic (Lesina and Varano), males are small (30–45 cm maximum) and all the eels over 45–50 cm TL are females (Rossi and Villani, 1980) (Figure 1.8).

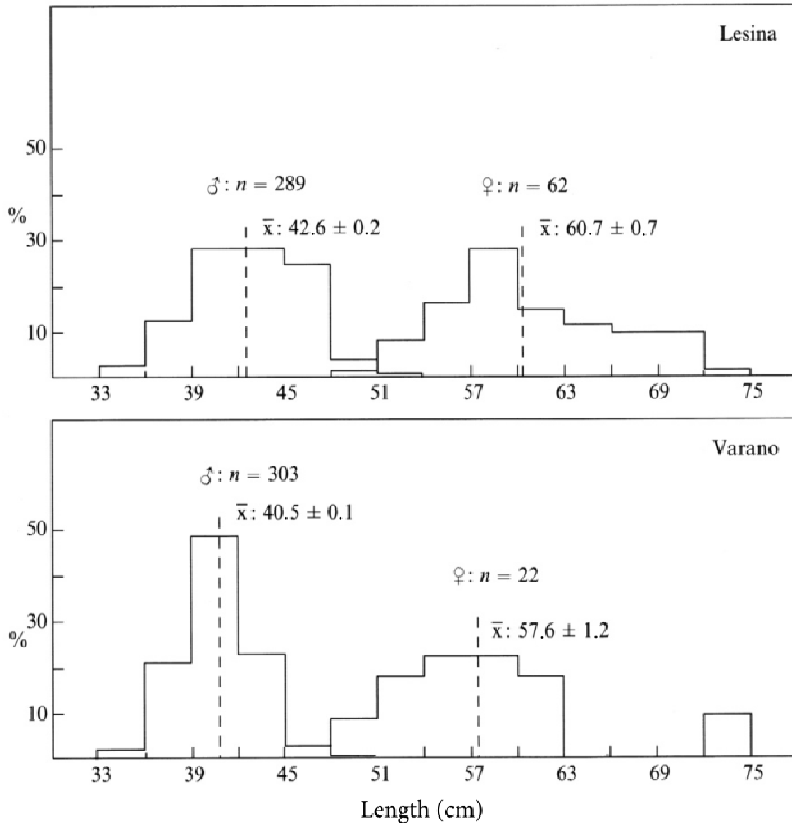


Figure 1.8. Size dimorphism in silver eels in two Italian lagoons from the Adriatic (according to Rossi and Villani, 1980)

There is little overlap between the two sexes, and therefore, sex determination via the “size method” is possible. It is accepted that yellow eels larger than 45 cm are females, but small females (about 37 cm TL) have also been reported (Tesch, 1991). Nordquist (1917) found that the pectoral fin, the eye and the head are broader in males. Holmgren and Wickstrom (1993) pointed out that in breeding males, the eyes are prominent in dorsal view.

Osteology, otoliths and scales: In *A. anguilla*, the basephenoid bone, normally located at the base of the skull, above the parasphenoid, is absent. A symplectic, linking the quadratic of the lower jaw to the hyomandibule and thus to the skull, does not exist. The narrowness of the head also entailed an adjustment in the position of the branchial apparatus. The latter moved behind the skull. The odd fins (dorsal, anal, caudal) are confluent. However, as shown by the caudal part of the spine, the skeletal elements of the caudal fin (the hypural bones) are still present (Bertin, 1956).

The scales are small and oval, deeply embedded in the skin. They appear rather late, according to a caudo-cephalic gradient, depending on the size, not on the age of the eel. As a result, these cannot be used for age assessment by scalimetry, because their appearance is late and their growth is irregular (Jellyman, 1979), hence the interest in otolithometry (Lecomte-Finiger, 1983a).

The eel's otoliths, and more particularly, the *sagitta*, have been the subject of many descriptions after Klein gave his own in 1740. In this area, Gandolfi-Hornoyd, who, between 1928 and 1937, devoted 16 notes to the otoliths of the European eel, was certainly the most prolific (Hureau and Monod, 1973). The otoliths from *A. anguilla* leptocephali and from glass eels are characteristic of eels (Hecht, 1977). The description of otoliths from leptocephalic to subadult stages was given by Appelbaum and Hecht (1978): in leptocephali and glass eels, the shape is circular, with a smooth border. The sulcus acusticus is open toward the front, closed behind, with a poorly individualized ostium and cauda. The collicula is homomorphic and relatively well developed. The upper and inner crista are well developed. The antiroster and the excisura ostii are absent; the rostrum is small, but present. The inner surface is flat; the lateral surfaces are strongly convex. The sagittae of larger individuals (>18 cm TL) differs from previous forms in that the antirostrend excisura ostii is absent and in that they have a more oval shape. In addition, the lateral edges become less convex. Capoccioni *et al.* (2011) examined intra- and interpopulation variations in the shape of otoliths in three eel stocks from different environments in Italy: two lagoons (Caprolace and Lesina) and one river (Tiber). In all three cases, the form evolved during ontogenetic development, presenting a better uniformity in small sizes than in larger ones. Depending on the environment, the otolith appeared as more elongated, with an accentuation of protrusions (rostrum and postrostrum) in both lagoons. Conversely, the shape of the otoliths appears as less elongated in the Tiber and does not seem to be subject to the influence of growth.

Not only does the eel's otolith serve as a growth marker and an age indicator, but it is also used as if it were the fish "black box". Because of its microstructure and the

values of its Sr/Ca, Sr/Si, O18/C13, etc., ratios, the otolith makes it possible to apprehend the biological past of the eel (leptocephalic larval life, metamorphosis, changes in glass eel environments, thermal or nutritional crises, etc.) and to retrospectively reconstruct its lifecycle (Lecomte-Finiger, 1999) (Figure 1.9).

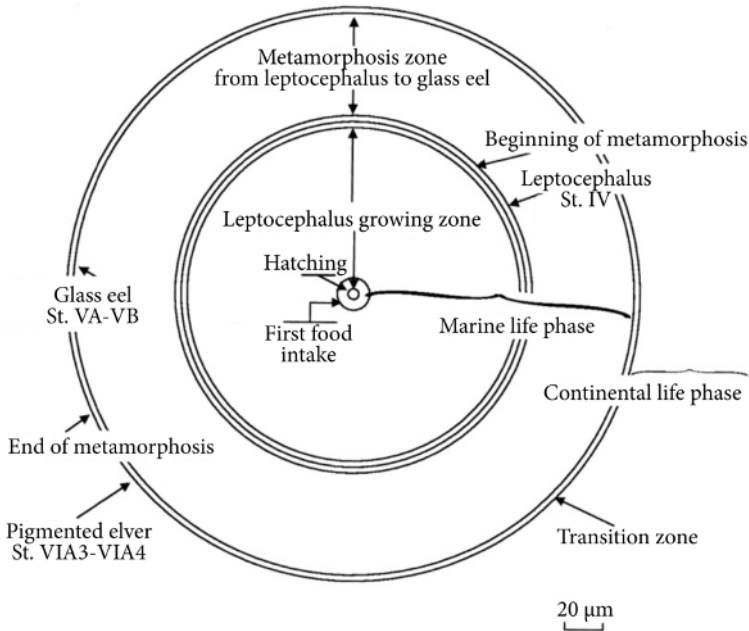


Figure 1.9. Reading of an eel glass eel otolith making it possible to trace the stages of its larval life (according to Lecomte-Finiger and Yahyaoui, 1989)

In fact, Lin *et al.* (2011) showed that the Sr/Ca ratio differed in the yellow eel otoliths from three sites sampled along the Asi River (in southern Turkey), possibly reflecting regional peculiarities of water chemistry. On the other hand, by subjecting juvenile pigmented eels to different diets for 8 weeks, Marohn *et al.* (2009) proved that feeding has no influence on the chemical composition of otoliths (Na, Sr, Ba, Mg, Mn, Cu, Y).

Karyology: $2n = 38$ (Sick *et al.*, 1962, 1967; Chiarelli *et al.*, 1969; Cucchi and Moritu, 1970; Passakas and Tesch, 1980; Passakas, 1981). Other investigations have revealed the existence of a distinct pair of heteromorphous female chromosomes (Ohno *et al.*, 1973; Kang, 1974; Passakas, 1976; Park and Kang, 1979).

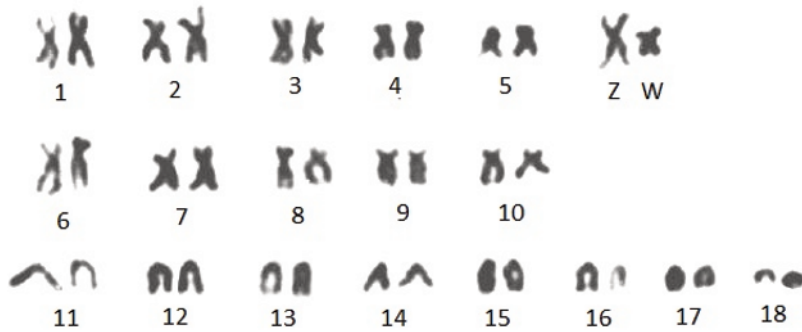


Figure 1.10. *Anguilla anguilla* ($2n = 38$) chromosomes: 1–5 metacentric, 6–10 submetacentric, 11–18 acrocentric and a heteromorphic pair female (ZW) (according to Passakas and Tesch, 1980)

Indeed, Figure 1.10 shows five metacentric pairs (1–5), five submetacentric pairs (6–10), eight acrocentric pairs (11–18) and a female heteromorphic pair. The latter is composed of two metacentric chromosomes, a large (Z) and a small (W) one. Males have two Z chromosomes. Wiberg (1983) has questioned the presence of sex chromosomes. Passakas and Tesch (1980) examined the relationship between gonadal sex and genotypic sex in yellow eels. They claimed that sexual differentiation is not entirely dependent on the genotype. The phenotypic sex also depends on the density of the population, nutrition and/or other factors, such as salinity.

Protein specificity and genetic diversity: Sick *et al.* (1967) showed the protein monomorphism of the European eel's hemoglobin, while that of the American eel *A. rostrata* is polymorphic. De Ligny and Pante-Louris (1973), Williams *et al.* (1973) and Rodino and Comparini (1978) found differences between the allelic frequencies for the malate dehydrogenase of these two species. Avise *et al.* (1986) also found differences in mitochondrial DNA. Larvae of both species from the Sargasso revealed genetic differences corresponding to differences in the number of myomers (Comparini and Schoth, 1982). Jacobsen *et al.* (2014) estimated the divergence time of the two species at 3.38 million years, coinciding with the closure of the Isthmus of Panama, which led to the strengthening of the Gulf Stream.

The serum protein frequencies in the transferring group are different, both between Atlantic and Mediterranean specimens, and between the eastern and western Mediterranean populations of *A. anguilla* (Drilhon *et al.*, 1966, 1967). A study of enzymatic polymorphism also highlighted the heterogeneity of the Mediterranean and near-Atlantic populations (Rodino and Comparini, 1978b). On

the other hand, with the same differentiation technique, Yahyaoui (1983) and Yahyaoui *et al.* (1983) found these homogeneous and considered them as having originated from the same “Sargassian” egg-laying area.

The genetic structure of the eel remains controversial (Maes and Volckaert, 2007; *et al.*, 2009; Pujolar *et al.*, 2009). The first genetic studies using mitochondrial DNA (Avisé *et al.*, 1986; Lintas *et al.*, 1998) or allozymes (De Ligny and Pante-Louris, 1973; Comparini *et al.*, 1977) did not reveal the genetic structuring of the *A. anguilla*. The hypothesis of a panmictic population was not retained by Daemen *et al.* (2001), Wirth and Bernatchez (2001) nor by Maes and Volckaert (2002), who proved a large-scale genetic differentiation using various genetic markers. Wirth and Bernatchez (2001), as well as Maes and Volckaert (2002), suggested the existence of a population subdivided into three subpopulations: the Mediterranean, the Atlantic and the North Baltic, interconnected by a large gene flow. The results of these studies showed signals that were associated with the clinal variation of allele frequencies, or to the haplotypic diversity related to distance isolation (Daemen *et al.*, 2001; Wirth and Bernatchez, 2001; Maes and Volckaert, 2002). These results are consistent with the ocean circulation patterns distributing eel larvae in Europe and a clinal variation in the number of vertebrae (Boëtius, 1980). The maintenance of such a large-scale stable geographical structure would require not only active migration routes and different breeding grounds for the three subpopulations, but also a restriction in the intermingling of larvae during the drift within the Gulf Stream (Andrelo *et al.*, 2011). Studies analyzing the genetic structure only using eels belonging to the same cohort have targeted genetic differentiation on a smaller scale. These studies have shown that the temporal genetic differences between groups of glass eels recruited on the same site during the same year may be greater than the large-scale spatial genetic differences of the same recruited cohort (Dannewitz *et al.*, 2005; Maes *et al.*, 2006, 2009; Pujolar *et al.*, 2006, 2007, 2009). In agreement with these observations, such small-scale genetic differentiation of glass eel waves would result from independent mating events, involving small groups of spawners separated by space or time (Maes *et al.*, 2006; Pujolar *et al.*, 2009). By studying the polymorphism of the cytochrome C oxidase region of the COI gene, Hassab El-Nabi *et al.* (2017) identified 14 haplotypes specific to the Burullus lagoon and 11 features typical of the Rosetta estuary in Egypt. They suggested considering these two environments as separate conservation units for the *A. anguilla*. In this context and looking for the origin of the genetic structure of the *A. anguilla*, Andrelo *et al.* (2011) found that:

1) even a very feeble intermingling during larval dispersal or adult migration is sufficient to completely eliminate any genetic differentiation between subpopulations;

2) temporal differences in small-scale recruitment may occur if the broodstock is subdivided into separate breeding groups;

3) geographic differentiation may be overestimated when a limited number of temporary recruits is analyzed. Taking these considerations into account, and in the absence of results based on appropriate sampling, the eel continues to be considered a panmictic species.

1.1.1.3. *Distribution*

These are the species with wide geographical distribution (Figure 1.11). Its distribution limits according to Ege (1939) are:

- to the north: until the North Cape and the Barents Sea (22° – 30° N);
- to the east: to the eastern Mediterranean and the Black Sea (48° – 65° E);
- to the south: as far as the coasts of Morocco and the Canary Islands (30° N);
- to the west: to Iceland, Madeira and the Azores (20° W).



Figure 1.11. *Geographic distribution of the A. anguilla*

The European eel was introduced in Japan for the first time in 1968 for aquaculture purposes (Tabeta *et al.*, 1977).

1.1.1.4. *Ecology*

Habitat: Within its wide range, the eel visits coastal waters (coastal areas, estuaries, lagoons) as well as continental waters (rivers, lakes, ponds, marshes, reservoirs). Glass eels are also able to flourish in very salty environments, such as

the hypersaline lagoons (40 g/L) of Tunisia (Lake of Tunis), Egypt (Bardawil) and South Sardinia (up to 70 g/L) (Rossi and Cannas, 1984). Pelagic leptocephali live only in the ocean and are located in the near-surface water layer (50–100 m) (Tesch, 1980). However, some larvae perform nyctohemeral migrations and dive as soon as the sun rises to the deeper layers of water (Tesch, 1980). Only the mainland phase of the eel's life is well known. The marine phase, particularly the one concerning the transoceanic migratory stage of the silver eel, remains hypothetical: marine trawling catches are certainly exceptional (Ernst, 1975). Only a few rare pieces of data provided by images filmed because of the Alvin American submarine are available (Robins *et al.*, 1979). The tagging and tracking of silver eels released west of the European continental shelf (Tesch, 1978), as well as in the Mediterranean (near Gibraltar) and in the Sargasso Sea (individuals treated with pituitary extracts) (Tesch, 1989), have shown that they dive up to 700 m during the day. During the dark hours, eels swim quite near the surface. The direction of the monitored individuals was west/southwest.

In brackish coastal waters and in fresh continental waters, eels reach the bottom with appropriate substrates in order to dig burrows where they can easily hide and move, freely shifting forwards and backwards, as well. Its smooth integument is advantageous for endogenous cryptic behavior. The glass eels prefer a particle size of 0.25 mm for the burrows, but they also show a preference for gravel larger than 2 mm, with interstices where they can penetrate (Lecomte-Finiger, 1979). Observations have revealed that eels stay in burrows or in hiding places during the day, but swim around during dusk and at night. They show almost no bathymetric preference, although younger individuals can be found in shallower waters than those frequented by adults (Neveu, 1981).

Multiple observations have led us to admit to the existence of a certain sexual segregation in the occupation of habitats: males probably remain in the downstream part of rivers and salt lagoons, whereas the females, perhaps more sensitive to population pressure, might seek less competitive habitats and occupy the upstream part of river basins (Svardson, 1976; Vollestad and Jonsson, 1988).

Migrations, displacements: The eel is the only large amphihaline and thalassotoc migrant in the Mediterranean. Its lifecycle is particularly complex, characterized by several metamorphoses, which can either be preliminary or consecutive to large-scale migrations (Figure 1.12):

- 1) transatlantic migration of leptocephalic larvae;
- 2) (mounted) anadromous migration of larval eels;

- 3) conquest of (freshwater or brackish) continental environments by the elvers and then, by the yellow eels;
- 4) catadromous (descent) migration of silver eels;
- 5) transatlantic migration back to the nesting area: the Sargasso Sea.

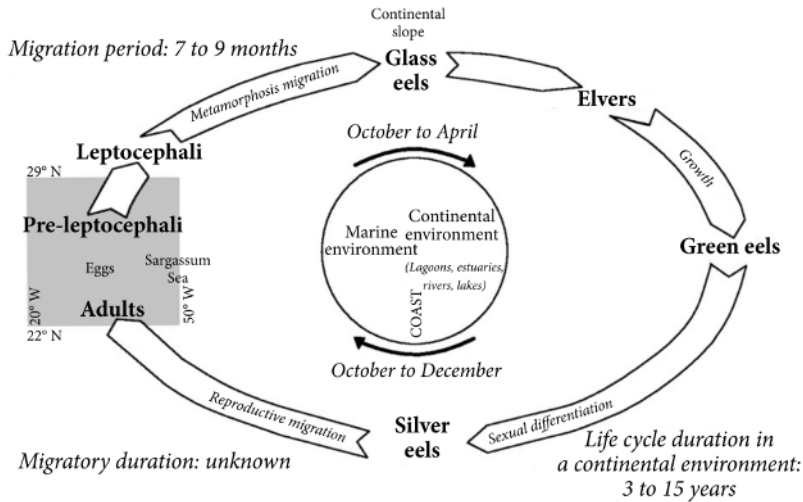


Figure 1.12. *Lifecycle of the European eel (according to Michaud, 1996)*

A photophobe fish, the eel especially, displays nocturnal activity. Therefore, its movements are difficult to observe, but in rivers, lakes and estuaries these have been specified because of tracking through markings: either metallic markings (Gundersen, 1979), colored markings (Cantrelle, 1984) or radionuclides (bromine 82, iodine 125) (Kruger, 1979) and through biotelemetry (*radiotracking* by ultrasonic transmitters) at sea (Tesch, 1974, 1978). The possibility of glass eels and eels crawling out of water makes it possible to conquer watersheds and water bodies isolated from the river systems, and it is one of the means of overcoming obstacles during anadromous migration (Legault, 1988). LaBar *et al.* (1987) studied local eel movements in a small lake in southwestern Spain (Acebrón, 1.2 ha). Individuals evolved in a surface ranging between 2,700 and 1,300 m² and cover a wider space at night than during the day. The individuals monitored during rainy and cloudy weather were more active during the day and used a larger area than those followed during the dry season or during more stable weather conditions.

– *Leptocephalic migration*: Leptocephalic larvae of the two eel species present at the Sargasso Sea are separated: geographical segregation (McCleave and Kleckner, 1987; McCleave *et al.*, 1987) (Figure 1.13) for hydrological reasons, toward the European continents for one species (*A. anguilla*) and toward the Americas for the other (*A. rostrata*).

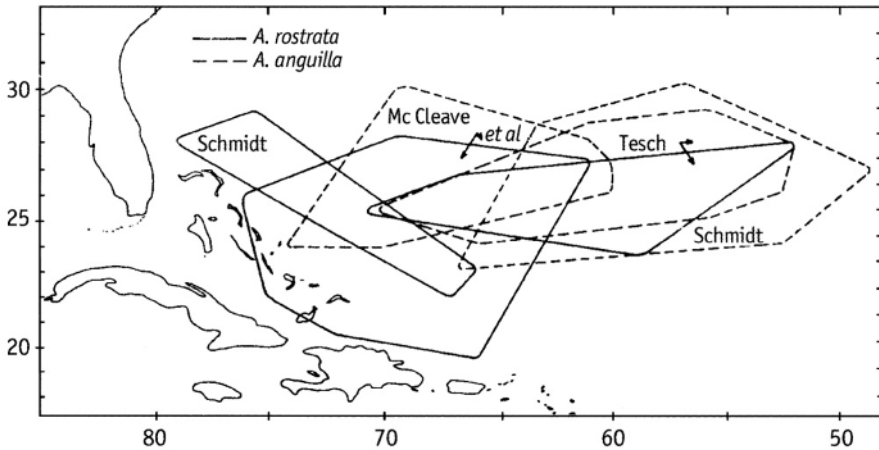


Figure 1.13. The respective egg-laying areas of the European eel and the American eel in the western Atlantic from the leptocephalic collections by three authors (according to McCleave and Kleckner, 1987)

The migration of the *A. anguilla* larvae from the Sargasso Sea to the European and African coasts was studied at the beginning of the 20th Century by Schmidt (1925), and then by Boëtius and Harding (1985). Research concerning larval distribution in the nesting area and assumed migration routes to Europe was conducted in 1979 and 1981 (Tesch, 1982a, 1982b; Kracht and Tesch, 1981; Tesch and Wegner, 1990). Hatching in areas with weak currents, leptocephalic larvae (size starting at 5 mm: Schoth and Tesch, 1984) are pelagic (–50 to –150 m: Tesch, 1980 and up to –500 m: Tesch *et al.*, 1986), and gradually driven north-east, toward the European continent, because of the current of the Gulf Stream and the North-Atlantic drift. The migratory journey involves more than a simple horizontal drift and supposes the existence of active swimming (Tesch, 1983, 1991), favoring vertical displacements according to a nycthemeral rhythm (at 50–100 m, then 30–70 m deep during the night and 100–150 m, then 250–300 m deep during the day) (Schoth and Tesch, 1982, 1984; Castonguay and McCleave, 1987). Several branches of the Gulf Stream and the North Atlantic drift might enable (Figure 1.14) the differentiation of three populations (Boetius, 1980):

- a northern population, pointing toward Iceland and Norway;
- a central population in the direction of the British Isles, the French coasts of the Atlantic, the North Sea and the Baltic;
- a southern population toward the coasts of Portugal, Morocco and the Strait of Gibraltar, that is to say, all the Mediterranean basin.

These three populations can be distinguished by their number of vertebrae (respectively, 114.46, 114.51 and 114.74) (Harding, 1985).

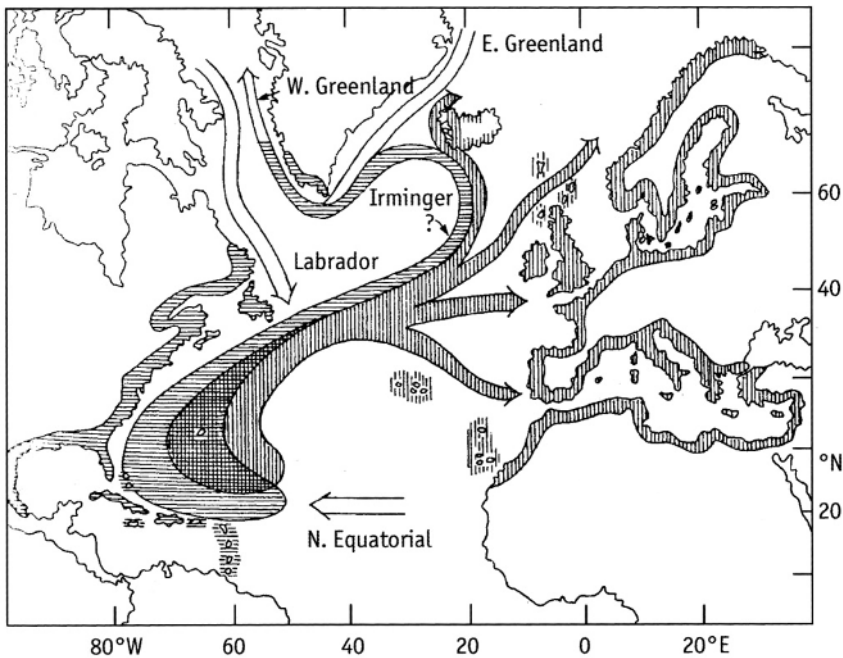


Figure 1.14. *Migration pathways of the leptocephali of the European eel (vertical lines) and American eel (horizontal lines) (according to Boëtius, 1980)*

Following Schmidt's work (1925), it seems clear that the migration of larvae from about 26° N–60° W to Europe takes about 2.5 years. Boëtius and Harding (1985) did not confirm this hypothesis and estimated this duration at around 11–18 months. It is unmistakable that the duration of leptocephalic migration has remained controversial to this day. This duration ranges between 7 and 9 months, estimated from the interpretation of otolith microstructures, and more than 2 years, determined from cohort analysis, otolith microstructures and numerical models (Figure 1.15).

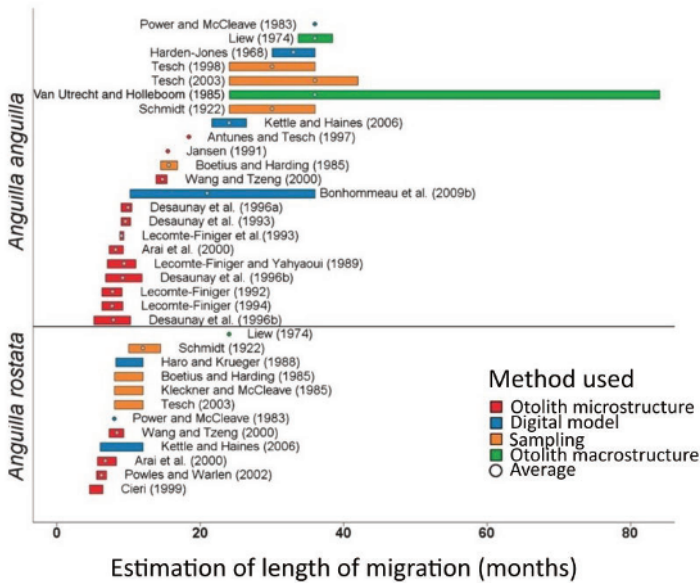


Figure 1.15. Interval and average values (circle) of the European eel's migration duration, according to different studies (from Bonhommeau *et al.*, 2010). For a color version of this figure, see www.iste.co.uk/kara/fishes3a.zip

A recent review of the work on this question tends to favor the hypothesis of a long migration period (Bonhommeau *et al.*, 2010). In light of current knowledge, these authors have expressed their reservations about the hypothesis of an active and oriented swimming ability, which might enable leptocephalic larvae to cross the Atlantic Ocean in less than a year: (1) fish larvae are not known to carry out large scale active migrations; (2) the required high speed is unrealistic (six somatic lengths per second for 35 mm larvae assuming perfect orientation); (3) the eel larvae do not have the necessary red muscles, able to support such a swimming speed; what is more, energy costs would be difficult to cover, given what is known about larval feeding and the low productivity of the tropical Atlantic.

As part of his hypothesis, Schmidt (1924) considered that the leptocephali coming from the Sargasso Sea penetrated the Mediterranean Sea, which was confirmed by harvesting leptocephalic larvae on both sides of the Strait of Gibraltar, as well as in the western and eastern basin of the Mediterranean. When they reach a size between 60 and 70 mm, the leptocephalic larvae metamorphose into glass eels on the continental shelf. This metamorphosis might effectively take place during the migration from west to east linked to the general circulation of marine currents

along the coasts (Lacombe and Chernia, 1972). The migratory movement of glass eels toward the northern Mediterranean coast (Adriatic Sea, Tyrrhenian Sea, Gulf of Genoa, Gulf of Lion) might take place along the currents that move upwards from the coast of North Africa, along Sicily and Italy, and to a lesser degree Sardinia and Corsica (LecomteFiniger, 1984). These data definitively invalidate the hypothesis put forward by Mazzarelli (1914) and Grassi (1914), concerning the existence of a Mediterranean spawning area. These last authors based their argument on ecological considerations, particularly those concerning certain similarities between the Ionian and Tyrrhenian seas and the Sargasso, and those on the harvest of some leptocephalic larvae, ranging between 30 and 50 mm, which are much superior to the ones collected by Schmidt in the Sargasso Sea (5–15 mm).

The orientation of the ocean navigation of glass eels might be influenced by electric fields (weak: 10^{-4} at 10^{-2} A/cm²), generated by ocean currents (McCleave and Power, 1978). It does not seem to be influenced by terrestrial geomagnetism (Zimmerman and McCleave, 1975) but appears to be more dependent on chemical signals (Sola and Tongiorgi, 1998).

– *Glass eel migration*: Eels or pibales, measuring around 6 cm and weighing 0.2 g, whose digestive tract is non-functional, are transparent at first (glass-eels, see Figure 1.16). They enter the littoral waters where they can stay (stabling is more or less prolonged, depending on the sites and seasons). Sensitive to the influence of desalinated continental waters (brackish estuarine, deltaic or lagoonal waters) at the ocean-continent interface, they search for the mouths of rivers, as well as the inlets of Mediterranean lagoons, even if oversaturated. Part of the stock settles in the lagoon and estuarine waters, while the other party is involved in the colonization of inland waters. Nevertheless, using the Sr/Ca ratio as a tracer (Secor *et al.*, 1995; Tzeng, 1996), the otolith microchemistry has shown that some individuals might carry out their entire growth phase at sea (Daverat *et al.*, 2004), at least in Atlantic Canada.



Figure 1.16. European eel elvers. Source: <http://www.migrateurs-loire.fr/quest-ce-que-le-programme-de-repeuplement>. For a color version of this figure, see www.iste.co.uk/kara/fishes3a.zip

In the Mediterranean, the entry of glass eels in continental waters is carried out according to a seasonal periodicity, especially in winter (December–March).

Places and authors	J	F	M	A	M	J	J	A	S	O	N	D
Egypt (Paget, 1923)	×	×	×	×								×
Lake of Tunis (Heldt and Heldt, 1929)	×	×	×	×	×	×	×					
Arno River, Italy (Gandolfi <i>et al.</i> , 1984)	×	×	×	×	×	×	×				×	×
Tiber River, Italy (Ciccotti <i>et al.</i> , 1995)	×	×	×								×	×
Mex Channel, Alexandria, Egypt (Ezzat and El-Serafy, 1977)		×	×	×	×	×						
Sagiada Lagoon, Greece (Zampola <i>et al.</i> , 2008)	×	×	×	×						×	×	×
Alfios River, Greece (Zampola <i>et al.</i> , 2008)	×	×	×	×							×	×
Gozlen River, Turkey (Kucuk <i>et al.</i> , 2005)	×	×	×	×	×	×	×					
Fourcade inlet, Camargue, France (Lefebvre <i>et al.</i> , 2003)	×	×	×	×							×	×
Fourcade inlet, Camargue, France (Crivelli <i>et al.</i> , 2008)	×	×	×	×	×	×	×	×	×	×	×	×

Table 1.1. Seasonal appearance of glass eels on the Mediterranean coasts (×: appearance, ××: maximum appearance)

In the Atlantic, tidal currents carry glass eels toward the coasts and to the estuaries (passive rise) (Deelder, 1958; Creutzberg, 1961), while in the Mediterranean areas where there are no strong tides, the entry of glass eels in lagoons and estuaries is active and occurs mostly at night (Lecomte-Finiger, 1976). The size and the age structure of migrating glass eels vary during the lagoon recruitment season. For example, for the glass eels caught between November 2000 and May 2001 at the Fourcade inlet (linking the Camargue Imperial and the Vaccarès ponds of the Mediterranean), the maximum abundances took place in January–February and, to a lesser extent, in April (Lefebvre *et al.*, 2003). Monitoring the monthly proportions of the different pigmentary stages (from VA to VI A₄) suggested a general aging of glass eels recruited between November and March, followed by the arrival of a second stream of young glass eels in April. At the same time, there was a marked decrease in monthly average masses and lengths, and this even considering only a given pigmentary stage (in this case, VB). The comparative analysis of these data with those obtained by Lecomte-Finiger (1976) for the “population” of the Bages-Sigean lagoon showed a completely different

monthly pigment composition and revealed a significant decrease in the length of glass eels of around 5% in 25 years. Zompola *et al.* (2008) analyzed the temporal migration patterns of glass eels on the west coast of Greece (the Sagiada marsh and the Alfios river) and found that it takes place simultaneously on the Atlantic coasts of southwestern Europe following the same pattern. However, the migratory dynamic is characterized by marked short-term fluctuations (migratory waves of 5–40 days) related to environmental factors, such as water temperature, atmospheric pressure, precipitation and the lunar cycle. A similar pattern is described by Lecomte-Finiger and Razouls (1981) regarding the Gulf of Lion, and by Ciccotti *et al.* (1995) with regard to the Tiber's estuary.

The seasonal and even the daily variations of the anadromous migration of glass eels have shown a clear influence of environmental, hydroclimatic and hydrometeorological factors. Temperature seems to be the key factor in this migration. In the wild, as in the laboratory, glass eels choose the coolest temperatures in comparison with the ones they are acclimated to, and which are actually the ones they encounter in nature (Tosi *et al.*, 1988, 1990). The long-term effects of global warming, linked to Global changes, are likely to modify their anadromous migration behavior (White and Knights, 1997). Several field studies have indicated that freshwater migration and recruitment are negatively correlated with temperature (Elie, 1979; Cantrelle, 1981; Gascuel 1986; Vollestad and Jonsson, 1988; McGovern and McCarthy 1992; Elie and Rochard 1994; Martin, 1995; Jessop, 2003). On the basis of experiments, Edeline *et al.* (2006) concluded that low temperatures might trigger the migration of glass eels and their recruitment into the river, due to a reduction in locomotor activity and their preference for freshwater. They suggested that the temperature might engage thyroid hormones. In addition to this, a drop in the condition of glass eels reduces the preference for freshwater and increases the preference for salt water. Depending on the condition, this behavioral plasticity might have an adaptive signification, limiting mortality by exhaustion, due to energy expenditure, induced by the passage to desalinated water. Desalination is also an inducing factor in the rise of glass eels in estuaries and the mouths of coastal rivers (Tosi *et al.*, 1988, 1989). Under experimental conditions, glass eels show a clear preference for freshwater over brackish or salty water; this salt-related factor clearly guides their choice and is more important than the thermal factor itself (Tosi *et al.*, 1990). Their ability to detect small differences in salinity (5 ppm) enables them to adopt a guided approach toward inland waters during recruitment. In addition, a clear influence of salinity (desalinated water at 2.5–3.5 g/l) on trophic activity, and therefore, on the growth of glass eels, has been experimentally proved (Yahyaoui, 1983). By combining several environmental parameters in the Italian lagoon of Fogliano (temperature, salinity, dissolved oxygen, lunar cycle, availability of benthic prey), Leone *et al.* (2016) proved the existence of a relationship between

the spatiotemporal dynamics of recruitment and the settlement of young individuals (glass eels, elvers, yellow eels) and the environmental characteristics of the host habitats. The most influential factors are temperature and salinity. While the tide mainly acts at the sea–lagoon interface and does not orient the eels which are already inside the lagoon, the availability of prey does not seem to attract more individuals.

Cosmic factors also play an important role in migration: there is a nycthemeral rhythm; in fact, anadromous migration begins during the hours immediately following sunset (Gandolfi *et al* 1980, 1984; Lecomte-Finiger, 1976). However, no lunar influence was detected. Bardonnet *et al.* (2005) found that with age, the light sensitivity of glass eels decreased, and that light avoidance was less stressed in unpigmented glass eels than in pigmented ones. This sensitivity might condition their migration as well as their vertical distribution in the water column, with consequences on the estimation of their abundance depending on fishing depths (Creutzberg, 1961). At the Fourcade inlet, in connection with the Vaccarès lagoon, Crivelli *et al.* (2008) suggested that it is essential to let the lagoons receive rainwater runoff from their watersheds. The elevation of their levels in winter, associated with the Mistral wind, carries low salinity water toward the sea, which favors the recruitment of glass eels. Local factors also play a role: odors or odor bouquets (especially the odors of decaying plant debris) are likely to play an attractive role (Sorensen, 1986). Another attractive role comes from conspecific chemical signals, as shown by experimental studies (Tosi *et al.*, 1990). These signals are epidermal pheromones emitted by yellow eels, established upstream of watercourses (Pesaro *et al.*, 1981; Saglio, 1982).

Transparent eels progressively become pigmented because of the development of cells enriched with melanic pigment (black), and thus become pigmented glass eels (elvers). In agreement with different authors, such metamorphosis ends with the completion of melanophore development (Elie *et al.*, 1982). Other types of reorganization accompany this loss of transparency: (1) *structural*, with the development of teeth, the modification of the digestive tract (resorption of shutter valves) (Elie, 1979) and the settlement of trophic activity (Lecomte-Finiger, 1983); (2) *anatomical*, with the differentiation of musculature, through an increase in diameter and in the number of fibers of the lateral musculature (Willemse and Lieuwma-Noordanus, 1984); (3) *sensory* (visual and olfactory) and *physiological*, with a change in the level thyroid hormone production (Monaco *et al.*, 1981, Yamano *et al.*, 2007) and in osmotic control capabilities (Sasai *et al.*, 2007). These changes continue during estuarine migration and at the beginning of lagoon life. The gaseous bladder remains non-functional during estuarine migration (Hickman 1981). After this first stage of subcontinental evolution, the scarcity of available studies does not allow us to provide details about the physiological, morphometric and behavioral changes that influence the migratory mode of river colonization.

– *Relative sedentarization of glass eels and yellow eels*: Young eels that have reached a suitable habitat tend to become sedentary, but they can make more or less, sometimes seasonal moves, depending on hydroclimatic conditions. The stay in brackish and even hyper-haline lagoon waters and in fresh continental waters may span between 3 and 12 years, and sometimes even 20 years. This favors a more or less rapid growth and an accumulation of energy-giving reserves (especially lipids), prior to the large reproductive migration back to the nesting area. The ecological preferences of the yellow eel, in terms of habitat, were specified by Pouilly (1994). An example was given by Rossi *et al.* (1987): three groups of yellow eels from the Po Delta (605 from Pila, 664 from Scardovari, 401 from Goro) were tagged and released 5 nautical miles offshore. Out of the 1670 tagged individuals (mean TL between 26.6 and 33.4 cm), 9.8% were fished over a 1-month period. Among the latter, 75% were caught in the nearest inland waters (9 km) from the release point and 8.6% at the mouth of the two branches of the Po River. However, there is no evidence that there is a real trend toward the *homings* of individuals, which previously adapted to brackish water. According to the authors, the massive return to the near-shore might only be a way of avoiding the relatively unfavorable conditions of the open sea.

From the microchemical analysis of Sr/Ca ratios in otoliths of 56 individuals from three Italian transition environments at the same latitude, Caprolace lagoon (N = 21), Lesina lagoon (N = 20) and the Tiber estuary (N = 15), Capoccioni *et al.* (2014) showed that in all the sites considered, the fraction of resident eels is significant (between 60 and 85.7%), but that the proportion of nomadic individuals varies according to the environment. According to these authors, the user profile of different habitats is related to local ecological conditions: nomadic behavior seems to be affected by food availability rather than by the salinity gradient. This consideration reinforces the hypothesis that the “optional catadromy” of the eel at the Mediterranean and the trophic changes shown by this species depend on the productivity of the environment rather than on salinity.

The movements of the yellow eel within its territory (home range) could be retraced because of various marking techniques. Through radiotelemetry, Baras and Jeandrain (1998) revealed a relative sedentarity of the eel, with a return to a diurnal place of residence corresponding to a highly structured cryptic habitat, with variable surface area (0.01–0.1 ha). As previously suggested, such fidelity to a given territory was interpreted as due to dependency on food resources and hunting strategies related to intraspecific competition. Motor activity responds to a nycthemeral cycle. It is essentially nocturnal; eels leave their habitats as soon as the sun sets. There is also a decrease in activity at temperatures below 13°C and an increase with increasing temperatures. In addition, there are variations related to the lunar cycle, with greater “agitation” during the full moon (Baras *et al.*, 1998).

– *Migration of silver eels*: At a certain age and size, and this varying greatly depending on the site, immature yellow (green) eels undergo an anatomical and physiological evolution corresponding to the metamorphosis into silver eels (third metamorphosis: leptocephalus/glass eel, glass eel/yellow or green eel, yellow eel/silver eel with a pre-adaptation value (or anticipatory adaptation according to Fontaine, 1989) to a meso-bathypelagic marine life (–600 to –2,000 m). These transformations concern:

- *skin changes*: (1) the skin becomes thicker, more elastic (rich in collagen fibers) and richer in mucus cells (Saglio *et al.*, 1988). This mucus shows differences in the concentration and chemical composition of glycoproteins between yellow eels and silver eels (Saglio and Fauconneau, 1988): the concentration of free amino acids is higher in yellow eels and three of these amino acids (taurine, glycine and alanine) decrease with the evolution toward silver eels; these changes possess an intraspecific chemical communication (pheromone attractiveness); (2) a change in the color of the integument takes place. The back darkens (it becomes rich in melanophores), the flanks and belly become poor in xanthophores (yellow pigment) and turn silvery-white due to the extension of purine-enriched guanophores (guanine and hypoxanthine), which are responsible for silvering;

- *muscle modifications*: an increase in muscular volume is due to muscle differentiation and reorganization (increase in the number and the size of the fibers of the white muscles because of hyperplastic and hypertrophic mechanisms). On the other hand, there is an increase in the volume of red muscles (due to an increase in the diameter of the fibers and their reorganization), which can range from 5% in the immature eel to >13% in the more sexually mature eel (Pankhurst, 1982b). These changes are coupled with a development of enzymatic glycolysis capabilities, all of which translates into an increase in their swimming abilities;

- *a certain involution of the digestive tract* generating a strict fasting throughout the reproductive migration and until the end of the lifecycle. Some tissue and cell changes take place. These are unrelated to digestion, but to osmoregulation as a response to a demineralization situation, which is responsible for hypotonicity (Fontaine, 1994). On the one hand, there is a transformation of the oesophageal epithelium which, having been pluristratified and rich in mucus cells in the freshwater eel, becomes unistratified and poor in mucus cells in the marine eel. These tissue and cell changes favor the acquisition of a selective permeability to Na^+ and Cl^- ions as a part of a necessary regulation of the hydromineral balance (Laurent and Kirsch, 1975);

- *an osmotic balance*, which is reached because of the absorption of water by the digestive tract, following water loss and an increase in ion concentration in the blood, after the passage to seawater. The intestine, kidneys and gills eliminate the

ions. Mucus is more abundant and the skin thickens in order to reduce water loss (Fontaine, 1975). A branchial specialization through the differentiation of many ionocytes or chloride cells makes osmoregulation possible because of Na^+ and Cl^- ion excretion mechanisms (Fountain *et al.*, 1995). The development of these cells (Sargent *et al.*, 1978), rich in mitochondria (ATP-producing) and in endoplasmic reticulum (synthesis of Na^+ - K^+ ATPases), and which have a pre-adaptation value (preparation for marine life), is controlled by the endocrine system (growth hormone or GH, thyroid hormones T3 and T4, cortisol). However, Aroua *et al.* (2005) concluded that the thyrotropic axis is not, or is only moderately, involved in silvering;

- *an increase in hematocrit values* (Johansson *et al.*, 1974) and *vascular revisions*, characterized by an increase (5×) in the capillary network or *rete mirabilis*, which enables an intensification of gas (Kleckner and Krueger, 1981) and pigmentary exchanges in the gas bladder (guanine enrichment that decreases gas conductance, that is to say, a reduction in diffusion losses). The physiology of the gaseous bladder, an organ intended to present a strong gas pressure at great depth, is based on the production made by the bladder's epithelium, CO_2 and lactic acid from glucose (anaerobic glycolysis) (Pelster and Scheid, 1991). Pelster (2015) gave a review of the functioning of the eel's gas bladder during their oviposition migration;

- *a development of sensory abilities*, with an increase in the diameter (5×) and the surface of the eye (Bertin, 1951; Stramke, 1972; Pankhurst, 1982b), a decrease in the number of cones in the retina due to degeneration (Pankhurst, 1982a) and changes in retinal pigments, related to the replacement of rhodopsin and porphyropsin by chrysopsin (Archer, 1998). The number of cone cells decreases and the number of rods increases (2×), varying from two to four layers (Es-Sounni *et al.*, 1987), favoring a monochromatic and scotopic vision. The lateral line becomes visible and the number of sensory cells increases (Zacchei and Tavoraro, 1988). Pankhurst and Lythgoe (1983) and Sorensen and Pankhurst (1988) showed that olfactory cells and associated mucus cells degenerate in males and females after the hormonal induction of sexual maturation, which suggests that olfaction becomes less important. However, later during sexual maturation, the development of sensitivity to sex pheromones is probably involved in the expression of sexual behavior;

- *an accumulation of energy reserves* to meet migratory needs (swimming) and gonadal development; these two functions mobilize 75% of stored energy. The reserves are essentially (80%) lipidic in the form of triglycerides, which are mainly accumulated in the muscle tissue (white muscle) and also in the liver; these deposits are then (partly) redistributed to the gonads. This accumulation of fat occurs specifically during the acquisition of silvering, since eels mainly accumulate glycogen (Barni *et al.*, 1985); between these two stages, it increases by 8–28% (Bergersen and Klemetsen, 1988; Larsson *et al.*, 1990). Lipids are in direct contact

with the muscles (Fontaine 1975, Pankhurst 1982a); they are also stored under the skin and in the liver. However, the silvering process and the moment of catadromic migration may not coincide with the acquisition of the optimum reserves;

- *progressive bone resorption* due to osteoclast activity in vertebral tissues, favoring a Ca^{2+} recycling that benefits the ovary (as co-factor of vitellogenesis);

- *activation of the endocrine glands*: the hypophysis (GH), the thyroid (T3 and T4), the interrenal (cortisol), as well as a correlative regression of the pituitary gland's prolactin secretion (PRL) (Olivereau and Olivereau, 1977). On the other hand, the rate of pituitary gonadotropins (GtH) remains particularly low in immature eels (2–100 ng/mg fresh hypophysis, 1,000 times lower than the rate of the *Cyprinus carpio* hypophysis carp), which reflects a shortfall in the gonadal stimulation by the pituitary gland during the continental lifelong phase (Dufour *et al.*, 1983). On the other hand, the gonads show a weak development and the silver individuals remain sexually immature. Their gonadosomatic index (GSI) increases slightly (0.38–1.86), distant from the one reached during maturity (30 at least) (Fontaine, 1989). Maturation is not correlated with age, but rather with size, and is mostly related to growth and to the accumulation of energetic reserves, which are necessary for the genital maturation that will take place as soon as the earliest opportunity arises (Svedang *et al.*, 1996). In males, differentiation takes place at the same time as silvering, whereas female gonads become different far earlier (Colombo *et al.*, 1984; Durif *et al.*, 2005).

Although “yellow and silver” have been described as two separate stages, the silvering process is actually gradual. Durif *et al.* (2005) could distinguish five different stages in 1,188 females fished in six localities in France, corresponding to different types of hydrosystems. For each of the individuals examined, a profile had been previously defined based on morphological and physiological characters. Thus, the silvering process is described as follows: stages I and II correspond to the yellow stage, separating sexually undifferentiated individuals (stage I) from females (stage II). At these stages, eels have undeveloped gonads with a GSI of 0.5% at most. There is still no production of vitellogenin or gonadotropin. Silvering is initiated in stage III, when vitellogenin significantly increases ($P < 0.05$). The level of GH reaches a maximum at this stage, suggesting a high growth rate before or at the start of silvering. The GSI of these presilvered eels is about 0.8%. The diameter of the eye also increases significantly ($P < 0.05$) and the average eye index is 7.6. The silver migratory stage is reached at stages IV and V. The levels of vitellogenin and GtH-II reach their maximum, as during gonad development. The digestive tract regresses significantly ($P < 0.05$) and the fish probably stop feeding. The eye index is about 1.0. The length of the pectoral fin continues to increase between stages IV and V. However, GH decreases significantly as from stage IV, suggesting that at this stage eels stop investing in somatic growth in favor of sexual maturation.

At the silver stage, eels seek to migrate to the sea. Migration begins in late summer or fall, which might allow them to reach the Sargasso sea-spawning area by the following spring. Their swimming speed is 2 km/h. Migratory activity is more intense during the night, but especially during the first hours of darkness (Bertin, 1951, Bräutigam, 1961) and for several authors, it is exclusively nocturnal (Winter *et al.*, 2005; Westerberg *et al.*, 2007; Aarestrup *et al.*, 2008; Billota *et al.*, 2011). According to the fishing statistics of lunar months, it is also clear that the peak of activity takes place at the time of, or a few days after, the last quarter (Figure 1.17) (Renström, 1979).

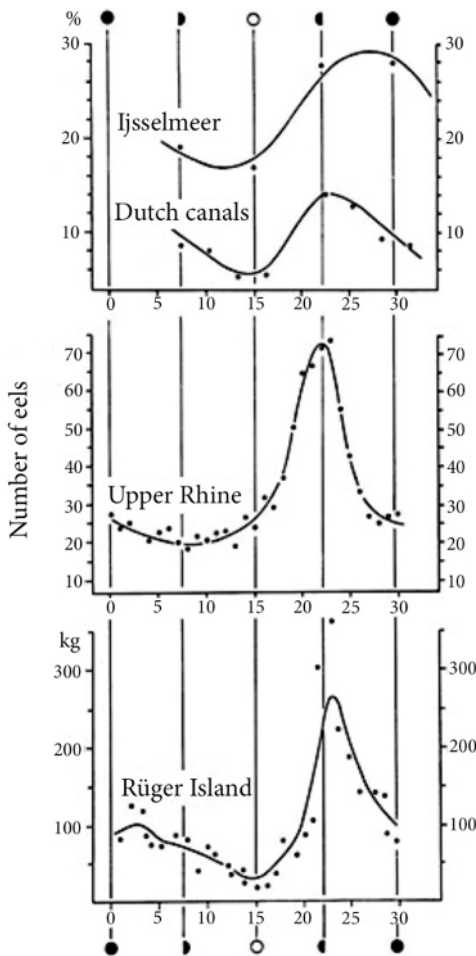


Figure 1.17. Average frequency of silver eels fished in different environments during the lunar month (according to Renström, 1979)

The participation of Mediterranean silver eels' egg-laying at the Sargasso Sea was questioned by Ekman (1932), who considered that the Mediterranean operates as "an eel trap". No silver eel catch in the vicinity of Gibraltar has made it possible to contradict this hypothesis. However, the "Sargassian" migration of Mediterranean eels has been generally accepted (Lecomte-Finiger, 1984). Because of tagging, Anilhat *et al.* (2016) have recently been able to reveal that Mediterranean eels can cross the Strait of Gibraltar. By simulating the optimal spawning migration conditions of eight silver eels (five females and three males, 4–11 years) caught in the Strait of Sicily, Capoccioni *et al.* (2014) suggested that only a small quota of Mediterranean males could reach the Sargasso Sea, and that only females from the central and western Mediterranean were able to reach it and lay their eggs.

– *Sea migration*: Transoceanic migration of future spawners might occur at depths ranging from 600–700 m to 2,000–3,000 m. Information on migratory routes and the behavior of silver eels after leaving continental waters is still rare. Two migratory routes toward the Sargasso have been suggested: a migratory route to the North via the central Atlantic Ocean (Tesch, 1986) and a route toward the South via the Azores current (Fricke and Kaese, 1995). In the latter case, the estimated duration of migration from simulation ranges between 4 and 6 months and is congruent with the period of departure of silver eels from Europe (September to November), and the first catches of the smallest larvae recorded in the Sargasso Sea range between February and June.

The beginning of silver eel migration toward the sea has been studied by conventional tagging (Westin, 1990) and by telemetry (Tesch, 1989; Westerberg *et al.*, 2007; Wysujack *et al.*, 2015) in the Baltic Sea, the North Sea, the North-East Atlantic and the Mediterranean. In the western Mediterranean, Bianchini *et al.* (2009) reported the capture of seven silver eels in two localities in the Strait of Sicily, 500 km apart from each other, at a depth of between 300 and 650 m. The tracking of silver eels for 6 days after their release near Gibraltar has shown that they rise at dusk and go down at dawn, making a medium horizontal movement at a speed of 0.3 m/s, but no exit through Gibraltar has been recorded (Tesch, 1989). In contrast, out of eight silver females carrying pop-up satellite tags, released in the coastal waters of Roussillon (French Mediterranean), two crossed the Strait of Gibraltar in depth and were followed throughout the Atlantic for around 2,000 km from their point of departure, the duration of the trip having lasted for 6 months (Amilhat *et al.*, 2016). In the North-East Atlantic, the average minimum migration speed is 1.5–17 km/day with vertical nychthemeral movements, which oscillate between 300 and 1,000 m (Wysujack *et al.*, 2015). According to these authors, silver

eels released at the Sargasso Sea occupy greater depths and a wider range of temperatures than those at the Northeast Atlantic.

The problems of orientation and navigation toward the Sargasso Sea remain unclear and various factors have been suspected: temperature (Westin and Nyman, 1977), light (Tesch *et al.*, 1992), electric and terrestrial magnetic fields (Karlsson, 1985; Hanson *et al.*, 1984), olfactory recognition, etc. Studies have suggested that there is a geomagnetic basis for the eel's orientation during its long Atlantic crossing (Tesch, 1974; *et al.*, 1992). Hanson *et al.* (1984) and Hanson and Westerberg (1986) measured the "magnetic" sensibility of the skull and spine. They concluded that the distribution and composition of the magnetic material in the fish is insufficient to justify magnetic orientation. In contrast, Moore and Riley (2009) proved the presence of biomagnetite in the mandibular canal region of the lateral line, which makes it suitable for a good magnetoreception. In addition, an imprint acquired during the leptocephalic transatlantic trip is suspected. In fact, silver eels deriving from transplanted glass eels for restocking and rearing are unable to find a proper return migration route (Westin, 1990). Whatever the factors of orientation toward the Sargasso, the duration of this transatlantic trip might last around 5 months, which would correspond to a maximum swimming speed of 40 km/d. This transatlantic migration ends at the Sargasso Sea, at the level of a thermal front located between 24° and 29° North latitude, in the vicinity of the subtropical convergence, a marine zone where temperature and salinity are constant.

Van Ginneken and Van den Thillart (2000) provided the first estimate of the energy cost of oceanic eel migration. They concluded that energy reserves are sufficient for migration and reproduction. The displacement cost, deduced from various studies (Palstra and Van den Thillart, 2010), oscillated between 11.5 and 17.5 milligram of fat per kilogram of somatic weight and per traveled kilometer. The average energy cost of reproduction is estimated at 57 ± 22 g of fat per kilogram (Palstra 2006, Palstra and Van den Thillart 2010) for GSI of 60%.

– *Ecological valence*: Eel larvae are among the most delicate organisms. In contrast, yellow and silver eels are comparatively more resistant to different environmental stresses. Their tolerance to salinity and their ability to survive exposed in the open air (Tesch, 1983) are well known. Glass eels tolerate low oxygen concentrations of approximately 2 mg/L at a temperature of 15°C (Gritzke, 1980). Silver eels can be stored in ponds at high densities for months. Mann (1960) stored fasting eels for 4 months in aquariums filled with fresh water. Boëtius and Boëtius (1967) kept silver eels that reached sexual maturity after a fasting period longer than 3 years. These same authors showed that the survival thermal amplitude

is between 0 and 30°C. Sadler (1979) reports a lethal temperature of 38°C for both yellow and silver eels. Fischer (1977) confirmed the eel's ability to fast, while Gadeau De Kerville (1918) tested their resistance out of water (168 h at 6.5°C).

– *Size, lifespan and growth*: The standard European eel usually measures up to 1 m (maximum 1.50 m) and weighs up to 3 kg (maximum 4 kg). An eel measuring 148.7 cm TL and weighing 5.54 kg, fished in a Croatian river in 2006, is considered the largest known specimen (Tutman *et al.*, 2007). The age of the *A. anguilla* is limited by the fact that after laying eggs in the Sargasso Sea, its lifecycle is complete. However, if its migration is prevented, it may live to a fairly advanced age (Walter, 1910; Tesch, 1983). According to otolithometric observations, its lifespan can extend from 3 to 18–20 years (4–11 years in the Mediterranean). Males stay in the fresh, lagoonal waters between 3 and 15 years, whereas females stay there for up to 20 years. Cases of larger lifespan (24, 30, 37 years) have been observed in captive Atlantic eels. The age of 50 was reached in a Swiss lake without an outlet, whereas it was 55 years old in Denmark, 57 years old in Ireland (Poole and Reynolds, 1998) and even 85 years old, according to Feunteun *et al.* (2011). The question of whether spawners survive spawning remains unresolved. Schmidt admitted that the Sargasso Sea was *both their cradle and their grave*, but at the laboratory, experimentally induced maturation and spawning were followed by a survival of spawners (Delerue-Le-Belle *et al.*, 1982).

Because of direct (individual labeling with tetracycline at a natural pond in the Camargue) and indirect methods (observation of the marginal appearance of growth marks over time in the case of Languedoc and Camargue populations), Panfili and Ximénès (1994) validated estimates for the age of Mediterranean eels from otoliths: a broad opaque zone is mainly formed in the spring, a broad hyaline zone is deposited during the summer months and a chromophilic “growth stop line” corresponds to the winter period. Otolithometry techniques were also applied to glass eels (Lecomte-Finiger, 1983a, 1992b) and yellow eels (Lecomte-Finiger, 1992a) in the lagoons at the Gulf of Lion (Narbonnais and Roussillon). The microstructure of the glass eel's otolith, analyzed by a scanning electron microscope (Lecomte-Finiger and Yahyaoui, 1989), revealed the history of larval life (hatching, first food intake, growth of the leptocephalus during the marine life phase, the metamorphosis to glass eels and the transition to continental life). The growth of glass eels is due to the resumption of food activity at the VIA3 stage (fully pigmented elver). It is faster during the summer months. Yahyaoui (1983) showed that this is closely related to temperature and desalination; the optimum growth might take place at 22–23°C (Sadler, 1979). Supernumerary stunting rings are visible in the otolith of samples captured in the Mediterranean lagoons in the Gulf of

Lionet and appear to be related to summer dystrophic crises (Lecomte-Finiger, 1985). Taking into account the inconsistencies between the nesting period determined from the larvae sampled at sea and the ones revealed through otolith analysis, McCleave (2008) questioned the value of daily growth streaks for determining the age of eel larvae. According to different authors, the metamorphosis age may vary between 159–212 days (Lecomte-Finiger, 1992; Désaunay *et al.* 1996a, 1996b; Arai *et al.*, 2000) and 318–397 days (Wang and Tzeng, 2000).

In the Mediterranean lagoons in the Gulf of Lion, eel growth is significant from April–May to October–November (Lecomte-Finiger, 1983a, 1985). A growth disharmony between the two sexes is classically observed, as shown by the example of the populations of the Adriatic lagoons of Lesina and Varano (Rossi and Villani, 1980) (Figure 1.8).

Indeed, as suggested by Panfili *et al.* (1994) and Melia *et al.* (2006) in the Camargue lagoons, females reach larger sizes and generally grow faster than males. However, these differences are difficult to detect in the early stages of development of eels and yellow eels, because gonad differentiation takes place when they reach a size of 15–25 cm, and also due to the existence of precocious intersex (Colombo *et al.*, 1984). Holmgren *et al.* (1997) observed a high rate of growth in females after the completion of sexual differentiation.

Somatic growth showed large variations at different scales: interindividual variations within the same population, and geographical variations between different habitats (Panfili *et al.*, 1994; Leo and Gatto, 1995). A classification based on 17 different eel populations revealed that growth is better in brackish water than in freshwater, but that latitude also has an influence (Ferandez-Delgado *et al.*, 1989). Panfili and Ximenes (1994), Acou *et al.* (2003) and Melia *et al.* (2006) also showed that growth in brackish environments is significantly higher than in freshwater environments. Capoccioni *et al.* (2014) compared the growth of eels in three transition environments in Italy (Caprolace and Lesina lagoons, Tiber estuary), located at the same latitude. The annual growth rate is higher in Lesina and Tiber, which are relatively productive, in comparison with the oligotrophic lagoon of Caprolace. Melia *et al.* (2006) studied the growth of male and female glass eels in the Vaccarès and Impériaux lagoons (Camargue, France), using samples fished between 1993 and 2003. The average size of glass eels is between 60 and 65 mm, whereas in the case of adults (both sexes), it ranges between 200 and 400 mm TL. It appears that males are rarely larger than 400 mm, whereas females are significantly larger (Figure 1.18).

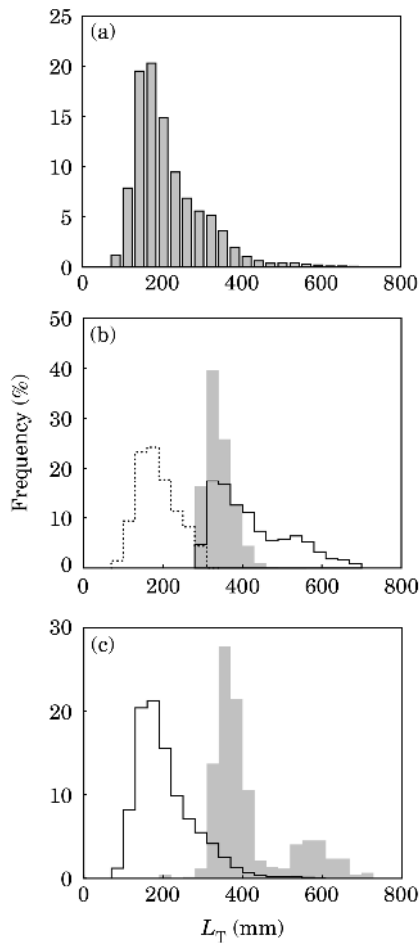


Figure 1.18. Distribution of the total length of 18,300 European eels fished between 1997 and 2003 at the Vaccarès and Impériaux lagoon systems: a) whole sample, b) by sex (undifferentiated represented by the dotted line, solid gray the males, and the females in continuous line), c) by stage of sexual maturity (yellow in continuous line, silver in solid gray). The frequency refers to the total number for each type of size (amplitude 30 mm) (according to Melia et al., 2006)

On the other hand, yellow eels are rarely bigger than 300 mm in size, whereas the silver eels have a bimodal distribution, with a first mode at 350 mm and a second one at 600 mm, respectively, corresponding to mature males and females. The age distribution of a sample of 291 eels fished between 1997 and 1998 is given in Figure 1.19 (Vaccarès and Impériaux).

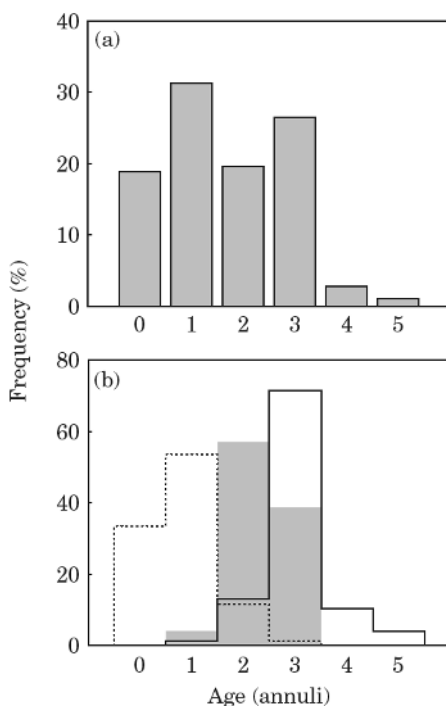


Figure 1.19. Age distribution of 291 European eels sampled between 1997 and 1998 in the Vaccarès and Impériaux lagoon system: a) whole sample, b) differentiated by sex (undifferentiated dashed, male in solid gray, females in solid line). The frequency is relative to the total number in each size class (according to Melia *et al.*, 2006)

The majority of eels undergo sexual maturation after 2–3 years of residence in the lagoon. Females remain in the lagoon for more than 5 years, whereas males do not stay there longer than 3 years.

The growth parameters of the von Bertalanffy model, as well as those regarding the length–weight relationship obtained at the Mediterranean, are given in Table 1.2.

In the Camargue, Melia *et al.* (2006) highlighted significant differences concerning relative growth between sexes and sexual maturation stages. In terms of size/mass relationships, silver eels have the lowest “a” and “b” values, which may indicate certain weight loss due to metamorphosis (gonad development and fasting). The value of “b” is higher in females, whereas the value of “a” is higher in males. These authors also showed interannual variations in “a” and “b” parameters. Parameter “a” has greater variability than “b” (variation coefficient VC = 39 and

2%, respectively). Parameters “a” and “b” are linked by a clear negative correlation ($r = -0.95$; $P < 0.01$). The value of “b” is also negatively correlated to the total length of eels for the same year ($r = -0.58$; $P < 0.01$), but it is positively correlated to the value of “a” ($r = 0.40$, $P < 0.01$). Analysis of the relationship between the length–weight of silver eels, following a latitudinal gradient (six countries: Denmark, Ireland, England, Belgium, France, Spain; 13 watersheds) showed significant differences between and among watersheds, probably implying differences in stoutness. This could suggest that the ability of eels to migrate and breed varies depending on the site (Boulenger *et al.*, 2015).

Places and authors	Sex or stage	Age (years)	N	a	b	L_{∞} (cm)	K	t_0
Valle Nuova Lagoon, Italy (Rossi and Colombo, 1976)	-	10	100	-	-	87.2	0.1873	-
Comacchio Lagoon, Italy (Rossi and Colombo, 1976)	-	11	212	-	-	73.6	0.1290	-
Lagoon of Porto Pino, Sardinia (Rossi and Cannas, 1984)	F	10	110	3.3×10^{-4}	3,405	72.8	0.336	-0.35
	M		150	0.0242	2,299	50.1	0.337	-0.31
Monaci Lagoon, Italy (Ardizzone and Corsi, 1985)	-	5	469	0.002	2.92	42.1	0.391	— 0.001
Kinneret Lake, Israel (Golani <i>et al.</i> , 1988)	-	4	32	4.04×10^{-6}	2,917	-	-	-
Camacchio Lagoon, Italy (Castaldelli <i>et al.</i> , 2013)	Yellow	0.5–8.5	565	0.00026	3,491	97.0	0.157	-
	Silver	4.5–10.5	360	0.006	2,780	125.97	0.124	-
	Mixed	0.5–10.5	925	0.00087	3,223	155.94	0.087	-
Homa Lagoon, Turkey (Acarli <i>et al.</i> , 2014)	-	-	103	0.0006	3,266	-	-	-

Table 1.2. Absolute (L_{∞} , K , t_0) and relative (a, b) growth parameters of the *Anguilla anguilla* in different Mediterranean lagoons

In addition to male- and female-specific growth patterns, for eels remaining at a sexually undifferentiated stage between 2 and 3 years, Melia *et al.* (2006) suggested

a third curve so as to describe the growth of undifferentiated eels. This curve takes into account in its mathematical expression the length and age during sexual differentiation. According to these authors, in the Camargue lagoons, the females are characterized by an asymptotic length, greater than that of males (580 ± 50 and 388 ± 13 mm respectively) and growing faster, while the growth rate is higher in males than in females (3.00×10^{-3} and 1.73×10^{-3} , respectively). Sexual differentiation begins at 204 ± 38 mm, that is to say, at the end of the second year of life in the lagoon, well before the length at which macroscopic differentiation becomes possible (300 mm). Experimentally, Kuhlmann (1975) obtained optimal growth at a temperature of 26°C and Sadler (1979) at $22\text{--}23^\circ\text{C}$. Under breeding conditions, in Italy, Deelder (1981) found that males can grow 12 cm/year and females can grow 17 cm/year, and the silver stage being reached between 2 and 4 years. Then, their average size is 44.5 and 59.8 cm, respectively.

– *Structure and population dynamics*: Studies on the dynamics of eel populations are rare. The recruitment of glass eels takes place later in the Mediterranean than in the Atlantic (Lecomte-Finiger, 1983). Interregional variations in recruitment depend not only on the arrival of leptocephali and their metamorphosis to elver on the continental shelf, but are directly related to local hydrological and hydrodynamic conditions. At the mouth of Moulouya (Morocco), the rise is the result of abundant fall season rains that cause a considerable increase in the river flow (Yahyaoui, 1983). Similarly, in Port-la-Nouvelle (Bages-Sigean lagoon), the outflow of a desalinated current, induced by northwesterly winds, is attractive for glass eels (Lecomte-Finiger, 1983). Nevertheless, elvers penetrate the lagoon all year round with a slowdown, or even a total stop, in summer (Finiger, 1976). At Mediterranean sites (Moulouya and Port-la-Nouvelle), the beginning of the recruitment season is characterized by the exclusive presence of transparent glass eels (from VA to VIA2, according to Elie *et al.*, 1982). Pigmented elvers (VIA4-VIB) are only found at the end of recruitment; on the other hand, at the Atlantic (Sebou estuary), the two categories are simultaneously present, even at the beginning of recruitment (Yahyaoui, 1988).

In the Sardinian lagoons of Porto-Pino, 60% of the fish caught are females and 90% of the sampled eels are at the silver stage, that is, around 5 years old (Rossi and Cannas, 1984). Silver males, aged 5.1 ± 0.5 years on average, measure 41.5 ± 2.6 cm and weigh 128 ± 21 g. Females, aged 6.4 ± 1.2 years, measure 58.5 ± 6.6 cm and weigh 370 ± 146 g. In the lagoon of Monaci (Italy), four age classes were identified (Ardizzone and Corsi, 1985). With regard to yellow undifferentiated eels, size frequency distribution (Figure 1.20) showed an average length of 25.35 ± 2.35 cm and 28.72 ± 2.22 cm for males and 40.37 ± 7 for females.

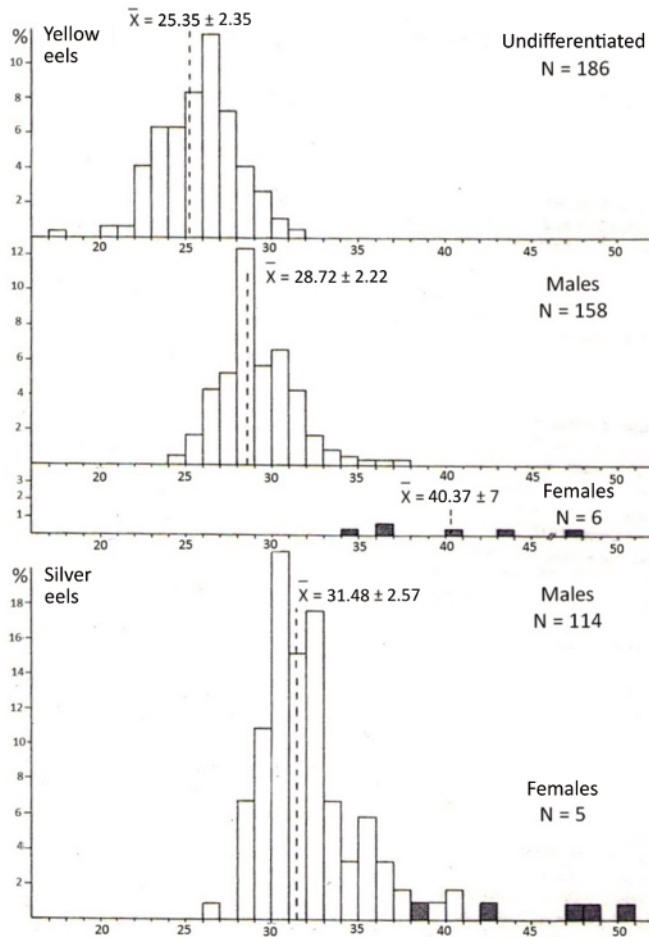


Figure 1.20. Size frequency distribution of silver and yellow eels at Monaci lagoon (according to Ardizzone and Corsi, 1985)

On average, silver eels measured 31.48 ± 2.57 cm. The sex ratio of yellow eels (undifferentiated individuals obviously being excluded, that is 53% of yellow eels) was 96.3% for males and 3.7% females. With regard to silver eels, males represented 95.8% and females represented 4.2%. Age structure showed a dominance of the 3-year olds for silver eels, as well as for undifferentiated individuals (26.1 ± 1.95 cm) and for males (28.6 ± 2.0 cm). A certain amount (11% out of the total number of yellow eels) in the undifferentiated group belonged to the 2-year-old group (23.1 ± 1.8 cm). Among silver eels, 3-year-old (30.8 ± 1.9 cm) and 4-year-old (33.6 ± 2.9 cm) males were the most frequent (Ardizzone and Corsi,

1985). In the Bages-Sigean and Canet-Saint-Nazaire lagoons, eels were between 1 and 12 years of age (15–97 cm TL) and 1 and 10 years of age (17–60 cm TL), respectively. Age group 3 dominated (34.2%) these two lagoons (Mallawa and Lecomte-Finiger, 1992). At the Vistonis (Greece) freshwater lake, the eel population was exclusively made up of silver females ranging from 68.7 to 113.8 cm in size (Macnamara *et al.*, 2014). Table 1.3 provided a structure of eel populations in different regions of the Mediterranean.

Authors	Places	Total population		Dominant age groups		Dominant age groups (%)
		Ages	Length (cm)	Age group	Lengths (cm)	
Rossi and Villani (1976)	Lesina and Varano lagoons, Italy	1–5	28–47	I–III	35–45	-
Gatto and Rossi (1979)	Comacchio Lagoon, Italy	1–14	26–80	Yellow eel I–III	25–29	-
				Silver eel IV–VII	41–59	
Ardizzone and Corsi (1985)	Poontin Lagoon, Italy	1–5	23–46.5	II–III	25–33	90
Purwanto (1981)	Piemanson, Camargue, France	1–4	17–49	I–II	17–21	-
GIS ARM (1986)	Languedoc, France:	1–6	15–80	I–II	15–25	84–95
	Mauguio lagoon	1–4		I–II	25–35	72
	Vic Lagoon	1–6		I–II	15–34	90
	Vaccarès lagoon	1–6		I–II	14–30	90
Mallawa (1987)	Narbonnais Roussillon, France:	1–12	15–97	II–IV	23–34	75
	Bages-Sigean lagoon Canet lagoon	1–10	17–60			80
Panfili (1988)	Languedoc, France:	1–5	23–56	I–II	-	-
	Vaccarès lagoon	1–7	28–46			
	Mauguio lagoon Vic Lagoon	1–3	26–37			

Table 1.3. Structure of eel populations in different Mediterranean regions (according to Mallawa and Lecomte-Finiger, 1992)

Predators: Eel predation is significant at the leptocephalic and glass eel stages. Predators are marine mammals such as whales (Vaillant, 1896), marine fishes such as myctophids and estuarine fish such as sticklebacks (Daniel, 1965). Predation is lower, but not negligible, at the elver and yellow eel stages by ictyophagous birds (cormorants, herons, grebes, seagulls, etc.) as well as by mammals (otters). According to Moriarty (1978), predation by the European conger *Conger conger* has a negative effect on eel stocks. The sea bass *Dicentrarchus labrax* not only competes with eels, but also feeds on glass eels and small yellow eels (Rossi and Cannas, 1984).

1.1.1.5. Food and eating behavior

Diet: At the moment of hatching, the digestive tract is barely formed and the mouth is closed (Prokhorchick, 1986). The digestive tract of the leptocephali, as well as its associated organs, is set in place in the first days after hatching. According to some authors (Hulet, 1978; Kracht and Tesch, 1981; Moser, 1981), the digestive tract might not be functional in leptocephali in general. According to other authors (Westerberg, 1989, 1990; Mochioka *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler *et al.*, 1998), larvae feed on plankton. It was Westerberg (1989, 1990) who first hypothesized the consumption of zooplanktonic organisms belonging to large gelatinous plankton (hydromeduses, siphonophores, scyphomeduses, ctenophores, thalias and appendicularians), in relation to the possibility of a wide mouth opening. Currently, the diet of leptocephali is still little known; no planktonic prey has been identified in the digestive tract (Kracht and Tesch, 1981). Its trophic resources have also been assumed to be particulate organic matter, such as the fecal pellets of copepods, or on the appendages of larvaceans (Desaunay and Guerault, 1997). According to Rasquin (1955), the leptocephalic larva does not feed during the whole metamorphosis, but it is at the gelatinous matrix, rich in GAGs glycosaminoglicans, and from lipids that the leptocephali will find the necessary energy for such transformations. Then, the gelatinous matrix will gradually be replaced by muscles and bone tissue. Between 70 and 80% of the GAGs, rich and highly energetic molecules will be catabolized during the metamorphosis (Pfeiler, 1984). Considering that GAGs have the property of retaining water, their degradation leads to a considerable loss of water and mineral salts, particularly of NaCl. Around 80% of the energy required for this ontogenetic stage comes from lipids (Pfeiler, 1996). During metamorphosis, the composition of lipids changes, manifesting their catabolism. The fasting phase ends at the VIA3 elver stage (complete pigmentation) (Lecomte-Finiger, 1983), corresponding to the reopening of the gastrointestinal tract (Monein-Langle, 1985), reflecting a close relationship between structural and functional development.

Pigmented elvers first consume planktonic prey, and later, they progressively feed on larger benthic prey. Their olfactory and gustatory sensitivity (chemoreception) is considerable in relation to amino acids at very low concentrations (10^{-8} at 10^{-9} M) (Crnjar *et al.*, 1992). Among the different pigmentary stages captured at a natural environment, the VIA4 stage (Elie *et al.*, 1982) is the first to contain prey in significant amounts (Tesch, 1983). In the lagoons of the Gulf of Lion, the elver's eating activity is only gradually established. Glass eels and those individuals at the beginning of pigmentation have no nutritional activity. Feeding begins only at stage VIA3 (according to the stages suggested by Elijah *et al.*, 1982), when pigmentation begins to develop (Lecomte-Finiger, 1983). For stages VIA4, VIB and yellow eels, there is a relationship between prey size and the number and length of fish. In fish measuring between 6 and 20 cm, and as they grow, eels tend to consume larger prey (although they continue to feed on small prey). The relationship between the size of fish and that of prey is: $P_1 = 0.49 \text{ TL}^{0.47}$ ($r = 0.82$). However, the average number of preys per stomach does not show significant variations with regard to fish size (6–20 cm) (Lecomte-Finiger, 1983).

Yellow eels are voracious carnivores with a broad food spectrum. They consume great diversity of benthic prey, usually the most available according to the seasons: isopod crustaceans (*Sphaeroma*), amphipods (*Gammarus*), mysids, annelids, molluscs, insects (Diptera, ephemeroptera, etc.) and fish. Their piscivorous tendencies increase with age, but we should observe that the ichthyophagia reported by several authors (Moriarty, 1972; Tesch, 1977) most often corresponds to a strict form of cannibalism, in that elvers occasionally serve as prey to eels, as already pointed out by Sinha and Jones (1967) and Tesch (1977). In the Mediterranean lagoons, the diet is quite diversified and offers seasonal variations: crustaceans (copepods, amphipods, isopods, decapods), insect larvae, polychaete annelids, gastropods and fish (*Atherina boyeri*), which reveals an obvious trophic opportunism (Lecomte-Finiger, 1983b). This type of diet has been described in the Prévost (Bouchereau *et al.*, 2006) and Mauguio lagoons (Bouchereau *et al.*, 2009) for fish measuring 23–87 cm TL and 15.6–72 cm TL. At three brackish ponds in Roussillon (Lapalme, Salses-Leucate, Bourdigou), glass eels and elvers (6–25 cm TL) also feed on crustaceans, annelids, insects, molluscs and fish (Lecomte-Finiger, 1983). Crustaceans represent the basis of the diet for each environment. Variations occur at the level of the consumed species. Thus, gammarids dominate at Lapalme (71–87%), idotheae are the main prey at Salses-Leucate (66–100%), while corophids are the main prey at Bourdigou (almost 100%). The dietary regime of eels (25–61 cm TL) from the Manzalah Lake (Egypt) is composed of fish, insect larvae, crustaceans and molluscs (Table 1.4; Ezzat and El-Seraffy, 1977). These differences confirm the opportunistic eating behavior.

Food items	Number	%
<i>Tilapia</i> spp.	153	49.28
Other fish	64	22.19
<i>Chironomidae</i> (larvae)	47	10.22
Shellfish	41	8.84
<i>Odonata</i> (larvae)	25	6.91
Shellfish	7	2.56

Table 1.4. Abundance and frequency of prey in the stomach of the *A. anguilla* at the Manzalah lagoon (from Ezzat and El-Seraffy, 1977)

The size of the prey consumed is correlated to the width of the eel's head (Sivertsen, 1938, Micheler, 1967). Thus, broad-headed eels, which are generally large individuals (40–60 cm TL), eat more fish than those with narrow heads. It is probable for silver eels not to feed during their migration (Morović, 1970), as evidenced by the degeneration of the intestinal tract (Tesch, 1983). This degeneration is unlikely to be reversible (Fontaine *et al.*, 1982).

Eating behavior: As a nocturnal species, eels feed mostly during the night (Morović, 1970; Deelder, 1984). The feeding activity mostly depends on temperature, being reduced when temperatures are too hot (28–30°C) and being interrupted below 10°C. Although voracious and cannibal, the eel is able to withstand prolonged fasting (up to 460 days) during which it uses its liver lipid (triglyceride) reserves, and then, its glycogen reserves are stored in its liver (Larsson and Lewander, 1973).

Three modes of food intake have been identified in yellow eels: sucking, cephalic shocks and body rotation (Helfman and Clark, 1986). The choice of each of these types of behavior is determined by the kind of prey (according to its consistency) and by the search for a ratio optimization between energetic costs and energetic benefits that these same prey may provide (Helfman and Clark, 1986). The existence of a regular plankton diet by eels, at various sizes, has been proven by parasitic infestations (for example *Pseudodactylogyrus anguillae*) because during the infestation cycle, planktonic copepods act as vectors for the parasite (Kennedy *et al.*, 1992). The same happens with the *A. crassus* nematode (Blanc, 1994; Bruslé, 1996). Silver eels do not feed during their catadromic migration. They are considered anorexic and as their gut has receded, and their transoceanic migration is carried out because of the exclusive use of (mainly lipidic) energy reserves accumulated during the yellow eel stage.

Intraspecific competition seems to be limited due to the adoption of territorial behavior by elvers and yellow eels, which allows for benthic resources to be shared. In addition, the diversification of diet and a change in the trophic spectrum during growth (increasing the consumption of gammarids) might reduce the risks of intraspecific competition. The eel has been considered able to compete interspecifically with the *Salmo trutta fario* trout, although their respective eating behavior and their activity rhythms are quite different. Nevertheless, in France, the eel is still deemed as harmful in the salmon farming zone (first category), where it was systematically destroyed until 1984 (CSP, 1998).

– *Variations and food rhythms*: In the brackish ponds of Roussillon (France), the values of the stomach vacuity coefficient are high in winter (50–95%) and in summer (60–78%), and seem to be related to water temperature fluctuations. Trophic activity is optimal between 15 and 25°C (Lecomte-Finiger, 1983). Similarly, in Lake Manzalah in Egypt, Ezzat and El-Seraffy (1977) revealed that feeding activity is active in spring and autumn, while it is very low in winter. In winter, eels only eat fish. In the Prévost (Bouchereau *et al.*, 2006) and Mauguio lagoons (Bouchereau *et al.*, 2009), the seasonal influence is manifested by a decrease in nutritional activity during the summer period, which reverses and increases at the following seasons. According to these authors, the seasonal variations observed reveal an opportunistic feeding behavior, characterized by the consumption of the most available benthic prey. Thus, the eel adapts its diet by adjusting it to the available energetic resources in the environment. As a result, this lagoon-resident is an indirect bioindicator of the trophic capacity and level of confinement present in the ecosystem.

In the Roussillon lagoons, glass eels consume small prey (annelids, diptera), which are present at shallow depths, whereas elvers (>10 cm and particularly those close to 20 cm TL) feed on more voluminous prey (idoths and gammarids) from the aquatic plant habitats (Lecomte-Finiger, 1983). In Manzalah Lake, feeding also changes with the size of fish (Ezzat and El-Seraffy 1977). The young (<35 cm TL) consume 62.07% crustaceans, 12.24% chironomid larvae, 13.79% odonate larvae, 3.45% gastropod molluscs and 3.45% fish. Older individuals (39.5–55.5 cm TL) consume 64.89% of fish, 13.28% of chironomid larvae, 10.93% of amphipods, 7.73% of gastropods and 5.15% of odonata larvae. Eels over 55.5 cm TL feed exclusively on fish.

Fishing was conducted every 2 h for 48 consecutive hours during the spring and summer at the Lapalme Pond (Lecomte-Finiger, 1983). Variations in the stomach vacuity coefficient (V) and the mean number of prey items by stomach (Nm) values were monitored over a 24-h cycle. In the spring, trophic activity shows two peaks.

The first and most important one is nocturnal and begins at around 10 pm ($V = 0\text{--}20\%$, $N_m = 5$) and continues until the morning (8 am). The second one presents a lower amplitude and takes place at around 4 pm ($V = 30\%$, $N_m = 2.5$). In summer, the fluctuations are of the same order, but of greater amplitude. Feeding activity periods reach their highest during the night (maximum at midnight: $V = 0\%$, $N_m = 4.2$) and to a lesser degree, during the afternoon (at around 4 pm): $V = 25\%$, $N_m = 5.5$).

1.1.1.6. *Reproduction and reproductive behavior*

Sexuality: The European eel is a secondary gonochoric species (Devlin and Nagahama, 2002), which is characterized by delayed sexual differentiation and a metagamic sexual determination. D’Ancona (1943) studied the development of the *A. anguilla* gonads from the pigmented elver stage onwards. At first, the gonads are undifferentiated, with parts with a male, female or intermediate tendency. This juvenile intersex stage is called “Syrski organ” (Colombo *et al.*, 1984; Colombo and Grandi, 1996). The histological development of the gonads of juvenile eels has been studied by many authors (Rodolico, 1934; Kuhlmann, 1975; Tesch 1983). The last stages of gonadal development are only known in hormonally mature specimens (Bieniarz *et al.*, 1978; Tesch, 1983; Colombo and Grandi, 1990), except for three stage III females collected in the Azores (Bast and Klinkhardt, 1988) and at the Rosemary bank in Scotland (Reinsch, 1968).

Eels smaller than 20 cm have undifferentiated gonads. The Syrski organ appears in eels measuring about 20–30 cm in the form of a thin lamina with primordial germ cells, isolated oocytes or in nests and spermatogonia (Grandi and Colombo, 1997). The first ovaries can appear in 22 cm eels; the first testicles are observed in individuals over 30 cm (Colombo and Grandi, 1996). These authors suggested a model for understanding the sexual differentiation of the *A. anguilla*, in which the testicles are lately derived from the Syrski organ, whereas the ovaries derive directly from undifferentiated gonads, and in some cases from the Syrski organ (Figure 1.21).

The genic determination of the sex is not univocus, but might be influenced by the environment and social factors. High temperatures and high densities might orient the sex ratio toward the male sex (Beullens *et al.*, 1997; Krueger and Oliveira, 1999; Oliveira and McCleave, 2002).

The testicle is an even organ with a lobular structure, in which spermatogonia are found throughout the lobule. Its external shape is different from that of other fish, with rounded lobules joining each other, as well as to the dorsal mesentery. The gonads of hormonally untreated males weigh 0.2–0.6% of the body weight, and in

laying conditions, between 3.6 and 9.6% (Meske and Cellarius, 1973; Bieniarz and Epler, 1977). The gonads of untreated hormonal females weigh 1.1–2.3% of the body weight and the artificially ripened gonads, 32–60% (Boëtius and Boëtius, 1980). The diameter of the oocytes in the gonads of untreated silver eels is 0.1–0.2 mm; in artificially ripened specimens, ready-to-lay eggs measure 0.9–1.6 mm in diameter (Boëtius and Boëtius, 1980). Two specimens captured in the eastern Atlantic contained oocytes measuring 0.12–0.15 mm (Reinsch, 1968) and 0.3–0.4 mm (Ernst, 1975) in diameter. The specimen caught the closest to the laying area (approximately 39° 32' N-50° W) displayed an oocyte diameter of 0.25 mm (Bast and Klinkhardt, 1988).

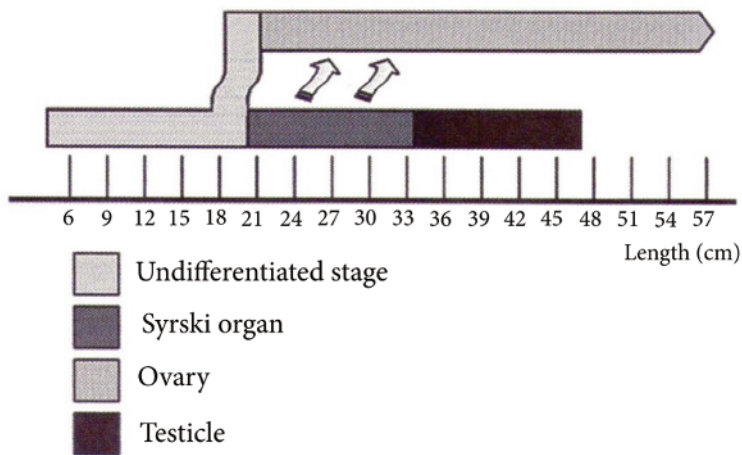


Figure 1.21. *Diagram of the eel's gonad development and differentiation in relation to the size of individuals (from Colombo and Grandi, 1996)*

Holmgren *et al.* (1997) argued that individuals with high growth at the beginning of sexual differentiation are more likely to develop into males. The possible link between the growth profile in the early stages of development and sex determination remains unknown (Melià *et al.*, 2006). The age of sexual differentiation is probably influenced by the environment. It occurs at 20–22 months old in Vaccarès-Impériaux and Comacchio and at 26 months old in Fumemorte, but the almost identical size (210–220 mm) at Vaccarès-Impériaux and Fumemorte is higher (270 mm) at Comacchio (Melià *et al.*, 2006). The fact that the age of sexual differentiation is different between the two sites in the Camargue (Vaccarès-Impériaux and Fumemorte), and that the size is still the same, reinforces the hypothesis that this could be one of the factors determining sexual differentiation, as already proposed by Bieniarz *et al.* (1981) and Colombo *et al.* (1984).

First sexual maturity: We have only few observations regarding the natural sexual maturity of eels: a trawl catch of a female in early ovarian development (GSI = 2.9) (Ernst, 1975) and a photograph by the American submarine Alvin of a “premature” female (Robins *et al.*, 1979). In captivity, ovarian maturation can be achieved by treating silver eels with carpal (*Cyprinus carpio*) pituitary extracts and mammalian gonadotropins (HCG or *human chorionic gonadotropin*), which induce ovarian development (GSI = 60.7) (Boëtius and Boëtius, 1980).

Yellow eels are immature. Their gonads are very weakly developed and barely contain germinal stem cells or at the very beginning of differentiation: spermatogonia and ovogonia-vitellogenic oocytes (Mallawa, 1987). When silver eels begin their oceanic migration in autumn, their gonads are poorly developed, with a gonadosomatic ratio oscillating between 1 and 2. At this stage, a prepubertal block occurs at the hypothalamic–pituitary–gonadal axis, inhibiting sexual maturation (Dufour, 1994). At the hypothalamic level, this blockage is the result of both a deficiency of the gonadotropin-releasing hormone (GnRH) and an inhibition in the release of gonadotropic hormone (GtH) by dopamine (Dufour, 1994). The consequence of this double blocking is an inhibition in the production of GtH, which consequently leads to an inhibition in maturation. The endocrine mechanism of this blockage remains unknown. Recently, the inhibition of the ovulatory peak of LH by dopamine could be lifted because of a triple treatment with testosterone, a GnRH agonist (GnRHa) and a dopamine receptor agonist (pimozide) (Vidal *et al.*, 2004). The question that still needs to be answered is: what is the environmental stimulus that lifts the prepubertal blockade and stimulates gonadal maturation? It has been suggested that the particular environmental conditions that eels encounter during the 6,000 km of reproductive migration may interact with the neuroendocrine mechanisms that control maturation. These factors are temperature (Boëtius and Boëtius, 1967), light and salinity (Nilsson *et al.*, 1981) and pressure (Fontaine, 1993). The first three show no clear effect on the hypothalamic–pituitary–gonadal axis (Boëtius and Boëtius, 1967; Nilsson *et al.*, 1981). The effect of pressure has been subject to laboratory research (Sebert and Barthelemy, 1985; *et al.*, 1988) and in natural conditions (Dufour and Fontaine, 1985). At the laboratory, no effects were observed on gonad maturation, although metabolic changes were confirmed. In contrast, at a more “natural environment”, the stimulation of the hypothalamic–pituitary–gonadal axis was obtained in silver females held for 3 months in cages 450 m deep in the Mediterranean (Dufour and Fontaine, 1985). Under these conditions, a slight gonad development (GSI = 2.3) was observed when compared to the control sample (GSI = 1.6). However, the GtH content was 27 times higher in the females kept deep in the Mediterranean. By experimentally subjecting females to an extended swim (5,500 km throughout 173 days), Van Ginneken *et al.* (2007), concluded that the latter may be a necessary physiological stimulus so as to start

gonad maturation. In fact, they found that at the end of the swimming period, maturation parameters (11-ketotestosterone, LH pituitary level and plasma estradiol level) were higher (although not significantly) in the group that had been subjected to swimming than in the control group. In addition, no significant difference was observed concerning the majority of measured morphometric and reproductive parameters (ocular index, GSI, hepatosomatic index, vitellogenin plasma level, cortisol, MSH). MSH and ACTH pituitary levels were not modified. On the other hand, the oocyte diameter was significantly higher in the group subjected to swimming.

Huertas *et al.* (2006) suggested the existence of “chemical communication” between (male or female) maturing eels and immature males, producing the gonad development of the latter. The pheromone involved is not known, although bile acids are possible candidates (Huertas *et al.*, 2008). Through the in-depth examination of the olfactory epithelium of *Anguilla* males, Churcher *et al.* (2015) showed that the acquisition of sexual maturity triggers the expression of specific chemoreceptors.

Normally, the eel does not reach sexual maturity in Mediterranean waters. The age at which emigration begins probably depends on the lipidic content (Larsson *et al.*, 1990). In natural waters, it is at 4–9 years for males and at 6–13 years for females (Tesch, 1983). Age may be much lower in aquaculture and considerably higher in areas where temperature is low.

– *Site and egg-laying period*: In 1922, Johannes Schmidt, Danish, located the eel spawning area in the Sargasso Sea, after capturing leptocephalic larvae. Several oceanographic surveys in the western Atlantic confirmed this hypothesis (reviewed by Tesch, 1977, 1991; Lecomte-Finiger, 1982; Bruslé, 1989). However, the spawning site is still unknown, but may be estimated from the collection of leptocephalic larvae of various ages. Schoth and Tesch (1984) found the most abundant larvae between 60 and 70° W longitude and 25° N latitude. What is more, age knowledge through the reading of otolith growth daily streaks (Castonguay, 1987) and the assessment of their growth makes it possible to estimate that the laying area may be set at approximately 23°–30° N latitude, 48°–74° W longitude, in the Sargasso Sea. The thermal front resulting from the meeting between the cold and less salty waters from the north and warmer (isothermal 18–19°C to 200 m deep) southern waters might be the determining factor that stops reproductive migration and concentrates broodstock in the southern part of the Sargasso Sea; the spawning isotherm is set at 16–17°C (Fontaine, 1994). On the other hand, larvae measuring less than 5 mm TL can be found up to –250 m (Schoth and Tesch, 1984), confirming egg-laying at such depths. Castonguay and McCleave (1987), as well as Tesch and Wegner (1990), reached similar conclusions from the analysis of larval collections.

The first laying might occur at the beginning of the year. According to Schmidt (1925) and Tesch (1983), the size of harvested larvae might indicate that the peak of reproductive activity is early March. It is very likely that spawning continues until July, since 5 mm larvae were fished by Schmidt (1925) in June, and 7 mm larvae by McCleave *et al.* (1987) in July. Wang and Tzeng (2000) reported prolonged spawning, which culminated in January. However, no large leptocephalic larva was fished during the various surveys conducted in March and April (Schoth and Tesch 1982, Kleckner and McCleave 1988, Tesch and Wegner 1990). McCleave (2008) found an inconsistency between the estimated spawning time from sea-collected specimens and the one provided by the counting of daily growth streaks in otoliths. Estimates from otoliths suggested a longer spawning season throughout the year than the one deduced from the size of larvae sampled at sea at different times of the year.

– *Fecundity*: The fecundity of females seems considerable. The GSI obtained by hormonal induction ranges between 32 and 60% (Boetius and Boetius, 1980). Evaluated after laboratory-induced maturation (pituitary carpal extracts + HCG), fecundity might be equivalent to 0.7–2.6 million and even 3 million oocytes/kg of the body's weight (Boetius and Boetius, 1980). Kokhnenko *et al.* (1977) calculated a fecundity rate of 3×10^6 /kg of body weight for an ovarian mass that might reach 90–120 g. At Vistonis lake (Greece), fecundity ranged from 3,287,500 to 10,832,000 oocytes ($6,413,250 \pm 1,719,874$ oocytes) in females measuring 68.7 to 99.4 cm (743–2,543 g). Fecundity is positively correlated to length and somatic weight, but independent from the infestation of fish by the *A. crassus* parasite (Macnamara *et al.*, 2014).

– *Reproductive behavior*: Reproduction has never been observed in nature, but information on some aspects of egg laying behavior has been obtained from laboratory observations of artificially “matured” eels. A male injected with pituitary extract swims close to a female, which is also artificially mature – sperm emission was obtained for the first time by Boëtius and Boëtius in 1980. More recently, the spawning behavior of artificially mature eels was observed in a group of two females and three males in a 4,000 l aquarium (Van Ginneken *et al.*, 2005a). Interactions between individuals suggest that eels probably set up spawning “aggregates” made up of both sexes, and not a coupled spawn, which was already suggested by Dou *et al.* (2007) concerning the *A. japonica*. Nowadays, it is acknowledged that eels have a high olfactory sensitivity to the substances produced by their congeners. Bile fluid and skin mucus are involved in the release of these odors, but other sources such as urine are not to be excluded. The nature of these pheromones depends both on the sex and on the sexual maturity of fish (Huertas *et al.*, 2008). Besides, noise emissions were recorded in salt marshes and attributed

to the European eel (Lagardère and Ernaude, 2004), but their relationship with potential reproductive behavior at the Sargasso Sea has not been established.

– *Egg, larva and ontogenesis*: Since Kaup's (1856) work on the "leptocephali", about 200 notes describing the egg, the larval and postlarval stages of the eel have been published.

The average diameter of intraovarian oocytes is 1.15 mm and probably smaller than 2 mm after fertilization. Kokhnenko *et al.* (1977) and Boëtius and Boëtius (1980) observed that eggs are pelagic. Boëtius and Boëtius (1980) found that oocytes obtained by the artificial induction of oviposition have a relatively uniform diameter of 1.05 ± 0.15 mm, and a very small perivitelline space. Half an hour after laying, this space reaches a width of about 0.2 mm; the yolk then measures 0.6 mm in diameter. The artificial fertilization of oocytes laid after hormone treatment and the hatching of larvae were described by Bezdenezhnykh *et al.* (1983). Because of induced maturation, Pedersen (2004) obtained eggs of only 763 ± 5.4 and 930 ± 5.5 μm . The number and the size of lipid globules in eggs are variable and fuse into a large globule.

The development of larvae measuring up to 75 mm in length from specimens collected at sea was described by Schmidt (1922). The growth in length seems to be greater in the postanal part than in the preanal part. In addition to the important change from the "olive leaf" shape into the eel shape, which is accompanied by a decrease in length and weight (Schmidt, 1922), the relative position of the dorsal and anal fins and the anus is remarkably altered. The first rays of the fins and the anus move forward and change position with regard to the myomeres. Under experimental conditions, Prokhorchik (1986) described the first 4.5 days of postembryonic development. Pedersen (2004) describes the development of some embryonic stages at 20–21°C (Figure 1.22).

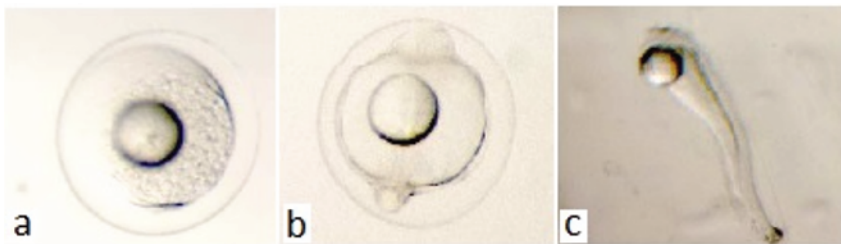


Figure 1.22. European eel egg and larva obtained by breeding: a) embryonic disc in an egg at 6-h postfertilization, diameter = 1 mm; b) gastrulation inside an egg at 28 h postfertilization, diameter = 1.073 mm; c) freshly hatched larva after 48 h after fertilization, total length = 2.35 mm (according to Pedersen, 2004). For a color version of this figure, see www.iste.co.uk/kara/fishes3a.zip

The metamorphosis (including the first morphological changes) matching the time when the leptocephalus reaches the continental shelf (Tesch, 1980; Cieri, 1999), which lasts about a month (Lecomte-Finiger, 1994), but Williamson *et al.* (1993) described a single-day prompt transformation having taken place at an aquarium. This is a complex process, controlled by internal factors and sequenced by environmental factors (Hourdry *et al.*, 1995; d'Hondt, 1999). It is of ribbon shaped (as a willow leaf), and the larva becomes cylindrical. It decreases in size and loses weight. The average size reduction is of the order of 2–6.4%, and weight loss represents 32–64% (Lecomte-Finiger, 1983). The reduction of the body surface area is impressive: a leptocephalus of 65 mm (total length) has a surface of 11 cm², whereas a glass eel of the same length only has a surface of 5.5 cm². Let us remember that the intestine becomes non-functional, following the establishment of a valve that prevents the transit of a possible food bolus. Most structures such as the gut, gills and kidneys develop or reorganize during this transition from the leptocephalic larval stage to the “glass eel stage” (Hulet and Robins, 1989). The pigmentation of the skin and internal tissues develop during this metamorphosis (Hulet and Robins 1989, Tsukamoto 1990), so that the larvae gradually lose their transparency (Schmidt 1909; Robins, 1989; Smith, 1989). The evolution of pigmentation is the support for the classification of metamorphosis stages from leptocephalic larvae (stages I–IV) to the glass eel stage (stages V and VI), corresponding to an analogous shape to that of the eel (Tesch, 2003). The “glass eel” to “elver” phases cover the V_A stages with no pigmentation, except for a spot on the caudal fin, V_B with the early development of pigmentation on the head and VI_{A0}, with the development of pigmentation along the base of the dorsal fin and with the first pigment cells placed behind the skull (Bertin, 1951; Elie *et al.*, 1982). The following stages VI_{A1}, VI_{A2}, VI_{A3}, VI_{A4} and VI_B (Strubberg, 1913; Bertin, 1951; Elie, 1979; Elie *et al.*, 1982) are based on the development of superficial pigmentation and the branchiostegal. We nowadays consider that the beginning of metamorphosis takes place between stages I and II. Metamorphosis ends at stage VI_B when elvers have completed their estuarine migration. Pigmentation is then complete, the mouth is filled with a new set of teeth, the intestine has become functional again after the VI_{A3} stage (Monein-Langle, 1985) and growth resumes: the “juvenile elver” stage is reached (Lecomte-Finiger, 1983; Jegstrup and Rosenkilde, 2003). Salinity and temperature have recently been confirmed as factors affecting the development of pigmentation during the “rise” of glass eels toward brackish and freshwater (Briand *et al.*, 2005). Temperature accelerates pigmentation, whereas salinity slows it down, which makes it possible to predict the residence time of glass eels at the estuary.

1.1.1.7. *Economic importance*

The eel is generally the most abundant species in Mediterranean lagoons, especially in the Adriatic and in the northern sector of the western basin. It is caught throughout the year, but the largest quantities are fished in autumn and in early winter, for example in December on the eastern Adriatic coast (Morović, 1970) and in the Mellah lagoon (Chaoui *et al.*, 2006). In addition, it has been shown that there is a relationship between the amount of fish caught, fish in the area and the moon phases (Deelder 1970, Lindroth 1979, Bach *et al.*, 1992), on the one hand, and atmospheric conditions (Deelder, 1970), on the other hand. Atmospheric disturbances, whatever these may be, are favorable for fishing.

The eel represents a major halieutic resource and its economic value is considerable. Its fishing generates significant income in Europe and all around the Mediterranean. Five types of products are commercialized: the glass eel (or pibale), intended for consumption or breeding (3,500 individuals/kg) and whose fishing is prohibited on the French Mediterranean coast, elvers weighing between 1 and 8 g, intended for growth and for stocking, fresh (mostly live) eels of 100–300 g (yellow eels) and 800 g/1 kg (yellow or silver eels), smoked eel (anonymous, 1994). A small portion of glass eel production is for human consumption and for restocking inland waters, but most of it (over 90%) is destined for fattening farms. Since 2009, the export of glass eels outside the European Community has been banned. Despite this, its selling price has steadily increased (up to 1,200 euros/kg in 2008), since it has gradually become scarce.

The global production of eels between 1985 and 2007 in the GFCM countries was 270–3,405 tons/year, with two main producing countries in 2005: Tunisia and Italy. This production is essentially lagoonal. In Italy, the lagoons of the Venetian region are the most productive. In Tunisia, the Tunis, the Ghar El Melh and the Ichkeul lagoons provide almost all the production. In Italy, eel yields are variable, from 40 kg/ha/year in the northern Adriatic (Rossi and Colombo, 1979) to 180 kg/ha/year in some Sardinian lagoons (Cottiglia, 1981). In the Orbetello lagoon, Cognetti *et al.* (1978) reported an average yield of 69 kg/ha/year for the period 1971–1975, while in the vicinity of Burano lagoon, Ardizzone *et al.* (1982) reported a total fish yield of 65.4 kg/ha/year, 50% of which was eel. In Tunisia, yields generally reach 10–20 kg/ha (Farrugio and Elie, 2010). In the Mellah lagoon (Algeria), the yield varied from 60.1 kg/ha/year between 1987 and 1991 to 1.4 kg/ha/year between 1992 and 2003 (Chaoui *et al.*, 2006).

In the Mediterranean, eels are exploited by small-scale fishing, which is mainly practiced in estuaries, lagoons, deltas and to a lesser extent, in lakes and rivers. In

France, fishing for yellow and silver eels is mainly carried out using traps. The main fishing gear is the triple fyke, more commonly known as the “*capéchade*”. Sometimes, *capéchade* alleys are temporarily set up through the passages leading to the sea, at the time of migrations (Farrugio *et al.*, 2007). In the valleys of the northern Adriatic, the fishing effort, based on fishing weirs (*lavorieri*) (De Angelis, 1960), mainly takes place in October–December and February–March, and is devoted to silver eels involved in the breeding migration. In central Italy, fishing is practiced using fyke nets, especially regarding yellow eels during the spring–summer, thus taking advantage of what is called the “summer migration” (Deelder, 1984). This fishing method is also used in Algeria, in the Mellah lagoon, where catches primarily comprise yellow eels (78%) and are carried out in winter, mainly in December (Chaoui *et al.*, 2006). Fishing with harpoons is practiced on the eastern coast of the Adriatic (Morović, 1970). In Tunisia, the eel is traditionally exploited in lagoons and wadis (Heldt, 1928, 1929). The main equipment used at Lake Ichkeul and El Bibane lagoon, to the south of Gabes, is *capéchades* and fixed fisheries (weirs). Only *capéchades* are used at Ghar El Melh lagoon (Tunisia). In Morocco, the fishermen at Nador lagoon catch the eel by means of a small longline, called the “*planza*”. In Egypt, silver eels are mainly captured by *capéchades* set up at the Upper Nile delta, at Manzalah, Edku and Burullus lakes, where fishing takes place during the winter, from November to March (Ezzat and El-Seraffy, 1977, 1984; Hosny and Dowidar 1988).

In the Monaci lagoon (Italy), four age classes are identified and 90% of total catches belong to age groups 2 and 3 (Ardizzone and Corsi, 1985). This interval can be considered as representing the most frequently exploited part in other Tyrrhenian lagoons (Ardizzone *et al.*, 1982). In the lagoons of Bages-Sigean and Canet-Saint-Nazaire (France), the catches are characterized by the abundance of small sizes: more than 95% are shorter than 35 cm TL, with a size dominance of 23–34 cm (75% of the population at Bages-Sigean, and 80% at Canet-Saint-Nazaire) (Mallawa and Lecomte-Finiger, 1992).

The application of the virtual population analysis modeling technique to the eels from the Monaci lagoon in 1983 (Ardizzone and Corsi, 1985) revealed a recruitment of 875,912 individuals aged 1 year. The fishing production was equivalent to 11,238 kg, from which 10,537 kg were males, that is to say, a 12 g yield per recruit (Y/R). The application of the Beverton and Holt (1957) analytical model for $F = 0.52$ ($M = 0.48$) mortality showed an optimal level of exploitation of the eel at that environment. The Z total mortality coefficient was estimated at 0.986 at Porto-pino lagoons, with a natural mortality coefficient (M) of 0.619 and 0.557 for males and females. In Valle Nuova, a lagoon on the north-west coast of the Adriatic where the

eel population mainly arises from restocking; Rossi and Papas (1979) estimated Z between 3.19 and 2.12 for glass eel recruits, and between 1.2 and 0.5 for the elver stage. In the Valli di Comacchio, Z was estimated to be 0.43 (Rossi, 1979).

The rearing of fished glass eels and elvers yielded between 3,117 and 10,811 tons/year during the period 1985–2007. In 2007, the main producing countries were the Netherlands (4,000 tons), Denmark (1,614 tons) and Italy (1,000 tons). Several lagoons have undergone a “reinforcement” of their eel population. For example, in the Monaci lagoon in 1983, the outpouring of elvers (date not shown) with a density of about 1 kg/ha resulted in a production of 112 kg/ha (mostly yellow eels) over a total of 284 kg/ha of various fish (Ardizzone and Corsi, 1985). In 1981, a repopulation was carried out in the same lagoon with elvers between 6 and 9 g at a density of 12 kg/ha. In 1984, this intervention raised the yield to 324 kg/ha over a total of 528 kg/ha (all fish species combined). We should observe that in the non-repopulated lagoons of the same region (Thyrrhenian Sea), yields were generally lower: 69 kg/ha/year on average for the period 1971–1975 in the Orbetello lagoon (Cognetti *et al.*, 1978) and about 33 kg/ha/year in the Burano Lagoon (Ardizzone *et al.*, 1982). In the case of the Comacchio lagoon (Italy), Rossi *et al.* (1988) showed that in the context of restocking programs, yellow eels from intensive aquaculture were effectively integrated into extensive lagoon aquaculture.

Stricto sensu, European eel aquaculture has not been put into practice yet since its lifecycle has not been mastered. The maturation of males was first induced by Fontaine (1936). Boëtius and Boëtius (1967) achieved an experimental induction of spermiation by using human chorionic gonadotropin (HCG). This hormone was also used by Lumare and Villani (1973). More recent work has shown that HCG may induce spermiation 3 months after a single injection (Kahn *et al.*, 1987), or earlier because of weekly repeated injections. Thus, eels become spermants after 10 weeks of being injected, according to Perez *et al.* (2000), after 5 weeks for Müller *et al.* (2002) and after 4 weeks, according to Pedersen *et al.* (2003).

Fontaine *et al.* (1964) managed the artificial maturation of a female that laid spontaneously, but fertilization was not attempted. Villani and Lumare (1975) were able to induce oogenesis by means of HCG and pituitary extract intramuscular injections. Boëtius and Boëtius (1980) were the first able to fertilize *A. anguilla* eggs. A few years later, a group of Belarusian researchers (Bezdenzhnykh *et al.*, 1983, 1984) obtained larvae, but these died 3.5 days after hatching. Pedersen (2003, 2004) recently induced the sexual maturation of European eels by subjecting them to a protocol successfully developed by Ohta *et al.* (1996) on the Japanese eel

A. japonica. As part of the PRO-EEL² European project, devoted to the control of reproduction and of larval production, 12-day-old larvae, ready to feed, were obtained.

In breeding, “*A. anguilla* male × *A. japonica* female” hybrids were obtained through artificial insemination by Okamura *et al.* (2004). These hybrids developed normally and survived 30 days after hatching. In addition, Burgerhout *et al.* (2011) kept postfertilization hybrids alive for 7 days, arising from the cross “*A. anguilla* male × *A. australis* female”. The hybrid showed typical characteristics of the *A. anguilla*, revealing the father’s gene expression. What is more, natural hybrids *A. anguilla* × *A. rostrata* might exist in the North Atlantic (Avisé *et al.*, 1990; Albert *et al.*, 2006).

1.1.1.8. Protection status, conservation

The European eel has experienced a sharp decline in population over the last 30 years (ICES, 2006; Aprahamian *et al.*, 2007; Castonguay *et al.*, 2007; Dekker *et al.*, 2007; Kimura *et al.*, 2008). The severity of this decline was officially recognized in 1998 when, on the basis of the analysis of fisheries statistics, the International Council for the Exploration of the Sea (ICES) informed the European Commission that “the European eel stock was outside its biosafety limits and that its exploitation was no longer sustainable”. Since this report, the populations of *A. anguilla* have continued to decline, and the ICES has corroborated its findings (ICES, 2006). Since June 2007, this species has been listed on Appendix II from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007). It has also been considered *critically endangered* by the International Union for the Conservation of Nature (IUCN) (Jacoby and Gollock, 2014).

Several hypotheses may be taken into consideration so as to account for the decline of the European eel. They include anthropogenic causes (Figure 1.23) such as:

- 1) the overexploitation during all the species’ development stages (Castonguay *et al.*, 1994; Dekker, 2003, 2004);
- 2) the loss of continental habitats, derived from the construction of obstacles to migration (Castonguay *et al.*, 1994);
- 3) mortality in hydroelectric turbines (Montén, 1985);

² Available on the <http://www.pro-eel.eu> website.

4) organic pollution (ICES, 2006), including contamination by PCBs which, released from fat reserves during catadromic migration has a negative effect on reproduction (Castonguay *et al.*, 1994);

5) the decrease in energy reserves resulting from insufficient food resources in inland waters (Svedäng and Wickstrom, 1997; Belpaire *et al.*, 2008);

6) oceanographic/climatic changes (Knights, 2003).

The explanations suggested also include natural causes (Figure 1.24), such as virus infections (van Ginneken *et al.*, 2004, 2005b) and the *Anguillicoloides crassus* haematophagous nematode parasite (Kuwahara *et al.*, 1974; ICES, 2006; Pelster, 2015). This parasite was introduced in Europe in the 1980s, from *A. japonica* Japanese eels, which had been imported for breeding (Bruslé, 1996). Its population explosion was so extended that the parasite is currently present in all European (Blanc, 1994, Ashworth and Blanc, 1997; Genç *et al.*, 2005) and North African populations (Rahhou *et al.*, 2001; Gargouri and Maamouri, 2006). *Anguillicola crassus* adversely affects migration, by reducing the oxygen transport capacity in the host fish (Molnar, 1993). Palstra *et al.* (2007) measured the infectious effect of this parasite on the energy consumption level throughout sustained swimming, and estimated an approximate 20% increase in the cost of movement in eels infected with the parasite.

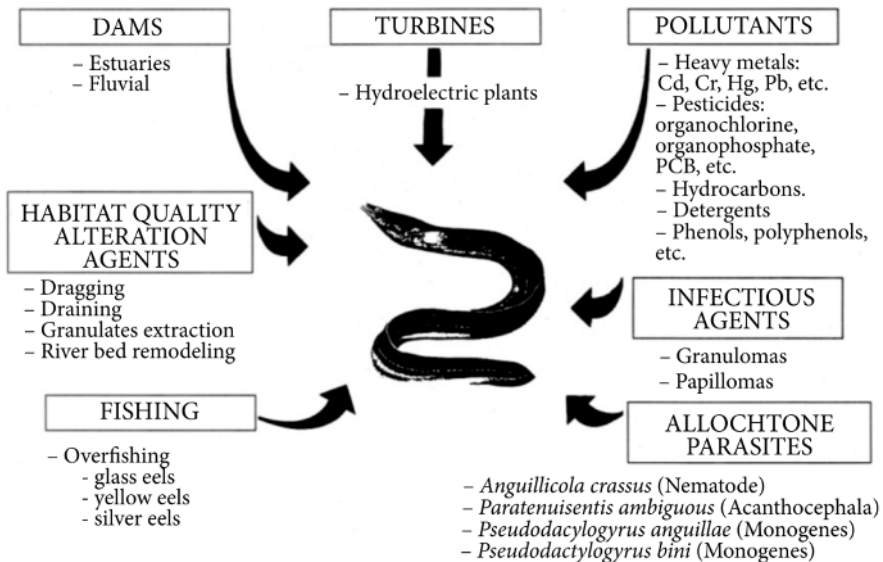


Figure 1.23. Anthropogenic threats to European eel populations (according to Bruslé and Quignard, 2013)

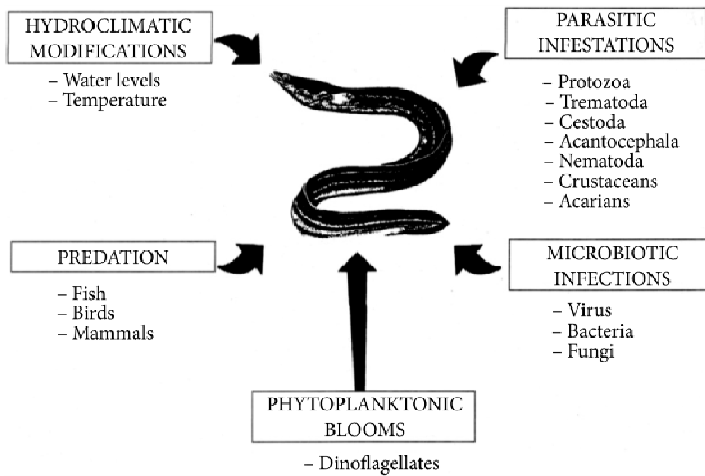


Figure 1.24. *Natural threats to European eel populations (from Bruslé, 1994)*

On another scale, climate change and changes to existing ocean routes have been suggested as possible causes for explaining the decline (Knights, 2003; Friedland *et al.*, 2007). Bonhommeau *et al.* (2008) mentioned the influence of environmental changes in the Sargasso Sea as far as larvae recruitment is concerned. They particularly suspected water warming at the eel's spawning area since the 1980s might have modified primary production negatively, thereby affecting the survival rate at early development stages. Recently, Clevestam *et al.* (2011) discussed the role of size in female reproductive individuals in achieving successful migration and maturation. This hypothesis is based on a possible fat reserve insufficiency in adults, which, as we have already mentioned, arises from the reduction of food resources in continental habitats, thus probably preventing silver females from reaching the spawning area (Svedäng and Wickström, 1997). Indeed, it is generally accepted that larger females are more likely to succeed in migration than smaller ones; swimming performance is related to the size of individuals (Brett, 1965; Brett and Glass, 1973; Ware, 1982; Palstra, 2006). In addition, larger females are more fertile than smaller ones (Wenner and Musick, 1974; Vollestad and Jonsson, 1986).

Given the dangers that threaten the eel, the European Commission has established a regulation (no. 1100/2007) requiring all member states with natural habitats occupied by this species to implement a management plan, so as to help rebuilding stocks. The purpose of this plan is to favor the escape toward the sea (breeding grounds) of at least 40% of the original biomass of silver eels. This measure is based on the assertion that limiting the fishing efforts during the final

phase of catadromic migration at lagoon and estuary inlet levels (channels) is practically the only stage in the eel's lifecycle that can be controlled. This management, which aims to maintain good broodstock levels, should have a positive impact on breeding success, and therefore on glass eels recruitment. Unfortunately, to date, very few studies have been conducted in view of estimating the size of the silver eel population, their exploitation rate or their effective escape rate.

In 2006–2007, using the mark and recapture technique, Amilhat *et al.* (2008, 2009) estimated the amount of migrating silver eels from the Bages-Sigean lagoon (France) to be 1,120,000 individuals (30 kg/ha), mainly males measuring between 36 and 42 cm TL. The exploitation rate by professional fishermen, estimated at 20% (6 kg/ha), suggested an escape rate of 80% (24 kg/ha). This rate was equivalent to 81.2% (342,221 individuals and a biomass of 200.2 tons) for the period of December 2013–February 2014 in the Ichkeul Tunisian lagoon (Derouiche *et al.*, 2016).

Bevacqua *et al.* (2007) used a demographic model in order to evaluate the effectiveness of suggested regulations for eels inhabiting the Camargue lagoons. They concluded that current fishery is inefficient so as to simultaneously allow for a sufficient escape of spawners and an acceptable fishery amount for fishermen.

Bilotta *et al.* (2011) developed a method for quantifying the number and biomass of eels migrating to the ocean using a high-frequency multibeam sonar. They highlighted the capabilities of this monitoring technique and its utility, both as a tool for analyzing the compliance with conservation objectives as well as a means for assessing the success of the measures implemented in order to preserve this species.

In a recent work considering 86 Mediterranean lagoons in nine countries, Aalto *et al.* (2015) confirmed a regional decline in eel catches since the mid-1970s, thus joining the general trend. The population dynamics model that they developed enabled them to estimate the overall escapement rate of silver eels at 35% from the level of pristine biomass. The authors predicted that the complete closure of lagoonal fishery could make it possible to reach a 57% escapement rate in comparison with current recruitment levels.

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