Long-term records (1781-2013) of European eel (*Anguilla anguilla L.*) production in the Comacchio Lagoon (Italy): evaluation of local and global factors as causes of the population collapse

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ABSTRACT

1. Several eel species have undergone extensive declines at both local and global level. The aim of this study is to identify the reasons for the collapse of the European eel (*A.anguilla*) stock in an important area for biodiversity conservation (Comacchio lagoon-Italy), in order to support the development of eel conservation plans.

2. The records of silver eel catches from Comacchio describe the total migratory population and cover the period 1781-2013. The data are accompanied by information related to habitat loss and other local factors. The role of local factors on the decline of the local stock was investigated, while additional information from the literature was also used to discuss the effects of global factors (including glass eel harvest for aquaculture, climate-oceanographic changes, habitat loss, pollution and parasitism) on the three eel species *A. anguilla*, *A. japonica* and *A. rostrata*.

3. The records from Comacchio provided significant information about the effects of local factors on local eel population in the past. However, the current population collapse, which started in the ‘70s, could not be explained by local factors.

4. The literature about global factors suggests that the three eel species are under a combined threat from various factors. The correlations between European aquaculture production data versus the Comacchio yields and other published data from other European eel and glass eel fisheries were found to be highly significant. Aquaculture, which depends entirely on wild-caught glass eels, seems to play a key role in the decline of natural stocks.

5. Conservative estimates using FAO data showed that the current numbers of glass eels needed to support aquaculture production in Europe and Asia exceeds 2×10^9 specimens. This requirement, largely supplied by *A. anguilla* glass eels, can explain the eel populations decline since the glass eel trade has been expanded at international level.

Keywords Comacchio Lagoon, *Anguilla* spp., population decline, local stressors, global stressors, aquaculture.

INTRODUCTION

The European eel (*Anguilla anguilla*, Linnaeus 1758) is a catadromous and semelparous species which spends most of its life as a yellow eel in fresh water, brackish and coastal habitats. When reaching sexual maturity it metamorphoses to a silver eel and returns to the Sargasso Sea in order to spawn and die. The larvae (leptocephalus) drift back to the coastlines and metamorphose into the transparent glass eels, which move upstream in fresh water habitats (recruitment), where they change to elvers thus initiatiating the yellow eel stage (Tesch, 2003).

Long-term records of eel species (*Anguilla* spp*.)* over the last four decades indicate an extensive world-wide reduction in numbers. *A. anguilla* has already been placed on the IUCN Red List of critically endangered species (Jacoby and Gollock, 2014). After the seventies, the commercially most important species, the European eel and the Japanese eel (*Anguilla japonica*, Temminck & Schlegel 1846), have shown population reductions of 99% and 80%, respectively, while the recruitment of American eel (*Anguilla rostrata*, Lesueur 1817) to Lake Ontario has reached critical levels (Dekker, 2003; IES, 2003; Dekker and Casselman, 2014; Cairns *et al*., 2014).

Reasons suggested for the population declines include habitat loss, pollution, parasitism, increased migration barriers, changes in oceanographic conditions, reduction of available prey in freshwater habitats, exotic fish invasions, and overexploitation of fisheries (Kennedy and Fitch, 1990; Westin, 1998; van Ginneken and Maes, 2005; Knights, 2003; Bevacqua *et al.*, 2007, 2009, 2012; Simon, 2007; Belpaire *et al.*, 2009; Bonhommeau *et al*., 2010; Clevestam *et al.*, 2011; Kettle *et al.*, 2011; Martino *et al*., 2011; Prchalová *et al.*, 2013; Katselis *et al*., 2013; Wickström and Sjöberg, 2014; Pratt *et al.*, 2014; Arai, 2014a). The critical levels of the eel populations in Europe led to the application of measures for stock recovery based on European Council Regulation 1100/2007 (E.U., 2007) and management plans for eel fisheries (http://ec.europa.eu/fisheries/marine_species/wild_species/eel/management_plans/).

Italy is one of the three top producers of farmed eels in Europe together with Netherlands and Denmark (http://www.fao.org/fishery/culturedspecies/Anguilla_anguilla/). The eel fishery of the Comacchio Lagoon in northeastern Italy was one of the most important localities in terms of production. Restocking in the lagoon has never been conducted and so the eel population is based only on natural recruitment. The lagoon is considered one of the most important centers for scientific research on eel, with available scientific literature which dates back to the eighteenth century (Friedlander, 1872; Colombo and Rossi, 1978; Gatto and Rossi, 1979; Rossi, 1979; Gatto *et al.*, 1982; Carrieri *et al.*, 1992; De Leo and Gatto, 1995, 1996; Bevacqua *et al.*, 2006; Castaldelli *et al.*, 2014; Dezfuli *et al.*, 2014; Aschonitis *et al*., 2015). The lagoon has been subjected to maximum exploitation because it is a semi-closed ecosystem in which the silver eel catches approach 100% of the migrating population. Thus, it presents an excellent opportunity for investigating the effects of the eel fishery management strategies that have been employed over the years. Additionally, it can be considered as an optimum location for monitoring population dynamics on a European scale. The annual variation in silver eel catches at this site is not only an indicator of the local stock but serves as an index of trends in the European eel population as a whole, which is considered a single, randomly mating population (hypothesis of panmixia) that spawns in the Sargasso sea and returns to the coasts of Europe and north-western Africa (Lintas *et al.*, 1998; Dannewitz *et al.*, 2005; Als *et al.*, 2011; Cagnon *et al.*, 2011).

The aim of the present study is to identify the local and global factors responsible for the collapse of the European eel (*Anguilla anguilla* L.) stocks in an important area for biodiversity conservation; the lagoon of Comacchio in the Po River delta (northeastern Italy. Historical records of silver eel catches which cover the period 1781-2013 are provided in this study. The data are used to illustrate the population decline, followed by a detailed discussion of the potential role of major local (habitat loss, changes in local environmental conditions) and global factors (aquaculture and fisheries, climate change, habitat loss, pollution and parasitism) which may be responsible for the population decline of this important eel species. The information provided in this study could support the development of future conservation plans for eel species.

MATERIALS AND METHODS

Study site

The eel fishing industry of Comacchio lagoon is of very considerable antiquity and constitutes one of the best examples for understanding the evolution of eel fishing activities over the centuries. According to Bertram (1873), the region was initially a great swamp with access to the sea. The precise date at which the lagoon was formed into a fish-pond is not known, but historical evidence indicates that in the year of 1229 the inhabitants (a community of fishermen) proclaimed Prince Azzo d'Este as Lord of Comacchio. From that time onwards prosperity increased, the fishermen began to adopt organization schemes and the first reclamation works began in order to facilitate fishing activities. The waters of the lagoon were dyked out from those of the Adriatic sea, and a series of canals and ponds were developed to cover the requirements of the fisheries. The operations were performed between the mouths of the Po di Volano River, on the north, and the Reno on the south, forming the boundaries of the great swamp. A number of entrances were constructed in the natural embankments of the lagoon. Bridges had also been built over all these channels by the munificence of various Popes, and very strong flood-gates were constructed to regulate the water inflow-outflow and the migration of the fish. The entire industry of Comacchio and other lagoons of the North-eastern coast of Italy (Emilia Romagna, Veneto and Friuli regions) was founded on the basis of eel fishing, which turned into an extremely important source of profit (Bertram, 1873).

The reported fishing technique for eels used in the region during the seventieth and eightieth century does not differ from the one used nowadays. Fishing was and is still performed through gateways where V-shaped screens of selective size, called lavorieri, are used to capture silver eels. The screens permit the entry of glass eel and elvers but entrap all silver eels when they begin migration. The similarity of lavorieri structures of the eighteenth century and now are shown in Figure 1a,b,c. Even in the previous centuries, the inhabitants of Comacchio had a good knowledge of the migration and recruitment periods. Friedlander (1872) and Bertram (1873) provide extensive details of this knowledge, which is quite surprising since fishermen also knew how to obtain measurements, to keep records of eel catches and to make estimations of fish stocks in the lagoon.

[FIGURE 1]

Nowadays, the Comacchio Lagoon comprises three main basins: Valle Campo, Valle Magnavacca, and Valle Fossa di Porto, which cover an area of $\sim 10^4$ ha (Figure 2). Valle Campo (~1600 ha) is completely separate and in private ownership, while the other two now constitute a single basin (8470 ha). The lagoon is connected to the Adriatic Sea by two canals (Bellocchio and Foce) that are hydraulically regulated by gateways where the lavorieri are placed and used to capture silver eels (Figure 2). The study site is recognized as one of the most important coastal wetlands in Europe for biodiversity conservation and since 1988 has been protected by the institution of the Regional Park of the Po Delta of the Emilia-Romagna (Regional Law 27/88) (http://www.parcodeltapo.it/pages/en/environment-territory/the-park.php).

[FIGURE 2]

Data and Methods

The silver eels of Comacchio lagoon were always caught in the lavorieri with approximately 100% efficacy and official estimates of the total biomass were being undertaken every year for more than two hundred years. Before 1988, the total catch was always sold off in the market. After 1988, the lagoon was recognized as important area for biodiversity conservation and the commercial fishing stopped, but measurements continued for monitoring purposes and all the captured specimens were being released again to continue migration. The Regional Park of the Po delta and the Management agency for the Parks and Biodiversity of Delta del Po were founded in 1988 and took over the infrastructures, official documents and records of the previous company managing the fishery. These historical records were organized and combined with new data to provide the following information, which covers the period 1781-2013:

a) Annual records which present the variation of fishing area coverage. The fishing area is the total area where migration was fully controlled by the lavorieri (Table S.1 in supplementary material).

b) Annual records of total weight of eels trapped in the lavorieri, which correspond to ~100% migrating silver eel population (Table S.1).

c) Records of mortality events from local stressors for the period 1787-1985. These records correspond to observations made by the managers of the fishery and they are not quantitative. They were noted by the managers as warning observations for possible production decline. They are unique historical records and they are provided here in order to assist the discussion on local stressors.

The silver eel production data from the Comacchio lagoon were used to investigate the role of local and global stressors on the eel stock. The investigation of the role of global stressors on eel populations collapse was based on additional information from the international scientific literature, which concerns the effects of aquaculture, climate-oceanographic changes, habitat loss, pollution and parasitism on eel species. Special attention was given in this study to the effects of aquaculture and for this reason official data of FAO for eel aquaculture production during the period 1950-2013 were also used (source: Fisheries and Aquaculture Information and Statistics Service of FAO – database of FishStatJ software v.2.12.4 for fishery time series, last date of data release: March of 2015, last accessed on 1/10/2015 (Table S.2 in supplementary material).

The analysis for evaluating the hypothesis of aquaculture as a major stressor for eel population decline was performed using Spearman correlation coefficients using SPSS 17.0 versus the dataset of silver eel catches from Comacchio. Additional data were also used a) CPUE data provided by Henderson *et al.* (2012), which concern yellow eel catches from Hinkley Point in Bridgwater Bay (Somerset, UK) for the period 1980-2010, and b) annual mean yields of glass eels from west European coastline sites provided by Feunteun (2002) for the period 1965-1996. The correlations were performed using European aquaculture production versus different yearly lag-time cases of the catches from Comacchio and Hinkley since the eels in natural environments are older than those of aquaculture. The 15-years lag-time case was chosen as the upper maximum threshold because older eels have never been captured in the Comacchio environment (Rossi, 1979; Aschonitis *et al*., 2015). For the comparison between aquaculture production and glass eel yield data of Feunteun (2002), the delay was applied on aquaculture data.

RESULTS AND DISCUSSION

Silver eel catches in the Comacchio lagoon for the period 1781-2013 and effects of local stressors

The total fishing area at the end of the seventeenth century, which was fully controlled by the lavorieri, was approximately 44 thousand hectares. The recorded changes in the fishing area coverage during the period 1781-2013 are shown in Table 1 and are illustrated in Figure 3a together with the total weight of silver eel catches over the same period. As indicated in Table 1 and Figure 3a, the most intensive habitat loss was observed in the periods 1916-1930 and 1966-1967. After 1970, the lagoon had already lost more than 80% of its initial coverage. The changes were mainly attributed to reclamation works for the formation of new agricultural land. The annual variation of biomass per unit area (ha), which also indirectly describes the abundance of silver eels, was estimated using the fishing area coverage (ha) and the annual catches (kg). The variation of biomass per unit area for the period 1781-2013 is given in Figure 3b.

[TABLE 1]

[FIGURE 3]

The recorded mortality events due to local stressors are given in Table 2. These records stop in 1985 since after 1988 professional fishing was banned. Moreover, the stock had already declined (Figure 3a) not permitting such observations. The main causes of documented mortality were hypersalinity, frost and ice coverage, and the flooding of the Reno River. The combination of hypersalinity and frost, followed by ice coverage, was the most serious local stressor due to the shallow nature of the lagoon (0.5-1.5 m) (Rossi and Cataudella, 1998). Table 2 also includes records of some unexplained high mortality events. The most likely explanations for these events may include the following:

1) Anoxia: in many cases unexpected flow of nutrients may change the system from mesotrophic to eutrophic with biomass accumulation of the dominant *Ruppia cyrrosa*, leading to oxygen depletion. Such events can't be excluded even in the eighteenth century because the lagoon was surrounded by agricultural land where manure application was already a widely applied fertilization practice.

2) Diseases: before 1900, the knowledge about eel diseases was limited and thus high mortality events due to disease outbreak could not easily be identified. The only case of disease identification in the past centuries concerns the "saltwater eel disease" which was already known in Italy since 1718 (Tesch, 2003). More recent cases of disease identification concern the case of *Argulus foliaceus* during 1970 (Table 2) while low levels of infections by *Anguillicoloides crassus* have been identified without significant impact on the population (Dezfuli *et al*., 2014).

[TABLE 2]

After the 1960s, the scientific community started to investigate more thoroughly the functions of the specific system and significant information was made available about the effects of anthropogenic activities. Before the 1970s, evidences of eutrophication started to be revealed mostly due to fertilizers application in the surrounding lands. Later, the phenomenon was intensified due to the effluents by a fish culture plant constructed by the SIVALCO cooperative (Sorokin and Zakuskina, 2010). In the mid 1970s, eutrophication in the lagoon was manifested by changes in the phytoplankton community and by the accumulation of labile sulfides in the bottom sediments (Cognetti *et al.*, 1975; Sorokin and Bilio, 1981; Sorokin and Zakuskina, 2010). These activities finally resulted in the outbreak of extremely dense and persistent blooms of picocyanobacteria in 1985, where their peak wet biomass reached over 60 g m^{-3} (Sorokin *et al.*, 1996a, b). The bloom was responsible for mortality of bottom vegetation, benthic fauna, eels, other fish and clams (Rossi and Cataudella, 1998; Sorokin and Zakuskina, 2010). Significant efforts for the recovery of the lagoon started after 1990, and a series of studies by Sorokin *et al.* (1996a, b) and Sorokin and Zakuskina (2010) were performed for the monitoring of the ecological status of the lagoon. Although, these studies revealed that the bloom of picocyanobacteria was still present, some signs of recovery of the benthic fauna started to appear after 1992 (Crema *et al.*, 2000; Munari *et al.*, 2003, 2005).

The latest updates of the eel stock were carried out in 2011 by Castaldelli *et al.* (2014, who investigated the yellow and silver eel morphology-physiology (sex, age, length), and by Aschonitis *et al.* (2015) which performed stock assessment analysis. The results of Aschonitis *et al.* (2015) showed that the estimated stocks and recruitment were at least ten times lower than the respective estimates of previous studies using data from the 80s (De Leo and Gatto, 1995; De Leo *et al.*, 2009). The results of Castaldelli *et al.* (2014) were compared with the previous study of Rossi (1979), which used data from 1974 and showed that a) the population reached ~98% feminization rate in 2011 from ~77% in 1974, b) the population exhibited faster maturation rates (younger, longer and heavier silver eels ready to migrate) and c) the observed age classes of eel population were reduced from 15 in 1974 to 11 in 2011 (14+ and 10+ years old, respectively, starting from 0+ age). These changes and especially the high feminization rate are the stronger evidences of the population collapse, which took place in the lagoon, since feminization is strongly negatively correlated with population density (Roncarati *et al.*, 1997; Krueger and Oliveira, 1999; Tzeng *et al.*, 2002; Han and Tzeng, 2006).

After 1970 the biomass production started to decline and after the year 2000 dropped to critical levels (Figure 3a). The loss of habitat during 1966-1967 for the reclamation of a big portion of the logoonal complex (Table 1), was almost certainly the most important local stressor causing a decline in terms of total mass (Figure 3a). The total catch was reduced significantly approximately 10 years after the land reclamations of 1966 and this suggests a probable stock-recruitment relationship with the habitat loss stressor. On the other hand, there was an increasing trend of abundance (mass of silver eel caught per unit area) during the period 1920-1980 and especially in 1960-1980 (period of large habitat loss (Figure 3b). After 1980 the abundance started to decrease and dropped below normal low values during 1990, which is 25 years after the last large habitat loss of 1966. Local stressors, and especially habitat loss and environmental degradation, may have influenced the local eel population, but special attention should also be paid to the effects of global stressors since a general decline of eel species was observed contemporaneously at the global level. Further discussion is reserved for global stressors in the next sections.

Effects of global stressors

The global trends of juvenile abundance for the three eel species of *A. anguilla*, *A. japonica* and *A. rostrata* showed a steep decline over the last forty years (Figure 4) (IES, 2003; Dekker and Casselman, 2014). This global decline merits consideration of the probable effects of global stressors on eel populations. Five hypotheses for the global decline are discussed in the following sections.

[FIGURE 4]

Aquaculture and glass eel harvest

Fishing has now almost been abandoned as a source of eels in favour of aquaculture, which is responsible for more than 90% of eels supply in the global trade (FAO, 2009; Crook, 2010). This percentage justifies the estimations of Dekker (2000) who reported that 80-95% of the glass eels are harvested. The basic feature of eel aquaculture is that it is totally dependent on wild-caught juveniles (glass eels or elvers). Significant progress in eel breeding and artificial reproduction in captivity have been achieved (Tanaka *et al.*, 2001; Kagawa *et al.*, 2005; Masuda *et al.*, 2012) but the proposed techniques have not yet become utilizable for commercial aquaculture due to reasons given in detail by Masuda *et al.* (2012). Thus, intensive eel farming is still fully dependent on natural eel reproduction and its effects can be easily assessed using official data of aquaculture production given by the Fisheries and Aquaculture Information and Statistics Service of FAO for *A. anguilla* and *A. japonica* (Figure 5a,b). An exponential increase of aquaculture production was observed in Europe after 1950 reaching a maximum around the year 2000 when a gradual decrease started (Figure 5a). This decrease may be attributed to two reasons: a) the decline of available glass eels and b) the increase of glass eel demand from markets outside Europe which enhanced glass eel export outside Europe. Ringuet *et al*. (2002) reported that the relatively abundant supplies of *A. anguilla* glass eels and their cheap price compared to *A. japonica* led many non-European eel farms to use *A. anguilla* glass eels at the end of the 1990s.

On the other hand, there was an unstoppable exponential increase of aquaculture production in Asia after 1950, which is currently two orders of magnitude higher than the one of Europe (Figure 5b). The continuous increase of Asian aquaculture production after 1990 (Figure 5b) raises questions about the origin of glass eels used, since the juvenile stocks of *A. japonica* declined to a minimum plateau after 1990 (Figure 4). This tremendous increase can only be explained by the use of imported glass eels of other species. This activity may also have enhanced the false labeling of eel products, which is already known to be a problem in Japan and China (Crook, 2010).

Unfortunately, FAO does not provide data about the use of *A. rostrata* in aquaculture production. The first reports of the *A. rostrata* glass eel trade to Asia are provided by Ooi *et al*. (1996). Significant information which indicates the role of glass eel trade for this species is given by Crook and Nakamura (2013) where the officially recorded imports of American eels to the Asian markets increased from 2 to 50 tons during the period of 1998-2011. ASMFC (2012), Cairns *et al.* (2014) and Stacey *et al*. (2014) provide important information about the natural populations and eel market of *A. rostrata* in North America.

[FIGURE 5]

The first evidence for the role of aquaculture in the decline of the European eel population can be provided by correlations between the total catches of Comacchio lagoon (Figure 3a) and aquaculture production in Europe (Figure 5a). For this reason, the values of aquaculture production, which correspond to the period 1950-1998, were correlated with 16 lag-time cases (from 0 to 15 years) of total catches from Comacchio (the case of 15-years lag-time corresponds to the period 1965-2013). The Spearman correlation ρ was maximized for 3-years lag-time with ρ=-0.949 (P<0.0001) (Figure 6a). Using the same procedure on CPUE data provided by Henderson *et al.* (2012), which concern yellow eel catches from Hinkley Point in Bridgwater Bay (Somerset, UK), the Spearman correlation was maximized for 2-years lag-time with ρ=-0.698 (P=0.002) (Figure 6b). Data on European aquaculture production after 1998 were not used in the above two cases in order to avoid inserting bias because aquaculture production started to decline after 2000 (Figure 5a) probably due to the intensification of glass eel export outside Europe.

For the case of mean glass eel yields provided by Feunteun (2002) only the data of 1974-1996 were used, because the mean data before 1974 correspond to fewer sites and present large variation. The Spearman correlation for Feunteun (2002) data was maximum for 0-years lag-time with ρ=-0.924 (P<0.0001) (Figure 6c). All the cases between 0 and 4 years lag-time showed values of ρ>0.8 with a tendency of gradual ρ decrease when the lag-time is increased. This finding is probably related to oscillations of aquaculture production caused by the degree of glass eel availability and price. For example, the price of glass eel drops when its availability is high and this fact may lead the aquaculture producers to release more product onto the market in order to achieve lower cost of production using the new cheaper glass eels.

[FIGURE 6]

It is also worth mentioning the additional problem of non-controlled or illegal trading for which there is official evidence from the early ‘90s (Kennedy and Fitch, 1990). Such activities have also been reported by Silfvergrip (2009), who cited a number of cases of illegal eel fishing and trade. Briand *et al.* (2008) estimated that the illegal trade of *A. anguilla* glass eel, derived from non-licensed fisherman and poachers, ranges between 20 to 40% of the total trade. They also noted that it is likely that the black market of *A. anguilla* glass eel will increase more in the near future due to their high price, caused by both the decline in natural stocks and the setting of export quotas associated with the listing of this species in CITES (https://www.cites.org/). The listing of only one eel species in CITES may also result in false declarations, as proved by two recent seizures of frozen eel declared as *A. japonica* (but in fact being a mixture of *A. anguilla* and *A. japonica*) reported by EU Member States (Crook, 2010). Additionally, it was found that world trade website platforms (due to legal issues information is not provided) are used for the trade of glass eels from Europe, America, Asia and Africa etc. The fact that African countries already participate in *A. anguilla* glass eel trade indicates that any control efforts from the European Union may fail since these countries are outside its jurisdiction. African countries may play the role of the stepping-stone for legalizing the trade of glass eels captured in the European coastlines of the Mediterranean.

Extremely interesting is also the fact that the probable initiation of the collapse of juvenile stocks appears first for *A. japonica* around 1968 or earlier, second for *A. anguilla* around 1978 and finally for *A. rostrata* around 1983, with interval periods of approximately 10 and 5 years, respectively (Figure 4). It is already known that the Asian aquaculture was, and is still the most demanding for glass eels while it has also been documented that after the 1970s, high amounts of other glass eel species were transferred to the Asian market and especially to Japan to expand aquaculture (Egusa, 1979; Briand *et al.*, 2008). In order to provide more robust evidence of the aquaculture contribution in global population collapse, a conservative estimate was undertaken of the global glass eel demands for aquaculture production, taking into account that: a) 200 g is the mean maximum weight of both male and female specimens reaching the market (Dekker, 2000; FAO, 2004), b) the mortality of eels after one year under aquaculture conditions ranges between 20-50% (Mezzani *et al.*, 1997), and c) the mortality of glass eels during catching, handling and transportation is more than 20% (Ciccotti *et al.*, 1999). Setting each one of the two mortalities at the minimum of 20% and using the total mean annual aquaculture production of Europe and Asia of the period 2008-2013, which approximates to ~255 thousands tones, the final number of glass eels required to support the current production is estimated at ~2 billions glass eels (97.8% of this estimate is to support the Asian aquaculture). This number is clearly a large underestimate, as it does not consider: a) the black market and the eel aquaculture production from other parts of the world and b) the part of the overall recruitment which finally reaches the natural habitats, and the remaining production related to fishing in the wild. If we consider a minimum weight per glass eel at 0.3 g (Dekker, 2000; FAO, 2004), the current glass eel demands for Europe and Asia exceed the value of 600 tones. Based on records of 1999, more than 300 tones of glass eels were caught by fishermen in Europe, of which 245 tones were caught by professional fishermen in France. Moreover, about 75 tones of glass eels were caught in France by non-professional fishermen (Castelnaud, 2002; Ringuet *et al.*, 2002).

Considering the above figures, approximately half of the global catch of glass eel seems to rely on *A. anguilla*. Since the Asian aquaculture is responsible for more than 97% of the global production, this indicates the existence of an extremely high, but still non-quantified, dependence on glass eel of other species; in particular *A. anguilla* (Zhang *et al.*, 1999; Katoh and Kobayashi, 2003; Sezaki et *al.*, 2005; Arai, 2014a) but also *A. rostrata* (Ooi *et al*., 1996; Crook and Nakamura, 2013). This dependence has been dramatically evidenced in the case of glass eel from France as widely reported by the media (http://news.bbc.co.uk/2/hi/europe/4432951.stm). Additional evidence in support of the hypothesis of glass eel being overharvested for aquaculture is a measurable increase of European eel recruitment after the application of the moratorium on the export of glass eel in 2010 (ICES, 2014; Briand et *al.*, 2015). Of course, it is still unknown if the activation of the moratorium has triggered the increase of illegal trade.

Oceonographic-climate changes

One of the most popular hypotheses to explain the global decline of eel populations was that oceanographic-climate changes have influenced the drift of eel larvae, resulting in lower recruitment. Tzeng *et al.* (2012) used long-term (1967–2008) glass eel catches to investigate climatic effects on the annual recruitment of *A. japonica* in Taiwan. The authors found significant correlations between the catches and climate indices, which describe ocean productivity and eddy activities. Their results showed that the variation of *A. japonica* recruitment is influenced by multi-timescale climate variability but their data of glass eel catches did not reveal any long-term recruitment collapse even though they exhibit high fluctuation (see Figure 1 in Tzeng *et al.*, 2012). The observed recruitment trends by the authors can not justify the trends of juvenile stocks of *A. japonica* presented in Figure 4. Aoyama *et al.* (2012) studied the status of *A. japonica* recruitment during 2009-2010 at the Sagani river estuary. Their observations demonstrated an unexpected late arrival of glass eels during early summer, which was considered a possible response to recent climate change, but there was no comparison with previous years in support of recruitment reduction.

In the case of European eel (*A. anguilla*) and American eel (*A. rostrata*), Bonhommeau *et al.* (2008) showed that indices of ocean circulation did not appear to explain variations in glass eel recruitment, while they found indications of bottom-up control of leptocephali survival-growth by primary production in the Sargasso Sea due to changes in oceanic temperature. Similar findings are reported by Knights (2003), Friedland *et al.* (2007) and Miller *at al.* (2009) stressing the effect of primary productivity in areas where leptocephali feed (for both *A. anguilla* and *A. rostrata*). Knights (2003) also indicated that concurrent gyre spin-up may affect major currents, slowing the oceanic migration which has probably enhanced starvation and predation losses. De Lafontaine *et al.* (2010), who analyzed the relationship between North Atlantic Oscillation index and catch per unit effort for the *A. rostrata*, found no significant relationships for any lag time

(0–20 years) while Dekker (2004), after analyzing the decline trends of *A. anguilla* in Lake Ijsselmeer (Netherlands), suggested that ocean and climate changes cannot explain the observed decline trends when taken individually. Pacariz *et al.* (2014) developed a model to simulate the passive drift of larvae from the spawning area in the Sargasso Sea to the European shelf for the period 1958–2008. The average drift time and latitudinal distribution of eel larval arrivals were explored for a range of constant depth levels and mortalities. The model showed that the proportion of eel larvae carried by the North-East Atlantic Current to landing sites of northern latitudes was greater before 1970, whereas there was an increase in the amount of larvae being entrained into the southbound current branches after this time (Pacariz *et al*., 2014). According to these results, the recruitment and stocks should be increased after 70s in the south-western coasts of Europe and in the Mediterranean.

Henderson *et al.* (2012) analyzed the abundance of both yellow eels of *A. anguilla* and *Conger conger* in Bridgwater Bay (Somerset, UK) for the period 1980-2010. The authors highlighted the population collapse of *A. anguilla* during the study period, while they also showed that this collapse was poorly correlated with the North Atlantic Oscillation Winter Index (NAOW, 4-month period of December-March). They also showed that the population of *C. conger*, which is a migratory fish with similar life cycle to *A. anguilla* (both species spawn in the Sargasso sea), did not show evidences of decline.

The above examples cast doubt on the hypothesis of climate-oceanographic changes as a stressor of the global recruitment collapse. In our opinion, this hypothesis is reliable to describe the high inter-annual and annual variation of recruitment, relocation of landing sites and changes of arrival periods. However, this hypothesis is not consistently able to explain the global populations collapse after 70s because it contradicts the explosion of aquaculture production which is a fact. The work of Henderson *et al.* (2012) provides probably the most robust proof, through the data of *C. conger*, that the oceanographic-climate change hypothesis is too weak to explain the large decline of *A. anguilla*. Climate changes were always part of earth's long life (Adams *et al.*, 1999) and eels have survived major oceanic and continental environmental changes over millions of years (Knights, 2009). It is quite surprising that the collapse of juvenile stocks of the three major eel species (Figure 4) took place in less than two decades.

Habitat loss

The data of area coverage for Comacchio lagoon (Table 1) provided a representative example of habitat loss but similar examples of eel habitat loss has also been observed worldwide, suggesting its inclusion in the list of global stressors. In the case of *A. anguilla*, a large portion of the suitable eel habitat has likely been lost during the second half of the past century, due to land reclamation, construction of barriers (e.g. dams) and other human-induced changes in the hydrological cycle (Kettle *et al*., 2011). Feunteun (2002) reports that a 50-90% of wetlands have been lost during the last century. The exact time over which this loss has taken place is not easy to determine but, on the basis of the available information, it occurred mostly between the 1950s and the 1990s in the northernmost parts of the eel distribution range (European coastlines in the Atlantic ocean and North-Baltic seas) and in a narrower time period (between the 1970s and the 1990s) in southern Europe and North Africa (Mediterranean sea) (Moriarty and Dekker, 1997; Bevacqua *et al*., 2015).

In the case of *A. japonica*, a very interesting study of eel habitat loss has been conducted by Chen *et al.* (2014). The authors analyzed Landsat imagery to assess the Japanese eel habitat reduction by human activities in 16 main rivers of East Asia, including Japan, Korea, Taiwan, and China. On average, 76.8% of the effective eel habitat area was lost in these 16 rivers in the period 1970–2010.

In the case of *A. rostrata*, representative paradigms of eel habitat loss are the cases of Lake Ontario and Champlain watersheds (Haro *et al*., 2000; de Lafontaine *et al*., 2010; Marsden and Langdon, 2012). Busch *et al.* (1998) estimated that up to 84% of river and stream habitats in east coast and eastern Lake Ontario basin, once available to migratory fishes (including *A. rostrata*), has been made inaccessible by dams. Marsden and Langdon (2012) also reported that there are 463 standing dams in the Champlain drainage in Vermont and that American eel migration was very likely impacted both by the dams and the targeted eel fishery associated with the dams. The effect of dams is expected to be extremely high in the case of *A. rostrata* since there are thousands dams in the rivers of east coast of USA (Graf, 1999), where eels can be found (Busch *et al.*, 1998; Geer, 2003; Phelps *et al*., 2014).

The effects of eel habitat loss and disturbance through habitat fragmentation, in-channel structures, hydropower facilities and water abstraction intakes (for irrigation, domestic, and industrial supply) can lead to reduction of the upstream colonization by glass eels (Piper *et al*., 2012) and delay of the downstream movement of silver eels, reduction of migration, injuries or direct mortality (Behrmann-Godel and Eckmann 2003; Gosset *et al.*, 2005; Durif and Elie, 2008; Calles *et al*., 2010; Piper *et al*., 2013). The elongated morphology and/or poor burst swimming capabilities of eels make them vulnerable at intake screens, pumps and turbines while the typical mortality in hydropower facilities has been estimated at between 15 and 38% per turbine encountered. Delay of fish at barriers also exacerbates pressures such as predation and diseases (Piper *et al*., 2013; Wright *et al*., 2015). Energy reserves, which are vital for successful oocyte production and oceanic migration of 5000-6000 km, may be depleted due to milling and searching while delayed at barriers (Behrmann-Godel and Eckmann, 2003; Travade *et al*., 2010; Piper *et al*., 2013).

Considering the above, habitat loss seems to contribute as a local and global factor of the decline in eel populations but special attention should be paid to the degree of its contribution. According to Moriarty and Dekker (1997) approximately half of the estimated surface of *A. anguilla* habitats include saline, closed and open waters which are not controlled by fisheries. Additionally, the majority of studies of eel habitat loss concern freshwater systems or lagoons associated with fisheries, which allow population assessment, without considering that eels can survive downstream of barriers located in open transitional fresh or saline environments. Eel populations may have been forced to live in such environments but their contribution to spawning and consequently recruitment is impossible of quantification although it could explain the existing sources of glass eels used in aquaculture.

Pollution

Eels are efficient bioaccumulators of toxic substances due to their high fat content and long life cycle (Feunteun, 2002) while their benthic lifestyle often leads to high exposure to contaminated sediments which increase the degree of bioaccumulation (Haro *et* *al*., 2000). Due to these characteristics, eels are considered ideal indicator species for bioaccumulation studies (Bruslé, 1994; Knights, 1997; Belpaire *et al*., 2008; Tabouret *et al*., 2011). Sublethal concentrations have many consequences on the physiology of eels. A wide range of contaminants such as PCBs, pesticides/herbicides, heavy metals and plastifiers disturb the reproductive hormonal cycles and therefore, reduce the breeding success (Feunteun, 2002; Robinet and Feunteun, 2002).

Robinet and Feunteun (2002) provided an extensive report on different pollutant types and body concentration ranges in both *A. anguilla* and *A. rostrata* while a more recent and more detailed report has been provided by Geeraerts and Belpaire (2010) only for *A. anguilla*. Robinet and Feunteun (2002) suggested that lipid mobilization during migration returns persistent lipophilic pollutants back into their circulation system, which are concentrated particularly in gonads at the crucial time of gametogenesis, reducing the quality of future spawners. Analysis of *A. rostrata* specimens by Dutil *et al*. (1987) and Hodson *et al.* (1994) showed that they may also suffer impaired osmoregulatory ability from direct exposure to water contaminated by pesticides. Fernández-Vega *et al*. (2015) found that herbicides led to higher mobilization of energy reserves on yellow *A.anguilla* leading to approximately 50% losses of reserves compared to control animals. Couillard *et al.* (1997) observed a relation between chemical contamination and pathological lesions in *A. rostrata*. The authors also suspected a relation between organochlorine contamination and oocyte diameter but this problem may only be temporary and may be diminished during migration since Palstra *et al.* (2007a) found that swimming for a period between 2-6 weeks significantly stimulated the gonadal mass and oocyte development in *A. anguilla*. Arai (2014b) showed that the concentrations of organochlorine compounds in the silver stage of *A. japonica* specimens were significantly higher than those in the yellow stage due to the higher lipid contents in the former versus the latter. The bioaccumulation was found to be proportional to the freshwater residence period. Thus, the chronic and intense exposure to pollutants may have serious impacts on eels such as growth rate, reduced fecundity, direct mortality, and reduced survival of offspring (Haro *et al*., 2000; Feunteun, 2002).

The aforementioned examples have led many scientists to propose the hypothesis of pollution as one of the main factors of eel populations decline (Robinet and Feunteun, 2002; Guimarães *et al*., 2009; Belpaire *et al*., 2011; Amilhat *et al*., 2014). On the other hand, a direct relationship between the reported effects and population decline has not yet been established (Byer *et al*., 2013; Giari *et al.* 2015). Knights (1997) suggested that there is no proof of significant mortality due to persistent pollutants except in some isolated accidents such as the Sandoz spill into the Rhine in 1986 which killed about 400 kg of eels (Meunier, 1994). The observed concentrations of bioaccumulated xenobiotics are most often below acute toxicity levels for eels, and Knights (1997) suggested that contamination, in particular by PCBs is not responsible for the decline of European eel. Despite the fact that the work of Knights (1997) is quite old compared to the current study, it was performed after the large decline of eels populations, which occurred after the 70s-80s. Additionally, Sancho *et al.* (1997) investigated the effects of Fenitrothion insecticide on the energy metabolism of *A. anguilla* and its recovery from intoxication. The authors found that most of the metabolic disorders did not persist after eels were allowed to recover in clean water for less than a week, which suggests that many non severe health implications due to pollution could be diminished during migration through swimming in the cleaner oceanic waters.

Parasitism

In the case of parasitism, many studies have shown that wide-spread infections of adult eels with *Anguillicoloides crassus* can reduce the potential migrating populations, and consequently the potential recruitment, since the infections reduce the swimming performance of the adult eels (Kennedy and Fitch, 1990; Sprengel and Luchtenberg, 1991; Moser *et al.*, 2001; Sures *et al.*, 2001; Kirk, 2003; Münderle *et al*., 2004; Palstra *et al*., 2007b; Wielgoss *et al*., 2008). Although some doubt exists over its precise origin (Lefebvre *et al.*, 2012), it is thought to be a natural parasite of the Japanese eel, which was spread to other eel species probably due to commercial movement of live eels (Hein *et al*., 2014). Our belief is that the appearance and spread of the parasite was coincidentally, rather than causally, related to the decline in European eels and it cannot be considered as a major cause of their declining populations. This can be supported by considering changes in *A. rostrata* populations, which showed a steep decline after 1983 (Figure 4), while the first documented observations of American eels infected by *A. crassus* started to appear at least ten years later (Fries *et al*., 1996; Ooi *et al*., 1996). It is worth mentioning that the observations of Ooi *et al*. (1996) on *A. crassus* infections concern *A. rostrata* eels which were imported to Taiwan as elvers from the United States and raised in a Taiwanese farm. This is also evidence that the Asian market had already established trade connections with America during the 90s for exploiting the American glass eels before the first observations of infected *A. rostrata* by *A. crassus*.

In recent years, it appears that the eel infections by *A. crassus* are not much of a problem either in Europe or in Asia, while a recent study by Dezfuli *et al.* (2014) showed that the levels of *A. crassus* in swim bladders of *A. anguilla* from Italian sites were significantly lower in prevalence and abundance in the coastal lagoons than in freshwater localities (rivers). Dezfuli *et al.* (2014) suggested that this parasite may have little impact in the decline of eel populations throughout Europe, because the contribution of lagoons to the eel migrating population is significantly higher than that of freshwater localities.

Taking into account all the existing findings from the literature, it is evident that eel species are under a combined threat from various stressors. Without diminishing the role of each global stressor, it seems that aquaculture plays a major and key role in the decline of natural stocks of all eel species. The high aquaculture production and the estimated high amount of glass eels caught and traded indicate that the spawning potential of eel populations has not collapsed. This is also proved by reports which still show high recruitment at specific locations (e.g. Shannon estuary in Ireland during 2014) (O'Connor, 2014) while there are still places with male-dominated populations (Bark *et al*., 2007) indicating high local population densities. The high number and biomass of glass eels needed to support the observed values of aquaculture production can also be used to question the IUCN Red List of species verifying the discussion made by Knights (2009) (http://www.glasseel.com/page17.html) which reported many errors, omissions and contradictions for the inclusion of eel species in the category of critically endangered species. At the same time, the role of the Convention on International Trade in Endangered

Species (CITES), which was developed in order to regulate the international trade, seems not to be fully updated and applicable in the case of eel species because glass eel and aquaculture derivatives are two completely different products. Moreover, the glass eel trade is an intermediate stage of aquaculture production and it is very difficult for it to be fully controlled.

CONCLUSIONS

The records of silver eel catches in the Comacchio Lagoon from 1781 to 2013 were used to discuss the combined effects of local and global stressors on the local population collapse. The discussion about the role of global stressors (aquaculture, oceonographic-climate changes, habitat loss, pollution, parasitism) was expanded to cover the three major species (*A. anguilla*, *A. japonica*, *A. rostrata*) providing an integrated view about their combined effects on eel populations decline. A more focused analysis on global aquaculture production showed that this factor plays a crucial role on the conditions of natural stocks.

The exponential increase of aquaculture production after the 70s is associated with a related expansion of the glass eel market since eels cannot reproduce in captivity. The conservative estimates of the amount of glass eels, which are needed to support the current aquaculture production, indicate the existence of an extremely large eel population farmed for human consumption. The consequent global demand for glass eel may also enhance illegal fishing, trade and false labeling of eel products, indicating that the case of eel is a global problem which can not be solved by one-sided interventions. For the case of *A. anguilla* these issues seem to have already reached a critical stage at which the European Council should intervene with stricter measures in cooperation with non-European countries since the glass eel trade has expanded at international and intercontinental level.

Supplementary Material

The supplementary material includes a) Table S.1 which provides the long time series of habitat loss and silver eel catches of the period 1781-2013 in Comacchio and b) Table S.2 which provides official data of FAO for eel aquaculture production during the period 1950-2013.

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References

Adams J, Maslin M, Thomas E. 1999. Sudden climate transitions during the Quaternary. *Progress in Physical Geography* **23**: 1-36.

Als TD, Hansen MM, Maes GE, Castonguay M, Riemann L, Aarestrup K, Munk P, Sparholt H, Hanel R, Bernatchez L. 2011. All roads lead to home: Panmixia of European eel in the Sargasso Sea. *Molecular Ecology* **20**: 1333-1346.

Amilhat E, Fazio G, Simon G, Manetti M, Paris S, Delahaut L, Farrugio H, Lecomte-Finiger R, Sasal P, Faliex E. 2014. Silver European eels health in Mediterranean habitats. *Ecology of Freshwater Fish* **23**: 49-64.

Aoyama J, Shinoda A, Yoshinaga T, Tsukamoto K. 2012. Late arrival of *Anguilla japonica* glass eels at the Sagami River estuary in two recent consecutive year classes: ecology and socio-economic impacts. *Fisheries Science* **78**: 1195-1204.

Arai T. 2014a. Do we protect freshwater eels or do we drive them to extinction? *SpringerPlus* **3**: Art.No.534

Arai T. 2014b. Variation in organochlorine accumulation in relation to the life history of the Japanese eel *Anguilla japonica*. *Marine Pollution Bulletin* **80**: 186-193.

Aschonitis VG, Castaldelli G, Lanzoni M, Merighi M, Gelli F, Giari L, Rossi R, Fano EA. 2015. A size-age model based on bootstrapping and Bayesian approaches to assess population dynamics of *Anguilla anguilla* L. in semi-closed lagoons. *Ecology of Freshwater Fish*, DOI: 10.1111/eff.12269 (in press).

ASMFC. 2012. American eel benchmark stock assessment. Atlantic States Marine Fisheries Commission, pp. 279.

Bark A, Williams B, Knights B. 2007. Current status and temporal trends in stocks of European eel in England and Wales. *ICES Journal of Marine Science* **64**: 1368-1378.

Behrmann-Godel J, Eckmann R. 2003. A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany. *Ecology of Freshwater Fish* **12**: 196-202.

Belpaire C, Goemans G, Geeraerts C, Quataert P, Parmentier K. 2008. Pollution fingerprints in eels as models for the chemical status of rivers. *ICES Journal of Marine Science* **65**: 1483-1491.

Belpaire CGJ, Goemans G, Geeraerts C, Quataert P, Parmentier K, Hagel P, De Boer J. 2009. Decreasing eel stocks: survival of the fattest? *Ecology of Freshwater Fish* **18**: 197-214.

Belpaire C, Geeraerts C, Evans D, Ciccotti E, Poole R. 2011. The European eel quality database: Towards a pan-European monitoring of eel quality. *Environmental Monitoring and Assessment* **183**: 273-284.

Bertram JG. 1873. *The Harvest of the Sea - Including sketches of fisheries & fisher folk*. Third edition. (source: http://www.electricscotland.com/lifestyle/sea/chapter3.htm)

Bevacqua D, Melià P, Crivelli AJ, De Leo GA, Gatto M. 2006. Timing and rate of sexual maturation of European eel in brackish and freshwater environments. *Journal of Fish Biology* (Supplement C) **69**: 200-208.

Bevacqua D, Melia P, Crivelli AJ, Gatto M, De Leo GA. 2007. Multi-objective assessment of conservation measures for the European eel (*Anguilla anguilla*): an application to the Carmargue lagoons. *ICES Journal of Marine Science* **64**: 1483-1490.

Bevacqua D, Melià P, Crivelli AJ, Gatto M, De Leo GA, Haro A, Smith KL. 2009. Assessing management plans for the recovery of the European eel: A need for multi-objective analyses. *American Fisheries Society Symposium* **69**: 637-647.

Bevacqua D, Capoccioni F, Melià P, Vincenzi S, Pujolar JM, Leo GA, Ciccotti E. 2012. Fishery-induced selection for slow somatic growth in European eel. *PLoS ONE* **7(5)**: e37622.

Bevacqua D, Melià P, Gatto M, De Leo GA. 2015. A global viability assessment of the European eel. *Global Change Biology* **21**: 3323-3335.

Bonhommeau S, Chassot E, Rivot E. 2008. Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso sea. *Fisheries Oceanography* **17**: 32-44.

Bonhommeau S, Castonguay M, Rivot E, Sabatié R, Le Pape O. 2010. The duration of migration of Atlantic *Anguilla* larvae. *Fish and Fisheries* **11**: 289-306.

Briand C, Bonhommeau S, Castelnaud G, Beaulaton L. 2008. An appraisal of historical glass eel fisheries and markets: landings, trade routes and future prospect for management. In: The Institute of Fisheries Management Annual Conference 2007. Ed. C. Moriarty. Wesport, Ireland.

Briand C, Beaulaton L, Chapon PM, Drouineau H, Lambert P. 2015. Eel density analysis (EDA 2.2) - Estimation de l'échappemement en anguilles argentées (*Anguilla anguilla*) en France. Repport of EPTB-Vilaine, ONEMA-INRA, IRSTEA, pp. 95.

Bruslé J. 1994. L'anguille Européenne *Anguilla anguilla*, un poisson sensible aux stress environnementaux et vulnerable à diverses atteintes pathogènes. *Bulletin Français de la Pêche et de la Pisciculture* **335**: 237-260

Busch WDN, Lary SJ, Castilione CM, McDonald RP. 1998. Distribution and availability of Atlantic coast freshwater habitats for American eel *(Anguilla rostrata).* Administrative Report #98-2. U.S. Fish and Wildlife Service, Amherst, NY.

Byer JD, Lebeuf M, Alaee MR, Stephen B, Trottier S, Backus S, Keir M, Couillard CM, Casselman J, Hodson PV. 2013. Spatial trends of organochlorinated pesticides, polychlorinated biphenyls, and polybrominated diphenyl ethers in Atlantic *Anguillid* eels. *Chemosphere* **90**: 1719-1728.

Cagnon C, Lauga B, Karama S, Mouches C. 2011. Temporal genetic variation in European eel *Anguilla anguilla* (Linnaeus, 1748): A fine scale investigation in the Adour estuary. *Marine Biology Research* **7**: 515-519.

Cairns DK, Chaput G, Poirier LA, Avery TS, Castonguay M, Mathers A, Casselman JM, Bradford RG, Pratt T, Verreault G, Clarke K, Veinott G, Bernatchez L. 2014. Recovery potential assessment for the American eel (*Anguilla rostrata*) for eastern Canada: life history, distribution, reported landings, status indicators, and demographic parameters. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/134. xiv + 157 p.

Calles O, Olsson IC, Comoglio C, Kemp PS, Blunden L, Schmitz M, Greenberg LA. 2010. Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. *Freshwater Biology* **55**: 2167-2180.

Carieri A, Cavallini G, Plazzi IM, Rossi R. 1992. Struttura della popolazione di anguille gialle ed argentine nelle Valli di Comacchio (Biennio 1989-1990). *Annali dell'Università di Ferrara* **2**: 1-24. (in italian)

Castaldelli G, Aschonitis V, Lanzoni M, Gelli F, Rossi R, Fano EA. 2014. An update of the length–weight and length–age relationships of the European eel (*Anguilla*

anguilla, Linnaeus 1758) in the Comacchio Lagoon, northeast Adriatic Sea, Italy. *Journal of Applied Ichthyology* **30**: 558-559.

Castelnaud G. 2002. *Caractéristiques de la pêcherie civellière du golfe de Gascogne*. Contrat européen n°99/023. IFREMER, CEMAGREF, Groupement de Bordeaux, pp. 32.(in french)

Chen J-Z, Huang S-L, Han Y-S. 2014. Impact of long-term habitat loss on the japanese eel *Anguilla japonica*. *Estuarine, Coastal and Shelf Science* **151**: 361-369.

Clevestam PD, Ogonowski M, Sjoberg NB, Wickström H. 2011. Too short to spawn? Implications of small body size and swimming distance on successful migration and maturation of the European eel *Anguilla anguilla*. *Journal of Fish Biology* **78**: 1073-1089.

Ciccotti E, Busilacchi S, Cataudella S. 1999. La pesca delle ceche di anguilla, tra conservazione ed uso responsabile di questa specie migratrice. *Laguna* **6**: 94-128. (in italian)

Cognetti G, De Angelis CM, Orlando E. 1975. Attuale situazione, ecologica delle valli di Comaccio. *Quaderni di Italia Nostra* **12**: 1-55. (in italian)

Colombo G, Rossi R. 1978. Environmental influences on growth and sex ratio in different eel populations (*Anguilla anguilla L.*) of Adriatic coasts. In: *Physiology and behaviour of marine organisms* (eds D.S. McLusky, A.J. Berry), Pergamon Press, Oxford, pp. 313-320.

Couillard CM, Hodson PV, Castonguay M. 1997. Correlations between pathological changes and chemical contamination in American eels, *Anguilla rostrata*, from St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1916-1927.

Crema R, Prevedelli D, Valentini A, Castelli A. 2000. Recovery of the macrozoobenthic community of the Comacchio lagoon system (Northern Adriatic Sea). *Ophelia* **52**: 143-152.

Crook V. 2010. *Trade in Anguilla species, with a focus on recent trade in European Eel A. anguilla*. TRAFFIC report prepared for the European Commission.

Crook V, Nakamura M. 2013. Assessing supply chain and market impacts of a CITES listing on *Anguilla* species. *Traffic Bulletin* **25**: 24-30.

Dannewitz J, Maes GE, Johansson L, Wickström H, Volckaert FAM, Järvi T. 2005. Panmixia in the European eel: a matter of time. *Proceedings of the Royal Society of London Series B* **272**: 1129-1137.

Dekker W. 2000. A procrustean assessment of the European eel. *ICES Journal of Marine Science* **57**: 938-947.

Dekker W. 2003. Status of the European eel stock and fisheries. In: *Eel biology* (eds K. Aida, K. Tsukamoto, K. Yamauchi), Springer-Verlag, Tokyo, pp. 237-254.

Dekker W, Casselman JM. 2014. The 2003 Québec Declaration of Concern about Eel declines – 11 years later: Are eels climbing back up the slippery slope? *Fisheries* **39**: 613-614.

Dekker W. 2004. What caused the decline of the Lake IJsselmeer eel stock after 1960? *ICES Journal of Marine Science* 61: 394-404.

De Lafontaine Y, Gagnon P,, Côté B. 2010. Abundance and individual size of American eel (*Anguilla rostrata*) in the St. Lawrence River over the past four decades. *Hydrobiologia* **647**:185–198

De Leo GA, Gatto M. 1995. A size and age structured model of the European eel (*Anguilla anguilla* L.). *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1351-1367.

De Leo GA, Gatto M. 1996. Trends in vital rates of the European eel: evidence for density dependence? *Ecological Applications* **6**: 1281-1294.

De Leo GA, Melià P, Gatto M, Crivelli AJ. 2009. Eel population modeling and its application to conservation management. *American Fisheries Society Symposium* **58**: 327-345.

Dezfuli BS, Giari L, Castaldelli G, Lanzoni M, Rossi R, Lorenzoni M, Kennedy CR. 2014. Temporal and spatial changes in the composition and structure of helminth component communities in European eels *Anguilla anguilla* in an Adriatic coastal lagoon and some freshwaters in Italy. *Parasitology Research* **113**: 113-120.

Durif CMF, Elie P. 2008. Predicting downstream migration of silver eels in a large river catchment based on commercial fishery data. *Fisheries Management and Ecology* **15**: 127-137.

Dutil J-D, Besner M, McCormick SD. 1987. Osmoregulatory and ionoregulatory changes and associated mortalities during the transition of maturing American eels to a marine environment. *American Fisheries Society Symposium* **1**: 175-190.

Egusa S. 1979. Notes on the culture of the European eel (*Anguilla anguilla* L.) in Japanese eel-farming ponds. *Rapports et Procès-Vérbaux des Reunions* **174**: 51-58.

European Union (EU). 2007. Council Regulation (EC) No. 1100/2007 "Establishing measures for the recovery of the stock of European eel".

FAO. 2004. Captured-based aquaculture. The fattening of eels, groupers, tunas and yellowtails. FAO, Rome, pp. 308.

FAO. 2009. Global exports and imports *Anguilla* spp. 1997–2007. FISHSTAT Fisheries Commodities Production and Trade Database: http://www.fao.org/fishery/statistics/global-commodities-production/en.

Fernández-Vega C, Sancho E, Ferrando MD. 2015. Energy reserves mobilization in the yellow eel as herbicide exposure effect. *Chemosphere* **135**: 94-100.

Feunteun E. 2002. Management and restoration of European eel population (*Anguilla anguilla*): An impossible bargain. *Ecological Engineering* **18**: 575-591.

Friedland KD, Miller MJ, Knights B. 2007. Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. *ICES Journal of Marine Science* **64**: 519-530.

Friedlander E. 1872. *La pesca nelle lagune di Comacchio*. Firenze, 100 pp. (in italian)

Fries LT, Williams DJ, Johnson SK. 1996. Occurrence of *Anguillicola crassus*, an exotic parasitic swimbladder nematode of eels, in the southeastern United States. *Transactions of the American Fisheries Society* **125**: 794-797.

Gatto M, Rossi R. 1979. A method for estimating mortalities and abundances of the Valli di Comacchio eels. *Memorie dell' Instituto Italiano di Idrobiologia* **37**: 107-114.

Gatto M, Laniado E, Rossi R. 1982. The management of eels in the Valli di Comacchio lagoon. *Oceanologica Acta* **4**: 303-307.

Geer PJ. 2003. Distribution, relative abundance, and habitat use of American eel *Anguilla rostrata* in the Virginia portion of the Chesapeake Bay. *American Fisheries Society Symposium* **33**: 101-115.

Geeraerts C, Belpaire C. 2010. The effects of contaminants in European eel: A review. *Ecotoxicology* **19**: 239-266.

Giari L, Guerranti C, Perra G, Lanzoni M, Fano EA, Castaldelli G. 2015. Occurrence of perfluorooctanesulfonate and perfluorooctanoic acid and histopathology in eels from north Italian waters. *Chemosphere* **118**: 117-123.

Graf WL. 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research **35**: 1305-1311.

Gosset C, Travade F, Durif C, Rives J, Elie P. 2005. Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications* **21**: 1095-1105.

Guimarães L, Gravato C, Santos J, Monteiro LS, Guilhermino L. 2009. Yellow eel (*Anguilla anguilla*) development in NW portuguese estuaries with different contamination levels. *Ecotoxicology* **18**: 385-402.

Han Y-S, Tzeng W-N. 2006. Use of the sex ratio as a means of resource assessment for the japanese eel *Anguilla japonica*: A Case Study in the Kaoping River,Taiwan. *Zoological Studies* **45**: 255-263.

Haro A, Richkus W, Whalen K, Hoar A, Busch W-D, Lary S, Brush T, Dixon D. 2000. Population decline of the American eel: Implications for research and management. *Fisheries* **25**: 7-16.

Henderson PA, Plenty SJ, Newton LC, Bird DJ. 2012. Evidence for a population collapse of European eel (*Anguilla anguilla*) in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom* **92**: 843-851.

Hein JL, Arnott SA, Roumillat WA, Allen DM, de Buron I. 2014. Invasive swimbladder parasite *Anguillicoloides crassus*: infection status 15 years after discovery in wild populations of American eel *Anguilla rostrata*. *Diseases of Aquatic Organisms* **107**: 199-209.

Hodson PV, Castonguay M, Couillard CM, Desjardins C, Pelletier E, McLeod R. 1994. Spatial and temporal variations in chemical contamination of the American eels, *Anguilla rostrata* captured in the estuary of the St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 464-478.

ICES. 2014. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eel, 3-7 November 2014, Rome, Italy. ICES CM 2014/ACOM:18. 203 pp.

IES – International Eel Symposium. 2003. Worldwide decline of eel resources necessitates immediate action-Quebec declaration of concern. *Fisheries Forum* **28**: 28-30.

Jacoby D, Gollock M. 2014. *Anguilla anguilla*. In: *IUCN 2014. IUCN Red List of Threatened Species. Version 2014.1*. (last accessed on 27 June 2014).

Kagawa H, Tanaka H, Ohta H, Unuma T, Nomura K. 2005. The first success of glass eel production in the world: basic biology on fish reproduction advances new applied technology in aquaculture. *Fish Physiology and Biochemistry* **31**: 193-199.

Katoh M, Kobayashi M. 2003. Aquaculture and genetic structure in the Japanese eel *Anguilla japonica*. *UJNR Technical Report* **30**: 87-92.

Katselis GN, Moutopoulos DK, Dimitriou EN, Koutsikopoulos C. 2013. Long-term changes of fisheries landings in enclosed gulf lagoons (Amvrakikos gulf, W Greece): Influences of fishing and other human impacts Estuarine. *Coastal and Shelf Science* 131, 31-40.

Kennedy CR, Fitch DJ. 1990. Colonization, larval survival and epidemiology of the nematode Anguillicola crassus, parasitic in the eel, *Anguilla anguilla*, in Britain. *Journal of Fish Biology* **36**: 117-131.

Kettle AJ, Vøllestad LA, Wibig J. 2011. Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? *Fish and Fisheries* **12**: 380-411.

Kirk RS. 2003. The impact of *Anguillicola crassus* on European eels. *Fisheries Management and Ecology* **10**: 385-394.

Knights B. 1997. Risk assessment and management of contamination of eels (*Anguilla* spp.) by persistent xenobiotic organochlorine compounds. *Chemistry and Ecology* **13**: 171-212.

Knights B. 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of *anguillid* eels of the Northern Hemisphere. *The Science of the Total Environment* **310**: 237-244.

Knights B. 2009. Comments on IUCN red list of threatened species citation for *Anguilla anguilla* (L.). Discussion on Freyhof J. and Kottelat, M. 2008. *Anguilla anguilla*. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. (http://www.glasseel.com/page17.html)

Krueger W, Oliveira, K. 1999. Evidence for environmental sex determination in the American eel, *Anguilla rostrata*. *Environmental Biology of Fishes* **55**: 381-389.

Lefebvre F, Wielgoss S, Nagasawa K, Moravec F. 2012. On the origin of *Anguillicoloides crassus*, the invasive nematode of anguillid eels. *Aquatic Invasions* **7**: 443-453.

Lintas C, Hirano J, Archer S. 1998. Genetic variation of the European eel (*Anguilla anguilla*). *Molecular Marine Biology and Biotechnology* **7**: 263-269.

Marsden JE, Langdon RW. 2012. The history and future of Lake Champlain's fishes and fisheries. *Journal of Great Lakes Research* **38**: 19-34.

Martino A, Syväranta J, Crivelli A, Cereghin R, Santoul F. 2011. Is European catfish a threat to eels in southern France? *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**: 276-281.

Masuda Y, Imaizumi H, Oda K, Hashimoto H, Usuki H, Teruya K. 2012. Artificial completion of the Japanese eel, *Anguilla japonica*, life cycle: challenge to mass production. *Bulletin of Fisheries Research Agency* **35**: 111-117.

Mezzani GC, Corbari L, Rossi R. 1997. Situazione e prospettive dell’allevamento intensivo di *anguilla* in Europa. *Il Pesce - Acquacoltura* **4**: p. *23*. (in italian)

Meunier FJ. 1994. Growth data of eel (*Anguilla anguilla* L.) in the Alsacian part of the river Rhine. *Bulletin Français de la Pêche et de la Pisciculture* **335**: 133-144.

Miller MJ, Kimura S, Friedland KD, Knights B, Kim H, Jellyman DJ, Tsukamoto K. 2009. Review of ocean-atmospheric factors in the Atlantic and Pacific Oceans influencing spawning and recruitment of *Anguillid* eels. *American Fisheries Society Symposium* **69**: 231-249.

Moriarty C, Dekker W. 1997. Management of the European eel. *Fisheries Bulletin* **15**: pp.110.

Moser ML, Patrick WS, Crutchfield JUJr. 2001. Infection of American eels, *Anguilla rostrata*, by an introduced nematode parasite, Anguillicola crassus, in North Carolina. *Copeia* **3**: 848-853.

Munari CS, Moduno F, Ghion G. 2003. Recovery of the macrobenthic communities in the valli di Comacchio, Northern Adriatic, Italy. *Oceanolica Acta* **26**: 67-75.

Munari CS, Rossi R, Mistri M. 2005. Temporal trends in macrobenthos community structure and redundancy in a shallow coastal lagoon (Valli di Comacchio, Northern Adriatic Sea). *Hydrobiologia* **550**: 95-104.

Münderle M, Sures B, Taraschewski H. 2004. Influence of *Anguillicola crassus* (Nematoda) and *Ichthyophthirius multifiliis* (Ciliophora) on swimming activity of European eel *Anguilla anguilla*. *Diseases of Aquatic Organisms* **60**: 133-139.

O'Connor W. 2014. Millions of glass eels in the Shannon estuary. source: http://europeaneel.com/2014/04/03/shannon-estuary-glass-eels/

Ooi H-K, Wang W-S, Chang H-Y, Wu C-H, Lin C-C, Hsieh M-T. 1996. An epizootic of anguillicolosis in cultured American eels in Taiwan. *Journal of Aquatic Animal Health* **8**: 163-166.

Pacariz S, Westerberg H, Björk G. 2014. Climate change and passive transport of European eel larvae. *Ecology of Freshwater Fish* **23**: 86-94.

Palstra A, Curiel D, Fekkes M, de Bakker M, Székely C, van Ginneken V, van den Thillart G. 2007a. Swimming stimulates oocyte development in European eel. *Aquaculture* **270**: 321-332.

Palstra AP, Heppener DFM, van Ginneken VJT, Székely C, van den Thillart GEEJM. 2007b. Swimming performance of silver eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*. *Journal of Experimental Marine Biology and Ecology* **352**: 244-256.

Phelps QE, Ridings JW, Herzog DP. 2014. American eel population characteristics in the upper Mississippi River. *American Midland Naturalist* **171**: 165-171.

Piper AT, Wright RM, Kemp PS. 2012. The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering* **44**, 329-336.

Piper AT, Wright RM, Walker AM, Kemp PS. 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. *Ecological Engineering* **57**: 88-96.

Pratt TC, Bradford RG, Cairns DK, Castonguay M, Chaput G, Clarke KD, Mathers A. 2014. Recovery potential assessment for the American eel (*Anguilla rostrata*) in eastern Canada: functional description of habitat. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/132. v + 49 p.

Prchalová M, Kubečka J, Říha M, Čech M, Jůza T, Ketelaars HAM, Kratochvíl M, Mrkvička T, Peterka J, Vašek M, Wagenvoort AJ. 2013. Eel attacks - A new tool for assessing European eel (*Anguilla anguilla*) abundance and distribution patterns with gillnet sampling. *Limnologica* **43**: 194-202.

Ringuet S, Muto F, Raymakers C. 2002. Eels: their harvest and trade in Europe and Asia. *TRAFFIC Bulletin* **19**: 80-106.

Robinet T, Feunteun E. 2002. Sublethal effects of exposure to chemical compounds: A cause for the decline in Atlantic eels? *Ecotoxicology* **11**: 265-277.

Roncarati A, Melotti P, Mordenti O, Gennari L. 1997. Influence of stocking density of European eel (*Anguilla anguilla*, L.) elvers on sex differentiation and zootechnical performances. *Journal of Applied Ichthiology* **13**: 131-136.

Rossi R. 1979. An estimate of the production of the eel population (*Anguilla anguilla* L.) in the Valli di Comacchio (Po Delta) in the period 1974-76. *Bollettino di Zoologia* **46**: 217-223.

Rossi R., Cataudella S. 1998. La produzone ittica nelle valle di Comacchio. *Laguna (Ferrara)* **5**: 67-83. (in italian)

Sancho E, Ferrando MD, Andreu E. 1997. Sublethal effects of an organophosphate insecticide on the European eel, *Anguilla anguilla*. *Ecotoxicology and Environmental Safety* **36**: 57-65.

Sezaki K, Itoi S, Watabe S. 2005. A simple method to distinguish two commercially valuable eel species in Japan *Anguilla japonica* and *A. anguilla* using polymerase chain reaction strategy with a species-specific primer. *Fisheries Science* **71**: 414-421.

Silfvergrip AMC. 2009. CITES identification guide to the freshwater eels (*Anguillidae*). Report 5943, Version 1.1. March 2009. The Swedish Environmental Protection Agency, Stockholm.

Simon J. 2007. Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). *ICES Journal of Marine Science* **64**: 1414-1422.

Sorokin YuI, Bilio M. 1981. Studies of microbial sulfate reduction and microplankton in fish culture ponds of the Comacchio region. Biology of the Sea, Vladivostok **2**: 50-58 (in Russian).

Sorokin YuI, Sorokin Pyu, Gnes A. 1996a. Structure and functioning of anthropogenically transformed Comacchio lagoon ecosystem. *Marine Ecology Progress Series* **133**: 57-71.

Sorokin YuI., Dallocchio F, Gelli F, Pregnolato L. 1996b. Phosphorus metabolism in anthropogenically transformed lagoon ecosystems: Comacchio lagoons (Ferrara, Italy). *Journal of Sea Research* **35**: 243-260.

Sorokin Y, Zakuskina O. 2010. Features of the Comacchio ecosystem transformed during persistent bloom of picocyanobacteria. *Journal of Oceanography* **66**: 373-387.

Sprengel G, Luchtenberg H. 1991. Infection by endoparasites reduces maximum swimming speed of European smelt *Osmerus eperlanus* and European eel *Anguilla anguilla*. *Diseases of Aquatic Organisms* **11**: 31-35.

Stacey JA, Pratt TC, Verreault G, Fox MG. 2014. A caution for conservation stocking as an approach for recovering Atlantic eels. *Aquatic Conservation: Marine and Freshwater Ecosystems* (in press). doi: 10.1002/aqc.2498

Sures B, Knopf K, Kloas W. 2001. Induction of stress by the swimbladder nematode *Anguillicola crassus* in European eels, *Anguilla anguilla*, after repeated experimental infection. *Parasitology* **123**: 179-184.

Tabouret H, Bareille G, Mestrot A, Caill-Milly N, Budzinski H, Peluhet L, Prouzet P, Donard OFX. 2011. Heavy metals and organochlorinated compounds in the European eel (*Anguilla anguilla*) from the Adour estuary and associated wetlands (France). *Journal of Environmental Monitoring* **13**: 1446-1456.

Tanaka H, Kagawa H, Ohta H. 2001. Production of leptocephali of Japanese eel (*Anguilla japonica*) in captivity. *Aquaculture* **201**: 51-60.

Tesch FW. 2003. *The eel*. Willey-Blackwell Publishing, Oxford, UK, pp.416.

Travade F, Larinier M, Subra S, Gomes P, De-Oliveira E. 2010. Behaviour and passage of European silver eels (*Anguilla anguilla*) at a small hydropower plant during their downstream migration. *Knowledge and Management of Aquatic Ecosystems* **398**: 1-19.

Tzeng WN, Han YS, He JT. 2002. The sex ratios and growth strategies of wild and captive Japanese eels *Anguilla japonica*. In: *Developments in understanding fish growth*. (eds B. Small and D. MacKinlay). International Congress on the Biology of Fish. Vancouver, Canada: Univ. of British Columbia, pp. 25-42.

Tzeng W-N, Tseng Y-H, Han Y-S, Hsu C-C, Chang C-W, Di Lorenzo E, Hsieh C-H. 2012. Evaluation of multi-scale climate effects on annual recruitment levels of the Japanese eel, *Anguilla japonica*, to Taiwan. *PLoS ONE* **7(2)**: e30805.

van Ginneken VJT, Maes GE. 2005. The European eel (*Anguilla anguilla,* Linnaeus), its lifecycle, evolution and reproduction: a literature review. *Reviews in Fish Biology and Fisheries* **15**: 367-398.

Westin L. 1998. The spawning migration of European silver eel (*Anguilla anguilla* L.) with particular reference to stocked eel in the Baltic. *Fisheries Research* **38**: 257-270.

Wickström H, Sjöberg NB. 2014. Traceability of stocked eels – the Swedish approach. *Ecology of Freshwater Fish* **23**: 33-39.

Wielgoss S, Taraschewski H, Meyer A, Wirth T. 2008. Population structure of the parasitic nematode *Anguillicola crassus*, an invader of declining North Atlantic eel stocks. *Molecular Ecology* **17**: 3478-3495.

Wright GV, Wright RM, Kemp PS. 2015. Impact of tide gates on the migration of adult European eels, *Anguilla anguilla*. *Estuaries and Coasts* **38**: 2031-2043.

Zhang H, Mikawa N, Yamada Y, Horie N, Okamura A, Uto T, Tanaka S, Motonobu T. 1999. Foreign eel species in the natural waters of Japan detected by polymerase chain reaction of mitochondrial cytochrome b region. *Fisheries Science* **65**: 684-686.

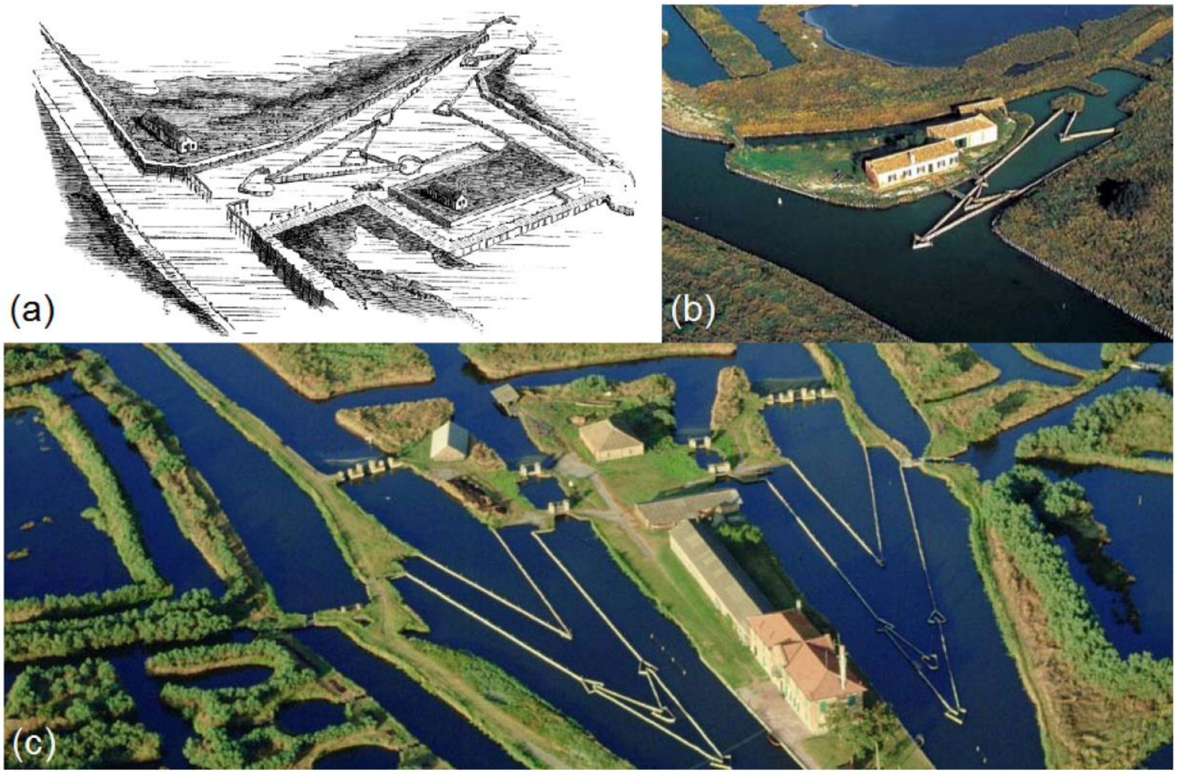

Figure 1. Structure characteristics of the lavorieri (a) in the lagoons of North-eastern Italy during the eightieth century according to drawings reported by Bertram (1873) (source: http://www.electricscotland.com/lifestyle/sea/chapter3.htm), (b) this is probably the lavorieri of Bertram drawing as it is nowdays after the reclamation works made during the nineteenth century (source: http://w3.quipo.it/libriliberi/l%20Comacchio%20Lavorieri1.JPG) and c) a panoramic view of a system of channels, ponds and lavorieri as they are nowadays (source: http://www.ferrarateraeacqua.it/it/parco-del-delta-del-po/cercatori/gallery-parco-del-delta-del-po/valli-e-lavorieri/image_ftaslider).

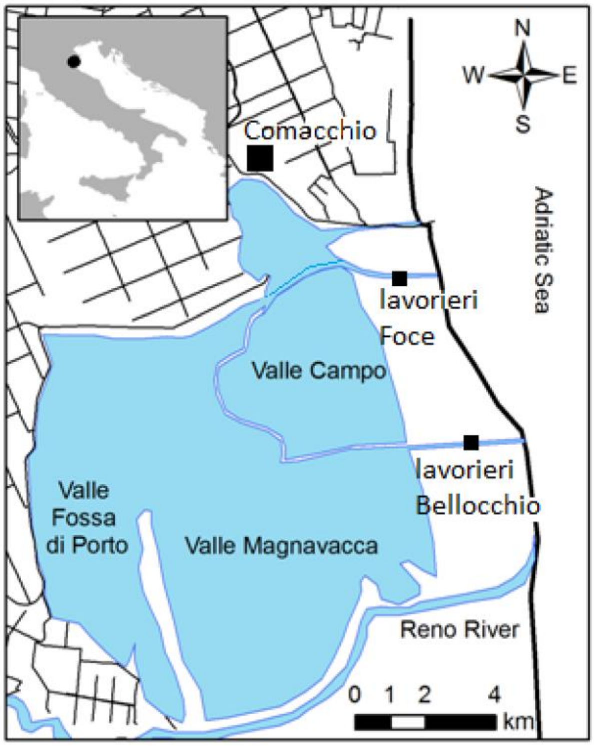

Figure 2. The boundaries of Comacchio Lagoon as they were formed after 1982 (44^{o} 36´ N, 12^{o} 10´ E).

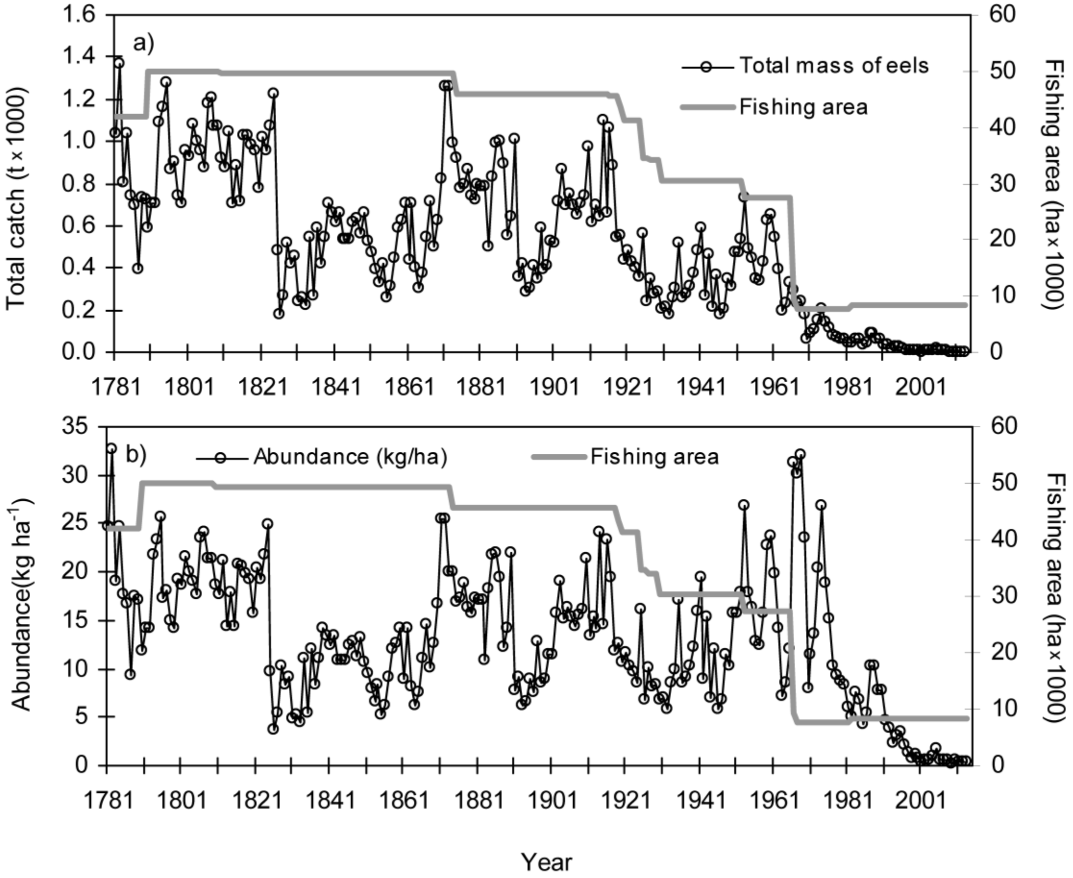

Figure 3. Eel fishing area coverage (ha) together with the (a) annual variation of silver eel catches (t×1000) and (b) abundance of silver eels (kg ha^{-1}) in the Comacchio lagoon for the period 1781-2013.

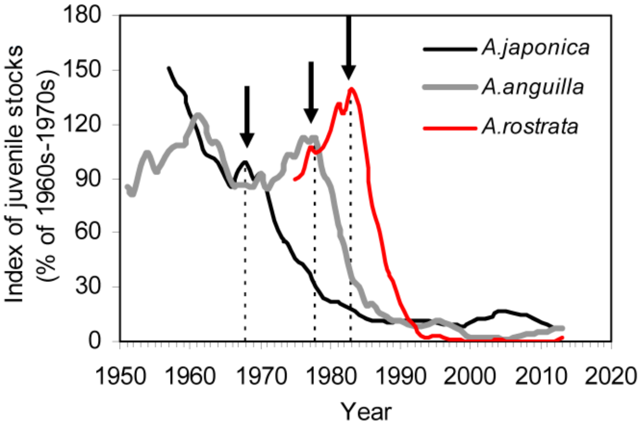

Figure 4. Time trends in juvenile abundance of the major eel stocks of the world (from Dekker and Casselman, 2014). The arrows and vertical lines indicate the probable year of the collapse initiation.

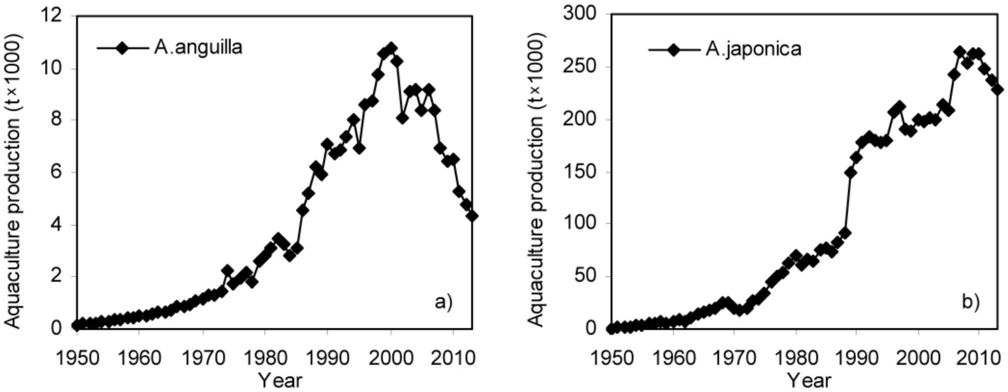

Figure 5. Official data of FAO for eel aquaculture production (a) in Europe for *A.anguilla* and (b) in Asia for *A.japonica* for the period 1950-2013 (source: Fisheries and Aquaculture Information and Statistics Service of FAO – database of FishStatJ software v.2.12.4 for fishery time series, last date of data release: March of 2015).

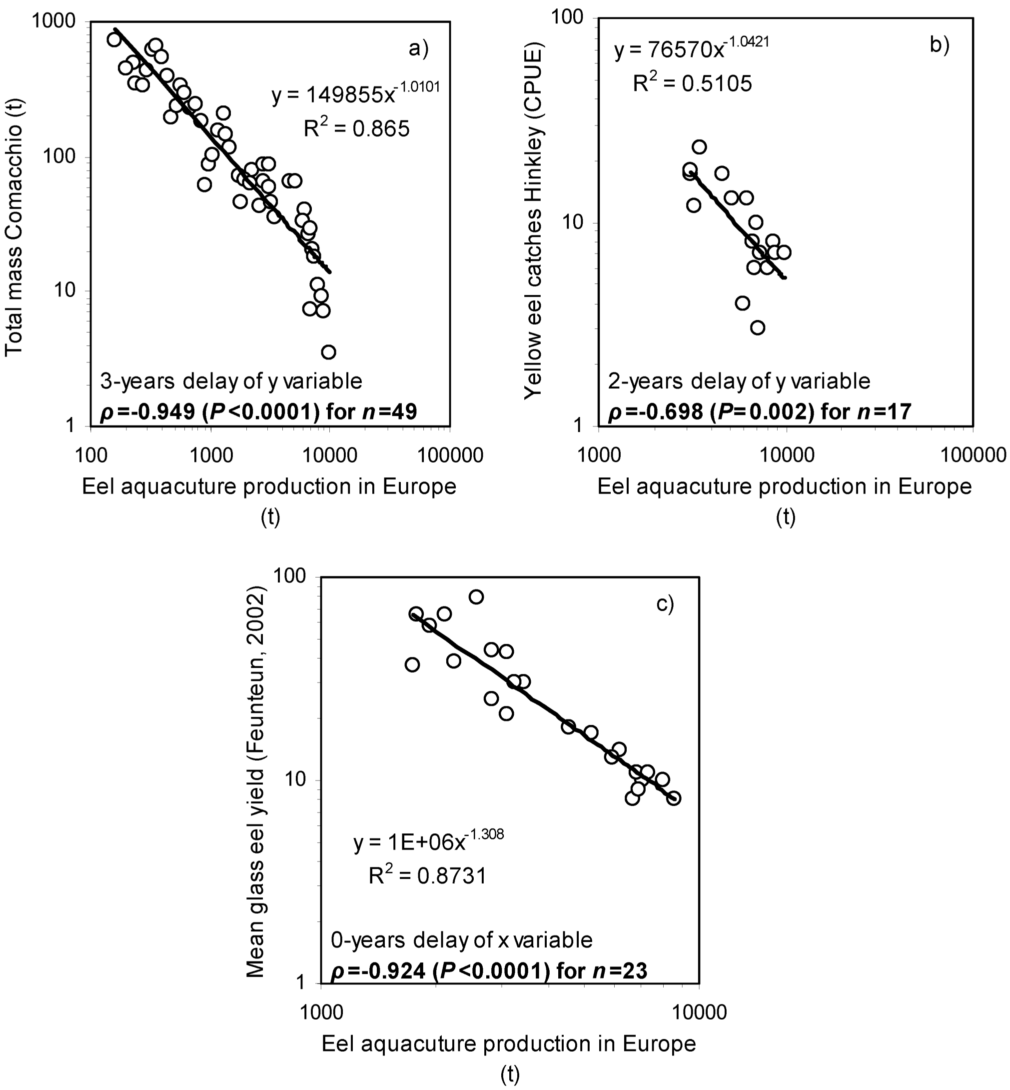

Figure 6. Correlations between eel aquaculture production in Europe versus a) total eel catches from Comacchio lagoon, b) CPUE values of yellow eel catches from Hinkley Point in Bridgwater Bay (Somerset, UK) provided by Henderson *et al.* (2012), c) mean glass eel yields from sites located in the west European coastlines estimated by Feunteun (2002).

TABLES

Table 1. Gain/loss of fishing area coverage during the period 1781-2013 in the Comacchio lagoon.

Year	Region (local nomenclature of different sub-basins of the lagoonal complex)	Fishing area (ha) gain[+]/loss[-]
1790	Scattered parts in the peripheral territory	+8000
1810	Ucceliera, Almentieri and Montalbano	-500
1874	Gallare	-3730
1916	Part of Ponti	-130
1919	Trebba	-2140
1920	Ponti and Raibosola	-2150
1925	Mantello	-6750
1927	Bosco and Poazzo	-500
1930	Isola and Volano	-3750
1953	Pega, Rillo and Zavelea	-2900
1966	Mezzano, Fattibello and Spavola	-17950
1967	Ravennate	-1870
1982	Part of Ravennate	+840
Total habitat gain/loss (ha) for the period 1781-2013		-33530

Table 2. Recorded mortality events in the Comacchio lagoon.

Year	Conditions
1787	Frost and ice coverage
1790	Hypersalinity
1822	Hypersalinity
1823	Hypersalinity
1824	Hypersalinity
1825	Hypersalinity + Frost and ice coverage
1826	Hypersalinity
1830	Frost and ice coverage
1834	Hypersalinity
1843	Flooding of Reno river
1850	Frost and ice coverage
1851	Frost and ice coverage
1859	Flooding of Reno river
1862	Flooding of Reno river
1869	Frost and ice coverage
1872	Hypersalinity
1877	Mortality from unidentified reasons
1879	Frost and ice coverage
1882	Mortality from unidentified reasons
1883	Mortality from unidentified reasons
1887	Mortality from unidentified reasons
1890	Frost and ice coverage + Mortality from undefined reasons
1891	Mortality from unidentified reasons
1892	Hypersalinity + Frost and ice coverage
1893	Hypersalinity
1896	Flooding of Reno river
1917	Hypersalinity
1918	Frost and ice coverage
1925	Frost and ice coverage
1927	Hypersalinity + Frost and ice coverage
1970	Outbreak of infection by *Argulus foliaceus*
1982	Mortality from unidentified reasons*
1985	Frost and ice coverage + Mortality from undefined reasons*

* Probably due to picocyanobacteria blooms (see text).

Table S.1 Historical records of habitat (fishing area) variation and silver eel catches in the Comacchio lagoon for the period 1781-2013.

Year	Fishing area	Mass of silver eels	Abundance
	ha	tn	kg/ha
1781	42000	1033.2	24.600
1782	42000	1369.2	32.600
1783	42000	802.2	19.100
1784	42000	1037.4	24.700
1785	42000	739.2	17.600
1786	42000	701.4	16.700
1787	42000	394.8	9.400
1788	42000	735.0	17.500
1789	42000	722.4	17.200
1790	50000	590.0	11.800
1791	50000	710.0	14.200
1792	50000	710.0	14.200
1793	50000	1090.0	21.800
1794	50000	1165.0	23.300
1795	50000	1280.0	25.600
1796	50000	865.0	17.300
1797	50000	905.0	18.100
1798	50000	745.0	14.900
1799	50000	705.0	14.100
1800	50000	960.0	19.200
1801	50000	930.0	18.600
1802	50000	1080.0	21.600
1803	50000	1005.0	20.100
1804	50000	955.0	19.100
1805	50000	880.0	17.600
1806	50000	1180.0	23.600
1807	50000	1205.0	24.100
1808	50000	1070.0	21.400
1809	50000	1070.0	21.400
1810	49500	920.7	18.600
1811	49500	876.15	17.700
1812	49500	1049.40	21.200
1813	49500	707.85	14.300
1814	49500	881.10	17.800
1815	49500	712.80	14.400
1816	49500	1029.60	20.800
1817	49500	1024.65	20.700
1818	49500	980.10	19.800
1819	49500	955.35	19.300
1820	49500	782.10	15.800
1821	49500	1014.75	20.500
1822	49500	955.35	19.300
1823	49500	1074.15	21.700
1824	49500	1227.60	24.800
1825	49500	480.15	9.700
1826	49500	183.15	3.700
1827	49500	272.25	5.500
1828	49500	514.80	10.400
1829	49500	415.80	8.400
1830	49500	455.40	9.200
1831	49500	237.60	4.800
1832	49500	257.40	5.200
1833	49500	222.75	4.500
1834	49500	549.45	11.100
1835	49500	267.30	5.400
1836	49500	594.00	12.000
1837	49500	415.80	8.400
1838	49500	549.45	11.100
1839	49500	702.90	14.200
1840	49500	663.30	13.400
1841	49500	613.80	12.400
1842	49500	663.30	13.400
1843	49500	539.55	10.900
1844	49500	534.60	10.800
1845	49500	539.55	10.900
1846	49500	618.75	12.500
1847	49500	638.55	12.900
1848	49500	559.35	11.300
1849	49500	658.35	13.300
1850	49500	524.70	10.600
1851	49500	470.25	9.500
1852	49500	391.05	7.900
1853	49500	326.70	6.600
1854	49500	415.80	8.400
1855	49500	257.40	5.200
1856	49500	311.85	6.300
1857	49500	450.45	9.100
1858	49500	594.00	12.000
1859	49500	628.65	12.700
1860	49500	702.90	14.200
1861	49500	440.55	8.900
1862	49500	702.90	14.200
1863	49500	400.95	8.100
1864	49500	306.90	6.200
1865	49500	376.20	7.600
1866	49500	544.50	11.000
1867	49500	717.75	14.500
1868	49500	504.90	10.200
1869	49500	623.70	12.600
1870	49500	826.65	16.700
1871	49500	1262.25	25.500
1872	49500	1257.30	25.400
1873	49500	990.00	20.000
1874	45770	919.977	20.100
1875	45770	778.090	17.000
1876	45770	796.398	17.400
1877	45770	865.053	18.900
1878	45770	746.051	16.300
1879	45770	723.166	15.800
1880	45770	796.398	17.400
1881	45770	782.667	17.100
1882	45770	782.667	17.100
1883	45770	498.893	10.900
1884	45770	833.014	18.200
1885	45770	993.209	21.700
1886	45770	1002.363	21.900
1887	45770	892.515	19.500
1888	45770	558.394	12.200
1889	45770	645.357	14.100
1890	45770	1006.940	22.000
1891	45770	357.006	7.800
1892	45770	421.084	9.200
1893	45770	283.774	6.200
1894	45770	302.082	6.600
1895	45770	411.930	9.000
1896	45770	347.852	7.600
1897	45770	585.856	12.800
1898	45770	389.045	8.500
1899	45770	411.930	9.000
1900	45770	526.355	11.500
1901	45770	521.778	11.400
1902	45770	718.589	15.700
1903	45770	869.630	19.000
1904	45770	695.704	15.200
1905	45770	750.628	16.400
1906	45770	700.281	15.300
1907	45770	654.511	14.300
1908	45770	709.435	15.500
1909	45770	741.474	16.200
1910	45770	974.901	21.300
1911	45770	613.318	13.400
1912	45770	700.281	15.300
1913	45770	645.357	14.100
1914	45770	1103.057	24.100
1915	45770	663.665	14.500
1916	45640	1063.412	23.300
1917	45640	885.416	19.400
1918	45640	543.116	11.900
1919	43500	552.450	12.700
1920	41350	442.445	10.700
1921	41350	483.795	11.700
1922	41350	430.040	10.400
1923	41350	401.095	9.700
1924	41350	355.610	8.600
1925	34600	560.520	16.200
1926	34600	238.740	6.900
1927	34100	344.410	10.100
1928	34100	279.620	8.200
1929	34100	286.440	8.400
1930	30350	209.415	6.900
1931	30350	212.450	7.000
1932	30350	179.065	5.900
1933	30350	261.010	8.600
1934	30350	303.500	10.000
1935	30350	518.985	17.100
1936	30350	261.010	8.600
1937	30350	279.220	9.200
1938	30350	315.640	10.400
1939	30350	373.305	12.300
1940	30350	482.565	15.900
1941	30350	588.790	19.400
1942	30350	270.115	8.900
1943	30350	464.355	15.300
1944	30350	212.450	7.000
1945	30350	364.200	12.000
1946	30350	179.065	5.900
1947	30350	209.415	6.900
1948	30350	345.990	11.400
1949	30350	315.640	10.400
1950	30350	476.495	15.700
1951	30350	476.495	15.700
1952	30350	540.230	17.800
1953	27450	735.660	26.800
1954	27450	491.355	17.900
1955	27450	450.180	16.400
1956	27450	351.360	12.800
1957	27450	340.380	12.400
1958	27450	430.965	15.700
1959	27450	625.860	22.800
1960	27450	653.310	23.800
1961	27450	546.255	19.900
1962	27450	389.790	14.200
1963	27450	194.895	7.100
1964	27450	236.070	8.600
1965	27450	332.145	12.100
1966	9500	297.350	31.300
1967	7630	229.663	30.100
1968	7630	244.923	32.100
1969	7630	179.305	23.500
1970	7630	61.040	8.000
1971	7630	86.982	11.400
1972	7630	103.768	13.600
1973	7630	156.415	20.500
1974	7630	205.247	26.900
1975	7630	143.444	18.800
1976	7630	115.213	15.100
1977	7630	79.352	10.400
1978	7630	70.959	9.300
1979	7630	66.381	8.700
1980	7630	64.092	8.400
1981	7630	45.780	6.000
1982	8470	43.197	5.100
1983	8470	64.372	7.600
1984	8470	58.443	6.900
1985	8470	35.574	4.200
1986	8470	45.738	5.400
1987	8470	88.088	10.400
1988	8470	87.241	10.300
1989	8470	66.066	7.800
1990	8470	65.219	7.700
1991	8470	39.809	4.700
1992	8470	33.033	3.900
1993	8470	20.328	2.400
1994	8470	26.257	3.100
1995	8470	29.645	3.500
1996	8470	17.787	2.100
1997	8470	11.011	1.300
1998	8470	7.300	0.862
1999	8470	9.100	1.074
2000	8470	7.070	0.835
2001	8470	3.526	0.416
2002	8470	4.796	0.566
2003	8470	4.841	0.572
2004	8470	7.434	0.878
2005	8470	15.311	1.808
2006	8470	5.0745	0.599
2007	8470	5.3340	0.630
2008	8470	4.6758	0.552
2009	8470	2.3830	0.281
2010	8470	4.3594	0.515
2011	8470	3.8115	0.450
2012	8470	3.7774	0.446
2013	8470	3.7860	0.447

Table S.2 Eel aquaculture production in the period 1950-2013 (source: Fisheries and Aquaculture Information and Statistics Service of FAO – database of FishStatJ software v.2.12.4 for fishery time series, last date release: March of 2015, http://www.fao.org/fishery/statistics/software/fishstatj/en#downlApp)

Country	Species (ASFIS species)	Aquaculture area (FAO major fishing area)	Environment (Environment)	Unit	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
China	Japanese eel	Asia - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Taiwan Province of China	Japanese eel	Asia - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	70	70	70	73	70	72	110	106	158	236	569	1550	1933	3851	6843
Taiwan Province of China	Japanese eel	Pacific, Northwest	Brackishwater	t	...	...	...	...	...	...	...	...	20	20	20	47	20	22	20	17	17	13	17	20	22	21	52
Japan	Japanese eel	Asia - Inland waters	Freshwater	t	339	1006	2261	2459	3139	3641	4901	5917	6737	5944	6403	8351	7804	10085	13609	16021	17015	19605	23819	23445	16936	14460	13631
Malaysia	Japanese eel	Asia - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Republic of Korea	Japanese eel	Asia - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	9	147	6
Total Japanese eel					**339**	**1006**	**2261**	**2459**	**3139**	**3641**	**4901**	**5917**	**6827**	**6034**	**6493**	**8471**	**7894**	**10179**	**13739**	**16144**	**17190**	**19854**	**24405**	**25020**	**18900**	**18479**	**20532**
Estonia	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Tunisia	European eel	Africa - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Algeria	European eel	Africa - Inland waters	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Spain	European eel	Atlantic, Northeast	Marine	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Portugal	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Bulgaria	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Romania	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Sweden	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ukraine	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Tunisia	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Morocco	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Morocco	European eel	Africa - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Lithuania	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
France	European eel	Europe - Inland waters	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
France	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Denmark	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Belgium	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Czech Republic	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Portugal	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Serbia and Montenegro	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Serbia and Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Malta	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ireland	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Greece	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Greece	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Greece	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Hungary	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Yugoslavia SFR	European eel	Mediterranean and Black Sea	Brackishwater	t	10	10	20	20	30	30	40	40	50	50	50	60	60	60	65	80	90	85	70	80	90	85	38
Netherlands	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Denmark	European eel	Atlantic, Northeast	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Denmark	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Spain	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Spain	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Germany	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	-	-	-
Italy	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Italy	European eel	Europe - Inland waters	Freshwater	t	105	151	127	154	170	186	204	224	246	270	297	326	358	393	431	473	520	570	626	687	750	850	900
Italy	European eel	Mediterranean and Black Sea	Brackishwater	t	45	65	54	66	73	80	88	96	106	116	127	140	153	168	185	203	223	244	268	295	323	355	390
Total European eel					**160**	**226**	**201**	**240**	**273**	**296**	**332**	**360**	**402**	**436**	**474**	**526**	**571**	**621**	**681**	**756**	**833**	**899**	**964**	**1062**	**1163**	**1290**	**1328**
Dominican Republic	American eel	America, North - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

continues….

continues….

Country	Species (ASFIS species)	Aquaculture area (FAO major fishing area)	Environment (Environment)	Unit	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
China	Japanese eel	Asia - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	60000	67672	80582	91655	100000	110000	120000
Taiwan Province of China	Japanese eel	Asia - Inland waters	Freshwater	t	11612	11788	13517	18716	21988	21269	26398	33058	27578	28852	30382	36621	36845	35975	42489	51577	48008	55169	52708	50956	39675	33109	25094
Taiwan Province of China	Japanese eel	Pacific, Northwest	Brackishwater	t	42	39	58	22	13	16	31	16	17	5	1	...	...	...	...	...	...	647	2933	67	284	255	452
Japan	Japanese eel	Asia - Inland waters	Freshwater	t	15038	17321	20715	26251	27630	32106	36781	36618	33984	36642	34489	38030	39568	36520	36994	39558	39704	38855	39013	36299	33860	29431	29131
Malaysia	Japanese eel	Asia - Inland waters	Freshwater	t	-	-	7	10	14	19	25	34	50	63	85	115	156	211	286	388	526	613	443	1572	2824	3354	2969
Republic of Korea	Japanese eel	Asia - Inland waters	Freshwater	t	36	85	150	100	100	150	303	200	211	233	347	448	732	557	2441	602	1046	1146	2386	3148	2451	2586	2345
Total Japanese eel					**26728**	**29233**	**34447**	**45099**	**49745**	**53560**	**63538**	**69926**	**61840**	**65795**	**65304**	**75214**	**77301**	**73263**	**82210**	**92125**	**149284**	**164102**	**178065**	**183697**	**179094**	**178735**	**179991**
Estonia	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-
Tunisia	European eel	Africa - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	144	...	151	...	...	18
Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Algeria	European eel	Africa - Inland waters	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	44	34	82	69	72	53	46	22	1	0	22	20
Spain	European eel	Atlantic, Northeast	Marine	t	-	-	-	-	...	...	...	...	...	...	...	15	20	26	29	31	61	125	98	105	175	134	153
Portugal	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	10	495	3	3	3
Bulgaria	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Romania	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-	-	-	-	-
Sweden	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	2	12	41	51	90	203	166	157	141	171	169	160	139
Ukraine	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1
Tunisia	European eel	Mediterranean and Black Sea	Marine	t	...	...	2	9	17	25	33	41	50	58	66	...	...	...	...	...	...	...	...	...	...	...	...
Morocco	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	60	35	41	68	85	55
Morocco	European eel	Africa - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Lithuania	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-
France	European eel	Europe - Inland waters	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	400	400	400	400	400	400	60
France	European eel	Europe - Inland waters	Freshwater	t	-	-	2	5	5	10	10	15	20	20	25	30	60	237	400	770	410	410	410	400	410	410	120
Denmark	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Belgium	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0	30	30	125	125	125	125	125
Czech Republic	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	4	4
Portugal	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	-	4	15	40	50	60	60	590	566	501	6	267	260	127	502	976	7
Serbia and Montenegro	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Serbia and Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	8	2	4
Malta	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-	-	-	3	3
Ireland	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-	-	-	-	-
Greece	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	42
Greece	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	6	4	18	50	45	94	145	337	341	366
Greece	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-	-	251
Hungary	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	115	90	39	98	73	33	...	...	...
Yugoslavia SFR	European eel	Mediterranean and Black Sea	Brackishwater	t	50	49	35	53	43	56	38	44	35	56	39	44	52	48	49	19	10	8	5	-	-	-	-
Netherlands	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	20	100	200	200	350	500	550	520	1250	1487	1535
Denmark	European eel	Atlantic, Northeast	Marine	t	...	...	...	...	...	...	...	...	...	...	...	-	-	-	-	-	-	-	-	-	-	-	-
Denmark	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	16	30	120	160	300	620	706	900	900	900	900	950
Spain	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	5	5	5	5	0	0	0	0	61
Spain	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Germany	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Italy	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	50	35	10	10	10	10
Italy	European eel	Europe - Inland waters	Freshwater	t	1000	1540	1200	1300	1450	1190	1750	1900	2100	2300	2000	1800	2000	2500	2700	3000	2500	2500	2000	1950	1985	2080	2280
Italy	European eel	Mediterranean and Black Sea	Brackishwater	t	428	660	516	566	621	510	749	822	902	991	1088	800	800	800	800	1000	1200	1550	1550	1305	1005	910	710
Total European eel					**1478**	**2249**	**1755**	**1933**	**2136**	**1791**	**2580**	**2826**	**3122**	**3465**	**3270**	**2821**	**3117**	**4560**	**5187**	**6209**	**5900**	**7101**	**6708**	**6880**	**7349**	**8052**	**6917**
Dominican Republic	American eel	America, North - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1	0	0	0	0	49	38

continues….

continues….

Country	Species (ASFIS species)	Aquaculture area (FAO major fishing area)	Environment (Environment)	Unit	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
China	Japanese eel	Asia - Inland waters	Freshwater	t	147316	155739	146317	144740	140067	135078	141721	139344	153828	154703	189754	207332	205325	214698	213811	208266	212464	206026
Taiwan Province of China	Japanese eel	Asia - Inland waters	Freshwater	t	24970	22232	17126	16399	28146	34032	34790	35027	33235	27862	23648	24570	20964	18888	19317	10521	2244	1904.27
Taiwan Province of China	Japanese eel	Pacific, Northwest	Brackishwater	t	93	105	115	144	2334	128	72	89	245	619	190	252	74	156	44	13.8	-	-
Japan	Japanese eel	Asia - Inland waters	Freshwater	t	28595	24171	21971	23211	24118	23123	21112	21526	21540	19495	20583	22241	20952	22406	20543	22006	17377	14204
Malaysia	Japanese eel	Asia - Inland waters	Freshwater	t	3635	6620	2250	1500	1980	2359	69	0	...	...	...	-	-	-	-	-	-	-
Republic of Korea	Japanese eel	Asia - Inland waters	Freshwater	t	1599	2287	2213	2037	2725	2644	2968	4312	5205	5575	7966	10557	6480	6621	7902	7185	4259	5149
Total Japanese eel					**206208**	**211154**	**189992**	**188031**	**199370**	**197364**	**200732**	**200298**	**214053**	**208254**	**242141**	**264952**	**253795**	**262769**	**261617**	**247992**	**236344**	**227283**
Estonia	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	5	15	7	40	40	45	47	30	20.3	2	...	...
Tunisia	European eel	Africa - Inland waters	Freshwater	t	28	10	15	17	20	11	9	7	28	19	18	20	15	15	10	3	2	3
Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	...	...	...	...	...	...	...	...	...	...	9	9	9	9	9	9	...	...
Algeria	European eel	Africa - Inland waters	Brackishwater	t	17	17	22	15	23	32	33	16	16	15	7	15	11.73	14.2	4.22	-	0.41	0
Spain	European eel	Atlantic, Northeast	Marine	t	189	255	217	238	302	259	13	10	16	3	2	2	-	1.58	2.1	0.96	0.9	-
Portugal	European eel	Atlantic, Northeast	Brackishwater	t	5	4	6	2	4	7	4	5	2	1	2	1	1	1	0.3	0.6	0.8	1
Bulgaria	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	0.24	-	-	...
Romania	European eel	Europe - Inland waters	Freshwater	t	-	-	1	-	-	-	-	-	-	-	1	1	...	...	0.1	...	...	...
Sweden	European eel	Europe - Inland waters	Freshwater	t	161	189	204	222	273	200	167	170	158	222	191	175	172	...	...	90	93	92
Ukraine	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Tunisia	European eel	Mediterranean and Black Sea	Marine	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Morocco	European eel	Mediterranean and Black Sea	Brackishwater	t	29	21	27	28	35	28	24	24	30	27	...	...	...	...	...	...	...	...
Morocco	European eel	Africa - Inland waters	Freshwater	t	...	100	40	60	20	12	23	40	38	50	50	100	50	60	110	68	80	340
Lithuania	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	11	12	...	...	...	...
France	European eel	Europe - Inland waters	Brackishwater	t	40	40	6	6	6	0	...	...	...	...	-	-	...	...	...	...	...	...
France	European eel	Europe - Inland waters	Freshwater	t	120	120	36	36	36	42	...	...	...	...	-	-	...	...	...	...	...	...
Denmark	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	...	43	44	720	...	-	-	-	...	...	...	...
Belgium	European eel	Europe - Inland waters	Freshwater	t	125	125	125	100	100	100	75	50	25	25	-	-	-	...	...	...	...	...
Czech Republic	European eel	Europe - Inland waters	Freshwater	t	3	3	1	1	1	1	1	1	0	1	1	0	0	0	-	-	1	-
Portugal	European eel	Europe - Inland waters	Freshwater	t	16	12	7	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-
Serbia and Montenegro	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	7	7	-	-	-	-	-	-	-	-
Serbia and Montenegro	European eel	Mediterranean and Black Sea	Brackishwater	t	2	2	3	7	5	7	4	6	9	9	-	-	-	-	-	-	-	-
Malta	European eel	Mediterranean and Black Sea	Marine	t	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ireland	European eel	Europe - Inland waters	Freshwater	t	-	-	20	25	1	...	...	...	...	...	...	-	-	-	-	-	-	-
Greece	European eel	Mediterranean and Black Sea	Marine	t	22	21	28	40	-	1	0	1	76	1	1	8	3	-	-	1.7	2	...
Greece	European eel	Europe - Inland waters	Freshwater	t	467	454	588	428	540	591	332	458	429	261	290	365	399	341	320	208.5	320	300
Greece	European eel	Mediterranean and Black Sea	Brackishwater	t	95	70	65	50	62	47	101	85	52	110	94	81	87	87	52	79	80	50
Hungary	European eel	Europe - Inland waters	Freshwater	t	...	...	...	...	...	73	36	11	11	5	-	-	0	-	-	-	-	-
Yugoslavia SFR	European eel	Mediterranean and Black Sea	Brackishwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Netherlands	European eel	Europe - Inland waters	Freshwater	t	2800	2443	2634	3228	3700	4000	3868	4200	4500	4000	5000	4000	3700	2800	3000	2050	1800	1800
Denmark	European eel	Atlantic, Northeast	Marine	t	-	-	-	-	-	-	145	103	104	71	918	742	82	1021.8	1000	800	661.1	...
Denmark	European eel	Europe - Inland waters	Freshwater	t	1400	1689	2468	2717	2674	2100	1021	1866	1675	882	781	872	813	636.9	532	354	399.85	498
Spain	European eel	Europe - Inland waters	Freshwater	t	60	80	130	145	109	80	390	306	380	385	382	461	520	475	412	427	373.2	305
Spain	European eel	Atlantic, Northeast	Brackishwater	t	...	...	...	...	...	...	21	23	28	39	19	16	14	11.8	8.5	6.15	-	-
Germany	European eel	Europe - Inland waters	Freshwater	t	-	-	-	-	150	150	150	150	322	329	567	440	447	385	398	660	460	471
Italy	European eel	Mediterranean and Black Sea	Marine	t	50	100	-	-	-	-	4	-	-	-	-	14	151.71	160	...	...	...	...
Italy	European eel	Europe - Inland waters	Freshwater	t	2500	2500	2800	2950	2450	2300	1618	1350	1034	955	656	898	392.8	400	383	470.5	450	450
Italy	European eel	Mediterranean and Black Sea	Brackishwater	t	450	500	350	250	250	200	77	200	186	177	151	88	6.23	7	264.19	39.1	50	50
Total European eel					**8579**	**8755**	**9793**	**10566**	**10761**	**10241**	**8121**	**9140**	**9177**	**8354**	**9180**	**8353**	**6932.47**	**6468.28**	**6525.95**	**5269.51**	**4774.26**	**4360**
Dominican Republic	American eel	America, North - Inland waters	Freshwater	t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-