Università degli Studi di Ferrara

DOTTORATO DI RICERCA IN
" BIOLOGIA EVOLUZIONISTICA E AMBIENTALE"

CICLO XXVIII

Assessment of European eel (*Anguilla anguilla* L.) population dynamics in the Comacchio lagoon using mathematical models and the role of global factors in population collapse

SETTORE SCIENTIFICO DISCIPLINARE BIO/07

TESI DI DOTTORATO DI
VASILEIOS ASCHONITIS

COORDINATORE DEL DOTTORATO	TUTOR
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Anni 2013/2015

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Dedicated to my wife Niki

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1 General background, objectives, structure and scientific derivatives of the thesis

1.1 General background

The eel (*Anguilla* spp.) is a catadromous and semelparous species which spends most of its life as yellow eel in fresh water, brackish and coastal habitats. When reaching maturity, it metamorphoses to silver eel and migrates to the ocean in order to spawn and die. The larvae (leptocephalus) drift back to the coastlines using oceanic currents and metamorphose into the transparent glass eels, which go upstream in fresh water habitats (process called "recruitment"), where they change to elvers setting the initiation of the yellow eel stage (Tesch, 2003) (Fig.1.1a).

The three most important eel species are the European eel (*Anguilla anguilla*, Linnaeus 1758), Japanese eel (*Anguilla japonica*, Temminck & Schlegel 1846) and American eel (*Anguilla rostrata*, Lesueur 1817). Both *A. anguilla* and *A. rostrata* spawn in the Sargasso Sea (Atlantic Ocean), which is bounded by a system of currents commonly called North Atlantic Gyre. Using the currents, the larvae of *A. anguilla* return back to the coastlines of Europe and north-western Africa, while the larvae of *A. rostrata* return back to the east coasts of north America in order to continue their biological cycle (Knights, 2003; van Ginneken and Maes, 2005). *A. japonica* spawns in the north-western Pacific Ocean near the seamounts of the West Mariana Ridge. These seamounts are located in the westward flow of the North Equatorial Current while *A. japonica* elvers return back to east coasts of Asia (Japan, Korea, China etc) (Tsukamoto et al., 2003).

Long-term records of juvenile stocks for the three aforementioned eel species indicate a severe reduction during the last four decades (Dekker and Casselman, 2014) (Fig.1.1b). Reasons suggested for the populations decline include habitat loss, pollution, parasitism, increased migration barriers, changes in oceanographic conditions, reduction of available prey, exotic fish invasions, overexploitation of fisheries (Kennedy and Fitch, 1990; van Ginneken and Maes, 2005; Knights, 2003; Belpaire et al., 2009; Bonhommeau et al., 2010; Kettle et al., 2011; Martino et al., 2011; Chen et al., 2014).

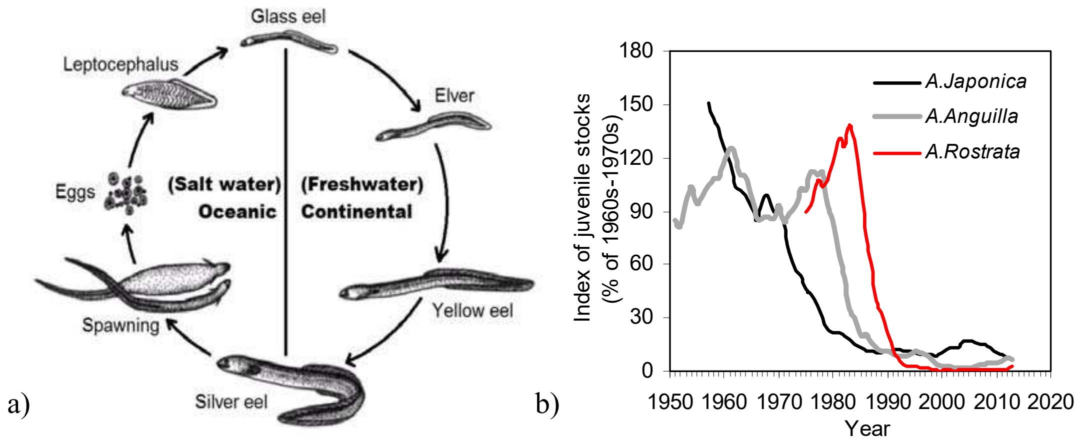

Fig.1.1 *a) Life cycle of eel species (Anguilla spp.) b) Time trends in juvenile abundance of the major eel stocks of the world (from Dekker and Casselman, 2014).*

Eel species are traded on a global scale for consumption. Smoked and stewed yellow or silver eels are favoured in Europe and North America, marinated grilled silver eels are favoured in Japan, while glass eels are also consumed in Spain, France and Italy (Ringuet et al., 2002; Briand et al., 2008). Therefore, eels of all life stages are exploited by commercial fisheries for consumption (Crook, 2010).

European glass eels are caught in southwest Europe and northwest Africa, mainly along the Atlantic coasts of France, Morocco, Portugal, Spain and UK. Yellow eels of *A. anguilla* are caught throughout the species's distributional area and silver eels mostly in northern Europe. Local fisheries are supplemented through the regular release into natural waters of juveniles (Crook, 2010). This is a form of low intensity farming, however, it is commonly referred to as "restocking" and it must not be confused with conservation restocking programs that aim to increase the escapement of silver eels (Dekker, 2000). In addition, wild juvenile eels are also caught and used in aquaculture production or farming. Eel farming, which is responsible for over 90% of all eel production worldwide (FAO, 2009), is capture-based. Prior to 1990, farming of eel species was almost exclusively carried out using species of local provenance. *A. anguilla* was farmed in Europe where Italy, Denmark and the Netherlands were the main producers, *A. japonica* was farmed in Asia (Japan, China, Korea etc) while *A. rostrata* was farmed in north America (Canada and USA) (Crook and Nakamura, 2013; ICES, 2014). After 1990, the regime of eel trade change completely and became an industry of global significance (Ringuet et al., 2002; Crook, 2010).

As concerns *A. anguilla*, its continental stock is widely distributed in Europe (Fig.1.2), supports small-scale fisheries in rural areas, and provides main incomes for over 25,000 people. Within the continental life stages, the *A. anguilla* population is fragmented over a multitude of small-scaled inland water bodies, and assessments of the local stocks have been accomplished in for a small fraction of the overall distribution (Dekker, 2004).

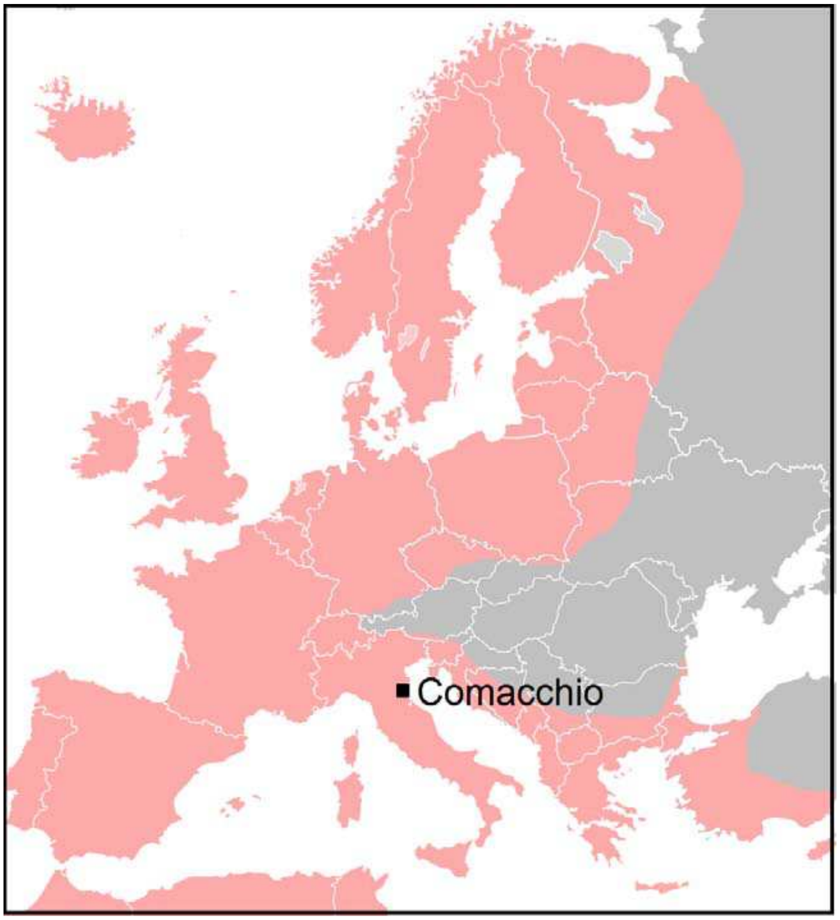

Fig.1.2 *Distribution of A. anguilla at continental scale (from wikipedia: European eel) and position of Comacchio lagoon.*

Italy is one of the top producers of farmed eels in Europe whereas the eel fishery in the Comacchio Lagoon (Fig.1.2) is one of the most interesting, as it is based only on natural recruitment while it has been studied since the eighteenth century. The lagoon has been subjected to maximum exploitation because it is a semi-closed ecosystem in which the silver eel catches correspond to the ~100% of the migrating population. This is succeeded because the canals, which connect the lagoon to the Adriatic Sea, are fully equipped with V-shaped screens of selective size that used to capture silver eel migrating population. Unfortunately, the local eel population started to decline after 1980 with no signs of recovery. Thus, it presents an excellent paradigm for investigating the effects of the eel fishery management strategies that have been employed over the years. Additionally, it can be considered an optimum location for monitoring population dynamics on a European scale since current evidence supports the view that glass eels originate from a single spawning stock in the Atlantic Ocean (hypothesis of panmixia) (Dekker, 2004; Als et al., 2011).

1.2 Objectives of the study

1. 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 using data of 2011 and comparison with the findings of previous surveys before the population collapse.
2. Development of a size-age model based on bootstrapping and Bayesian approaches to assess population dynamics of *Anguilla anguilla* L. in semi-closed lagoons. Application on the population of Comacchio lagoon.
3. Presentation of long-term series (1781-2013) of European eel (*Anguilla anguilla* L.) catches in the Comacchio Lagoon (Italy) and literature review about the contribution of local and global stressors on the population collapse. Specific analysis is performed to prove the hypothesis that aquaculture, which totally depends on glass eels harvested from the wild, is the major factor of global and local (Comacchio) eel population collapse.
4. Supplemental study: A review and synthesis of bivariate non-linear models to describe the relative variation of ecological, biological and environmental parameters. The doctoral thesis concerned the application of mathematical models for the assessment of eel population dynamics and morphometric characteristics. Such models consist of many bivariate functions which describe isolated attributes of the populations. For this reason, an expanded literature review was performed on various types of such functions which are used in ecological, biological and environmental problems. This is a supplementary chapter in the thesis.

1.3 Structure and scientific derivatives of the study

The research on the topic led to the production of four scientific articles for impact factor journals, which are provided as individual chapters in the thesis. The three of them have already been published, while one is under major revision. The titles of the articles are the following:

1. Castaldelli, G., Aschonitis, V., Lanzoni, M., Gelli, F., Rossi, R., Fano, E.A., 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 (3), pp. 558-559. DOI: 10.1111/jai.12392 (derivative of Objective 1 – Chapter 2). Chapter 2 is more expanded in comparison to the published article due to article size limitations required for the journal, while more recent data from FishBase were additionally included due to FishBase update.

2. Aschonitis, V.G., Castaldelli, G., Lanzoni, M., Merighi, M., Gelli, F., Giari, L., Rossi, R., Fano, E.A., 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, Article in Press. DOI: 10.1111/eff.12269 (derivative of Objective 2 – Chapter 3).
3. Aschonitis, V.G., Castaldelli, G., Lanzoni, M., Rossi, R., Kennedy, C., Fano, E.A., 2016. Long-term series (1781-2013) of European eel (*Anguilla anguilla* L.) catches in the Comacchio Lagoon (Italy): local and global stressors of the population collapse. Aquatic Conservation: Marine and Freshwater Ecosystems. Submitted article for publication (the article is under review for a second time after major revision) (derivative of Objective 3 – Chapter 4).
4. Aschonitis, V.G., Castaldelli, G., Bartoli, M., Fano, E.A., 2015.A review and synthesis of bivariate non-linear models to describe the relative variation of ecological, biological and environmental parameters. Environmental Modeling and Assessment, 20 (2), pp. 169-182. DOI: 10.1007/s10666-014-9421-7 (derivative of Objective 4 – Chapter 5).

Additionally, supplementary material is also provided at the end of the thesis and contains the long time series of habitat loss and silver eel catches of the period 1781-2013 in Comacchio lagoon, official data of FAO for eel aquaculture production during the period 1950-2013 and non official documentation for glass eel trade. The supplementary material is used for the analysis of Chapter 4.

1.4 References

Als, T.D., Hansen, M.M., Maes, G.E., 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.

Belpaire, C.G.J., 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.

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.

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.

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.

Dekker, W. 2004. Slipping through our hands - Population dynamics of the European eel. PhD thesis, University of Amsterdam, pp 186, ISBN 90–7454910–1.

Dekker, W., 2000. A procrustean assessment of the European eel. ICES Journal of Marine Science 57, 938–947.

Dekker, W., Casselman, J.M., 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.

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.

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.

Kennedy, C.R., Fitch, D.J., 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, A.J., Vøllestad, L.A., 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.

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. Science of the Total Environment 310, 237–244.

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.

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

Tesch, F.W., 2003. The eel. Willey-Blackwell Publishing, Oxford, UK, pp.416.

Tsukamoto, K., Otake, T., Mochioka, N., Lee, T.-W., Frickee, H., Inagaki, T., Aoyama, J., Ishikawa, S., Kimura, S., Miller, M.J., Hasumoto, H., Oya, M., Suzuki, Y., 2003. Seamounts, new moon and eel spawning: The search for the spawning site of the Japanese eel. Environmental Biology of Fishes 66, 221–229.

van Ginneken, V.J.T., Maes, G.E., 2005. The European eel (*Anguilla anguilla,* Linnaeus), its lifecycle, evolution and reproduction: a literature review. Reviews in Fish Biology and Fisheries 15, 367–398.

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2

An update of the length-weight and length-age relationships of the European eel in the Comacchio Lagoon

2.1 Summary

An update of length-weight and length-age relationships for yellow, silver and mixed population of European eels (*Anguilla anguilla* L.) of the Comacchio Lagoon, Italy, is provided in this study using data obtained in 2011. This historically important eel stock has undergone 99% feminization, probably due to the significant density reduction over the past three decades. The results showed that the extremely lower density conditions did not affect significantly the length-weight relationships, which approximate those of the ’70 and ‘80s but they affect the length-age relationships leading to faster maturation rates. These conditions led to younger, longer and heavier silver eels before their migration to the Sargasso sea.

2.2 Introduction

Long-term records of the European eel (*Anguilla anguilla* L.) show a dramatic reduction in recruitment and stock over the past 3 decades (Dekker and Casselman, 2014). The conditions are considered critical and for this reason *A. anguilla* is already placed on the IUCN Red List of critically endangered species (Jacoby and Gollock, 2014). This reduction may have affected growth patterns, which seem to be highly influenced by population density in semi-closed environments (De Leo and Gatto, 1996). Information on growth patterns has been derived from enclosed environments, such as lakes, stocked with glass eels or artificially bred eels (Simon et al., 2013a; Trautner, 2013).

The aim of the study is to provide new information on length-weight (LWR) and length-age (LAR) relationships in yellow and silver eels collected in 2011 in the Comacchio Lagoon, Italy, a managed, semi-closed lagoon where stocking is not applied, and the population relies only on natural recruitment.

2.3 Materials and methods

The Comacchio Lagoon is located on the Adriatic coast, south of the Po Delta, in Northern Italy (44° 36´ N, 12° 10´ E) and covers an area of 8470 ha. The lagoon is connected to the sea through two main canals, the Canal Fosse and Canal Gobbino, controlled with gates and permanent fish-traps consisting of V-shaped metal screens, locally called *lavorieri*. The *lavorieri* are used for capturing silver eels when they begin migrating, with efficacy of essentially 100%, while they permit the passage of glass eels. Silver eels were sampled at the *lavorieri* on six occasions in November and December, 2011.

Yellow eels were captured using a set of 20 trap nets, evenly distributed over the entire lagoon surface. This fishing gear is a modified fyke net consisting of a leader 50 m long and 1.5 m high that drives the fish toward two cone-shaped trap nets positioned on either side of the leader at its outer end. The structure is made of 8 mm^2 mesh. The nets were monitored every second day during September and October, a period when metamorphosis to silver eels is considered to be complete, preventing overlap of the two monitored groups. A total of 366 silver and 573 yellow eels were randomly extracted from the traps for the determination of total length L (cm), weight W (g) and age X (years). Otoliths were prepared and examined for age determination according to the grinding and polishing technique (ICES, 2009). Sex was determined by macroscopic examination of the gonads. For LWR, the following function was used:

$$W = aL^b \tag{2.1}$$

where a and b are coefficients. Log-log plots of length and weight values were created for visual identification and removal of outliers before the fitting procedure (Froese, 2006; Liu et al., 2013).

For the LAR relationship, the following von Bertalanffy growth equation was used:

$$L = L_\infty(1-e^{-kX})+L_0e^{-kX} \tag{2.2}$$

where L_∞ (cm) and k ($year^{-1}$) are coefficients. The parameter L_0 (the length of elvers at metamorphosis from the glass stage) was assumed to be 7.5 cm, following the procedure of De Leo and Gatto (1996), which used data from late seventies and eighties from the same site. The fitting procedure was performed using the StatGraphics Centurion XV software (Statpoint Technologies, Warrenton, VA, USA).

Comparison of the measured weight and length ranges and estimated coefficients of LWR and LAR was performed using data from other studies (www.fishbase.org, last accessed in 23/1/2016) (Table 2.1, 2.2). Analysis was also performed in the $\log_{10}(a)$ versus b graphs of LWR before and after the inclusion of the new data of this study. These graphs are provided in FishBase in order to examine the relationship of a, b datasets from different populations and the response of LWR of the same species under various environmental conditions and to verify the robustness of new LWR datasets.

Table 2.1 Values of *a* and *b* coefficients for LWR based on 19 case studies as they provided in FishBase database (FishBase.org, last accessed in 23/1/2016).

No.	a coef.	b coef.	Sex	Length (cm) range	r^2	Number of specimens	Country	Location	Reference
1	0.007	2.63	unsexed	-	0.929	7	Spain	Lake Hondo, 2000 (summer)	Blanco et al., 2003
2	0.005	2.767	unsexed	45.1 - 61.8	0.844	212	Turkey	Hatay Region, Mar-May 2003	Özcan, 2008
3	0.00181	2.962	juvenile	15.0 - 35.0	-	-	France	Étang de Thau	Campillo, 1992
4	0.0016	3	unsexed	-	0.974	69	France	*miscelaneous*	Bauchot[2], 1978
5	0.00203	3	female	-	-	-	Iran	Caspian Sea	Sheikh, 2000
6	0.00111	3.095	juvenile	15.0 - 35.0	-	-	France	Étang de Thau	Campillo, 1992
7	0.0011	3.13	unsexed	6.8 - 121.5	0.980	17586	Belgium	Flanders (Yser, Scheldt and Meuse drainage basin), 1992-2009	Verreycken et al., 2011
8	0.00119	3.15	unsexed	-	0.950	418	France	Camargue lagoons, Rhône delta, 1997-2003	Melia et al., 2006
9	0.00115	3.15	male	-	0.790	1585	France	Camargue lagoons, Rhône delta, 1997-2003	Melia et al., 2006
10	0.001	3.16	unsexed	17.0 - 68.6	0.985	-	Portugal	Arade estuary, central Algarve, 2004-2007	Veiga et al., 2009
11	0.00085	3.18	mixed	-	0.920	579	Italy	Comacchio lagoons	De Leo & Gatto, 1995
12	0.00087	3.22	female	-	0.960	940	France	Camargue lagoons, Rhône delta, 1997-2003	Melia et al., 2006
13	0.00064	3.22	unsexed	-	-	85	Ireland	River Shannon	Moriarty, 1986
14	0.0007	3.243	female	21.6 - 66.2	0.968	199	Germany	River Havel system, Elbe River, 2001	Simon, 2007
15	0.00056	3.313	unsexed	10.0 - 60.0	0.990	957	UK	Tadnoll Brook, Dorset	Mann & Blackburn, 1991
16	0.00049	3.319	unsexed	-	-	412	Portugal	Quinta da Rossiada lagoon, Albufeira and Aveiro Estuary	Bessa & Pestana, 1981
17	0.00052	3.37	unsexed	-	0.960	15311	France	Camargue lagoons, Rhône delta, 1997-2003	Melia et al., 2006
18	0.0003	3.47	unsexed	25.9 - 61.5	0.988	8	Croatia	River Neretva estuary, middle Adriatic, 2000-2004	Dulčić & Glamuzina, 2006
19	0.0003	3.47	unsexed	5.7 - 49.5	0.998	7	Greece	Rihios estuary, NW Aegean, 1997-99	Koutrakis & Tsikliras, 2003

Table 2.2 Values of L_∞ (cm) and k (year^{-1}) coefficients for LWR based on 40 case studies as they provided in FishBase (FishBase.org, last accessed in 23/1/2016).

No.	L_∞ (cm)	k (1/y)	Sex	Country	Location	Reference
1	37.5	0.98	Male	Italy	Acquatina (Southwest Adriatic)	Rossi & Corbari, 1982; Rossi et al., 1988
2	38.8	1.1	Male	France	Camargue lagoons, Rhône delta	Melia et al., 2006
3	41.8	0.35	Male	Italy	Comacchio lagoons	De Leo & Gatto, 1995
4	42.1	0.39	Male	Italy	Monaci lagoon	Ardizzone & Corsi, 1985; Rossi et al., 1988
5	44.9	0.62	Male	Italy	Varano lagoon	Rossi & Villani, 1980; Rossi et al., 1988
6	45.3	0.62	Male	Italy	Lesina lagoon	Rossi & Villani, 1980; Rossi et al., 1988
7	47	0.47	Male	Italy	Comacchio lagoon	Rossi et al., 1988
8	49.3	0.34	Male	Italy	Comacchio lagoon	Rossi et al., 1988
9	50.1	0.34	Male	Italy	Sardinia	Rossi & Cannas, 1984; Rossi et al., 1988
10	51.3	0.38	Male	Italy	Valle Nuova lagoon	Rossi & Colombo, 1976; Rossi et al., 1988
11	58	0.63	Female	France	Camargue lagoons, Rhône delta	Melia et al., 2006
12	65.9	0.04	Male	Ireland	Burrishoole system (9°55'W, 53°55'N)	Poole & Reynolds, 1996
13	70	0.03	Male	Ireland	Burrishoole system (9°55'W, 53°55'N)	Poole & Reynolds, 1996
14	70.4	0.16	Female	Germany	East of the Darss Sill, Mecklenburg-Vorpommern	Simon et al., 2013b
15	70.8	0.06	-	UK	Tadnoll Brook, Dorset	Mann & Blackburn, 1991
16	72.4	0.15	Female	Germany	West of the Darss Sill, Mecklenburg-Vorpommern	Simon et al., 2013b
17	72.8	0.34	Female	Italy	Sardinia	Rossi & Cannas, 1984; Rossi et al., 1988
18	73	0.08	Female	Germany	Lake Sacrow, River Havel system	Simon, 2007
19	74.2	0.15	Female	Germany	Bodden around Ruegen Island, Mecklenburg-Vorpommern	Simon et al., 2013b
20	76.2	0.23	Female	Italy	Comacchio lagoons	De Leo & Gatto, 1995
21	77.8	0.14	Female	Germany	Mecklenburg-Vorpommern (all coastal areas)	Simon et al., 2013b
22	80	0.07	Female	Germany	Lake Jungfernsee, River Havel system	Simon, 2007
23	82	0.13	Female	Germany	North and east of Ruegen Island, Mecklenburg-Vorpommern	Simon et al., 2013b
24	82.3	0.25	Female	Italy	Lesina lagoon	Rossi & Villani, 1980; Rossi et al., 1988
25	82.9	0.14	Female	Germany	Darss-Zingst Bodden chain, Mecklenburg-Vorpommern	Simon et al., 2013b
26	83	0.06	Female	Germany	Lake Pritzerbe, River Havel system	Simon, 2007
27	83	0.07	Female	Germany	Lake Eiserbude, River Havel system	Simon, 2007
28	83.2	0.08	-	Germany	Helgoland, North Sea	Penáz & Tesch, 1970; Tesch, 1991
29	84	0.09	Female	Germany	Lake Rangsdorf, River Havel system	Simon, 2007

30	85.2	0.13	Female	Germany	Wismar Bay/Salzhaff, Mecklenburg-Vorpommern	Simon et al., 2013b
31	87	0.2	Female	Italy	Comacchio lagoon	Rossi et al., 1988
32	87.2	0.19	Female	Italy	Valle Nuova Lagoon	Rossi & Colombo, 1976; Rossi et al., 1988
33	90	0.07	Female	Germany	Lake Blankensee, River Havel system	Simon, 2007
34	99.5	0.13	Female	Italy	Comacchio lagoon	Rossi et al., 1988
35	105	0.05	Female	Ireland	River Barrow	Moriarty, 1983; Tesch, 1991
36	112	0.11	Female	France	Lagoon of Arcachon	Tae-Won, 1979; Tesch, 1991
37	112	0.15	Female	Italy	Varano lagoon	Rossi & Villani, 1980; Rossi et al., 1988
38	135	0.06	Female	France	Mediterranean coast	Campillo, 1992
39	143	0.01	Female	Ireland	Burrishoole system (9°55'W, 53°55'N)	Poole & Reynolds, 1996
40	150	0.01	Female	Ireland	Burrishoole system (9°55'W, 53°55'N)	Poole & Reynolds, 1996

2.4 Results

Up to 99% of both the yellow and silver eels were female. Only 8 yellow and 6 silver males observed. The almost complete feminization is explained by the low density of the eel population, as the mean capture of silver eels in the period 1963-1973 (Rossi, 1979) was 19.32 kg ha^{-1}, while the mean capture in the period 2008-2012 was 0.45 kg ha^{-1}, indicating a reduction of 98%. Due to the low number of male specimens, analysis was conducted only on the female population. The results of LWR and LAR analyses of yellow and silver populations of the female eels are shown in Table 2.3. The log-transformed LWRs ($\log W = b \log L + \log a$) are linear and ANOVA allowed comparisons of the slope b and intercept $\log a$ of between the yellow and silver eels. The comparison between the log-transformed LWRs showed that slopes and intercepts are significantly different at 99% confidence level suggesting that morphometric relationships must be treated separately for yellow and silver eels. Morphometric relationships for the mixed population are also given in Table 2.3 for comparisons with other studies (Table 2.1) where mixed populations are commonly used.

The comparison of a and b between the LWR for the mixed female population (Table 2.3) and the values provided by De Leo and Gatto (1995, 1996) (No.11 in Table 2.1) showed that they are approximately equivalent since the later are inside the estimated 95% confidence limits of the coefficients of Table 2.3. These results suggested that the reduction of population density did not affect the LWR in the specific site. The a and b parameters of the mixed population were also approximately equivalent to the respective mean values given for *A.*

anguilla in the FishBase (a = 0.0009 and b = 3.19) (Table 2.1) (www.fishbase.org, last accessed in 23/1/2016).

Table 2.3 Length-weight (LWR) and length-age (LAR) relationships for yellow and silver female eels in Comacchio lagoon, Italy, in 2011.

LWR		**Total length *L* range (cm)**		**Weight *W* range (g)**		**Length-weight relationship**				
	N	Min	Max	Min	Max	*a*	±95% CL	*b*	±95% CL	r^2
Yellow	565	13.5	85	8.9	1413.4	0.00026	0.0002-0.00032	3.491	3.439-3.542	0.97
Silver	360	40.5	105	102	2248.3	0.006	0.0019-0.01	2.780	2.632-2.929	0.79
Mixed	925	13.5	105	8.9	2248.3	0.00087	0.00058-0.0012	3.223	3.005-3.441	0.961

LAR		**Total length *L* range (cm)**		**Age *X* range (years)**		**Length-age relationship**				
	N	Min	Max	Min	Max	L_∞ (cm)	±95% CL	k (year^{-1})	±95% CL	r^2
Yellow	565	13.5	85	0.5	8.5	97.0	87.49-106.52	0.157	0.135-0.179	0.834
Silver	360	40.5	105	4.5	10.5	125.97	119.79-132.14	0.124	0.113-0.134	0.866
Mixed	925	13.5	105	0.5	10.5	155.94	147.49-164.4	0.087	0.08-0.093	0.97

N, number of individuals; *a* and *b*, regression coefficients of LWR; L_∞ and k, regression coefficients of LAR; r^2, square correlation coefficient; ±95% CL, confidence limits (95%) of the regression coefficients.

Using the 19 pairs of a and b coefficients provided in Table 2.1 and the additional three pairs provided in Table 2.3 the $\log_{10}(a)$ versus b graphs were constructed. Fig.2.1a shows the $\log_{10}(a)$ versus b relationship as it is provided in FishBase while Fig.2.1b shows the change of the relationship after the inclusion of the new data of Table 2.3. The values of slope, intercept and R^2 of the regression line did not significantly change after the inclusion of the new data verifying the robustness of the procedure used for the implementation of the study, while the three new cases are well distributed along and very close to the regression line (Fig.2.1b).

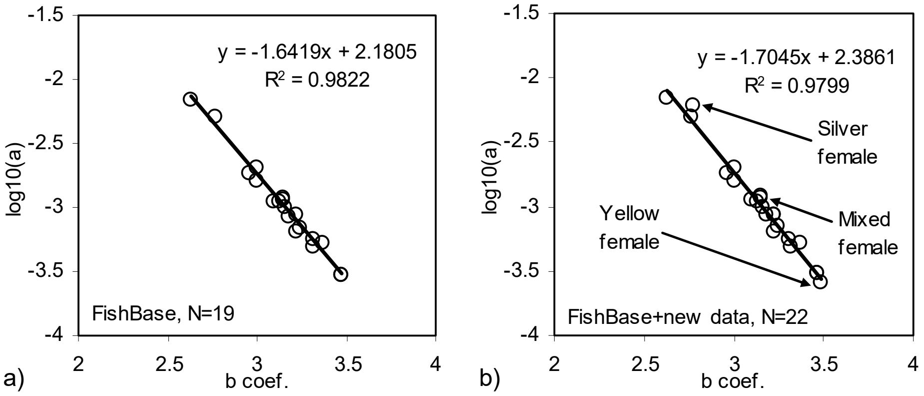

Fig.2.1 *a) Graph of* $\log_{10}(a)$ *versus b as it is provided in FishBase using the 19 cases of Table 2.1 and b) Graph of* $\log_{10}(a)$ *versus b after the inclusion of the three new cases provided in Table 2.3.*

For the case of LAR and the respective changes in L_∞ and k coefficients, the three cases of FishBase for mixed yellow+silver female populations from Comacchio (No. 20, 31, 34 in Table 2.2) were compared with the respective mixed female population of 2011 (Table 2.3). The updated values of L_∞ value (155.94 cm) was much higher while the updated k value (0.087) was much lower (Table 2.3) from the respective values of No. 20, 31, 34 cases of Table 2.2. The observed coefficients of L_∞ and k in these cases were all outside the estimated 95% confidence limits of the coefficients of Table 2.3. The findings indicate that the reduction of population density affects LAR favouring longer and heavier eels. The observed morphometric changes were accompanied by increased maturation rates in comparison to the late 1970s. Accordingly, age classes were reduced in number compared to those reported by Rossi (1979), when the older age class for both yellow and silver eels was 14.5, while in the current study it was 8.5 for the yellow eels and 10.5 for the silver eels.

2.5 Discussion

Apart from the updated LWRs and LARs of *A. anguilla* in Comacchio lagoon, other significant observations during monitoring were the faster maturation rates (younger, longer and heavier silver eels ready to migrate), the reduction of age classes and the extremely high feminization rate. 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).

Apart from the common approach, which is widely used for the presentation of LWRs relationships (e.g. Table 2.3), the additional analysis of $\log_{10}(a)$ versus b graphs was included. Our opinion is that this additional element in the LWR analysis can be used a) to evaluate and compare the estimated a, b coefficients with those from other studies and b) to evaluate the contribution of new LWR coefficients in the $\log_{10}(a)$-b graphs which are extremely valuable for assessing the LWR response of a species under different environmental conditions. An additional element which was observed during this analysis and by the Tables 2.1 and 2.2 was that the existing data provided by FishBase include the sex differentiation but not the yellow/silver differentiation. As indicated by Table 2.3 and Fig.2.1b, the LWR and LAR of yellow and silvers are significantly different and this should be taken into account since silver and yellow eels are two different trading products.

2.6 References

Ardizzone, G.D., Corsi, F., 1985. Eel population structure, dynamics and fishing yield in a coastal lagoon of central Italy. Oebalia II, 547–560.

Bauchot, R., Bauchot, M.L., 1978. Coefficient de condition et indice pondéral chez les téléostéens. Cybium 4, 3–16.

Bessa, R., Pestana, G., 1981. Contribuicao para o estudo da enguia europeia *Anguilla anguilla* L. em Portugal. Relat. Act. Aquar. Vasco da Gama, Lisb. (11) 21 p.

Blanco, S., Romo, S., Villena, M.-J., Martínez, S., 2003. Fish communities and food web interactions in some shallow Mediterranean lakes. Hydrobiologia 506–509, 473–480.

Campillo, A., 1992. Les pêcheries françaises de Méditeranée: synthèse des connaissances. Institut Francais de Recherche pour l'Exploitation de la Mer, France. 206 p.

Dekker, W., Casselman, J.M., 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.

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

Dulčić, J., Glamuzina, B., 2006. Length-weight relationships for selected fish species from three eastern Adriatic estuarine systems (Croatia). Journal of Applied Ichthyology 22, 254–256.

Froese, R., 2006. Cube law, condition factor and weight–length relationships: History, meta-analysis and recommendations. Journal of Applied Ichthyology 22, 241–253.

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.

ICES, 2009. Workshop on Age Reading of European and American Eel (WKAREA), 20-24 April 2009, Bordeaux, France. ICES CM 2009\ACOM, 48, pp. 66.

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).

Koutrakis, E.T., Tsikliras, A.C., 2003. Length-weight relationships of fishes from three northern Aegean estuarine systems (Greece). Journal of Applied Ichthyology 19, 258–

260.

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

Liu, L.W., Luo, Y.L., Liang, X-F., 2013. Length–weight relationship for nine freshwater fish species from Wujiang River in China. Journal of Applied Ichthyology 29, 681–682.

Mann, R.H.K., Blackburn, J.H., 1991. The biology of the eel *Anguilla anguilla* (L.) in an English chalk stream and interactions with juvenile trout Salmo trutta L. and Salmo salar L. Hydrobiologia 218, 65–76.

Melia, P., Devacqua, D., Crivelli, A.J., de Leo, G.A., Panfili, J., Gatto, M., 2006. Age and growth of *Anguilla anguilla* in the Camargue lagoons. Journal of Fish Biology 68, 876–890.

Moriarty, C., 1983. Age determination and growth rate of eels *Anguilla anguilla* (L.). Journal of Fish Biology 23, 257–264.

Moriarty, C., 1986. Riverine migration of young eels *Anguilla anguilla (L.).* Fisheries Research 4, 45–58.

Özcan, G., 2008. Length-weight relationships of five freshwater fish species from the Hatay Province, Turkey. Journal of FisheriesSciences.com 2(1), 51–53.

Penáz, M., Tesch, F.-W., 1970. Geschlechtsverhältnis und Wachstum beim Aal (*Anguilla anguilla*) an verschiedenen Lokalitäten von Nordsee und Elbe. Ber. Dt. Wiss. Komm. Meersforsch 21, 290–310.

Poole, W.R. Reynolds, J.D., 1996. Growth rate and age at migration of *Anguilla anguilla*. Journal of Fish Biology 48, 633–642.

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., Colombo, G., 1976. Sex ratio, age and growth of silver eels in two brackish lagoons in the northern Adriatic (Valli di Comacchio and Valle Nuova). Arch. Oceanogr. Limnol. Venezia 18, 227–310.

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. Boll. Zool. 46, 217–223.

Rossi, R., Villani, P., 1980. Biological analysis of eel catches (*Anguilla anguilla* L.) from the lagoons of Lesina and Varano. Journal of Fish Biology 16, 413–423.

Rossi, R., Corbari, L., 1982. Analisi biologica del pescato del lago di Acquatina (Adriatico sud-occidentale) nel periodo 1976-1979. Mem. Biol. Mar. Oceanogr. 12, 111–126.

Rossi, R., Cannas, A., 1984. Eel fishing management in a hypersaline lagoon of Southern Sardinia. Fisheries Research 2, 285–298.

Rossi, R., Carrieri, A, Franzoi, P., Cavallini, G., Gnes, A., 1988. A study of eel (*Aguilla anguilla* L.) population dynamics in the Comacchio lagoons (Italy) by mark-recapture method. Oebalia XIV, N.S.:1–14.

Sheikh, G., 2000. European eel in the Caspian Sea. I.F.R.O. Newsletter 24, 1–3.

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 Sciences 64, 1414–1422.

Simon, J., Dörner, H., Scott, R.D., Schreckenbach, K., Knösche, R., 2013a. Comparison of growth and condition of European eels stocked as glass and farm sourced eels in lakes in the first 4 years after stocking. Journal of Applied Ichthyology 29, 323–330.

Simon, J., Ubl, C., Dorow, M., 2013b. Growth of European eel *Anguilla anguilla* along the southern Baltic coast of Germany and implication for the eel management. Environmental Biology of Fishes 96, 1073–1086

Tae-Won, L., 1979. Dynamique des populations d'anguilles des lagunes d'Arcachon. Thèse Université des Sciences et Technique du Languedoc, Montpellier. 218 p.

Tesch, F.W., 1991. *Anguilla anguilla* (Linnaeus 1758). p.389-437. In H. Hoestlandt (ed.) The freshwater fishes of Europe. Vol. 2. Clupeidae, Anguillidae. AULA-Verlag Wiesbaden.

Trautner, J.H., 2013. Stocking the right eel species: A fast PCR-based identification assay to discriminate European (*Anguilla anguilla*), American (*A. rostrata*) and Japanese eel (*A. japonica*). Journal of Applied Ichthyology 29, 912–915.

Tzeng, W.N., Han, Y.S., He, J.T., 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.

Veiga, P., Machado, D., Almeida, C., Bentes, L., Monteiro, P., Oliveira, F., Ruano, M., Erzini, K., Gonçalves, J.M.S., 2009. Weight-length relationships for 54 species of the Arade estuary, southern Portugal. Journal of Applied Ichthyology 25, 493–496.

Verreycken, H., Van Thuyne, G., Belpaire, C., 2011. Length-weight relationships of 40 freshwater fish species from two decades of monitoring in Flanders (Belgium). Journal of Applied Ichthyology 27, 1416–1421.

3

A size-age model based on bootstrapping and Bayesian approaches to assess population dynamics of Anguilla anguilla L. in semi-closed lagoons

3.1 Summary

A size-age modelling technique is presented for assessing the vital rates, stock and recruitment of eel populations in semi-closed lagoons with fully monitored migration of silver eels. Data for yellow and silver European eels (*Anguilla anguilla* L.) were obtained in 2011 from the Comacchio lagoon (Italy). The analysis was performed in three steps: a) correction of yellow eel data, which are affected by the fyke nets selectivity during samplings, b) estimation of survival curve, stock, recruitment and metamorphosis rates of the population (calibration using data from 2011), c) validation of the model using the observed amount of silver eel migrating population of the next year. A bootstrap procedure was used to assess the level of uncertainty for each parameter using the 95% intervals of the highest posterior density distribution HPDD (Bayesian approach). The measured abundance of silver eels was 0.56 ind ha^{-1}, while the yellow eel abundance and recruitment were estimated by the model for 2011 at 8.77 ind ha^{-1} and 5.99 ind. ha^{-1}, respectively. The model performance during validation was satisfactory since the observed total mass of migrating population of 2012 (3777 kg) was inside the 95% HPDD intervals (3197-3839 kg) of model's predictions. The estimated stocks and recruitment were at least ten times lower from the respective estimations of previous studies of 1989 highlighting the crucial conditions of the population. The proposed modeling approach can provide significant information about eel population conditions, facilitating the evaluation of a range of management options in the context of eel conservation plans.

3.2 Abbreviations

A(L)	size of trunk section as a function of body length *L* (mm^2)
A_{50}(m)	size of trunk section at 50% selectivity as a function of mesh size *m* of fyke nets (mm^2)
AC	age class as a parametric number (i.e. the *AC* values for the age classes 0+,1+...*X*+ are respectively 0.5, 1.5…*X*+0.5)

F_i	survival of both yellow and silver eels per age class i
G_i	frequency of yellow eels per age class i
L	total body length of eel (mm)
L_0	constant which describes the length of elvers at age 0 (mm)
L_∞	regression coefficient of length-age relationship which describes the maximum reachable length of fish (mm)
M	eel body mass (g)
N	total number of individuals in a population (e.g. population of yellow or silver eels)
RF_i	survival rate (range 0-1, dimensionless)
S_i	abundance per age class i of silver eels (ind. ha^{-1})
TR_i	relative rate of metamorphosis (range 0-1, dimensionless)
Y_i	abundance of yellow eels per age class i (ind. ha^{-1})
W	body weight of eel equivalent to M (g)
a	regression coefficient of weight-length relationship
b	regression coefficient of weight-length relationship
c	regression coefficient of survival curve
d	regression coefficient of survival curve
f	abundance of the total population of silver eels (ind. ha^{-1})
i	serial integer number of eel age class (i=1, 2, 3…)
j	serial integer number for years in sequence
k	regression coefficient of survival curve which is used to convert the frequency of yellow eels to abundance per age class
k_L	regression coefficient of length-age relationship which describes growth rate (year^{-1})
m	fyke net mesh size (mm)
n_i	number of individuals per age class i
$\eta(m)$	shape parameter as a function of net mesh size (mm^{-2})
ρ	density of eel mass (~0.001 g mm^{-3})
$\varphi(L,m)$	fyke net selectivity as a function of length L and mesh size m (relative rate 0-1)

3.3 Introduction

Long-term records of glass eel recruitment for European eel populations from the past five decades indicate a dramatic reduction of 99% magnitude (Dekker, 2004; Dekker and Casselman, 2014; ICES, 2014**.** Conservation efforts have been intensified in order to establish measures for stock recovery (EU, 2007) and to designate management plans to reduce known anthropogenic mortality factors such as eel fisheries (Moriarty and Dekker, 1997; De Leo and Gatto, 2001; Feunteun, 2002; Starkie, 2003; Bark et al., 2007; Bevacqua et al., 2007, 2009a; Wickström and Sjöberg, 2013; Briand et al., 2015). Measures such as the recent application of the moratorium on the export of glass eel in 2010 showed already positive effects on the recruitment (ICES, 2014; Briand et al., 2015).

Basic element for the designation of site-specific management and conservation plans is the description of eel population dynamics using models. Eel population models can identify critical components of the species life history and its responses to different environmental forces (De Leo et al., 2009). The modelling of complex life cycle of eels for different habitats (lagoons, estuaries, rivers, streams, lakes) is extremely difficult and for this reason various modelling approaches adjusted to the features of each environment have been proposed (Dekker, 2000a,b; Feunteun et al., 2000; Aprahamian et al., 2007; Dorow et al., 2009; De Leo et al., 2009; Oeberst and Fladung, 2012; Macnamara and Mccarthy, 2014; Schiavina et al., 2015). The development and application of different modelling techniques face several problems, which are summarized in the following paragraphs.

Many models are based on a plethora of assumptions. For example, many models, which predict vital rates and yields, assume constant recruitment and stable age and size distribution of the eel population (Gatto and Rossi, 1979; Gatto et al., 1982; De Leo and Gatto, 1995, 1996, 2001), constant fishing mortality or no density dependence of vital rates (Francis and Jellyman, 1999; Hoyle and Jellyman, 2002).

Calibration and validation of the models require significant sampling efforts and data collection, which are extremely time, labour and cost demanding. It is indicative that many models have been applied with no calibration due to data mining limitations (Lambert and Rochard, 2007; Prigge et al., 2013). The model of Vøllestad and Jonsson (1988) is considered the most demanding in data because it minimizes the use of assumptions. For this model, the recruitment and escapement must be fully known but in the majority of cases, a quantitative measurement of recruitment is almost impossible to be performed while the sampling effort in order to create a robust dataset of yellow and silver eels has been significantly increased due to the decline of eel populations.

Additionaly, there is lack of information about the oceanic portion of eel life history. For this reason, the majority of demographic models describe only the continental phase. Although eels may occupy fresh, brackish, or salt waters during their continental period, most models deal only with eels in fresh or brackish waters. Some attempts have been made to model the full life cycle by using many simplifications in the continental phase (De Leo et al., 2009; Bonhommeau et al., 2009; Pacariz et al., 2014).

Given the high number of unknown and untested hypotheses and assumptions, De Leo and Gatto (2001) and De Leo et al. (2009) stressed the need to use stochastic approaches in order to explicitly describe the uncertainty in the parameters, which regulate models performance (e.g. by using bootstrap techniques, Monte Carlo simulations, Bayesian techniques). Eel population models based on such techniques are of urgent need because they can be used not only for the analysis of population vital rates and production but also for the development of conservation plans in sites with limited data availability.

The aim of this study is to present and apply a size-age modelling approach based on bootstrapping and Bayesian techniques in order to describe the population dynamics of eels in semi-closed ecosystems with fully monitored migration of silver eels. The specific environments are considered the most important in terms of fisheries production but also for populations monitoring. Detailed data of eel population from the Comacchio Lagoon (Italy) were obtained in 2011 and are used for the application of the proposed modelling approaches.

3.4 Materials and methods

3.4.1 Study site and measurements

The eel fishery in the Comacchio Lagoon of Italy (44° 36′ N, 12° 10′ E) (Fig.3.1a) is a semi-closed ecosystem and has always been exploited for commercial fishery with no permission for any recreational fishing activity. The silver eel catch in this system represents ~100% of the silver eel migrating population. Additionally, the eel populations are based only on natural recruitment and no stocking has been conducted either to the Comacchio Lagoon or to neighbouring areas. The lagoon comprises three main basins (Fig.3.1a): Valle Campo, Valle Magnavacca, and Valle Fossa di Porto, which cover an area of ~10^4 ha. Valle Campo (~1600 ha) is in private ownership and completely separate, while the other two, which constitute the study site (8470 ha), are now a single basin recognized as the most important area for biodiversity conservation within the Regional Park of the Po River Delta of the Emilia-Romagna Region. The lagoon is connected to the Adriatic Sea by two canals (Bellocchio and Foce) (Fig.3.1a) which are hydraulically regulated by gateways where V-shaped screens of selective size, called *lavorieri,* are used to capture silver eels (Fig.3.1b). The screens permit the entry of elvers but entrap all silver eels when they begin their migration.

Yellow and silver eel populations were monitored during 2011. Silver eels were sampled at the screens during the period of seaward migration (November and December), while continuous monitoring during the entire year was conducted to assess the total catch. Silver eel migration was null in the period January-October. The total catch of silver eels of 2011 in the screens (for the fishing area of 8470 ha) was 3811.5 kg with a total population abundance f equal to 0.56 ind. ha^{-1}.

Since yellow eels can not be caught by the screens, their monitoring was performed by a set of 20 trap nets evenly distributed over the entire lagoon area. The fishing gear was a modified fyke net, locally called *cogollo*, which is typically used for eel fishing in the shallow lagoons of the northern Adriatic. It consists of a leader, 50 m × 1.5 m, that directs the fish toward two conical trap nets positioned at its distal ends. The structure consists of 8×8 mm mesh, large enough to prevent blocking by macroalgae, periphyton and detritus, but small enough to prevent loss of small age class specimens. The mesh allowed smaller elvers to escape from the net, and for this reason a correction has to be performed for this sampling error. The nets were monitored every two days in September and October, a period when metamorphosis to silver eels is considered complete, preventing overlap of the two monitored groups (van Ginneken et al., 2007).

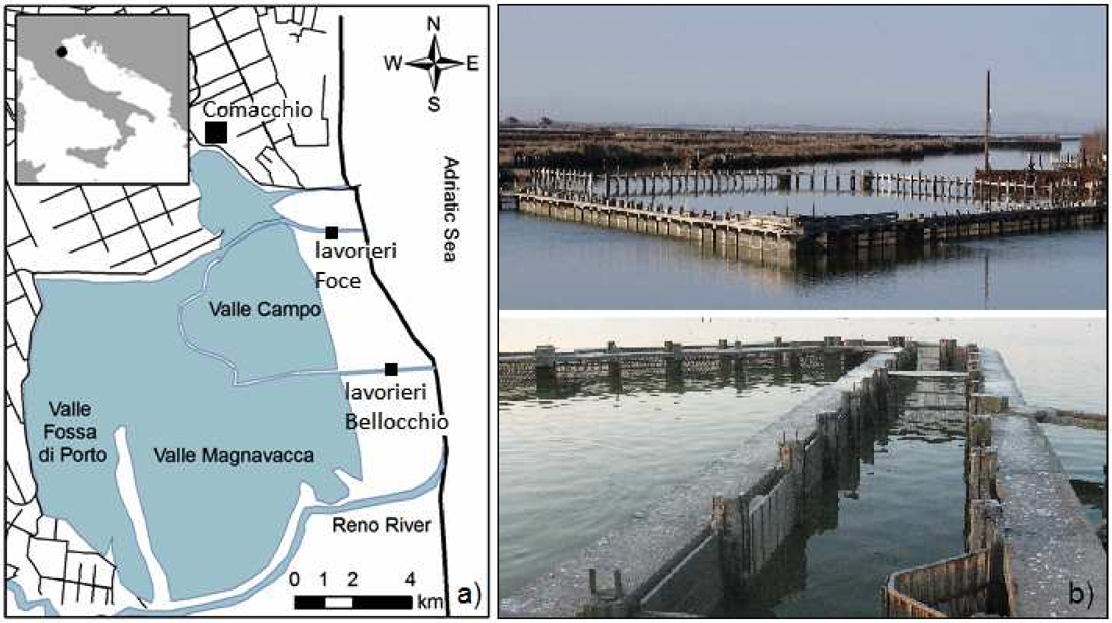

Fig.3.1 *a) Study site –The boundaries of Comacchio Lagoon as they formed after 1982 (44^{o} 36′ N, 12^{o} 10′ E) and b) V-shaped screens "lavorieri" of selective size used to capture silver eels.*

A total of 2627 yellow and silver eels were caught (73% yellow and 27% silver). Eels were counted and anaesthetized with ice to measure length and weight before being released. Sub-samples of 573 yellow and 366 silver eels were randomly selected for age and sex determination (Tables 3.1 and 3.2). Additional measurements for the gonado-somatic index, the hepato-somatic index and the gut index were performed for the specimens of Table 3.1 and 3.2 in order to assess the silvering stage based on the classification of Durif et al. (2005, 2009). All the captured silver eels in the screens were found to be at the V silvering stage while the silvering stage of eels captured in the trap nets was up to the III and in very few cases (<1%) up to the IV stage (the specimens of IV stage were not included in Table 3.1). The age of specimens was determined by double reading after grinding and polishing the otoliths (ICES, 2009). Age was expressed as the number of years from the elvers' entry into the enclosed waters. Since elvers always enter in spring and are captured in autumn, the age classes are given as 0+,1+,…*X*+ (corresponding to the respective parametric numbers AC of 0.5, 1.5,…*X*+0.5), respectively. Sex was determined by macroscopic examination of the gonads and when specimens were smaller than 35 cm microscopic examination of the gonads was performed (Colombo and Grandi, 1996; Tesch, 2003). The eels, which had the characteristically lobed Syrsky's organ, were recorded as male; those with a typically pleated gonad, as female; and those in which reproductive organs could not be distinguished were recorded as undifferentiated.

Table 3.1 Number of individuals n per age class, mean length L (cm), and mean weight W (g) of yellow eels for different age and sex classes (Total number of yellow eels $N = 573$).

Age Class i	**Females**			**Males**			**Undifferentiated**		
	n	L±S.D.	W±S.D.	n	L±S.D.	W±S.D.	n	L±S.D.	W±S.D.
0+	83	18.4±1.2	14.5±4.6				3	11.1 ± 0.2	9.9 ± 0.5
1+	212	25.1±3.2	30.4±12.1	5	21.2 ± 2.5	22.4 ± 10.1	7	19.5 ± 1.7	24 ± 10.4
2+	102	36.7±4.8	87.8±40.2	1	33	49			
3+	78	45.9±5.3	183.3±79.9	1	40.5	106			
4+	35	56.1±6.5	345.3±141.4	1	43.5	162			
5+	25	59.6±5.5	402.9±130.2						
6+	12	64.6±6.3	527.2±192.1						
7+	6	76.8±1.7	995.9±145.3						
8+	2	84.8	1380.5						

Table 3.2 Number of individuals n per age class, mean length L (cm), and mean weight W (g) of silver eels for different age and sex classes (Total number of silver eels $N = 366$).

Age Class i	**Females**			**Males**		
	n	L±S.D.	W±S.D.	n	L±S.D.	W±S.D.
4+	11	61.9 ± 3.7	488.3 ± 100.4	4	42 ± 1.0	133.9 ± 18.7
5+	51	68.1 ± 1.8	675.5 ± 144.6	1	41.5	102
6+	137	70.8 ± 3.8	890 ± 247.2	1	41	107
7+	108	80.3 ± 2.7	1269.6 ± 191			
8+	38	84.8 ± 0.9	1330.9 ± 168.7			
9+	12	88.5 ± 1.2	1534.2 ± 240.3			
10+	3	96.1 ± 7.7	1957.3 ± 265.5			

Additional data of silver eel catches for the period (1960-2013) (Fig.3.2) were also collected in order to provide indirect justifications about the assumptions used in the modelling approaches. According to Fig.3.2, the silver eel migrating population has been declined significantly after 1995. During the period 1998-2012, the silver eel population shows extremely low and almost constant abundance which can support the assumption that the density effects on the morphometric characteristics and maturation behaviour were not differentiated during the period 2000-2011 (the population density conditions during this period affect the data of 2011 because the oldest eels belong to 10+ age class, Table 3.1 and 3.2). Additionally, it adequately supports the assumption of constant recruitment, which is prerequisite in many size-age modelling approaches (De Leo et al. 2009).

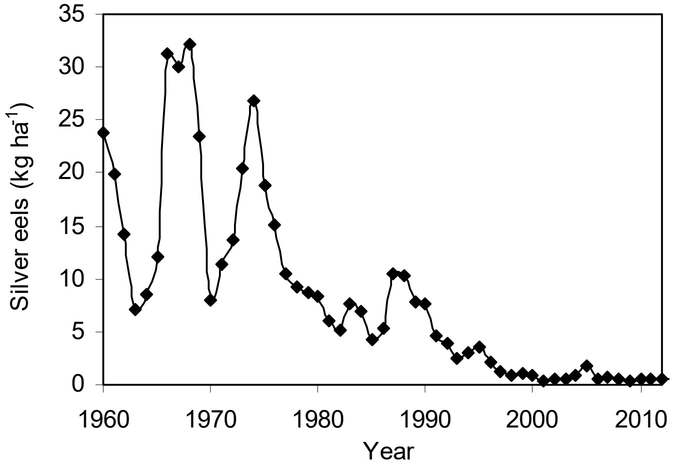

Fig.3.2 *Silver eel catches (total of the migrating population) expressed as abundance (kg ha^{-1}) for the period 1960-2012.*

3.4.2 Modelling approach to correct the fyke net effects in yellow eel samplings

The small age class specimens can escape from fyke nets introducing error in the frequency distribution of individuals per age class of yellow eel population. The frequency of yellow eels in each age class i is defined as the ratio n_i/N from Table 3.1. The error was corrected using the method of Bevacqua et al. (2009b), in which fyke net selectivity φ can be estimated as a function of eel body length and net mesh size using the equation:

$$\varphi(L,m)=\left\{1+\exp\left[-\eta(m)\left(A(L)-A_{50}(m)\right)\right]\right\}^{-1} \tag{3.1}$$

where L is body length (mm), m is the mesh size (mm), $\eta(m)$ is a shape parameter expressed as a function of the fyke net mesh size (mm^{-2}), $A(L)$ is the section size of the fish trunk expressed as a function of body length (mm^2), and $A_{50}(m)$ is the trunk section at 50% selectivity expressed as a function of the fyke net mesh size (mm^2).

The functions of $\eta(m)$ and $A_{50}(m)$ are estimated by the following equations (Bevacqua et al., 2009b):

$$\eta(m) = \exp\left(-0.06m - 1.65\right) \text{ and } A_{50}(m) = \exp\left(0.09m + 3.26\right) \tag{3.2a,b}$$

where m is mesh size (mm).

The trunk section was estimated using the assumption that eel shape is a cylinder of body mass M, density ρ (equal to water density 0.001 g mm^{-3}), and body length L (Gatto and Rossi, 1979). Eel mass and body size are significantly related, and M can be substituted as a function of L. The above define the function of trunk $A(L)$ as follows (Gatto and Rossi, 1979; Bevacqua et al., 2009b):

$$A = \frac{M}{\rho L} \rightarrow A(L) = \frac{M(L)}{\rho L} \tag{3.3}$$

and

$$M(L) = aL^b \text{ and } A(L) = a\rho^{-1}L^{b-1} \tag{3.4a,b}$$

where a and b are regression coefficients, M in g and L in mm. In this study, the morphometric relationship $M(L)$ (Eq.3.4a) was derived from regression using length and weight (equivalent to mass for Eq.3.4a: $W=a \cdot L^b$). Log-log plots of length and weight values ($\log W=\log a+b \cdot \log L$) were created using simple linear regression for the identification and removal of outliers before the fitting procedure (Froese, 2006). Outliers were identified using as threshold value the studentized residual >2 using the StatGraphics XVII software (Statpoint Technologies, Warrenton, VA, USA).

Additionaly the length-age relationship was examined using a von Bertalanffy growth equation:

$$L = L_\infty \left(1 - e^{-k_L \cdot AC}\right) + L_0 e^{-k_L \cdot AC} \tag{3.5}$$

where L_∞ (mm) and k_L ($year^{-1}$) are coefficients, AC is the parametric age class in years and L_0 is the length of elvers at metamorphosis from the glass stage (age 0). L_0 was considered equal to 75 mm according to De Leo and Gatto (1996) which used older data from the same site. Outliers in the observations were identified by the same criterion used in weight-length relationship.

Using the aforementioned equations, correction was performed to the number of individuals n_i of yellow eel age classes (Table 3.1) which were affected by fyke net selectivity. The morphometric relationships Eq.3.4a and Eq.3.5 were applied using only the specimens of $L<400$ mm in order to increase their accuracy for the smaller specimens. This threshold was chosen using indications from selectivity graphs of different mesh size obtained by Bevacqua et al. (2009b) and initial trials using the data of this study. After the correction of n_i values of the age classes affected by selectivity, their values were used to recalculate the frequency n_i/N of yellow eels per age class, symbolized as G_i. Correction was not required for the data of silver eels since they were not affected by the fyke net selectivity. The abundance S_i (ind. ha^{-1}) for each age class i of silver eels was estimated by multiplying the frequency for each age class n_i/N from Table 3.2 with $f = 0.56$ ind. ha^{-1} ($S_i = f \cdot n_i/N$). The G_i and S_i were used for the calculation of a) the eel survival curve and the survival rates per age class of the entire population to the time of migration, b) the stock of yellow eels, c) the recruitment, and d) the rate of metamorphosis from yellow to silver eels.

3.4.3 Modelling approach to estimate the survival curve, stock of yellow eels, recruitment and metamorphosis

The survival curve describes the degree of survival of both yellow and silver eels per age class after the occurrence of natural mortality. The survival for each age class i is symbolized F_i and is given by values relative to G_i. The F_i is equal to G_i for the first four age classes (0+, 1+, 2+, and 3+), in which metamorphosis to silver eels was not observed (Table 3.2). A preliminary analysis was performed to select the optimum form of the survival curve using the known F_i values of the first four age classes versus the parametric age class AC. The aim of the analysis was to find the optimum transformations of F and AC for providing a linear relationship of the two transformed parameters with an intercept which can be used for the derivation of the recruitment when AC=0. The optimum transformations for F and AC were $F'=F^{-1/2}$ and $AC'=[\ln(AC+1)]^2$, respectively, and the general form of the transformed and non-transformed survival curve is the following:

$$F' = cAC' + d \quad \text{and} \quad F = \left[c\left(\ln(AC+1)\right)^2 + d \right]^{-2} \quad \text{for } c, d > 0 \qquad (3.6a,b)$$

The value of 1 in the natural logarithm of AC transformation was used to solve the equation for AC=0. For AC=0 in Eq.3.6b the value of F is equal to d^{-2} which is used in the following steps for the estimation of glass eel recruitment.

The survival rate of an age class i is described by the ratio of sequential F values as follows:

$$RF_i = \frac{F_i}{F_{i-1}} \qquad (3.7)$$

The parameters of the survival curve were estimated based on the concept that the G_i of an age class i of yellow eels is equal to the value of survival F_i minus the proportional frequency of silver eels of the same age class. The proportional frequency of silver eels is equal to S_i of each age class i multiplied by a correction factor k. The factor k is also used a) to convert the frequencies G_i to abundance Y_i (ind. ha^{-1}) of yellow eels per age class according to $Y_i=G_i/k$, b) to convert the F_i values to total population abundance per age class according to F_i/k (ind. ha^{-1}) and c) to convert the parameter d^{-2} to recruitment abundance according to d^{-2}/k (ind. ha^{-1}). The concept of the conversion factor k was first proposed by Gatto and Rossi (1979). The connection between G_i, F_i and S_i using k is performed by the following expression:

$$G_i = F_i - kS_i \qquad \text{or} \qquad G_i / k = F_i / k - S_i \qquad \text{for } k > 0 \qquad (3.8\text{a,b})$$

Eq.3.8a using Eq.3.6b can be restated as:

$$G_i = \left[c\left(\ln(AC_i + 1)\right)^2 + d \right]^{-2} - kS_i \qquad \text{for } c, d, k > 0 \qquad (3.9)$$

Eel population presented eleven age classes (0+, 1+, ...10+) (Tables 3.1 and 3.2) each of which could be described by Eq.3.9. S_i was equal to 0 for the first four age classes (0+,1+,2+, and 3+) while G_i was equal to 0 for the final two age classes (9+ and 10+). The eleven age classes provided a set of eleven observations of $(G, S \text{ and } AC)_i$ which were used to estimate the three unknown parameters c, d, and k after fitting Eq.3.9.

The estimated values of c and d are used in Eq.3.6 to describe the survival curve. The value of k is also used to estimate the relative rate (i.e. values 0-1) of metamorphosis to silver eels TR_i for each age class according to the following:

$$TR_i = \frac{kS_i}{G_i + kS_i} = \frac{S_i}{Y_i + S_i} \qquad (3.10)$$

3.4.4 Validation method

A method to validate the performance of the model (Eqs.3.1-3.10) is to compare the observed and predicted silver eel catch (total migrating population) of the next year. The calibrated model can predict the abundance of silver eels per age class for the next year according to the following:

$$S_i^{j+1} = Y_{i-1}^{j} \times RF_i \times TR_i \qquad (3.11)$$

where S_i^{j+1} is the abundance of silver eels in the age class i for the year j+1, Y_{i-1}^{j} is the abundance of the yellow eels in the age class $i-1$ for the current year j, RF_i and TR_i are the rates of survival and metamorphosis to silver eels of the age class i, respectively. The sum of

S_i^{j+1} predictions from all age classes of silver eels provides an estimation of the migrating population of the next year as abundance (ind. ha^{-1}). The above method assumes that the RF_i and TR_i rates remain constant. Since the data of 2011 were used for the calibration of the model, the observed silver eel catch of 2012 was used for validation. Following the same sampling procedure as in 2011, the total catch of silver eels in the screens for 2012 was 3777.4 kg with a biomass per unit area equal to 0.446 kg ha^{-1} and a median weight of silver eel specimens equal to 1.253 kg (value obtained from 400 randomly selected specimens).

3.4.5 Bootstrap regression and Bayesian uncertainty analysis

The Eq.3.6b and consequently Eq.3.9 were built under the assumption that recruitment was constant during the period, which covers the respective age classes of Tables 3.1 and 3.2. Additional uncertainties are also introduced by the corrected G_i observations using Eq.3.1 and the morphometric relationships (Eq.3.4a and 3.5) which can be affected by the variation of population density and environmental factors (Castaldelli et al., 2014). Considering the above, De Leo and Gatto (1995) and De Leo et al. (2009) proposed the use of bootstrap or Monte Carlo techniques in order to explicitly investigate the inserted errors by the above monitoring and modelling assumptions and to assess the uncertainty in parameters estimation. In our study, bootstrap non linear regression (NLR) was selected to be used which is based on the generation of a large number of new datasets by randomly sampling data with replacement (Efron and Tibshirani, 1993). Since the overall modelling approach starts with the morphometric relationships, the bootstrap NLR was performed on Eq.3.4a and Eq.3.5 by applying the “nls” function (Ritz and Streibig, 2008) together with the non-linear least-squares algorithm “nl2sol” (Dennis et al., 1981) in R package. The procedure produced 10,000 respective bootstrap pairs of a, b coefficients and pairs of L_∞, k_L coefficients for Eq.3.4a and Eq.3.5, respectively. The modelling technique continues using either with the 10,000 curves of Eq.3.4a or the respective curves of Eq.3.5 (De Leo and Gatto, 1995; De Leo et al., 2009) (for this study Eq.3.4a was selected due to better performance, while for Eq.3.5 the median values of the curves were used). The bootstrap curves of Eq.3.4a were used to develop a respective number of a) selectivity curves (Eq.3.1) and b) corrected frequencies of yellow eels per age class G_i. The bootstrap sets of G_i frequencies were used to solve Eq.3.9 which led to a respective number of (c,d,k) estimations and consequently a respective number of estimations for a) the recruitment according to d^{-2}/k (ind. ha^{-1}), b) the abundance of yellow eels per age class Y_i (ind. ha^{-1}) according to $Y_i = G_i/k$, c) the survival rates per age class RF_i (Eq.3.7) and d) the rates of metamorphosis to silver eels TR_i (Eq.3.10).

For all bootstrapped variables, a 95% probability interval, also called Bayesian confidence interval (Gelman et al., 2014), was estimated based on the probability distribution of their 10,000 estimations. This method was applied in order to estimate the values of the posterior probability density distribution (HPDD) that indicate the 2.5% and 97.5% thresholds, which contain the central 95% of the distribution. The probability interval was computed using the "`p.interval` {LaplacesDemon}" of the R package (Bernardo, 2005) which returns unimodal or multimodal Highest Posterior Density Intervals (HPDIs), depending on the form of the probability distributions. In many occasions, regression analysis with bootstrapping may lead to non symmetrical frequency-probability distributions of bootstrap estimations of the coefficients. In order to describe both normal and skewed distributions, the median values of the estimations were used in all cases because they are more appropriate to be used as a measure of central tendency.

The bootstrap sets of Y_i, RF_i and TR_i parameters of all age classes from 2011 were also used in the validation procedure which produced a respective number of predictions of the silver eel catches for the next year of 2012. These predictions were also subjected to HPDD analysis. The calibrated model with the data of 2011 was considered successful in the case where the observed value of silver eel catches of 2012 was inside the intervals, which define the 95% of the HPDD of the predicted values by the model.

3.5 Results

3.5.1 Fyke net effects and estimate of yellow and silver eel abundance per age class

The coefficients a and b of the weight-length relationship (Eq.3.4a) were estimated using the specimens of L<400 mm. From the initial dataset of the 2627 specimens, 1725 had L<400 mm, while 66 were considered outliers. The remaining 1659 observations were subjected to bootstrap regression for the estimation of a and b coefficients of Eq.3.4a. The weight-length relationship (Eq.3.4a) using the median values of the bootstrap curves together with the intervals which define the 95% highest posterior density (HPDIs-95%) are given in Fig.3.3a. The respective frequencies and the HPDDs of bootstrap pairs of a and b coefficients are given in Fig.3.4a and Fig.3.4b, respectively. The squared correlation coefficient between observed and predicted values of specimens weight from Eq.3.4a (using the median values of a and b coefficients) was estimated at R^2=0.91.

For the case of length-age relationship (Eq.3.5), only 492 observations from specimens with age up to 3+ were used in the analysis because specimens with L<400 mm exist only in the first four age classes. After the removal of 14 outliers, 478 observations were used in the bootstrap regression. The length-age relationship (Eq.3.5) using the median values of the bootstrap estimations together with the intervals which define the 95% highest posterior density (HPDIs-95%) are given in Fig.3.3b. The respective frequencies and HPDDs of bootstrap pairs of k_L and L_∞ coefficients are given in Fig.3.4c and Fig.3.4d, respectively. The squared correlation coefficient between observed and predicted values of specimens length from Eq.3.5 (using the median values of k_L and L_∞ coefficients) was estimated at R^2=0.84.

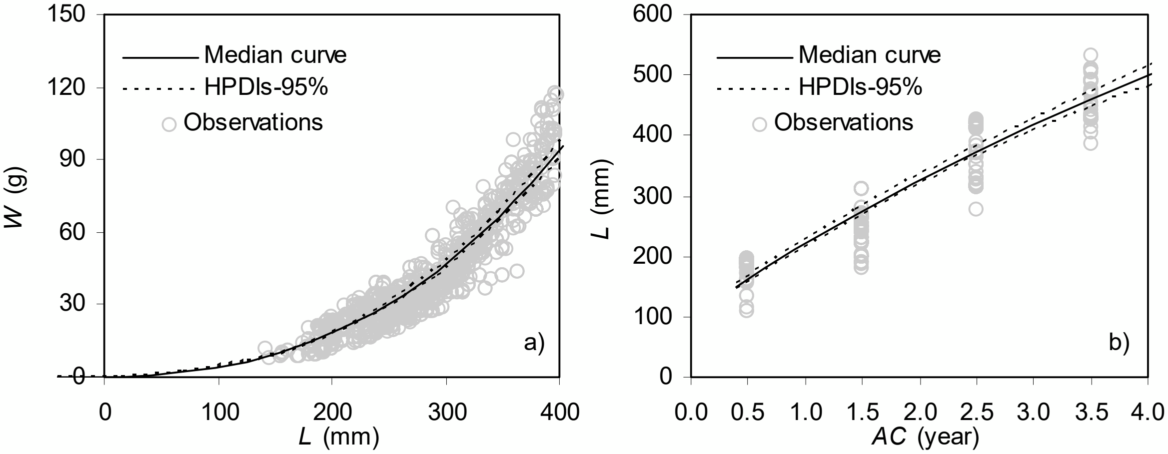

Fig.3.3 *Results based on the 10,000 bootstraps a) weight-length curves for eels with L<400 mm b) length-age curves for eels of age up to 3+ (solid line: Median values; dotted lines: 95% highest posterior density intervals HPDIs-95%).*

The abundance per age class of silver eels S_i (ind. ha^{-1}) and the initial frequency G_i per age class of yellow eels before correction are given in Fig.3.5a and Fig.3.5b, respectively. Using a mesh size of fyke nets equal to m=8 mm, the parameters of $\eta(m)$ and $A_{50}(m)$ (Eqs.3.2a,b) were estimated at 0.119 mm^{-2} and 53.517 mm^2, respectively. The bootstrap pairs of a, b coefficients of Eq.3.4a together with the estimated values $\eta(m)$ and $A_{50}(m)$ were used to build a respective number of curves for fyke net selectivity φ (Eq.3.1). The median values of φ estimations together with their 95% HPDIs are given in Fig.3.5c. Considering the median estimated length of individuals for each yellow eel age class, it was found that the median φ values for 0+ age class (with L_{median}=141 mm) and 1+ age class (with L_{median}=259 mm) were equal to 16.98% and 99.93%, respectively, while for the rest age classes the selectivity was 100% (Fig.3.5c). Taking into account the bootstrap φ curves, a respective number of corrections was made on the frequency distribution G_i of yellow eels. The median values of corrected G_i estimations together with the intervals of 95% highest posterior density (HPDIs-95%) are given in Fig.3.5d.

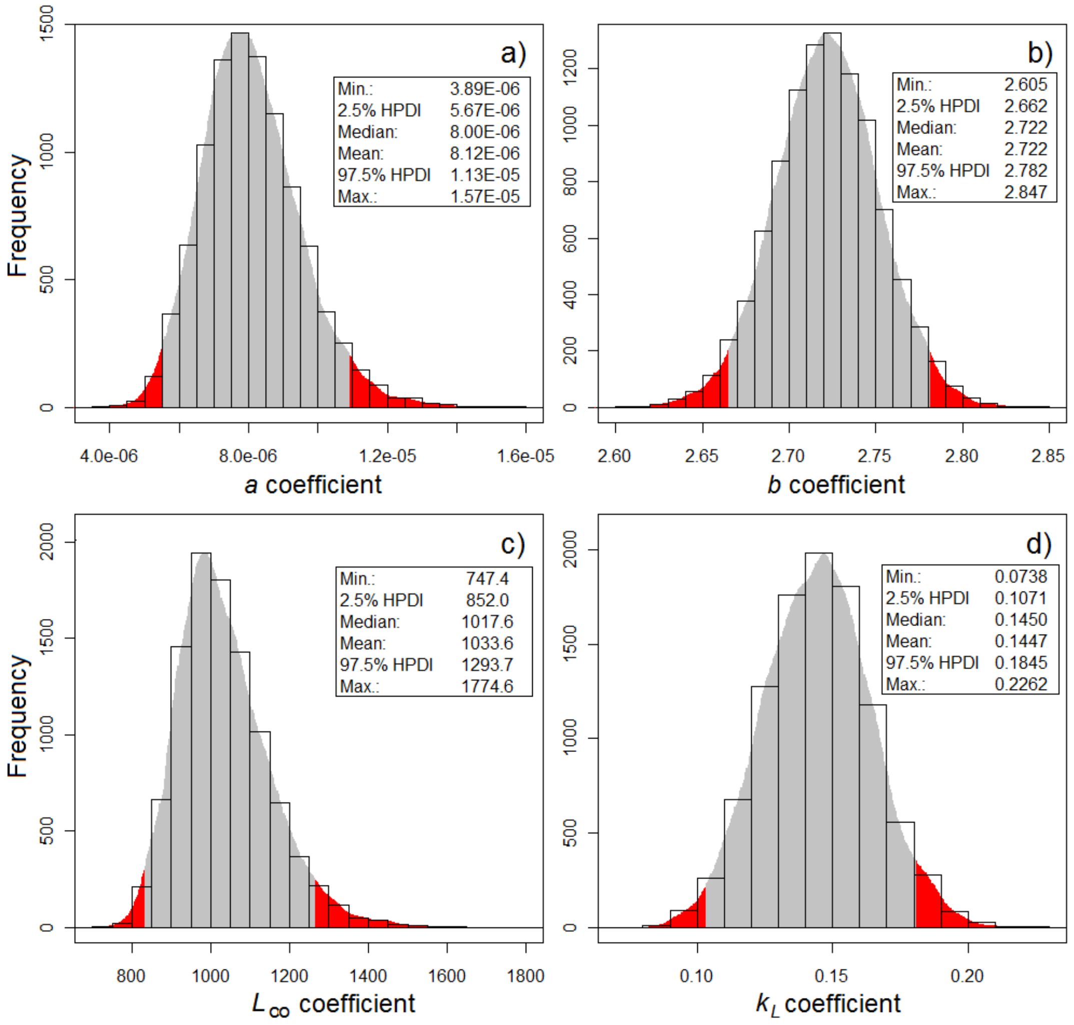

Fig.3.4 *Frequency and highest posterior density distributions (HPDDs) based on the 10,000 bootstrap estimations of a) a coeficient of Eq.3.4a, b) b coeficient of Eq.3.4a, c) L_∞ coefficient of Eq.3.5 and d) k_L coefficient of Eq.3.5 (the grey zone defines the regions of the 95% highest posterior density).*

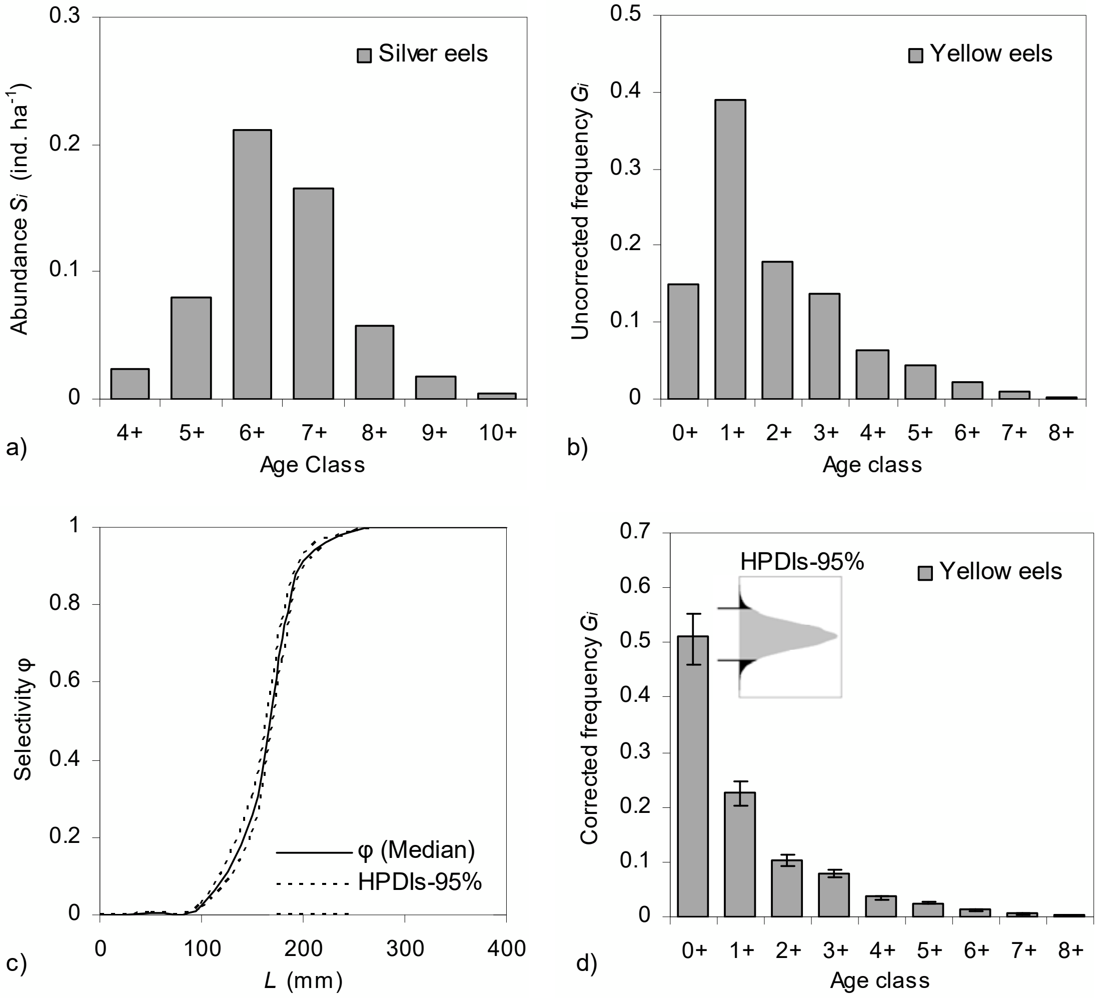

Fig.3.5 *a) Abundance per age class S_i (ind. ha^{-1}) of silver eels, b) initial uncorrected frequency G_i of yellow eels per age class i, c) the median values of the 10,000 selectivity curves φ (Eq.3.1) together with their HPDIs-95%, d) the median values of the 10,000 corrected frequencies G_i together together with their HPDIs-95%.*

3.5.2 Survival curve, stock, recruitment and metamorphosis

The eleven age classes provide a set of eleven observations of $(G, S$ and $AC)_i$ which are used to estimate the three unknown parameters *c*, *d,* and *k* after fitting Eq.3.9. The fitting procedure for Eq.3.9 was performed using each one of the 10,000 cases of G_i frequencies (Fig.3.5d) and the one dataset of S_i values (Fig.3.5a). This procedure produced a respective number of (*c*, *d*, *k*) estimations and a respective number of recruitment estimations for 2011 as (ind. ha^{-1}) according to the parameter d^{-2}/k. The frequencies and HPDDs of bootstrap sets of *c*, *d*, *k* and d^{-2}/k coefficients together with their intervals of 95% highest posterior density (HPDIs-95%) are given in Fig.3.6a,b,c,d respectively. The squared correlation coefficient between observed and predicted values of the corrected G_i values from Eq.3.9 (using the median values of c, d, k coefficients) was estimated at R^2=0.95.

The corrected G_i frequencies (Fig.3.5d) together with their respective k values (Fig.3.6c) obtained from Eq.3.9 were used to generate a respective number of estimations for the abundance of yellow eels per age class Y_i (ind. ha^{-1}) according to $Y_i=G_i/k$ (Fig.3.7a). Using Eq.3.8b, a respective number of estimations of F_i/k was derived (abundance of both yellow and silver eels per age class as ind. ha^{-1}) and they are given in Fig.3.7b while the recruitment of 2011, before the catch of silver eels, was estimated at 5.99 ind. ha^{-1} according to the median value of d^{-2}/k (Fig.3.6d and Fig.3.7b).

A respective number of bootstrap survival rates RF_i (Eq.3.7) and metamorphosis rates TR_i (Eq.3.9) per age class were estimated and they are given in Fig.3.7c and Fig.3.7d, respectively. The survival rate RF_i of the 0+ age class was calculated using the estimated recruitment and it was found higher than the survival of 1+, 2+… age classes (Fig.3.7c). This result occurred because the population of 0+ age class, which was sampled during September-October of 2011, is composed by the same specimens which arrived as glass eels through natural recruitment during spring of 2011. Thus, the survival rate of 0+ age class is a half-year rate and not a full-year rate (as in the case of the rest age classes). The half-year rate corresponds only to the warm season, while it does not include the winter period where frost is an additional factor for mortality increase especially in the case of elvers (mortality due to low water temperature may start to appear even from 12°C for *A. anguilla* according to Wu et al. (2010)). The above fully justify the higher value of half-year survival rate of the 0+ class in comparison to the full-year rates of some of the next age classes (e.g. 1+ to 5+ in Fig.3.7c) which are affected by winter effects. The above contradict the assumption of De Leo and Gatto (1995) who assumed that natural mortality during winter is negligible because eels can strongly reduce feeding activities and metabolic rate by entering to a state of torpor. Indeed, eels respond in such way in order to overcome cold water conditions by moving to deeper waters >5m (Westerberg and Sjöberg, 2014) but the mortality due to low water temperature can not be considered negligible since high mortality events have been recorded in the lagoon in periods of frost (Rossi and Cataudella, 1998). The probability of such phenomena is quite high in Comacchio lagoon due to its shallow water depth (0.5-1.5 m).

The total abundance of yellow eels was estimated at 8.77 ind. ha^{-1} (sum of age classes of Fig.3.7a), while the total abundance of the population (yellow + silver) before migration was estimated at 9.33 ind. ha^{-1} (sum of 8.77+0.56 ind. ha^{-1}). The stock of yellow eels remaining in the lagoons after silver eel migration in 2011 was estimated at 0.66 g ha^{-1} based on the weights of each age class of yellow eels, which is equal to a total of 5601 kg after extrapolation for the entire lagoon.

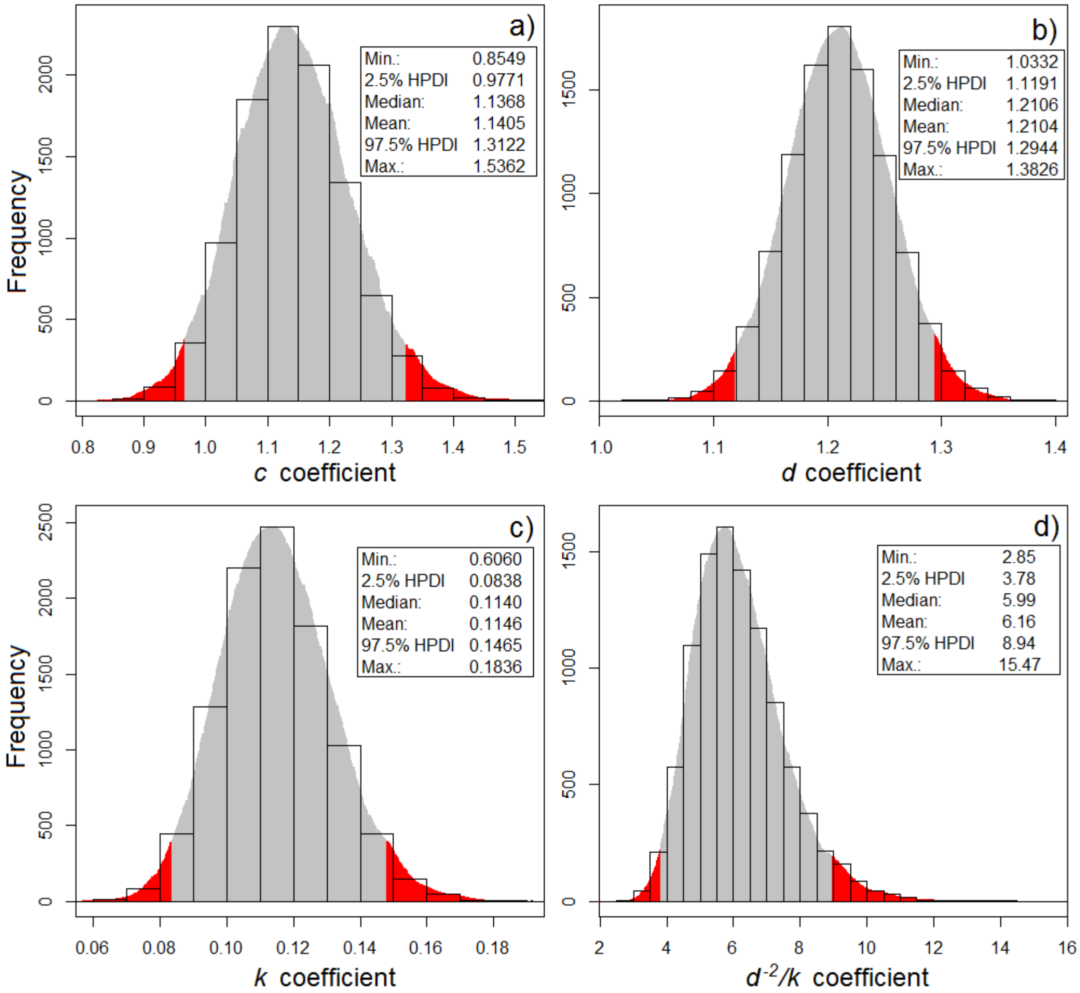

Fig.3.6 *Frequency and highest posterior density distributions (HPDDs) based on the 10,000 bootstrap estimations of a) c coeficient of Eq.3.9, b) d coefficient of Eq.3.9, c) k coefficient of Eq.3.9 and d)* d^{-2}/k *which is equivalent to the estimated recruitment of 2011 as ind.* ha^{-1} *(the grey zone defines the regions of the 95% highest posterior density).*

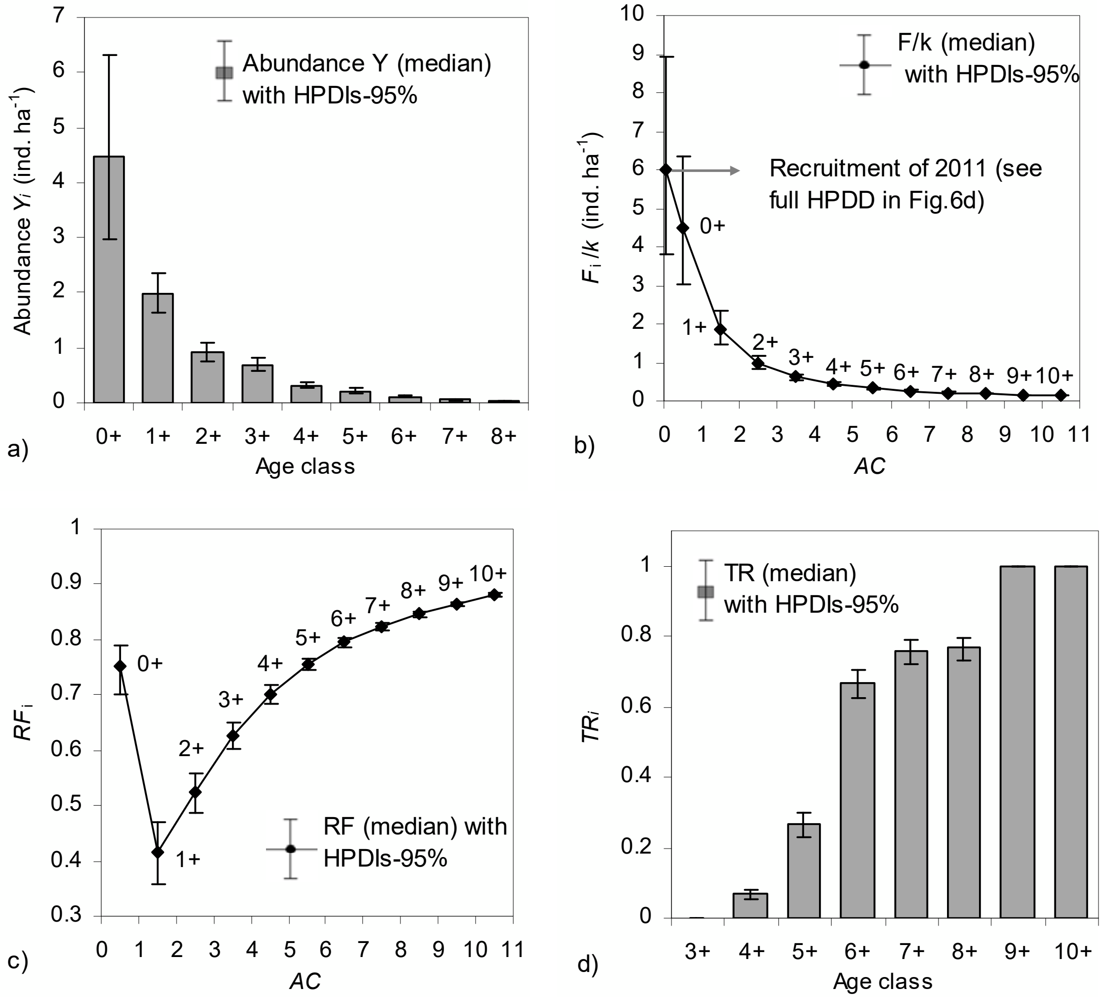

Fig.3.7 *a) Abundance per age class Y_i (ind. ha^{-1}) of yellow eels together with their HPDIs-95%, b) abundance per age class F_i/k (ind. ha^{-1}) of both yellow+silver eels together with their HPDIs-95%, c) survival rates per age class RF_i together with their HPDIs-95%, and d) metamorphosis per age class TR_i to silver eels together with their HPDIs-95%.*

3.5.3 Validation

The Eq.3.11 was used to estimate the abundance S_i^{j+1} (ind. ha^{-1}) per age class of silver eels for 2012 (migrating population of the next year) using the 10,000 sets of Y_i, RF_i and TR_i parameters. The sum of predicted S_i^{j+1} values for 2012 was estimated at f=0.329 ind. ha^{-1} (median value). Each one of the bootstrap estimations of f for 2012, was multiplied with the total fishing area (8470 ha) and the median weight of silver eel specimens (1.253 kg) in order to provide a respective number of predictions for the total silver eel catch in kg. The frequency distribution and HPDDs of the predicted catches for 2012 and their comparison with the observed value is given in Fig.3.8. According to Fig.3.8, the observed value is inside the HPDI-95% of the predictions while the median predicted value by the model (3495 kg) was found approximately 8% lower from the observed one.

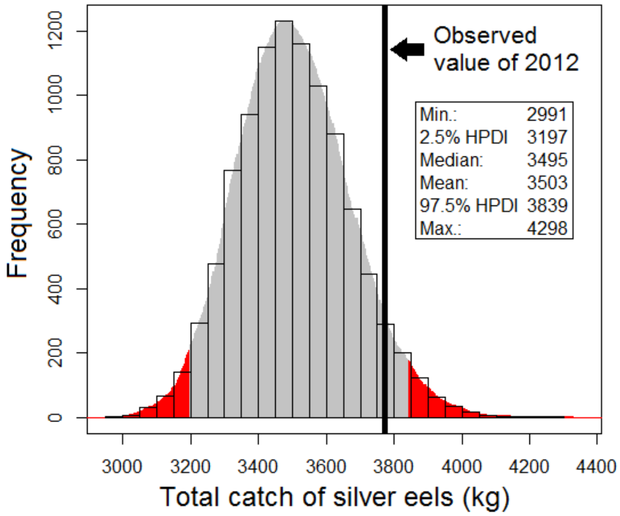

Fig.3.8 *Predicted values of silver eel catch of 2012 together with their HPDIs-95% and comparison with respective observed value.*

3.6 Discussion

Despite the satisfactory performance of the proposed model to assess the population dynamics, it is required to discuss the assumptions used in the modeling approach and the observed limitations during data acquisition, which were both regulated by the type of the local environment and the characteristics of the local population.

For example, the preliminary analysis for the derivation of the survival curve and the adoption of the final form of Eq.3.6 was based on the corrected G_i values of the yellow eel age classes in which metamorphosis to silver eels was not observed. Since silver eels below the age 4+ were not found in our study, the preliminary analysis for the development of the survival curve was based on four classes (four observations). This number of observations is satisfactory for this type of problem, since in many occasions they can be fewer because transformation to silver eels may occur even in the 3+ age class (Rossi, 1979; Laffaille et al., 2006). If we also consider the fact that some of the initial G_i values were corrected due to the selectivity of the fyke nets (one was corrected in our case), then the real and correct observations of G_i can be even fewer. An additional value that could be used is the quantitative measurement of recruitment but in this case the G_i values correspond to frequency while recruitment is considered directly as abundance, and these two parameters are not comparable since the conversion parameter k is unknown (k is estimated in the next steps of the mathematical procedure). If recruitment is a known parameter, a prediction-correction analysis has to be performed in order to correct the form of the survival curve. In our case, the proposed survival curve worked well to identify the population dynamics but its ability to estimate the recruitment must be further investigated since recruitment measurements were not available. Further investigations on the theoretical concept are also required for the validity of the procedures in the section which describes the development of selectivity curve since local environmental conditions and fish behavior are also likely to affect fyke-net selectivity (Naismith and Knights, 1990a,b; Desprez et al., 2013).

Semi-closed lagoons (such as Comacchio), which are connected to the sea only through managed canals, facilitate the monitoring of silver eels migration but a quantitative assessment of recruitment is restricted for various reasons. The recruitment takes place in a three month period (for Comacchio this period is from February to April; unpublished data) and all the possible pathways, which connect the lagoon to the sea, must be blocked on the whole cross section. Blockage is performed with fine mesh nets (2 mm size) connected to fyke nets in order to capture glass eels. Such attempts for quantitative measurements are impossible in practice because a) the small size of glass eels allows them to exploit any possible opening to enter in the lagoon increasing the number of nets needed, b) it is almost impossible to keep stable, clean and effective a 2 mm barrier net for such a long time in swift waters because their mesh may get obstructed by debris and be washed away by the strong tidal currents and c) the use of such structures for a long time may cause implications on ecosystem functioning (e.g. to impede other species recruitment, decrease of the tidal activity etc). A more detailed description of the factors, which regulate glass eel recruitment, and the techniques which can be used for sampling and abundance estimations are given in Harrison et al. (2014). Drouineau et al. (2016) also proposed the use of recruitment indices to overcome the aforementioned problems. The use of such indices can assist the evaluation of models like the one of this study but they require more years of recruitment observations.

One of the targets of the proposed modelling approach is to estimate the abundance per age class of yellow eels and consequently the total population, which remains in the lagoon after the migration of silver eels. The only way to validate the yellow eel stock results of such models is to perform quantitative samplings using trawl nets and electrofishing during the same operation period of the fyke nets, or to use the enclosed system of fyke nets which was proposed by Ubl and Dorow (2015) for non-tidal coastal waters. In our case, these methods were not possible to be performed due to basic limitations. For example, quantitative samplings can not be used because eels are not homogeneously distributed in the lagoon, they show extremely sedentary behaviour and they stay hidden in shelters such as holes on the bottom or inside the stones of the lagoonal coastline. Trawl nets and electrofishing samplings are affected by selectivity, as the fyke nets, and additional analysis for each method is required to correct the respective errors. For the case of Comacchio, where water is saline to hyper-saline and turbidity is quite high (Sorokin and Zakuskina, 2010), the efficiency of electrofishing is expected to be almost null due to its limitations under these conditions (SFCC, 2007; Baldwin and Aprahamian, 2012). The sampling structure, which was proposed by Ubl and Dorow (2015), could be a useful solution for further evaluation of model's assumptions and estimated stock densities.

Additional problem in this study was the low number of observed males (~1%) which is attributed to the low eel population density that favours female dominance (Davey and Jellyman, 2005). Sexual dimorphism is usually considered in such models, but in our case it was not applied due to the low number of male specimens. During the procedure of outliers removal, before the fitting procedure of Eq.3.4a and Eq.3.5, it was observed that almost all of the few observations from male specimens in the data were excluded as outliers. Thus, the modelling approach, which was followed in this study, described the population dynamics of a female dominated population. For eel populations with higher % of males, which allow robust analysis of their morphometric characteristics, the inclusion of sexual dimorphism must be included in the modelling approach (De Leo and Gatto, 1995).

The application and validation of the proposed modelling approach can be performed only when the migration of silver eels is fully monitored in such way to obtain their total population abundance (parameter f). During the validation procedure, it was assumed that the RF_i and TR_i rates remain the same for the next year. This assumption can be considered valid when there is no significant variation in the population density between the calibration and validation years. In our case this assumption was indirectly considered valid by Fig.3.2.

The application of the proposed modelling approach and the monitoring datasets of this study provided significant information about the recent conditions of eel population in the Comacchio lagoon allowing the comparison with scientific studies of the past. The data presented in Table 3.1 and 3.2 were used by Castaldelli et al. (2014) to analyze the length-weight, length-age relationships and feminization of 2011 in comparison to previous studies which were conducted using data from the 70s and 80s (Rossi, 1979; De Leo and Gatto, 1996). The results showed faster maturation rates (fewer age classes) and higher feminization (reaching 99%), for the population of 2011 in comparison to the past conditions which indicates that the population density was reduced to critical levels (Colombo and Rossi, 1978; Svedäng et al., 1996; De Leo and Gatto 1996; Desprez et al., 2013). The critical conditions of the population density are verified by the records of silver eels catches of the period (1960-2013) which show evident collapse of the population during 90s (Fig.3.2). For the period 1998-2013, the migrating population of silver eels is stabilized to the lowest observed values with a mean±st.dev. equal to 0.68±0.36 kg ha^{-1}, while for the period of 1960-1997 was 11.8±8.6 kg ha^{-1} (Fig.3.2). The comparison between the two periods indicates a reduction of silver eels approximately to 94%. Further comparison was also performed between the estimated recruitment of 2011 by our modelling approach and the estimated recruitment using data from 1989 (De Leo and Gatto 1995, 1996, 2001; De Leo et al. 2009). Using a bootstrapping procedure, De Leo et al. (2009) showed that the highest probability of recruitment intensity for 1989 is in the range between 50-100 ind.ha^{-1}, which is more than ten times higher that the estimated value of 5.99 ind.ha^{-1} in 2011.

The plethora of past and recent scientific studies of the eel population dynamics in Comacchio lagoon sets this study area as one of the most important places to investigate exemplary the development of a local eel stock. Apart from Comacchio, many European semi-closed lagoons already have the appropriate infrastructure (e.g. *lavorieri*) to monitor the total migrating population of silver eels, which reduces significantly the monitoring cost and time in comparison to other monitoring methods, which focus on recruitment. These places can be used as reference sites not only for estimations of the local eel production and the development of models but also for estimation of the spawning potential of the total European eel population. Decision makers and scientists, which are responsible for the development of management plans for the recovery of European eel population, can exploit the advantages of such semi-closed lagoons to analyze the potential consequences of different conservation strategies.

3.7 References

Aprahamian, M.W., Walker, A.M., Williams, B., Bark, A., Knights, B., 2007. On the application of models of European eel (*Anguilla anguilla*) production and escapement to the development of Eel Management Plans: the River Severn. ICES Journal of Marine Science 64(7), 1472–1482.

Baldwin, L., Aprahamian, M., 2012. An evaluation of electric fishing for assessment of resident eel in rivers. Fisheries Research 123–124, 4–8.

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.

Bevacqua, D., Melia, P., Crivelli, A. J., Gatto, M., De Leo, G.A., 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, A.J., Gatto, M., De Leo, G.A., 2009a. 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., De Leo, G.A., Gatto, M., Melià, P., 2009b. Size selectivity of fyke nets for European eel *Anguilla anguilla*. Journal of Fish Biology 74, 2178–2186.

Bernardo, J.M., 2005. Intrinsic credible regions: An objective Bayesian approach to interval estimation. Sociedad de Estadistica e Investigacion Operativa 14, 317–384.

Bonhommeau, S., Le Pape, O., Gascuel, D., Blanke, B., Tréguier, A.-M., Grima, N., Vermard, Y., Castonguay, M., Rivot, E., 2009. Estimates of the mortality and the duration of the trans-Atlantic migration of European eel *Anguilla anguilla* leptocephali using a particle tracking model. Journal of Fish Biology 74, 1891–1914.

Briand, C., Beaulaton, L., Chapon, P.M., 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.

Castaldelli, G., Aschonitis, V., Lanzoni, M., Gelli, F., Rossi, R., Fano, E.A., 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.

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

Colombo, G., Grandi, G., 1996. Histological study of the development and sex differentiation of the gonad in the European eel. Journal of Fish Biology 48, 493–512.

Davey, A.J.H., Jellyman, D.J., 2005. Sex determination in freshwater eels and management options for manipulation of sex. Reviews in Fish Biology and Fisheries 15, 37-52.

Dekker, W., 2000a. The fractal geometry of the European eel stock. ICES Journal of Marine Science 57, 109–121.

Dekker, W., 2000b. A Procrustean assessment of the European eel stock. ICES Journal of Marine Science 57, 938–947.

Dekker, W., 2004. Slipping through our hands - Population dynamics of the European eel. PhD thesis, University of Amsterdam, pp 186, ISBN 90–7454910–1.

Dekker, W., Casselman, J.M., 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.

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

De Leo, G.A., Gatto, M., 2001. A stochastic bioeconomic analysis of silver eel fisheries. Ecological Applications 11, 281–294.

De Leo, G., Melia, P., Gatto, M., Crivelli, A., 2009. Eel population modeling and its application to conservation management. American Fisheries Society Symposium 58, 327–345.

Dennis, J.E.Jr., Gay, D.M., Welsh, R.E., 1981. An adaptive nonlinear least-squares algorithm. ACM Transactions on Mathematical Software 7, 348–368.

Desprez, M., Crivelli, A.J., Lebel, I., Massez, G., Gimenez, O., 2013. Demographic assessment of a stocking experiment in European Eels. Ecology of Freshwater Fish 22, 412–420.

Dorow, M., Beardmore, B., Haider, W., Arlinghaus, R., 2009. Using a novel survey technique to predict fisheries stakeholders' support for European eel (*Anguilla anguilla* L.) conservation programs. Biological Conservation, 142 (12), 2973–2982.

Drouineau, H., Briand, C., Lambert, P., Beaulaton, L., 2016. GEREM (Glass Eel Recruitment Estimation Model): A model to estimate glass eel recruitment at different spatial scales, Fisheries Research 174, 68–80.

Durif, C.M.F., Dufour, S., Elie P., 2005. The silvering process of the eel: a new classification from the yellow resident stage to the silver migrating stage. Journal of Fish Biology 66, 1025–1043.

Durif, C.M.F., van Ginneken, V., Dufour, S., Müller, T., Elie P., 2009. Seasonal evolution and individual differences in silvering eels from different locations. In: Van den Thillart G., Dufour S., Rankin J.C. (Eds.) Spawning migration of the European eel: Reproduction index, a useful tool for conservation management, Fish and Fisheries Series 30, Springer, pp 13–38.

Efron, B., Tibshirani, R.J., 1993. An introduction to the bootstrap. New York: Chapman & Hall.

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

Feunteun, E., Acou, A., Laffaille, P., Legault, A., 2000. European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. Canadian Journal of Fisheries and Aquatic Sciences 57, 1627–1635.

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

Francis, R.I.C.C., Jellyman, D.J., 1999. Are mean size data adequate to monitor freshwater eel fisheries? Marine and Freshwater Research 50, 355–366.

Froese, R., 2006. Cube law, condition factor and weight–length relationships: History, meta-analysis and recommendations. Journal of Applied Ichthyology 22, 241–253.

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

Gatto, M., Laniado, E., Rossi, R., 1982. The management of eels in the Valli di Comacchio lagoon. Oceanologica Acta V(4, Suppl.), 303–307.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2014. Bayesian data analysis. Third Edition, Chapman & Hall/CRC press, Taylor and Francis Group, pp. 675.

Harrison, A.J., Walker, A.M., Pinder, A.C., Briand, C., Aprahamian, M.W., 2014. A review of glass eel migratory behaviour, sampling techniques and abundance estimates in estuaries: implications for assessing recruitment, local production and exploitation. Reviews in Fish Biology and Fisheries 24, 967–983.

Hoyle, S.D., Jellyman, D.J., 2002. Longfin eels need reserves: modelling the effects of commercial harvest on stocks of New Zealand eels. Marine and Freshwater Research 53, 887–895.

ICES, 2009. Workshop on Age Reading of European and American Eel (WKAREA), 20-24 April 2009, Bordeaux, France. ICES CM 2009\ACOM, 48, pp. 66.

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

Laffaille, P., Acou, A., Guillouët, J., Mounaix, B., Legault, A., 2006. Patterns of silver eel (*Anguilla anguilla* L.) sex ratio in a catchment. Ecology of Freshwater Fish 15, 583–588.

Lambert, P., Rochard, E., 2007. Identification of the inland population dynamics of the European eel using pattern-oriented modelling. Ecological Modelling 206, 166–178.

Macnamara, R., Mccarthy, T.K., 2014. Silver eel (*Anguilla anguilla*) population dynamics and production in the River Shannon, Ireland. Ecology of Freshwater Fish 23, 181–192.

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

Naismith, I.A., Knights, B., 1990a. Modelling of unexploited and exploited populations of eels *Anguilla anguilla* (L.), in the Thames estuary. Journal of Fish Biology 37, 975–986.

Naismith, I.A., Knights, B., 1990b. Studies of sampling methods and of techniques for estimating populations of eels, *Anguilla anguilla* L.. Aquaculture Research 21, 357–367.

Oeberst, R., Fladung, E., 2012. German Eel Model (GEM II) for describing eel, *Anguilla anguilla* (L.), stock dynamics in the river Elbe system. Inf. Fischereiforsch 59, 9–17.

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

Prigge, E., Marohn, L., Oeberst, R., Hanel, R., 2013. Model prediction vs. reality - testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ*observation of silver eel escapement in compliance with the European eel regulation. ICES Journal of Marine Science 70, 309–318.

Ritz, C., Streibig, J.C., 2008. Nonlinear regression with R. Springer, New York.

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. Boll. Zool. 46, 217–223.

Rossi, R., Cataudella, S., 1998. La produzione ittica nelle valli di Comacchio. Atti del Convegno Scientifico Laguna "Risanamento e tutela delle vallidi Comacchio fra conservazione ambientale e valorizzazione produttiva, pp 67–76. (in Italian)

Schiavina, M., Bevacqua, D., Melià, P., Crivelli, A.J., Gatto, M., De Leo, G.A., 2015. A user-friendly tool to assess management plans for European eel fishery and conservation. Environmental Modelling and Software 64, 9-17.

SFCC, 2007. Fisheries Management SVQ Level 2: Catch fish using electrofishing techniques. Scottish Fisheries Co-ordination Centre, pp. 44.

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

Starkie, A., 2003. Management issues relating to the European eel, *Anguilla anguilla*. Fisheries Management and Ecology 10 (6), 361–364.

Svedäng, H., Neuman, E., Wickström, H., 1996. Maturation patterns in female European eel: Age and size at the silver eel stage. Journal of Fish Biology 48, 342–351.

Tesch, F.W., 2003. The eel. Willey-Blackwell Publishing, Oxford, UK, pp.416.

Ubl, C., Dorow, M., 2015. A novel enclosure approach to assessing yellow eel (*Anguilla anguilla*) density in non-tidal coastal waters. Fisheries Research 161, 57–63.

van Ginneken, V.J.T., Durif,C., Balm, S.P., Boot, R., Verstegen, M.W.A., Antonissen, E., Guido van Den Thillart, G., 2007. Silvering of European eel (*Anguilla anguilla* L.): seasonal changes of morphological and metabolic parameters. Animal Biology 57, 63–77.

Vøllestad, L.A., Jonsson, B., 1988. A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. Journal of Animal Ecology 57, 983–997.

Westerberg, H., Sjöberg, N., 2014. Overwintering dormancy behaviour of the European eel (*Anguilla anguilla* L.) in a large lake. Ecology of Freshwater Fish 24, 532–543.

Wickström, H., Sjöberg, N.B., 2013. Traceability of stocked eels – the Swedish approach. Ecology of Freshwater Fish 23, 33–39.

Wu Ning, Li Wenjing, Li Zhongbao, Zheng Weigang, 2010. Preliminary study on tolerance of elver of 5 *Anguilla* species to ultimate water temperature. South China Fisheries Science 6(6), 14–19.

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Long-term series (1781-2013) of European eel production in the Comacchio lagoon: local and global stressors of the population collapse

4.1 Summary

Several eel species (*Anguilla* spp.*)* have undergone an extensive decline at the global level. The aim of the study is to identify the reasons of collapse of the European eel (*Anguilla anguilla* L.) stock in an important area for biodiversity conservation (Comacchio lagoon-Italy), in order to support the development of eel conservation plans. The records of silver eel catches from Comacchio are equivalent to the total migrating population and cover the period 1781-2013. The data are accompanied with information related to habitat loss and other local stressors. The role of the local stressors on the decline of local stock was investigated while additional information from the literature was also used to discuss the effects of global stressors (such as glass eel harvest for aquaculture, climate-oceanographic changes, habitat loss, pollution and parasitism) on the three eel species *A. anguilla*, *A. japonica*, *A. rostrata*. The records from Comacchio provided significant information about the effects of local stressors in the past but the population collapse, which started in the '70s with no signs of recovery, could not be explained. The literature about the global stressors suggests that the three eel species are under a combined threat from various directions. Aquaculture, which depends entirely on wild-caught glass eels, seems to play a key role in the decline of natural stocks. 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 significantly high exposing the crucial role of aquaculture. Conservative estimations using FAO data showed that the current amount of glass eels needed to support aquaculture production in Europe and Asia exceeds the 2×10^9 specimens. This demand, largely covered by *A. anguilla* glass eel, can justify eel populations decline since glass eel trade has been expanded at international level.

4.2 Introduction

European eel (*Anguilla Anguilla*, Linnaeus 1758) is a catadromous and semelparous species which spends most of its life as yellow eel in fresh water, brackish and coastal habitats. When reaching maturity, it metamorphoses to 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 go upstream in fresh water habitats (recruitment), where they change to elvers setting the initiation of the yellow eel stage (Tesch, 2003).

Long-term records of eel species (*Anguilla* spp*.)* from the last four decades indicate an extensive reduction world-wide, while *A. anguilla* is already placed on the IUCN Red List of critically endangered species (Jacoby and Gollock, 2014). After the seventies, the commercially most important species; European eel and 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 decline are 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 conditions 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). The eel fishery of the Comacchio Lagoon at northeastern Italy was one of the most important in terms of production. Restocking in the lagoon has never been performed and 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 correspond to the ~100% of the migrating population. Thus, it presents an excellent paradigm for investigating the effects of the eel fishery management strategies that have been employed over the years. Additionally, it can be considered 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 of trends in the European eel population as a whole, since it 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 study is to identify the local and global stressors of 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); in order to support the development of future conservation plans for eel species. Historical records of silver eel catches which cover the period 1781-2013 are provided in this study. The data are used to highlight the population decline, while a detailed discussion is performed for the potential role of major local (habitat loss, changes in local environmental conditions) and global stressors (aquaculture and fisheries, climate change, habitat loss, pollution and parasitism) which may be responsible for the populations decline of this important eel species.

4.3 Materials and methods

4.3.1 Study site

The eel fishing industry of Comacchio lagoon is of very considerable antiquity and constitutes one of the best paradigms to understand the evolution of eel fishing activities over the centuries. According to Bertram (1873), the region was initially a great swamp accessible to the sea (Fig.4.1a).

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 the place grew in prosperity, its fisheries 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.

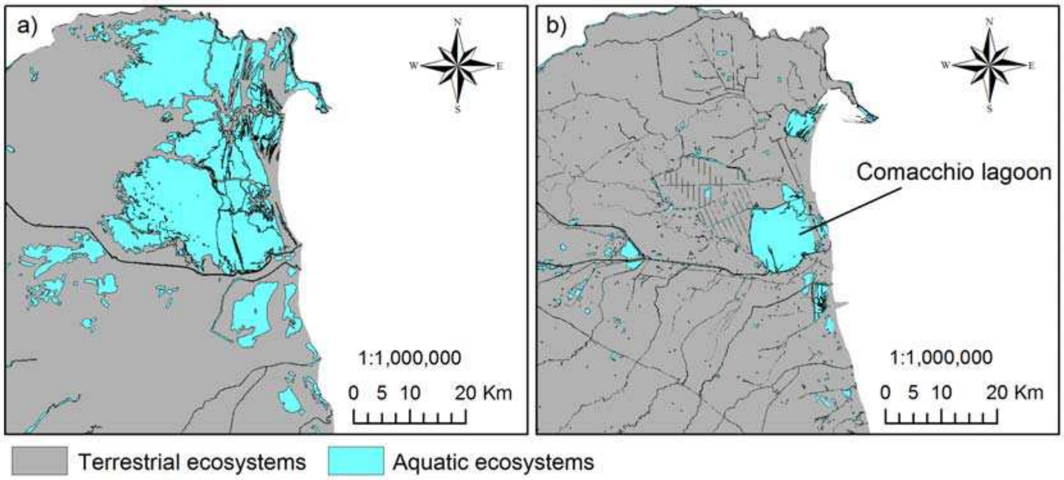

Fig.4.1 *a) System of lagoons in the Po River delta and Comacchio region during 1853 and b) coverage of Comacchio lagoon region in 2008 (source: http://geoportale.regione.emilia-romagna.it/).*

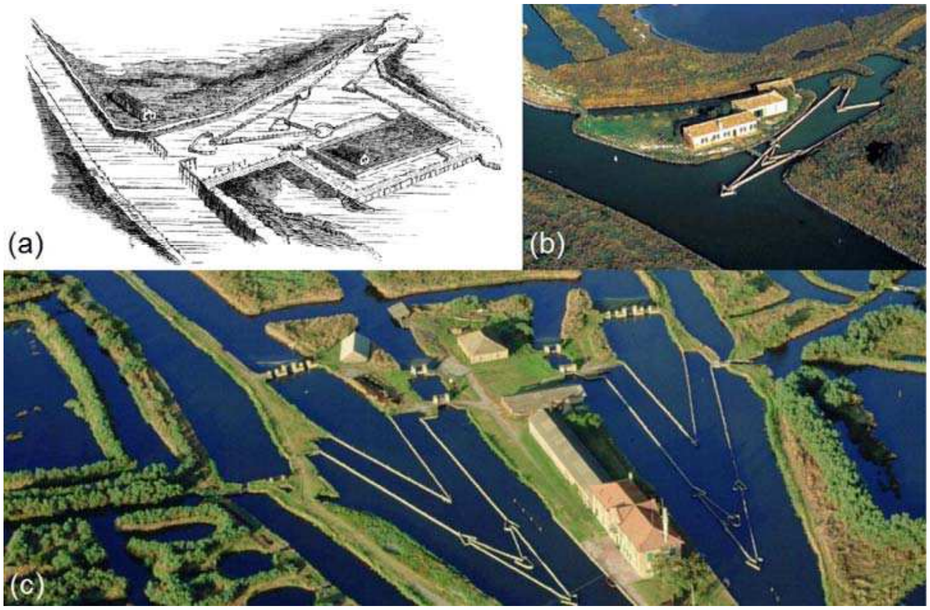

Fig.4.2 *Structure characteristics of the lavorieri, a) in the lagoons of North-eastern Italy during the eightieth century according to drawings reported in Bertram (1873) (source: http://www.electricscotland.com/lifestyle/sea/chapter3.htm), b) this is probably the lavorieri of Bertram drawing as it 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.ferrararaterraeacqua.it/it/parco-del-delta-del-po/cercatori/gallery-parco-del-delta-del-po/valli-e-lavorieri/image_ftaslider).*

Bridges had also been built over all these trenches 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 Fig.4.2a,b,c. Even in the previous centuries, the inhabitants of Comacchio had good knowledge about the migration and recruitment periods. Friedlander (1872) and Bertram (1873) provide extensive details of this knowledge, which is quite surprising since fishermen knew also how to obtain measurements, to keep records of eel catches and to make estimations of the young fish which were hosted in the lagoon.

Nowadays, the Comacchio Lagoon comprises three main basins: Valle Campo, Valle Magnavacca, and Valle Fossa di Porto, which cover an area of ~10^4 ha (Fig.4.1b). Valle Campo (~1600 ha) is completely separate and in private ownership, while the other two constitute now 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. The study site is recognized as one of the most important coastal wetlands in Europe for biodiversity conservation and in 1988 was 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).

4.3.2 Data and Methods

The silver eels of Comacchio lagoon were always caught in the lavorieri at approximately 100% efficacy and official measurements of the total biomass were being performed 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 the infrastructures, official documents, and records of the previous company managing the fishery. These historical records were organized and combined with new data providing 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 about the Comacchio lagoon were used to investigate the role of local and global stressors on the eel stock. The investigation about 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. A special focus was given in this study on 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 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.

4.4 Results and discussion

4.4.1 Silver eel production 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 given in Table 4.1 and are illustrated in Fig.4.3a together with the total weight of silver eel catches of the same period. As indicated in Table 4.1 and Fig.4.3a, the most intensive habitat loss was observed in the periods 1916-1930 and 1966-1967, while after the 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 lands. 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 Fig.4.3b.

The recorded mortality events due to local stressors are given in Table 4.2. These records stop in 1985 since after 1988 professional fishing was banned while the stock had already declined (Fig.4.3) not allowing such observations. The main reasons of documented mortality were hypersalinity, frost and ice coverage, and the flooding of Reno River. The case of hypersalinity and frost followed by ice coverage were the most serious local stressor due to the shallow nature of the lagoon (0.5-1.5 m) (Rossi and Cataudella, 1998). Table 4.2 also includes records of some unexplained high mortality events. Probable explanations for these events may be 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 cannot 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 4.2) while low levels of infections by *Anguillicoloides crassus* have been identified without significant impact on the population (Dezfuli et al., 2014).

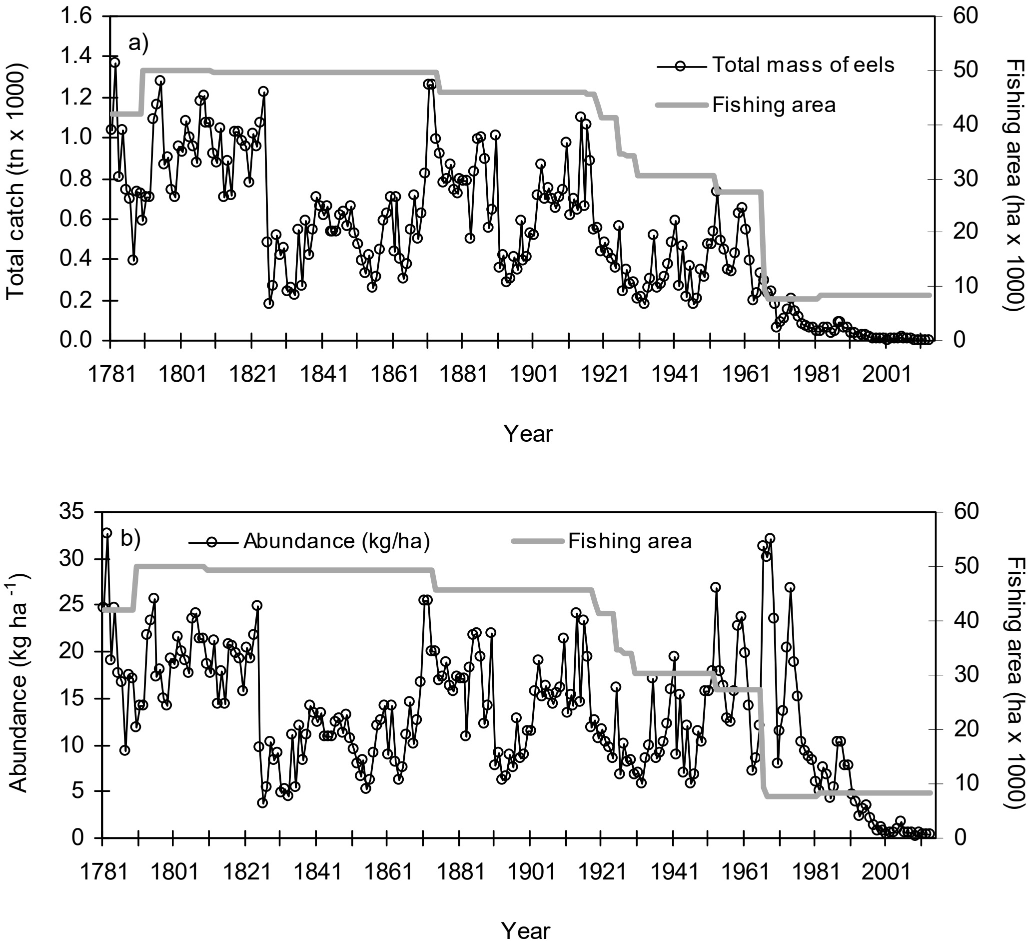

Fig.4.3 *Eel fishing area coverage (ha) together with the a) annual variation of silver eel production (tn×1000) and b) abundance of silver eels (kg ha*$^{-1}$*) in the Comacchio lagoon for the period 1781-2013.*

Table 4.1 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 1781-2012		-33530

Table 4.2 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).

After the 1960, the scientific community started to investigate 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 caused the mortality of bottom vegetation, benthic fauna, eels, mullets 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 after that ecosystem shift was performed in 2011 by Castaldelli et al. (2014) which 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 from the respective estimations 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 presented 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 the 1960 the biomass production started to decline and after the year 2000 dropped to critical levels (Fig.4.3a). The loss of habitat during 1966-1967 for the reclamation of a big portion of the logoonal complex (Table 4.1), was almost certainly the most important local stressor causing a decline in terms of total mass (Fig.4.3a). 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, it was observed 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 (Fig.4.3b), while 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 be given to the effects of global stressors since a general decline of eel species was observed contemporaneously at the global level. Thus, further discussion is performed about the global stressors in the next sections.

4.4.2 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 the last forty years (Fig.4.4) (IES, 2003; Dekker and Casselman, 2014). This global decline triggers the interest to investigate the probable effects of global stressors on eel populations collapse and for this reason five hypotheses for the global decline are discussed in the following sections.

4.4.2.1 Aquaculture and glass eel harvest

Fishing has almost been abandoned as a source of eels in favour of aquaculture, which covers more than 90% of eels in the global trade (FAO, 2009; Crook, 2010). This percentage justifies the estimations of Dekker (2000) which reported that 80-95% of the glass eels is harvested. The basic feature of eel aquaculture is that it is totally dependent on wild-caught juveniles (glass eels or elvers).Significant steps of 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 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* (Fig.4.5a,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 (Fig.4.5a). This decrease may be attributed to two reasons: a) the decline of available glass eel 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*, whose population had already declined, led many non-European eel farms to use *A. anguilla* glass at the end of the 1990s.

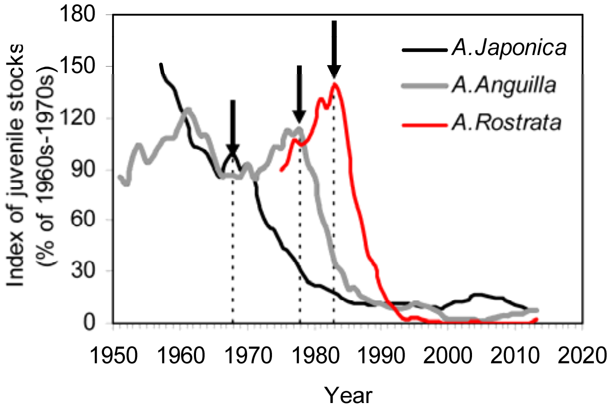

Fig.4.4 *Time trends in juvenile abundance of the major eel stocks of the world (from Dekker and Casselman, 2014). The arrows and vertical lines indicate the year of the collapse initiation.*

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 (Fig.4.5b). The continuous increase of Asian aquaculture production after 1990 (Fig.4.5b) raises questions about the origin of glass eels used, since the juvenile stocks of *A. japonica* declined to a minimum plateau after 1990 (Fig.4.4). This tremendous increase can only be explained by the use of imported glass eels of other species. This activity may also 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 about *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. (2015) provide important information about the natural populations and eel market of *A. rostrata* in North America.

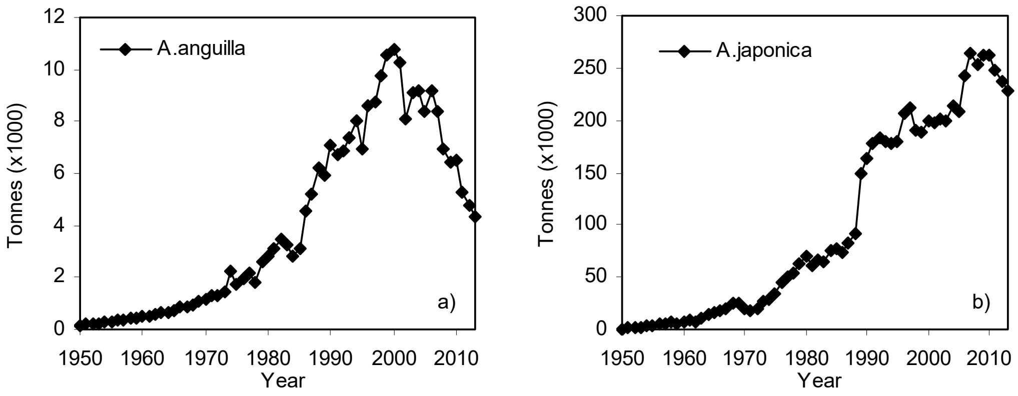

Fig.4.5 *Official data of FAO for eel aquaculture production: a) in Europe for A. anguilla and b) in Asia for A. japonica for the period 1950-2013 (source: Fisheries and Aquaculture Information and Statistics Service of FAO – database of FishStatJ software v.2.12.4 for fishery time series, last date of data release: March of 2015).*

A first evidence about the role of aquaculture in the decline of European eel population can be provided by correlations between the total catches of Comacchio lagoon (Fig.4.3a) and aquaculture production in Europe (Fig.4.5a). 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 was maximized for 3-years lag-time with ρ=-0.949 (P<0.0001) (Fig.4.6a).

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) (Fig.4.6b). Data of 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 (Fig.4.5a) 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 on Feunteun (2002) data was maximun for 0-years lag-time with ρ=-0.924 (P<0.0001) (Fig.4.6c). 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 to the market in order to achieve lower cost of production using the new cheaper glass eels.

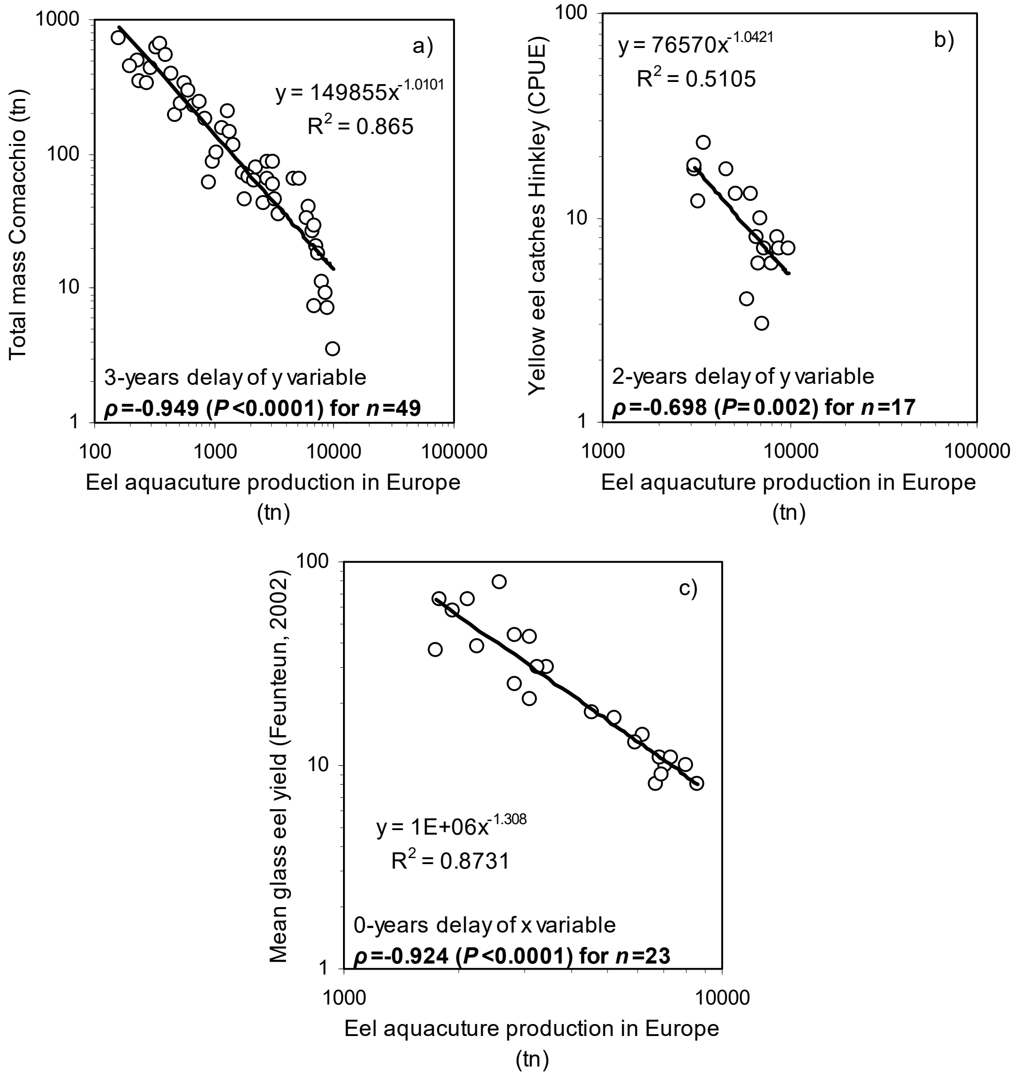

Fig.4.6 *Correlations between eel aquaculture production in Europe versus a) total eel catches from Comacchio lagoon, b) CPUE values of yellow eel catches from Hinkley Point in Bridgwater Bay (Somerset, UK) provided by Henderson et al. (2012), c) mean glass eel yields from sites located in the west European coastlines estimated by Feunteun (2002).*

It is also worth mentioning the additional problem of non-controlled or illegal trading for which official evidences date back to the early '90s (Kennedy and Fitch, 1990). Such activities have also been reported by Silfvergrip (2009), who provided 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 the black market of *A. anguilla* glass eel will increase more in the near future due 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 (Fig.S.1 in supplementary material) 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 efforts of the European Union to control it 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 initiation of collapse of juvenile stocks appears first for *A. japonica* around 1968, second for *A. anguilla* around 1978 and finally for *A. rostrata* around 1983, with interval periods of 10 and 5 years, respectively (Fig.4.4). It is already known that the Asian aquaculture was and still is the most demanding for glass eels while it is also documented that after the 1970s, high amounts of other glass eel species were transferred to Asian market and especially to Japan to expand aquaculture (Egusa, 1979; Briand et al., 2008). In order to provide a more robust evidence of the aquaculture contribution in global population collapse, a conservative estimation was performed for the global glass eel demands for aquaculture production, taking into account that: a) 200 g is the mean maximum weight of both produced 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 are 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 ~255 thousands tones, the final number of glass eels, which is required to support the current production, is estimated at ~2 billions glass eels (97.8% of this estimation 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 rest part of the recruitment, which finally reaches the natural habitats, and the 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 are caught in France by non-professional fishermen (Castelnaud, 2002; Ringuet et al., 2002).

Considering the above, 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-rated, dependence on glass eel of other species, particularly *A. anguilla* (Zhang et al., 1999; Katoh and Kobayashi, 2003; Sezaki et al., 2005; Arai et al. 2014a) but also *A. rostrata* (Ooi et al., 1996; Crook and Nakamura, 2013). This dependence has been dramatically expressed in the case of glass eel from France as widely reported by the media (http://news.bbc.co.uk/2/hi/europe/4432951.stm). An additional proof to support the hypothesis of glass eel overharvest for aquaculture is a distinguishable increase of European eel recruitment after the application of the moratorium on the export of glass eel in 2010 (ICES, 2014; Briand, 2015) (Fig.4.7). Of course, it is still unknown if the activation of the moratorium has triggered the increase of illegal trade.

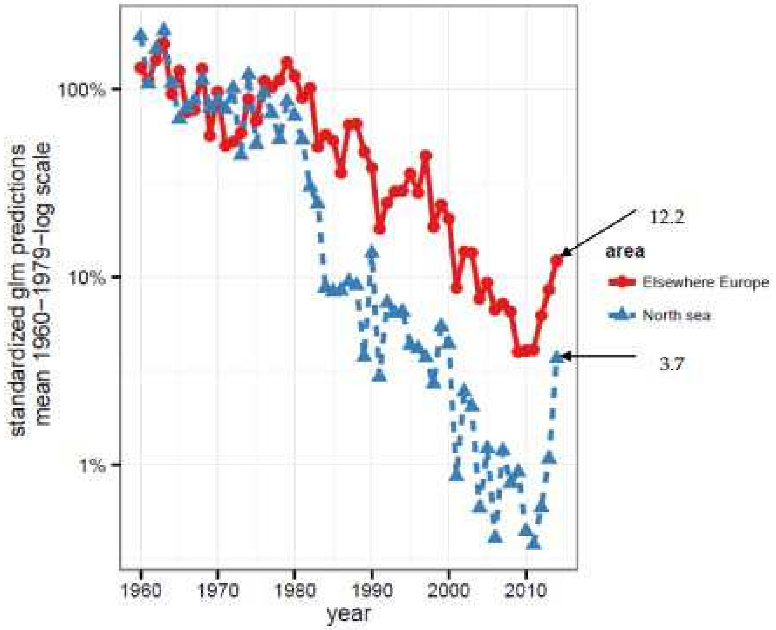

Fig.4.7 *WGEEL recruitment index: mean of estimated glass eel recruitment for the continental North Sea and elsewhere in Europe updated to 2014 (from ICES, 2014).*

4.4.2.2 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 present high fluctuation (Fig.4.8). The observed recruitment trends by the authors can not justify the trends of juvenile stocks of *A. japonica* presented in Fig.4.4. 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 not a comparison with previous years to support recruitment reduction.

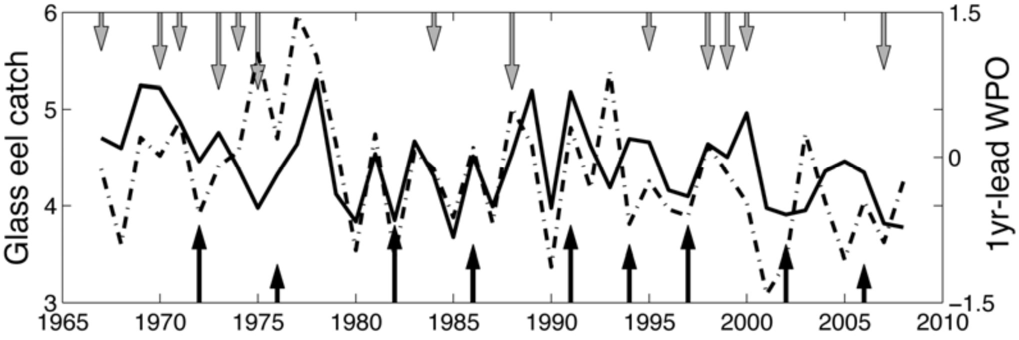

Fig.4.8 *Time series of log$_{10}$(glass eel catch) (bold line) and 1-year leading summer Western Pacific Oscilation index - WPO index (dashed line). The black arrows represent the El Nino years, and the gray arrows represent La Nina years. The length of arrow indicates the strength of the events. The glass eel catches were significantly correlated with summer WPO with 1-year lag. (source: Tzeng et al., 2012)*

For the case of European eel (*A. anguilla*) and American eel (*A. rostrata*), Bonhommeau et al. (2008) showed that indices of ocean circulation did not seem 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 larvae arrivals were explored for a range of constant depth levels and instantaneous 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 to 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 aforementioned opinions may throw 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 consistent 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 justify 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 (Fig.4.4) took place in less than two decades.

4.4.2.3 Habitat loss

The data of area coverage for Comacchio lagoon (Table 4.1) provided a representative example about habitat loss while similar intensity 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 the *A. japonica*, a very interesting study for 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 the *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 habitat in east coast and eastern Lake Ontario basin, once available to migratory fishes (including *A. rostrata*), has been made inaccessible by dams. Marsden et al. (2012) also reported that there are 463 standing dams in the Champlain drainage in Vermont and that American eel 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 et al., 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, 2009; Calles et al., 2010; Piper et al., 2013). The elongated morphology and 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 eel populations decline but special attention should be given regarding the degree of its contribution. According to Moriarty and Dekker (1997) approximately half of the estimated surface of *A. anguilla* habitats includes saline closed and open waters which are not controlled by fisheries. Additionally, the majority of studies for eel habitat loss concern freshwater systems or lagoons associated to 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 and their contribution to spawning and consequently recruitment is impossible to be quantified but it could explain the existing sources of glass eels used in aquaculture.

4.4.2.4 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, 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 on *A. rostrata* specimens by Dutil et al. (1987) and Hodson et al. (1994) showed that 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. (2007) 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 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, 2000; Feunteun, 2002).

The aforementioned aspects 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 in respect to the current study, it was performed after the large decline of eels populations, which was occurred after 70s-80s. Additionally, Sancho et al. (1997) investigated the effects of Fenitrothion insecticide on the energy metabolism of the *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.

4.4.2.5 Parasitism

For the case of parasitism, many studies have shown that wide-spread infections of adult eels from *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., 2007; Wielgoss et al., 2008; Székely et al., 2009). 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 problem of the parasite was coincidental especially with the decline in European eels and cannot be considered as a major cause of populations decline. This can be justified using the case of *A. rostrata* populations which showed a steep decline after 1983 (Fig.4.4), while the first documented observations of American eels infected by *A.crassus* started to appear at least ten years after (Fries et al. 1996; Ooi et al., 1996). It is worth mentioning that the observations of Ooi et al. (1996) for *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 a proof that the Asian market had already established trade connections with America during 90s for exploiting the American glass eels before the first observations of infected *A. rostrata* by *A. crassus*.

The last years, the eel infections by *A.crassus* is not as much of a problem not only in Europe but also in Asia, while a recent study by Dezfulli et al. (2014) showed that the levels of the *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). Dezfulli 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 eel migrating population is significantly higher than freshwater localities.

Taking into account all the existing findings from the literature about the global stressors, it is evident that eel species are under a combined threat from various directions. Without diminishing the role of each global stressor, it seems that aquaculture plays a key role in the decline of natural stocks of all eel species. The high aquaculture production and the estimated high amount of glass eel 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 amount 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 difficult to be fully controlled.

3.5 Conclusions

The records of silver eel catches in the Comacchio Lagoon, equivalent to the local migrating population 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 covering the three major species (*A. anguilla*, *A. japonica*, *A. rostrata*) and provided 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 to a respective expansion of the glass eel market since eels are not reproduced in captivity. The conservative estimations about 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 to non European countries since glass eel trade has been expanded at international level.

3.6 References

Adams, J., Maslin, M., Thoma,s E., 1999. Sudden climate transitions during the Quaternary. Progress in Physical Geography 23, 1–36.

Als, T.D., Hansen, M.M., Maes, G.E., 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, V.G., Castaldelli, G., Lanzoni, M., Merighi, M., Gelli, F., Giari, L., Rossi, R., Fano, E.A., 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 in press 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, C.G.J., 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, J.G., 1873. The Harvest of the Sea - Including sketches of fisheries & fisher folk. Third edition. (http://www.electricscotland.com/lifestyle/sea/chapter3.htm)

Bevacqua, D., Melià, P., Crivelli, A.J., De Leo, G.A., 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, A. J., Gatto, M., De Leo, G.A., 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, A.J., Gatto, M., De Leo, G.A., 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, J.M., Leo, G.A., 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, G.A., 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, P.M., 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, W.D.N., Lary, S.J., Castilione, C.M., McDonald, R.P., 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, J.D., Lebeuf, M., Alaee, M.R., Stephen, B., Trottier, S., Backus, S., Keir, M., Couillard, C.M., Casselman, J., Hodson, P.V., 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, D.K., Chaput, G., Poirier, L.A., Avery, T.S., Castonguay, M., Mathers, A., Casselman, J.M., Bradford, R.G., 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, I.C., Comoglio, C., Kemp, P.S., Blunden, L., Schmitz, M., Greenberg, L.A., 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, I.M., 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, E.A., 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, P.D., Ogonowski, M., Sjoberg, N.B., 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, C.M., 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: McLusky, D.S., Berry, A.J., (Eds.), Physiology and behaviour of marine organisms, Pergamon Press, Oxford, pp. 313–320.

Couillard, C.M., Hodson, P.V., 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 thecomacchio 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, G.E., Johansson, L., Wickström, H., Volckaert, F.A.M., 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 stock. 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., 2004. What caused the decline of the Lake IJsselmeer eel stock after 1960? ICES Journal of Marine Science 61, 394–404.

Dekker, W., Casselman, J.M., 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.

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, G.A., 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, G.A., Gatto, M., 1996. Trends in vital rates of the European eel: evidence for density dependence? Ecological Applications 6, 1281–1294.

Dezfuli, B.S., Giari, L., Castaldelli, G., Lanzoni, M., Rossi, R., Lorenzoni, M., Kennedy, C.R., 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, C.M.F., 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, S.D., 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.

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, M.D., 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, K.D., Miller, M.J., 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, L.T., Williams, D.J., Johnson, S.K., 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, Supplemento 37, 107–114.

Gatto, M., Laniado, E., Rossi, R., 1982. The management of eels in the Valli di Comacchio lagoon. Oceanologica Acta V(4, Suppl.), 303–307.

Geer, P.J., 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, E.A., Castaldelli, G., 2015. Occurrence of perfluorooctanesulfonate and perfluorooctanoic acid and histopathology in eels from north Italian waters. Chemosphere 118, 117–123.

Graf, W.L., 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, L.S., 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, P.A., Plenty, S.J., Newton, L.C., Bird, D.J., 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, J.L., Arnott, S.A., Roumillat, W.A., Allen, D.M., 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, P.V., Castonguay, M., Couillard, C.M., 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, pp. 203.

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, G.N., Moutopoulos, D.K., Dimitriou, E.N., 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, C.R., Fitch, D.J., 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, A.J., Vøllestad, L.A., 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, R.S., 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., Crivelli, A.J., 2007. Interaction between severity of the infection by the nematode *Anguillicola crassus* and the tolerance to hypoxia in the European eel, *Anguilla anguilla*. Acta Parasitologica 52, 171–175.

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

Marsden, J.E., Langdon, R.W., 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, G.C., Corbari, L., Rossi, R., 1997. Situazione e prospettive dell’allevamento intensivo di *anguilla* in Europa. Il Pesce - Acquacoltura 4, p. *23.*

Meunier, F.J., 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, M.J., Kimura, S., Friedland, K.D., Knights, B., Kim, H., Jellyman, D.J., 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, M.L., Patrick, W.S., Crutchfield, J.U.Jr., 2001. Infection of American eels, *Anguilla rostrata*, by an introduced nematode parasite, *Anguillicola crassus*, in North Carolina. Copeia 3, 848–853.

Munari, C.S., Moduno, F., Ghion, G., 2003. Recovery of the macrobenthic communities in the valli di Comacchio, Northern Adriatic, Italy. Oceanolica Acta 26, 67–75.

Munari, C.S., 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.P., Heppener, D.F.M., van Ginneken, V.J.T., Székely, C., van den Thillart, G.E.E.J.M., 2007. 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.

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

Phelps, Q.E., Ridings, J.W., Herzog, D.P., 2014. American eel population characteristics in the upper Mississippi River. American Midland Naturalist 171, 165–171.

Piper, A.T., Wright, R.M., Kemp, P.S., 2012. The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. Ecological Engineering 44, 329–336.

Piper, A.T., Wright, R.M., Walker, A.M., Kemp, P.S., 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, T.C., Bradford, R.G., Cairns, D.K., Castonguay, M., Chaput, G., Clarke, K.D., 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, H.A.M., Kratochvíl, M., Mrkvička, T., Peterka, J., Vašek, M., Wagenvoort, A.J., 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. Boll. Zool. 46, 217–223.

Rossi, R., Cataudella, S., 1998. La produzione ittica nelle valli di Comacchio. Atti del Convegno Scientifico Laguna "Risanamento e tutela delle vallidi Comacchio fra conservazione ambientale e valorizzazione produttiva, pp 67–76. (in Italian)

Sancho, E., Ferrando, M.D., 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, A.M.C., 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, Y.I., 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, Y.I., Sorokin, P.Y., Gnes, A., 1996a. Structure and functioning of anthropogenically transformed Comacchio lagoon ecosystem. Marine Ecology Progress Series 133, 57–71.

Sorokin, Y.I., 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 bBloom 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, J.A., Pratt, T.C., Verreault, G., Fox, M.G., 2015. A caution for conservation stocking as an approach for recovering Atlantic eels. Aquatic Conservation: Marine and Freshwater Ecosystems 25 (4), 569–580.

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.

Székely, C., 1994. Paratenic hosts for the parasitic nematode *Anguillicola crassus* in Lake Balaton, Hungary. Diseases of Aquatic Organisms 18, 11–20.

Tabouret, H., Bareille, G., Mestrot, A., Caill-Milly, N., Budzinski, H., Peluhet, L., Prouzet, P., Donard, O.F.X., 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, F.W., 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, W.N., Han, Y.S., He, J.T., 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, V.J.T., Maes, G.E., 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, N.B., 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, G.V., Wright, R.M., Kemp, P.S., 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.

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5

A review and synthesis of bivariate non-linear models to describe the relative variation of ecological, biological and environmental parameters

5.1 Summary

The application of mathematical models for the assessment of eel population dynamics and morphometric characteristics were presented in the previous chapters of the doctoral thesis. The general structure of such models consists of many bivariate functions which describe isolated attributes of the populations. For this reason, an expanded literature review was performed on various types of such functions which are used in ecological, biological and environmental problems. This is a supplementary chapter in the thesis.

There is a plethora of non-linear models to describe bivariate relationships related to ecological, biological and environmental problems and this makes difficult to have a general aspect about the suitable models for a new-born dataset. Additionally, there is a special interest for bivariate Non-Linear models which can describe the Relative variation of the dependent variable (NLR models) (i.e. these models provide a restricted range of values between 0 and 1) because they can easily be adjusted to fit different datasets which describe the same relationship. The aim of this study is to provide a review and synthesis of NLR models which can be used to describe bivariate relationships which follow bell-shaped, simple-double sigmoid, bilinear and periodical patterns. This attempt aims to save time and effort for the selection of a NLR model based on five steps a) preparation of data, b) visual identification of the suitable model based on pre-constructed graphs, c) a starting point using the simpler form (base function) of the selected models which are given in complex general forms, d) directions to increase the number of coefficients in order to improve fitting and e) techniques to modify the given NLR models in order to derive new ones with inverted patterns.

5.2 Introduction

The mathematical description of ecological, biological and environmental phenomena begins from the analysis of isolated relationships between two parameters. During such analyses, several problems may occur when the graphical representation and modelling of the relationship between two parameters require for their description a non linear curve. Due to the large number of non linear models and the time-consuming procedure for the selection of the optimum one, the researchers usually adopt those which are presented in similar published works. This is not necessarily wrong, but in many cases, it may be misleading to choose a model *a priori* without systematic comparison (Chen et al., 1992). Although, there are advanced software packages that provide automated procedures to fit and compare a wide collection of curves, there are limitations to describe complex non-linear patterns. In these cases, the users must select *a priori* the general form of the model and to provide initial conditions for the coefficients in order to run optimization algorithms (Motulsky and Ransnas, 1987) for its calibration such as the Gauss-Newton method (Nocedal and Wright, 1999), the Steepest-Descent method (Cauchy, 1847; Meza, 2010) and the Levenberg-Marquardt method (Levenberg, 1944; Marquart, 1963) etc. This procedure may lead to a low quality result or even to no result due to the following reasons i) the pre-selected model by the user is not suitable to describe the relationship, ii) the data are few to be fitted by a model with many coefficients, iii) wrong selection of the initial values of the coefficients and iv) no availability of the appropriate software package or low knowledge to handle it properly.

Process-based mathematical models such as AQUACROP (Raes et al., 2009), AQUATOX (Park and Clough, 2004), SWAT (Neitsch et al., 2010), HYDRUS (Simunek et al., 2013) etc are widely used in ecological-environmental studies and they include a significant amount of inter-related non-linear functions to describe isolated internal processes. Such functions are listed in several review and application articles and they are commonly used to describe the relative rates of bio-chemical transformations (Chen et al., 2010), physiological and morphological attributes of plants and animals (Chen et al., 1992; Zeide, 1993; Castaldelli et al., 2014; Archontoulis and Miguez, 2013; Grimm et al., 2011) metabolic and limiting growth factors of plants and animals (Zwietering, et al., 1990; Lopez et al., 2004; Aschonitis et al., 2013) population dynamics versus environmental gradients (Oksanen and Minchin, 2002), energy dynamics and attribute variations of natural systems (Höök et al., 2011; Lenzen et al., 2013; Johansson et al. 2007), matrix properties (e.g. soil) (Seki, 2007). Even though the general non linear models from the aforementioned works are for general use and they can be applied easily in various datasets, there is a special interest for **N**on-**L**inear models which have the ability to provide results which are restricted in the range of values between 0 and 1 in order to describe the **R**elative variation of a dependent variable (**NLR** models). NLR models can be formed by modifying many general non linear models and they can easily be adjusted to fit different datasets which describe the same phenomenon providing information for the general patterns of a bivariate relationship.

Although NLR models appear in many works, there are no review papers or technical reports that provide a list of them, general guidelines for their development from existing general non-linear models and information about their properties. The aim of this study is to provide a review and synthesis of NLR models which can be used to describe bivariate non-linear relations having always in mind their connection to ecological, biological and environmental problems. This attempt aims to decrease the time and effort for the selection of the optimum model providing valuable information about their behaviour and potential use.

5.3 Methodological approaches and NLR categories

5.3.1 Preparation of the data

The most significant step before the selection of a NLR model is the rescaling of the dependent variable y to relative values between 0 and 1. This can be performed using the following function (Gatto and Rossi, 1979):

$$f = \begin{cases} \dfrac{y - y_{\min}}{y_{\max} - y_{\min}} & \text{for } y_{\min} \leq y \leq y_{\max} \\ 1 & \text{for } y > y_{\max} \end{cases} \tag{5.1}$$

In the first part of Eq.5.1, y_{min} can be either equal to the minimum observed y value or it can be set directly equal to zero. The selection depends on the nature of the physical problem. For example if we want to describe the height variation of a plant versus time, we set $y_{min}=0$ when the plant was established in the soil as a seed, whereas if the plant was transplanted then the y_{min} is equal to its height at the day of transplanting. The second part of Eq.5.1, where $f=1$, can be used when observed y values greater than a preset maximum threshold value y_{max} are considered outliers. All the non-linear models which are presented in the next sections provide values between 0 and 1 (relative rates) for a dependent parameter f (rescaled y using Eq.5.1) as a function of an independent variable T.

Many non-linear models include the exponential function in internal calculations. In this case special attention must be given on the values of the independent variable T because programming languages and software packages (e.g Excel) present numeric limitations and they cannot store values with more than 307 digits. For this reason calculations inside exponentials which give values greater than 709 return error {i.e. exp(709)=8e+307 and exp(710)=error}. This problem can be solved by changing the units of the independent variable in order to have smaller values.

5.3.2 Bell-shaped NLR models

The models of this section describe symmetric and non-symmetric bell-shaped curves similar to the most popular distributions (e.g. Laplace, Normal, Gumbel, Beta, inverse Gaussian etc). These models can describe general patterns similar to the ones observed in studies which concern the relative metabolic-growth rates of organisms versus environmental parameters or versus time (Yin et al., 1995; Polak et al., 2011), the relative abundance of organisms and the variation of landscape characteristics versus environmental gradients (Austin, 2002; Ivits et al., 2011) or the variation of biochemical parameters as a function of other environmental variables (Pallavicini et al., 2009; Kokkinou et al., 2012). The following models contain the coefficient T_{opt}, where $f(T)$ is equal to the maximum value 1 when $T=T_{opt}$. Boundary conditions and coefficients' restrictions are given when necessary. Rules to add coefficients are provided using a "base function" which describes the simplest form of the model.

5.3.2.1 Symmetric bell-shaped models

The first model of this category is a modification of the most popular equations which have been used to describe the metabolic activity of phytoplankton as a function of temperature (Lehman et al., 1975; Jørgensen, 1976; Jørgensen et al., 1978; Grimm et al., 2011). These equations were transformed to one multi-purpose model according to the following (Fig.5.1):

$$f(T) = \exp\left(-a \cdot \left|T - T_{opt}\right|^{n}\right) \text{ for } a>0 \text{ and } n>0 \qquad (5.2)$$

- For $n=1$, the curve follows the patterns of Laplace distribution, while n reduction below 1 provides symmetrical sphenoid curves.
- For $1<n<2$, the increase of n provides a gradual transition from Laplace distribution to normal distribution patterns, while for $n=2$ the curve follows the patterns of normal distribution.
- For $n>2$, the model provides curves where a larger range of T values around T_{opt} provides $f(T)$ values closer to maximum (Fig.5.1). Such patterns have been observed in the daily variations of algae gross primary production (Martin et al., 2006). Changing the shape of the curve by increasing the n value must be followed by parallel reduction of parameter a in order to keep the curve in a specific range of T values.
- The base function is given for $n=1$ (Laplace distribution patterns) or $n=2$ (Normal distribution patterns).

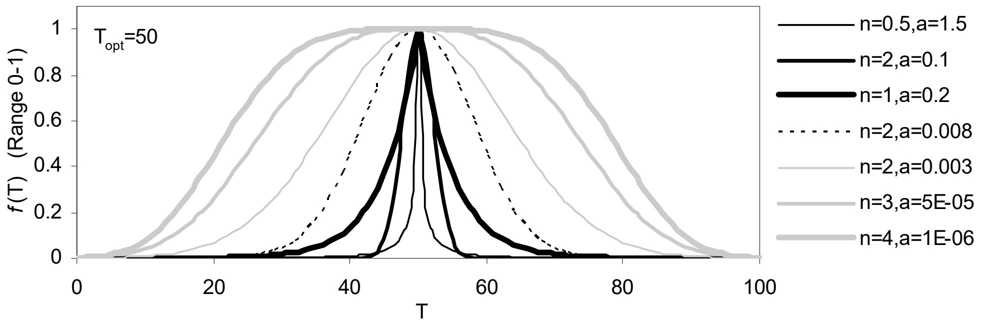


Fig.5.1 *Graphical representation of different symmetric bell-shaped curves produced by Eq.5.2 for different variations of n and a coefficients and constant* T_{opt}*=50.*

The second model of the category can describe Beta type bell-shaped patterns. Such patterns have been observed in crop development as a function of temperature (Yin et al., 1995). A new modified power-Beta type I model to describe only symmetric patterns similar to beta distribution is the following (Fig.5.2):

$$\left.\begin{array}{l} f(T)=\left[\dfrac{2(T-a)}{T_{opt}-a}-\left(\dfrac{T-a}{T_{opt}-a}\right)^2\right]^n \\ \text{for } T \geq a \text{ and } T \leq 2T_{opt}-a \end{array}\right\} \quad \text{where } n>0 \text{ and } T_{opt} \neq a \qquad (5.3)$$

- For $n \leq 1$, the model provides convex bell-shaped curves. The decrease of *n* below 1 increases the convexity of the curve.
- For $n>1$, the model provides concave bell-shaped curves. The increase of *n* above 1 leads to concavity increase.
- The base function is given for $n=1$ (Convex patterns similar to Beta distribution when the beta-shaped coefficients are equal).

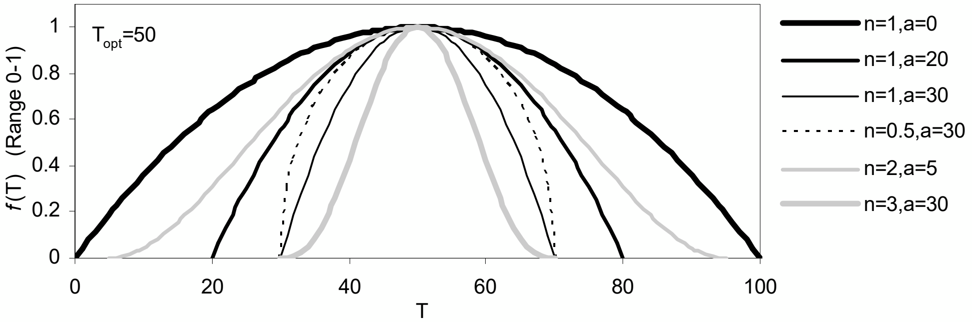


Fig.5.2 *Graphical representation of different symmetric bell-shaped curves produced by Eq.5.3 for different variations of n and a coefficients and constant* T_{opt}*=50.*

The third model of the category is based on cosine functions that are commonly used in climatology (Peixoto, 1984; Shumway and Stoffer, 2006). The following power-cosine function is a modified version of the model proposed by van de Beek et al. (2011) to describe the spectral analysis trends of rainfall time series (Fig.5.3):

$$\left.\begin{array}{l} f(T)=\left\{\cos\left[\left(a\dfrac{\left(T-T_{opt}\right)}{2\pi}\right)^{m}\right]\right\}^{n} \\ \text{for } T\geq T_{opt}-\dfrac{2\pi}{a}\left(\dfrac{\pi}{2}\right)^{(1/m)} \text{ and } T\leq T_{opt}+\dfrac{2\pi}{a}\left(\dfrac{\pi}{2}\right)^{(1/m)} \end{array}\right\} a\neq0, n>0,\ m\in\mathbb{Z}\geq1 \qquad (5.4)$$

- For $n\leq1$, the model provides convex bell-shaped curves while the increase of n value above 1 changes the shape to concave.
- For $m=1$, the curve has a clear pick at T_{opt} while further m increase provides particular shapes with a larger range of T values around T_{opt} where $f(T)$ is close to maximum (Fig.5.3).
- The base function is given for $n=m=1$ (Cosine patterns).

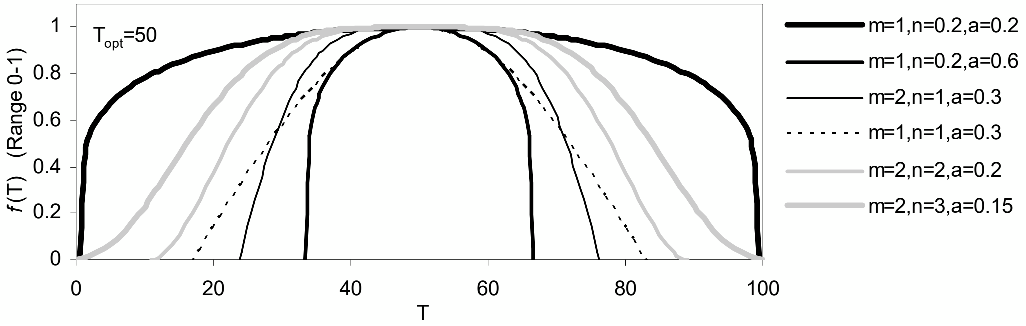


Fig.5.3 *Graphical representation of different symmetric bell-shaped curves produced by Eq.5.4 for different variations of m, n and a coefficients and constant* $T_{opt}=50$.

5.3.2.2 Non-symmetric bell-shaped models

The first model of this category is a modified version of the Weibull (1951) probability density function and it was given by Steele (1962) who used it to describe the relation between photosynthesis and light intensity in aquatic ecosystems. The function was further modified by adding the m power which allows curvature changes according to the following (Fig.5.4):

$$f(T)=\left\{\left(\frac{T}{T_{opt}}\right)^{n}\exp\left[1-\left(\frac{T}{T_{opt}}\right)^{n}\right]\right\}^{m} \text{ for } T\geq0,\quad T_{opt}\neq0,\ n\neq0 \text{ and } m>0 \qquad (5.5)$$

- For $0<n\leq1$, the left part (for $T< T_{opt}$) becomes convex; otherwise, is concave.
- For $n<0$, the boundary condition changes to $T>0$.

- The base function is given for $n=m=1$.

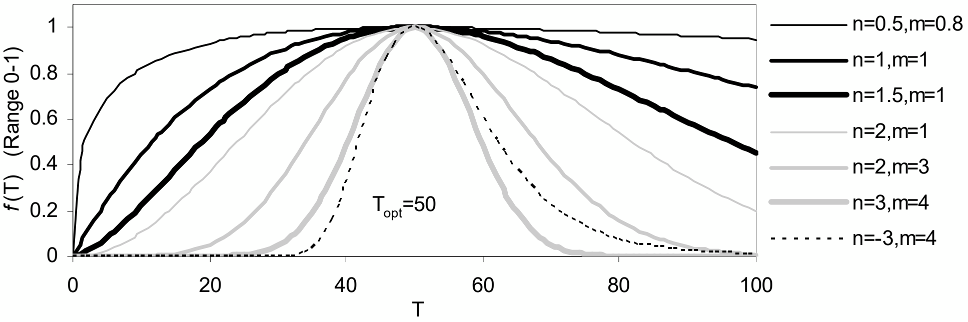


Fig.5.4 *Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.5 for different variations of m and n coefficients and constant $T_{opt}=50$.*

Curves which follow similar patterns of skewed Gaussian distributions can be plotted by the following power-Gaussian model which is a modified version of the one provided by Archontoulis and Miguez (2013) for the description of the phenological development rates of crops as a function of temperature (Fig.5.5):

$$f(T) = \exp\left[\left(\frac{a\left(T - T_{opt}\right)^2}{2T_{opt}^2\left(s - T\right)}\right)^{2n+1}\right] \quad \text{for } T > s,\ a>0 \text{ and } n \in \mathbb{Z} \geq 0 \qquad (5.6)$$

- The s coefficient was introduced in order to solve the limitation of using $T=0$. The value of s defines the left boundary condition of the curve by shifting the left edge of the curve at x–axis without shifting its maximum which is always found at T_{opt}.
- The increase of n provides shapes with a larger range of T values around T_{opt} where $f(T)$ is close to maximum.
- The base function is given for $n=0$ (skewed Gaussian distribution patterns).

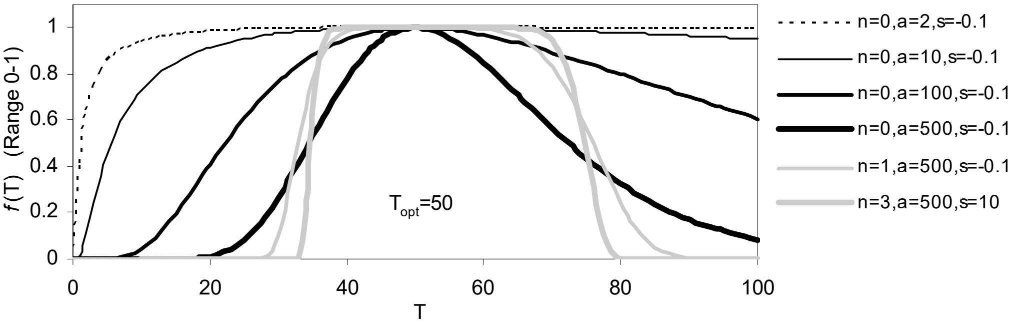


Fig.5.5 *Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.6 for different variations of n, a and s coefficients and constant $T_{opt}=50$.*

Gumbel distribution has been used to describe the distribution of fitness effects of mutations in adaptation models of DNA (Orr, 2006), the probability of extreme climatologic-hydrologic events (Zwiers and Kharin, 1998) etc. Curves which follow the patterns of Gumbel distribution can be plotted by the following modified power-Gumbel model (Fig.5.6):

$$f(T) = \left\{ \exp\left[\left(1 + \frac{T - T_{opt}}{a} - \exp\left(\frac{T - T_{opt}}{a} \right) \right)^{2n+1} \right] \right\}^{m} \quad \text{for } a \neq 0,\ m > 0 \ \text{ and } n \in \mathbb{Z} \geq 0 \qquad (5.7)$$

- For $a>0$ the curve follows the patterns of a skewed smallest extreme Gumbel distribution, while for $a<0$ follows the patterns of a skewed largest extreme Gumbel distribution.
- The increase of m increases the steepness of the curve while the increase of n provides shapes with a larger range of T values around T_{opt} where $f(T)$ is close to maximum.
- The base function is given for $n=0$ and $m=1$ (Gumbel distribution patterns).

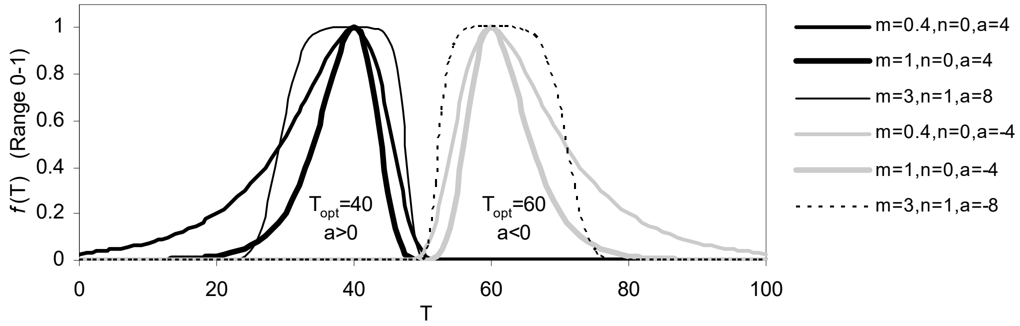


Fig.5.6 *Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.7 for different variations of m, m and a coefficients based on two* T_{opt} *cases equal to 40 and 60.*

The power-Beta type I (Eq.5.3) provides strictly symmetric patterns similar to beta function. When there is need to describe non symmetric patterns of beta function similar to the ones observed by Yin et al. (1995), the power-Beta type II (Eq.5.8) and III (Eq.5.9) can be used. The difference between models II and III is that they provide different curvature changes due to the different effects of the power n.

The power-Beta model II is given by the following function (Fig.5.7):

$$f(T) = 1 - \left| \frac{2\left(T - T_{opt}\right)}{a - T_{opt}} \cdot \left(1 - \frac{T - T_{opt}}{2\left(a - T_{opt}\right)} \right) \right|^{n} \quad \text{for } a \neq T_{opt},\ n > 0 \qquad (5.8)$$

- For $a<T_{opt}$ and boundary conditions $a \leq T \leq \sqrt{2}\, T_{opt}$, the function provides curves as the ones at the left side of Fig.5.7.
- For $a>T_{opt}$ and boundary conditions $a+\sqrt{2}\ (T_{opt} - a) \leq T \leq a$ the function provides curves as the

ones at the right side in Fig.5.7.

- The increase of *n* provides shapes with a larger range of *T* values around T_{opt} where *f(T)* is close to maximum.
- The base function is given for *n*=2 (Beta distribution patterns when the beta-shaped coefficients are not equal).

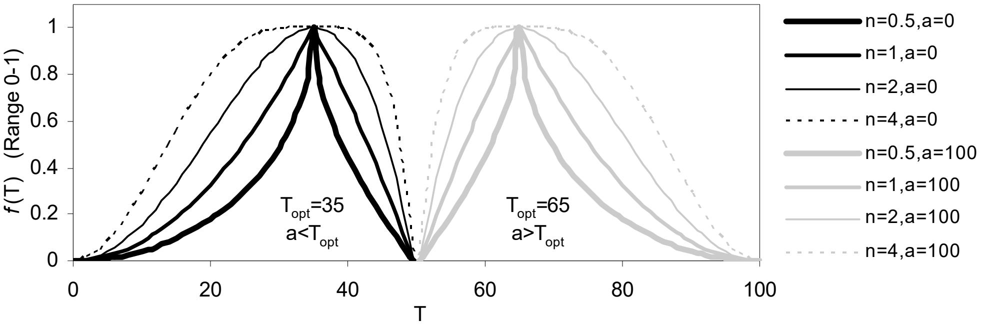


Fig.5.7 *Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.8 for different variations of n and a coefficients based on two* T_{opt} *cases equal to 35 and 65.*

The power-Beta model III is given by the following function (Fig.5.8):

$$f(T)=\left\{\left(\frac{T-a}{2\left(T_{opt}-a\right)}\right)\left[3-\left(\frac{T-a}{T_{opt}-a}\right)^2\right]\right\}^n \quad \text{for } a\neq T_{opt} \text{ and } n>0 \qquad (5.9)$$

- For $a<T_{opt}$ and boundary conditions $a\leq T\leq\sqrt{3}\,(T_{opt}-a)+a$, the function provides curves as the ones at the left side of Fig.5.8.
- For $a>T_{opt}$ and boundary conditions $\sqrt{3}\,(T_{opt}-a)+a\leq T\leq a$, the function provides curves as the ones at the right side of Fig.5.8.
- For $0<n\leq1$, the curvature is convex while for $n>1$ the curvature changes to concave form.
- The base function is given for *n*=1.

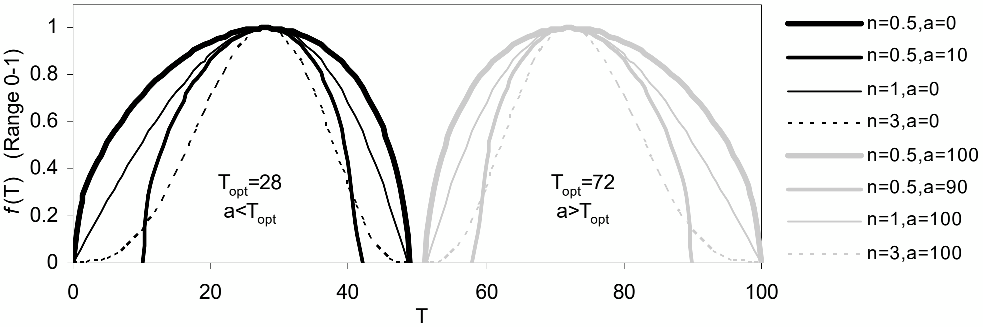


Fig.5.8 *Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.9 for different variations of n, a coefficients based on two* T_{opt} *cases equal to 28 and 72.*

The next curve was obtained by inversing and modifying the linear Bezier equation (no citation available, Bezier equations were based on Bernstein's polynomials and they were publicized on 1962 after their use by the French engineer P.Bezier to design the bodies of Renault automobiles). The Bezier polynomials are commonly used in computer graphics analysis (Thanutong and Dejdumrong, 2013) and geographical information systems (Dale, 2004). A power *n* was also introduced in the inversed linear Bezier formula, which allowed curvature changes (Fig.5.9):

$$\left.\begin{array}{l} f(T)=\left(\dfrac{T-a}{T_{opt}-a}\right)^{n}, n>0 \text{ and } a\neq T_{opt}, \text{for } a\leq T\leq T_{opt} \\ f(T)=\left(\dfrac{T-b}{T_{opt}-b}\right)^{n}, n>0 \text{ and } b\neq T_{opt}, \text{for } T_{opt}\leq T\leq b \end{array}\right\} \quad (5.10)$$

- For 0<*n*<1 the curvature becomes convex.
- For *n*=1 the curvature becomes straight line (base function).
- For *n*>1 the curvature becomes concave.

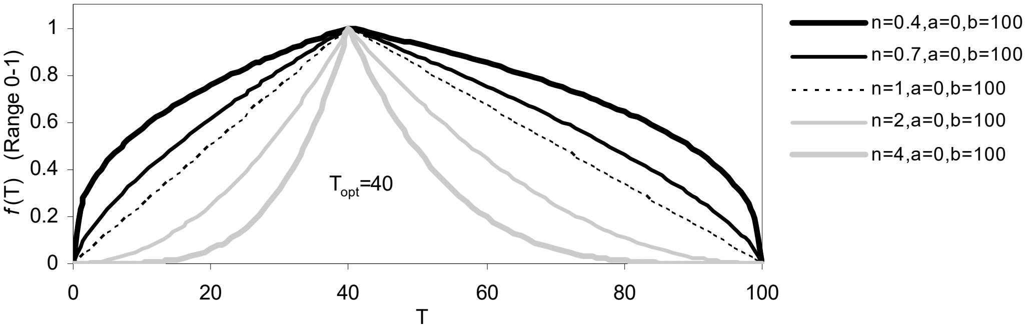


***Fig.5.9** Graphical representation of different non symmetric bell-shaped curves produced by Eq.5.10 for different variations of n, a and b coefficients and constant T_{opt}=54.*

5.3.3 Convex, simple and double sigmoid NLR models of saturation-growth type

This section is dedicated to convex, simple and double sigmoid of saturation-growth type models. Boundary conditions and coefficients' restrictions are given when necessary. Rules to remove or add coefficients are provided using a "base function", which describes the simplest form of the equation. Since most of the given NLR models provide "saturation-growth" type curves, we also provide the respective functions which calculate the *T* value for the half saturation or half growth rate (i.e. *f(T)*=0.5). The sigmoid curves *f(T)* also present an inflection point at a specific T_i value where the slope of the curve is maximum (*df(T)/dT*=max), while the curvature becomes zero and can be identified using $d^2f(T)/dT^2=0$.

The function which calculates the T value at inflection point for sigmoid curves is also provided. Results from complex derivations and integrations for steps shown in the next sections were conducted using the on-line free equation and derivative solvers of Wolfram Alpha Widgets (http://www.wolframalpha.com/widgets/).

5.3.3.1 Convex and simple sigmoid models of saturation-growth type

The first model is based on the saturation-growth equation of Michaelis and Menten (1913) which is often used to describe the growth response of bacteria, phytoplankton and plants as a function of nutrient concentration in the water and soil, respectively (Anastacio et al.,1999; Kayombo et al., 2003; Antonopoulos, 2010). The initial Michaelis-Menten model was modified to the following form by adding the parameter s and the power n (Fig.5.10):

$$f(T) = \left(\frac{(T-s)}{(T-s)+a} \right)^n \text{ for } T \geq s \text{ , } a>0 \text{ and } n>0 \tag{5.11a}$$

- The s coefficient is equal to the left boundary condition at x-axis where $f(T)=0$.
- The decrease of n and a parameters increases the steepness of the curve.
- For $n>1$, $f(T)$ becomes sigmoid.
- The base function is given for $n=1$ and $s=0$.
- The T values for half-saturation and inflection point are given by the following equations, respectively:

$$T_{0.5} = \frac{a + s\left(2^{1/n} - 1\right)}{2^{1/n} - 1} \tag{5.11b}$$

$$T_i = \frac{1}{2} a(n-1) + s \text{ for } n>1 \tag{5.11c}$$

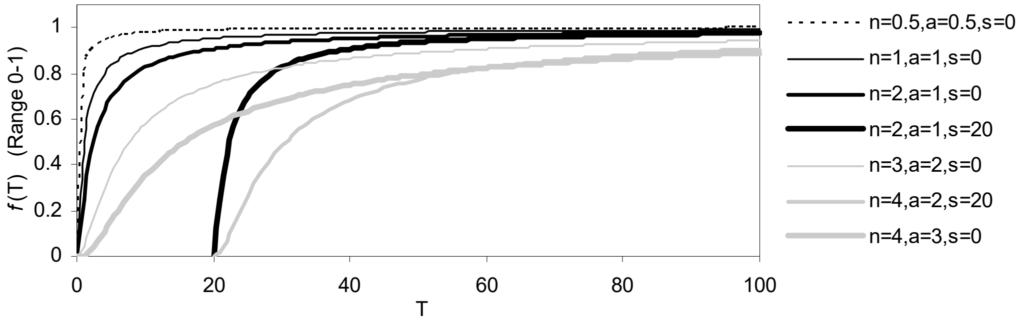


Fig.5.10 *Graphical representation of different convex and simple sigmoid curves of saturation-growth type produced by Eq.5.11a for different variations of n, a and s coefficients.*

The next function is a convex growth curve which was derived after modification of the model of Kosugi (1994) for the description of unsaturated hydraulic properties (Fig.5.11):

$$f(T)=1-\left[erfc\left(a\ln(T-s)\right)\right]^{n} \quad \text{for } T\geq s+1,\ a>0 \text{ and } n>0 \tag{5.12a}$$

- The $s+1$ coefficient defines the left boundary condition at x-axis where $f(T)=0$.
- The increase of n and a parameters leads to convexity increase.
- The base function is given for $n=a=1$.
- There is no T_i for $f(T)$ between 0-1 while $T_{0.5}$ is given by the following equation:

$$T_{0.5}=s+\exp\left[a^{-1}erfc^{-1}\left(2^{-1/n}\right)\right] \tag{5.12b}$$

where $erfc^{-1}$ is the inverse complementary error function {e.g. if $erfc(w)=z$ then $erfc^{-1}(z)=w$}. In case where *erf* and *erfc* functions do not work in Excel, the Analysis ToolPak add-in has to be installed, or alternatively the following formulas, which approximate *erf* and *erfc*, can be used, respectively:

```
ERF(x) = GAMMADIST(x^2; 0.5; 1; TRUE)
ERFC(x) = CHIDIST(2*x^2; 1) = 2*NORMSDIST(-x*SQRT(2))
```

The cases of inverse erf^{-1} and inverse complementary error function $erfc^{-1}$ are not included in Excel but they can be calculated using the following formulas, which approximate erf^{-1} and $erfc^{-1}$, respectively:

```
ERFINV(x) = SQRT(GAMMAINV(x; 0.5; 1))
ERFCINV(x) = -NORMSINV(x/2)/SQRT(2)
```

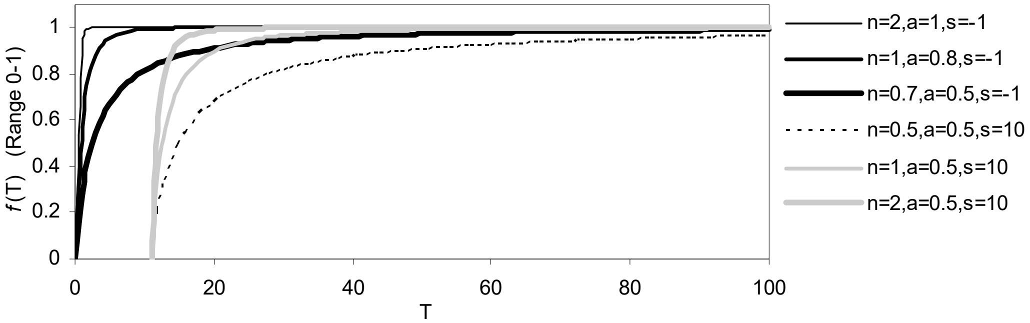


Fig.5.11 *Graphical representation of different convex curves of saturation-growth type produced by Eq.5.12a for different variations of n, a and s coefficients.*

The next curve is a modified power function of the symmetrical expolinear function which was used to describe the patterns of leaf area expansion based on principles of light interception (Goudriaan and Monteith, 1990; Goudriaan, 1994) (Fig.5.12):

$$f(T)=\left[\frac{1}{a}\ln\left(\frac{1+\exp\left[a(T-s)\right]}{1+\exp\left[a(T-s-1)\right]}\right)\right]^{n} \quad \text{for } a>0,\ n>0 \qquad (5.13a)$$

- The parameter *s* shifts the whole curve at *x*-axis.
- The decrease of *a* parameter leads to concavity decrease.
- The decrease of *n* parameter leads to concavity increase. For n=1 the sigmoid curve becomes symmetrical.
- The base function is given for n=1.
- For n=1, the *T* values for half-saturation and inflection point are given by $T_{0.5}=T_i=s+1/2$. For $n\neq1$ there is not general analytical solution for T_i while the *T* value for half saturation is given by:

$$T_{0.5}=\frac{1}{a}\ln\left[\frac{\left[\exp\left(2^{-1/n}a\right)-1\right]\ \exp\left(as+a\right)}{\exp\left(a\right)-\exp\left(2^{-1/n}a\right)}\right] \qquad (5.13b)$$

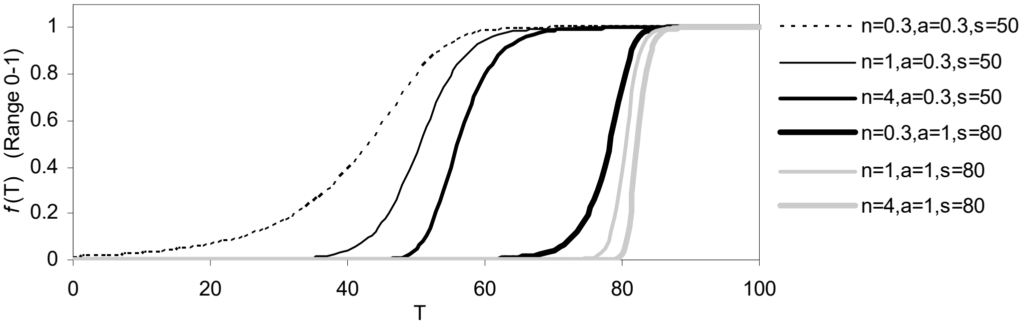


Fig.5.12 *Graphical representation of different convex curves of saturation-growth type produced by Eq.5.13a for different variations of n, a and s coefficients.*

The equation of Weibull (1951) and its modified versions have been used to describe the patterns of trees, algae and bacterial growth (Yang et al., 1978; Chalker, 1981; Martin et al., 2006) etc. The initial model was modified by adding the shifting factor *s* according to the following (Fig.5.13):

$$f(T)=1-\exp\left[-\left[\left(\frac{T-s}{a}\right)^{b}\right]\right] \quad \text{for } T\geq s,\ a>0 \text{ and } b>0 \qquad (5.14a)$$

- For $0<b\leq1$ the shape of the curve is convex with no inflection point in the range (0-1) while for $b>1$ the curvature becomes sigmoid.

- The factor s shifts the whole curve and defines the left boundary condition at x-axis where $f(T)=0$.
- The base function is given for $b=1$.
- The T value for the half-saturation and for the inflection point are given by the following equations, respectively:

$$T_{0.5} = s + a\left[-\ln\left(0.5\right)\right]^{1/b} \tag{5.14b}$$

$$T_i = s + a\left[\frac{b-1}{b}\right]^{1/b} \tag{5.14c}$$

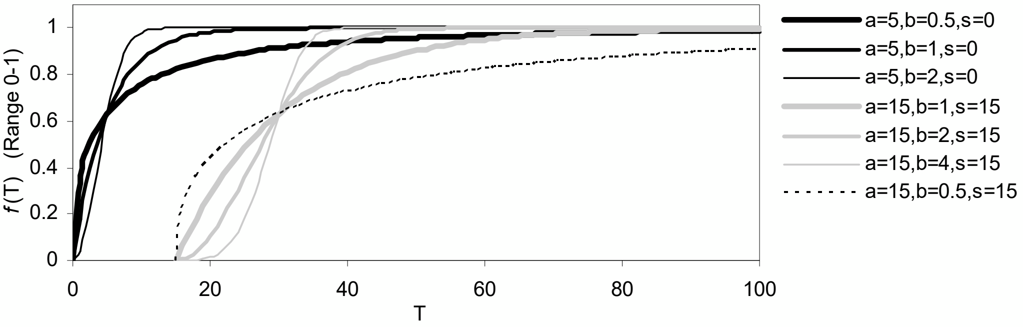


Fig.5.13 *Graphical representation of different convex and simple sigmoid curves of saturation-growth type produced by Eq.5.14a for different variations of a, b and s coefficients.*

The next curve is a modified version of the descending sigmoid function given by van Genuchten (1980) for the description of water retention curve. The curve was inverted in order to be growth sigmoid while an additional factor b was introduced in order to solve the problem for $T=0$, where the initial curve returns error. The curve provides sigmoid and convex growth patterns without the use of exponential function in inter-calculations (Fig.5.14):

$$f(T) = \left[1 + (aT + b)^n\right]^{-m} \text{ for } T > -b/a,\ a > 0,\ n < 0 \text{ and } m > 0 \tag{5.15a}$$

- The term $-b/a$ defines the left boundary condition.
- The base function is given for $n=-1$, $m=1$, $b=0$.
- The curve is convex with no inflection point when $nm=-1$, while it becomes sigmoid for $nm\neq-1$.
- The T value for the half-saturation and for the inflection point are given by the following equations, respectively:

$$T_{0.5} = a^{-1}\left[\left(2^{1/m}-1\right)^{1/n} - b\right] \tag{5.15b}$$

$$T_i = \frac{1}{a}\left[\left(\frac{n-1}{nm+1}\right)^{1/n} - b\right] \quad \text{for } nm \neq -1 \tag{5.15c}$$

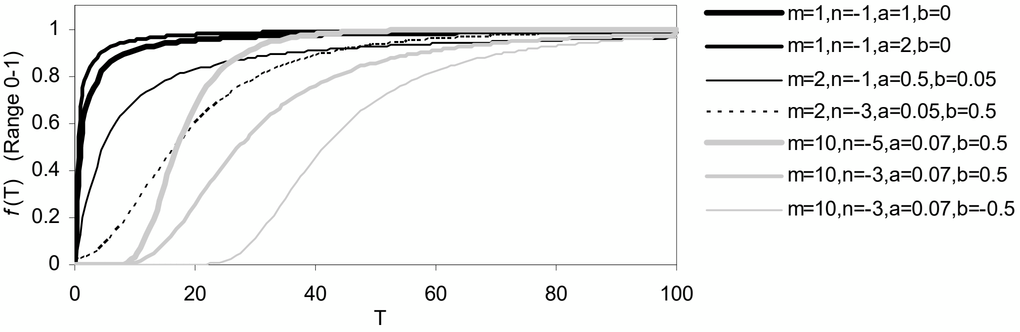


Fig.5.14 *Graphical representation of different convex and simple sigmoid curves of saturation-growth type produced by Eq.5.15a for different variations of m, n, a and b coefficients.*

One of the most popular functions which has been used extensively in biology ecology, medicine, engineering and economic studies is the one given by Richards (1959). The basic and the most applicable modifications of the Richards equation are the Bertalanffy-Richards and the Schnute-Richards equation (von Bertalanffy, 1957; Yuancai et al., 1997). It is commonly used to describe the length-age relationship of fishes (Castaldelli et al., 2014), while it has been used to describe weight-age relationship of animals (Erickson et al., 2001). Detailed analyses and presentations of different approaches to handle Richards function are also given to other studies (Tjørve and Tjørve, 2010; Wang et al., 2012). In this study a simplified NLR version is provided allowing the curve to provide sigmoid patterns according to the following (Fig.5.15):

$$f(T) = \left\{1 + n\exp\left[-a\left(T-s\right)\right]\right\}^{-m} \qquad \text{for } m>0,\ n>0 \text{ and } a>0 \tag{5.16a}$$

- The parameter s shifts the whole curve along the x-axis.
- For $m=n=a=1$, the curve is transformed to the basic symmetrical sigmoid logistic function (Verhulst, 1838; Lipovetsky, 2010).
- The T value for half-saturation and for the inflection point are given by the following equations, respectively:

$$T_{0.5} = s - \left(\frac{1}{a}\right)\ln\left(\frac{2^{1/m}-1}{n}\right) \tag{5.16b}$$

$$T_i = \frac{1}{a}\ln\left(mn\right) + s \tag{5.16c}$$

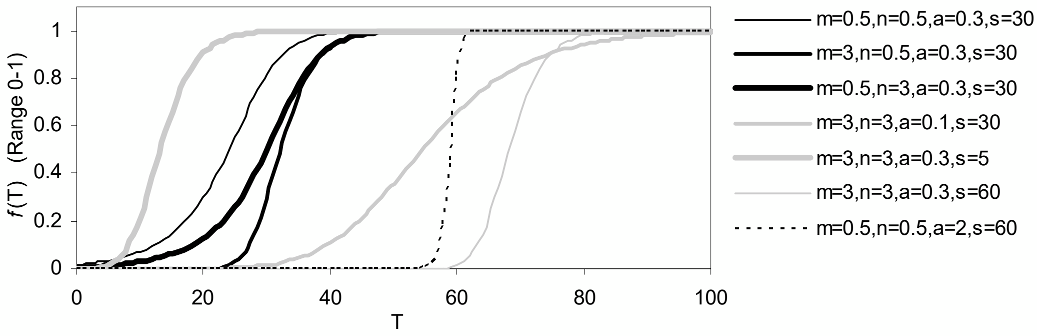


Fig.5.15 *Graphical representation of different convex and simple sigmoid curves of saturation-growth type produced by Eq.5.16a for different variations of m, n, a and s coefficients.*

5.3.3.2 Double sigmoid models of saturation-growth type

The following model is a modified version of the ones used to describe the disease progress curves and growth curves of sugarcane smut (Hau et al., 1993; Amorin et al., 1993). The model describes double-sigmoid patterns with an easily adjusted horizontal intermediate plateau (Fig.5.16):

$$f(T) = \left\{ \exp\left[-\exp\left[\left(\frac{s-T}{a} \right)^{2n+1} \right] \right] \right\}^{m} \quad \text{for } a>0,\ m>0 \text{ and } n \in \mathbb{Z} \geq 0 \tag{5.17a}$$

- For n=0 the curve is simple sigmoid while for n>0 the curve becomes double-sigmoid exhibiting three horizontal plateaus with no boundary conditions.
- The increase of a leads to the length increase of the intermediate plateau.
- The decrease of m shifts upwards the intermediate plateau, while a further increase of n above 1 increases the steepness of the double sigmoid curve.
- The base function is given for n=0 and m=1, where the function is transformed to the simple sigmoid Gumbel-Gompertz (Gompertz, 1825; Yin et al., 2003) which has been used to describe the wood formation dynamics (Cuny et al., 2013).
- The parameter s shifts the whole curve along the x-axis.
- The T value for half saturation is given by the following equation:

$$T_{0.5} = s - a\left[\ln\left(-\frac{1}{m}\ln\left(0.5\right)\right)\right]^{1/(2n+1)} \tag{5.17b}$$

- Analytical solution for inflection point can be found only when n=0 (simple sigmoid case of

Eq.5.17a) according to the following:

$$T_i = s - a\ln\left(-\frac{1}{m}\right) \tag{5.17c}$$

For $n>0$ (double sigmoid), there is not general analytical solution for inflection points of *maxima extrema* while there is a local minimum extreme of the first derivative of Eq.5.17a which connects the two sigmoid parts and it is given for $T=s$.

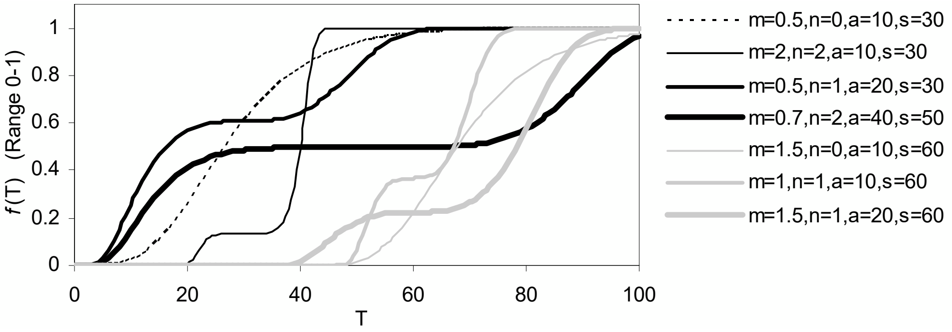


Fig.5.16 *Graphical representation of different simple and double sigmoid curves of saturation-growth type produced by Eq.5.17a for different variations of m, n, a and s coefficients.*

The next model was used to describe hydraulic properties of double-porosity soils (Durner, 1994) and to fit fatigue profiles of mouses (Cairns et al., 2008). A shifting factor *s* was also included in the original model according to the following (Fig.5.17):

$$f(T) = 1 - \left\{(1-c)\left[1+\left(\frac{T-s}{a_1}\right)^n\right]^{-1} + c\left[1+\left(\frac{T-s}{a_2}\right)^m\right]^{-1}\right\} \tag{5.18a}$$

for $T \geq s$, $a_{1,2}>0$, $0 \leq c \leq 1$, $n>0$, $m>0$

- The parameter *s* shifts the whole curve along the x-axis.

- For $c=1$ or $c=0$, the model provides simple sigmoid curves with one inflection point. Analytical solutions for the simple sigmoid cases are the following:

$$\left.\begin{array}{l} \text{for } c=0 \quad \rightarrow \quad T_{0.5} = a_1 + s \;\; \text{and} \;\; T_i = a_1\left(\dfrac{n-1}{n+1}\right)^{1/n} + s \\ \text{for } c=1 \quad \rightarrow \quad T_{0.5} = a_2 + s \;\; \text{and} \;\; T_i = a_2\left(\dfrac{m-1}{m+1}\right)^{1/m} + s \end{array}\right\} \tag{5.18b}$$

- For $c \neq 0,1$ the curve becomes double sigmoid. There is not general analytical solution for $T_{0.5}$, while inflection points which correspond to the *maxima extrema* of the first derivative of Eq.5.18a can be found according to the following:

$$\text{for } c \neq 0,1 \quad \rightarrow \quad T_{i,1} = a_1\left(\frac{n-1}{n+1}\right)^{1/n} + s \quad \text{and} \quad T_{i,2} = a_2\left(\frac{m-1}{m+1}\right)^{1/m} + s \qquad (5.18c)$$

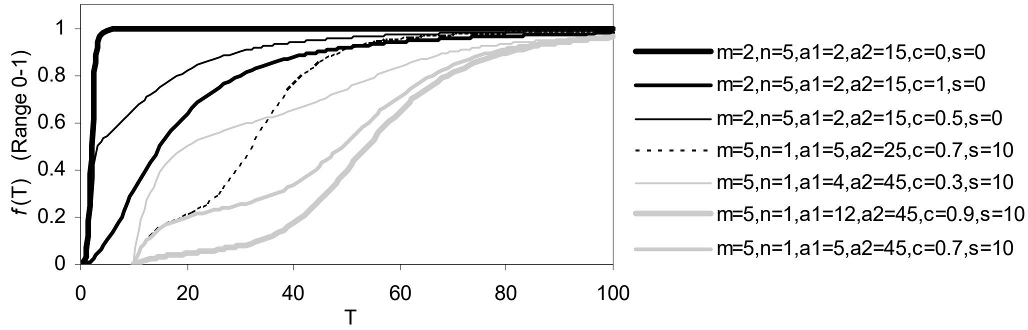


Fig.5.17 *Graphical representation of different simple and double sigmoid curves of saturation-growth type produced by Eq.5.18a for different variations of m, n,* a_1*,* a_2*, c, and s coefficients.*

The next double sigmoid model is a modified version of the hyperbolic tangent function which has been used to describe earth state transitions (Roper, 2000) (Fig.5.18):

$$f(T) = \frac{1}{2}\left\{(1-c)\tanh\left(\frac{T-a_1}{b_1}\right) + c\tanh\left(\frac{T-a_2}{b_2}\right) + 1\right\} \quad \text{for } b_{1,2}>0 \text{ and } 0 \leq c \leq 1 \qquad (5.19a)$$

- There are three cases where Eq.5.19a becomes simple sigmoid:

$$\left.\begin{array}{l} \text{for } c = 0 \rightarrow T_{0.5} = T_i = a_1 \\ \text{for } c = 1 \rightarrow T_{0.5} = T_i = a_2 \\ \text{for } c \neq 0,1 \text{ and } a_1 = a_2 = a \rightarrow T_{0.5} = T_i = a \end{array}\right\} \qquad (5.19b)$$

- For $c \neq 0,1$ and $a_1 \neq a_2$ the curve becomes double sigmoid. There is not general analytical solution for $T_{0.5}$, while inflection points which correspond to the *maxima extrema* of the first derivative of Eq.5.19a can be found according to the following:

$$T_{i,1}=a_1 \text{ and } T_{i,2}=a_2 \qquad (5.19c)$$

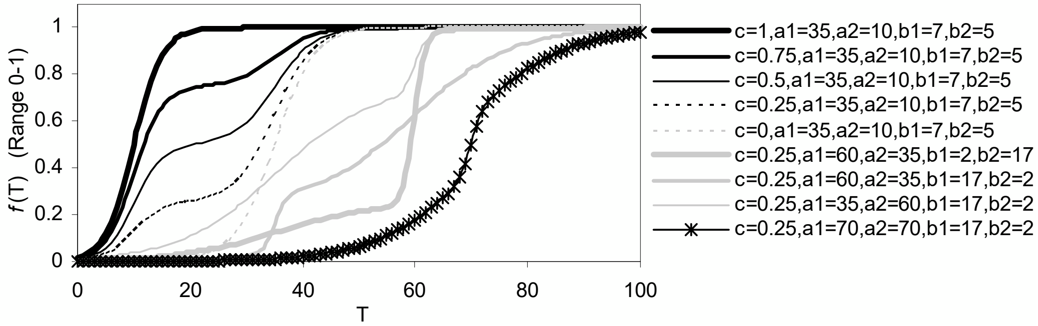


Fig.5.18 *Graphical representation of different simple and double sigmoid curves of saturation-growth type produced by Eq.5.19a for different variations of c,* a_1*,* a_2*,* b_1 *and* b_2*.*

5.3.4 Special curves

5.3.4.1 A bilinear curve

Linear models are widely used but they cannot be applied for data that have a turning- or rate-change-point. To describe such bilinear-type data, a completely generalized version of a linearized biexponential model (LinBiExp) was proposed by Buchwald (2007) to make possible smooth and fully parametrizable transitions between two linear segments maintaining a clear connection between them. The full form of LinBiExp function (Buchwald, 2007) solves the problem of Eq.5.10 (for *n*=1), which changes form in order to describe the linearity changes but it was not possible to be transformed in such way to provide relative rates between 0-1 and for this reason is not discussed in this study. Two modified forms of the LinBiExp were derived which can provide transition between two linear segments describing relative rates and they are given by the following equations (Fig.5.19):

$$f(T) = b \cdot \ln\left[\exp\left(\frac{a(T-c)}{b}\right)+1\right]+1 \qquad (5.20)$$

for $T \geq \dfrac{b \cdot \ln\left[\exp(-1/b)-1\right]}{a}+c$, *α*≠0 and *b*<0

$$f(T) = 1 - b \cdot \ln\left[\exp\left(\frac{a(T-c)}{b}\right)+1\right] \qquad (5.21)$$

for $T \leq \dfrac{b \cdot \ln\left[\exp(1/b)-1\right]}{a}+c$, *α*≠0 and *b*>0

In Eq.5.20 the right linear segment is always horizontal describing the *f*(*T*)=1, while in Eq.5.21 the left linear segment is always horizontal describing the *f*(*T*)=1. The full form of LinBiExp (Buchwald, 2007) does not have these restrictions where the slopes of the two linear segments can be adjusted at any slope. The adjustment of both Eqs.5.20 and 5.21 can be performed by the following:

- The coefficient *c* defines the value of *T* where the breakpoint between the two lines exists.
- The decrease of *a* increases the angle between the two linear segments.
- The increase of the absolute value of *b* provides a smoother transition between the two linear segments.

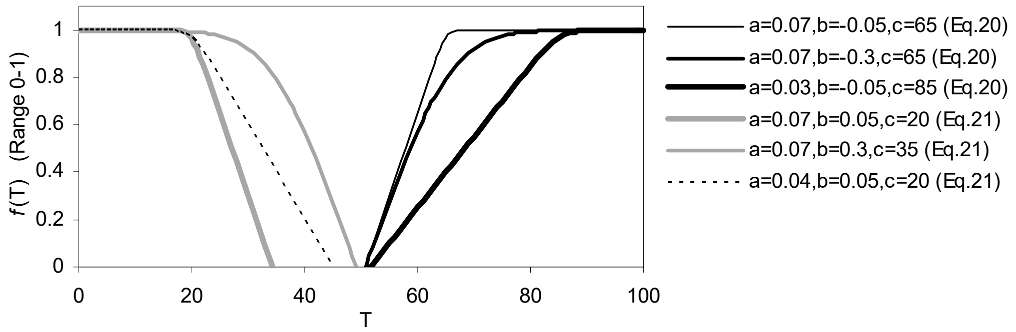


Fig.5.19 *Graphical representation of different bilinear curves of saturation-growth or descending type produced by Eqs.5.20 and Eqs.5.21 for different variations of a, b and c coefficients.*

5.3.4.2 A periodical curve

Periodical curves can be used when there is a need to describe the diurnal or seasonal variation of climatologic parameters. The following function is for general use to describe the relative rate (0-1) of constant periodical variations and it is a modified version of the models used to describe the diurnal light intensity (Schroeder, 1997) and the seasonal variation of river flow (Righetto et al., 2012) (Fig.5.20):

$$f(T)=\left[\frac{1}{2}\left[\cos\left(\frac{T}{a}+b\right)+1\right]\right]^{n} \quad \text{for } \alpha\neq 0 \text{ and } n>0 \qquad (5.22)$$

- The increase of parameter *a* decreases the length of the period.
- The parameter *b* shifts the curve along the *x*-axis.
- The decrease of *n* below 1 changes the cosine shape curve to convex while the increase of *n* above 1 increases the concavity of the cosine shape.
- Eq.5.22 has the advantage that it is not restricted by boundary conditions.

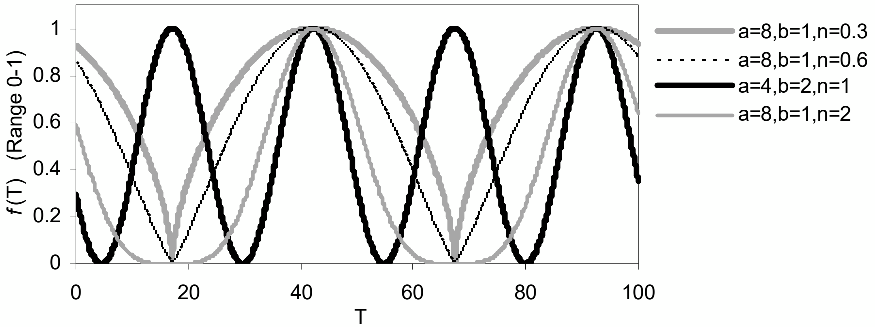


Fig.5.20 *Graphical representation of periodical curves produced by Eq.5.22 for different variations of a, b and n coefficients.*

5.3.5 Inverting the NLR models

The inversion of growth sigmoid and bell-shaped curves leads to new categories, the descending sigmoid and the inverted bell-shaped curves, respectively. Descending sigmoid curves are used in soil physics (van Genuchten, 1980; Kosugi, 1996; Khlosi et al., 2008; Dexter et al., 2008), tolerance-survival of organisms versus age (Aschonitis et al., 2015), while inverted bell-shaped curves can be used to describe the patterns of metabolic rate reduction of organisms during hibernation or nightly torpor {such patterns have been observed in Geiser (2004)}.The inversion can be performed either by violating the given restrictions of the coefficients for each of the aforementioned functions (when is possible) or by using the following general rule which is valid only for NLR models:

$$Invf(T) = 1 - f(T) \tag{5.23}$$

where $f(T)$: is a function which describes the relative variation (i.e. $f(T)$=0-1) of a rescaled dependent variable and $invf(T)$: is the respective inverted form of $f(T)$. Restrictions can be violated to invert curves only in the following cases a) Eq.5.6 for $n \in \mathbb{Z}<0$, b) Eq.5.7 for $n \in \mathbb{Z}<0$, c) Eq.5.13 for $a<0$, d) Eq.5.15 for $n>0$, e) Eq.5.16 for $a<0$ and f) Eq.5.17 for $a<0$. For the inverted bell-shaped curves the term of T_{opt} describes the value of T which provides $Invf(T)=0$.

For the descending sigmoid curves the equations which provide the T value for half saturation and inflection point are the same with their respective growth curves $f(T)$ either when they are derived by using Eq.5.23 or by violating coefficient restrictions. The boundary conditions (when exist) remain the same for all the models. Examples of inversion using Eq.5.23 which provide symmetric bell-shaped, non symmetric bell-shaped, descending sigmoid and descending double sigmoid curves are given in Fig.5.21.

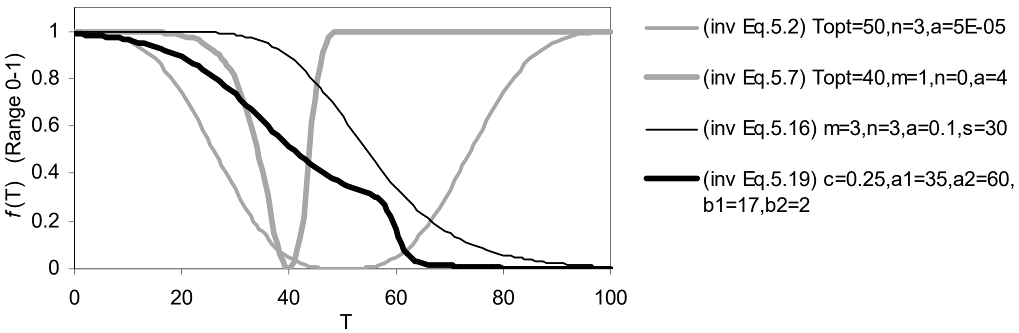


Fig.5.21 *Examples of inversion using Eq.5.23 which provide symmetric bell-shaped, non-symmetric bell-shaped, descending sigmoid and descending double sigmoid curves.*

5.4 Conclusions

A review and synthesis of NLR models, which can describe a wide range of relative patterns of phenomena related to ecology, biology and environmental sciences, were conducted aiming to provide an integrated aspect of their potential use. The description of their behaviour and their graphical representation is the key element to decrease the time and effort for the exploration and selection of the optimum models to describe a new-born dataset. Two basic advantages of NLR models in comparison to general non linear models were identified and used to modify and improve their flexibility, namely a) the simpler form of a NLR model can be raised to a power allowing curvature changes without affecting the minimum (~0) and maximum (~1) relative value of the rescaled dependent variable, and b) if a NLR model is described by the function *f*, it can easily be modified to another NLR model which provides inverted mirror curves *invf* using the general rule $invf = f - 1$.

All the NLR models and their graphical representations which are described in this study can be found in a single Excel file "NLRmodels.xls" https://www.researchgate.net/publication/280567934_NLRmodels

5.5 References

Amorin, L., Bergamin-Filho, A., Hau, B., 1993. Analysis of progress curves of sugarcane smut on different cultivars using functions of double sigmoid patterns. Phytopathology 83, 933–936.

Anastacio, P.M., Nielsen, S.N., Frias, A.F., Marques, J.C., 1999. CRISP (crayfish and rice integrated system of production): 4.Modelling water, algae and oxygen dynamics. Ecological Modelling 123, 29–40.

Antonopoulos, V.Z., 2010. Modelling of water and nitrogen balances in the ponded water and soil profile of rice fields in Northern Greece. Agricultural Water Management 98, 321–330.

Archontoulis, S.V., Miguez, F.E., 2013. Nonlinear regression models and applications in agricultural research. Agronomy Journal 105, 1–13.

Aschonitis, V.G., Lekakis, E.H., Petridou, N.C., Koukouli, S.G., Pavlatou-Ve, A., 2013. Nutrients fixation by algae and limiting factors of algal growth in flooded rice fields under semi-arid Mediterranean conditions: case study in Thessaloniki plain in Greece. Nutrient Cycling in Agroecosystems 96(1), 1–13.

Aschonitis, V.G., Castaldelli, G., Lanzoni, M., Merighi, M., Gelli, F., Giari, L., Rossi, R., Fano, E.A., 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, (Article in Press) DOI: 10.1111/eff.12269

Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157, 101–118.

Buchwald, P., 2007. A general bilinear model to describe growth or decline time profiles. Mathematical Biosciences 205, 108–136.

Cairns, S.P., Robinson, D.M., Loiselle, D.S., 2008. Double-sigmoid model for fitting fatigue profiles in mouse fast- and slow-twitch muscle. Experimental Physiology 93(7), 851–862.

Castaldelli, G., Aschonitis, V.G., Lanzoni, M., Gelli, N., Rossi, R., Fano, E.A., 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(3), 558–559.

Cauchy, A., 1847. Méthode générale pour la résolution des systèmes d'équations simultanées. Compte Rendu des Séances de L'Académie des Sciences XXV, Vol. A, 25, 536–538.

Chalker, B.E., 1981. Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. Marine Biology 63, 135–141.

Chen, Y., Jackson, D.A., Harvey, H.H., 1992. A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences, 49, 1228–1235.

Chen, W.W., Niepel, M., Sorger, P.K., 2010. Classic and contemporary approaches to modeling biochemical reactions. Genes & Development 24, 1861–1875.

Cuny, H.E., Rathgeber, C.B.K., Kiessé, T.S., Hartmann, F.P., Barbeito, I., Fournier, M., 2013. Generalized additive models reveal the intrinsic complexity of wood formation dynamics. Journal of Experimental Botany 64(7), 1983–1994.

Dale, P., 2004. Introduction to mathematical techniques used in GIS. CRC Press, 224 pp.

Dexter, A.R., Czyż, E. A., Richard, G., Reszkowska, A., 2008. A user-friendly water retention function that takes account of the textural and structural pore spaces in soil. Geoderma 143, 243–253.

Durner, W., 1994. Hydraulic conductivity estimation for soils with heterogeneous pore structure. Water Resources Research 30(2), 211–223.

Erickson, G.M., Rogers, K.C., Yerby, S.A., 2001. Dinosaurian growth patterns and rapid avian growth rates. Nature 412, 429–433.

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

Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. Annual Review of Physiology 66, 239–74.

Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philosophical Transactions of the Royal Society 182, 513–585.

Goudriaan, J., Monteith, J.L., 1990. A mathematical function for crop growth based on light interception and leaf area expansion. Annals of Botany 66, 695–701.

Goudriaan, J., 1994. Using the expolinear growth equation to analyze resource capture. In J.L. Monteith, R.K. Scott, M.H. Unsworth (eds.), Resource capture by crops (pp. 99–100), Nottingham University Press.

Grimm, K. J., Ram, N., Hamagami, F., 2011. Nonlinear growth curves in developmental research. Child Development 82(5), 1357–1371.

Hau, B., Amorin, L., Bergamin-Filho, A., 1993. Mathematical functions to describe disease progress curves of double sigmoid patterns. Phytopathology 83, 928–932.

Höök, M., Li, J., Oba, N., Snowden, S., 2011. Descriptive and predictive growth curves in energy system analysis. Natural Resources Research 20(2), 103–116.

Ivits, E., Buchanan, G., Olsvig-Whittaker, L., Cherlet, M., 2011. European farmland bird distribution explained by remotely sensed phenological indices. Environmental Modeling and Assessment 16, 385–399.

Johansson, H., Brolin, A.A., Håkanson, L., 2007. New approaches to the modelling of lake basin morphometry. Environmental Modeling & Assessment 12, 213–228.

Jørgensen, S.E., 1976. A eutrophication model for a lake. Ecological Modelling 2, 147–165.

Jørgensen, S.E., Mejer, H., Friis, M., 1978. Examination of a lake model. Ecological Modelling 4, 253–278.

Kayombo, S., Mbwette, T.S.A., Katima, J.H.Y., Jørgensen, S.E., 2003. Effects of substrate concentrations on the growth of heterotrophic bacteria and algae in secondary facultative ponds. Water Research 37, 2937–2943.

Khlosi, M., Cornelis, W.M., Douaik, A., van Genuchten, M.Th., Gabriels, D., 2008. Performance evaluation of models that describe the soil water retention curve between saturation and oven dryness. Vadose Zone Journal 7(1), 87–96.

Kokkinou, M., Theodorou, L., Papamichail, G., Emmanuel M., 2012. Aspects on the catalysis of lipase from porcine pancreas (type VI-s) in aqueous media: development of ion-pairs. Brazilian Archives of Biology and Technology 55(2), 231–236.

Kosugi, K., 1994. Three-parameter lognormal distribution for soil water retention. Water Resources Research 30 (4), 891–901.

Kosugi, K., 1996. Lognormal distribution model for unsaturated soil hydraulic properties. Water Resources Research 32, 2697–2703.

Lehman, J.T., Botkin, D.B., Likens, G.E., 1975. The assumptions and rationales of a computer model of phytoplankton population dynamics. Limnology and Oceanography 20, 343–364.

Lenzen, M., Dey, C., Foran, B., Widmer-Cooper, A., Ohlemüller, R., Williams, M., Wiedmann T., 2013. Modelling interactions between economic activity, greenhouse gas emissions, biodiversity and agricultural production. Environmental Modeling & Assessment 18, 377–416.

Levenberg, K., 1944. A method for the solution of certain non-linear problems in least squares. Quarterly of Applied Mathematics 2, 164–168.

Lipovetsky, S., 2010. Double logistic curve in regression modeling. Journal of Applied Statistics 37(11), 1785–1793.

Lopez, S., Prieto, M., Dijkstra, J., Dhanoa, M.S., France, J., 2004. Statistical evaluation of mathematical models for microbial growth. International Journal of Food Microbiology 96, 289–300.

Marquart, D.W., 1963. An algorithm for least-squares estimation of non linear parameters. Journal of the Society for Industrial and Applied Mathematics 11(2), 431–441.

Martin, S., Castets, M.-D., Clavier, J., 2006. Primary production, respiration and calcification of the temperate free-living coralline alga *Lithothamnion corallioides.* Aquatic Botany 85, 121–128.

Meza, J.C., 2010. Steepest descent. WIREs Computational Statistics 2(6), 719–722.

Michaelis, L., Menten, M.L., 1913. Die kinetik der invertinwirkung. Biochemische Zeitschrift 49, 333–339.

Motulsky, H.J., Ransnas, L.A 1987. Fitting curves to data using nonlinear regression: a practical and nonmathematical review. FASEB Journal 1(5), 365–374.

Neitsch, S.L., Arnold, J.G., Kiniry, J.R., Srinivasan, R., Williams, J.R., 2010. Soil and Water Assessment Tool. Input/output file documentation. Version 2009 Agricultural Research Service, Texas, USA pp. 604

Nocedal, J., Wright, S., 1999. Numerical optimization. Springer Series in Operations Research. (Eds.) Glynn, P., Robinson, S.M., Springer, New York, pp.634.

Polak, M., Tukaj, Z., Karcz, W., 2011. Effect of temperature on the dose–response curves for auxin-induced elongation growth in maize coleoptile segments. Acta Physiologiae Plantarum 33, 437–442.

Oksanen, J., Minchin P.R., 2002. Continuum theory revisited: what shape are species responses along ecological gradients? Ecological Modelling 157, 119–129.

Orr, A.H., 2006. The distribution of fitness effects among beneficial mutations in Fisher's geometric model of adaptation. Journal of Theoretical Biology 238, 279–285.

Pallavicini, P., Diaz-Fernandez, Y.A., Pasotti, L., 2009. Smoothly shifting fluorescent windows: a tunable ''off-on-off'' micellar sensor for pH. Analyst 134, 2147–2152.

Park, R.A., Clough, J.S., 2004. AQUATOX (Release 2): Modeling environmental fate and ecological effects in aquatic ecosystems. Technical Documentation, EPA/823/R-04/002. Office of Water, United States Environmental Protection Agency, Washington, DC.

Peixoto, J.P., 1984. Physics of climate. Reviews of Modern Physics 56(3), 365–429.

Raes, D., Steduto, P., Hsiao, T.C., Fereres, E., 2009. AquaCrop-the FAO crop model to simulate yield response to water: ii. Main algorithms and software description. Agronomy Journal 101, 438–447.

Richards, F.J., 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10(2), 290–301.

Righetto, L., Casagrandi, R., Bertuzzo, E., Maria, L., Gatto, M., Rodriguez-Iturbec, I., Rinaldo, A., 2012. The role of aquatic reservoir fluctuations in long-term cholera patterns. Epidemics 4, 33–42.

Roper, L.D., 2000. Using sigmoid and double-sigmoid functions for earth states transitions. Personal copy not assigned to a journal, available online: http://www.roperld.com/Science/DoubleSigmoid.pdf.

Schroeder, F., 1997. Water quality in the Elbe estuary: Significance of different processes for the oxygen deficit at Hamburg. Environmental Modeling and Assessment 2, 73–82.

Seki, K., 2007. SWRC fit - a nonlinear fitting program with a water retention curve for soils having unimodal and bimodal pore structure. Hydrology and Earth Systems Science Discussions 4, 407–437.

Shumway, R.H., Stoffer, D.S., 2006. Time series analysis and its applications – with R examples, Springer, NY, 2nd edition.

Simunek, J., Van Genuchten, M., Sejna, M., 2013. The HYDRUS-1D software package for simulating the one-dimensional movement of water, heat, and multiple solutes in variably saturated media, Version 4.16 HYDRUS Software Ser. Department of Environmental Sciences, University of California Riverside, Riverside.

Steele, J.H., 1962. Environmental control of photosynthesis in the sea. Limnology and Oceanography 7, 137–150.

Thanutong, C., Dejdumrong, N., 2013. A new scan conversion technique for Bézier curves. Advanced Science Letters 19(5), 1292–1295.

Tjørve, E., and Tjørve, K.M.C., 2010. A unified approach to the Richards-model family for use in growth analyses: Why we need only two model forms. Journal of Theoretical Biology 267, 417–425.

van de Beek, C.Z., Leijnse, H., Torfs, P.J.J.F., Uijlenhoet, R., 2011. Climatology of daily rainfall semi-variance in the Netherlands. Hydrology and Earth System Sciences 15, 171–183.

van Genuchten, M.Th., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Science Society of America Journal 44, 892–898.

Verhulst, P.F., 1838. A note on population growth. Correspondence Mathematiques et Physiques 10, 113–121.

von Bertalanffy, L., 1957. Quantitative laws in metabolism and growth. Quarterly Review of Biology 32, 217–231.

Wang X.-S., Wu, J., Yang, Y., 2012. Richards model revisited: Validation by and application to infection dynamics. Journal of Theoretical Biology 313, 12–19.

Weibull, W., 1951. A statistical distribution function of wide applicability. Journal of Applied Mechanics 18, 293–297.

Yang, R.C., Kozak, A., Smith, J.H.G., 1978. The potential of Weibull-type functions as flexible growth curves. Canadian Journal of Forest Research 8(4), 424–431.

Yin, X., Kropff, M.J., McLaren, G., Visperas, R.M., 1995. A nonlinear model for crop development as a function of temperature. Agricultural and Forest Meteorology 77, 1–16.

Yin, X., Goudriaan, J., Lantinga, E.A., Vos, J., Spiertz, H.J., 2003. A flexible sigmoid function of determinate growth. Annals of Botany 91, 361–371.

Yuancai, L., Maques, P.C., Macedo, W.F., 1997. Comparison of Schnute's and Bertalanffy-Richards' growth functions. Forest Ecology and Management 96, 283–288.

Zeide, B., 1993. Analysis of growth equations. Forest Science 39(3), 594–616.

Zwiers, F.W., Kharin, V.V., 1998. Changes in the extremes of the climate simulated by CCC GCM2 under CO_2 doubling. Journal of Climate 11, 2200–2222.

Zwietering, M.H., Jongenburger, I., Rombouts, F.M., van't Riet, K., 1990. Modeling of the bacterial growth curve. Applied and Environmental Microbiology 56(6), 1875–1881.

Supplementary material

Table S.1 Historical records of habitat (fishing area) variation and silver eel production 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….

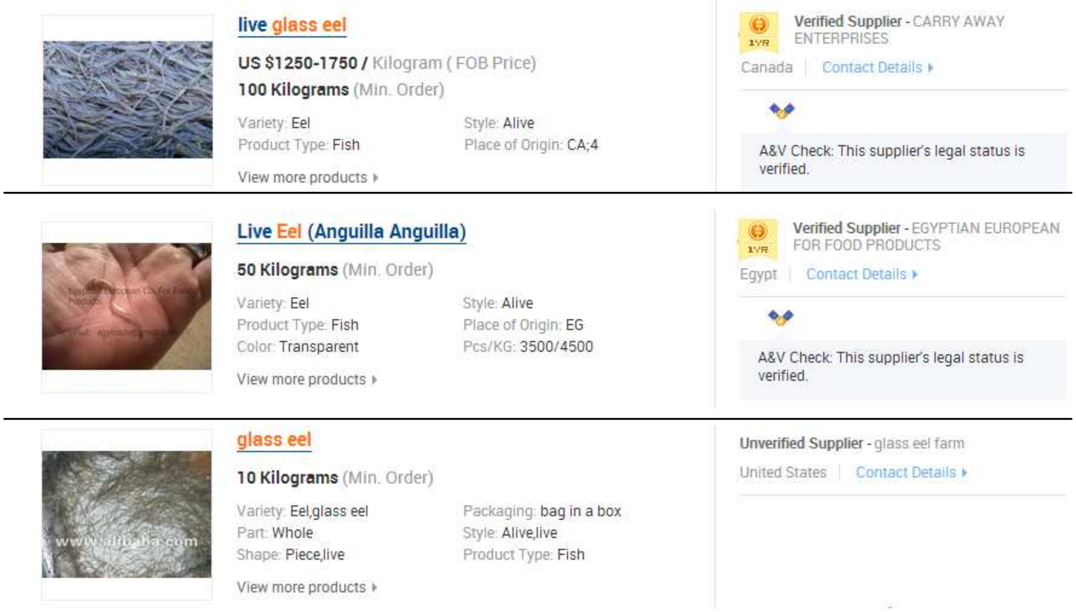
Country	Species (ASFIS species)	Aquaculture area (FAO major fishing area)	Environment (Environment)	Unit	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
China	Japanese eel	Asia - Inland waters	Freshwater	t	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	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	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

The examples given in Figure below provide evidence of the uncontrolled glass eel trade through international trade websites.



live glass eel

US $1250-1750 / Kilogram (FOB Price)

100 Kilograms (Min. Order)

Variety: Eel
Style: Alive
Product Type: Fish
Place of Origin: CA;4

View more products

Verified Supplier - CARRY AWAY ENTERPRISES

Canada | Contact Details

A&V Check: This supplier's legal status is verified.

Live Eel (Anguilla Anguilla)

50 Kilograms (Min. Order)

Variety: Eel
Style: Alive
Product Type: Fish
Place of Origin: EG
Color: Transparent
Pcs/KG: 3500/4500

View more products

Verified Supplier - EGYPTIAN EUROPEAN FOR FOOD PRODUCTS

Egypt | Contact Details

A&V Check: This supplier's legal status is verified.

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glass eel

10 Kilograms (Min. Order)

Variety: Eel,glass eel
Packaging: bag in a box
Part: Whole
Style: Alive,live
Shape: Piece,live
Product Type: Fish

View more products

Unverified Supplier - glass eel farm

United States | Contact Details

Fig.S.1 *Examples of glass eel trade through world trade website platforms (suppliers data were derived from the world trade website platform: http://www.alibaba.com - last accessed on 28/01/2015).*