A modelling approach for conservation of european eel (anguilla anguilla) and related fisheries

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A MODELLING APPROACH FOR CONSERVATION OF EUROPEAN EEL (*Anguilla anguilla*) AND RELATED FISHERIES

Ph. D. thesis

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Preface

Most of the work presented in this thesis, besides the field work, was performed at the Department of Environmental Sciences in Parma, since January 2006. Most of the field data analyzed have been provided by the work conducted by Dr. Alain Crivelli at Tour du Valat Biological Station (Le Sambuc, France).

Since 2006 and 2009 I had the opportunity to join the ICES/EIFAC Working Group on eels and I participated in writing the annual reports on eel status provided by the Group. This experience provided me with new ideas and perspectives that became part of this thesis. In the same period I also had the possibility to present my works at different international workshops and congresses (see below).

The personal relationships established during above mentioned meetings and the excellent scientific network in which my supervisor Professor Giulio A. De Leo was already involved permitted me to spend some fruitful months as visiting student at:

- Poole Lab. Marine Institute (Mayo, Ireland) in March 2007
- Micheli Lab. Hopkins Marine Station, Stanford University (Monterey, CA, USA) from June to September 2007
- Crivelli Lab. Tour du Valat Biological Station (Le Sambuc, France) in March and July 2008
- Tsukamoto Lab. Oceanic Research Institute, University of Tokyo (Tokyo, Japan) in October-November 2008

Most of the contents of this work of thesis have been presented as oral presentations at the following international conferences:

- Andrello M., **D. Bevacqua**, P. Melià, A.J. Crivelli & G.A. De Leo (2008). Impact of the invasive European catfish on the dynamics of a European eel population in a freshwater canal. MALIAF 2008 "Managing Alien Species for Sustainable Development of Aquaculture and Fisheries", Firenze, Italy, 5-7 November 2008
- **Bevacqua D**., P. Melià, A.J. Crivelli, G.A. De Leo & M. Gatto (2008). A demographic model for the continental phase of anguillid eels. WFC 2008, 5th World Fisheries Congress, Yokohama, Japan, 20-24 October 2008
- **Bevacqua D**., P. Melià, A.J. Crivelli, M. Gatto & G.A. De Leo (2008). Market preferences and conservation measures for the European eel. Aquaculture Europe 08, Krakow, Poland, 15-18 September
- **Bevacqua D**., P. Melià, A.J. Crivelli, M. Gatto & G.A. De Leo (2007). A multi objective, bioeconomic analysis of a small scale eel fishery in Camargue. 6th European Conference on Ecological Modelling, ECEM'07, Trieste, Italy, 27-30 November
- **Bevacqua D**., P. Melià, A.J. Crivelli, G.A. De Leo & M. Gatto (2007). Market preferences and conservation measures. The case of the European eel. Challenges for Diadromous Fishes in a Dynamic Global Environment, 137th Annual Meeting of the American Fisheries Society 2007, Halifax, Nova Scotia, Canada, June 18-21
- **Bevacqua D**., P. Melià, A.J. Crivelli, G.A. De Leo & M. Gatto (2006). Effectiveness of EU conservation measures for the European eel (*Anguilla anguilla*): an analysis for the Camargue lagoons. Estuarine & Coastal Sciences Association 41st International Conference 2006, Venice, Italy, 15-20 October
- **Bevacqua D**., M. Andrello, P. Piovani, P. Melià, G.A. De Leo & M. Gatto (2006). How variations in the oceanic conditions can affect population genetics of a catadromous fish. The

case of the European eel. Estuarine & Coastal Sciences Association 41st International Conference 2006, Venice, Italy, 15-20 October
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- M. Andrello, **D. Bevacqua**, P. Melià, A. Crivelli, M. Gatto & G.A. De Leo (2006). A simulation model of population genetic to unravel the panmictic nature of European eel. The Fisheries Society of the British Isles Annual International Symposium 2006, Aberdeen, UK, 10-14 July
- **Bevacqua D**., P. Melià, A. Crivelli, G.A. De Leo & M. Gatto (2006). A demographic model for the management of the eel fisheries in the Camargue lagoons. The Fisheries Society of the British Isles Annual International Symposium 2006, Aberdeen, UK, 10-14 July
- **Bevacqua D**., P. Melià, A. Crivelli, G.A. De Leo & M. Gatto (2006). Timing and rate of sexual maturation of European eel in brackish and freshwater environments. The Fisheries Society of the British Isles Annual International Symposium 2006, Aberdeen, UK, 10-14 July

The thesis is structured in nine chapters. Except for the first introductive chapter and the last one that provides an overall conclusion of my work, the remaining seven chapters are based on manuscripts that have been published, submitted or devised for submission to international peer reviewed journals.

- Charter 2: Melià P., **D. Bevacqua**, A. J. Crivelli, J. Panfili, G. A. De Leo & M. Gatto 2006. Sex differentiation of the European eel in brackish and freshwater environments: a comparative analysis. *Journal of Fish Biology* 69, 1228-1235.
- Charter 3: Melià P., **D. Bevacqua**, A. J. Crivelli, De Leo G., J. Panfili, and M. Gatto 2006. Age and growth of the European eel *Anguilla anguilla* in the Camargue lagoons. *Journal of Fish Biology***,** 68:876-890.
- Charter 4: **Bevacqua D**., P. Melià, A. J. Crivelli, G. A. De Leo and M. Gatto 2006. Timing and rate of sexual maturation of European eel in brackish and freshwater environments. *Journal of Fish Biology* 69:200-208
- Charter 5: **Bevacqua D**., P. Melià, A. J. Crivelli, M. Gatto and G. A. De Leo. Size selectivity of fyke nets in eel fishing. Submitted to *Journal of Fish Biology*
- Charter 6: **Bevacqua D**., P. Melià, A. J. Crivelli, M. Gatto and G. A. De Leo. An age-length structured demographic model for anguillid eels. In preparation
- Charter 7: **Bevacqua D**., P. Melià, A. J. Crivelli, M. Gatto and G. A. De Leo 2007. Multi-objective assessment of conservation measures for the European eel (Anguilla anguilla): an application to the Camargue lagoons. *ICES Journal of Marine Science* 64(7):1483-1490
- Charter 8: **Bevacqua D**., P. Melià, A. J. Crivelli, M. Gatto and G. A. De Leo 2007. Assessing Management Plans for the recovery of the European eel (*Anguilla anguilla*): a need for multi-objective analyses. Proceedings of the 137th Annual Meeting of the American Fisheries Society 2007. Challenges for Diadromous Fishes in a Dynamic Global Environment, Halifax, Nova Scotia, Canada, June 18-21. *Fisheries* (in press).

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1
General introduction

The urgency for a conservation and management plan for the European eel

The interest in the biology and ecology of European eel has rapidly shifted in a just a decade from the anecdotic curiosity for its complex and fascinating natural history and its still mysterious life-cycle, to the growing concern for the status of eel stocks due to the dramatic decline of recruitment, which is now less than 10% of what was observed in the past (ICES, 2007). Concerns exist not only at the biological and ecological level, but also for the huge number of small-scale fisheries exploiting eels. In September 2007 a Council Regulation "establishing measures for the recovery of the stock of European eel" (EC 1100/2007) has been approved. The objective of the Regulation is "to achieve a recovery of the stock of European eel to previous historic levels of adult abundance and the recruitment of glass eel", and to ensure the sustainable use (fishing) of the stock. The principal element of the Regulation is the establishment of eel management plans for each River Basin according to which it shall be permitted, "with high probability, the escapement to sea of at least 40% of the biomass of adult eels"

A brief review of eel life cycle

The European eel (*Anguilla anguilla* L., 1758) is a highly migratory amphihaline species. The geographic distribution of *A.anguilla* comprises most of Europe, ranging from Northern Scandinavia to Northern Africa, and from the Eastern Mediterranean region to the Azores. Its life cycle, elucidated in the 1920's by Johannes Schmidt, is considered unique and extraordinary, but still cannot be considered completely known. Spawning takes place, according to Schmidt's findings, in the Atlantic Ocean, probably in the Sargasso Sea where the smallest *larvae* (the leptocephali) were observed (Schmidt, 1912). After hatching, leptocephali are probably driven towards east by the Gulf Stream and this drift is believed to take from a few months (Lecomte-Finiger, 1994) to a few years (Schmidt, 1925; Kettle and Haines, 2006). On the continental shelf, leptocephali metamorphose into glass eels (small unpigmented eels), which colonize coastal and inland waters of the Atlantic and Mediterranean coasts. Once entered the new environment, glass eels undergo a series of physiological and behavioural changes, develop pigmentation, and become able to swim actively, thus entering the "elver" stage (small yellow eel). Yellow eels grow and feed in continental waters in this pre-reproductive stage for a variable number of years, ranging from about 3 to 8 years for males and from about 5 to 20 years for females, until they reach maturation size (around 400 mm for males and 600 for females). Eels eventually undergo metamorphosis to the silver stage, begin sexual maturation and migrate back to the spawning areas where they complete maturation processes (van Ginneken et al. 2007), spawn and die. While eels are commonly believed to colonize inland waters, recent analysis shows that a fraction of eels might develop their full life cycle in coastal waters (Tsukamoto, 1998; Daverat et al.; 2006).

The eel decline

After having constituted most of the fish biomass in many European fresh and brackish water bodies and sustained thousands of small scale fisheries spread all over the continent, in the last decades the overall European eel stock faced a severe decline and today the species is to be considered beyond safe biological limits (ICES, 2007). Fisheries data indicate that the eel stock is at its historical minimum; only 1% of the 1960 recruitment level is reached at the moment.

Scientists proposed several potential causes to explain the observed decline. On the one hand, there are processes occurring in the oceanic phase, such as variation in the North Atlantic Oscillation (NAO) and the possibility of a weakening of the Gulf Stream due to global climate change (Castonguay et al., 1994; Desaunay and Guerault, 1997; Bonhommeau et al., 2008). These processes can reduce both larval survival and the adult reproductive success, thus affecting the stock as a whole. On the other hand, there are continental factors ranging from water pollution and contamination, to overexploitation of either glass eels or yellow and silver eels, to man-made

transfers of parasites and diseases, to habitat loss due to land reclamation and the presence of barriers and dams (ICES, 2007).

Open questions on eel demography and management

Despite the fact that European eel has recently gathered considerable attention, there are very few detailed studies on eel population dynamics. In fact, the eel life cycle presents several distinctive features that have been usually neglected in demographic modelling analysis, such as high plasticity in body growth, marked sexual dimorphism, sexual maturation depending upon size rather than upon age, annual fluctuations in recruitment, and effects of density on body growth, survival and sex ratio. Some of these issues have been explicitly accounted for in past works and this has allowed a preliminary estimation of otherwise unknown demographic parameters for some North-Adriatic populations (De Leo and Gatto 1995; 1996). Nevertheless, further investigation is needed to extend such demographic analyses to other sites in order to allow comparison and provide a useful tool for defining eel management plans requested by the new Regulation (EC 1100/2007). Indeed, eel management needs to be further investigated at both local and global scale, possibly with the support of an adequate modelling effort so as to identify the effects of alternative management strategies. The continental population extends throughout Europe and northern Africa, and fisheries are scattered over literally thousands of large and small water bodies, both marine and freshwater. Local management of over 10,000 small, fragmented and weakly regulated fisheries has not been adequately addressed yet in a formal quantitative framework.

Aims and outlines of the thesis

Demographic models that have been proposed to describe the continental phase of eel life cycle can be divided into site specific and general models. Site specific models (see for example Vøllestad and Jonsson (1988) or De Leo and Gatto (1995)) are usually devised, calibrated and, in same cases, validated upon data from particular dataset. Such models help in describing local population dynamics but can be hardly applied to different populations. On the other hand, very general model (see Dekker, 2000 or Lambert and Rochard, 2007) can be easily applied to different contexts but usually neglect parameter calibration and prediction validation on field data. The aim of this thesis is to develop modelling approaches for describing eel demography that can be easily applied to different contexts where a suitable dataset is provided (chapters 2, 3, 4, 5 and 6). Then, I show the effectiveness of such models when defining management plans, requested by the new European regulation (EC 1100/2007), with particular emphasis on eel fisheries and multiobjective analyses (chapters 7 and 8).

Chapter 2 provides a body growth model for eels that explicitly accounts for different growth patterns in undifferentiated, males and females individuals. The model permits to assess asymptotic lengths and for the first time the body size that triggers sexual differentiation.
In Chapter 3, the above mentioned body growth model is applied to different populations characterized by different levels of salinity. The emerging results confirm that brackish waters allow for higher growth rates and suggest that an average size of around 22 cm, independently from growth rates and salinity, might trigger gonadal development and consequent sexual differentiation.
Chapter 4 provides a sexual maturation model, then calibrated on three different populations characterized by different salinity levels. The model confirms that sexual maturation process is likely to depend on size rather than on age and provides mathematical evidence to the hypothesis that males and females follow different strategies when attaining maturation size.
Chapter 5 provides, through a meta-analysis, a model to assess size selectivity of meshed fishing gears.
In Chapter 6, all the models presented in previous chapters are merged in a unique model, length and age structured, able to describe eel population dynamics in the continental phase: from glass eel recruitment to silver eel escapement. This model retains the main features of eel biology and

explicitly considers fishing mortality due to different fishing policies. Although the model has been devised to be suited to different eel population, here I present its calibration and validation to the eel population of the Camargue lagoons (southern France).
In chapter 7, a preliminary version of the model presented in chapter 6 is used to assess ecological and social (here intended as harvest biomass) consequences of different eel fishery management in the Camargue lagoons with particular regards to the requests of the Council Regulation (EC 1100/2007). In order to show optimal policies with regard to different and somehow contrasting objectives, I perform a multi-objective analysis to highlight possible tradeoffs between different policies in order to avoid conflicts between different stakeholders. The main result is that historical management of Camargue eel fishery seems to be far from being optimal under both ecological and social aims.
Chapter 8 provides a review of different approaches in dealing with eel population dynamics and their potential application to eel fishery management. The review suggests that, despite the existence of some studies on local population dynamics, just a few of them have been used to develop sound management policies. Moreover, multicriteria analysis, explicitly accounting for conflicting objective, is almost absent in fishery management.
Finally, in chapter 9, I discuss the obtained results of my work in order to show what has been added to previous knowledge on eel ecology and management and what still need to be done.

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2

Age and growth of the European eel in the Camargue lagoons

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Abstract

Although the main features of the continental phase of European eel's (*Anguilla anguilla*) biological cycle are currently well-known, realistic and well tuned demographic models based on long-term studies are still needed. Age-length data from a 11-year monitoring of the European eel population of the Camargue lagoons (Rhône delta, Southern France) were collected for glass, yellow and silver eels. Three distinct models were calibrated to describe the growth process of undifferentiated eels, females and males, respectively. Uncertainty of parameter estimates was evaluated by bootstrapping. Females were characterized by larger asymptotic body size than males (580±50 vs. 388±13 mm) and faster growth, whilst the Brody growth coefficient was larger for males than for females ($3.00 \cdot 10^{-3} \pm 1.68 \cdot 10^{-3}$ vs. $1.73 \cdot 10^{-3} \pm 0.50 \cdot 10^{-3}$). Sexual differentiation was estimated to begin at 204±38 mm, i.e., at the end of the second year of permanence in the lagoons, well before the length at which macroscopic differentiation becomes possible (about 300 mm), but consistently with histological observations. Males are likely to leave the lagoon or die (due to either natural or fishing mortality) within the first three years, whilst females can remain up to five years. Sexual differentiation and maturation have a major role in shaping the length structure of the population. Length-weight data were fitted by allometric curves ($W = aL^b$). The calibration of distinct curves for data from different years evidenced that the allometric coefficient a is subject to wider inter-annual fluctuations than the allometric exponent b. A negative correlation links average body length and allometric exponent ($r = -0.58$, $P << 0.01$).

Introduction

The European eel *Anguilla anguilla* (L.) has long been an important economic resource for fishermen in many Atlantic and Mediterranean coastal areas. The European eel stock, however, has been declining since the early 1970's, with official catches diminishing from more than 20,000 t in 1968 to about 7,000 t at the end of the 1990's (FIGIS, 2004). Although true catches in the 1990's may be almost twice larger than official data, due to illegal and unreported catches (ICES, 1988; Moriarty and Dekker, 1997), there is general agreement that European eels are now seriously threatened (Moriarty and Dekker, 1997; EIFAC/ICES, 2003). Therefore, the development of sustainable exploitation strategies and active conservation policies is fundamental for the maintenance of the European eel and other *Anguilla* stocks all over the world (Dekker *et al.*, 2003).

Despite the concern of the scientific community about the fate of European eels, the present knowledge of the stock status is chiefly based on indirect measures (as total harvests or catches per unit effort). Detailed and time-extensive demographic data are indeed lacking since the mid 1980's, when Vøllestad and Jonsson (1988) published the results of their 13-year monitoring in the Imsa River (SW Norway). Recent studies have mostly been limited to short-term surveys. This might be due to reduced funding for long-term investigation because the European eel is losing its commercial interest after being heavily exploited.

For this reason, the extensive dataset presented and analysed here is of particular importance. It has been collected during a long-term survey in the Rhône delta lagoons (Camargue, Southern France), where the body length structure of the local population was monitored during 11 years, from 1993 to 2003. A statistical analysis is performed on the data to single out the main features of the population and determine the factors that influence its structure. The dataset is then used to calibrate a growth model that is specifically suited for eel populations.

Although a number of studies have been carried out to describe body growth of the European eel since the late 1970's (see, e.g., Rossi and Colombo, 1976*a*, 1976*b*; Moriarty, 1983; Vøllestad, 1985; Fernández-Delgado *et al.*, 1989; De Leo and Gatto, 1995; Poole and Reynolds, 1996; Svedäng, 1999; Aprahamian, 2000), most of them have been limited to the recording of growth rates. Only

few recent studies have led to the formulation or calibration of a growth model. De Leo and Gatto (1995), for instance, calibrated a von Bertalanffy growth model, with parameters differentiated by sex, on data from the intensively exploited eel population of the Comacchio lagoons (NE Italy). Poole and Reynolds (1996) calibrated an analogous model on data from an unexploited system at Burrishoole (W Ireland). No model, however, has ever accounted for a realistic description of eel growth before sexual differentiation. The main features of the European eel's biological cycle are currently rather well-known, at least for its continental phase, but there is still a need for realistic and well tuned demographic models based on large datasets from long-term studies and derived by means of rigorous calibration procedures. Devising reliable growth models is the basis for the development of sound population models. These, in turn, can provide an effective framework for a better understanding of the consequences of different management policies on the long-term demography of the European eel. Herein, three distinct growth curves are calibrated for undifferentiated eels, males and females, under the hypothesis that eels follow the same growth path before sexual differentiation. Non-parametric statistics (bootstrapping) are used to derive probability distributions for parameter estimates and assess their uncertainty.

Materials and methods

Eels were collected at two sites in the brackish waters of the Rhône delta (Camargue, Southern France; see Fig. 1): Capelière, in the Vaccarès lagoon (6,400 ha) and Malagroy, in the Impériaux lagoon (4,600 ha). The lagoons are connected to the Mediterranean Sea at Grau de la Fourcade, near Saintes Maries de La Mer, by sluice gates which regulate the water flow to and from the lagoons.
From March 1993 to November 1996, 1,808 eels were caught at Capelière. The fishing device was the capétchade, an eel pot with a 6 mm mesh size and a 40 m guiding net, called paradière. The total length of the eels was measured, and, occasionally, the weight. From January 1997 to November 2003, 18,300 eels were caught at Capelière and Malagroy with the same fishing devices. Their total length, weight, sex, stage of sexual maturation (yellow or silver eel) were determined. Eels shorter than 300 mm were classified as undifferentiated, whilst longer eels were sexed by gonad inspection. The stage of sexual maturation was determined according to Pankhurst's (1982) ocular index. A sub-sample of 352 individuals caught between October 1997 and September 1998 was subject to otolith inspection. For each individual, the whole right and left otoliths were read immersed into rosemary essential oil (in order to enhance the visualisation of the growth marks) under a binocular microscope with reflected light against a dark background. Otolith examination was helped by a digital image acquisition and the construction of an image data bank. Both otoliths were then read twice by one reader from the core area to the edge and then back to the centre again: opaque zones were read as annual

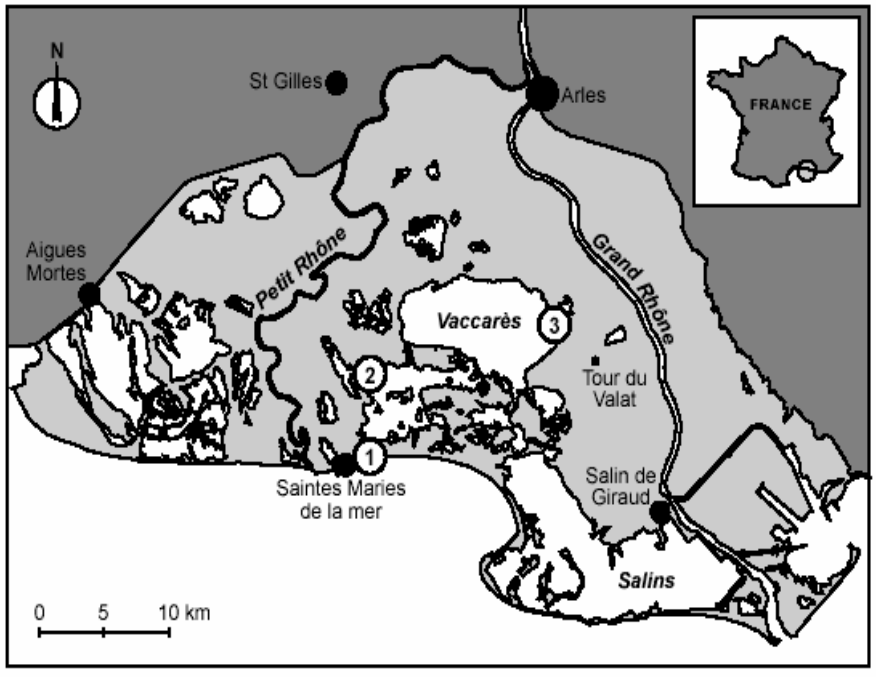


Figure 1. *The Camargue lagoons (1, the position of Fourcade sluice gates; 2, the sampling station at Impériaux; 3, the sampling station at Vaccarès)..*

increments. Age estimation was done according to the validated method described in Panfili and Ximénès (1994). 291 individuals were successfully aged, the otoliths of the others remaining non interpretable. Between 1993-2003, glass eels were also sampled at different sites in the Vaccarès and Impériaux lagoons with a fry net (with a 0.5 mm mesh size and a 20 m leading net) and close to Fourcade sluice gates (with a hand net). 1,327 individuals were caught and their total length and weight were measured.

Results

Length and age structure of the population

Table I reports the basic length statistics of the 1,327 glass eels sampled between 1993-2003. The average length has been varying between 60 and 65 mm. The basic statistics of length data for the 20,108 adult eels (yellow and silver) caught between 1993-2003 at Capelière and Impériaux are reported in Table II. The average length of adult eels has been varying between approximately 200 and 400 mm. Fig. 2*a* shows the length structure of the adult population.

Table I – *Basic statistics of length data (by year) for the 1993-2003 glass eel sample.*

Year	Number of eels	Mean ± S.D. (mm)	Min (mm)	Max (mm)
1993	16	65 ± 5	58	77
1994	238	62 ± 4	52	74
1995	34	65 ± 6	54	91
1996	13	61 ± 3	57	66
1997	47	60 ± 4	52	68
1998	258	60 ± 3	52	69
1999	74	62 ± 4	54	70
2000	381	61 ± 3	52	72
2001	8	61 ± 2	58	63
2002	145	63 ± 4	53	72
2003	113	63 ± 3	56	71

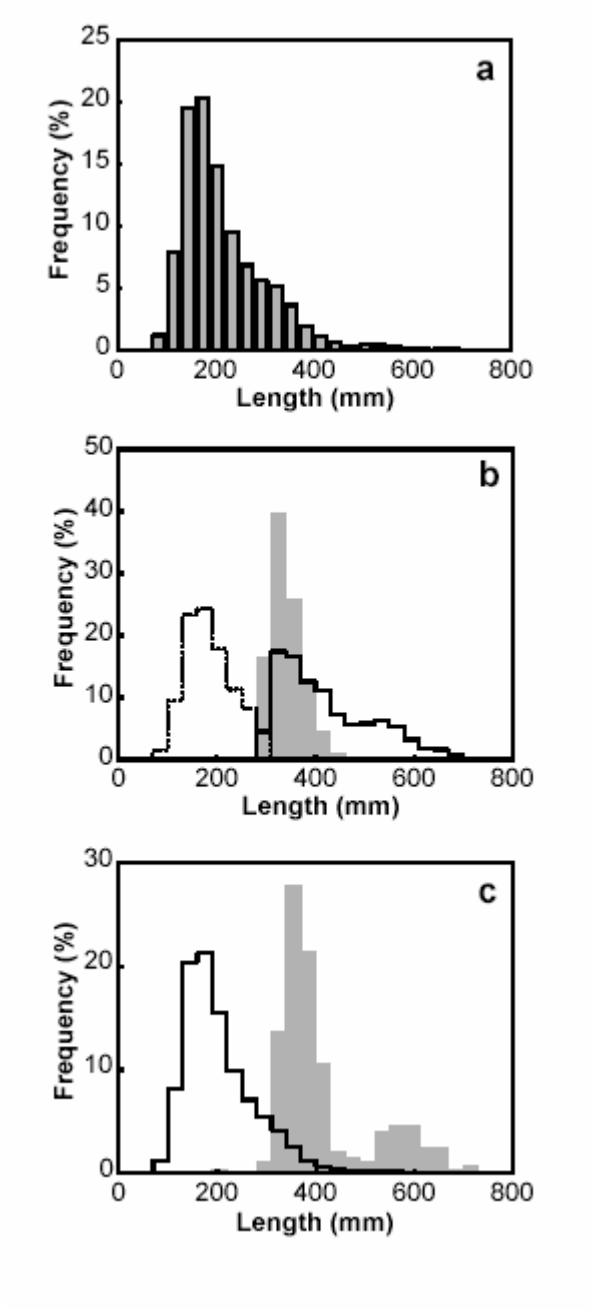
To analyse the population structure in more detail, data were divided into groups according to sex and sexual maturation stage. As data collected between 1993-1996, however, include only body length (not sex and maturation stage), only the 1997-2003 dataset has been considered in the following.

Table II – *Basic statistics of length data (by year) from the 1993-2003 sample of adult eels*.

Year	Number of eels	Mean ± S.D. (mm)	Min (mm)	Max (mm)
1993	576	392 ± 108	102	748
1994	665	294 ± 182	57	762
1995	282	383 ± 157	76	784
1996	285	342 ± 117	138	733
1997	4243	220 ± 82	68	661
1998	7842	190 ± 71	60	688
1999	1774	219 ± 84	73	735
2000	1736	233 ± 106	64	717
2001	1009	254 ± 88	80	722
2002	1105	291 ± 91	75	700
2003	591	287 ± 99	62	664

The basic length statistics for the different categories considered are reported in Table III. Length distributions by sex and maturation categories are displayed in Fig. 2*b* and Fig. 2*c*. Some key features of the length structure are immediately apparent from the histograms: Fig. 2*b* shows that males rarely exceed 400 mm, whereas female length has a much wider range. As for the structure by maturation stage, Fig. 2*c* shows that the length of yellow eels rarely exceeds 300 mm, whilst the

length distribution of silver eels is bimodal, with a lower mode at about 350 mm and a higher mode around 600 mm, corresponding to mature males and females, respectively.
Fig. 3*a* shows the age distribution of the subset of 291 eels aged between 1997-1998. The age structure is bimodal, with peaks at one and three annuli. Fig. 3*b* shows the age distribution of the sample by sex. It is apparent from the histogram that most eels undergo sexual maturation after two or three years of residence in the lagoon. Females can remain in the lagoon up to five years, whereas no males stay longer than three years. A classification by sexual maturation stage (i.e., yellow vs. silver eels) was not possible because the aged sample comprised only three silver eels.



Length-weight curve

Length and weight are usually linked by an allometric relationship, with weight W being a power of length L:

$$W = aL^b \quad (1)$$

This relationship can be written in a linear form after a logarithmic transformation of data, which allows estimating a and b by linear regression. A length-weight curve was calibrated on the entire 1997-2003 dataset and separately on the data of each maturation and sex category cited in the previous section. The uncertainty of the parameter estimates was assessed by bootstrapping (Efron, 1979) the original data (1000 iterations for each dataset). Results are reported in Table IV. Parameter estimates are significantly different between maturation stages and among sex categories (t-test, $P<0.01$ for all pairwise comparisons). Silver eels are the category characterized by the lowest value of a and b. This is indeed obvious, as they are slimmer because of the metamorphosis they are undergoing (gonads develop, the digestive tube reduces, feeding stops). The estimates of a and b for undifferentiated eels are practically identical to those of yellow eels. This is not unexpected, if one considers that undifferentiated eels are the overwhelming majority of yellow eels. The allometric exponent b of females is greater than that of males, whilst a is higher for males.

Figure 2. *Total length distribution (30mm classes) of 18300 European eels caught between 1997 and 2003 at Vaccarès and Impériaux: (a) entire sample, (b) divided by sex (dotted line: undifferentiated; grey: males and white, females) and (c) divided by maturation stage (white: yellow eels; grey: silver eels). The frequency is relative to total numbers in each class.*

Table III – *Basic statistics of length data for the 1997-2003 adult eel sample. Notice that sex and maturation categories do not sum up to 18,300 because for a few eels sex and/or maturation stage could not be determined.*

Group	Number of eels	Mean ± S.D. (mm)	Min (mm)	Max (mm)
undifferentiated	15317	186 ± 48	60	299
males	1585	342 ± 31	300	476
females	941	423 ± 95	300	722
yellow	17421	208 ± 77	60	714
silver	418	416 ± 96	300	722
total	18300	217 ± 87	60	735

Table IV – *Results of calibrating the length-weight allometric relationship from the 1997-2003 data. a and b are the parameters of the allometric relationship (mean ± S.D.) and* σ^2_{expl} *is the percent of explained variance. Eel numbers are slightly lower than those reported in Table II because a few eels were not weighed.*

Group	Number of eels	*a*	*b*	σ^2_{expl}
undifferentiated	15311	$2.24 \cdot 10^{-7} \pm 0.06 \cdot 10^{-7}$	3.37 ± 0.01	0.96
males	1585	$8.14 \cdot 10^{-7} \pm 2.12 \cdot 10^{-7}$	3.15 ± 0.04	0.79
females	940	$5.25 \cdot 10^{-7} \pm 0.72 \cdot 10^{-7}$	3.22 ± 0.02	0.96
yellow	17414	$2.29 \cdot 10^{-7} \pm 0.05 \cdot 10^{-7}$	3.36 ± 0.00	0.98
silver	418	$8.43 \cdot 10^{-7} \pm 1.64 \cdot 10^{-7}$	3.15 ± 0.03	0.95
total	18293	$2.36 \cdot 10^{-7} \pm 0.04 \cdot 10^{-7}$	3.36 ± 0.003	0.98

To find out possible inter-annual variation in allometric parameters, *a* and *b* were estimated for each year from 1993 to 2003 (data from 1993 to 1996 were not used in the preceding analysis due to the lack of data about sex and maturation). Results are synthesized in Fig. 4. The coefficient *a* is affected by a considerably higher degree of variability than the allometric exponent *b* (between-year coefficients of variation were 39 and 2%, respectively). The two parameters are linked by a conspicuous negative correlation ($r = -0.95$, $P \ll 0.01$, see Fig. 4*a*). Also, the allometric exponent correlates negatively with the average length of eels in the same year ($r = -0.58$, $P \ll 0.01$, see Fig. 4*b*), which in turn is positively, yet more loosely, correlated with coefficient *a* ($r = 0.40$, $P \ll 0.01$, not shown).

Growth model

The classical von Bertalanffy (1957) model was used as a basis to describe eel growth. In its differential form, it links body length to age by means of the following equation:

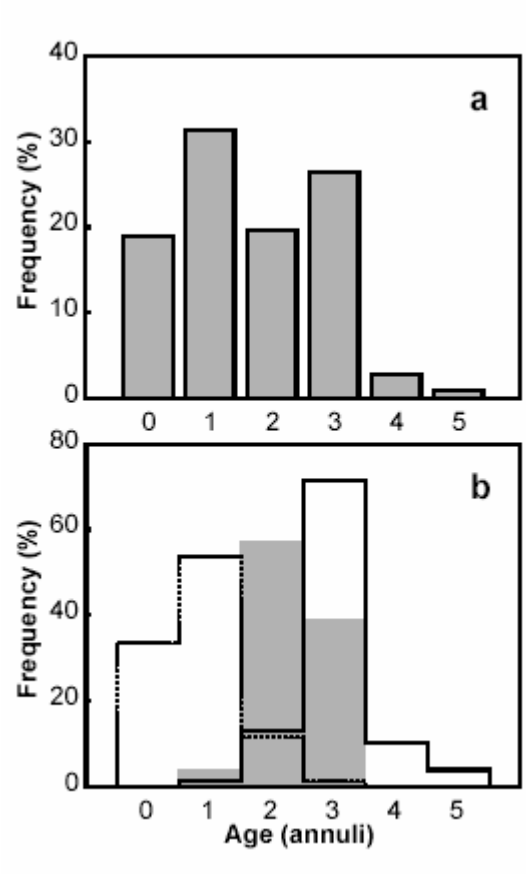
$$\frac{\mathrm{d}L}{\mathrm{d}x} = k \cdot (L_\infty - L) \qquad (2)$$

where L_∞ is the asymptotic mean length and k is the Brody growth constant. Due to the strong sexual differentiation of eels, calibrating a single growth curve would indeed provide a scarcely realistic description of growth. For this reason, previous growth models have usually contemplated different growth curves for females and males, respectively (De Leo and Gatto, 1995; Poole and Reynolds, 1996). However, since eels remain sexually undifferentiated for about two to three years and sex is not genetically determined, a third growth curve is introduced here to describe the growth of undifferentiated eels. All eels are assumed to share the same growth curve until age x^* (to be estimated together with the other parameters), at which sexual differentiation takes place, and then follow two distinct growth paths according to the sex they have assumed. The equations of the growth model are therefore the following:

$$L(x) = \begin{cases} L_0 + (L^* - L_0)\dfrac{1-\exp(-k_U x)}{1-\exp(-k_U x^*)} & \text{for } x \le x^* \quad \text{(undiff.)} \quad (3a) \\ L_{\infty F} - (L_{\infty F} - L^*)\exp\left(-k_F (x - x^*)\right) & \text{for } x > x^* \quad \text{(females)} \quad (3b) \\ L_{\infty M} - (L_{\infty M} - L^*)\exp\left(-k_M (x - x^*)\right) & \text{for } x > x^* \quad \text{(males)} \quad (3c) \end{cases}$$

where L_0 is the length at age zero (which is conventionally set to the age at which glass eels become pigmented and metamorphose to elvers), $L^* = L(x^*)$ is the length at age x^*, k_U, k_F, and k_M are the Brody growth constants for undifferentiated eels, females and males, and $L_{\infty F}$ and $L_{\infty M}$ are the asymptotic mean lengths of females and males, respectively. Note that Eq. (3*a*) is still a von Bertalanffy curve, albeit written in a slightly unusual form. In fact, this formulation evidences the length at sexual differentiation instead of the asymptotic mean length for undifferentiated eels, as this latter parameter would lack any biological meaning (the growth process begins to slow down only when eels are already differentiated). However, Eq. (3*a*) can be derived straightforwardly from the equivalent, yet more usual form $L(x) = L_{\infty U} - (L_{\infty U} - L_0)\exp(-k_U x)$.

The growth model was calibrated with the data from the 291 eels caught between 1997-1998, for which length, age, and sex data were available. As data were collected in different years (1997 and 1998) and at different stations (Vaccarès and Impériaux), a three-way ANOVA was performed with respect to fishing station, catch year and sex to verify the homogeneity of the dataset. Results showed that neither spatial location (ANOVA, P = 0.12) nor catch year (P = 0.21) significantly affected the mean length in 1997-1998, whilst sex had a strong, statistically significant effect ($P<10^{-15}$).



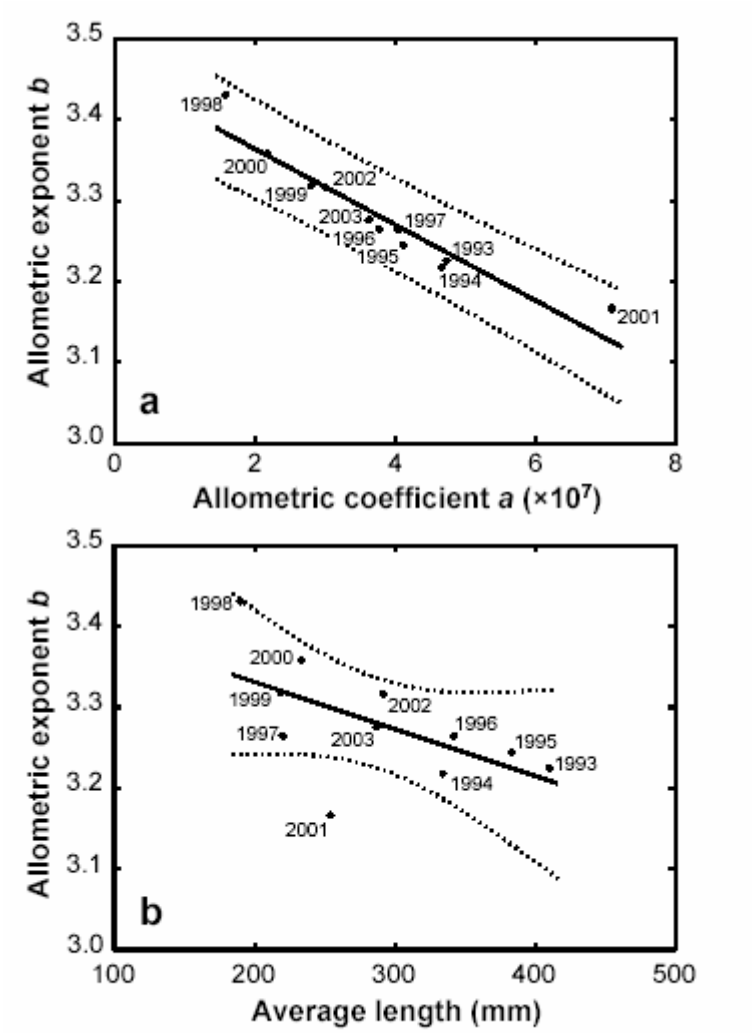
To perform a rigorous calibration of the growth curves, the number of annuli in the otolith (which is indeed the only age indicator available) must be transformed to a 'true' age (in days). However, the precise assignment of age to an eel requires the assumption that all eels recruited in a given year enter the lagoon simultaneously at a given (average) date. As glass eel recruitment in the Camargue usually peaks between March-April, this date was set at April 1st. Then age was calculated as the difference between the day of capture and the day of recruitment plus a number of years equalling the number of annuli counted via otolith inspection. The number of annuli in the otolith corresponds indeed to the number of years an eel has spent in the lagoon.

Eq. (3) has eight unknown parameters (L_0, x^*, L^*, k_U, k_F, k_M, $L_{\infty F}$ and $L_{\infty M}$), to be estimated from data. Since the three curves must intersect in a unique point, corresponding to age and length at which

Figure 3. *Age distribution of 291 European eels sampled between 1997-1998: (a) entire sample; (b) by sex (dotted line: undifferentiated; grey: males and white, females). The frequency is relative to total numbers in each class.*

sexual differentiation occurs, the calibration of the three curves must be carried out concurrently. However, the simultaneous estimation of the eight parameters would be computationally difficult. Hence, the calibration procedure was split in three sequential steps. First, L_0 was estimated as the average length of glass eels caught between 1997-1998. Then, $L_{\infty F}$ and $L_{\infty M}$ were estimated by fitting two distinct von Bertalanffy growth curves (for females and males, respectively) to adult eel data, and discarding the corresponding values of k_F and k_M. In fact, asymptotic mean length estimates depend mostly upon length data at older ages, and are likely to be less influenced than Brody coefficients by the values assumed by the other parameters. The optimal values of $L_{\infty F}$ and $L_{\infty M}$ were found by minimizing the mean squared error between the logarithms (under the hypothesis of multiplicative error) of observed and predicted age-length data of females and males, respectively. Finally, having fixed the values of L_0, $L_{\infty F}$ and $L_{\infty M}$, Eqs. 3*a*, 3*b* and 3*c* were fitted on age-length data of undifferentiated eels, females and males (again by minimizing the mean squared error between the logarithms of observed and predicted data) to estimate the remaining five parameters (x^*, L^*, k_U, k_F and k_M).

Age and length at sexual differentiation are to be estimated from the data; however, eels less than 300 mm long had not been sexed due to the impossibility of macroscopically distinguishing males from females. Therefore, to use also age-length data of those individuals having a length comprised between L^* and 300 mm (i.e., for which sexual differentiation is supposed to have occurred but not to be detectable yet), the model calibration was performed in the following way: first, the length an eel would have if it were a female and if it were a male was estimated on the basis of current parameter values; then, the corresponding prediction errors were calculated; finally, each error was multiplied by the fraction of individuals of the corresponding sex at differentiation and the overall error was derived as the sum of the two.



Note that sex ratio at differentiation cannot be simply calculated from the overall catch. The corresponding estimate would indeed be biased in favour of females, which mature later and consequently spend a longer time in inland waters compared to males. As males stay in the Camargue lagoons no longer than three years, an unbiased estimate of the sex ratio could be obtained by considering only those eels that are already sexually differentiated but are less than three years old. However, the subsample of 291 eels aged between 1997-1998 contained only 41 individuals satisfying these

Figure 4. *Interannual variation of the total length and mass relationship between 1993 and 2003. (a) Comparison of the allometric coefficients and (b) comparison of the allometric coefficients and mean total length.- linear regression; -- 95%confidence intervals.*

constraints, too small a number to obtain a significant estimate. Hence, 90% confidence intervals for length were calculated from the subset of sexually differentiated eels under three years (306–530 mm for females and 305–388 mm for males, respectively). Then, all eels with a length comprised within the previously calculated confidence intervals were selected from the whole set of 12,085 eels caught between 1997-1998, obtaining 301 females and 467 males. The resulting estimate of the sex ratio at differentiation is skewed in favour of males and is about 1:1.55. Thus, the corresponding weights used to calculate the prediction error for sexually differentiated eels under 300 mm were 0.39 and 0.61 for females and males, respectively.

The uncertainty associated to parameter estimates was assessed with the bootstrap (Efron, 1979; see De Leo, 1995 for an application of the bootstrap to eel demography). During the extraction of the subset of eels to be aged, eels were divided into 25 mm length classes, and an approximately constant number of eels per class (independent of the relative abundance of that class) was aged. Therefore, the bootstrap procedure was stratified (Efron and Tibshirani, 1986) in length classes to follow the original sampling scheme. Original data were resampled 1000 times, generating an empirical probability distribution for each parameter. The basic statistics for the model parameters are reported in Table V. Fig. 5 shows the original dataset and the fitting curves. Note that the median values of parameters' distributions were used instead of the means, as the first are much less influenced by extreme values.

Table V – *Basic statistics of growth curves' parameters, as obtained by bootstrapping the 1997-1998 dataset.*

Parameter		**Mean ± S.D.**	**Median**	**Percentiles**	
				5th	**95th**
L_0	(mm)	60.0 ± 0.2	60.0	59.7	60.3
x^*	(d)	609 ± 126	653	317	690
L^*	(mm)	204 ± 38	215	115	240
k_U	(d^{-1})	$7.18 \cdot 10^{-2} \pm 45.5 \cdot 10^{-2}$	$0.10 \cdot 10^{-2}$	$0.01 \cdot 10^{-2}$	$19.9 \cdot 10^{-2}$
$L_{\infty F}$	(mm)	580 ± 50	573	511	668
k_F	(d^{-1})	$1.73 \cdot 10^{-3} \pm 0.50 \cdot 10^{-3}$	$1.66 \cdot 10^{-3}$	$1.11 \cdot 10^{-3}$	$2.66 \cdot 10^{-3}$
$L_{\infty M}$	(mm)	388 ± 13	386	370	410
k_M	(d^{-1})	$3.00 \cdot 10^{-3} \pm 1.68 \cdot 10^{-3}$	$3.05 \cdot 10^{-3}$	$1.66 \cdot 10^{-3}$	$4.65 \cdot 10^{-3}$

Table VI – *Correlation matrix of the eight parameter estimates. Stars indicate statistically significant coefficients (P<0.01).*

	L_0	x^*	L^*	k_U	$L_{\infty F}$	k_F	$L_{\infty M}$	k_M
L_0								
x^*	0.045							
L^*	0.046	0.973*						
k_U	0.136	–0.356*	–0.364*					
$L_{\infty F}$	-0.072	0.138	0.125	–0.087				
k_F	0.058	0.295*	0.284*	–0.065	-0.726*			
$L_{\infty M}$	0.087	–0.008	0.008	0.080	–0.128	0.047		
k_M	–0.007	0.563*	0.467*	–0.186	0.278*	0.064	–0.554*	

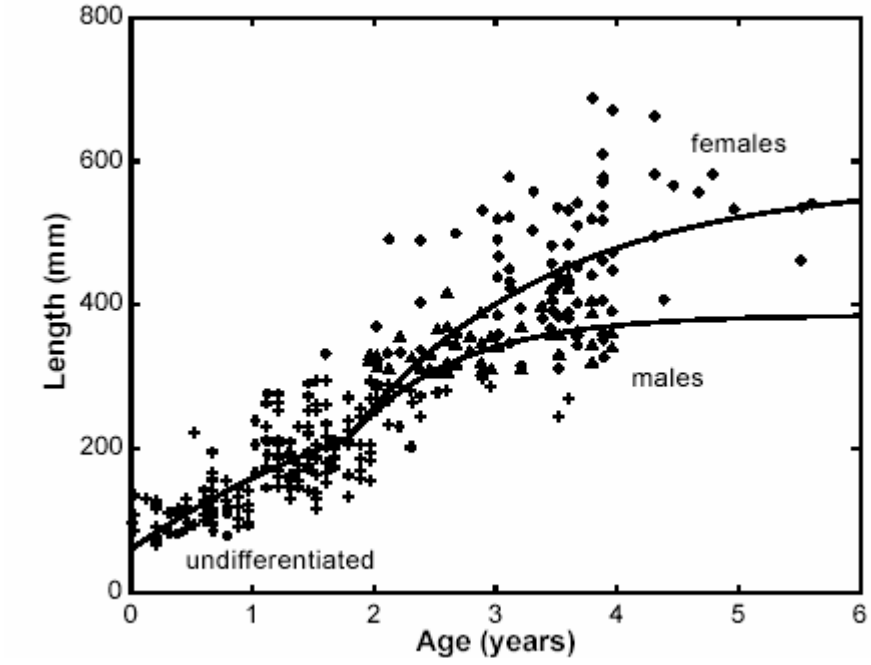
The correlation matrix of the eight parameters (Table VI) shows some significant correlations between parameter estimates. In particular, as evidenced in Fig. 6*a*, there is a negative correlation between Brody coefficients and length at differentiation/asymptotic length (for sexually undifferentiated/differentiated eels, respectively). Age x^* and length L^* at sexual differentiation are also clearly correlated, though positively (Fig. 6*b*).

Discussion

Eels reach the Camargue lagoons as glass eels, with an average length comprised between about 60-65 mm, and then become elvers around 65-75 mm. They undergo sexual differentiation approximately after two years, and become sexually mature after two to three years of residence in the lagoon. Sexual differentiation and maturation have a major role in shaping the length structure of the population. Males are likely to leave the lagoon or die (due to either natural or fishing mortality) within the first 3 years, whilst females can remain up to 5 years. These are rather short times compared to those observed by De Leo and Gatto (1995) at Comacchio (up to 8 years for males and 15 for females), and much shorter than those recorded by Poole and Reynolds (1996) at Burrishole (up to 33 and 57 for males and females, respectively). In addition to geographical variation, a major cause of this huge difference is likely to be the different management of these populations: whilst yellow eels are intensively fished in the Camargue, only migrating silver eels are caught at Comacchio and Burrishole.

Length-weight data are very well fitted by allometric curves. The calibration of distinct curves for data from different years evidences that the allometric coefficient a is subject to wider inter-annual fluctuations than the allometric exponent b. The negative correlation linking average body length and allometric exponent is possibly due to differences in the composition of the catch: samples with higher average length are, in fact, likely to comprise a higher fraction of sexually mature eels, which are characterized by lower values of b.

The length structures at Vaccarès and Impériaux were not significantly different during 1997-1998, thus allowing the aggregation of age-length data over space and time to calibrate the growth model. One could wonder, however, if the length structures at the two study sites have remained similar also over the whole study period, and if there have been significant inter-annual variations of eel length. A three-way ANOVA was therefore performed on the 1997-2003 dataset (no data were recorded at Impériaux before 1997). Results confirm that sex is the factor with the strongest influence ($P<10^{-15}$), but reveal that both fishing station ($P = 6.74 \cdot 10^{-8}$) and catch year ($P = 1.23 \cdot 10^{-12}$) have a significant effect on length over a wider time horizon. Due to possibly high spatial and temporal variability of the growth process, one should be particularly cautious when trying to aggregate data from different stations and from different surveys, as this operation could lead to unreliable results.

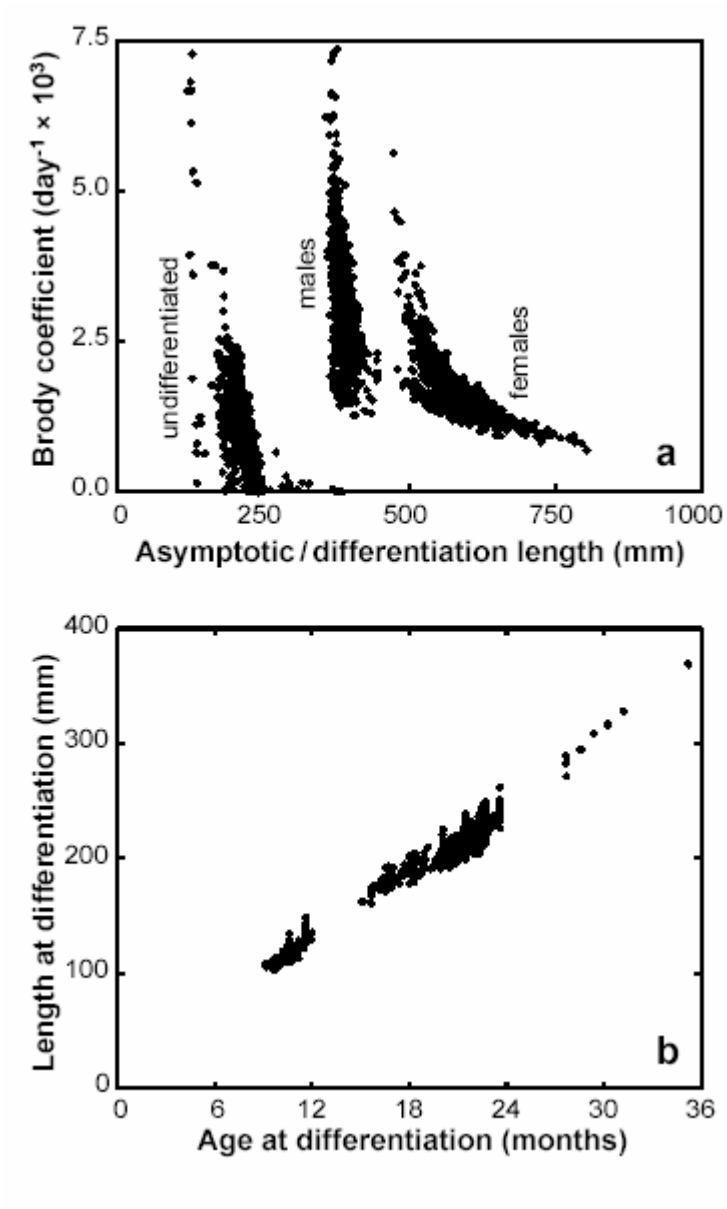


The model proposed here provides a realistic description of the growth process of the European eel, which is characterised by strong sexual differentiation and delayed sex determination. The introduction of a growth curve for undifferentiated eels overcomes a major drawback of earlier growth models (De Leo and Gatto, 1995; Poole and Reynolds, 1996), in which the growth paths of males and females were differentiated from the early developmental stages.

Figure 5. *Median growth curves of undifferentiated (+), female (o) and male (Δ) European eel.*

Like in other fish species (Parker, 1992), females grow faster than males (as can be noted by comparing the slopes of the corresponding growth curves of Fig. 5) and become larger, as their asymptotic body size is about 50% higher than that of males (Table V; see also Poole and Reynolds, 1996). Data suggest that growth is more variable in females than in males (compare the dispersion of observed data around the median growth curves). The higher variability in female growth is reflected in the uncertainty of parameter estimates, and in particular the asymptotic body size (coefficient of variation 9% and 3% for females and males, respectively). The parameter affected by the highest uncertainty is k_U, the Brody coefficient of undifferentiated eels. In fact, a von Bertalanffy curve was used to describe their growth mainly for the sake of consistency with the curves for differentiated eels. However, a linear approximation would have performed equally well, because from the data there is no evidence of a slowing down of the growth process before sexes differentiate. Sexual differentiation occurs at about 21 months. Length at differentiation is between 210 and 220 mm, which is fairly less than the length at which macroscopic differentiation becomes possible (300 mm). However, Colombo and Grandi (1996) revealed that eels under 200 mm are also undifferentiated histologically, whilst the formation of the early Syrski organ (a small testis initially containing both male and female germ cells) begins just between 200-220 mm.

The model proposed here can be used as a powerful tool to describe the growth process of eels and, combined with information about recruitment, mortality, and migration rates, provide a robust basis for the development of reliable demographic models of eel populations. It can be applied to other eel populations, provided that a sufficient number of length, age and sex data is available. As the number of parameters to be estimated is rather high, one could perhaps want to reduce it by fixing some of them *a priori*. However, this should be done with extreme caution, because of the high plasticity of eel body growth (De Leo and Gatto, 1995). Eel growth is indeed controlled by ecological factors, such as food availability and water temperature (Panfili et al., 1994), and might also be influenced by demographic factors such as population size (see, e.g., Moriarty, 1973, although Aprahamian, 2000, found no significant relationship between growth rate and eel density or biomass at 15 English sites). Length at sexual differentiation L^* is likely to vary less than other parameters, but age at sexual differentiation x^* could vary from one population to another due to different environmental conditions.



It is indeed likely that the actual trigger for sexual maturation is associated to a critical body size rather

Figure 6. *Bootstrap distribution of body growth parameters from 1997-1998 dataset.(a)Total length at differentiation and asymptotic total lengths (for sexually undifferentiated and differentiated European eels, respectively) and the Brody coefficient and (b) age and total length at sexual differentiation.*

than a given age. Asymptotic length can vary as well from site to site. De Leo and Gatto (1995) obtained higher values for both $L_{\infty F}$ (762±14 mm) and $L_{\infty M}$ (418±23 mm) of the Comacchio eel population. Poole and Reynolds (1996) reported even higher ranges for $L_{\infty F}$ (varying between 1433-1507 mm) and $L_{\infty M}$ (659-700 mm) at Burrishole. Estimates of the Brody growth constant are even more variable: De Leo and Gatto (1995) report $k_F = 0.23 \pm 0.01$ yr^{-1} = $6.30 \cdot 10^{-4} \pm 0.27 \cdot 10^{-4}$ d^{-1}, $k_M = 0.35 \pm 0.056$ yr^{-1} = $9.59 \cdot 10^{-4} \pm 1.53 \cdot 10^{-4}$ d^{-1}, whilst Poole and Reynolds estimated $k_F = 0.013$ yr^{-1} = $3.56 \cdot 10^{-5}$ d^{-1}, $k_M = 0.031$-0.036 yr^{-1} = $8.49 \cdot 10^{-5}$-$9.86 \cdot 10^{-5}$ d^{-1}. Note, however, that a direct comparison of these values is not possible, as previous models did not contemplate a distinct growth curve for undifferentiated eels. Length at recruitment L_0 can also vary, depending upon the time glass eels need to reach their final environment. Vøllestad and Jonsson (1988) reported an average length of glass eels of 75±8 mm, and Poole and Reynolds (1996) found a similar figure (72 mm).The application of the present growth model to different populations, or to the same population in different periods, would be important to identify parameters that are invariant because of physiological and genetic constraints, and variable parameters that require the collection of age-length data sets for the characterization of a specific eel population. In particular, it would be very interesting to test, through an extensive comparisons of data from different sites, the hypothesis of size-dependent (instead of age-dependent) sex differentiation.

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3

Sex differentiation of European eel

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Abstract

Body growth parameters, age and total length at sex differentiation were compared in three European eel populations from Mediterranean sites with different salinity. Whilst body growth is faster in brackish than in freshwater environments, the present analysis shows that body size at sex differentiation might be a physiological invariant.

Main text

The European eel *Anguilla anguilla* (L.) is a secondary gonochoristic species (Devlin and Nagahama, 2002) characterised by delayed sex differentiation and metagamic sex determination. Gonad differentiation and development are likely triggered by reaching a certain body size rather than age (Bieniarz *et al.*, 1981; Colombo *et al.*, 1984). Sex determination in *Anguilla* species is not univocally determined by genes, but is presumably influenced by environmental and social factors, with high temperatures and high densities biasing sex ratio towards males (Beullens *et al.*, 1997; Krueger and Oliveira, 1999; Oliveira and McCleave, 2002). Eels also show clear sexual dimorphism (Krueger and Oliveira, 1999), with females growing faster and attaining greater body size than males (although this last statement has been recently questioned; see, e.g., Holmgren and Mosegaard, 1996; Holmgren *et al.*, 1997). Body growth shows extreme variability at different spatial scales, from inter-individual variation within the same population to geographic variation among different habitats (Vøllestad, 1992; Panfili *et al.*, 1994; De Leo and Gatto, 1995).

The aim of the present chapter is to use mathematical modelling to test the invariance of sex differentiation and body growth parameters of the European eel in different environmental conditions. Although mathematical models have already been used to describe eel growth (De Leo and Gatto, 1995; Poole and Reynolds, 1996), so far the only way to investigate sex differentiation has been to perform expensive histological analyses. In the present chapter a body growth model and a flexible calibration procedure described in chapter 2 are used to compare three European eel populations from Mediterranean sites with different salinity and subject to different fishing policies. The model explicitly accounts for sexual dimorphism by introducing three distinct von Bertalanffy growth curves for undifferentiated fish, females and males (see chapter 2, for details). Besides the classical von Bertalanffy growth parameters – L_0 (total length at age zero, i.e., at metamorphosis from glass eel to elver), k_U, k_F, and k_M (Brody coefficients for undifferentiated, females and males), $L_{\infty F}$ and $L_{\infty M}$ (asymptotic mean lengths of females and males) – the model has two additional parameters for sexual differentiation, namely L^* (total length at sex differentiation) and x^* (age at sex differentiation). These two parameters, along with the other six von Bertalanffy growth parameters, are estimated from available data.

The calibration requires data on total length (L_T) and sex at different ages, possibly covering the whole age span of the population being investigated. The model was applied to three datasets. The first was collected in the brackish waters of the Impériaux and Vaccarès lagoons (Rhône river delta, Southern France). These data were used in chapter 2 to develop the growth model used in this work. A second dataset was collected in the adjacent Fumemorte drainage canal, where salinity is much lower. The third was collected in the Valli di Comacchio lagoons (Po river delta, Northern Italy), another brackish environment, and was used by De Leo and Gatto (1995) to develop a demographic model for the Comacchio eel population. Table I provides a concise overview of the three sites and the corresponding data.

The results of applying the growth model to the three datasets are reported in Table II. Uncertainty associated to parameter estimates and relevant statistics were assessed by stratified bootstrapping of the original data (Efron and Tibshirani, 1986; see chapter 2, for details about the application of the bootstrap to this specific problem). Fig. 1 shows the original datasets and the corresponding fitting curves.

Table I – *Main features of the three study sites and corresponding datasets*.

	Vaccarès - Impériaux	Fumemorte	Valli di Comacchio
latitude	43°30'N	43°30'N	44°40'N
longitude	4°30'E	4°30'E	12°10'E
salinity (g L^{-1})	3.8–12.4*	0.9	23–37
winter temperature (°C)	7	7	2
summer temperature (°C)	21–22	21–22	24
sampling period	1997–1998	1988–1990	1974–1975
sample size	290	287	758
L_T (mm)	66–688	120–685	123–709
age (yr)	0–6	0–11	0–12

Salinity and temperature data from Dallocchio *et al.* (1998), Acou *et al.* (2003), Poizat *et al.* (2004)

* at Vaccarès; salinity is higher and more variable at Impériaux (5.7–38.0 g L^{-1}; Poizat *et al.*, 2004).

To fit data, median values of parameters distributions were used instead of means, due to the higher robustness of the median, especially when distributions are strongly skewed.
Females attained a larger size (asymptotic body size about 30–50% larger than that of males) and grew faster than males. This is in accordance with other field studies (Vøllestad and Jonsson, 1986; Vøllestad, 1992; Panfili *et al.*, 1994; Poole and Reynolds, 1996), but in partial contrast with Holmgren and Mosegaard (1996) and Holmgren *et al.* (1997), which claimed that individuals growing faster at the beginning of sex differentiation might develop with higher probability into males. To highlight subtler differences between growth paths of females and males, growth rates were calculated as $dL/dt = k\,(L_\infty - L_T)$ for both sexes at 3 ages: age at sex differentiation x^*, $x^* + 1$ yr and $x^* + 2$ yr. Estimates are reported in Table III, and confirm faster female growth at all sites (Mann-Whitney test, $P<0.001$), except for Fumemorte, where the growth rate of males was higher at age x^*.

Table II – *Basic statistics of growth curves' parameters. For each parameter, the first row reports mean ± S.D., whilst the second row shows median and 90% C.I. (between parentheses). Parameter distributions were obtained by stratified bootstrapping of the original age-length data (1000 iterations).*

Parameter		Vaccarès - Impériaux	Fumemorte	Valli di Comacchio
L_0	(mm)	60.01 ± 0.19*	60.01 ± 0.19*	60.0**
		60.01 (59.71–60.33)	60.01 (59.71–60.33)	60.0
x^*	(yr)	1.67 ± 0.35	2.16 ± 0.22	1.62 ± 0.25
		1.79 (0.87–1.89)	2.18 (1.77–2.42)	1.65 (1.01–1.91)
L^*	(mm)	204.34 ± 38.47	209.23 ± 21.32	268.65 ± 23.86
		215.15 (114.78–239.56)	217.04 (171.06–235.23)	275.58 (206.52–290.50)
k_U	(yr^{-1})	26.22 ± 166.23	3.55 ± 3.43	19.36 ± 78.66
		0.37 (0.03–72.70)	1.42 (0.70–9.46)	1.68 (1.40–142.38)
$L_{\infty F}$	(mm)	579.73 ± 50.35	515.91 ± 17.84	547.61 ± 4.28
		573.00 (510.66–667.71)	514.74 (488.88–547.16)	547.47 (540.85–554.67)
k_F	(yr^{-1})	0.63 ± 0.18	0.39 ± 0.05	0.52 ± 0.05
		0.61 (0.40–0.97)	0.38 (0.31–0.48)	0.53 (0.45–0.60)
$L_{\infty M}$	(mm)	387.84 ± 12.77	396.27 ± 13.15	429.87 ± 2.22
		386.43 (369.76–409.75)	395.00 (379.96–414.35)	429.76 (426.13–433.56)
k_M	(yr^{-1})	1.10 ± 0.61	1.47 ± 2.33	0.86 ± 2.57
		1.11 (0.60–1.70)	0.67 (0.44–6.39)	0.75 (0.64–0.93)

* L_0 was calculated as the average length of glass eels entering the Camargue water system.
** as no data about glass eels was available for Comacchio, L_0 was *a priori* set equal to the value of the 2 French sites.

Although this outcome is consistent with those obtained by Holmgren *et al.* (1997), it should be taken with caution, as male growth at Fumemorte was assessed with a considerably higher level of uncertainty compared to the other sites.

Table III – *Basic statistics of growth rates (mm yr $^{-1}$) as a function of age for females (r_F) and males (r_M). For each parameter, the first row reports mean ± S.D., whilst the second row shows median and 90% C.I. (between parentheses).*

Parameter	Vaccarès - Impériaux	Fumemorte	Valli di Comacchio
$r_F(x^*)$	227.93 ± 31.79	117.64 ± 10.57	145.23 ± 10.25
	224.45 (186.53–282.04)	116.68 (102.73–137.41)	144.20 (130.22–162.69)
$r_M(x^*)$	198.28 ± 39.48	269.63 ± 382.43	123.56 ± 27.87
	192.58 (151.14–266.56)	120.61 (83.48–1203.36)	117.90 (100.19–158.32)
$r_F(x^* + 1)$	120.89 ± 8.95	79.68 ± 5.17	86.07 ± 5.89
	121.64 (107.87–133.58)	78.87 (72.38–89.04)	84.59 (79.56–99.48)
$r_M(x^* + 1)$	64.35 ± 13.30	54.61 ± 19.68	56.70 ± 8.10
	62.58 (45.78–90.52)	57.25 (2.23–79.28)	54.75 (48.99–76.12)
$r_F(x^* + 2)$	65.97 ± 13.35	54.12 ± 4.27	51.06 ± 4.69
	66.99 (41.99–86.15)	53.35 (47.91–61.34)	49.97 (46.07–62.77)
$r_M(x^* + 2)$	23.28 ± 11.89	26.13 ± 11.76	26.50 ± 5.11
	20.37 (8.68–48.73)	29.83 (0.00–38.69)	25.56 (21.57–39.47)

In general, growth was more variable in males than in females (as evidenced by standard deviations and confidence intervals in Table III), especially in the ages immediately following sex differentiation. Holmgren *et al.* (1997) found indeed scarcely significant differences in L_T increases between the two sexes under 300 mm, whilst they observed significantly higher growth rates in females after complete sex differentiation. However, the assessment of possible links between growth patterns in early developmental stages and sex determination remains an open question and accurate otolith analyses might be very useful to solve it. Irrespective of their sex, European eels grew faster in brackish than in freshwater environments. This is in accordance with the literature (see., e.g., Panfili and Ximénès, 1994; Acou *et al.*, 2003), although the causes are still unclear. Salinity might indeed affects growth rates by influencing food availability, the feeding behaviour or the trophic level at which eels feed (Edeline and Elie, 2004; Harrod *et al.*, 2005). Asymptotic body size of females was higher in Vaccarés-Impériaux and Comacchio, whilst there was no clear result for males.

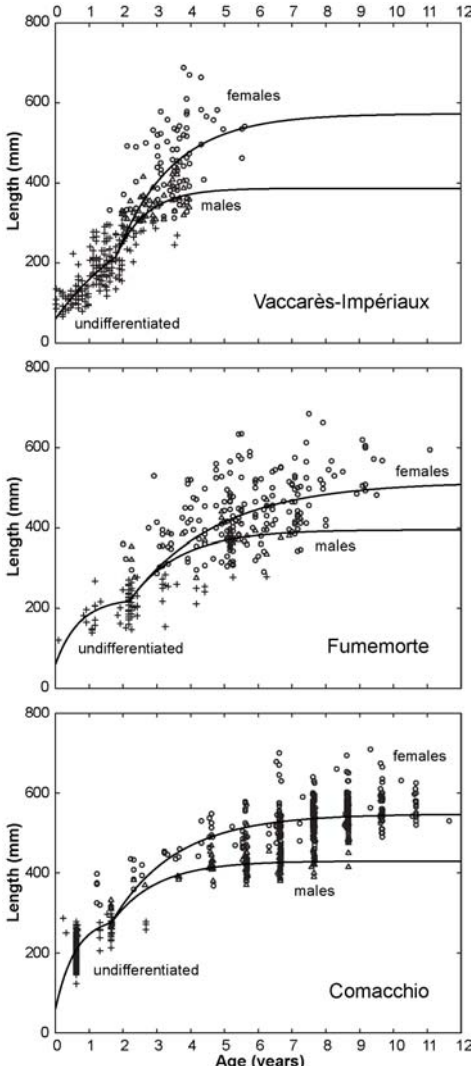

Figure 1. *Growth curves of undifferentiated (┼), female (○) and male (△) European eels for the 3 populations. Symbols identify observed age-length data, whilst solid lines show median fitting curves.*

Age at sex differentiation was also likely to be influenced by the environment, as it occurred at 20–22 months at the 2 brackish-water sites (Vaccarés-Impériaux and Comacchio) and at about 26 months at Fumemorte. On the contrary, L^* was almost identical (210–220 mm) in the two Camargue populations (Vaccarés-Impériaux and Fumemorte) and higher (270 mm) at Comacchio. At all sites, however, sex differentiation occurred before macroscopic differentiation became possible (300 mm), in accordance with both histological evidence (Colombo and Grandi, 1996) and the

results obtained via mathematical models.

To test for possible invariance of growth and differentiation parameters, empirical bootstrap distributions of all parameters were compared pair-wise (two sites at a time). L^* was not significantly different at Vaccarés-Impériaux *v.* Fumemorte (Mann-Whitney test, $P = 0.27$; Wilcoxon matched pairs test, $P = 0.14$). Borderline results were obtained for k_U and k_M at Fumemorte *v.* Comacchio (Mann-Whitney test, $P<0.001$ for both parameters; Wilcoxon matched pairs test, $P = 0.20$ and 0.30, respectively). All other parameter estimates were significantly different among the 3 sites ($P<0.001$ with both tests for all pair-wise comparisons).

The two French populations analysed (Vaccarés-Impériaux and Fumemorte) share the same recruitment. Glass eels must indeed pass through the lagoons, which are connected to the Mediterranean Sea through sluice gates, to enter into the Fumemorte canal. The comparison of sex differentiation parameters between the two populations is therefore of particular interest to highlight the effect of environmental factors on some life-history traits, especially on sexual differentiation.

Age at sex differentiation is different between the two sites, whilst length is not, as shown in Fig. 2, thus supporting the idea of a critical size as a trigger for sex differentiation (Bieniarz *et al.*, 1981; Colombo *et al.*, 1984). The empirical distribution of x^* and L^* for Comacchio and Vaccarés-Impériaux shows a minor mode at a lower value of both parameters. This might be explained by the fact that some individuals differentiate very early, or indicate a dubious age determination for some eels, or simply be caused by particularly odd recombinations of data during bootstrap resampling. The different estimate of L^* obtained for Comacchio suggests that this parameter can vary from site to site, at least over a very wide geographical range. It should be noted, however, that the three datasets analysed were collected in different periods. This might have influenced our results if, as suggested by Dannewitz *et al.* (2005), temporal genetic variability in the European eel is as important as (or even the cause of) spatial variability. Also, the three populations are subject to different fishing policies: fishing is indeed not allowed in the Fumemorte canal, whilst it is mainly focused on yellow eels in the Vaccarés-Impériaux lagoons and concentrated on silver eels at Comacchio. For this reason, and due to the use of a mesh size (16 mm) much larger than in Camargue (6 mm), only very few data were available in Comacchio for eels between 250–400 mm. The lack of small fish in the sample might therefore have skewed the estimation of size at sexual differentiation towards larger sizes. A comprehensive comparative analysis based on recent data from different sites would be of great interest to clarify the fascinating issue of determining possible physiological invariants in the European eel, a species characterised by high plasticity of vital rates.

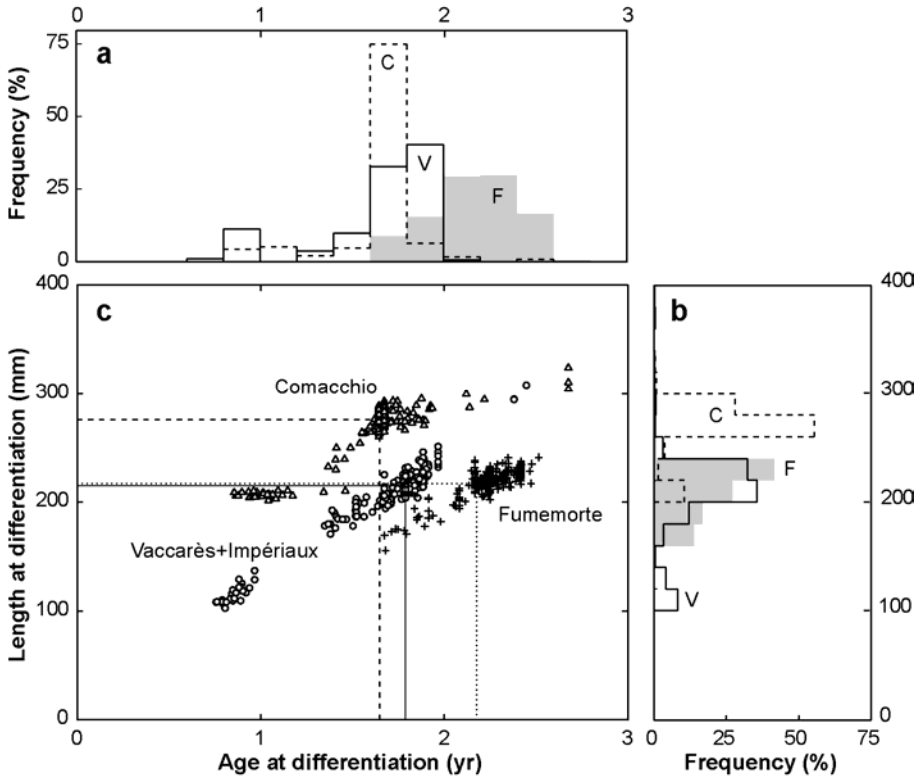

Figure 2. *Bootstrap distributions of age x* and total length L* at sex differentiation for the 3 populations. a: marginal distribution of x*; b: marginal distribution of L*; c: joint distribution (each symbol represents a bootstrap replicate, whilst lines show the median point of marginal distributions).* ○ , ⎯ *and* □ *Vaccarès-Impériaux (V);* +, ... *and* ▒: *Fumemorte (F);* △, - - - *and* ⬚: *Comacchio (C).*

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4

Timing and rate of sexual maturation of European eel in brackish and freshwater environments

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Abstract

Understanding physiological and environmental triggers for sexual maturation in eels can help developing reliable demographic models. Maturation rates in three European eel populations increased from September to October and were slightly lower in freshwater than in brackish waters. Average and variance of total length (L_T) at maturation were larger in females than males.

Introduction

The European eel *Anguilla anguilla* (L.) is a catadromous fish: individuals grow and feed in brackish and fresh waters as yellow eels until sexual maturation, when they metamorphose to the silver stage and leave continental waters to reach their spawning grounds in the Sargasso sea. Sexual maturation of eels, as well as sex differentiation, depends upon body size rather than age, with fast-growing individuals maturing earlier than slower ones (Vøllestad and Jonsson, 1988; De Leo and Gatto, 1995). Sex differentiation and maturation, along with the differences in the growth paths of males and females, play a key role in determining the size and sex structure of *A. anguilla* populations. European eels show indeed delayed sex differentiation and clear sexual dimorphism, with females attaining larger body size and starting sexual maturation later than males (Vøllestad 1992; Krueger and Oliveira, 1999). Accordingly, the population size structure of the spawning stock is clearly bimodal. The differences in maturation between males and females affect the timing of migration, alter the sex ratio and influence the effective output of spawners of eel populations. Identifying the triggers for metamorphosis and understanding the way environmental factors affect sex maturation of eels is one of the preliminary steps needed to develop reliable demographic models which, in turn, can provide effective tools for the management and conservation of this charismatic, yet endangered fish species.

Metamorphosis processes have been deeply debated in the last years (Beullens *et al*., 1997; Svedäng and Wickstrom, 1997; Durif *et al*., 2005). Most studies have been aimed at describing the morphological and physiological changes occurring during metamorphosis, but only very few of them have been oriented to the estimation of maturation rates by calibrating mathematical models on available data (De Leo and Gatto, 1995; 1996). In fact, although modelling approaches have already been used to describe different aspects of the complex life cycle of *A. anguilla*, such as natural recruitment (Lambert, 1994; Dekker, 2000a; Dekker, 2003), body growth (De Leo and Gatto, 1995; Poole and Reynolds, 1996), and fishing mortality (Moriarty and Dekker, 1997; Dekker, 2000b), studies on maturation have usually been limited to estimating the mean total length and/or age at metamorphosis (Vøllestad and Jonsson, 1988; Vøllestad, 1992; Poole and Reynolds, 1996; Svedäng *et al*., 1996). The few attempts to compute maturation rates as a function of L_T were carried out in different ways, either by empirical estimation of the parameters so as to match model predictions with field observations (Sparre, 1979), or by rigorously fitting parameterised demographic models to available data (De Leo and Gatto, 1995), or by using length-structured cohort analysis models on catch data (Dekker, 2000c). In the present work a simple maturation model, explicitly accounting for sexual dimorphism and temporal variation of maturation rates, was used to test the influence of different environmental conditions on maturation parameters.

The model

According to field observations and previous demographic studies (Vøllestad, 1992; De Leo and Gatto, 1995), the maturation rate (here intended as a finite rate, *i.e.* the probability that a yellow eel becomes silver within a given time step, for instance a month or a year) was assumed to be an increasing and saturating function of L_T:

$$\gamma(L_T) = \gamma_{max}\left[1 + e^{(\lambda - L_T)\eta^{-1}}\right]^{-1} \quad (1)$$

where γ_{max} is the asymptotic maturation rate, λ is a semisaturation constant and η is a shape parameter which is inversely proportional to the slope of the curve at $L_T = \lambda$.
The model was applied to three datasets. The first was gathered between 1997–2003 in the brackish waters of the Vaccarès and Impériaux (VandI) lagoons (Rhône river delta, Southern France), where both yellow and silver eels are commercially exploited. A second dataset was collected between 1989–2002 in the adjacent Fumemorte (FM) drainage canal, a fresh water body where fishing is forbidden. The third was collected between 1974–1976 in the Valli di Comacchio (VC) lagoons (Po river delta, Northern Italy), another brackish environment, where only silver eels are fished. This last dataset was originally analysed by Gatto *et al*. (1982) and then used by De Leo and Gatto (1995, 1996) to develop a demographic model for the VC eel population. Table I provides a concise overview of the three sites and the corresponding data. In Camargue (VandI and FM), yellow and silver eels were caught with the same fishing gear during the same sampling sessions. Hence, the observed proportion of silver eels in each length class of the sample was assumed to accurately reflect the distribution of silver eels in the population. At VC silver eels were sampled from the professional catch of 1975–1976 at the so-called *lavorieri* (screens located at the sluice gates of the canals connecting the lagoons to the sea), whilst yellow eels were caught by a shallow water trawl at the beginning of autumn 1976.

Table I – *Main features of the three study sites and corresponding datasets.*

	Vaccarès - Impériaux	**Fumemorte**	**Valli di Comacchio**
latitude	43°30'N	43°30'N	44°40'N
longitude	4°30'E	4°30'E	12°10'E
salinity	3.8–38.0	0.9	23–37
winter temperature (°C)	7	7	2
summer temperature (°C)	21–22	21–22	24
sampling period	1997–2003	1989–2002	1974–1976
sample size			
males (yellow/silver)	622/275	19/37	8/159*
females (yellow/silver)	354/62	126/96	29/334*
L_T (mm)	74–722	67–825	123–709

Salinity and temperature data from Dallocchio *et al.* (1998), Acou *et al.* (2003), Poizat *et al.* (2004)

* Yellow and silver counts in Comacchio are not directly comparable as the fishing procedures used were different (see text for details)

Yellow abundances in the VC sample were rescaled by a proportionality coefficient [estimated by Gatto *et al*., (1982)] to account for the differences in fishing effort and selectivity of the fishing gear between the two samples. Since silvering takes place in autumn, only data collected from September to November were used for the estimation of maturation rates.
For all populations, maturation rates were calculated on an annual basis. For the VandI population, the number of data was sufficient to calculate also monthly maturation rates. On an annual horizon, the maturation rate was calculated simply as the proportion π_S of silver eels in every length class of the autumn population structure. In fact, mature eels abandon the study sites shortly after maturation (usually in winter), so silver eels observed in autumn samples must have silvered during the current season and the silvering probability coincides with the fraction of silver eels within the length class. To calculate monthly maturation rates, the effect of progressive maturation was accounted for as follows. Let $N_Y(t)$ and $N_S(t)$ be the number of yellow and silver eels, respectively, in a given

population and in a given month t, and let γ and σ be the maturation and survival rates. The number of silver eels at time $t + 1$ was derived as the number of silver already present plus that of those matured in the meanwhile, multiplied by the survival rate:

$$N_S(t + 1) = \sigma [N_S(t) + \gamma N_Y(t)] \quad (2)$$

Dividing both members by the total number of eels at time $t + 1$, considering that $N(t + 1) = \sigma N(t)$, and indicating with $\pi_Y(t)$ and $\pi_S(t)$ the proportions of yellow and silver eels at time t, respectively, Eq. (2) was rewritten as

$$\pi_S(t + 1) = \pi_S(t) + \gamma\pi_Y(t) \quad (3)$$

Noting that $\pi_S + \pi_Y = 1$ by definition, and solving the equation with respect to γ, the maturation rate was finally calculated as

$$\gamma = \left[\pi_S(t+1) - \pi_S(t)\right]\left[1 - \pi_S(t)\right]^{-1} \quad (4)$$

The equations above are valid only if γ and σ are constant in time and equal for yellow and silver eels. This assumption is likely to be verified with good approximation if one divides the population by sex and in sufficiently narrow length classes. 30 mm classes were used for males and 50 mm ones for females, whose body size spans over a wider range. Optimal values for maturation curves' parameters were found by minimizing the mean squared error between the maturation rates predicted by the model (Eq. 1) and those calculated from catch data with Eq. (4). Maturation parameters γ_{max}, η and λ were estimated independently for male and females at the three sites. Uncertainty of parameter estimates and relevant statistics were assessed with the Bootstrap (Efron, 1979). Bootstrapping was stratified in length and sex classes to follow the original sampling procedure (Efron and Tibshirani, 1986).

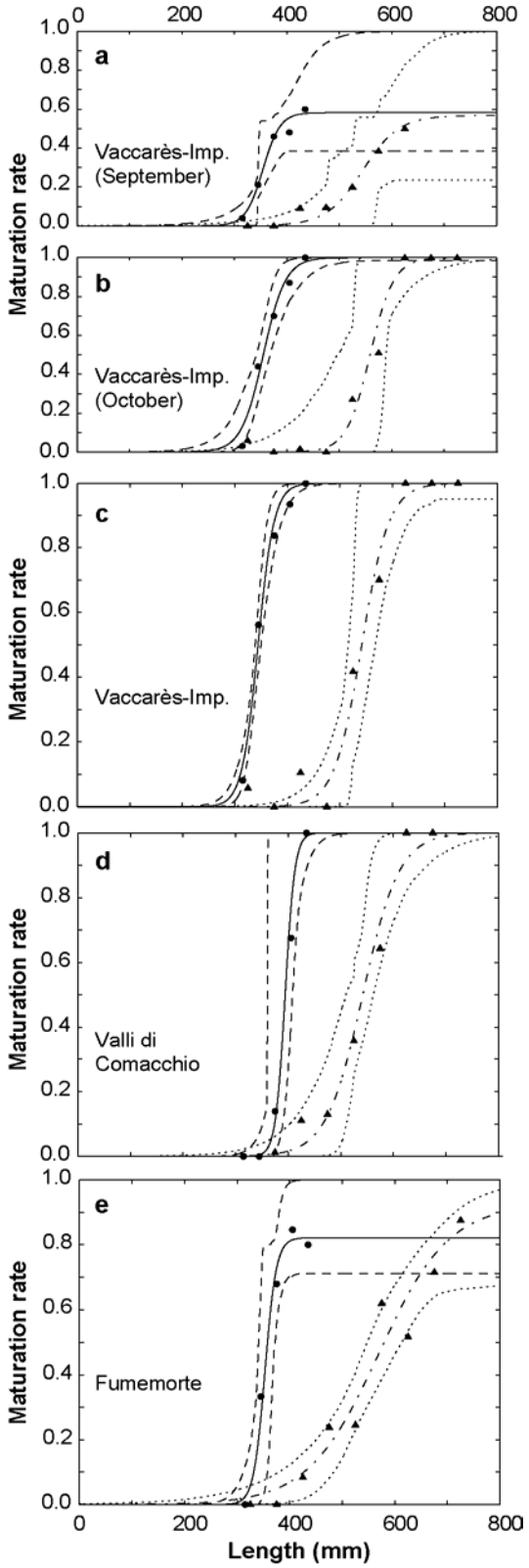
Results and discussion

The results of calibrating the maturation models are reported in Table II. Fig. 1 shows maturation rates calculated from the original datasets and the corresponding fitting curves. Monthly maturation curves for the VandI populations are shown in Fig. 1(*a*) and (*b*), whilst Fig. 1(*c*), (*d*) and (*e*) compare annual maturation curves of the three populations.

As for monthly maturation rates in VandI, the dependency of maturation parameters upon sex and time was assessed by statistical tests on bootstrapped distributions obtained from the September and October subsets. λ was significantly influenced by sex (*c.* 550 *v.* 360 mm for females and males, respectively) and slightly less significantly by time (2-way ANOVA: $P<0.001$ for sex, $P = 0.001$ for time). On the contrary, γ_{max} changed remarkably with time (from *c.* 0.65 in September to 1 in October) but was not affected by sex (2-way ANOVA: $P<0.001$ for time, $P = 0.18$ for sex). Finally, η varied with both time and sex (2-way ANOVA: $P<0.001$ for both factors).

The effect of the environment on silvering was assessed in the same way by comparing parameter distributions of the annual maturation curves obtained for the 3 populations. All maturation parameters varied with both sex and site (2-way ANOVA: $P<0.001$ for both factors).

However, the strong sex dimorphism of maturation paths could have masked some subtler differences as regards the influence of the site. Therefore, bootstrap distributions of all parameters were compared pair-wise (two populations at a time) by means of a Wilcoxon matched pairs test. Inter-site differences were significant (P<0.001) for all parameters except λ of females and γ_{max} of males, which did not differ significantly between the two brackish water populations (P = 0.64 and P = 0.13, respectively). Although this was only partially confirmed by statistical tests, average L_T at metamorphosis was very similar at all sites for both sexes. In all populations average L_T at sexual maturation was higher in females than in males in accordance with the current knowledge (*e.g.* Vøllestad, 1992; De Leo and Gatto, 1995; Svedäng *et al*., 1996; Dekker, 2000c; Acou *et al*., 2003). It is interesting to notice that in all investigated populations η (which is inversely correlated to the slope of maturation curves) and the standard deviation of λ were higher in females than in males (Wilcoxon test, P<0.001; Levene's test, P<0.001). This confirms the empirical observation by Vøllestad (1992) that the average L_T at sexual maturation is more variable in females than in males and corroborates the hypothesis that males undergo sexual maturation as soon as they attain the minimum body size necessary to afford migration, whilst for females there is trade-off between maximising fecundity (by continuing growth and postponing reproduction) and minimising the probability of dying in continental waters (Vøllestad, 1992).



The asymptotic maturation rate was equal to 1 for both sexes in the 2 brackish water populations, whilst it was slightly lower in freshwater (0.9 for females and 0.84 for males), suggesting that silvering is more difficult in freshwater environments. So far, appreciable differences in maturation between fresh and brackish water were found only for the average age at metamorphosis. In fact, growth is known to be slower in freshwater and, consequently, eels take longer to reach the suitable size for metamorphosis (Acou *et al*., 2003; chapter 3). Asymptotic maturation rates derived in the present analysis are appreciably higher than those found by Dekker (2000c) for the IJsselmeer population and by De Leo and Gatto (1995, 1996) for Comacchio. A comparative analysis with Dekker (2000c) estimates is not possible due to the different approaches used in his and this work. It is instead interesting to remark the difference between present estimates and those obtained by De Leo and Gatto (1995) using the same dataset for VC. In fact, they estimated that the asymptotic maturation rate for females was equal to 0.34 ± 0.09, far below the present estimate (1.00 ± 0.00). This discrepancy is probably due to the different procedures used to calibrate the models. In fact, the estimate of De

Figure 1. *Estimated length-specific maturation rates (± 90% confidence limits) for male(solid line) and female(dash-dotted line). European eels at Vaccarès-Impériaux (a, b, and c), Valli di Comacchio (d) and Fumemorte (e). a and b are monthly maturation curves (September and October, respectively), whilst c, d and e are annual. Symbols identify length-specific maturation rates calculated from data for each length class, whilst lines show median fitting curves.*

Leo and Gatto (1995) is the result of the concurrent calibration of 8 unknown demographic parameters and might be biased by overparameterisation. In contrast, the present estimate has been obtained by calibrating only the 3 parameters of a single maturation curve. Although this estimate might also be affected by some biases (*e.g.* the fact that yellow and silver eels' counts are not directly comparable), splitting the calibration of complex demographic models into several small models focused on specific life-history events can help bypass some computational problems and obtain more reliable results.

Table II – *Basic statistics of maturation curves' parameters. For each parameter, the first row reports mean ± S.D., whilst the second row shows median and 90% C.I. (between parentheses). Parameter distributions were obtained by stratified bootstrapping (sex and length classes) of the original datasets (1000 iterations).*

Parameter	VandI (September)	VandI (October)	VandI (annual)	VC (annual)	F (annual)
λ_m (mm)	363.4 ± 21.14	355.0 ± 6.61	344.2 ± 2.92	389.0 ± 12.71	352.5 ± 8.8
	354.8 (343.0–406.2)	354.8 (345.1–365.9)	344.2 (339.3–349.1)	394.3 (375.5–406.9)	352.9 (338.8–368.0)
η_m (mm)	18.9 ± 12.59	22.2 ± 5.97	15.4 ± 2.60	7.4 ± 5.90	10.6 ± 4.96
	16.6 (0.8–41.8)	21.5 (14.1–32.9)	15.4 (11.2–19.9)	9.2 (0.8–17.0)	10.8 (0.8–18.6)
$\gamma_{max, m}$	0.65 ± 0.20	1.00 ± 0.00	1.00 ± 0.01	1.00 ± 0.01	0.84 ± 0.08
	0.58 (0.41–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)	1.00 (1.00–1.00)	0.82 (0.73–1.00)
λ_f (mm)	553.4 ± 51.89	555.3 ± 26.21	541.5 ± 13.12	540.4 ± 14.79	567.0 ± 26.95
	552.8 (475.1–632.1)	559.1 (514.9–587.1)	541.8 (520.6–564.0)	541.8 (522.3–559.5)	568.7 (522.0–607.3)
η_f (mm)	35.0 ± 25.61	23.7 ± 16.10	25.4 ± 8.69	34.2± 14.14	65.8 ± 16.61
	35.9 (1.3 –77.0)	23.0 (2.1–51.8)	26.2 (8.5–37.6)	34.7 (12.2–48.9)	67.2 (37.3–90.5)
$\gamma_{max, f}$	0.67 ± 0.27	1.00 ± 0.00	1.00 ± 0.01	1.00 ± 0.01	0.90 ± 0.11
	0.60 (0.30–1.00)	1.00 (1.00–1.00)	1.00 (0.98–1.00)	1.00 (1.00–1.00)	0.93 (0.71–1.00)

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5

Size selectivity of fyke nets for European eel

Chapter submitted for publication: D. Bevacqua, P.Melià, G.A. De Leo, M. Gatto. Size selectivity of fyke nets for European eel *Anguilla anguilla*

Abstract

Size selectivity of fyke nets for European eels was investigated by reviewing the results of published experimental studies. A general size selectivity model was then derived, that can be easily incorporated into demographic models to assess fishing mortality under different management options.

Main text

Fishery management of European eel (*Anguilla anguilla*) has received increasing attention by both the scientific community and fisheries agencies in the last years (ICES, 2007). There is indeed growing concern on the fate of the European eel stock (Dekker *et al.*, 2003), which has experienced a 99% recruitment drop in the last three decades and is presently outside safe biological limits (ICES, 2007). *A. anguilla* has been recently listed in Annex B of CITES, and the European Council adopted a regulation (EC 1100/2007) aimed at recovering the stock through the drawing up of Eel Management Plans (EMPs) at a river basin scale. EMPs are required to reduce anthropogenic mortality so as to permit the escapement of at least 40% of the adult eel biomass relative to pristine conditions. Despite anthropogenic mortalities encompass a broad range of disturbance factors (including pollution, habitat loss, human-driven transfer of parasites and viral diseases, obstacles to upstream and downstream migration), it is likely that EMPs will focus mainly on the reduction of fishing mortality. Commercial fishing alone can indeed have a severe impact on the escapement of adult eels from continental waters (Dekker, 2000), and a reduction of fishing disturbance can be attained in the short term if sound fishery policies are devised. During the continental phase of their life cycle, European eels are fished with a variety of fishing gears at all developmental stages. In particular, size-selective trapping devices (such as fyke nets), aimed at fishing European eels during their movement within continental habitats (Tesch, 2003), contribute to the majority of overall catches (Dekker, 1999).

Sound mathematical models, explicitly accounting for fishing mortality under different management scenarios, might help scientists and decision makers devising targets and means of EMPs and forecasting their consequences on the future viability of the European eel stock. In demographic models of exploited fish populations, the fishing mortality rate F is commonly expressed as the product of three factors: *i*) a catchability coefficient q, which depends from the characteristics of the target species and the specific fishing gear used; *ii*) the fishing effort E, typically measured as the number of gears used multiplied by the total fishing time; and *iii*) the selectivity φ, namely the fraction of fish intercepted by the gear that are effectively retained: $F = qE\varphi$. For most fishing gears, fish liability to capture depends upon body size, to which φ can be linked through a so-called size selectivity curve, and whose determination is a key component of fishery assessment (Myers and Hoenig, 1997). In this chapter, size selectivity of fyke nets for European eels was investigated by reviewing the results of published experimental studies, with the aim to derive a general size selectivity model that can be easily used to assess fishing management policies.

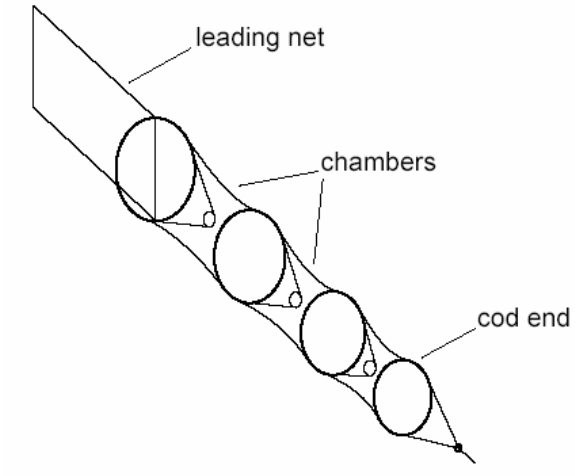


Figure 1. *Structure of a typical fyke net composed by a leading net, 2 chambers and a cod end.*

Fyke nets (Fig. 1) belong to towed gears, from which fish can escape if they are able to force the passage through meshes. In eels, similarly to

what observed for most fish species (Ferno and Olsen, 1994), escape attempts usually occur in the cod end part of the gear. Therefore, size selectivity is mostly determined by the size *m* of the mesh openings at the cod end, with larger individual more likely retained than smaller ones. In contrast with the size selectivity of gill nets, which is typically a unimodal, bell-shaped function of fish size, that of fyke nets is generally a monotone, non-decreasing function of fish size with an upper asymptote at unity (indicating that, beyond a given body size, almost 100% of the fish are retained). A sigmoid curve is most commonly used to provide a mathematical description of this pattern:

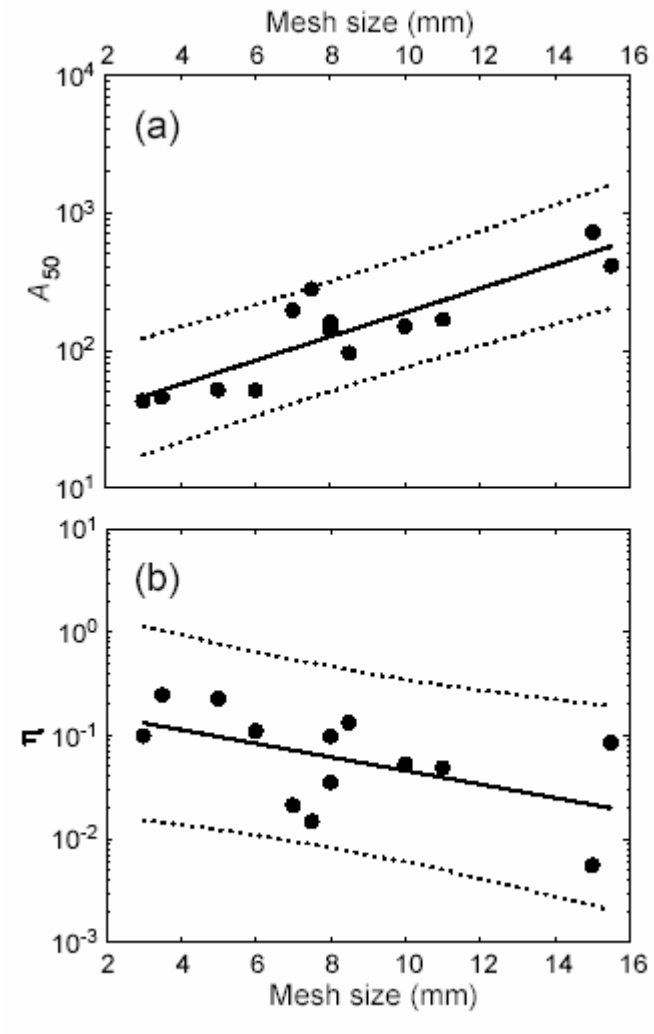
$$\varphi(S) = \{1 + \exp[-\eta(S - S_{50})]\}^{-1}, \quad (1)$$

where S is fish size (*e.g.* its body length, mass or cross section), S_{50} is S at which 50% of the fish are retained and η is a shape parameter defining the slope of the curve at $S = S_{50}$. $\varphi(S)$ is symmetric about S_{50} and the value of η determines the size range of the catch.

Logically, size selectivity of a meshed gear should be expressed as a function of fish cross section (Gatto and Rossi, 1979; De Leo and Gatto, 1995). Yet, body length *i*) is considerably easier to measure than section, *ii*) can be simply related to fish section trough an allometric relationship, and *iii*) is a standard biometric measure which is commonly used in fisheries management models. For this reason, net selectivity is often expressed as a function of body length. To this end, fish section A can be derived as a function of total body length L_T if an allometric relationship is available, such as that used in De Leo and Gatto (1995):

$$A(l) = a\rho^{-1}L_T^{\,b-1} \quad (2)$$

where ρ is the density of the fish (assumed to be constant and equal to water density, *i.e.* 0.001 g mm^{-3}), whilst a and b are the scale and shape parameters of an allometric body mass and length relationship.



Despite the socio-economical importance of thousands of small scale eel fisheries scattered all over Europe (Dekker, 2003), only a few studies explicitly investigated the link between net selectivity and mesh size for European eels (*e.g.* Gatto and Rossi, 1979; Naismith and Knights, 1990). These studies determined empirical selectivity curves for specific mesh sizes by using direct (*i.e.* based on the knowledge of the population length structure and the opportunity to monitor escapement) or indirect methods (comparing catches obtained from an experimental gear with those of a control one). Typical outputs of the experiments were the minimum body length (l_{min}) retained by the gear of a given mesh size m and the body length (l_{max}) over which all individuals are retained. Yet, none of these studies provided an analytical relationship linking mesh size with the parameters characterising the size selectivity curve. The parameters of the size selectivity curve (equation 1) were derived from l_{min} and l_{max}. First, the cross sections A_{min} and A_{max} corresponding to l_{min} and l_{max} were estimated from equation 2 by imposing *a*

Figure 2. *Variation of size selectivity parameters A_{50} (a) and η (b) for different cod end mesh sizes. ●, parameter estimates derived from literature data (Table I); ——, fitting line; ....., 95% CI.*

= 2.36 10^{-7} and b = 3.36, the values proposed in chapter 2 for a French European eel population. Then, A_{50} was calculated as the average of $A_{\min}$ and $A_{\max}$. Finally, η was determined from equation 1 by supposing that a fraction α of the fish retained by the gear had a cross section comprised between $A_{\min}$ and $A_{\max}$. By imposing $\varphi(A_{\min}) = (1-\alpha)/2$ and $\varphi(A_{\max}) = (1+\alpha)/2$, one obtains indeed:

$$\eta = \ln\left[(1+\alpha)(1-\alpha)^{-1}\right](A_{\min} - A_{50})^{-1} = \ln\left[(1-\alpha)(1+\alpha)^{-1}\right](A_{\max} - A_{50})^{-1} \quad (3)$$

Data for the present analysis were gathered from six experimental studies on net selectivity for European eels, encompassing a range of 13 mesh sizes between 3–15.5 mm (knot-to-knot). Of these, only three were published in peer reviewed scientific journals (Gatto and Rossi, 1979; Naismith and Knights, 1990; De Leo and Gatto, 1995), whilst the others were described in two PhD theses (Lee, 1979; Adam, 1997) and a technical report (Ximénès, 1986). Most studies reported gear selectivity at the cod end of fyke nets. Naismith and Knights (1990), however, reported the results of lab tests in which eels were placed in a netted bag and suspended in tanks to control escapement. The findings of the studies are summarized in Table I, along with the relevant estimates of A_{50} and η (obtained by imposing α = 0.95 in equation 3). Fig. 2 displays estimated A_{50} and η against the mesh size m of the fishing gear, showing that A_{50} increased and η decreased for increasing values of m. These data were used to investigate possible relationships between the two parameters and m. A linear regression of $\ln A_{50}$ and $\ln\eta$ against m was performed to prevent the resulting models from assigning negative values to A_{50} for m near zero and to η for large m values. Significant correlations were found between $\ln A_{50}$ and m (r^2 = 0.77, $P << 0.01$) and between $\ln\eta$ and m (r^2 = 0.28, $P < 0.1$). Fitting lines are superimposed to data in Fig. 2. The relevant equations are the following:

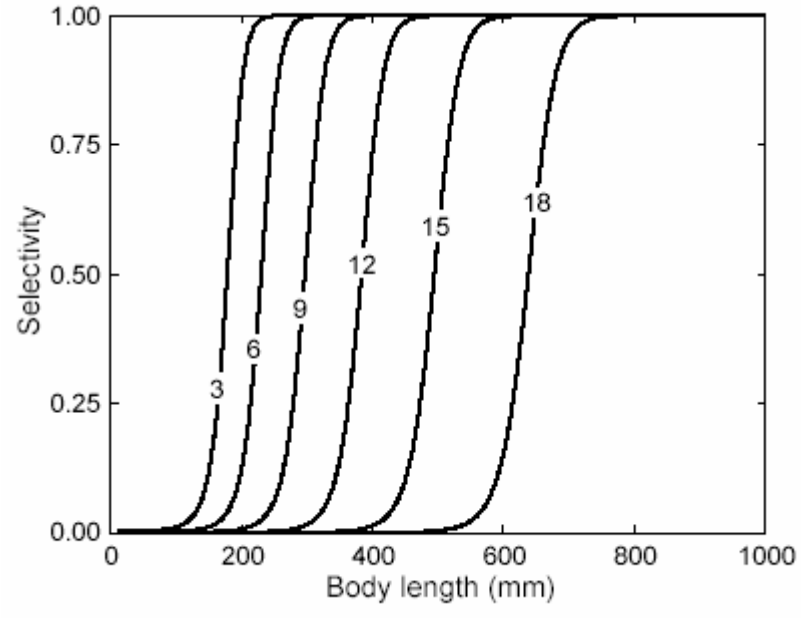
$$\ln A_{50} = 3.23 + 0.2m \quad (4)$$

$$\ln\eta = -1.57 - 0.15m \quad (5)$$

Through equations 4 and 5 it is easy to generalize equation 1 to encompass different values of the mesh size m:

$$\varphi(l,m) = \left\{1 + \exp\left[-\eta(m)\left(A(l) - A_{50}(m)\right)\right]\right\}^{-1} \quad (6)$$

where A is given by equation 2 and A_{50} and η by equations 4 and 5, respectively. Equation 6 can be adapted to European eel populations with different morphometric characteristics by substituting appropriate values of a and b in equation 2, and has therefore a general validity. Fig. 3 shows the estimated selectivity curves of fyke nets having a mesh size ranging between 3–18 mm resulting from using the values of the body mass and length relationship proposed in chapter 2.



The model proposed here is not exempt from weaknesses. Environmental conditions and fish behaviour are also likely to affect gear selectivity. For instance, studies on towed gears suggest that very small mesh cod ends might be avoided more than larger ones, probably because the first create more drag and turbulence through water (Wileman *et al.*, 1996). Unfortunately, however, the influence of these factors on selectivity is poorly documented and available

Figure 3. *Estimated size selectivity curves for eel fyke nets for different cod end meshes. Mesh sizes (in mm, knot-to-knot) are superimposed to the relevant curves.*

data do not allow incorporating these effects in a reliable way. We are also aware that assuming fyke net selectivity to be determined only by the mesh size of the cod end, and disregarding the selectivity of the leading net and that of the chambers, is another weak assumption of the model. Despite these reservations, the general size selectivity curve formulated in this chapter, based on empirical evidence from data gathered both in the lab and on the field, can be easily adapted to specific gears, fishing practices or fish stocks. It can be incorporated into demographic models, such as those required for the development of EMPs, which will be crucial to simulate demographic dynamics and assess the consequences of different management options.

Table I – *Mesh size (knot-to-knot), minimum (l_{min}) and maximum (l_{max}) total length of the catch from the studies analysed in this chapter, along with relevant estimates of the selectivity function parameters A_{50} and η (see equations 2 and 3).*

Mesh size (mm)	l_{min} (mm)	l_{max} (mm)	A_{50} (mm^2)	η (mm^{-2})	Method†	Fishing device	Reference
3	75	225	43	0.099	dir.	cod end	Adam (1997)
3.5	150	200	46	0.245	dir.	mesh-bag	Naismith and Knights (1990)
5	160	210	52	0.227	dir.	mesh-bag	Naismith and Knights (1990)
6	120	230	51	0.111	dir.	cod end	Ximenes (1986)
7	130	430	196	0.021	dir.	cod end	Lee (1979)
7.5	150	500	279	0.015	dir.	cod end	Ximenes (1986)
8	160	360	139	0.035	dir.	cod end	De Leo and Gatto (1995)
8	270	330	160	0.098	dir.	cod end	Ximenes (1986)
8.5	210	270	96	0.133	ind.	mesh-bag	Naismith and Knights (1990)
10	225	345	150	0.052	ind.	cod end	Adam (1997)
11	240	360	168	0.049	ind.	mesh-bag	Naismith and Knights (1990)
15	200	752	720	0.006	ind.	cod end	Gatto and Rossi (1979) ‡
15.5	430	470	412	0.085	ind.	mesh-bag	Naismith and Knights (1990)

† dir.: direct method; ind.: indirect method (see text for details)
‡ In this work l_{min} and l_{max} were estimated from minimum and maximum fish section.

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6

A 14 years population dynamics analysis of European eel

Introduction

Natural fish populations undergo abundance variations during intergeneration time due to changes in fishing pressure, physical (e.g. environmental factors) or biological conditions (e.g. insurgency of diseases). Similarly, variations in local population abundance and structure show marked seasonal patterns; this is especially evident in temperate seas, but also occurs in tropical areas. Nevertheless, most fishery models and stock assessments, and therefore the management strategies based upon them, focus on overall population biomass dynamics on intergeneration time scales ignoring population structure and seasonal dynamics. While this approach may be reasonable for determining general long term patterns and demographic attributes (e.g. population carrying capacity, growth rates etc.), sound fisheries management needs to explicitly account for size and maturation stage and to be implemented on a finer time scale. This is particularly true for all those species that undergo seasonal variation in structure and abundance and are exploited at different size and ontogenetic stages in different periods of the year.

What mentioned above is particularly true for different eel species. On a broad spatial and time scale, continental eel catches of the three most valuable species of the Northern hemisphere (*A. anguilla, A. rostrata* and *A. japonica*) abandoned natural fluctuations, observed until the 60s, and seem to have begun a regular decrease (ICES 2007). Recruitment of the three species has also declined considerably since the late 1970s (Castonguay et al. 1994, Moriarty and Dekker 1997). European eel stock is currently considered outside safe biological limits (ICES 2007). On a local scale**,** eel populations, along the year, undergo abrupt variations in terms of individual abundance, size and maturation structure. Juvenile recruitment, and consequent increase in individual abundance, occurs in spring. Sexual maturation, and consequent changes in population structure due to migration to the open sea of big mature individuals, occurs in autumn. In addition, commercial fisheries severely affect eel stock at different development stage or body size, depending on the period of the year and on the local demand (e.g. mature eels are consumed in Italy, while newly recruited glass eels are consumed in Spain and Portugal), altering natural population structure. European Commission recently (June 2007) approved an EU Regulation to force Member States to implement Eel Management Plans (EMPs) at river basin scale with the aim to achieve the objective of a 40% escapement of adult eel from each river basin (measured with respect to undisturbed conditions) (EC 2007). Similar protection measures are being debated to protect American eel (ICES, 2007). To assess effective EMPs is necessary to (i) evaluate the present status of local stocks and related fisheries, (ii) estimate the potential eel production of different local populations and, (iii) develop management tool to *a priori* assess efficacies of different management measures.

Herein, is presented a model of eel demography accounting for the main features of the continental phase of eel life cycle never pieced together in a unique study, namely: (1) density dependent survival of juvenile eels (Vøllestad and Jonsson, 1988; De Leo and Gatto 1996); (2) body growth characterized by strong sexual dimorphism and high inter-individual plasticity (Vøllestad 1992, Panfili et al. 1994; De Leo and Gatto, 1995, Krueger and Oliveira 1999); (3) sex differentiation and maturation, as well as natural mortality, related to body size rather than age (see chapters 2 and 4); (4) fishing mortality depending on fishing gear device and body size (see chapter 5); (5) huge fluctuations of annual recruitment at the glass eel stage (De Leo and Gatto, 1995). The model, accounting for monthly time step, has been calibrated and validated on an exceptionally detailed 14 years data set from the Camargue lagoons (Rhône River delta, Southern France). That illustrated in the present work thus represents, up to now, the most sophisticated functional and data-driven modeling approach to the analysis of eel demography in the continental phase of its life cycle. The model has been used to accomplish two main goals. First, increase the knowledge on biological features that are likely to influence continental dynamics of eels worldwide. Second, develop e flexible tool to assess both local eel stock and harvest for variable recruitment and fishing effort, turning out to be of great help in defining efficient EMPs.

The presented model has been tightly calibrated on eel data from the Camargue lagoons, nevertheless it is likely that a similar approach can be used to assess and manage local populations for all those fishes for which juvenile recruitment is mainly independent from local adult stock, vital features are related to body size rather than age and seasonal changes trigger important aspects of life cycle (e.g. sexual maturation, migrations, natural mortality etc.)

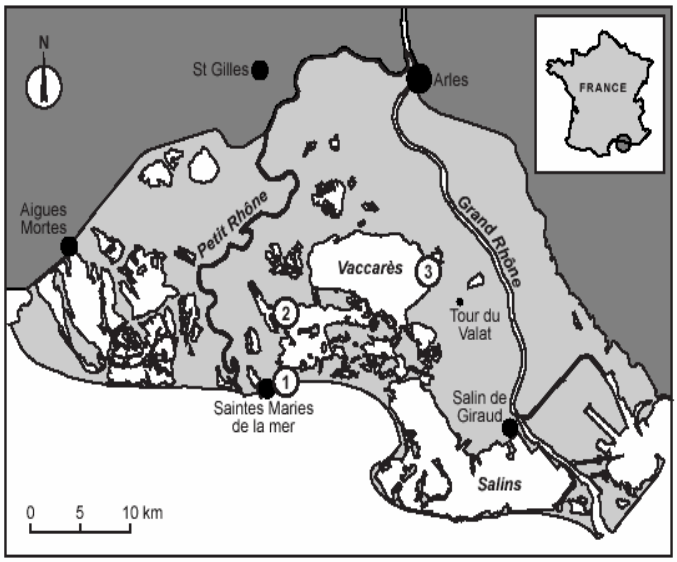
General information and data

Study site

The Camargue water system (Rhône River delta, Southern France) comprises two major watersheds (Fig. 1): the Impériaux lagoon (4,600 ha) and the Vaccarès lagoon (6,400 ha). The lagoons are isolated from the two arms of the Rhône River (Grand Rhône and Petit Rhône) and from the Mediterranean Sea by dykes. The water flow from the lagoons to the sea and back is regulated by Fourcade sluice gates, near Saintes Maries de la mer. Water management is mainly aimed at maintaining low water levels (around 1-2 m to prevent the inundation of Saintes Maries de la mer) and low salinity levels (around 4-12 to avoid damage to rice fields) in the lagoons. Commercial fishery takes place both in Impériaux and Vaccarès through the use of fyke nets while recreational fishing is banned. From the socio-economic viewpoint, the European eel is the most important fish species along Mediterranean coasts of France, as its fishery covers about 70% of total revenues by professional fishermen (Lefebvre et al. 2003).

European eel life history in the Camargue lagoons

Similarly to other eel species living at temperate latitudes such as American and Japanese eels, European eel is a semelparous and panmictic fish. Reproduction takes place in open ocean, at tropical latitudes, *larvae* undergo a long distance migration to the continental waters, young eels colonise marine, brackish and freshwater environments where they feed and grow until they reach the maturation size (van Ginnneken and Maes, 2005). Eels reach the Camargue lagoons as glass eels (the ontogenetic stage following the larval one), with an average length comprised between 55–65 mm. They enter into the Camargue water system through Fourcade sluice gates. The number of glass eels reaching the Camargue lagoons depends upon the effective recruitment to the continental platform and by water exchanges between the sea and the lagoons (i.e., when sluices are open and there is a sufficient freshwater call). After settling in the lagoons, eels start feeding and growing, and undergo a first metamorphosis to the elver stage (small, sexually undifferentiated yellow eels) around 65–75 mm. Sex differentiation occurs around 200-230 mm (Colombo et al., 1984), approximately two years later their entry to the lagoons (see chapter 2). Metamorphosis to the last stage of sexually mature eels, referred to also as silver eels, is also a body size driven process after which silver eels leave the lagoon to begin their journey towards the spawning grounds in the Sargasso Sea. Males become sexually mature (around 350 mm) within the first three years, whilst females can remain in the lagoons up to six years (around 550 mm) (see chapter 4).



Available data

During a long-term survey conducted by Tour du Valat (TdV in the following)

Figure 1. *The Camargue water system (43°30'N, 4°30'E). Circled numbers indicate the position of Fourcade sluice gates (1) and the two sampling stations at Impériaux (2) and Vaccarès (3).*

biological station from 1993 to 2006, 25,704 adult eels were caught at two sampling sites (Vaccarès, and Impériaux). Eels were measured (total length and body mass) and, since 1997, sexed (eels longer than 300 mm were sexed by gonad inspection, whilst shorter eels were classified as undifferentiated). Their stage of sexual maturation was determined according to Pankhurst's (1982) ocular index, and a sub-sample of 291 individuals was aged by otolith inspection. In the same period, 2,885 glass eels were sampled at Vaccarès and total length and mass were measured in a sub-sample of 1327 individuals. Biometric data were used to derive a body growth and a maturation model in chapters 2 and 4. In addition a mark-recapture program on glass eels, conducted in 2004, permitted to mark 1,224,719 glass eels belonging to 2004 cohort. Individuals of the same cohort have been recaptured in autumn of the same year (176 individuals) and in spring 2005 (144 individuals). In both cases 4 of those recaptured eels were even marked (Crivelli et al., in prep).
The fishing effort of TdV biological station has been regularly recorded since 1993. Adult eels were caught through fyke nets with a 6 mm mesh size and a 40 m guiding net. TdV researchers fished approximately 4 days per month with a single capétchade at each fishing station. Catch statistics for adult eels at Capelière and Impériaux between 1993-2006 are reported in Table I. Glass eels were caught, at Vaccarès, with a fry net having a 0.5 mm mesh size and a 20 m leading net; fishing took place about 4 days per month. Statistics are reported in Table II. Fishing effort of professional fishermen is inferred from available information (see Appendix for details).

Table 1 – *Adult eels (numbers and biomass) caught with a 6 mm mesh-sized capétchade at Vaccarès and Impériaux during 1993-2006 by TdV biological station.*

Year	Vaccarès Number of eels	Biomass (kg)	Effort (days net)	Impériaux Number of eels	Biomass (kg)	Effort (days net)
1993	381	59.5	30.4	–	–	–
1994	317	59.9	40.1	–	–	–
1995	268	42.9	30.7	–	–	–
1996	260	27.4	26.0	–	–	–
1997	2561	84.0	45.5	1516	44.6	44.4
1998	8443	132.3	44.9	1970	29.8	47.1
1999	882	34.7	41.6	653	14.4	45.9
2000	1155	47.3	45.4	395	19.6	47.0
2001	490	28.8	29.8	489	16.8	26.8
2002	404	41.1	27.7	677	31.8	23.7
2003	437	30.9	27.4	123	5.6	23.9
2004	620	33.3	31.6	–	–	–
2005	1790	48.7	28.3	1481	30.8	19.8
2006	271	28.0	23.7	121	11.7	23.8

Table 2 – *Glass eels (in numbers) caught with a 0.5 mm mesh-sized fry net at Vaccarès during recruitment seasons (February-April) 1993-2006 by TdV biological station*

Year	Number of glass eels	Effort (days net)	CPUEg
1993	2	9.9	0.2
1994	190	15.9	12.0
1995	61	15.9	3.9
1996	5	3.9	1.3
1997	25	16.2	1.6
1998	217	12.5	17.4
1999	56	10.7	5.3
2000	2079	11.7	177.7
2001	4	12.1	0.3
2002	146	11.9	12.3
2003	8	11.8	0.7
2004	62	11.7	5.3
2005	2	10	0.2
2006	28	12	2.3

Model formulation

Eel population is divided into five classes by sexual maturation stage (yellow/silver) and by sex (undifferentiated/females/males). Classes are indicated with the following acronyms, where the first letter indicates the maturation category (yellow/silver) and the second the sex category (undifferentiated/female/male): YU, YF, YM, SF, SM. Temporal population dynamics are simulated through a monthly time step.

Let $n_i(x,l,t)$ (i = YU, YF, YM, SF, SM), be the joint probability densities for a x-months old eel to have length l at time t and being in stage i. The length and stage structure of a cohort evolves in time, as a consequence of body growth, survival, sexual differentiation and maturation processes. The change of the population structure from time t to time t^+ can be written as:

$$\begin{cases} \int_{l_1^+}^{l_2^+} n_{\mathrm{YU}}(x^+,l,t^+)\,\mathrm{d}l = \int_{l_1}^{l_2} \sigma\cdot(1-h)\cdot(1-d)\cdot n_{\mathrm{YU}}(x,l,t)\,\mathrm{d}l \\ \int_{l_1^+}^{l_2^+} n_{\mathrm{YF}}(x^+,l,t^+)\,\mathrm{d}l = \int_{l_1}^{l_2} \sigma\cdot(1-h)\cdot\left[f_{\mathrm{F}}\cdot d\cdot n_{\mathrm{YU}}(x,l,t)+(1-\gamma)\cdot n_{\mathrm{YF}}(x,l,t)\right]\mathrm{d}l \\ \int_{l_1^+}^{l_2^+} n_{\mathrm{YM}}(x^+,l,t^+)\,\mathrm{d}l = \int_{l_1}^{l_2} \sigma\cdot(1-h)\cdot\left[f_{\mathrm{M}}\cdot d\cdot n_{\mathrm{YU}}(x,l,t)+(1-\gamma)\cdot n_{\mathrm{YM}}(x,l,t)\right]\mathrm{d}l \\ \int_{l_1^+}^{l_2^+} n_{\mathrm{SF}}(x^+,l,t^+)\,\mathrm{d}l = \int_{l_1}^{l_2} \sigma\cdot(1-h)\cdot\left[\gamma\cdot n_{\mathrm{YF}}(x,l,t)+(1-\xi)\cdot n_{\mathrm{SF}}(x,l,t)\right]\mathrm{d}l \\ \int_{l_1^+}^{l_2^+} n_{\mathrm{SM}}(x^+,l,t^+)\,\mathrm{d}l = \int_{l_1}^{l_2} \sigma\cdot(1-h)\cdot\left[\gamma\cdot n_{\mathrm{YM}}(x,l,t)+(1-\xi)\cdot n_{\mathrm{SM}}(x,l,t)\right]\mathrm{d}l \end{cases} \quad (1)$$

where σ is the fraction of eel surviving from time t to time t^+, h the fraction of eels harvested by fishermen, d the probability for an undifferentiated eel to undergo sex differentiation, f_{F} and f_{M} the fraction of differentiating eels becoming female/male, γ the probability for a yellow eel to metamorphose to silver eel and, ξ is the probability for a silver eel to move out off the lagoon to migrate toward the spawning site. The parameters σ, h, d, γ, ξ can be function of time, age, body size, sex and developmental (see Appendix for details). The integral

$$\int_{l_1}^{l_2} n_i(x,l,t)\,\mathrm{d}l \quad (2)$$

gives the probability of an eel of age x at time t to have body length between l_1 and l_2 ($l_1 < l_2$).

Eel recruitment is considered to occur each year at the beginning of the spring. Age is counted conventionally starting when glass eels become pigmented, metamorphose to elvers and settle in the lagoon. At age $x = 0$, the length structure of a newly recruited cohort at time t is supposed to be distributed as a random variable with assigned probability density $r(l)$:

$$n_{\mathrm{YU}}(0,l,t) = r(l)\,, \quad (3)$$

therefore if $l_{\max}$ is the maximum length:

$$\int_0^{l_{\max}} r(l)\,\mathrm{d}l = 1 \quad (4)$$

If the total number of recruited elvers at time t-x is $R(t\text{-}x)$, the total number $N_i(x,t)$ of x-months old eels at time t, in stage i is given by

$$N_i(x,t) = R(t-x)\int_0^{l_{\max}} n_i(x,l,t)\,\mathrm{d}l \quad (5)$$

Then, catches abundances C of eels in stage i, in the age interval [x, x^+] and, in the time interval [t, t^+] can be computed, using the Baranov catch equation as:

$$C = \frac{F}{F+M} \cdot \left(1 - e^{-(F+M)}\right) \cdot N_i(x,t), \quad (6)$$

where F and M are the instantaneous fishing and natural mortality rates.

The total number of eels, at time t, in stage i can be computed by summing up the abundances of each cohort (eels of different ages x) obtained by eq.4. Eel abundances (in numbers) can be easily transformed in biomasses by using the allometric relationships between total length and body mass calculated in chapter 2. Finally, is interesting to note that, varying the integral limits of equation 4, stock and catch abundances can be easily structured in desired length classes.

Recruitment and glass eel survival

Annual variation of glass eel recruitment can be estimated from glass eels captures per unit effort ($CPUE_g$) recorded by TdV Biological Station in 1993-2006 at Vaccarès lagoon (tab. 2). Mark recapture experiments conduced on 2004 cohort (Crivelli et al., in prep.) permitted to assess, through the refined form of Lincoln Petersen, the effective abundance G_{2004} of glass eel recruited in spring 2004 be around 40 millions. In 2004 the relationship Φ between effective glass eel recruitment and $CPUE_g$ is equal to:

$$\Phi = \frac{G_{2004}}{CPUE_g(2004)} = 7{,}425{,}200 \quad (7)$$

then, supposing Φ not to vary from year to year, effective glass eel recruitment G at year y can be easily inferred by observed $CPUE_g$ at year y as:

$$G(y) = \Phi \cdot CPUE_g(y) \quad (8)$$

Given the remarkable fluctuations in glass eel recruitment, one would expect, in absence of density dependent effects, to observe the same variability in the CPUE of small yellow eels, possibly with a time lag of 12-18 months, that is the time needed by newly recruited glass eels to reach the minimum size (around 180 mm) to be trapped into fyke nets (see chapter 5). Yet fluctuations in catch of small eels are indeed much smaller than those of glass eels (not shown data). It is assumed that density-dependent survival of juveniles, that is from glass eels to elvers, might play a role in damping fluctuations observed in glass eel recruitment. As a consequence, it is assumed that the fraction σ_g of glass eels surviving to the elver stage is a decreasing function of glass eels abundance G, namely:

$$\sigma_g = \frac{\sigma_0}{1 + \rho \cdot G} \quad (9)$$

where, the maximum survival σ_0 at low density corresponds to natural survival as described in following sections, while the constant ρ is an unknown parameter to be estimated. Thus annual elver recruitment, net of glass eel mortality, is calculated as:

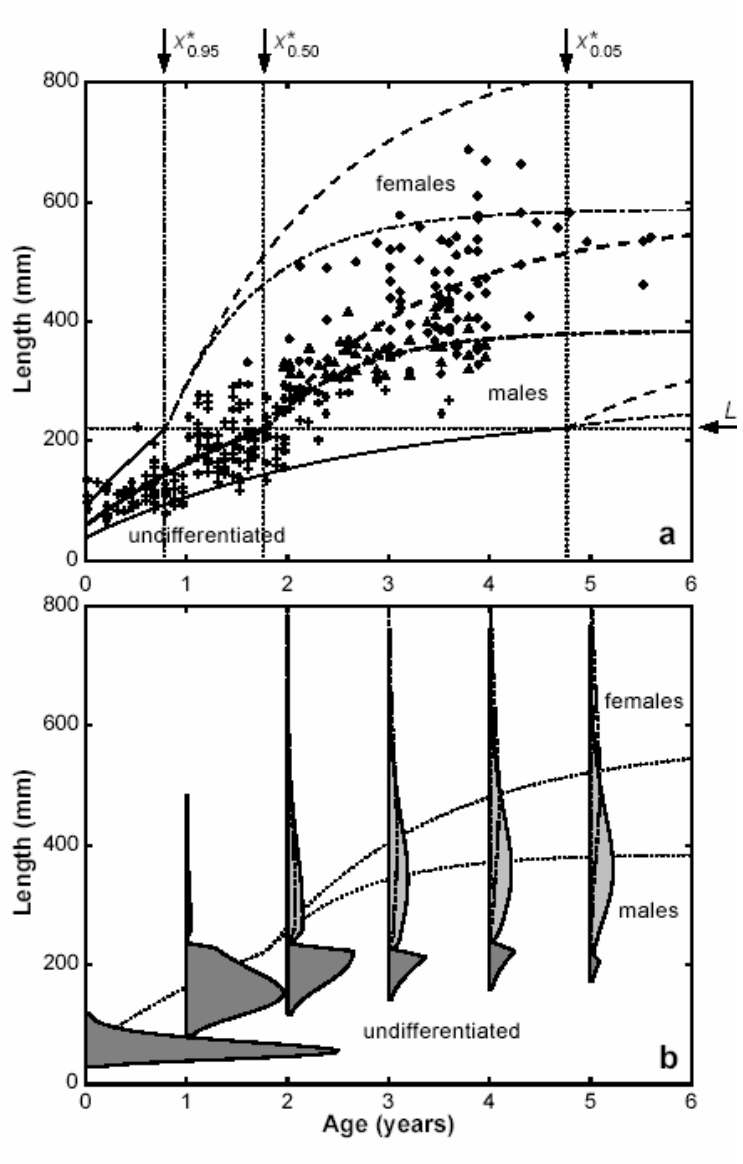
$$E = \sigma_g \cdot G \quad (10)$$

According with chapter 2, it is conventionally assumed that recruitment occurs at the beginning of April and is negligible otherwise.

Body growth and sex differentiation

Eel growth is characterized by evident sexual dimorphism (Krueger and Oliveira, 1999) and high inter-individual variability (Vøllestad 1992, De Leo and Gatto 1995). Sex determination is

metagamic, and is influenced by environmental factors and population density (Oliveira and McCleave 2002). Also, sex differentiation is delayed in time and it is likely triggered when a minimum body size threshold is exceeded (Colombo et al. 1984; chapter 2). All these peculiar features have been explicitly accounted for by using a stochastic version of the model proposed in chapter 2 and summered in the Appendix. A stochastic formulation (see Appendix for details), which follows the assignment-at-birth approach (Kirkpatrick 1984), already applied to eel growth by De Leo and Gatto (1995), allows us accounting for inter-individual variability. Notice that, in the stochastic version of the model, the age of sexual differentiation x^* is no longer a constant, as fast-growing eels reach the critical body length L^* at lower ages than slower ones. Fig. 2a shows the growth curves for undifferentiated, females and males, respectively, along with their confidence bounds. As evidenced in the figure, L^* is considered to be a physiological invariant, while x^* is not, as suggested in chapter 3. Fig. 2b shows the evolution of the size structure within a cohort and the sex differentiation process. While fast-growing eels can undergo sex differentiation already during their first year of life in the lagoons, a small fraction of slow-growing eels can remain sexually undifferentiated for many years. Thus, parameter d, reported in eq.1, is equal to 0 for individuals having body length l minor than L^* and equal to 1 afterwards. The fraction of differentiating eels becoming females f_F is set equal to 0.39 (while $f_M = 1 - f_F$) as assessed in chapter 2 for the same lagoons.



Sexual maturation and adult migration

Sexual maturation of eels, like sex differentiation, depends upon body size rather than age, with fast-growing individuals maturing earlier than slower ones (Vøllestad and Jonsson 1988, chapter 4). Also, length at metamorphosis differs between sexes with females metamorphosing to silver eels at a higher length than males. The fraction γ of eels that reaches sexual maturity is here assumed to be a function of length and to be represented by a sigmoid curve as suggested in chapter 4. Sexual and temporal variations of the silvering rate are accounted for, by introducing six metamorphosis curves, for the two sexes (female/male) and for the three months in which most of the eels are assumed to undergo metamorphosis to the silver stage (September/October/November).

Finally it is been assumed that silver eels leave the lagoon at the end of the month to start their journey to the spawning site. Notice that silver eels might encounter physical obstacles that can severely impair migration to the open sea. Therefore, a parameter ξ, that is the probability for a silver eel to escape from the lagoon in a given month, was

Figure 2. *Stochastic growth model. (a) Median growth curves (thick lines) and 90% prediction intervals (thin lines) of undifferentiated (solid), female (dash) and male (dash-dot) eels. Symbols identify observed age-length data (cross: undifferentiated eels; circles: females; triangles: males). Vertical dotted lines evidence age at sex differentiation of eels with initial sizes corresponding to different percentiles of the length distribution at recruitment. (b) Propagation of eel length distribution within a cohort.*

introduced in the model. In this study case ξ = 1 since, at Fourcade sluice gates, a passage to the sea is constantly guaranteed. However the possibility to vary this parameter permits to simulate the effect of different management of the sluice gates and to use the model in different contexts where silver eel migration might be impaired.

Natural mortality

Natural mortality instantaneous rate is needed to assess the fraction σ of eels surviving from time t to time t^+. The natural mortality rates of fish are closely related to their body size (McGurk, 1996). This has been demonstrated empirically within fish populations, as well as in comparison between populations and species (Lorenzen, 1996). Unluckily, similar allometric studies have never been conducted on eel species and today what is known from empirical studies is that natural mortality is in the order of 75 – 95% over the total continental life span (Moriarty and Dekker, 1997; Dekker, 1999). Although Gulland (1987) pointed out that size dependent mortality models make stock assessments more realistic, most authors used constant mortality rates when dealing with eel dynamics. Only De Leo and Gatto (1995) and recently Lambert and Rochard (2007) considered natural mortality as a decreasing function of age. If size is closely related to age, then size dependent vital rates can be calculated as a function of age but this is not the case of the eels whose plasticity in growth processes is well known (see chapter 2). Thus eel natural mortality rate M is here considered as a power function of body weight w as successfully used in many other fish species (Lorenzen, 1996):

$$M(w) = \alpha \cdot w^{\beta} \tag{11}$$

where α and β are respectively a scale and a shape parameter. When considering annual mortality rates, the shape parameter of equation 10 can be assumed equal to -0.29 for a broad range of fish species, while scale parameter varies more within populations, species or family groups (Lorenzen, 1996). Thus, information on the cumulative mortality rate for eels on the continental life span is used to specifically assess a value of α for eels. Supposed that the cumulative mortality rate M_{tot} over the continental life span is equal to 2.52 (such a value corresponds to a continental mortality of 92%) as suggested by Dekker (2000) one obtains:

$$\int_0^{x_{\max}} M(x)dx = 2.52 \tag{12}$$

where $x_{\max}$ corresponds to the average continental life span, equal to 6 years in the Camargue lagoons (see chapter 2). Note that, separately for males and females, body weight w can be estimated by body length l by using weight-length relationships and body length l can be estimated by age x using a body growth model. Then, allometric relationships and the body growth model proposed in chapter 2 are used to rewrite the mortality rate M (eq.10) as a function of age x, as it appears in equation 11. Then α remains the only unknown parameter of equation 11 and its value can be easily calculated as equal to 1.00 and 1.08 for males and females respectively. Estimated survival for the Camargue lagoons, as function of body length, are reported in fig 3.

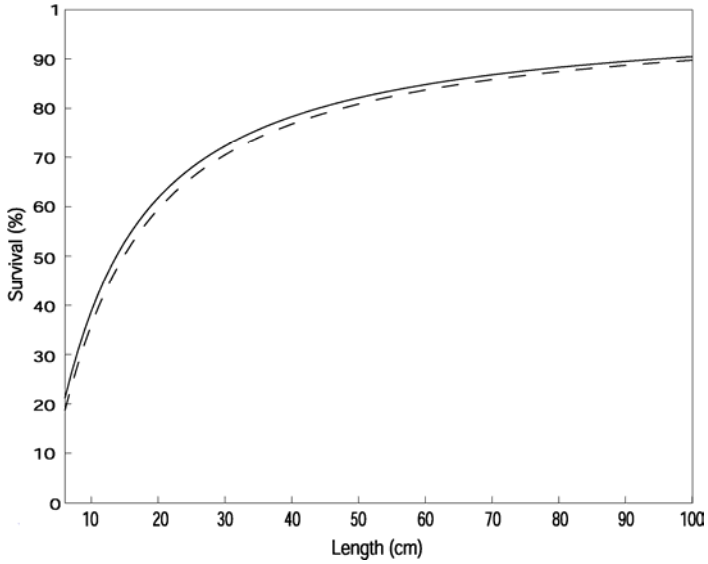


Figure 3. *Natural annual survival probability of males (dotted line) and females (solid line) as a function of total body length.*

Fishing mortality

Fishing mortality instantaneous rate F is needed to assess the fraction h of eels fished from time t to time t^+. F is assumed to be proportional, through catchability q and selectivity η coefficients, to the fishing effort E:

$$F_{ms}(l,t) = q_{ms} \cdot \varphi(l) \cdot E(t) \qquad (13)$$

where ms indicates the maturation stage ($ms = y$ for yellow eels, $ms = s$ for silver), the gear selectivity varies with eels body length l and fishing effort varies with time t.

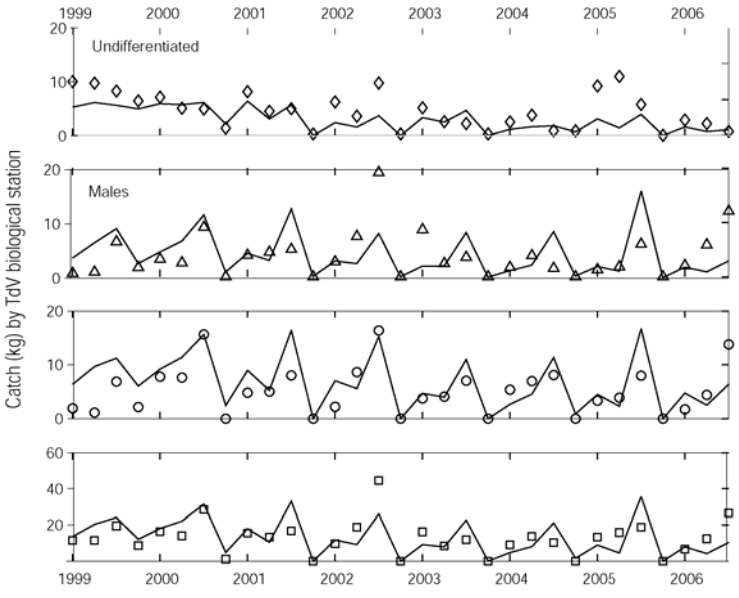
Catchability coefficient is a crucial parameter; it represents the effectiveness of the fishing gear. Such effectiveness depends upon the kind of fishing gear, its location, eels' behavior, characteristics of the environment etc. Catchability is likely to be different for silver and yellow eels; in fact while silver eels are frenetically moving to find the way to the open sea yellow eels show a more sedentary behavior. Catchability coefficients q_y and q_s, for yellow and silver eels, are unknown parameters that must be estimated.

In the case of fyke nets, the gear selectivity depends upon eel body length l and can be represented by means of a selectivity curve $\eta(l)$ as shown in chapter 5.

Fishing effort $E(t)$ in month t is here intended as the number of nets-day cast in the lagoons in that month. The fishing effort and relative catch of TdV biological station is exactly known and largely negligible compared with that performed by professional fishermen that has been estimated on the field experience of A.J. Crivelli (see Appendix for details).

Model calibration and validation

The entire demographic model is made up by different sub-models, described in the previous sections, regarding different aspect of the eel life cycle. Concurrent estimations of many different parameters can lead to good fit on some observed data, yet not being able to correctly describe the biological processes that are the linchpin of these observed data. In this study, thanks to an excellent dataset, it was possible to assess, through independent calibrations, most of the parameters needed (see Appendix for details). The only parameters (ρ, q_y and q_s) that could not be estimated *a priori* on available data were estimated by fitting the simulated eel abundances of TdV catch, structured by time-length-sex and maturation stage, to those observed during 1993-2003 (see Appendix for details). The last three years of data (2004-2006) were used to validate the model. Uncertainty of parameter estimates was assessed by means of a Bootstrap procedure (Efron and Tibshirani 1993), which allowed us to account for the variability of the population structure.



Results

Expected versus observed catches by TdV in terms of biomass, from spring 1999 to autumn 2006 are reported in fig 4. Besides fitting on catch biomasses, the model fits on catch structure by maturation stage, sex and body size. Correlation coefficients between expected and observed data, both in calibration (1999-2003) and validation (2004-2006) are reported in table 3. The model provides a fairly good fit of the observed dynamics of the biomasses harvested by TdV, especially for

Figure 4. *Predicted (lines) vs. observed (symbols) harvested biomass from spring 1999 to fall 2006. From 2004 symbols identify data used for validation.*

females and the overall catch while in some years (1999, 2002 and 2005) it underestimates the catch of undifferentiated and/or male eels. The model excellently fits the observed catch in terms of length structure, both in calibration and validation, for any sex and maturation stage, as confirmed by correlation coefficients always higher than 0.85 (Table 3). Concurrently estimated values of the unknown model parameters (ρ, q_y and q_s), along with their basic statistics, are reported in table 4. A value of ρ equal to 6.7×10^{-8} indicates a maximum successful settlement of about 15 millions of elvers and consequent existence of density dependent regulation of juvenile survival. Estimated relationship between elver settlement and glass eel recruitment is shown in Fig. 5. Although the number of glass eels that in given year enter the lagoons can considerably vary (from ca. 1 million to ca.1 billion), the following number of elvers successfully colonizing the lagoons rarely exceeds 11 millions individuals (ca.1,000 per hectare). Catchability parameters (q_y and q_s) estimates, equal to ca. 2.2×10^{-4} and 1.7×10^{-2} respectively for yellow and silver eels, clearly show that fyke nets impact much more on silver rather than on yellow eels.

Once all the parameters have been accurately calibrated, the demographic model provided an excellent tool for assessing the whole eel stock and the harvest by professional fishermen; it offered a detailed view on the status of the local stock and the impact of fishing on its dynamics. During 1999-2006, the biomass of the stock has been varying between 50 and 250 t (4.5 – 22.7 kg/ha) (Fig. 6). In the same period, the total number of eels in the lagoons has varied between about 1 and 18 millions (Fig.6). Both biomasses and individual abundances show strong seasonal oscillations, with biomasses slumping in autumn due to silver eel migration and high fishing pressure and individual abundances quickly rising in spring due to elver settlement. Averaging stock abundances on an annual basis, one can disregard seasonal oscillations and interestingly assess that both biomasses and abundances are significantly declining in 1999-2006 ($p = 0.014$ for abundances and $p = 0.0018$ for biomasses). When one separately considers yellow and silver eels composing the stock (both in terms of biomass and abundance), it is appears that while the yellow compound of the stock is decreasing (p = 0.014 and 0.0017 for abundance and biomass), the silver compound does not show any trend.

Professional fishermen monthly harvest shows severe oscillations varying from 1 and 25 tons (fig 8c) and from 50,000 and 350,000 individuals (fig 6). Total annual yields by professional fishermen varied between 55.2 and 95.5 t (5.0–8.7 kg/ha) and, despite seasonal oscillations, shows a significant decrease during 1999-2006 (p = 0.0005 and 0.015 for abundance and biomass). Similarly to the stock, even for the harvest, the decrease is lead by a decrease in the yellow eel harvest (p = 0.00032 and 0.0042 for abundance and biomass) while silver eel catches do not show any significant trend in the same period. Being minor the fishing effort of 6 fishermen from Impériaux, we can roughly estimate an annual catch around 5-9 tons per fishermen in Vaccarès.

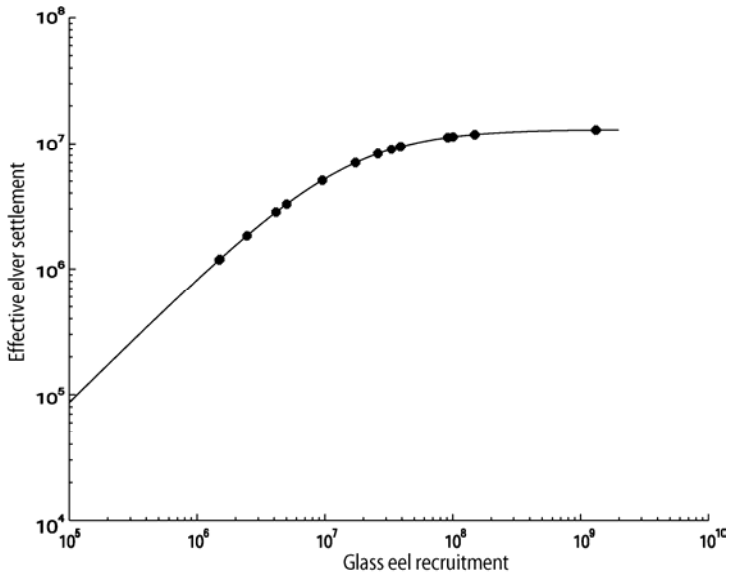


Figure 5. *Relationship between elver abundance and glass eels' CPUE. Dots indicate observed CPUE values and the corresponding elver abundance estimated by the model. Confidence limits on elver abundance are too narrow to be shown in the figure.*

Silver eels account on average for 25% in biomass of the annual catch, with minimum in 2006 (19%) and a maximum in 2004 (38%). The exceptional catch of silver eels of 2004 is probably due to the high recruitments of 1998 and 2000. These estimates agree with the annual catch declared by some fishermen in recent interviews.

Discussion

The demographic model here developed allowed a deep insight on Camargue eel population and related fisheries and, highlights some features that might be common to other eel populations.

Recruitment and density dependence

The model permitted to assess both annual glass eel recruitment and the fraction that successfully establish, as elvers, in the lagoons. Figure 5 shows that the Camargue lagoons are unlikely to shelter more than 15 millions elvers per year (around 1364 elver/ha) and that, however, even annual glass eel recruitment is often far below this threshold. Similarly, Klein-Breteler et al., (1990), through field experiments in Holland, concluded that glass eel stocking at 1600 individuals per hectare lead to strong density dependent limitations. During 1993-2006, estimated elver recruitment in Camargue fluctuated, with a decreasing yet not significant trend ($p = 0.41$), around an average of 7 millions (640 elvers/ha), with a minimum of about 1.2 millions (107 elvers/ha) in both 1993 and 2005 and a maximum of 12.8 millions (1,170 elvers/ha in 2000). Such a figure is close to the values of elver settlement (200-700 elvers/ha) estimated in Lough Neagh in the period 1960-1977 (ICES, 2007) before the recruitment drop of the 80s. De Leo and Gatto (1996) estimated that elver density in Comacchio lagoons dropped during 1974-1989 from 1806.2 to 202 individuals per hectare so that actual situation of the Camargue lagoon ranks between the "golden age" of Comacchio and the "bad times" forerunning eel fishery crisis observed in northern Adriatic sea in the last decade.

Density dependent juvenile mortality plays an important role in determining effective elver recruitment (recruitment net of glass eel mortality). This work suggests that competition underlying such mechanism is intra-cohort and not simply intra-specific. Similar results were found for both European (Vollestad and Jonssonn,1988; Klein Breteler et al., 1990; Svedang, 1999) and American (Jessop, 2000) eels. Newly recruited individuals probably compete among them, and not with adult eels, for food and space. The reason of this could be found in differentiation of diets and shelters for juvenile and adults. Moreover is to note that, in close lagoons, eels have no chance to move upstream to avoid high densities as observed in estuaries environments (Lambert and Rochard, 2007). Rodriguez et al., (2005 JFB) found that ability of elvers to withstand starvation decreases with salinity; Crean et al., (2005) assert that abrupt change in salinity, typical in the passage between open sea and closed lagoons, impair glass eel survival. Thus, is not surprising that high recruitment densities in the Camargue lagoons are associated with high juvenile mortalities.

Another feature that, together with juvenile mortality, is often related to density is sex ratio, with females predominant at low densities (Davey and Jellyman, 2005; Han and Tzeng, 2006). In Camargue lagoons about 61% of young eels become males (see chapter 2), and this percentage has not significantly varied in 1993-2006 (not shown data). This is another clue that juvenile eel density has been maintained constant in the same period and, high enough to produce more males than females.

Although local recruitment of glass eels in the Camargue lagoons is likely to have declined in the last decades following the global trend (unluckily there are no data prior to 1993), due to the presence of density dependent effects is difficult to imagine that, in last decades, elver recruitment, net of glass eel mortality, could be much higher than the one estimated in last 14 years. While, in the last 20 years, glass eel recruitment dramatically declined in the Adriatic sea, impairing profitability of commercial fishery in Comacchio and surrounding areas (De Leo and Gatto, 2001), natural recruitment in Southern France is still enough to sustain eel populations and related fisheries.

Natural mortality

In the past, other authors considered eel mortality rates as age dependent (De Leo and Gatto, 1995; Lambert and Rochard, 2007), probably assuming that older eels would have been bigger and probably less subject to natural mortality. Although such an approach represents a step forward from constant mortality rates, it neglects inter-population and inter-individual variability in growth processes. As a consequence those survival models assessed on a certain population are unlikely to fit on other population characterized by very different growth patterns and can not take advantage from the use of stochastic growth model that explicitly consider inter-individual variability in

growth processes. It is likely that such limitations have been overcome by the length dependent approach here used. Disentangling the contribution of natural and fishing mortality to the overall dynamics of exploited fish populations is always a tough task for researchers (Gulland, 1965). Here a survivorship model for adult eels has been calibrated *a priori* and permitted to separately account for natural and fishing mortality, both depending on body length.

Harvest and stock

Apart from estimating elver settlement the model permits to assess stock abundance and to compare it with data from other studies. Eel density in the Vaccarès-Impériaux water system has fluctuated between 73 and 1690 eels/ha (fig. 6). The average was 628 eels/ha, a figure comparable to those reported by De Leo and Gatto (1996) for the Comacchio population in the late 1980s (300–600 eels/ha) and by Moriarty and Dekker (1997) for the Bourgneuf marsh in the early 1990s (600 eels/ha), but one order of magnitude lower than densities reported by Feunteun (2000) for a river Basin in N Brittany (4,500 eels/ha) and by De Leo and Gatto (1996) for Comacchio in the mid 1970s (3,388 eels/ha). Moreover, figure 8 shows that undifferentiated eels are an overwhelming fraction of the standing population (49–94%). Their relative abundance reaches its maximum at the beginning of spring, when the emigration of mature eels and the recruitment of juveniles are almost complete. Yellow females and males account for 3–31% and 2–25% of the population respectively, whilst silver eels are only a minor fraction (0–1% for females and 0–3% for males), reflecting the fact that only a very small fraction of population succeeds in undergoing sexual maturation and avoiding fishermen nets when trying to find the way back to the sea. Such a detailed figure, made possible by the model structure, clearly indicates that the Camargue eel stock is currently overexploited. According to chapter 7 the reason of such overexploitation is the high selectivity of the fishing gear, even for small eels (200-300 mm), coupled with an high fishing effort. In terms of biomass, the density of the Camargue stock has been varying between 5.1 and 23.5 kg/ha (13.9 kg/ha on average), lower than the one estimated in Comacchio (149 kg/ha in the 1970s, 55–65 kg/ha in the late 1980s). The reason is probably due to differences in fishing practices (only silver eels fished at Comacchio) rather than on different productivity of the two sites. Yellow females (44–69%) represent the major fraction of the stock, undifferentiated eels account for a 10–39% of the total biomass, whilst biomass of yellow males (10–30%), silver females (0–8%) and silver males (0–7%) have a minor importance.

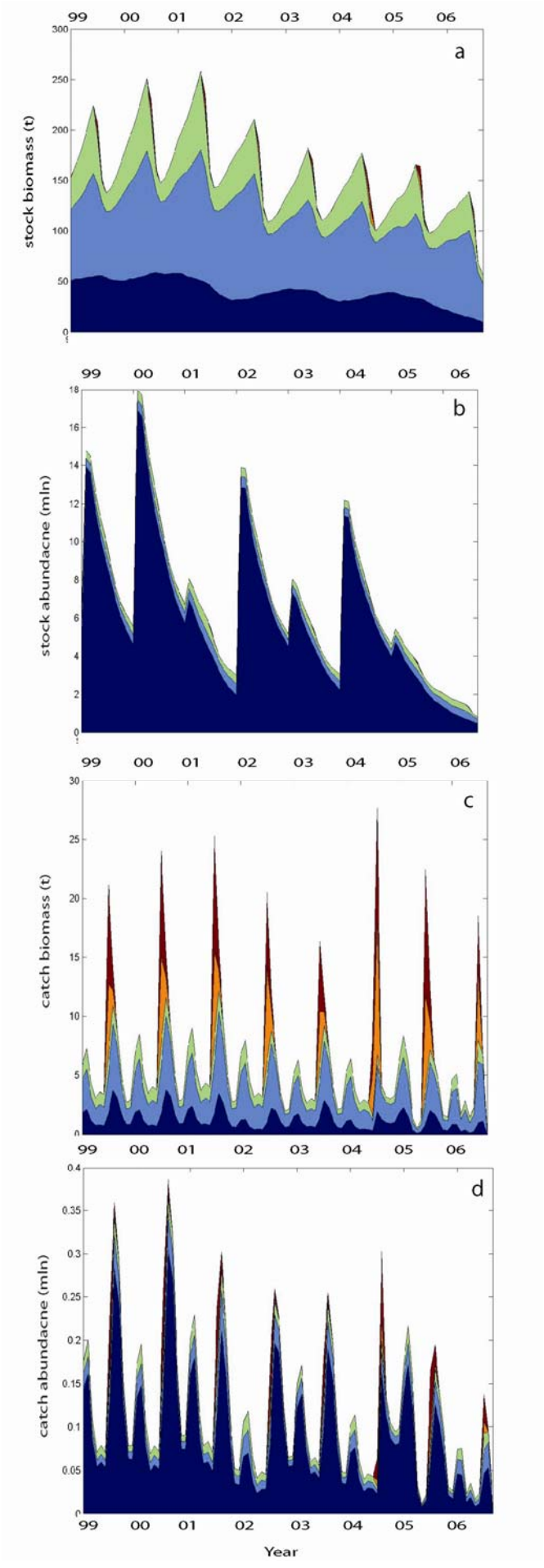
The results related to standing stock and harvest show that particular trends, e.g. a significant decrease in standing stock biomass, can be evidenced by analysing the yellow eel compound of yields but are masked by other commonly used indicators. Indeed, the sole analysis of silver eel yield or elver recruitment does not show any significant decreasing trend.

Silver eel dynamics, with respect to yellow eel ones, are delayed in time (the time needed by an eel to reach the silvering length) and probably smoothed by mortality rate accumulated during the continental life span. Figures of constant silver eel yields can mask a severe decline of underlying yellow eel stock and induce policy makers to postpone urgent conservation actions.

Due to the nature of the eel life cycle, monitoring entrance and/or escapement of eels from a local habitat is a common practice (De Leo and Gatto 1995). However, this work evidences that a clear picture of the state of the standing stock can be given only by accurate, constant and long term samples of standing stock or in alternative by sound demographic models. Inadequate models or sample campaigns can induce to dangerous mistakes in stock assessment, this is particularly true for those species having a complex life cycle and particularly dangerous for those species outside biological limits.

Spawning stock recovery

In June 2007 the Council of the European Union approved a Regulation (EC 1100/2007) establishing measures for the recovery of the European eel stock. Each Member State is required to elaborate EMPs in order to achieve an escapement to the sea of at least 40% of the potential



spawner biomass (with respect to undisturbed conditions) from each river basin. Scientists and policy makers shall take up the challenge to design management plans that will affect thousands of small scale fisheries operating in Europe. Thus, for any demographic model, is crucial to be able to assess both potential and actual spawning escapement. In the period 1999-2006, average of annual silver eel escapement in the Camargue lagoons was 20.6 tons (around 65,000 males and 25,000 females) with a maximum of 33.8 in 2004 and a minimum of 10.8 in 2006. On average, in 1999-2006, only 1.3% of recruited elvers succeeded in leaving the lagoons as silver eel. Effective spawner escapement agrees with our previous estimates (chapter 6) of about 14 tons. On the contrary, potential silver eel escapement (here simply intended as in absence of fisheries as in chapter 6) is around 280 tons, a figure much higher than the 62 tons previously estimated. Consequently, spawners' escapement in 1999-2006 turns out to be equal to 7% of the potential one, far away from the benchmark imposed by the Regulation. In chapter 7 fyke nets efficacy (related to catchability parameter *q*) has been supposed to be the same for yellow and silver eels, and the impact of fisheries on silver eel stock was underestimated. In fact silver eel catchability seems to be almost two orders of magnitude bigger than yellow eel catchability; it means that silver eels are much more likely to face the nets and being caught and this is probably due to the major movements of silver eels when searching the way to the open sea. Silver eel fishing through fyke nets is a common practice all over Europe and inferring silver eel mortality, due to fyke nets, by studies conducted on yellow eels can distort the results and impair the efficacies of conservation policies all over Europe. The estimated potential silver eel production of 25 kg/ha is much higher than the ones estimated in freshwater environments in northern Europe (3.51 kg/ha in the Imsa River (Norway) by Vollestad and Jonsson, 1988, 4.4 kg/ha in the Lake IJsslemeer (Netherlands) by Dekker, 2000a, 1.3 kg/ha in the Fremur catchment (northern France) by Feunteun et al., 2000) and similar to other estimates in

Figure 6. *Simulated dynamics of stock (a, in biomass; and b, in numbers) and harvest (c, in biomass; and d, in numbers) from March 1999 to November 2003 structured by sex and maturation class. Dark blue: undifferentiated; light blue: yellow females; green: yellow males; orange: silver females; ochre: silver males*

Mediterranean lagoons [20 kg/ha in Comacchio by Rossi (1979) and 19 kg/ha in Sardinia by Rossi and Cannas (1984)]. However is to note that, while silver production estimates in Comacchio have been validated by direct observation of the catches (we remind that in Comacchio silver eel catches corresponds to the silver eel production), our value of 25 kg/ha is only an assessment that might be overestimated by the absence of density dependent effects on body growth and adult eel natural mortality in the model. Nevertheless this result invites policy makers to seriously consider the high contribution that Mediterranean lagoons can give in restoring the global spawning stock. This contribution has been historically neglected, probably, due to the fact that eel production of Mediterranean lagoons (with the exception of Comacchio) have not been extensively studied in the past and, despite half of the European eel catches come from Mediterranean areas (Dekker, 2000b), long term data are often lacking (ICES, 2007). We still ignore many aspects on eel reproduction and we can not disregard the hypothesis that only some populations (e.g from the Baltic Sea or the one from freshwater habitats) constitute the effective spawning stock. Then, on a precautionary approach, we should hope that eel conservation concern both brackish and freshwater habitats, both Mediterranean and Atlantic waters. However, the high productivity of Mediterranean areas (Dekker, 2000b), the minor impact of the parasite *Anguillicola crassus* in brackish rather than in freshwater, the absence of impediments to migration typical of freshwater habitats (e.g. hydroelectric dams) and the faster effect of protection measures on spawner production due to the faster life cycle in brackish and warmer areas (chapter 3) are aspects to be considered when distributing conservation efforts.

Table 3– *Correlation coefficients of observed vs. estimated catches by TdV, in terms of biomass and individual abundance*

	Biomass				*Abundance length structure*				
	Undif.	Mal. (Y+S)	Fem. (Y+S)	Tot.	Undif.	Mal.(Y)	Fem.(Y)	Mal.(S)	Fem.(S)
Calibration (1999-2003)	0.65	0.47	0.79	0.70	0.95	0.98	0.95	0.82	0.96
Validation (2004-2006)	0.59	0.33	0.63	0.53	0.96	0.95	0.97	0.85	0.96

Table 4 – *Basic statistics of model parameters, as resulting by bootstrapping (100 iterations) of the 1999-2006 data set.*

Parameter		**Mean ± SD (CV)**	**Median (90% CI)**
Recruitment			
ρ	(–)	$6.74\times10^{-8} \pm 0.32\times10^{-8}$ (0.05)	6.72×10^{-8} (6.27×10^{-8}–7.28×10^{-8})
Catchability			
q_y	(nets^{-1} d^{-1})	$2.28\times10^{-4} \pm 0.60\times10^{-4}$ (0.07)	2.29×10^{-4} (2.01×10^{-4} –2.53×10^{-4})
q_s	(nets^{-1} d^{-1})	$1.72\times10^{-2} \pm 0.11\times10^{-2}$ (0.07)	1.72×10^{-2} (1.51×10^{-4} –1.93×10^{-4})

Conclusions

The presented model accounts for the major features of the continental phase of eel life cycle and overcomes some important drawbacks of earlier models, such as constant recruitment and stable age and size-distribution. Its stochastic formulation allows us to account for the intrinsic uncertainty of eel demography. This is the first functional model, assessed on a long time dataset, able to simulate

both harvest and stock dynamics structured by sex, maturation stage and length structure. A monthly time step permitted to account for seasonal changes both in natural and anthropogenic features. It permitted to assess the effect upon stock and catches of i) spring recruitment, ii) autumnal escapement and iii) monthly fishing effort peaks. Although is well known that in eels, similarly to many other fish species, ecological consequences of size on vital parameters (e.g., survivorship, fecundity, sexual maturity) are more important than those due to age (De Leo and Gatto, 1995) this is the first time that plasticity in body growth is coupled with size dependence of *i*) natural mortality, *ii*) fishing mortality and, *iii*) maturation processes. Despite the model explicitly accounts for the major features of eel biology, most of the biological parameters have been independently estimated in order to avoid over-parameterization and guarantee biological reliability of parameter values. The European eel is presently considered as a threatened species (ICES, 2007). Despite this, eel fisheries remain an important source of revenues for a number of local economies. Decision makers in management agencies require effective tools to analyze the potential consequences of different conservation policies for eel stocks all over Europe. The model proposed here can provide a robust conceptual framework for the development of both specific models for local populations and more general, yet realistic, models of the whole European eel stock. Finally, presented findings highlight the central role that Mediterranean lagoons might play in recovering global spawning stock.

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Appendix

Body growth and sex differentiation

The growth model proposed in chapter 2 is a modified von Bertalanffy (1957) model, in which three distinct growth curves are used for undifferentiated individuals, males and females, explicitly accounting for the strong sexual differentiation of eels. Its deterministic form is the following (see chapter 2 for further details):

$$L(x) = \begin{cases} L_0 + (L^* - L_0)\dfrac{1-\exp(-k_{\mathrm{U}}x)}{1-\exp(-k_{\mathrm{U}}x^*)} & \text{for } x \le x^* \quad \text{(undiff.)} \\ L_{\infty F} - (L_{\infty \mathrm{F}} - L^*)\exp\big(-k_{\mathrm{F}}(x-x^*)\big) & \text{for } x > x^* \quad \text{(females)} \\ L_{\infty M} - (L_{\infty \mathrm{M}} - L^*)\exp\big(-k_{\mathrm{M}}(x-x^*)\big) & \text{for } x > x^* \quad \text{(males)} \end{cases} \tag{A.1}$$

where L_0 is the length at age zero (conventionally set to the age at which glass eels become pigmented and metamorphose to elvers), L^* and x^* are length and age at sexual differentiation, k_{U}, k_{F}, and k_{M} are the Brody growth constants for undifferentiated eels, females and males, and $L_{\infty\mathrm{F}}$ and $L_{\infty\mathrm{M}}$ are the asymptotic mean lengths of females and males, respectively. Eq. (A.1*a*) is a von Bertalanffy curve, albeit reformulated to put in evidence length and age at sexual differentiation, L^*

and x^*, instead of the asymptotic mean length for undifferentiated eels $L_{\infty U}$. This latter parameter lacks indeed any biological meaning, as growth begins to slow down only when eels are already differentiated. However, Eq. (A.1*a*) can be straightforwardly transformed into the equivalent, yet more usual form

$$L(x) = L_{\infty U} - (L_{\infty U} - L_0)\exp(-k_U x) \tag{A.2}$$

The model was calibrated with age-length data from 291 eels caught between 1997-1998 in the Vaccarès and Impériaux lagoons. A stratified bootstrap procedure (Efron and Tibshirani, 1993) was used to assess the uncertainty associated to parameter (see chapter 2 for details).
To account for inter-individual variability, a stochastic formulation of Eq. (A.1) has been derived. The assignment-at-birth approach (Kirkpatrick 1984) was followed, applied to eel growth by De Leo and Gatto (1995). In their model, the actual length of an individual is given by $l(x) = L(x)\cdot g$, where $L(x)$ is the expected length at age x (as given by the deterministic growth model) and g is a log-normally distributed random factor assigned at birth according to the length structure at recruitment. In the present study, the application of the assignment-at-birth approach to Eq. (A.1) requires to express x^* as a function of g, as fast-growing eels reach the critical body length at lower ages than slower ones. It is supposed, as in chapter 3, that L^* is a physiological invariant, while x^* is not.
The link between x^* and g can be determined from the stochastic form of Eq. (A.1):

$$l(x^*) = \left[L_{\infty U} - (L_{\infty U} - L_0)\exp\left(-k_U x^*\right)\right]\cdot g = L^* \tag{A.3}$$

from which one obtains

$$x^*(g) = \frac{1}{k_U}\ln\frac{L_{\infty U} - L_0}{L_{\infty U} - L^*/g} \tag{A.4}$$

The stochastic version of the growth model can be therefore be written as

$$l(x,g) = \begin{cases} \left[L_0 + (L^* - L_0)\dfrac{1-\exp(-k_U x)}{1-\exp(-k_U x^*)}\right]\cdot g & \text{for } x \le x^*(g) \quad \text{(undiff.)} \\ \left[L_{\infty F} - (L_{\infty F} - L^*/g)\exp\left(-k_F(x - x^*(g))\right)\right]\cdot g & \text{for } x > x^*(g) \quad \text{(females)} \\ \left[L_{\infty M} - (L_{\infty M} - L^*/g)\exp\left(-k_M(x - x^*(g))\right)\right]\cdot g & \text{for } x > x^*(g) \quad \text{(males)} \end{cases} \tag{A.5}$$

The actual length l of an eel is then determined by its age x and a growth factor g, randomly assigned at birth according to a log-normal distribution function $r(l)$ with unitary geometric mean and variance σ_r^2 which has been estimated on age-length data as the prediction error variance of the deterministic growth model.

Fishing effort by professional fishermen

Fishing pressure at Impériaux and Vaccarès has been approximated in the following way. Between 1993-2006, 19 commercial fishermen have fished in the Impériaux lagoon and 12 in the Vaccarès lagoon. A recent survey among fishermen permitted to assess the average number of nets that they use depending on the month and on the location (Impériaux or Vaccarès). These data have been adjusted considering that Impériaux fishermen fish about 3 days per week for 10 months per year (fishing is forbidden in the Impériaux lagoon in July and August) while at Vaccarès, fishermen have

been fishing about 5 days per week from December to February and from July to August, and 6 days per week for the rest of the year..

Model calibration

The unknown parameters of the demographic model (ρ for recruitment survival q_y and q_s for fishing mortality) were estimated by fitting the simulated catch abundance by TdV biological station, structured by time, length, sex and maturation stage, to that observed in 1999-2003. Catch data were aggregated into trimesters, length classes (50 mm wide), sex (undifferentiated, males and females) and maturation stage (yellow and silver).

Being $\overline{\pi}_{i,L,T}$ the total number of eels of stage i (i = YU, YM, YF, SM, SF), in length class L at trimester T caught by TdV biological station. We have used the residual variance as a cost function. Hence,

$$C(\psi) = \sum_i \frac{\sum_T \sum_L \left[\overline{\pi}_{i,T,L} - \hat{\pi}_{i,T,L}(\boldsymbol{\psi})\right]^2}{\sum_T \sum_L \left[\overline{\pi}_{i,T,L} - \overline{\overline{\pi}}_i\right]^2} \tag{A.6}$$

is the sum of the residual variances of the abundances of the five sex/maturation categories structured by length classes (N_L = 20) and time (N_T = 19 from March 1999 to November 2003). $\hat{\pi}_{i,T,L}(\boldsymbol{\psi})$ is the corresponding estimate, associated to parameter set $\boldsymbol{\psi}$ (ρ, q_y, q_s), and $\overline{\overline{\pi}}_i$ is the observed average abundance of individuals of class i over time and length classes.

It is important to notice that, to calculate the structure and abundance of the catch, we would need to know the structure and abundance of the stock. However, there is not any *a priori* structure and abundance of the stock. Yet, as age data show that no eels remain more than six years in the Camargue lagoons, the structure and abundance of the stock in a given year are not influenced by the state of the population six years before, but depend only upon eel recruitment, mortality and escapement during the last years. Therefore, population dynamics has been simulated starting from a theoretical length distribution and population size in 1993, and compared the structure of the catch predicted by the model six years later with that observed during the following five years (1999-2003). The parameter set $\boldsymbol{\psi}$ that minimize $C(\boldsymbol{\psi})$, was found with the Nelder-Mead simplex algorithm (Nelder and Mead 1965).

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7

Multi-objective assessment of conservation measures for the European eel

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Abstract

The European eel (*Anguilla anguilla*) stock has declined since the early 1970s and is presently considered outside safe biological limits. The European Commission proposed a regulation (COM 2005/472 final) to establish measures for the recovery of the stock, with the aim to achieve the escapement to the sea of a 40% of adult eel biomass (with respect to undisturbed conditions) from each river basin. The proposed regulation imposes an effective reduction of fishing activities until implementation of an approved eel management plan. A demographic model, explicitly accounting for age, length and sex structure and for the peculiar features of the continental phase of eel life cycle, was used to assess the effectiveness of the regulation proposal. Alternative management options were explored with reference to the Camargue (Southern France) eel population. Using multi-criteria methods different fishing policies were compared with respect to two potentially conflicting objectives: preserving a sufficient spawner escapement and guaranteeing an acceptable harvest to fishermen. Current fishery is shown to be inefficient and appropriate management policies (like limiting the fishing season and increasing the mesh size of the fishing gears) are likely to have a doubly positive effect, by achieving the conservation target of the regulation and increasing fishermen revenues.

Introduction

Available information on the status of the European eel *Anguilla anguilla* (L.) stock and its fisheries supports the view that the European eel stock has experienced a severe decline in most of its distribution area. The stock is presently considered outside safe biological limits and current fisheries are not sustainable (Dekker, 2003a; Dekker, 2003b; ICES, 2003). The observed decline is likely to be caused by a number of factors, whose relative importance is still debated: oceanic climate change, water pollution and contamination, habitat loss, overexploitation at all developmental stages, human-caused transfer of parasites and diseases (Castonguay *et al.*, 1994; Robinet and Feunteun, 2002; Dekker, 2003b; Knights, 2003; Palstra *et al*., 2005; Palstra *et al*., 2006).

The development of active conservation policies has been recognized as a fundamental task for the maintenance of the European eel stock and the sustainability of a huge number of small-scale fisheries depending upon the commercial harvest of eels (Dekker, 2003a). A EU Regulation for the recovery of the European eel stock was proposed in 2005 by the European Commission and is currently under discussion. The main point of the proposed regulation is the establishment of eel management plans at a river basin scale, with the aim to "achieve the objective of a 40% escapement of adult silver eel from each river basin (measured with respect to undisturbed conditions)" (Commission of the European Communities, 2005). One option in the proposal was to impose the closure of the fishery for 15 days each month in a river basin until the relevant Member State has implemented an approved eel management plan aimed at achieving the 40% escapement objective.

The choice of conservation measures to ensure eel survival rests with Member States. Possible conservation measures that could form part of eel management plans include reduction of yellow eel fishing, reduction of silver eel fishing during the autumn to facilitate downstream migration of adult eels, increases in restocking, improvements in water quality, modifications to water management aimed at improving eel migration, reduction of recreational fishing and assisted migration. Social and economic consequences of different choices among proposed measures should be assessed on a local scale. The key element of the proposal is that "a failure to act will result in a disappearance of all eel fishing and aquaculture sectors if the stock decline continues" (Commission of the European Communities, 2005).

As expected, the proposal generated great concern among fishermen. Along the Mediterranean coasts of France, the European eel is the most important fish species from a socio-economic viewpoint (Loste and Dusserre, 1996). Its artisanal fisheries account for about 70% of total revenues

of professional fishermen (Lefebvre *et al.*, 2003). Eel catches from French Mediterranean lagoons reached their peak in the 1970s and started dropping in the mid 1980s. In the early 1990s they reached a minimum and remain at this level today (COGEPOMI, 2006). Local fishermen claimed that the decline is not ascribed to fishing pressure, but is likely to be caused by habitat loss, pollution and climate change. A recent ICES report argued, in contrast, that overfishing might have a major impact also in the Mediterranean Sea (ICES, 2005). Also, fishermen declared that the objective of a 40% escapement of mature eels is already met in southern France, because many coastal streams would not be exploited.

In order to assess the effectiveness of the proposed EU Regulation and its impact on the existing fishing activities, it is necessary to (1) evaluate the present status of local stocks, (2) estimate their abundance under undisturbed conditions, and (3) assess the potential effects of different conservation measures. As alternative management strategies may have different ecological and socio-economic consequences, the effectiveness of the measures to be implemented should be evaluated according to at least two (potentially contrasting) criteria: preservation of a sufficient spawner escapement and maintenance of an acceptable harvest by fishermen.

In this work, an updated version of the demographic model proposed by De Leo and Gatto (1995) is used to assess the consequences of different management policies on the status of the Camargue eel stock. De Leo and Gatto's (1995) model is modified to account for the specific characteristics of the Camargue eel population. The model is then used to estimate the output of silver eels from the lagoons and the harvest by local fishermen corresponding to different mesh sizes of the nets and different levels of fishing effort. Finally, a Pareto analysis is performed to identify those fishing policies that provide the best compromise between the two conflicting objectives of maximizing the escapement of silver eels and maximizing the harvest.

Materials and methods

Study site

The Camargue water system (Rhône River delta, southern France) comprises two major watersheds (Figure 1): the Impériaux lagoon (4 600 ha) and the Vaccarès lagoon (6 400 ha). The lagoons are isolated from the two arms of the Rhône River (Grand Rhône and Petit Rhône) and from the Mediterranean Sea by dykes. The water flow between the lagoons and the sea is regulated by sluice gates at Grau de la Fourcade, near Saintes Maries de La Mer. Water management is mainly aimed at maintaining low water levels inside the lagoons (to prevent the flooding of Saintes Maries de La Mer and ensure the drainage of cultivated land) and low salinity levels (to avoid damage to rice fields).

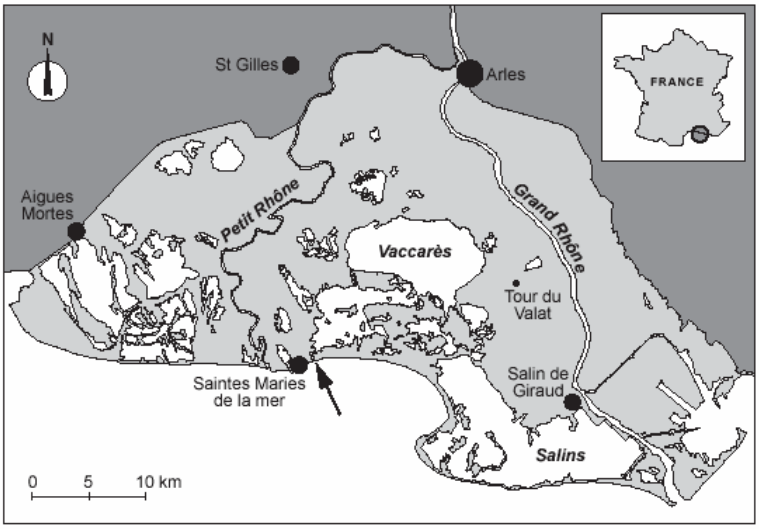


Figure 1. *The Camargue water system. The arrow indicates the position of Fourcade sluice gates.*

Demographic model

De Leo and Gatto (1995) developed a size- and age-structured demographic model for the European eel population of the Comacchio lagoons (Po River delta, northern Italy). The model is based on a multiple classification of individuals by sex, size and age classes. It was successfully used to describe the demography of the local eel stock and to perform a bioeconomic analysis of the silver eel fishery in the same lagoons (De Leo and

Gatto, 2001). The model accounts for the main features of the eel life cycle: strong sexual dimorphism, high plasticity in body growth, size-dependence of differentiation and maturation processes. Body growth was described by a classical von Bertalanffy curve, with different parameters for females and males. In this work, a modified version of De Leo and Gatto's (1995) model was used, suitably adapted to account for the peculiarities of the Camargue eel population and for some features which were not included in the original model (inter-annual variability of glass eel recruitment and density-dependent juvenile survival). To describe body growth, the model presented in chapter 2 for the Camargue eel population, which accounts for delayed sex differentiation by adopting three distinct growth curves for undifferentiated, female and male eels was used. Then, sexual maturation was linked to body length through a sigmoid curve (De Leo and Gatto 1995, adapted to the Camargue in chapter 4).

As the total number of glass eels entering the Camargue water system each year is unknown, it was assumed to be proportional to the catch per unit effort (CPUE) of glass eels observed each year. Experimental catches of glass eels were made periodically between 1993-2003 by Tour du Valat Biological Station (using a fry net with a 0.5 mm mesh and a 20 m leading net) to monitor recruitment variability. Since fluctuations in glass eel abundance are strongly dampened in the yellow eel population, a density-dependent survival rate from the glass eel to the elver stage (small, sexually undifferentiated yellow eels of about 65–75 mm) was assumed. This is in accordance with previous work reporting evidence of density-dependent juvenile survival in the European eel (Vøllestad and Jonsson, 1988; De Leo and Gatto, 1996). Therefore, elver abundance was linked to glass eel CPUE through a Beverton-Holt function. To represent natural mortality the relationship proposed by De Leo and Gatto (1995), which links the survival rate to eel age through a Weibull function, was used. As for fishing mortality, the rate was assumed proportional, through a catchability and a selectivity coefficient, to the fishing effort.

The effectiveness of the fishing device used in Camargue, the so-called capétchade (an eel pot with a 40 m guiding net, called paradière), is linked to eel body length and mesh size through a selectivity curve (Figure 2) obtained with the method proposed by De Leo and Gatto (1995). The average monthly fishing effort during the last decade is reconstructed on the basis of information gathered by Tour du Valat Biological Station and is shown in Figure 3. Mathematical details on the formulation of the model are provided in the Appendix. The model was calibrated by fitting the simulated length structure and biomass of the catch to that observed by Tour du Valat Biological Station during 1993-2003. Data were aggregated into 50 mm length classes and into trimesters. Also, due to the small fraction of silver eels in the catch, maturation categories (yellow/silver) were pooled together, whilst sex categorization (undifferentiated/male/female) was maintained.

The model allow to estimate the present structure of the Camargue eel population and provides us with a tool to predict its fate under different scenarios. To this end, the model was run from the present state of the stock onwards by feeding it with a constant eel input (958 000 elvers per year), corresponding to the median recruitment estimated by the model for 1993-2003. To characterize candidate management policies, two decision variables were considered: the mesh size of fishing devices and the fishing effort. The nets currently used in the Camargue have a 6 mm (knot-to-knot) mesh in derogation to the national law that enforces a 10 mm mesh size for eel fishery in the rest of France. The selectivity of a 6 mm mesh

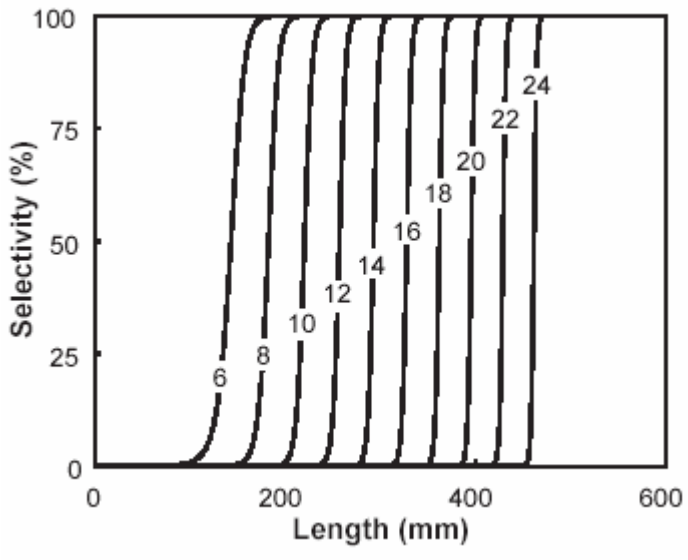


Figure 2. *Selectivity of capétchade nets with different mesh sizes.*

size is zero for eels with total length <100 mm, and becomes 100% for fish longer than 176 mm (Figure 2). As Camargue eels reach this length after about one year's growth in the lagoons (see Figure 5 in chapter 2), 6 mm capétchade nets are definitely very selective, especially if we consider that in most northern European countries fishing devices start being effective only over 300 mm. For these reasons, we analyse the consequence of increasing mesh size up to 24 mm.
As for the fishing effort, six effort limitation rules representing different management alternatives were considered, that is:

(a) to maintain the present fishing effort (baseline scenario);

(b) to impose a complete closure of the fishery (an approximation of undisturbed conditions);

(c) to halve the present fishing effort by imposing a 15-day closure each month (original EU proposal in the absence of approved management plans);

(d) to impose a seasonal summer closure (following fishermen practice to reduce the fishing effort in this season);

(e) to impose a seasonal autumn closure (to facilitate downstream migration of adult eels);

(f) to impose a seasonal winter closure (following fishermen practice to reduce the fishing effort in this season).

The model was run over a 7-year period (i.e., from 2003 until 2010). As the maximum residence time of an eel in the Camargue lagoons is about 6 years (chapter 2) this time horizon is sufficient to ensure that the population structure has approximately reached the regime.

Multi-objective analysis

By running the model with different values of the decision variables, the performances of all management policies were evaluated, resulting from the combination of mesh sizes comprised between 6 and 24 mm with the different effort limitation rules listed above. The performance of each policy is evaluated with respect to two potentially conflicting objectives: to maximize the spawner output from the lagoons and to maximize the harvest by Camargue fishermen. Whilst, with our model, the optimal management of the fishery with respect to the maximization of spawner output alone is straightforward (the spawning output is maximum when the fishing effort is zero), the same does not hold for the maximization of the harvest. In fact, if the stock is exploited beyond its productive limits, because the effort is too high or the mesh size too small, the fishery may become inefficient. The maximum harvest is usually achieved at intermediate exploitation levels (Clark, 1990). Therefore, to identify the best management policies with respect to the socio-economic objective we looked for the optimum mesh size corresponding to the different effort limitation rules considered.

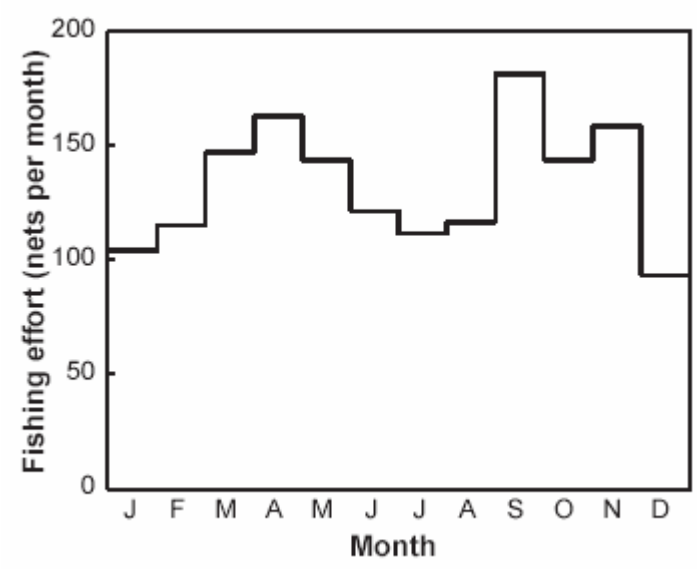


Figure 3. *Average fishing effort in the Camargue lagoons during 1993-2003, by month.*

Then, to highlight possible trade-offs between the two objectives and find out the management policies providing the best compromise between them, a multi-objective analysis was performed. Multi-objective analysis provides a useful framework for the development of realistic management policies in fisheries, when multiple and conflicting objectives are to be considered (Enriquez-Andrade and Vaca-Rodriguez, 2004), and has been used to rationalise the management of a range of fisheries (Sylvia, 1992; Pan *et al.*, 2001; Enriquez-Andrade and Vaca-Rodriguez, 2004). Following classical theory for multi-objective analysis, the Pareto-efficient alternatives were identified, that is those management policies for which it is not possible to modify decision variables to improve one performance indicator (for instance, the abundance of the spawner output) without worsening at the same time the other performance indicator (i.e. catch abundance). Then all the Pareto-dominated policies were excluded, i.e. those management alternatives for which there exists at least another feasible policy that guarantees both a higher harvest and a higher spawner output. The non-dominated policies identify the so-called Pareto boundary. In the following, the term 'optimal' will be used to refer to the best performing policies with respect to a single objective, whilst will be denoted as 'Pareto-efficient' the policies belonging to the Pareto boundaries determined through the multi-objective analysis.

Results

Single-objective analysis

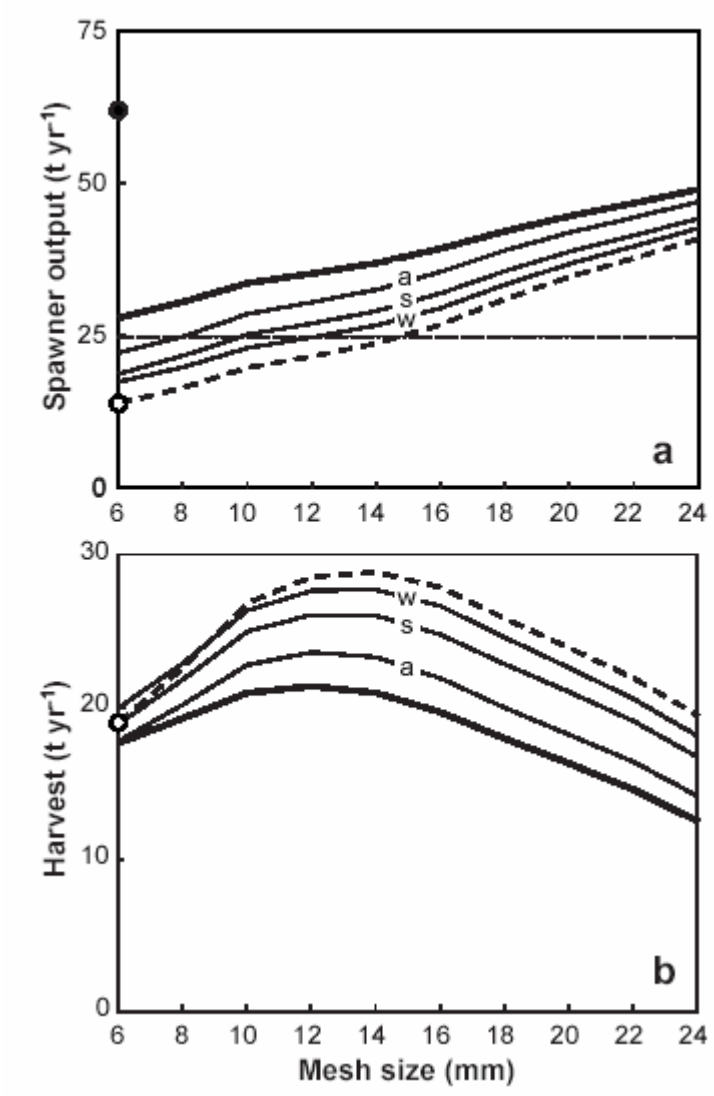


Figure 4 shows the effect of different fishing policies on the local stock with respect to the two objectives, considered one at a time. Under the hypothesis that recruitment remains constant and equal to the median of the last 11 years, and assuming that the closure of every fishing activity provides a reliable proxy for the "undisturbed conditions" referred to by the regulation proposal, a maximum potential spawner output of about 62 t was estimated. However, the annual output of silver eels under the present fishing pressure is estimated to be about 14 t. Under the current management, the spawner output would therefore be only 22% of the potential output, far below the conservation target of the regulation (40% of the potential output), which is about 25 t.

The spawner output (Figure 4a) increases almost linearly with the mesh of the fishing gear, at least in the range of mesh sizes considered. To ensure the achievement of the conservation target under the present fishing effort, the mesh of the nets should be increased from the present value of 6 mm to at least 16 mm. Alternatively, a 50% reduction of the effort would guarantee

Figure 4. *Performances of different fishing policies as determined by different mesh sizes: (a) spawner output and (b) total annual harvest. Dashed lines: present fishing effort; bold lines: halved effort (15-day monthly closure); thin lines: seasonal closures (s: summer, a: autumn, w: winter); filled circle: complete closure; open circle: current fishery. The dotted line indicates the 40% of the spawner output in undisturbed conditions. Recruitment was assumed to be constant and equal to the median of that observed between 1993-2003.*

the required escapement even if the mesh size remained unchanged. Among seasonal effort reduction policies, the most effective is the closure of the fishery in autumn, which preserves silver eels from being captured just before leaving for the ocean.
As for annual catches (Figure 4b), these are estimated to stabilize, given the present fishing effort, mesh size and a constant recruitment, at around 19 t per year. However, an increase of the harvest up to 29 t yr^{-1} (under the same effort) could be achieved by increasing the mesh size to 16 mm. This would indeed shift the fishing pressure from younger, undifferentiated eels shorter than 200 mm to older fishes over 300 mm (Figure 2). Present analysis shows that for all fishing policies considered, the optimal mesh size (with respect to maximizing catches) would be between 12 and 14 mm (Table 1). Within this range, all effort limitation rules would guarantee higher catches compared to present management. Above 14 mm, catches are expected to decrease, but to remain higher than the ones predicted under current management scenarios, for mesh sizes up to 18-24 mm (depending on the effort).

Table I – *Optimal and Pareto-efficient mesh sizes (in mm) corresponding to different effort limitation rules as obtained with the single-objective (maximizing harvest) and the multi-objective (maximizing harvest and spawner output) analyses, respectively. Note that scenario b (complete fishery closure) is Pareto-efficient (and obviously does not depend upon mesh size) and has no interest for the single-objective analysis, as harvest is equal to zero. On the contrary, a 14-mm mesh (although optimal/Pareto-efficient) does not respect the EU conservation target under the baseline scenario.*

Effort limitation rule	**Optimal mesh size (single-objective)**	**Pareto-efficient mesh range (multi-objective)**
a) baseline scenario	14	14–24
b) complete closure	–	–
c) 15-day closure	12	20–24
d) summer closure	12	16–24
e) autumn closure	12	16–24
f) winter closure	14	22–24

Multi-objective analysis

Changing fishing effort with respect to the present level obviously has an opposite effect on spawner output and catch: spawner stock always decreases with increasing fishing effort, whilst catch increases with the fishing effort. Similarly, spawner output and catch react differently to changes of the fishing gear, with the first increasing with mesh size, and the latter being a unimodal function of mesh size. The results of the multi-objective analysis can help decision makers to understand the trade-off between the two objectives. Figure 5 shows the performances of the fishing policies considered above in relation to the two objectives. It is evident that there is a range of Pareto-efficient policies (summarized in Table 1), corresponding to different effort limitation rules and mesh sizes. The current fishery is clearly inefficient, as there are several policies, also outside the Pareto-set, providing both higher catches and a larger adult escapement. Whatever the effort, the minimum mesh necessary to achieve efficiency is always larger or equal than 14 mm (Table 1). This corroborates the belief that the current mesh is far too selective to preserve the reproductive potential of this population. It is worth noting that a simple reduction of the fishing effort, not associated with the development of a specific management

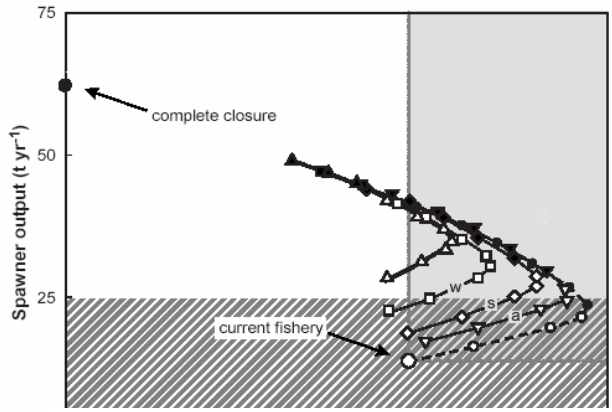


Figure 5. *Pareto analysis with respect to the two management objectives (maximizing spawner output and catches). Each symbol represents a management policy (effort limitation rule plus mesh size). Filled symbols: Pareto-efficient policies (Pareto boundary); open symbols: non-efficient policies; dashed line connecting circles: present fishing effort; bold line connecting upwards triangles: helved effort (15-day monthly closure); thin lines connecting downwards triangles, diamonds and squares: seasonal closures (a: autumn, s: summer, w: winter). Policies within the shaded area dominate the current fishery with respect to both objectives, whilst the hatched area identifies non-feasible policies, namely those not respecting the conservation target.*

plan, would achieve the conservation target, but would be unfavourable to fishermen, whose catches would be reduced with respect to present management.

Transient to regime

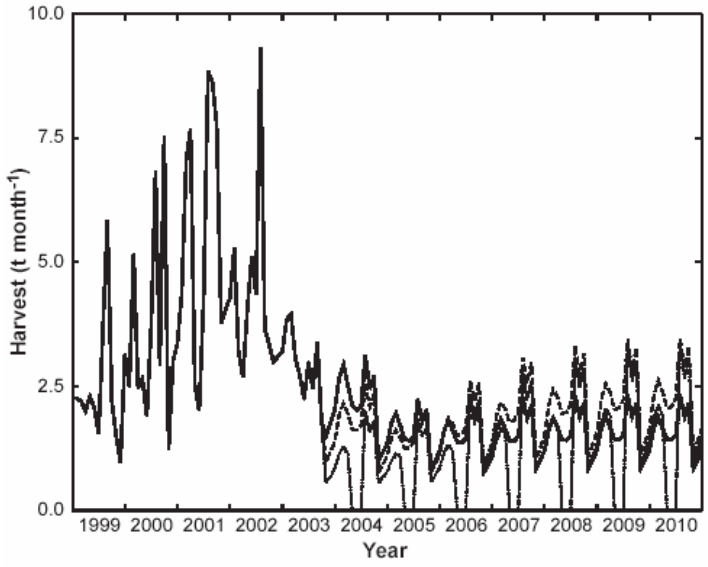
Predictions of harvest and spawner output reported before refer to a regime situation, provided that recruitment remains constant through time. However, increasing the mesh from the current to a larger size would certainly cause a temporary drop of the catch, until juvenile eels (currently the main target of the fishery) have grown up to the minimum size caught by the new mesh size. To assess the impact of this phenomenon on the fishery, the dynamics of the catch during the transient were focused. Figure 6 shows estimated catches between 1999-2003 and those predicted between 2004-2010 under three different policies respectively aimed at: (1) maintaining current exploitation levels (both effort and mesh size), (2) maximizing the catch while respecting the conservation target of the regulation (current effort, 16 mm mesh size), and (3) maximizing the spawner output without decreasing the catch at regime (summer closure, 22 mm mesh size). Monthly catches are characterized by extremely wide oscillations between 1999-2003, due to the combined effect of recruitment variability and seasonal fluctuations of the fishing effort. On the contrary, predicted catches between 2004-2010 show only seasonal fluctuations, as recruitment is supposed to remain constant from year to year. Moreover, annual catches between 1999-2002 were influenced by two exceptional recruitment abundances in 1998 and 2000.

At current exploitation levels, annual catches are expected to decrease from about 32 t in 2003 (and a median catch of 45 t yr^{-1} between 1999-2003) to about 19 t. Under the second scenario, catches are expected to remain below those obtained under current exploitation levels during the first two years (–5.4 and –1.7 t, respectively), but to exceed 20 t yr^{-1} by the third year after changing the mesh size. On the long run, the second management scenario would produce an annual catch of about 29 t. Under the third scenario, catches would undergo a marked decrease during the first three years (–15.2, –8.5 and –5.5 t, respectively), and reach the figure of 19 t yr^{-1} only after roughly seven years, with an overall loss around 39 t before the end of the transient.

Discussion

The results of our analysis support the view that, at present, the Camargue eel fishery is inefficient with respect to the two objectives of maximizing spawner output and catches biomass.

In fact, the use of highly selective fishing devices, such as those employed by Camargue fishermen, decreases productivity by focusing the fishing pressure on younger stages. The goal to guarantee a 40% escapement of adult eels from the Camargue lagoons could be achieved without reducing the productivity of the fishery, provided that a suitable management policy is adopted.



One wonders what the reasons are for this inefficiency, in particular considering that the current mesh size is far below the minimum allowed by French law. A major cause is that the current mesh allows fishermen to catch also small-size fish species, such as the sandsmelt *Atherina boyeri* (30-70 mm length). Although eels are still the most important target of the fishery, the decline of the catch occurred during the

Figure 6. *Estimated (1993-2003) and predicted (2004-2010) monthly harvest during the transient towards different regimes determined by different management scenarios. Solid line: current fishery; dashed line: maximum harvest compatible with EU adult escapement targets; dotted line: maximum adult escapement not affecting current annual catches.*

last two decades might have induced fishermen to decrease the mesh size to compensate the harvest reduction, causing a further increase of the fishing pressure on eels. Moreover, there could be a market demand for catches containing small eels to be resold to aquaculture plants in France and abroad. A comprehensive analysis of the eel market would provide a deeper understanding of fishermen behaviour and possibly influence the range of acceptable management policies. Decision makers should take into account these points when trying to identify feasible ways to increase the efficiency of the local fishery.

Our results suggest that an effort limitation rule based on a 15-day fishery closure each month would have a very positive effect on the spawner output. However, it would have a negative effect on fishermen revenues if no action were taken to impose the use of fishing devices with a larger mesh. Also, a severe monitoring of the fishing effort by local authorities would be necessary to ensure that the effort is not intensified during periods in which fishing is allowed to compensate losses due to closures. A seasonal closure of the fishery is likely to be easier to manage than intermittent monthly closures. In any case, the analysis shows that decision makers can choose among a number of management policies that should achieve the regulation's objectives, whilst considerably increasing the catch.

In present analysis, recruitment is assumed to remain constant, consistently with the available data from the Camargue, which do not suggest any decline since the early 1990s. However, the effectiveness of different management policies will depend critically upon the actual number of elvers settling in the lagoons each year. If recruitment decreases appreciably during the following years, the conservation target of the regulation might become unreachable even if the fishery were completely closed. On the contrary, a substantial increase in recruitment might allow fishermen to meet the target even without changing the current fishing policy, at least if density-dependent effects are limited to juvenile survival and do not have appreciable effects on older stages (as assumed in our model). In this case the results of the Pareto analysis are indeed independent from the recruitment, as all scenarios are equally affected by a change in its magnitude.

Another critical point of the EU's regulation proposal is how to assess the "undisturbed conditions" that set the benchmark for the conservation target. The regulation makes a generic reference to "the absence of human activities affecting the fishing area or the stock". Such a pristine state, however, seems quite impractical to determine. If one refers to the pre-industrial era, he would lack any reference data. ICES (2006) suggests using, whenever possible, historical abundance data from the 1950s to the 1970s (depending on the specific stock) to set a reference point for undisturbed conditions. For sites where no historical data are available, such as the Camargue lagoons, the availability of a demographic model is of fundamental importance to assess the dynamics of local populations in the absence of exploitation with respect to the different level of recruitment. It is important to point out, however, that fishing is not the only source of disturbance (although anthropogenic impacts in the Camargue natural reserve are likely to be relatively small compared to other environments). Hence, fishermen might try to shift the attention on alternative conservation measures, aimed at improving environmental conditions (such as a different management of sluice gates regulating water exchanges with the sea) rather than at rationalizing fishing. It cannot be disregarded, however, that the efficiency of the fishery depends only upon the choice of an appropriate fishing policy.

It should be noted that our results refer to a brackish water system which forms only a part of a wider river basin, that of the Rhone River. The guidelines emerging from this study cannot be simply extended to the management of the whole basin without further investigation. However, correct management of the lagoons would have a positive impact on the spawner output of the whole basin and on local economy. Whilst the ideas analysed in the present work are based on a detailed understanding of eel demography in the Camargue lagoon, the mathematical model here derived can be adapted to simulate eel population dynamics in other coastal lagoons and rivers, provided the necessary data for calibration are available. Also, the multi-objective approach can be easily extended to include a complete bio-economic analysis, integrating demographic knowledge

and socio-economic information (such as market prices and fishing costs). For these reasons, the conceptual framework proposed here can provide a useful tool to reveal existing trade-offs between conservation and production objectives and assess different exploitation policies from contrasting viewpoints.

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Appendix

In this section a concise description of the model structure is provide, and in particular the equations of the sub-models describing juvenile mortality from the glass eel to the elver stage, recruitment of elvers to the lagoons, body growth and sex differentiation, sexual maturation, natural and fishing mortality of yellow and silver eels.

Recruitment

Recruitment to the Camargue lagoons is monitored since 1993 by Tour du Valat Biological Station. The absolute number G of juveniles entering into the lagoons cannot be directly measured in the field, but the observed annual catch per unit effort of glass eels (CPUE) can be used as a recruitment indicator. Observed fluctuations in the adult population are strongly reduced compared to those of juveniles, suggesting density-dependent survival from glass eel to elver. As cannibalism by adult eels on juveniles can be excluded on the basis of the analysis of gastric contents (Crivelli, unpubl. data) and no overcompensation effects have ever been observed in the Camargue population, recruitment at the elver stage E was expressed as a Beverton-Holt function of glass eel CPUE C:

$$E = \frac{\alpha C}{\beta' + C} \qquad \text{with } \beta' = \beta / \kappa_R$$

The calibration of the model (see main text) provided an estimate of α (8.97×10^6nets months) and β' (14.22 eels net^{-1} month^{-1}).

Body growth and sex differentiation

Body growth was described with the model proposed in chapter 2 for the Camargue population, which accounts for sexual dimorphism and sex differentiation by using three distinct growth curves for undifferentiated eels, males and females:

$$L(x) = \begin{cases} L_0 + (L^* - L_0)\dfrac{1-\exp(-k_{\mathrm{U}} x)}{1-\exp(-k_{\mathrm{U}} x^*)} & \text{for } x \le x^* \quad \text{(undiff.)} \\ L_{\infty F} - (L_{\infty \mathrm{F}} - L^*)\exp\left(-k_{\mathrm{F}}(x - x^*)\right) & \text{for } x > x^* \quad \text{(females)} \\ L_{\infty M} - (L_{\infty \mathrm{M}} - L^*)\exp\left(-k_{\mathrm{M}}(x - x^*)\right) & \text{for } x > x^* \quad \text{(males)} \end{cases}$$

where L_0 is the length at metamorphosis to elver, L^* and x^* are length and age at sexual differentiaton, k_{U}, k_{F}, and k_{M} are the Brody growth constants for undifferentiated eels, females and males, and $L_{\infty \mathrm{F}}$ and $L_{\infty \mathrm{M}}$ are the asymptotic mean lengths of females and males, respectively (see chapter 2 for further details and parameter estimates).

Sexual maturation

Following De Leo and Gatto (1995), we link sexual maturation to body length by assuming that the silvering rate is a sigmoid function of eel length L:

$$\gamma(L) = \frac{\gamma_{\max}}{1 + \exp\left[(\lambda - L)/\eta\right]}$$

where $\gamma_{\max}$ is the maximum silvering rate, λ is the average length at maturation and η is a shape parameter. Here we use the curves calibrated in chapter 4 for the Camargue eel population. These retain the formula proposed by De Leo and Gatto (1995), but with different parameter sets accounting for the differences between the two sexes and for monthly variations of silvering rates (see Bevacqua et al. 2006 for further details and parameter estimates).

Natural mortality

Under the hypothesis that density dependence acts only in the early life stages, and that yellow and silver eel survivorship depends only upon age, we use the model proposed by De Leo and Gatto (1995), describing adult annual survivorship σ as function of age x:

$$\sigma(x) = \exp\left[\left(\frac{x}{b}\right)^c - \left(\frac{x+1}{b}\right)^c\right]$$

where b and c are scale and shape parameters, respectively, of a Weibull age-at-death distribution. Whilst their demographic model had an annual step, ours has a step of 1 month. Assuming that natural mortality acts only during spring and summer (De Leo and Gatto, 1995), we spread its effect along a 6-month span, from April to September.

Fishing mortality

We assume the fishing mortality rate to be proportional, through a catchability coefficient q and a selectivity coefficient φ (depending upon eel length L) to the fishing effort E, measured as the number of nets multiplied by the fishing time:

$$F(L,t) = q\,E(t)\,\varphi(L)$$

Selectivity φ is linked to body length through the sigmoid model proposed by De Leo and Gatto (1995):

$$\varphi(L) = \frac{1}{1+\exp\left[(\overline{A} - \rho^{-1} a L^{b-1})/\zeta\right]}$$

where $\overline{A}$ is the average section retained by the mesh of the net (29.07 mm^2 for the fishing device used by Camargue fishermen, the so-called capétchade), ρ is the relative density of an eel (assumed = 1g/cm^3), a and b are the parameters of the length-weight relationship (estimates for the Camargue population are provided in chapter 2) and ζ is a shape parameter (= 3.5 mm^2 for the capétchade). The calibration of the model (see main text) provided an estimate of q (6.13×10^{-4} $nets^{-1}$ $month^{-2}$).

8

Assessing Management Plans for the recovery of the European eel

Chapter in press on *Fisheries*: D. Bevacqua, P.Melià, A.J. Crivelli, M. Gatto 2006 , G.A. De Leo. Assessing Management Plans for the recovery of the European eel (*Anguilla anguilla*): a need for multi-objective analyses.

Abstract

The European eel (*Anguilla anguilla*) stock has been declining since the early '70s and is currently considered to be outside safe biological limits. In June 2007, the Council of the European Union approved a Regulation establishing measures for the recovery of the European eel stock. Each Member State is required to develop Eel Management Plans (EMPs) in order to achieve an escapement of at least 40% of the potential spawner biomass (with respect to undisturbed conditions) from each river basin. A reliable estimate of the potential spawner output of local stocks is crucial for the development of EMPs. Given the complexity of the eel life cycle, the use of mathematical models explicitly accounting for specific demographic traits and incorporating fundamental socio-economic information is necessary to thoroughly assess the effectiveness of alternative management strategies. Here, using a case study approach, how mathematical modeling, based on sound field data, can contribute to the assessment of potential spawning stock and to the development of sound management plans is shown. Then, it is discussed how a multi-objective approach can be used to examine trade-offs between conservation and fishery goals and to help decision-makers identifying effective management policies.

Introduction

The European eel (*Anguilla anguilla*) is found and exploited in most European water bodies and a number of sites in northern Africa (Dekker, 2000a). More than 25,000 people obtain a substantial income from eel fisheries (Moriarty and Dekker, 1997). In recent decades, however, eel recruitment and eel catches have dramatically declined throughout the range of this species, which is presently considered outside safe biological limits (ICES 2005). The causes of its widespread decline are still poorly understood, but most likely include changes in oceanic circulation (Castonguay et al. 1994; Knights, 2003; Friedland et al., 2007), impact of new parasites (Lefebvre et al., 2002), habitat disruption, chemical contamination and overfishing at different developmental stages (Dekker, 2000b; Feunteun, 2002; ICES, 2005).

Devising suitable strategies for the recovery of the stock is made particularly difficult by the unique and complex life cycle of the European eel. *A. anguilla* is a catadromous amphihaline fish, whose biological cycle is fairly well-known in the continental phase, but whose oceanic phase remains surrounded by much mystery. Spawning areas are believed to occur in the Sargasso Sea. Larvae (leptocephali) reach the North African and European continental shelf where they develop into glass eels (small, unpigmented eels) and then metamorphose to elvers (small, pigmented eels). Although eel catadromy may be facultative (Tsukamoto et al., 1998; Daverat et al., 2006), a significant proportion of glass eels colonize brackish and freshwater environments. There they gradually become yellow eels (larger, still immature, pigmented eels) and grow for 2–20 years until they attain the critical size triggering sexual maturation and metamorphosis into the silver stage. Silver eels begin a 5,000 km journey that brings them back to the spawning grounds, where they eventually mate and die.

Although decline of eel catches began in the late 1960s and recruitment collapse became evident in the '80s (ICES, 2005), the first comprehensive restoration plans are only now being developed (Dekker, in press). Dekker (in press) provides an exhaustive description of the political and scientific process that contributed to developing these conservation plans. Briefly summarized, in 2003, the European Commission issued a "Proposal for a Community Action Plan for the Management of European Eel" (Commission of the European Communities 2003), further developed in a proposal for a "Council Regulation Establishing Measures for the Recovery of the Stock of European Eel" (Commission of the European Communities 2005). A revised version of the text was unanimously approved by the European Parliament and finally endorsed by the Council in June 2007. Its main target is to permit "the escapement to the sea of at least 40% of the biomass of adult eel relative to the best estimate of the potential escapement from the river basin in the absence of human activities affecting the fishing area or the stock" (Commission of the European

Communities 2005). Member States are required to provide an Eel Management Plan (EMP) for each river basin, with the aim of achieving this target via locally implemented measures. Those Member States that do not submit an EMP to the Commission for approval by 31 December 2008 "shall either reduce the fishing effort by at least 50% relative to the average effort deployed from 2004 to 2006 or reduce the fishing effort to ensure a reduction of eel catches by at least 50% relative to the average catch from 2004 to 2006" (Commission of the European Communities 2005). The Regulation's target escapement of at least 40% of the potential adult eel biomass is not clearly defined. The Regulation refers to the "absence of human activities affecting the fishing area or the stock", a pristine state which may be unrealistically difficult to determine due to lack of historical data. ICES (2005) recommends, when possible, the use of existing and scientifically reviewed historical data on eel abundance and glass eel recruitment to derive a reference point. However, historical data are often missing and, when present, they usually come from sites where eel exploitation has a long history. The longest European datasets on eel catches have been collected in Lake IJsselmeer (the Netherlands), Lough Neagh (northern Ireland), Baltic Sea and Comacchio lagoons (northern Italy) (Moriarty and Dekker, 1997). These local eel populations have been strongly affected by fishing activities in the last century and even before (Moriarty and Dekker, 1997). Therefore, estimating the potential spawning stock in the absence of human activities is a very hard task even for these sites, as human pressure began far before the collection of data. Long-term data from unexploited systems are often missing. In any case, inferring the productive potential of exploited areas from data collected in unexploited areas (though with similar characteristics) could cause serious underestimates, since fisheries activities are likely to have developed where stock densities were higher, while historically unexploited areas were probably the less productive ones (Dekker, 2003). Where the fishery targets only silver eels and almost all individuals are caught at the outlet of the lagoons (like, for instance, at Comacchio), the potential spawning output can be easily estimated from historical silver eel catches. For the fisheries where yellow eels are also caught (like, for instance, at Lake IJsselmeer and Lough Neagh), or where the fraction of silver eels caught is not reliably known (like, for instance, in the Baltic sea), the potential spawning stock cannot be easily assessed. In cases where few data are available, the development of suitable mathematical models is often the only way to examine the consequences of different management strategies (De Leo et al., in press).

Here the process for developing a conceptual framework to assess different management policies via mathematical modeling supporting the decision process is illustrated. The starting point is a review of existing efforts to estimate the potential spawner production, which is the key reference point of an EMP. According to ICES (2005) guidelines, only models based on field data from well-studied local eel populations are considered. Then, it is shown how demographic models have been used to assess the consequences of different management policies on the viability of eel populations, and how socio-economic information has been integrated into demographic models to evaluate the productivity and profitability of the fishery under different management scenarios. Finally, the potential contribution of multi-objective analysis supporting the identification of optimal management policies is discussed, particularly when decision-makers are faced with contrasting objectives (typically, eel conservation and profitability of the fishery).

Bioeconomic assessment of eel populations

A reliable estimate of the potential (pristine) spawner output of local stocks is the starting point for the development of EMPs in accordance to the Regulation. However, conservation measures aimed at achieving the conservation target set by the Regulation also affect, through possible limitations of fishing effort, the profitability of the fishery and, consequently, the social acceptability of a management plan. Therefore, the effectiveness of proposed EMPs must be evaluated not only from a conservation viewpoint, but also an economic one. To promote consensus among fishermen, decision-makers should look for optimal fishing policies that achieve compromise between maximizing the viability of the stock and maximizing the profitability of the fishery. To this aim, it

is crucial to have suitable tools to (1) estimate spawner output under undisturbed conditions, (2) predict the impact of different management policies on spawner output and (3) estimate their influence on revenues.

Estimating potential spawner outputs

Estimating potential spawner output (i.e., the biomass of mature silver eels that, in the absence of any fishing activity, would abandon a given site to begin their oceanic migration) provides a reference point to assess the impact of the fishery on the reproductive success of eel populations. Historically, most studies on eel population dynamics have been conducted in locations where commercial fisheries were present, and fishing activities themselves provided the data used to develop models. These were usually aimed at assessing potential yields rather than spawner outputs. However, were the fishery targets only silver eels, estimating maximum yield also provides an assessment of potential spawner output. In contrast, where yellow eels are also exploited, estimating potential spawner output requires the development of demographic models explicitly accounting for fishing mortality at all developmental stages. In the following, the main studies that, in the last decades, provided reliable estimates of silver eel productions are briefly reviewed. Estimates are all expressed as a silver eel biomass per hectare, in order to favor the comparison among results of different studies.

A first attempt to assess silver eel escapement trough mathematical modeling was made by Rossi (1979) for the Comacchio lagoons and by Rossi and Cannas (1984) for the Porto Pino lagoons (southwestern Sardinia) through a simple life-table analysis. They provided an estimate of silver eel production before the recruitment drop of the ‘80s, equal to 20 and 19 kg/ha at Comacchio and Porto Pino, respectively. Rossi (1979) reported also that silver eel production at Comacchio was much bigger in the period between the two world wars than in the ‘70s, thanks to a water system configuration favoring juvenile recruitment.

Vøllestad and Jonsson (1988) used a long-term data series from the Imsa River (SW Norway) to develop an input-output model predicting total biomass and age distribution of silver eels from annual recruitment data. They estimated an overall yield of 3.51 kg/ha for the period 1975-1979. The mortality rate (assumed to be constant with age) was inversely correlated with the number of recruiting elvers, thus giving the first evidence for density dependence in eel mortality. Vøllestad and Jonsson’s (1988) approach provides a powerful tool to predict yields at sites where elver recruitment and silver eel migration can be monitored and where the impact of commercial harvest is also reliably known. However, recruitment and silver eel migration cannot be readily measured in most eel fishing areas.

De Leo and Gatto (1995) developed the first model for the European eel including a multiple classification of individuals by age and size. The model was based on data from the Valli di Comacchio lagoons (Northern Italy) and accounted for inter-individual life history variability by means of a stochastic formulation. This represented a major improvement, as accounting for variability in the life cycle provides fundamental information about the uncertainty associated to harvest and the risk of stock decline. De Leo and Gatto (1995) estimated a silver yield of 6.15 kg/ha at Comacchio for the period 1989-1990. This figure is almost one third of that estimated for the same lagoons by Rossi (1979) 15 years before, likely reflecting a recruitment drop in the ‘80s. Later on, De Leo and Gatto (1996) applied their model to three data sets from the same sites, though from different periods (mid ‘70s vs. late ‘80s) and revealed the dependence of prereproductive survival and mean body size at silvering upon eel density.

Dekker (2000), through a length-structured cohort analysis estimated, a potential silver eel production of about 4.4 kg/ha for Lake IJsselmeer. By using data from commercial catches, he calculated length-specific rates of total mortality and, under the assumption of constant natural mortality and silvering and escapement rates, he estimated fishing mortality. He argued that ceasing yellow eel exploitation in Lake IJsselmeer would lead to a many-fold increase in the adult eel

population. He concluded that current, uncontrolled exploitation levels in the major eel fisheries might have negative consequences on the entire stock of European eel spawners.
Feunteun et al. (2000) used electrofishing and mark-recapture techniques in the Fremur catchment (Northern France) to identify the relationship between silver eels dynamics, standing stock structure and environmental factors such as flow, atmospheric pressure, rainfall, and lunar phase at a river basin scale. According to their study, silver eels represented almost 10% of the sedentary population in the catchment. However, only a small fraction of the silver eels (around 20%) effectively contributed to spawner output in the following migration period. In the Fremur catchment, where both natural and fishing mortality are low, the authors estimated an average spawner production of 1.3 kg/ha.
Rosell et al. (2005) examined data from tagging experiments and commercial sources at Lough Neagh (Northern Ireland) by means of cross spectral analysis to investigate the relationship between explanatory variables (natural glass eel input, additional purchased glass eel input, mean water flow and temperature) and response variables (yellow and silver eel yield). They found a significant dependence between yellow and silver eel yield on natural glass eel input 8 and 18 years before, probably reflecting the different life span of males and females. Their study revealed, despite the presence of commercial fisheries, a silver eel escapement of 2.5-3.5 kg/ha. This quite high estimate (considering Lough Neagh latitude and the fact that the local fishery exploits both yellow and silver eel) led the authors to consider the current management to be sustainable. Yet, the authors did not provide any assessment of the potential spawner production in undisturbed conditions.
In chapter 8 the approach proposed by De Leo and Gatto (1995) was extended to account for inter-annual variability of glass eel recruitment and density-dependent juvenile survival while retaining the multiple classification of individuals by age and size and stochasticity in individual growth rates. In chapter 8 peculiarities of the eel life cycle such as delayed sex differentiation and sexual dimorphism in body growth were accounted for through the model proposed in chapter 2 and described monthly variations in maturation rates with the model proposed in chapter 4. By applying the model to a long-term data series from the Camargue lagoons (S France), in chapter 8 current spawner escapement were estimated to be far below the potential escapement (5.6 kg/ha) achievable in the absence of fishing at present recruitment levels.
Potential spawner escapement varies significantly among different sites, ranging between 1 and 20 kg/ha. Eel production is influenced by a number of environmental factors, such as temperature, salinity and food availability, as well as by juvenile recruitment. Production is generally higher in brackish water bodies and at higher temperatures (up to 20 kg/ha before the recruitment drop of the last decades, around 6 kg/ha at present recruitment levels). In freshwater environments, lakes are usually more productive (about 4 kg/ha) than rivers (around 2–3 kg/ha). At sites where no historical data are available, gathering data on environmental parameters and present levels of juvenile recruitment is crucial to obtain preliminary estimates of potential production (through comparison with sites with similar conditions) and to provide the basis for the development of sound demographic models.

Assessing the consequences of different management scenarios on spawner output

Conservation of the European eel stock requires action in a number of fields, including structural measures to make rivers passable and to improve habitats, control of predators and parasites, improvement of water quality, and glass eel restocking. However, sustainable management of the fishery will certainly remain the central element of most EMPs due to their immediate consequences on spawner escapement. For this reason, our analysis focuses on management measures oriented to the regulation of the fishing effort. While it is easy to quantify the reduction in spawning output biomass due to silver eel fisheries, the consequences of yellow eel fishing on the spawning stock are not always easy to quantify. The impact of exploiting yellow eel was usually underestimated and often neglected, assuming strong compensatory density-dependent effects

(ICES 2005). Recent works on different eel species, however, show that overfishing of yellow eels can dramatically impair spawner escapement.
Dekker (2000) established, through a length-structured cohort analysis, the historical impact of the well-documented fisheries of Lake IJsselmeer on both silver eel escapement and commercial catches. He concluded that yellow eel overexploitation in Lake IJsselmeer reduced female escapement to 0.14% and male escapement to 1.43% of pristine levels, and that the fishing pressure on yellow eels precluded them from attaining a sufficient size to undergo sexual maturation and metamorphose into silver eels. Consequently, most of the catch was made up of yellow eels and spawner output was virtually absent.
Hoyle and Jellyman (2002) assessed the consequences of different management policies on yield and spawner biomass per recruit of two sympatric eel species in New Zealand, the longfin eel *Anguilla dieffenbachii* and the shortfin eel *Anguilla australis*. The local fishery targets both species, which are characterized by life cycles of different duration (*A. dieffenbachii* spends longer in freshwater and attains bigger sizes than *A. australis*). They estimated that current exploitation rates have reduced the spawning per recruit of *A. dieffenbachii* and *A. australis* females by about 95% and 40%, respectively. Then, they explored the effects of different decision variables, such as minimum legal weights and exploitation rates, on the spawning and fishing yield per recruit of both species concluding that the two species require different management policies due to their different life cycles. Given the difficulty of developing different management policies for species that are hardly distinguished by fishermen, the authors suggested establishment of no-take reserves to protect New Zealand eels.
Doole (2005) applied a multiple-cohort bioeconomic model to the longfin eel fishery of the Waikato River (New Zealand) to investigate its optimal management and ascertain the appropriateness of current regulatory policies. He argued that using historical harvest data to calculate presently sustainable catches is inappropriate in light of the recent recruitment collapse. The author explored the consequences of management policies based on individual transferable quotas and the enforcement of protected areas on the status of the stock and the harvest. He argued that area closure and the spatial definition of harvest rights are attractive management options due to the territoriality of longfin eels, and that limiting the exploitation of older cohorts would increase yields. However, this last finding critically depends upon the specific spawner-recruitment relationship adopted. In fact, the author assumed that the number of juvenile eels entering the river in a given year and sustaining the local population depends on the abundance of local spawning stock two years before. Unfortunately, this assumption is not valid for local European eel populations, so that neither Dole's (2005) method nor his conclusions can be given for granted in the management of European eel fisheries.
In chapter 7 the consequences of different management policies for the Camargue eel fishery were evaluated. Both silver eel escapement and harvest by local fishermen corresponding to different mesh sizes of the nets and different levels of fishing effort were estimated. By using realistic recruitment estimates, effective harvest and spawning output in absolute numbers and not only in terms of values per recruit could be assessed.
All these studies clearly show that eels are particularly susceptible to overexploitation due to the singularity of their life cycle. In particular, downstream migration of silver eels facilitates their catch at particular places (e.g., bottlenecks). Also, their long lifespan is responsible for accumulation of high mortality rates as demonstrated by the major impact of fisheries on eel females and, in general, on long-living species (Dekker, 2000; Jackson et al., 2001; Hoyle and Jellyman, 2002). In addition, the absence of apparent stock-recruitment relationships at a local scale impairs the acceptance of sustainable management policies by fishermen communities.

Calculating eel fishery profits

In addition to theoretical studies on the economics of fisheries (since the seminal works by Gordon 1954; Schaefer 1954), there are several studies regarding the exploitation of specific fish stocks in

the literature (see, e.g., Myers et al., 1997; Orensanz et al., 1998; Kulmala et al., 2007). With regard to eels, however, examples of thorough bioeconomic analyses predicting the profitability of a fishery under different management scenarios are rare. While studies from other fisheries can provide useful information on the general guidelines to be followed to pursue sustainability in eel fisheries, the eel life cycle is so distinctive that general guidelines can be hardly applied to the development of specific policies for the management of eel stock. Here the main results of the few bioeconomic analyses specifically focused on eel fisheries are summarized.

Gatto et al. (1982) assessed the profitability of different management strategies for the eel fishery of the Comacchio lagoons. The effort was traditionally exerted only on silver eels, which are fished by special devices called *lavorieri* intercepting the entire flux of migrating fish. Gatto et al. (1982) concluded that extending the fishery to also target a fraction of yellow eels would allow fishermen to improve their gross economic return by about 10%. Almost 20 years later, De Leo and Gatto (2001) performed a stochastic bioeconomic analysis of eel fishing in the same lagoons aimed at optimizing the economic return from the Comacchio eel fishery. The authors explored the effect of extending the fishery to yellow eels and tested whether the decline of natural recruitment could be effectively supplemented by elver restocking. The authors analyzed different management policies in terms of fishing effort on yellow eels (defined as number of nets placed), net selectivity (mesh size) and restocking density. Net selectivity was expressed as a function of the fish size and the mesh size of the net. They explicitly considered harvesting costs, different selling prices for yellow and silver eels, and different discount rates to assess the optimal management policy for maximizing the average net economic benefit. They found that the highest profits could be obtained by fishing silver eels by *lavorieri* and fishing a fraction of yellow eels with 160 nets of 21-mm mesh. A stochastic approach allowed the authors to derive not only a point estimate of the economic benefit associated with the different management alternatives considered, but also the uncertainty of their estimates.

A call for multi-objectives analyses

Fisheries managers must often cope with multiple, and possibly conflicting, objectives (Charles, 1989; Hilborn, 2007) such as maximizing catches, minimizing costs, minimizing bycatch, and maximizing spawning output per recruit. Considering several objectives at once provides a framework for the decision process, promotes a more appropriate role in the process for the analyst, and usually identifies a wider range of alternatives than those obtained by a single-objective analysis (Cohon, 1978).

Multi-objective techniques represent an improvement with respect to traditional, single-objective approaches to planning problems (e.g., cost-benefit analysis), because they allow decision-makers to address a number of objectives that cannot be reduced to a single dimension such as revenue (Meier and Munasinghe, 1994). Multi-objective analysis can indeed help decision-makers identify and highlight possible trade-offs among conflicting viewpoints. However, while it is widely agreed that the use of a multi-objective approach is highly desirable (Vaca-Rodriguez and Enríquez-Andrade, 2006), substantial difficulties are encountered in identifying the ultimate goals of the different stakeholders and in providing a framework for the comparison between objectives. For these reasons, the use of multi-objective methods in fisheries research has been scarce over the last decades, although pioneering studies have been conducted since the early 1980s (e.g., Bishop et al. 1981; Charles, 1989) and a few recent examples can also be found in the literature (e.g., Sylvia and Enríquez-Andrade, 1994; Pan et al., 2001; Melià and Gatto, 2005). Nevertheless, most efforts remain directed to the development of analytical tools to evaluate the impact of management strategies in a single-objective perspective.

The key concept of multiple-objective analysis is Pareto efficiency. An alternative (for instance, a fishing policy) is called Pareto-efficient when it is not possible to modify decision variables to improve a performance indicator (e.g., the viability of a fish stock) without worsening another performance indicator (e.g., the revenue of fishermen exploiting the stock). All other alternatives,

for which there exists at least one feasible solution guaranteeing both higher viability and higher revenues, are called Pareto-dominated. The set of non-dominated policies is called Pareto boundary (or Pareto set) and represents the suite of alternatives among which the decision-maker can reasonably choose. The Pareto optimal set and associated trade-offs supply a useful reference and important information to decision-makers. Eventually, for any given problem, only one solution has to be selected by the decision-makers. This solution is usually not the result of a formal maximization problem, but rather of a subjective evaluation of the relative importance of the objectives by the decision-makers. Hence it must be clear that the multi-objective approach concentrates on providing information to the decision-makers regarding the range of effective choices and the consequences of different options rather than suggesting a single optimal solution (Gatto and De Leo, 2000).
An example of applying this approach to eel management is provided in chapter 7. There a Pareto analysis is performed to identify the fishing policies providing the best compromise between two partially conflicting objectives in the management of the eel fishery of the Camargue lagoons: maximizing the escapement of silver eels towards the ocean and maximizing the harvest by commercial fishermen. Their results support the view that, at present, the Camargue eel fishery is inefficient with respect to the two objectives of maximizing spawner output and catch biomass. The main reason of such inefficiency is the use of highly selective fishing devices, which focus the fishing pressure on younger stages. In order to maximize the spawning output, the fishery would need to be closed, while yield maximization would require adopting a larger mesh size than currently used.

Yields or profits?

Many local European eel fisheries are likely as inefficiently managed as the Camargue fishery. However, assuming the main goal of fishermen is the maximization of fishing yield is not always realistic. Indeed, informed fishermen are usually more interested in maximizing the revenues deriving from selling their eel catches rather than maximizing yields (Hilborn, 2007). Estimating the profitability of a fishery requires socio-economic information on costs and revenues, which is often difficult to collect, especially for small-scale fisheries. Selling prices vary widely depending on a number of factors, such as seasonal fluctuations in demand, provenance of the catch, and size of the fish. In most fish markets, bigger individuals are preferred to smaller ones (see, e.g, De Leo and Gatto, 2001). In these cases, the fishing strategies adopted by fishermen cannot be correctly interpreted without explicitly incorporating the size price structure into the analysis. In the Camargue, for instance, the main cause of inefficiency of the fishery is the overexploitation of young yellow eels (see chapter 7), a practice that affects the size composition of the catch and, if the eel price per mass unit is related to the fish size or the maturation stage, can also affect profits. If one applied De Leo and Gatto (2001) price structure to the analysis of the Camargue fishery, the inefficiency of current exploitation practices would become even more evident. In recent years, however, local market demand has shifted towards a marked preference for small-sized eels required by aquaculture. Therefore, the reduction of the overall harvestable catch caused by the use of a small mesh size might be compensated by the extra profit generated by selling the lucrative small eels to the aquaculture market. Despite the difficulty of gathering the necessary information, including fishing costs and revenues in the quantification of fishermen's objectives is of critical importance and can lead to very different management scenarios from those obtained by aiming to maximize yields. This approach is even more compelling when eels are exploited in a multi-species fishery where other species may also drive or influence the fishing strategy.

Final considerations

The collapse of the European eel stock and glass eel recruitment requires immediate action to halt their decline. Although habitat considerations such as pollution and dams and hydropower stations certainly contribute to the decline, there is little doubt that, given the present level of recruitment,

reducing fishing mortality is the most practical and effective short-term strategy to increase the spawning stock (ICES, 2005). For some fisheries this might simply require the reduction of the catch and consequently the profit – which, understandably, is strongly opposed by fishermen. Yet, recent analyses show that cases exist where the conservation target can be achieved without reductions in harvest (chapter 7). Given the complexity of the eel life cycle and the duration of its continental life span, the only way to assess the efficacy of an EMP at the local level is to make use of demographic models of eel dynamics that allow the investigation of the effects of a large number of fishing alternatives (in terms of fishing effort, fishing gears and length of the fishing season). The results can be surprising, as both spawning stock and catches can be substantially improved by using a suitable combination of fishing effort and mesh size, as demonstrated in chapter 7.

As the European eel is a panmictic species, sustainable management strategies must have a both a local and global scope. All bioeconomic analyses conducted on local eel populations have disregarded the existence of a global stock-recruitment relationship, considering spawner output as unrelated to recruitment. To date, the only attempts to assess the whole European eel stock and describe its dynamics have by Dekker (2000c) and Åström and Dekker (2007). Although these studies were chiefly focused on eel conservation rather than with the sustainability of the fishery from the fisherman viewpoint, they represent a useful starting point for a comprehensive bioeconomic analysis of the European eel stock and its fishery.

Another often neglected aspect in the design of eel recovery plans is the inclusion of the economic component in fishery management. It is well known, in fact, that fishery dynamics are generally driven by economic forces occurring at the market level that try to match supply and demand (Pinnegar et al. 2006). A change in market price reflecting the consumer's willingness-to-pay to purchase eels at a given level of production can strongly affect fishermen's profits and consequently influence the set of optimal policies. For instance, in the late 1990s, the increasing Asian demand for glass eels on European and North American markets pushed selling prices to exceptionally high prices (up to 4500 €/kg; Tesch 2003). In the following years, Japanese demand for glass eels was mostly satisfied on Asian markets, and glass eel prices in Europe began to decline. Market price fluctuations remain driven by the balance between Asian and local demand which prizes small size eels for aquaculture (Allen et al. 2006). Given this global consideration, the European eel was included in Appendix II of the Convention on International Trade in Endangered Species (CITES) in June 2007. This listing will likely have consequences on the international eel trade that will be important in shaping market scenarios and in producing cascading impacts on local fisheries. Moreover, after years of almost complete absence of regulation, EU Member States are now required by the end of 2008 to implement EMPs that will certainly affect thousands of small artisan fisheries scattered all around Europe. An effective enforcement of the EU Regulation could is difficult to achieve in such a fragmented situation, as free-riding incentives are always present.

Nevertheless, conflicts that are likely to arise between fishermen and policy makers as a result of the implementation of EMPs can be reduced and enforcement enhanced if the interests of fishermen are explicitly accounted for in the definition of the recovery plans. This implies that a detailed analysis of fishermen's preferences should be carried out. This task is far from trivial, as fishermen operating in small-scale fisheries affected by unpredictable environmental conditions do not always aim to maximize profits, but rather to minimize the variability of annual revenues (Chaboud 1995). Curiously enough, a similar attitude has been observed in small-scale African farmers who preferred to reject technological innovations when the potential increase in yield was associated with an increase in yield variance (Brossier, 1989). In these cases, the use of stochastic models, explicitly accounting for the uncertainty in predictions, may allow decision-makers to formulate risk-averse management policies that are more likely to be supported by fishermen.

Finally, when developing management plans it should be remembered that small-scale fishing is not just a source of income, but is often perceived also as a valuable "way of life" (Apostole et al., 1985). Factors such as sense of independence (i.e., being one's own boss), lack of options, socialization processes, cultural traditions, etc. can indeed play a central role in defining

fishermen's responses to regulations. Multi-objective methods can provide a way to explicitly account for several contrasting objectives which cannot be reduced or evaluated to just monetary terms. Last but not least, multi-objective analysis also offers the further advantage of identifying a whole set of Pareto-efficient policies rather than just a single optimal policy simply expressed in economic terms. This approach provides decision-makers with more opportunities to manage potential conflict among contrasting stakeholders while applying a rigorous and quantitative assessment of the conservation effectiveness of different fishing policies and conservation plans.

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9
Conclusions

The study of eel population dynamics is more than thirty years old. Significant progresses have been done since the first attempts of the 1970's to describe eel demography by mathematical modelling (Sparre, 1979; Gatto and Rossi, 1979) and when this work of thesis started the continental phase of the eel biological cycle could be considered fairly well-known (De Leo et al., 2003). However some key factors, responsible for regulating continental phase of eel life cycle (such as, for instance, the role of body size as a trigger for sexual differentiation and maturation, or the dependence of survival upon eel size) still missed assessment of quantitative relationships. Moreover, comparisons among vital parameters in different eel populations were often impaired by the use of different models or calibration techniques by different authors. In this work of thesis I tried to overcome these gaps and I analyzed vital features of eel life cycle providing models that, after proper calibration, could suit to different eel populations.

Particularly, in chapter three I applied the same body growth model and the same parameter calibration technique to three eel populations characterized by different environmental and demographic conditions. This exercise permitted to highlight invariance of sexual differentiation size in eel populations having different body growth rates. Similarly, in chapter four I analyzed the probability of sexual maturation, in three different populations, and its relationship to individuals' sex and body size. In this case my findings provided analytical support to the hypothesis that males and females have developed different maturation strategies. In fact males attain sexual maturation at a smaller and relatively fixed size in order to minimize the growing phase and consequently the probability to die before spawning. Differently, females mature at higher and more variable size in order to find an optimum compromise between shortening the growing period and attaining larger body sizes to increase fertility.

Although scientific literature provides many studies on particular aspects of European eel life cycle, just a few works (Vøllestad and Johnson, 1988; De Leo and Gatto, 1995; Dekker, 2000; Lambert and Rochard, 2007) considered them all and described the entire dynamics of an eel cohort, from juvenile recruitment to adult migration toward spawning areas. These works provided deep insights in eel dynamics but they still could be improved. Most of them neglect inter-individual variability in body growth patterns [all with the exception of De Leo and Gatto (1995)]; others analyzed virtual populations and their goodness was not tested on real data (Lambert and Rochard, 2007), others disregarded interannual variability in juvenile recruitment (De Leo and Gatto, 1995) or in fishing effort (Vøllestad and Johnson, 1988) and others considered size invariant mortality and sexual maturation rates (Dekker, 2000). In addition, all the previous models used an annual time step that impaired to simulate the seasonal fluctuations, in stock abundance and catch, depending on eel particular life cycle (i.e. juvenile recruitment in spring and adult migration in autumn) and fishing effort variability during the year. In the demographic model described in chapter six, thanks to an exceptionally detailed and long term dataset 1993-2006, I could overcome all above mentioned limitations. The resulting model, calibrated and even validated on field data, takes into account stochasticity in body growth and recruitment variations observed between 1993-2006. Moreover all vital parameters are linked to size rather than age, age is indeed a poor indicator of size for all those species that exhibit high plasticity in growth processes. In addition the model permitted to assess for the first time the density level over which density dependent mortality severely affect juvenile settlement.

After a decade of alarming reports by the International Council for the Exploration of the Sea (ICES), European eel has recently (2007) listed in Annex B of CITES and IUCN red list of threatened species (2008). At the same time, the Council of the European Union approved a Regulation establishing measures for the recovery of the European eel stock. The main target of the Regulation is to achieve "the escapement to the sea of at least 40% of the biomass of adult eel relative to the best estimate of the potential escapement from the river basin in the absence of human activities affecting the fishing area or the stock" (EC 1100/2007). Member States are required to develop Eel Management Plans (EMPs) defining appropriate measures to pursue this objective at a river basin scale by the end of 2008. Fishermen will be directly affected by the

implementation of the EU Regulation, as commercial harvesting is easier to control than other pressures such as pollution, parasitism or habitat disruption. Devising appropriate policies for the management of eel fisheries is therefore crucial to safeguard eel population viability and to achieve socio-economic sustainability. Thus, in chapter seven I used the developed demographic model (described in chapter six) to estimate the output of silver eels from a Mediterranean lagoon and the harvest by local fishermen corresponding to different mesh sizes of the nets and different levels of fishing effort. Then, I performed a Pareto analysis to identify those fishing policies that provided the best compromise between the two conflicting objectives of maximizing the escapement of silver eels and maximizing the harvest. Finally in chapter eighth, I showed how demographic models have been historically used to assess the consequences of different management policies on the viability of fish populations, and how socio-economic information has been integrated into demographic models to evaluate the productivity and profitability of the fishery under different management scenarios. I also discussed the potential contribution of multi-objective analysis supporting the identification of optimal management policies, particularly when decision-makers are faced with contrasting objectives (typically, eel conservation and profitability of the fishery).

Although I am confident that my work provided new perspectives in eel demography and some useful tools for developing sound fishery management policies, I am convinced that a lot of work on modelling eel population dynamic still needs to be done. In particular I think that there is still a lack of knowledge upon the role of density and environmental factors in determining sex ratio. Yet some studies (Oliveira et al., 2001) evidenced that female relative abundance increases at lower densities, these results need to be properly quantified and analytically assessed before being integrated in demographic analyses. Additionally, up to now, demographic studies upon European eel have actually neglected the oceanic phase of eel life cycle and stock-recruitment relationship. Only Astrom and Dekker (2007) provided a first attempt to consider the full eel life cycle through modelling the dynamics of the overall European eel stock. Although their work has the invaluable merit to have opened the era of full life cycle models for eels, it neglects many recent findings on eel physiology (van Ginneken et al., 2007a,b; Belpaire and Goemans 2007) and oceanography (Kettle and Haines, 2006; Bonhommou et al., 2008) that are likely to affect eel reproductive success. Additionally, molecular studies recently provided interesting insights into the oceanic phase of the life cycle and the interpretation of the results would take great advantage of modelling approaches coupling genetics and demography (Maes and Volckart 2007). Then, I am convinced that the next challenge for scientists involved in eel population dynamics will consist in strengthening cooperation with different research fields in order to find quantitative ways of expressing new insights and integrate them in more exhaustive studies of population dynamics.

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