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# A demographic model for the conservation and management of the European eel: an application to a Mediterranean coastal lagoon

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Abstract :

We present a general size and age-structured demographic model of the continental phase of catadromous eels' life cycle, allowing for the incorporation of (i) fluctuations of juvenile recruitment, (ii) density-dependent settlement and sex determination, (iii) plastic body growth and sexual dimorphism, and (iv) vital rates driven by body size rather than age. The model can be used to assess (i) standing stock, (ii) fishing yield, and (iii) spawner production under different recruitment and management scenarios. We demonstrate the model by applying it to a European eel stock (Camargue lagoons, southern France) that was continuously monitored for 17 years (1993–2009). Results indicate that the upper limit to settlement in the Camargue water system is  $\sim 419$  eels  $\text{ha}^{-1}$  per year. A balanced sex ratio occurs for a settlement of  $\sim 94$  eels  $\text{ha}^{-1}$ , shifting towards males at higher densities. Catchability is higher in adult silver eels than in sub-adult yellow eels, possibly due to behavioural differences. Estimated standing stock ranged between 7 and 19 kg  $\text{ha}^{-1}$ . Fishing yield was 5–7 kg  $\text{ha}^{-1}$  per year, while spawner escapement ranged between 0 and 13 kg  $\text{ha}^{-1}$  per year (<30% of what would occur in the absence of fishing and obstacles to migration).

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**Keywords:** *Anguilla anguilla, density dependence, European eel, fish population dynamics, life history variation, plasticity in vital traits, size-dependent demography, stochastic demographic models, stock assessment*

## Introduction

The European eel (*Anguilla anguilla*) poses an extraordinary challenge to scientists and fishery managers. Its peculiar life history, characterized by long-ranging catadromous migrations between the ocean and continental waters, has stimulated the flourishing of a large body of literature in the last century (Righton et al., 2012). Sustainable management of catadromous eels of the genus *Anguilla* is made particularly difficult by the different spatial scales at which the life history of these species takes place (Dekker, 2000, 2016; Dekker and Beaulaton, 2016). Feeding and growing places are widely distributed, mostly at temperate latitudes, from northern Africa to the White Sea (Dekker, 2003). However, reproduction is presumed to take place in restricted areas at tropical latitudes, in the Sargasso Sea (Schmidt, 1923).

Eel stocks have been an important income source for local communities in the past centuries. In the 1990s, the European eel fishery provided revenues for over 25 000 people in rural areas (Dekker, 2003). However, a range of concurrent pressures, including overfishing, habitat loss and alteration, parasitic diseases, obstacles to migration and changes in oceanic conditions has driven eel stocks towards a generalized decline in the past three decades (Bevacqua et al., 2015; Drouineau et al., 2018). The European eel has been listed in Appendix II of the Convention on International Trade in Endangered Species (CITES) in 2007, and has been added to the IUCN red list and classified as critically endangered (Jacoby and Gollock, 2014; Jacoby et al., 2015; Miller et al., 2016). The Council of the European Union has approved a regulation (Council Regulation 1100/2007, indicated as "EU Regulation" in the following) that imposes to all Member States comprehending natural habitats for the European eel to develop and implement eel management plans (EMPs) for the recovery of the eel stock.

Demographic models provide valuable tools to better understand the consequences of different management policies on eel conservation. Significant progress has been made during the last 50 years in modelling the continental demography of eels. However, few studies have led to the development of models suited to support an informed conservation management of eel stocks (but see Fenske et al., 2011), either because most studies have been restricted to specific life-history traits (Bevacqua et al., 2011b; Drouineau et al., 2016) or because they have not been subject to rigorous calibration procedures involving field observations from long-term time series (De Leo and Gatto, 1995; Schiavina et al., 2015; Aschonitis et al., 2017b).

The goal of the present work is to propose a model that can help decision-makers to (i) evaluate the present status of local eel stocks and fisheries, (ii) assess the link between juvenile recruitment and spawner production, and (iii) forecast the consequences of different management measures on spawner production and fishing yield. The model includes the most important features of eel species and encompasses a set of sub-models, describing the main vital traits, which can be customized to account for sitespecific features. The modelling framework includes a multiple classification of the stock by developmental stage, age and body size, along with a stochastic formulation accounting for interindividual variability in body growth and its consequences on vital rates. Sub-models describe (i) juvenile recruitment and settlement in continental waters; (ii) body growth; (iii) sex differentiation; (iv) natural and (v) fishing mortality; (vi) sexual maturation; and (vii) spawner escapement. We demonstrate the model by calibrating it against a long-term time series (1993–2009) from the European eel stock of the Camargue lagoons (Rhône River delta, Southern France) and using it to assess spawner production and fishing yield under different management scenarios.

## The Camargue eel fishery

### Study site

The Camargue water system (Figure 1) encompasses two major interconnected basins: the Vaccarès lagoon (6400 ha) and the Impériaux lagoon (2800 ha). For the sake of brevity, we will refer to them in the following as the “Camargue lagoons,” although the system comprises other minor watersheds. The Camargue lagoons are isolated by dikes from the two arms of the Rhône River (Grand Rhône and Petit Rhône) and from the Mediterranean Sea. Water exchanges from the lagoons to the sea and back are regulated by sluice gates at Grau de la Fourcade, near Saintes Maries de la Mer (Crivelli et al., 2008). A limited number of professional fishers is allowed to fish within the lagoons, while recreational fishing is banned. Scientific monitoring of the Camargue eel stock has been carried out by Tour du Valat (TdV) Biological Station in the lagoons since the early '90s using the same fishing gear (i.e. fyke nets) of the professional fishery.

### Available data

Scientific monitoring of the Camargue eel stock is performed by TdV Biological Station in the Camargue lagoons since the early '90s. Between 1993 and 2009, 3021 glass eels were fished at Vaccarès with a fry net having a 0.5-mm mesh and a 20-m leading net. Sampling took place ~4 days per month during the recruitment season (February–April). Annual glass eel catches are reported in Table 1. In 2004, 2008, and 2009, mark–recapture experiments were carried out to assess the magnitude of glass eel recruitment to the lagoons. In each of the 3 years, between 500 000 and 1.2 million glass eels were intercepted by an eel trap at their passage through sluice gates at Grau de la Fourcade, marked with tetracycline and released into the lagoons (A. J. Crivelli, unpublished data). Some months later, marked eels were recaptured with fry nets placed in Vaccarès, allowing the estimation, through the Lincoln–Petersen refined method (Seber, 1982), of a recruitment ranging between 11.2 and 55.7 million glass eels per year. This information was used to transform the time series of glass eel recruitment from a relative measure (catches per unit effort, CPUE) to an absolute abundance  $R = \Theta \text{CPUE}$ , where the proportionality coefficient  $\Theta = 7,76 \times 10^6$  was estimated from the data provided by the mark–recapture experiments. In the same period, 26 690 adult eels (yellow and silver) were caught in the Camargue lagoons with fyke nets with a 6-mm mesh and a 40-m leading net. The sampling effort was ~4 days per month with a single fyke net set in each lagoon. Annual adult eel catches are reported in Table 2. Until 1997, only total length and, occasionally, body mass of fish were recorded. Since 1997, all eels were measured, weighed and sexed. Sex was determined by gonad inspection in fish >30 cm long, while smaller individuals were classified as sexually undifferentiated. Maturation stage (yellow or silver) was determined according to Pankhurst's (1982) ocular index. A sub-sample of 291 individuals was aged by otolith reading and provided data for the calibration of a body growth model (Melia` et al., 2006a). Fishing effort exerted by TdV scientists is largely negligible compared to that performed by professional fishers (12 operating at Vaccarès and 7 at Impériaux, corresponding to an average of 184 nets per day in the lagoons, with peaks in fall and spring attaining ~290 nets per day). The commercial fishery targets both yellow and silver eels and is carried out with the same fishing gear used by TdV (fyke nets with a 6-mm mesh). During the study period (1993–2009), water salinity underwent large fluctuations, ranging between 5 and 25

(annual average), while water temperature ranged between 7 °C in winter and 22 °C in summer, with an annual average of ~14 °C.

## General model

After hatching in the open sea, the larvae of catadromous eels (leptocephali) are transported by currents to feeding areas in fresh and coastal waters (Bonhommeau et al., 2010; Munk et al., 2010). As soon as they approach the continental platform, they first metamorphose into glass eels and then into elvers. After acclimation to the new environment, elvers develop into yellow eels, which feed and grow until sexual differentiation. Sex determination is metagamic (i.e. determined by environmental rather than genetic factors; Geffroy and Bardonnnet, 2016), and gonad differentiation is likely triggered by reaching a critical body size. After differentiation, eels show clear sexual dimorphism (Krueger and Oliveira, 1999), with females growing faster and attaining greater body size than males (Vøllestad, 1992; Poole and Reynolds, 1998; Melia` et al., 2006a; Daverat et al., 2012). Finally, yellow eels metamorphose into silver eels, which become more active and head to the open sea to migrate back to spawning grounds, where they reproduce and eventually die (Aoyama, 2009).

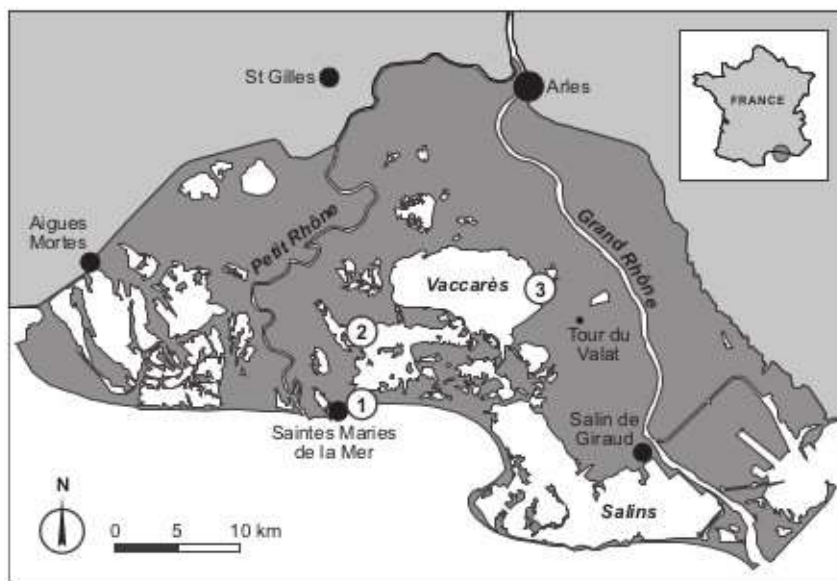


Figure 1. The Camargue water system (43 300N 4 300E). Circled numbers indicate the position of sluice gates at Grau de la Fourcade (1) and the two sampling stations in the Impériaux (2) and Vaccarès (3) lagoons.

Year	Catch (ind.)	Fishing effort (net day)	CPUE (ind. net <sup>-1</sup> day <sup>-1</sup> )
1993	2	9.9	0.2
1994	161	11.9	13.5
1995	53	11.9	4.5
1996	5	3.9	1.3
1997	27	7.7	3.5
1998	217	10.9	20.0
1999	55	10.6	5.2
2000	2 079	11.7	177.6
2001	4	12.1	0.3
2002	146	11.9	12.3
2003	8	11.9	0.7
2004	62	11.7	5.3
2005	2	10.0	0.2
2006	28	12.0	2.3
2007	6	10.8	0.5
2008	55	11.7	4.7
2009	14	11.7	1.2
Total	2 924	171.7	17

Table 1. Glass eels caught by TdV biological station with a fry net (0.5-mm mesh size) in the Vaccarès lagoon between 1993 and 2009.

The conceptual scheme of the model is illustrated in Figure 2. The model encompasses only the continental phase of eel life history, disregarding the oceanic phases. Despite the key role of the reproductive oceanic phase for the conservation of eel species, the link between the two phases can be interpreted only within a global perspective (Bevacqua et al., 2015) while, at the local scale, recruitment from the sea can be considered as independent of the local population dynamics (Dekker, 2000; De Leo and Gatto, 2001; Bornarel et al., 2018). The stock is subdivided into five classes on the basis of maturation (Yellow/Silver) and sex (Undifferentiated/Female/Male). They are identified by the following acronyms (where the first letter indicates the maturation stage and the second one the sex): YU, YF, YM, SF, SM. Within each class, we ascribed changes in vital rates to interindividual variation, and in particular to differences in body size among individuals of the same age, as detailed in the following section. We described inter-individual variability in body size through an assignment-at-birth approach (Kirkpatrick, 1984; De Leo and Gatto, 1995). Under this approach, observed body size variability at a given age can be interpreted as due to differences among individuals that are completely determined at birth (e.g. at the genetic level). Therefore, the body length  $l$  of an individual of age  $x$  can be written as

$$l(x) = L(x)g, \quad (1)$$

where  $L(x)$  is the median body length at age  $x$  ( $x0 \geq 0$  is arbitrarily set as the age of elvers at the time of first settlement in continental waters) and  $g$  is a growth factor accounting for the individual potential for body growth. If  $g$  is randomly assigned to each individual according to a known probability density  $s(g)$ , the integral

$$\int_{g_1}^{g_2} s(g)dg \quad (2)$$

represents the probability that a recruited individual has a growth factor comprised between  $g_1$  and  $g_2$ . A typical choice (De Leo and Gatto, 1995; De Leo et al., 2009) is to use a log-normal probability density function for  $g$ .

Year	Vaccarès			Impériaux		
	Catch (ind.)	Biomass (kg)	Effort (net day)	Catch (ind.)	Biomass (kg)	Effort (net day)
1993	381	59.5	30.7	–	–	–
1994	317	59.9	40.6	–	–	–
1995	268	42.9	31.3	–	–	–
1996	260	27.4	26.5	–	–	–
1997	2 561	84.0	46.3	1 516	44.6	44.0
1998	8 443	132.3	45.3	1 970	29.8	48.0
1999	882	34.7	42.0	653	14.4	46.8
2000	1 155	47.3	45.8	395	19.6	48.2
2001	490	28.8	30.3	489	16.8	27.1
2002	404	41.1	28.6	677	31.8	24.4
2003	437	30.9	28.0	123	5.6	24.4
2004	620	33.3	35.9	–	–	–
2005	1 790	48.7	25.2	1 481	30.8	24.1
2006	271	28.0	23.7	121	11.7	24.2
2007	313	45.6	24.3	121	8.3	24.3
2008	350	58.5	24.3	108	19.4	24.1
2009	57	11.5	24.4	37	3.7	24.3
Total	18 999	814.4	553.2	7 691	236.5	383.9

Table 2. Adult eels caught by TdV biological station with a fyke net (6-mm mesh size) in the Vaccarès and Impériaux lagoons during 1993–2009.

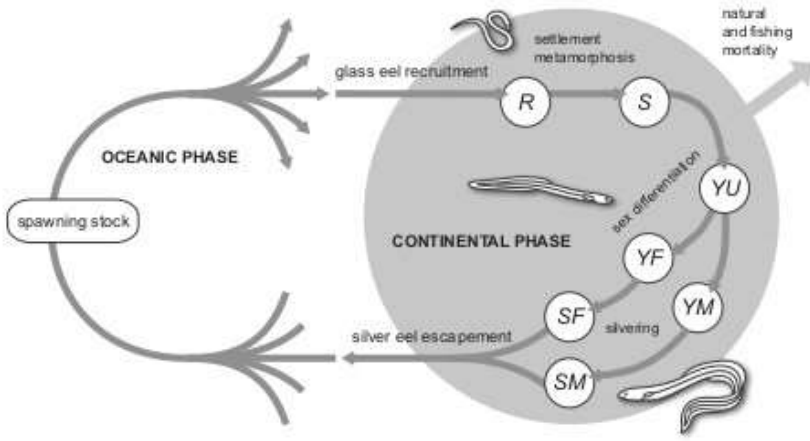


Figure 2. Schematic view of the life cycle of catadromous eel species (genus *Anguilla*). The proposed model encompasses the whole continental phase of the life cycle (grey shading). White circles indicate the life-history stages considered by the model (R, glass eel recruitment; S, elver settlement; YU, sexually undifferentiated yellow eels; YF, yellow females; YM, yellow males; SF, silver females; SM, silver males).

If  $S(t)$  is the settlement density of elves at time  $t$ , the density (with respect to  $g$ ) of sexually undifferentiated yellow eels, with growth factor  $g$ , at time  $t$  is given by

$$N_{YU}(x_0, g, t) = s(g)S(t). \quad (3)$$

The structure of a newly recruited cohort evolves through time, as a consequence of body growth, natural and fishing mortality, sexual differentiation and maturation, and silver eel escapement from continental sites. Thus, the dynamics of the stock can be described by the following partial differential equations governing the variables  $N_i(x, g, t)$ , namely the densities with respect to  $x$  and  $g$  of eels in the stage  $i$  ( $= YU, YM, YF, SM, SF$ ):

$$\frac{\partial N_{YU}}{\partial x} + \frac{\partial N_{YU}}{\partial t} = -DN_{YU} - (M + F)N_{YU}, \quad (4)$$

$$\frac{\partial N_{YF}}{\partial x} + \frac{\partial N_{YF}}{\partial t} = (1 - f_M)DN_{YU} - (M + F + \Lambda)N_{YF}, \quad (5)$$

$$\frac{\partial N_{SF}}{\partial x} + \frac{\partial N_{SF}}{\partial t} = \Lambda N_{YF} - (M + F + \Gamma)N_{SF}. \quad (6)$$

$$\frac{\partial N_{YM}}{\partial x} + \frac{\partial N_{YM}}{\partial t} = f_M DN_{YU} - (M + F + \Lambda)N_{YM}, \quad (7)$$

$$\frac{\partial N_{SM}}{\partial x} + \frac{\partial N_{SM}}{\partial t} = \Lambda N_{YM} - (M + F + \Gamma)N_{SM}. \quad (8)$$

where  $D$  is the rate at which undifferentiated eels undergo sexual differentiation;  $f_M$  and  $1 - f_M$  are the fractions of differentiating eels becoming males and females, respectively;  $M$  is the natural mortality rate;  $F$  is the fishing mortality rate;  $\Lambda$  is the rate at which yellow eels metamorphose to silver eels; and  $\Gamma$  is the rate at which silver eels leave the system to begin their oceanic migration. These rates can be expressed as functions of body size, sex, maturation stage, and/or time, as described in the following sections.

Equations (4)–(8) are a modified version of the McKendrick– von Foerster model, adapted to account for the classification of the population by sex and developmental stage [readers unfamiliar with continuous-time models with age structure may refer to Rees and Ellner (2009) for a first introduction to the topic]. After having set appropriate initial conditions, the equations can be numerically integrated from an initial time  $t_0$  to a final time  $t_f$ . Abundance and biomass of standing stock and catch, structured into sex/maturation classes, can be computed through the equations reported in the Supplementary material.

## Sub-models for specific life-history traits

### Glass eel recruitment and settlement in continental water

Eel recruitment takes place mainly in winter and spring, with peaks depending on latitude and the variability of oceanic factors (Harrison et al., 2014); recruitment intensity shows wide interannual fluctuations (Drouineau et al., 2016). Only a fraction of the glass eels recruiting to a water system successfully settle as elvers: settlement success may be affected by the presence of predators and/or competition for food and space (Bevacqua et al., 2011a). To account for possible density-dependent effects on the survival of new recruits during the settlement phase, we linked elver settlement  $S$  at time  $t$  to glass eel recruitment  $R$  at time  $t - s$  through a simple Beverton–Holt relationship:

$$S(t) = \frac{\delta_0 R(t - \tau)}{1 + \rho R(t - \tau)}, \quad (9)$$

where  $\delta_0$  is the survival probability of a glass eel from recruitment to settlement as elver (which can be estimated with an appropriate mortality model, see “Natural and fishing mortality” section), and  $\rho$  reflects the intensity of density dependence.

### Body growth, sex determination, and sex differentiation

Eels show high plasticity in body growth, resulting in wide interindividual variation within the same population and in geographical variation among habitats (Daverat et al., 2012; Côté et al., 2014). In a relatively homogeneous habitat, the median body growth of an eel cohort can be described with the model proposed by Melia` et al. (2006a), which explicitly considers a unique growth curve during the sexually undifferentiated phase with a subsequent splitting into two curves, one for males and one for females, when body length  $L^*$  at sexual differentiation is attained. The model has been used for different eel stocks from both brackish and freshwater environments (Melia` et al., 2006b), and its parameters can be estimated also when site-specific age–length data are available only for silver eels (Melia` et al., 2014). The rate of sexual differentiation is considered to be zero when body length is  $< L^*$  and infinity when it is  $\geq L^*$ .

There is evidence that sex determination within a cohort shifts in favour of males as eel density increases (Geffroy and Bardonnat, 2016). The fraction of  $f_m$  of eels differentiating as males within a cohort can be linked to the initial density  $S$  of that cohort (at first settlement) through a sigmoid function (like in Bevacqua et al., 2015):

$$f_m = \frac{1}{1 + \exp(\eta_{SR}(\lambda_{SR} - S))}, \quad (10)$$

where  $\lambda_{SR}$  indicates the density at which sex ratio at sexual differentiation is balanced (1:1) and  $\eta_{SR}$  is a shape parameter.

### Natural and fishing mortality

Bevacqua et al. (2011b) have shown that body size, water temperature, stock density, and sex are the primary determinants of natural mortality rate in the European eel. Their model links natural mortality rate  $M$  to body mass  $m$ , through an allometric relationship

$$M = \mu_1 m^b, \quad (11)$$

where  $\mu_1$  is mortality rate at unit mass (1 g) and  $b = -0.46$ . In turn,  $\mu_1$  is expressed as a function of water temperature  $\mu_1 = \exp(-E/kT)$  where  $a$  is a proportionality coefficient accounting for the effect of stock density and sex,  $\exp(-E/kT)$  is the Boltzmann–Arrhenius factor,  $k$  is Boltzmann constant ( $8.62 \times 10^5 \text{ eV K}^{-1}$ ) and  $E$  (eV) is the activation energy (see Bevacqua et al., 2011b). We used this general model to derive the natural mortality rate  $M$  of the different stages and size classes into which the stock is subdivided.

We linked fishing mortality rate  $F$  to gear efficiency, selectivity, and fishing effort through the following relationship:

$$F = q\phi E, \quad (12)$$

where  $q$  is a catchability coefficient,  $\phi$  is gear selectivity and  $E$  is the fishing effort. Parameter  $q$  represents the ability of a specific gear to intercept a fish, and depends on the characteristics of the gear and the fish behaviour. In fact, while migrating silver eels move actively when seeking the way to the ocean, resident yellow eels show a more sedentary behaviour (McCleave, 1999; Aoyama et al., 2002; Hedger et al., 2010) and are likely less prone to be captured by passive devices. For this reason, we considered two possibly different values for the catchability coefficient, one for yellow eels and one for silver eels. Gear selectivity  $\phi$  can be expressed as a function of net mesh size and body length, at least for fyke nets, which are frequently used for eel fishing (Bevacqua et al., 2009). Fishing effort  $E$  can be computed as the number of fishing gears set in place per unit time, whenever this information is directly available (like in our case study), or indirectly inferred from the number of operating boats, fishing licences, etc.

### Sexual maturation and escapement

Silvering occurs mainly in autumn, when water temperature decreases, and is triggered by body size rather than age (Krueger and Oliveira, 1999; Arai et al., 2009). Also, size at silvering differs between sexes, with females metamorphosing at a bigger size than males. In particular, size at silvering in female eels is generally considered the result of a trade-off between survival and fecundity (Mateo et al., 2017). According to De Leo and Gatto (1995), we linked the fraction of eels undergoing sexual maturation to the silver stage to body length  $l$  through a sigmoid function:

$$\Lambda = \frac{\chi}{1 + \exp[\eta_{SILV}(\lambda_{SILV} - l)]}, \quad (13)$$

where  $\chi$  is the maximum rate of metamorphosis,  $\lambda_{SILV}$  is a semi-saturation constant, and  $\eta_{SILV}$  is a shape parameter. Different parameter sets can be used to account for differences between sexes and among different environments (Bevacqua et al., 2006).

Silver eels leave continental waters when environmental conditions are most favourable to migration (Brujns and Durif, 2009; Béguer-Pon et al., 2018). Usually, a minimum water flow is needed to trigger migration towards the open sea (Acou et al., 2008). Hence, we assumed that the escape rate of silver eels is an increasing, yet saturating function of the water flow  $WF$  from inland waters towards the open sea (or a proxy for it):

$$\Gamma = \frac{1}{1 + \exp(\eta_{ESC}(\lambda_{ESC} - WF))}, \quad (14)$$



where  $\lambda_{ESC}$  is a semi-saturation constant and  $\eta_{ESC}$  is a shape parameter. When the water flow is regulated by sluice gates that can be open or closed, like in the Camargue lagoons, the number of open gates can be used as a proxy for water flow. Thus, in this case parameter  $\lambda_{ESC}$  indicates the number of open gates that would allow the escapement of half of the silver eels from the basin. We assumed that silver eels that do not find the way to the sea when water exchanges are interrupted can resume feeding (according to Feunteun et al., 2000) and wait up to 2 years for favourable conditions (Vøllestad et al., 1994).

### Model calibration

The calibration of all the parameters included in the different sub-models requires a careful approach because of the complexity of the overall model. In general, we can distinguish data of different kind that all concur to the estimation of the model parameters: (i) data coming from samples of the studied population that describe vital traits, such as body growth as a function of age; (ii) data that derive from meta-analyses and describe general relationships (although species-specific) such as natural mortality rate as a function of body size; and (iii) time series of eel densities and catches coming from commercial harvesting and/or scientific monitoring. Data of the first two types allow what we will call an off-line calibration, which does not require the simulation of an inter-annual demographic model. Results of the off-line calibration can then be input to the dynamic demographic model which, via the estimation of the remaining parameters, is then fitted to time series data through appropriate, usually computer-intensive, techniques.

### Off-line calibration

In this first phase we derived parameter values or functional relationships from (i) previous studies conducted on the same stock and (ii) existing models regarding specific life-history traits of the species. Several studies have analysed specific traits of eel life history, and can therefore provide trait-specific models that can be used as a basis for the construction of the general model (Figure 3). In a previous work, we calibrated a deterministic body growth model from age-length data from the Camargue lagoons (see Melia et al., 2006a). We used the deterministic model calibrated by Melia et al. (2006a) on age-length data from the Camargue lagoons as the baseline to describe the median body growth pattern, and used the same data set to quantify the stochastic component of body growth. Under the assignment-at-birth approach, this was done by deriving the probability distribution of the body growth factor  $g$ , calculated as the ratio between observed body lengths and those predicted by the deterministic growth model. More precisely, we estimated a lognormal probability density function  $s(g)$ , after verifying that  $\ln(g)$  follows a Gaussian distribution (Jarque-Bera test,  $p > 0.2$ ) with mean zero and standard deviation  $\delta_g = 0.23$ . We described natural mortality, including  $\delta_0$ , with the model proposed by Bevacqua et al. (2011b). This requires a qualitative evaluation of eel density in the stock under analysis and the availability of data about the annual average water temperature of the site. We used the morphometric relationship  $M = \alpha l^\beta$ , derived from length-weight data (see Melia et al., 2006a), to transform body lengths into body masses. To assess fishing mortality, we could not use commercial catches, due to the lack of comprehensive and reliable data. However, the fishing effort of commercial fishers (average number of nets set per day) was known with sufficient precision on a monthly basis, and was hence used to describe seasonal variations in fishing pressure. We linked gear selectivity  $\phi$  to body length through the model described in Bevacqua et al. (2009), and we expressed silvering rate as a function of body length and sex through the model proposed in Bevacqua et al. (2006).

### On-line calibration

All those parameters than cannot be set off-line should be estimated through a robust calibration procedure, including the estimation of parameter uncertainty (De Leo et al., 2009). We performed parameter estimation by comparing observed and predicted catches by TdV and minimizing a cost function. We used only scientific catches because, as explained in the previous section, reliable data on commercial catches were not available. Observed catches were subdivided into sex/maturation classes and then pooled by trimester to derive sufficiently representative body size distributions. The state of the model was arbitrarily initialized as  $N_i(x, g, t_0) = 0$  ( $i = YU, YF, YM, SF, SM$ ), where time  $t_0 = 0$  corresponds to winter 1993. In accordance with the recruitment schedule observed

in the Camargue, we assumed that settlement takes place during April and that the acclimation of glass eels and subsequent metamorphosis to elver lasts 1 month [ $\tau=1$  month in Equation (9)]. The model was then run by feeding it with the reconstructed recruitment series. According to the information available on the maximum permanence of eels in the Camargue lagoons (Melia` et al., 2006a), the first 6 years of simulation were used as a model warm-up and excluded from the comparison to experimental data to ensure that the model had completely forgot its initial state. Therefore, the comparison between observed and simulated catches encompassed the period from spring 1999 to fall 2009.

Since data comprise also a classification by sex and maturation stage, different time series were available, and it was necessary to minimize different cost functions at a time. To overcome this problem, we used the fraction of variance unexplained (FVU) for each sex/maturation class as a cost function:

$$FVU_i = \frac{\sum_T [\bar{y}_{i,T} - \tilde{y}_{i,T}(\theta)]^2}{\sum_T [\bar{y}_{i,T} - \bar{y}_i]^2}, \quad (15)$$

where  $\bar{y}_{i,T}$  is the observed abundance of eels in class  $i$  ( $\frac{1}{4}$  YU, YM, YF, SM, SF) at time step  $T$  (in our case, a trimester),  $\tilde{y}_{i,T}$  is the corresponding estimate obtained from the model with a parameter set  $\theta$ , and  $\bar{y}_i$  is the result of averaging  $\bar{y}_{i,T}$  over all time steps. The advantage of using FVUs instead of mean squared errors is that FVUs are by definition constrained between 0 and 1 and are therefore comparable independently of the magnitude of abundance of the different classes. Note that in our study case eel sex was determined through a visual inspection of the gonads, and sex determination was possible only in individuals  $>30$  cm in length. Therefore, individuals below that size were classified as undifferentiated in samples used for model calibration. For this reason, after simulating the dynamics of the stock, eels  $<30$  cm were reclassified as undifferentiated to allow a consistent comparison of simulated and observed catch structure. We found the optimal parameter set by minimizing the sum of the FVUs obtained for the five sex/maturation classes using the nonlinear programming algorithm “fminsearch” implemented in MATLAB. Finally, we performed an assessment of the uncertainty affecting parameter estimates via nonparametric bootstrap (see De Leo et al., 2009 for a discussion on the topic).

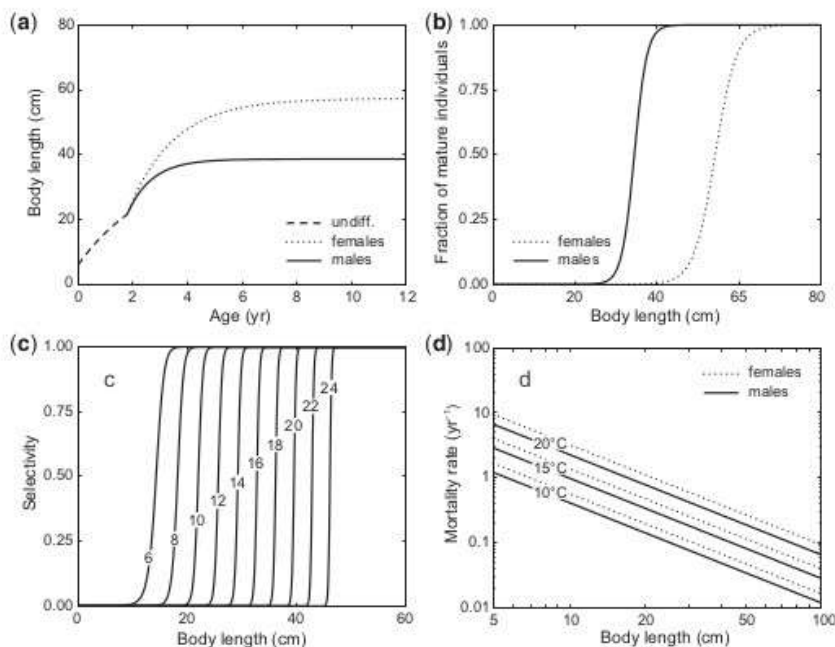


Figure 3. Models used to describe specific life-history traits of the European eel *A. anguilla* in the Camargue lagoons: (a) body growth from Melia` et al. (2006b); (b) sexual maturation from Bevacqua et al. (2006); (c) selectivity of fyke nets with different mesh size (knot-to-knot distance, in mm; from Bevacqua et al., 2009); (d) natural mortality rate as a function of body size and water temperature from Bevacqua et al. (2011b).

## Assessment of spawner production under different scenarios

Once calibrated for a given site, the model allows the assessment of spawner production and fishing yield under different recruitment and management scenarios. We used the time series of silver eel escapements and catches (reconstructed for the period 1999–2009 on the basis of historical glass eel recruitment, fishing effort, and sluice gate regulation) as a baseline. Then, we estimated escapements and catches that would have derived from the same recruitment time series, but under different scenarios of anthropogenic impact, namely: (i) in the absence of fishing pressure and without obstacles to silver eel migration (i.e. by setting fishing effort to zero and considering that all the sluice gates connecting the lagoons with the sea are open); (ii) under a fishing pressure regulated according to the actual French EMP (decree NOR: TRAM1331211A, 27 January 2014) imposing a closure of the yellow eel fishery from 15 July to August and from 15 October to 1 January, a closure of the silver eel fishery from 16 February to 15 September, and assuming no obstacles to migration. Finally, we estimated the pristine silver eel escapement from the Camargue water system by assuming that, under pristine conditions, glass eel recruitment was so abundant that elver settlement attained its upper limit  $S_{max} = r_0/q$ , that fishing was absent and that there was no obstacle to silver eel migration.

## Results

### Model fitting and parameter estimates

The model provides a reconstruction of the stock dynamics in the Camargue lagoons over the study period. It succeeds in reproducing the magnitude of experimental catches by TdV with good approximation, although its disaggregation into sex/maturation classes (Figure 4a) is not always precise, and the most intense fluctuations are sometimes damped down in the simulated time series. In contrast, the performances of the model are very satisfactory in reproducing the body size distribution of the catch (Figure 4b). The expected values for unknown model parameters  $(\rho, \lambda_{SR}, \eta_{SR}, q_y, q_s, \lambda_{ESC}, \eta_{ESC})$ , resulting from the calibration against the Camargue data set, are reported in Table 3, together with estimated uncertainty.

Parameter  $\rho$  determines the fraction of glass eels that successfully settle in the lagoon as elvers. The relationship between glass eel recruitment  $R$  and elver settlement  $S$  is shown in Figure 5a, suggesting that the highest values of glass eel recruitment are dampened down by density dependence. The upper limit to elver settlement  $S$  is calculated as  $S_{max} = \delta_0/\rho$ , where  $\delta_0 = 0.86$  is glass eel survival in the absence of density-dependent effects (as resulting from the natural mortality model) and  $\rho = 2.05 \times 10^{-3} \text{ (eels ha)}^{-1}$  (Table 3). The corresponding estimate of  $S_{max}$  is  $\sim 419$  (90° CI:407-431) eels  $ha^{-1}$ .

Sex determination is also influenced by eel density: sex ratio (measured as the fraction of elvers that will differentiate as males) increases with the abundance of the cohort at the time of first settlement (Figure 5b). During the study period, the estimated fraction of males at sex differentiation varied between 0.51 and 0.77. A balanced sex ratio is expected to occur in correspondence with a settler abundance of about 94 elvers  $ha^{-1}$ .

Estimated catchability coefficients for yellow and silver eels are equal to  $6.38 \times 10^6$  and  $7.75 \times 10^6 \text{ net}^{-1} \text{ day}^{-1} \text{ month}^{-1}$ , respectively. Considering an average monthly fishing effort  $E = 184 \text{ net} \times 30.5 \text{ day}$  and a 100% selectivity, the fishing mortality rate  $F$  equals 0.036 and 0.044  $\text{months}^{-1}$  (corresponding to 0.43 and 0.53  $\text{years}^{-1}$ ) for yellow and silver eels, respectively. Values of fishing mortality vary from month to month depending on the actual value of the fishing effort (which ranges between 49 and 290 net day) and that of net selectivity  $\phi$ , which (for the fishing gears used in the Camargue lagoons) is negligible for small yellow eels (<15 cm in length) and approaches unity for eels >18 cm (Bevacqua et al., 2007).

Parameters  $\lambda_{ESC}$  and  $\eta_{ESC}$  determine the escapement rate of silver eels as a function of the average number of open sluice gates at Grau de la Fourcade. Resulting parameter estimates suggest that escapement probability is almost zero when <2.7 gates (monthly average) are open, while it is close to one over this threshold value. In other words,

the escapement of potential spawners from the Camargue is possible only when the water flow from the lagoons to the sea overcomes a certain threshold (i.e. the water exchange occurring when  $\sim 3$  sluices per month are kept open).

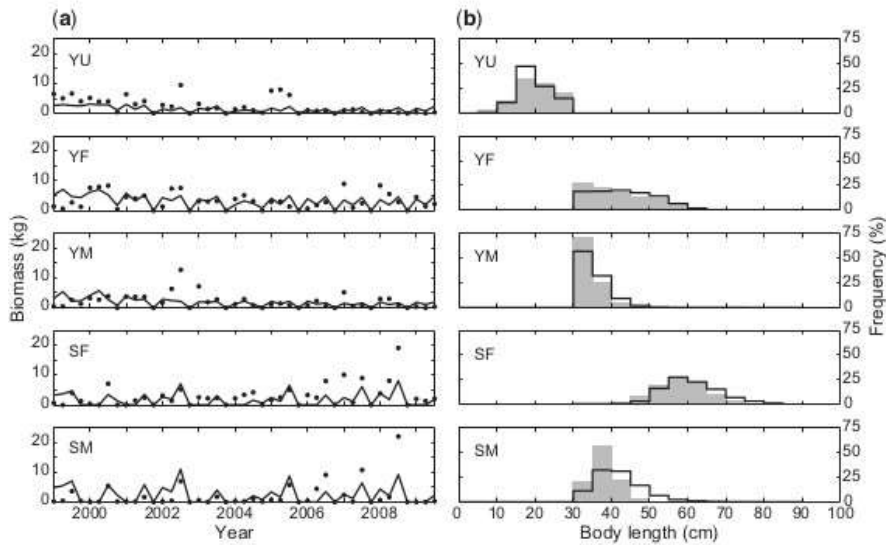


Figure 4. (a) Predicted (lines) vs. observed (dots) European eel catches of TdV biological station from spring 1999 to fall 2009 by sex and maturation (see Figure 2 for the explanation of the acronyms). (b) Predicted (solid lines) vs. observed (grey shading) size structure of the catch aggregated over the whole study period.

Parameter	Median	5th percentile	95th percentile
Elver settlement $\rho$ (individuals <sup>-1</sup> ha)	$2.05 \times 10^{-3}$	$2.00 \times 10^{-3}$	$2.11 \times 10^{-3}$
Sex determination $\lambda_{SR}$ (-)	94.06	36.84	122.91
$\eta_{SR}$ (-)	$3.72 \times 10^{-3}$	$2.94 \times 10^{-3}$	$4.32 \times 10^{-3}$
Catchability $q_Y$ (nets <sup>-1</sup> day <sup>-1</sup> month <sup>-1</sup> )	$6.38 \times 10^{-6}$	$5.62 \times 10^{-6}$	$7.22 \times 10^{-6}$
$q_S$ (nets <sup>-1</sup> day <sup>-1</sup> month <sup>-1</sup> )	$7.75 \times 10^{-6}$	$6.70 \times 10^{-6}$	$9.11 \times 10^{-6}$
Escapement $\lambda_{ESC}$ (-)	2.73	2.63	2.81
$\eta_{ESC}$ (-)	24.33	17.27	87.69

Table 3. Model parameter estimates and relevant statistics resulting from bootstrapping (100 iterations) the 1999–2003 data set.

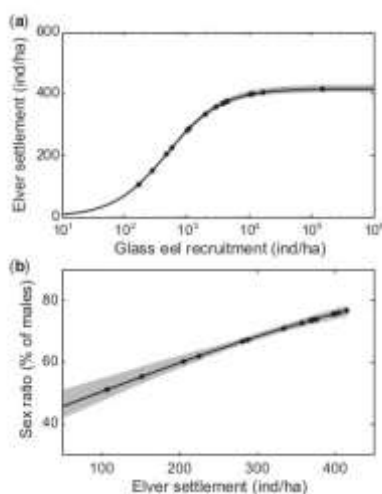


Figure 5. Relationships linking (a) glass eel recruitment and elver settlement [Equation (9)] and (b) elver settlement and sex ratio [Equation (10)]. Dots indicate the estimates of the variables for each year of the study period (1993–2009). Shaded areas indicate 90% confidence intervals for the curves as obtained via bootstrapping.

### Estimates of standing stock, catch, and spawner production

Between 1999 and 2009, the density of the Camargue eel stock (as reconstructed through the calibration of the demographic model) ranged between 7 and 19 kg ha<sup>-1</sup>, with an average of 12 kg ha<sup>-1</sup> (Figure 6a). In numbers, it varied between 135 and 720 eels ha<sup>-1</sup>, with an average of 338 eels ha<sup>-1</sup> (Figure 6b). Both biomass and numbers undergo wide seasonal fluctuations: biomass falls rapidly in autumn, under the combined effect of high fishing pressure and the migration of silver eels, and increases during the re of the year due to body growth of resident and newly recruited eels. Density rises suddenly in spring, due to juvenile recruitment, and then decreases until the next recruitment peak. The productivity of the commercial fishery also fluctuates widely throughout the year, ranging between 0.08 and 1.13 kg ha<sup>-1</sup> per month (Figure 6d) with an annual average of 5.3 kg ha<sup>-1</sup> per year (corresponding to almost 50 tons per year in the lagoons considered in the study). Silver eels represent a considerable fraction (40%) of the overall biomass caught, although in numbers they represent only 12% of the catch (Figure 6c).

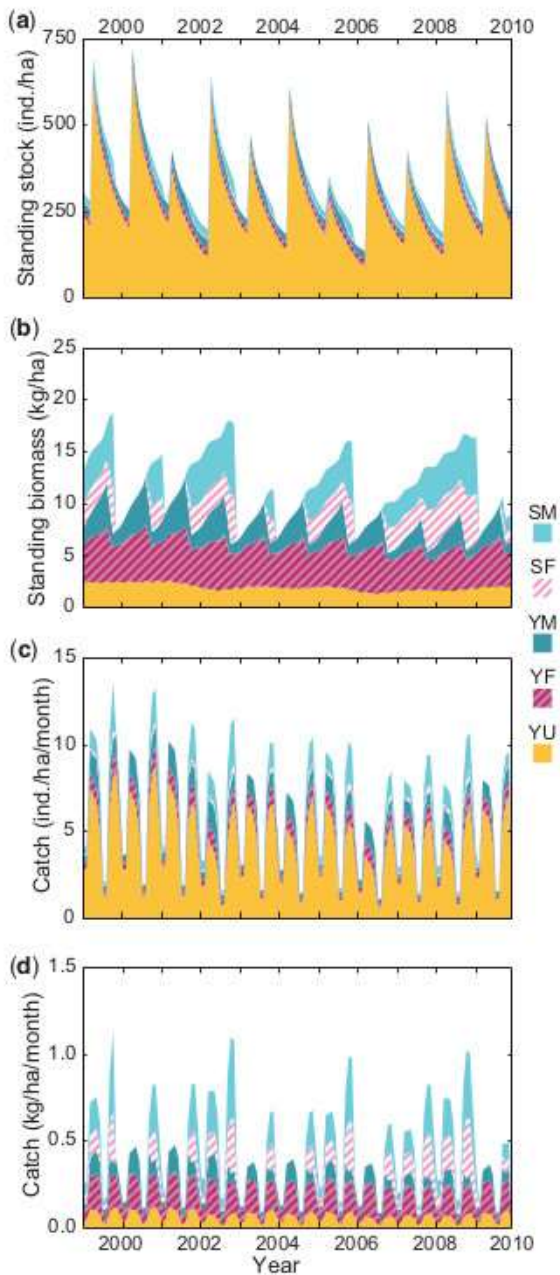


Figure 6. Simulated dynamics of commercial European eel catch (a, in numbers; and b, in biomass) and standing stock (c, in numbers; and d, in biomass) in the Camargue lagoons between March 1999 and November 2009.

The estimated escapement of migratory silver eels is shown in Figure 7a. Migration is conditioned on the presence of favourable environmental conditions. In the Camargue this means, in particular, that a sufficient number of sluice gates must be open to allow for the escapement of spawners (Figure 7b). The amount of silver eel escaping each year varies from almost zero up to 12.6 kg ha per year, with an average over the whole study period of 5.1 kg ha<sup>-1</sup> (27 silver eels ha<sup>-1</sup>). The expected escapement from the Camargue lagoons is almost 47 tons per year. Silver males account, on average, for 57% of migrating silver eel biomass and for 85% in terms of abundance. Escapement was negligible when sluice gates were kept closed in winter (e.g. in 2004 and 2008) and maximum in the following years.

Estimates of annual spawner production and fishing yield under the historical management and under alternative management scenarios are reported in Table 4. For the period 1999–2009, we estimate a historical spawner production around 5.1 kg ha<sup>-1</sup>. Potential spawner production in the same period would have been more than three times the historical one (15.9 kg ha<sup>-1</sup> on average) in the absence of fishing pressure and without obstacles to migration. Under pristine conditions (as approximated by assuming elver settlement to attain its upper limit) escapement would have been even higher, namely 18.2 kg ha<sup>-1</sup>, while under the actual French EMP it would be, on average, 6.5 kg ha<sup>-1</sup>. As for the annual fishing yield, we estimate that it was, on average, equal to 5.3 kg ha<sup>-1</sup>, during the study period, and that it would have been equal to 3.3 kg ha<sup>-1</sup> if the fishery had been regulated according to the French EMP and all obstacles had been removed.

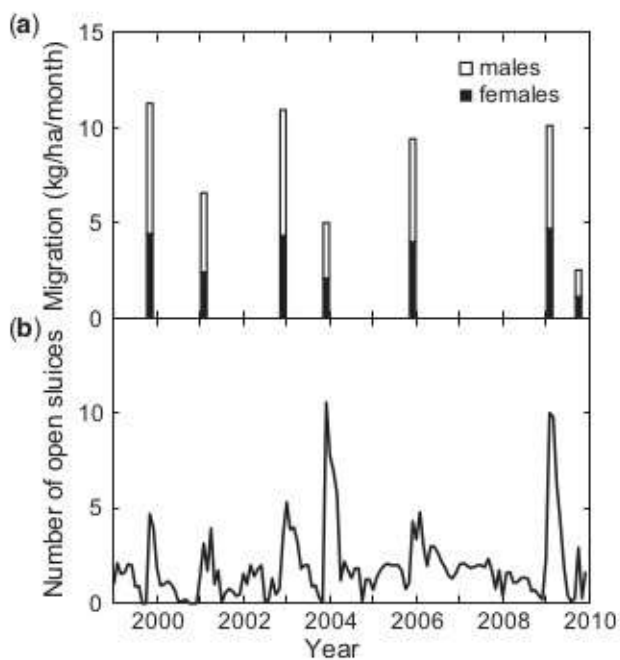


Figure 7. (a) Estimated biomass of silver eels migrating from the Camargue lagoons between March 1999 and November 2009. (b) Average number of open sluice gates connecting the lagoons to the open sea in the same period.

## Discussion

In this work, we have presented an age and size-structured model accounting for the major life-history traits of the European eel. The model builds up on the model developed by De Leo and Gatto (1995) and introduces a number of novel components, namely: density-dependent settlement and sex determination; allometric scaling of natural mortality rate as a function of body size and temperature rather than age; time-varying recruitment (it was assumed to be constant in De Leo and Gatto, 1995) estimated on the basis of experimental glass eel catches. The model has been tuned using a rigorous calibration procedure based not only on size distribution data (as in De Leo and Gatto, 1995) but also on a historical time series of scientific catches classified by sex and maturation stage. A reliable calibration of the proposed model requires a rather considerable amount of information, which is not often

available, except for the few fisheries that are subject to long-term scientific monitoring. A simplified version of the model (such as the one described by Schiavina et al., 2015) can provide an easier way to assess eel stocks in datapoor conditions.

In the following sections, we discuss our main findings regarding the Camargue case study, as well as the general suitability of the model to provide information for the assessment and management of eel stocks.

### Survival from glass eel to elver

Survival from glass eel to elver in the Camargue lagoons varies between 0.3% (at a density of  $\sim 150\,000$  glass eels  $\text{ha}^{-1}$ ) and 64% (at a density of  $\sim 170$  glass eels  $\text{ha}^{-1}$ ) depending on glass eel density. As far as we know, this is the first estimate of glass eel survival in the wild (see Simon et al., 2009 for an assessment under controlled conditions). Our results suggest the existence of density-dependent processes regulating eel survival during their acclimation to the continental environment. Density-dependent survival in the continental growing phase had already been claimed for yellow eels (Vøllestad and Jonsson, 1988; De Leo and Gatto, 1996; Lobon-Cervia and Iglesias, 2008; Acou et al., 2011), but not for glass eels, despite density-dependent survival has been observed in the early life stage of a number of other fish species. It is also worth noting that in our case study glass eels are constrained within a confined lagoon and have limited possibility to avoid intraspecific competition by migrating upstream, as it is the case in river estuaries, where the effects of density dependence may become less intense.

Detecting the existence of density-dependent processes and quantifying mortality rates in early life-history stages, as well as the carrying capacity of different environments, is a crucial issue for the management of fishery and recovery practices. The EU Regulation encourages restocking of newly recruited eels to increase spawner production. However, the efficacy of restocking measures can be limited by density-dependent mechanisms, as already evidenced by some previous studies. Müller (1975) recommended stocking at no  $>100$  to  $500$  eels  $\text{ha}^{-1}$  in northern Europe, while Moriarty et al. (1990), by reviewing the success of glass eel restocking in 68 Polish lakes, found that stocking  $>275$  eels  $\text{ha}^{-1}$  was detrimental for subsequent catches. Moreover, the actual ability of stocked eels to migrate from continental waters to oceanic spawning grounds once they become sexually mature is questioned. Some studies report that stocked eels lack a correct imprint of directional cues (Westin, 2003; Prigge et al., 2013), whereas others reported no differences in migratory patterns of stocked and non-stocked eels (Limburg et al., 2003; Westerberg et al., 2014).

Scenario	Spawner escapement			Fishing yield		
	Mean	Min	Max	Mean	Min	Max
Historical recruitment, fishing and water management	5.1	0	12.6	5.3	3.4	7.1
Historical recruitment, no fishing, no barriers	15.9	13.0	18.9	–	–	–
Historical recruitment, regulated fishing (French EMP), no barriers	6.5	5.0	8.1	3.3	2.8	4.0
Pristine recruitment, no fishing, no barriers	18.2	–	–	–	–	–

Table 4. Annual spawner production and fishing yield ( $\text{kg ha}^{-1}$ ) of the Camargue lagoons between 1999 and 2009 as estimated by simulation under different recruitment, water management, and fishing scenarios.

### Sex determination

We provided the first quantitative relationship between sex ratio at sex differentiation and the abundance of a cohort at the time of first settlement. Population density is considered a key factor for the determination of eel sex, with high densities shifting sex ratio in favour of males. A generally accepted interpretation of the effect of stock density on sex determination is that it might allow the maximization of fitness (Geffroy and Bardonnnet, 2016). As females mature at larger sizes and require more energy to complete the yellow eel phase, an overcrowded habitat would not be able to sustain a female-skewed stock. Some field studies support this hypothesis (Parsons et al., 1977; Laffaille et al., 2006), but without proposing any quantitative relationship. Han and Tzeng (2006), reviewing data from the literature, derived a set of linear relationships linking eel density with the proportion of males in stocks of different catadromous eel species. However, the relationship for the European eel was based only on three data

points, two of which came from cultured stocks characterized by extremely high densities and thus not necessarily representing the typical density range observed in the wild. Our relationship, which is based on a long-term data series from a wild stock, suggests that cohort density has a remarkable effect on sex determination. In the Camargue, a settlement around 94 (90% CI 37–123) elvers  $\text{ha}^{-1}$  corresponds to a balanced (1:1) sex ratio, while increasing settlement density shifts sex ratio at sex differentiation in favour of males. Although extrapolation to stocks characterized by very different environmental conditions should be made with extreme caution, because the actual effect of eel density on sex determination is likely affected by other parameters such as habitat quality and productivity (two crucial factors determining intra-specific competition for space and resources), we are confident that similar relationships may hold also for other eel stocks.

### Fishing mortality

The results of estimating two different coefficients for yellow and silver eels suggest that catchability by fyke nets is higher for silver eels than for yellow eels. Catchability is known to depend on fish behaviour, which can vary remarkably from one stage to another (Quinn and Deriso, 1999). Yellow eels have a sedentary behaviour, while silver eels move actively, seeking the way to the open sea and are therefore more easily intercepted by passive fishing devices like fyke nets. However, as catchability is affected also by a number of local environmental factors (Arreguin-Sanchez, 1996), it is unlikely that parameter estimates for the Camargue lagoons are valid also for other eel stocks. Moreover, while fyke nets are probably the most used fishing gear in Mediterranean eel fisheries, other tools are commonly used across the geographic range of the European eel, such as “lavorieri” (used in Italy for silver eel fishing), trawl nets, or longlines. Although we are not aware of any study reporting estimates of catchability for these latter tools, the inclusion of the associated fishing mortality would be easily integrated in our modelling framework provided that sufficient information is available for the parameterization of the relevant sub-model (see Schiavina et al., 2015 for a discussion). The same holds if different fleet segments exert their fishing pressure on distinct life stages with different fishing gears.

### Silver eel escapement

Downstream migration of silver eels is triggered by a number of environmental variables; however, silver eel escapement can be strongly reduced or completely prevented by the presence of anthropogenic obstacles (Jansen et al., 2007; Trancart et al., 2018). Delayed migration caused by unfavourable hydrological conditions has been often observed in regulated river basins, yet the consequences of such a delay in the migration and the breeding success remain unknown (Acou et al., 2008; Verhelst et al., 2018). Our results provide an example of how to quantify this effect: in the Camargue lagoons migration is possible only when at least three sluice gates (monthly average) are open. However, sluice gate management in the Camargue aims at maintaining a low water level ( $\sim 1\text{--}2$  m) in the lagoons to prevent flooding and avoid damage to surrounding fields. For this reason, gates are closed for most of the year, forcing silver eels to delay their seaward migration. This is yet another example of the trade-off between the two contrasting objectives of sound hydrological management at the local level and species preservation at the global level. As said above, eel escapement may also be impaired by obstacles like hydropower facilities, which can cause mass mortalities of migrating silver eels. Although this is not the case for the Camargue lagoons, this effect can be included in the model via an additional mortality parameter, as discussed in Schiavina et al. (2015).

### Stock assessment

Estimated eel settlement in the Camargue varies around 360 eels  $\text{ha}^{-1}$  per year between 1993 and 2009, with minima of 108 eels  $\text{ha}^{-1}$  in 1993 and 2005 and a maximum of 418 eels  $\text{ha}^{-1}$  in 2000. These figures fall within the broad range of estimates (17 – 1800 eels  $\text{ha}^{-1}$ ) obtained in past studies conducted in very different sites (e.g. Vøllestad and Jonsson, 1988 in a Scandinavian stream; De Leo and Gatto, 1996 in coastal lagoons of northern Italy; Lobon-Cervia and Iglesias, 2008 in a northern Spain river). Differences in effective eel settlement depend on the magnitude of glass eel recruitment from the open sea, which is higher along the Atlantic coasts of Western Europe (Dekker 2000; Bornarel et al., 2018), and habitat productivity, which is generally higher in warmer and brackish waters (Aalto et al., 2016). Our estimate is comparable to that (306 eels  $\text{ha}^{-1}$ ) derived by De Leo and Gatto (1996) for



Valle Campo (a lagoon of the Po river delta, northern Italy) in 1989. However, the estimated standing stock is much lower in the Camargue than in Valle Campo (12 vs. 60 kg ha<sup>-1</sup>, on average). This discrepancy is most likely due to the different fishing policy applied in the two sites, because fishers in the Camargue target both yellow and silver eels, while in Valle Campo they fish only migrating silver eels. In contrast, estimated settlement and productivity are higher in the Camargue than in the IJsselmeer, the largest Dutch watershed (Dekker, 2004).

### **Assessment of spawner production under alternative management scenarios**

The EU Regulation imposes Member States to adopt EMPs to 'reduce anthropogenic mortalities so as to permit, with high probability, the escapement to the sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock' (article 2.4).

This policy is commendable, though not easy to implement. Here, we show how our model can be used to estimate the pristine escapement of silver eels. In the Camargue lagoons it turns out to be ~18 kg ha<sup>-1</sup> per year, which is consistent with pristine silver eel production of other brackish lagoons of the northern Mediterranean (Bevacqua et al., 2015; Schiavina et al., 2015; Aschonitis et al., 2017a). This is a really crucial figure, as it allows us to determine the 40% target (~7 kg ha<sup>-1</sup>) of the EU Regulation, and to use it as a benchmark to assess the consequences of different management scenarios. The present spawner production (averaged between 1999 and 2009) is only 28% of the estimated pristine one. Silver eel escapement would have attained 88% of the pristine production if the fishery had been closed and all obstacles to migration removed.

Interestingly, if the French EMP were rigorously applied to the fishery management of the Camargue lagoons (i.e. if yellow and silver eels accidentally caught outside the period in which fishing is allowed were released without damage) silver eel escapement would attain 6.5 kg ha<sup>-1</sup>, which corresponds just to the 36% of the estimated pristine escapement and is five times the silver eel escapement per hectare recently estimated, in the absence of fishery, for two northern European rivers systems (Poole et al., 2018). The possibility of obtaining 40% of the pristine silver eel production at current recruitment levels, ~1% of the pristine one, is highly debated in the scientific community (ICES, 2018). Our results suggest that accomplishing the EU Regulation targets would be possible through a severe reduction of fishing mortality rates, at least in sites similar to the Camargue lagoons.

### **Applicability of the model to heterogeneous environments**

Our model is spatially implicit and, hence, suited to describe the dynamics of eel stocks in habitats where eel density and environmental features can be assumed to be homogeneously distributed in space, such as coastal lagoons or inland lakes. The hypothesis of spatial homogeneity might provide a satisfactory approximation also for river basins where, due to the depletion of recruitment and the presence of human-made obstacles to upstream migration, the major part of the eel stock is concentrated in the lower part of the basin. In contrast, these assumptions might not hold in more complex river basins: river networks have specific topologies that may determine spatially heterogeneous patterns of habitat suitability, recruitment, and eel productivity, which may prove difficult to describe via a spatially implicit model (Schiavina et al., 2015). Nevertheless, our approach could be extended to describe eel population dynamics also at the scale of an entire river basin, if this can be decomposed into a limited number of homogeneous compartments (e.g. estuary, main stem, minor tributaries, coastal lagoons, inland lakes) and if eel movement among compartments can be adequately quantified. Each compartment would then be characterized by a specific parametrization, since settlement potential, body growth patterns, natural and fishing mortality, maturation and escapement rates, all would possibly vary among compartments according to the spatial patterns of environmental variables (such as water temperature, salinity, and food availability) and eel density. Spatial heterogeneity of eel recruitment could be considered through generalizations of the Beverton–Holt model able to take into account the level of fish aggregation (see Brännström and Sumpter, 2005) or by considering distinct values of settlement potential for the different compartments (Schiavina et al., 2015). Individual movement among compartments could be described as a diffusion process (for instance as in Lambert and Rochard, 2007, who linked eel movement to eel age and inter-compartmental density gradients). A compartmental approach could be used also to describe other heterogeneous systems, like those at the interface between inland waters and the open sea,

where some individuals become residents (either settling in freshwater bodies or completely skipping the freshwater phase) and some become habitat switchers (Daverat et al., 2006).

## Conclusion

Our work provides a modelling framework that can be adapted to describe the demography of different eel stocks. Its generality makes it potentially suitable to describe not only the dynamics of European eel, but also that of other catadromous eel species. The application proposed here exemplifies how a satisfactory description of the continental phase of eel life history can be obtained by combining information already available from the literature with original parameter estimates derived from a rigorous calibration procedure based on available experimental data. The application of the model to specific eel stocks allows decision-makers to forecast the consequences of different management measures on the productivity of the fishery and on the output of spawners. It provides, therefore, a powerful tool to identify more sustainable management policies for these endangered, yet still heavily exploited, fish species.

## Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

## Acknowledgements

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