

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

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

**Key words:** *Anguilla anguilla*; eel management; stock assessment; bootstrap regression; Bayesian probability

## Introduction

European eel (*Anguilla anguilla* L.) is a catadromous and semelparous species which spends most of its life as yellow eel in fresh water, brackish and coastal habitats. When reaching maturity, it metamorphoses to silver eel and returns to the Sargasso Sea in order to spawn and die. The larvae (leptocephalus) drift back to the coastlines and metamorphose into the transparent glass eels, which enter in transitional waters (e.g. coastal lagoons) or go upstream in fresh water habitats (processes of recruitment) and then change to elvers setting the initiation of the yellow eel stage (Tesch 2003; Bonhommeau et al. 2009;

ICES 2014). The European eel population is considered a single, randomly mating population (hypothesis of panmixia) that spawns in the Sargasso sea and returns to the coasts of Europe and north-western Africa (Als et al. 2011).

Long-term records of recruitment for European eel populations from the past five decades indicate a dramatic reduction of 99% magnitude (Dekker 2004; Dekker & Casselman 2014; ICES 2014). Reasons for this decline include habitat loss, pollution, parasitism, increased migration barriers, changes in oceanographic conditions, relocations of glass eels, reduction of available prey in freshwater habitats and overexploitation of fisheries (Feunteun 2002;

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Belpaire et al. 2009; Amilhat et al. 2014; Dekker & Casselman 2014). Conservation efforts have been intensified to establish measures for stock recovery (EU 2007) and to designate management plans to reduce known anthropogenic mortality factors such as eel fisheries (De Leo & Gatto 2001; Bark et al. 2007; Bevacqua et al. 2007, 2009a; Wickström & Sjöberg 2013; Briand et al. 2015). Measures such as the recent application of the moratorium on the export of glass eel in 2010 showed already positive effects on the recruitment (ICES 2014; Briand et al. 2015).

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

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

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

Additionally, there is a lack of information about the oceanic portion of eel life history. For this reason, the majority of demographic models describe only the continental phase. Although eels may occupy

fresh, brackish or salt waters during their continental period, most models deal only with eels in fresh or brackish waters. Some attempts have been made to model the full life cycle using many simplifications in the continental phase (Bonhommeau et al. 2009; De Leo et al. 2009; Pacariz et al. 2014).

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

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

## Materials and methods

### Study site and measurements

The eel fishery in the Comacchio Lagoon of Italy (44°36' N/12°10'E) (Fig. 1a) has been studied since the eighteenth century (Friedlander 1872; Colombo & Rossi 1978; Gatto & Rossi 1979; Rossi 1979; Gatto et al. 1982; De Leo & Gatto 1995, 1996; Melià et al. 2006; Castaldelli et al. 2014). The lagoon is a semi-closed ecosystem and has always been exploited for commercial fishery with no permission for any recreational fishing activity. The silver eel catch in this system represents ~100% of the silver eel migrating population. Additionally, the eel populations are based only on natural recruitment, and no stocking has been conducted either to the Comacchio Lagoon or to neighbouring areas. The lagoon comprises three main basins (Fig. 1a): Valle Campo, Valle Magnavacca and Valle Fossa di Porto, which cover an area of ~10<sup>4</sup> ha. Valle Campo (~1600 ha) is in private ownership and completely separated, while the other two, which constitute the study site (8470 ha), are now a single basin recognised as the most important area for biodiversity conservation within the Regional Park of the Po River Delta of the Emilia-

Romagna Region. The lagoon is connected to the Adriatic Sea by two canals (Bellocchio and Foce) (Fig. 1a) which are hydraulically regulated by gateways where V-shaped screens of selective size, called *lavorieri*, are used to capture silver eels (Fig. 1b). The screens permit the entry of elvers but entrap all silver eels when they begin their migration.

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

As yellow eels cannot be caught by the screens, their monitoring was performed by a set of 20 trap nets evenly distributed over the entire lagoon area. The fishing gear was a modified fyke net, locally called *cogollo*, which is typically used for eel fishing in the shallow lagoons of the northern Adriatic. It consists of a leader, 50 × 1.5 m, that directs the fish towards two conical trap nets positioned at its distal ends. The structure consists of 8 × 8 mm mesh, large enough to prevent blocking by macroalgae, periphyton and detritus, but small enough to prevent the loss of small age class specimens. The mesh allowed smaller elvers to escape from the net, and for this reason, a correction has to be performed for this sampling error.

The nets were monitored every 2 days in September and October, a period when metamorphosis to silver eels is considered complete, preventing overlap of the two monitored groups (van Ginneken et al. 2007).

A total of 2627 yellow and silver eels were caught (73% yellow and 27% silver). Eels were counted and anaesthetised with ice to measure length and weight before being released. Sub-samples of 573 yellow and 366 silver eels were randomly selected for age and sex determination (Tables 1 and 2). Additional measurements for the gonadosomatic index, the hepatosomatic index and the gut index were performed for the specimens of Tables 1 and 2 in order to assess the silvering stage based on the classification by Durif et al. (2005, 2009). All the captured silver eels in the screens were found to be at the V silvering stage, while the silvering stage of eels captured in the trap nets was up to the III and in very few cases (<1%) up to the IV stage (the specimens of IV stage were not included in Table 1). The age of specimens was determined by double reading after grinding and polishing the otoliths (ICES 2009). Age was expressed as the number of years from the elvers' entry into the enclosed waters. As elvers always enter in spring and are captured in autumn, the age classes are given as 0+, 1+, ... X+ (corresponding to the respective parametric numbers AC of 0.5, 1.5, ... X+ 0.5) respectively. Sex was determined by macroscopic examination of the gonads, and when specimens were smaller than 35 cm, microscopic examination of the gonads was performed (Colombo & Grandi 1996;

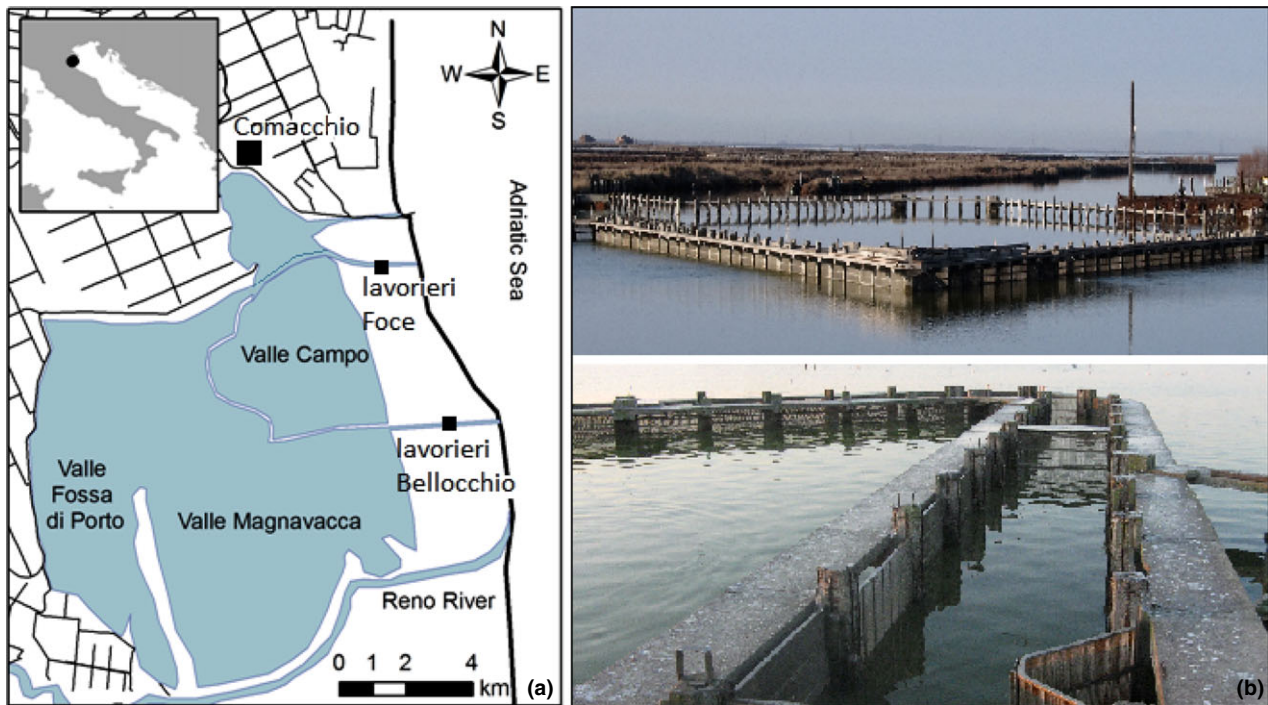


Fig. 1. (a) Study site – Comacchio Lagoon and (b) V-shaped screens ‘*lavorieri*’ of selective size used to capture silver eels.



Table 1. Number of individuals  $N$  per age class, mean length  $L$  (cm) and mean weight  $W$  (g) of yellow eels for different age and sex classes (Total number of yellow eels  $N = 573$ ).

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

Tesch 2003). The eels that had the characteristically lobed Syrsky's organ were recorded as male, those with a typically pleated gonad, as female and those in which reproductive organs could not be distinguished were recorded as undifferentiated.

Additional data of silver eel catches for the period (1960–2013) (Fig. 2) were also collected to provide indirect justifications about the assumptions used in the modelling approaches. According to Fig. 2, the silver eel migrating population has been declined significantly after 1995. During the period 1998–2012, the silver eel population shows extremely low and almost constant abundance which can support the assumption that the density effects on the morphometric characteristics and maturation behaviour were not differentiated during the period 2000–2011 (the population density conditions during this period affect the data of 2011 because the oldest eels belong to 10+ age class, Tables 1 and 2). Additionally, it adequately supports the assumption of constant recruitment, which is prerequisite in many size-age modelling approaches (De Leo et al. 2009).

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

The small age class specimens can escape from fyke nets introducing error in the frequency distribution of individuals per age class of yellow eel population.

The frequency of yellow eels in each age class  $i$  is defined as the ratio  $n_i/N$  from Table 1. The error was corrected using the method of Bevacqua et al. (2009b), in which fyke net selectivity  $\phi$  can be estimated as a function of eel body length and net mesh size using the equation:

$$\phi(L, m) = \{1 + \exp[-\eta(m)(A(L) - A_{50}(m))]\}^{-1}, \quad (1)$$

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

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

$$\begin{aligned} \eta(m) &= \exp(-0.06m - 1.65) \text{ and } A_{50}(m) \\ &= \exp(0.09m + 3.26), \end{aligned} \quad (2a,b)$$

where  $m$  is mesh size (mm).

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

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

Table 2. Number of individuals  $N$  per age class, mean length  $L$  (cm) and mean weight  $W$  (g) of silver eels for different age and sex classes (Total number of silver eels  $N = 366$ ).

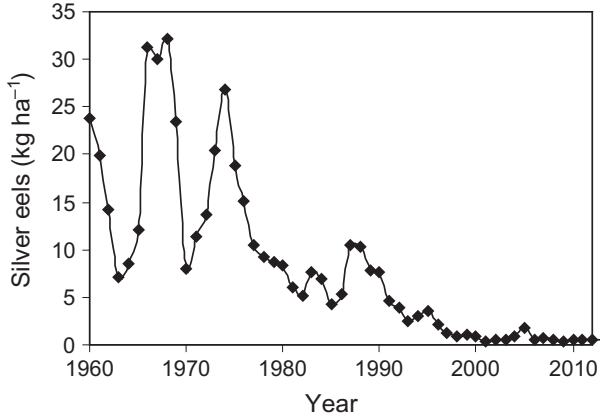


Fig. 2. Silver eel catches (total of the migrating population) expressed as abundance ( $\text{kg ha}^{-1}$ ) for the period 1960–2012.

1979; Bevacqua et al. 2009b):

$$A = \frac{M}{\rho L} \rightarrow A(L) = \frac{M(L)}{\rho L} \quad (3)$$

and

$$M(L) = aL^b \text{ and } A(L) = a\rho^{-1}L^{b-1}, \quad (4a,b)$$

where  $a$  and  $b$  are regression coefficients for  $M$  in  $g$  and  $L$  in  $mm$ . In this study, the morphometric relationship  $M(L)$  (Eq. 4a) was derived from regression using length and weight (equivalent to mass for Eq. 4a:  $W = a \cdot L^b$ ). Log-log plots of length and weight values ( $\log W = \log a + b \cdot \log L$ ) were created using simple linear regression for the identification and removal of outliers before the fitting procedure (Froese 2006). Outliers were identified using as threshold value the studentised residual  $>2$  using the StatGraphics XVII software (Statpoint Technologies, Warrenton, VA, USA).

Additionally, the length–age relationship was examined using a von Bertalanffy growth equation:

$$L = L_{\infty}(1 - e^{-k_L \cdot AC}) + L_0 e^{-k_L \cdot AC}, \quad (5)$$

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

Using the aforementioned equations, correction was performed to the number of individuals  $n_i$  of yellow eel age classes (Table 1) which were affected by fyke net selectivity. The morphometric relationships Eqs 4a and 5 were applied using only the specimens of  $L < 400$   $mm$  to increase their accuracy for the smaller specimens. This threshold was chosen using

indications from selectivity graphs of different mesh sizes obtained by Bevacqua et al. (2009b) and initial trials using the data of this study. After the correction of  $n_i$  values of the age classes affected by selectivity, their values were used to recalculate the frequency  $n_i/N$  of yellow eels per age class, symbolised as  $G_i$ . Correction was not required for the data of silver eels as they were not affected by the fyke net selectivity. The abundance  $S_i$  ( $\text{ind. ha}^{-1}$ ) for each age class  $i$  of silver eels was estimated by multiplying the frequency for each age class  $n_i/N$  from Table 2 with  $f = 0.56 \text{ ind. ha}^{-1}$  ( $S_i = f \cdot n_i/N$ ). The  $G_i$  and  $S_i$  were used for the calculation of (i) the eel survival curve and the survival rates per age class of the entire population to the time of migration, (ii) the stock of yellow eels, (iii) the recruitment and (iv) the rate of metamorphosis from yellow to silver eels.

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

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

$$F' = cAC' + d \text{ and } F = \left[ c(\ln(AC+1))^2 + d \right]^{-2} \text{ for } c, d > 0 \quad (6a,b)$$

The value of 1 in the natural logarithm of  $AC$  transformation was used to solve the equation for  $AC = 0$ . For  $AC = 0$  in Eq. 6b, the value of  $F$  is equal to  $d^{-2}$  which is used in the following steps for the estimation of glass eel recruitment.

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

$$RF_i = \frac{F_i}{F_{i-1}} \quad (7)$$

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

$$G_i = F_i - kS_i \text{ or } G_i/k = F_i/k - S_i \text{ for } k > 0 \quad (8a,b)$$

Equation (8a) using Eq. (6b) can be restated as follows:

$$G_i = \left[ c(\ln(AC_i + 1))^2 + d \right]^{-2} - kS_i \text{ for } c, d, k > 0 \quad (9)$$

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

The estimated values of  $c$  and  $d$  are used in Eq. 6 to describe the survival curve. The value of  $k$  is also used to estimate the relative rate (i.e. values 0–1) of metamorphosis to silver eels  $TR_i$  for each age class according to the following:

$$TR_i = \frac{kS_i}{G_i + kS_i} = \frac{S_i}{Y_i + S_i} \quad (10)$$

## Validation

A method to validate the performance of the model (Eqs 1–10) is to compare the observed and predicted silver eel catch (total migrating population) of the next year. The calibrated model can predict the abundance of silver eels per age class for the next year according to the following:

$$S_i^{j+1} = Y_{i-1}^j \times RF_i \times TR_i \quad (11)$$

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

## Bootstrap regression and Bayesian uncertainty analysis

The Eq. 6b and consequently Eq. 9 were built under the assumption that recruitment was constant during the period, which covers the respective age classes of Tables 1 and 2. Additional uncertainties are also introduced by the corrected  $G_i$  observations using Eq. 1 and the morphometric relationships (Eqs 4a and 5) which can be affected by the variation of population density and environmental factors (Castaldelli et al. 2014). Considering the above, De Leo & Gatto (1995) and De Leo et al. (2009) proposed the use of bootstrap or Monte Carlo techniques in order to explicitly investigate the inserted errors by the above monitoring and modelling assumptions and to assess the uncertainty in parameters estimation. In our study, bootstrap nonlinear regression (NLR) was selected to be used which is based on the generation of a large number of new data sets by randomly sampling data with replacement (Efron & Tibshirani 1993). As the overall modelling approach starts with the morphometric relationships, the bootstrap NLR was performed on Eqs 4a and 5 by applying the 'nls' function (Ritz & Streibig 2008) together with the nonlinear least-squares algorithm 'nl2sol' (Dennis et al. 1981) in R package. The procedure produced 10,000 respective bootstrap pairs of  $a$ ,  $b$  coefficients and pairs of  $L_\infty$ ,  $k_L$  coefficients for Eqs 4a and 5 respectively. The modelling technique continues using either with the 10,000 curves of Eq. 4a or the respective curves of Eq. 5 (De Leo & Gatto 1995; De Leo et al. 2009) (for this study, Eq. 4a was selected because of better performance, while for

Eq. 5, the median values of the curves were used). The bootstrap curves of Eq. 4a were used to develop a respective number of (i) selectivity curves (Eq. 1) and (ii) corrected frequencies of yellow eels per age class  $G_i$ . The bootstrap sets of  $G_i$  frequencies were used to solve Eq. 9 which led to a respective number of  $(c, d, k)$  estimations and consequently a respective number of estimations for (i) the recruitment according to  $d^{-2}/k$  (ind. ha<sup>-1</sup>), (ii) the abundance of yellow eels per age class  $Y_i$  (ind. ha<sup>-1</sup>) according to  $Y_i = G_i/k$ , (iii) the survival rates per age class  $RF_i$  (Eq. 7) and (iv) the rates of metamorphosis to silver eels  $TR_i$  (Eq. 10).

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

The bootstrap sets of  $Y_i$ ,  $RF_i$  and  $TR_i$  parameters of all age classes from 2011 were also used in the validation procedure which produced a respective

number of predictions of the silver eel catches for the next year of 2012. These predictions were also subjected to HPDD analysis. The calibrated model with the data of 2011 was considered successful in the case where the observed value of silver eel catches of 2012 was inside the intervals, which define the 95% of the HPDD of the predicted values by the model.

## Results

### Fyke net effects and estimate of $G_i$ and $S_i$

The coefficients  $a$  and  $b$  of the weight-length relationship (Eq. 4a) were estimated using the specimens of  $L < 400$  mm. From the initial data set of the 2627 specimens, 1725 had  $L < 400$  mm, while 66 were considered outliers. The remaining 1659 observations were subjected to bootstrap regression for the estimation of  $a$  and  $b$  coefficients of Eq. 4a. The weight-length relationship (Eq. 4a) using the median values of the bootstrap curves together with the intervals which define the 95% highest posterior density (HPDIs-95%) is given in Fig. 3a. The respective frequencies and the HPDDs of bootstrap pairs of  $a$  and  $b$  coefficients are given in Fig. 4a and b respectively. The squared correlation coefficient between observed and predicted values of specimens weight from Eq. 4a (using the median values of  $a$  and  $b$  coefficients) was estimated at  $R^2 = 0.91$ .

For the case of length-age relationship (Eq. 5), only 492 observations from specimens with age up to 3+ were used in the analysis because specimens with  $L < 400$  mm exist only in the first four age classes. After the removal of 14 outliers, 478 observations were used in the bootstrap regression. The length-age relationship (Eq. 5) using the median values of

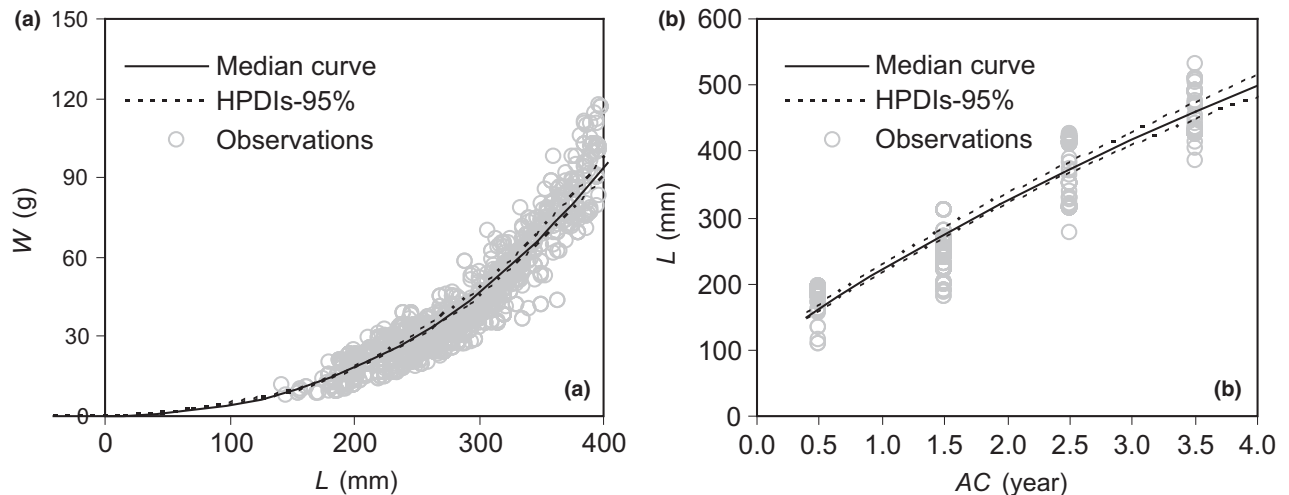


Fig. 3. Results based on the 10,000 bootstraps: (a) weight-length curves for eels with  $L < 400$  mm and (b) length-age curves for eels of age up to 3+ [solid line: median values; dotted lines: 95% highest posterior density intervals (HPDIs-95%)].

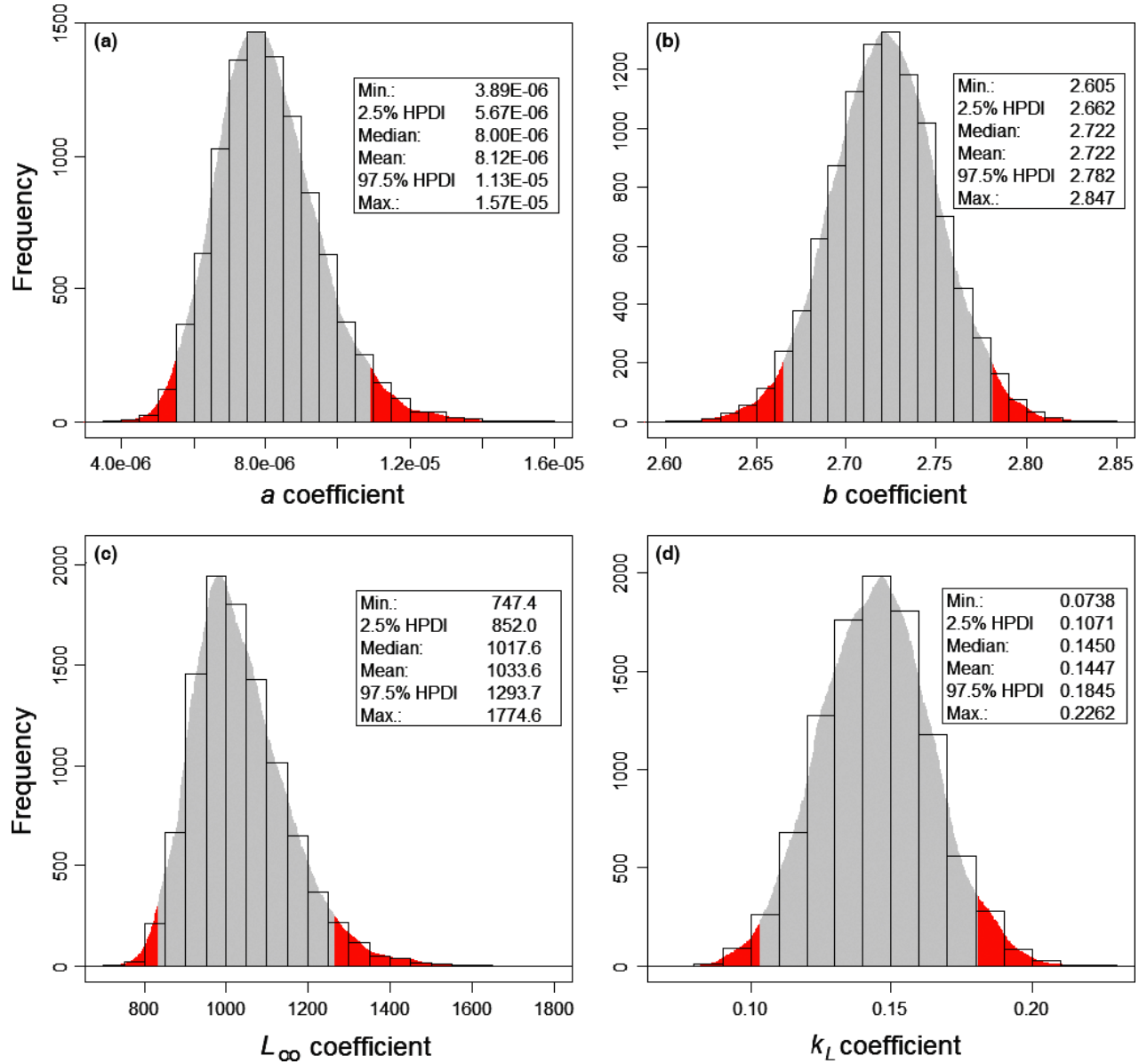


Fig. 4. Frequency and highest posterior density distributions (HPDDs) based on the 10,000 bootstrap estimations of (a)  $a$  coefficient of Eq. 4(a), (b)  $b$  coefficient of Eq. 4(a), (c)  $L_{\infty}$  coefficient of Eq. 5 and (d)  $k_L$  coefficient of Eq. 5 (the grey zone defines the region of the 95% highest posterior density).

the bootstrap estimations together with the intervals which define the 95% highest posterior density (HPDIs-95%) is given in Fig. 3b. The respective frequencies and HPDDs of bootstrap pairs of  $k_L$  and  $L_{\infty}$  coefficients are given in Fig. 4c and d respectively. The squared correlation coefficient between observed and predicted values of specimens length from Eq. 5 (using the median values of  $k_L$  and  $L_{\infty}$  coefficients) was estimated at  $R^2 = 0.84$ .

The abundance per age class of silver eels  $S_i$  (ind.  $ha^{-1}$ ) and the initial frequency  $G_i$  per age class of yellow eels before correction are given in Fig. 5a and b respectively. Using a mesh size of fyke nets equal to  $m = 8$  mm, the parameters of  $\eta(m)$  and  $A_{50}(m)$

(Eq. 2a,b) were estimated at  $0.119 \text{ mm}^{-2}$  and  $53.517 \text{ mm}^2$  respectively. The bootstrap pairs of  $a$ ,  $b$  coefficients of Eq. 4a together with the estimated values  $\eta(m)$  and  $A_{50}(m)$  were used to build a respective number of curves for fyke net selectivity  $\phi$  (Eq. 1). The median values of  $\phi$  estimations together with their 95% HPDIs are given in Fig. 5c. Considering the median estimated length of individuals for each yellow eel age class (Fig. 3b), it was found that the median  $\phi$  values for  $0+$  ( $L_{median} = 141$  mm) and  $1+$  ( $L_{median} = 259$  mm) age classes were equal to 16.98% and 99.93% respectively, while for the rest age classes, the selectivity was 100% (Fig. 5c). Taking into account the bootstrap  $\phi$  curves, a respective



number of corrections were made on the frequency distribution  $G_i$  of yellow eels. The median values of corrected  $G_i$  estimations together with the intervals of 95% highest posterior density (HPDIs-95%) are given in Fig. 5d.

#### Survival curve, stock, recruitment and metamorphosis

The eleven age classes provide a set of eleven observations of  $(G, S \text{ and } AC)_i$  which are used to estimate the three unknown parameters  $c, d$  and  $k$  after fitting Eq. 9. The fitting procedure for Eq. 9 was performed using each one of the 10,000 cases of  $G_i$  frequencies (Fig. 5d) and the one data set of  $S_i$  values (Fig. 5a). This procedure produced a respective number of

$(c, d, k)$  estimations and a respective number of recruitment estimations for 2011 as  $(\text{ind. ha}^{-1})$  according to the parameter  $d^{-2}/k$ . The frequencies and HPDDs of bootstrap sets of  $c, d, k$  and  $d^{-2}/k$  coefficients together with their intervals of 95% highest posterior density (HPDIs-95%) are given in Fig. 6a–d respectively. The squared correlation coefficient between observed and predicted values of the corrected  $G_i$  values from Eq. 9 (using the median values of  $c, d, k$  coefficients) was estimated at  $R^2 = 0.95$ .

The corrected  $G_i$  frequencies (Fig. 5d) together with their respective  $k$  values (Fig. 6c) obtained from Eq. 9 were used to generate a respective number of estimations for the abundance of yellow eels per age

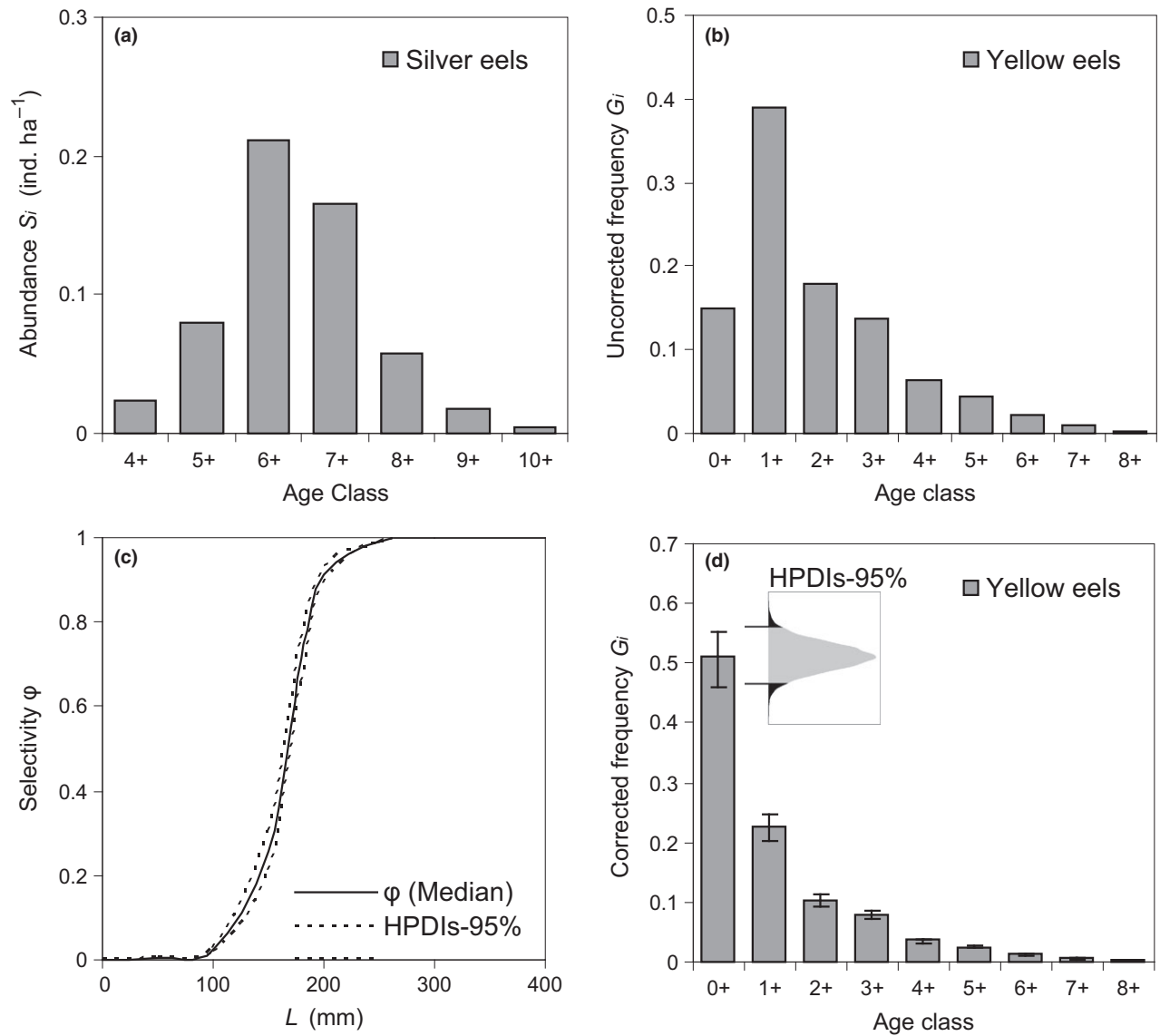


Fig. 5. (a) Abundance per age class  $S_i$  (ind. ha<sup>-1</sup>) of silver eels, (b) initial uncorrected frequency  $G_i$  of yellow eels per age class  $i$ , (c) the median values of the 10,000 selectivity curves  $\phi$  Eq. (1) together with their HPDIs-95%, (d) the median values of the 10,000 corrected frequencies  $G_i$  together with their HPDIs-95%.

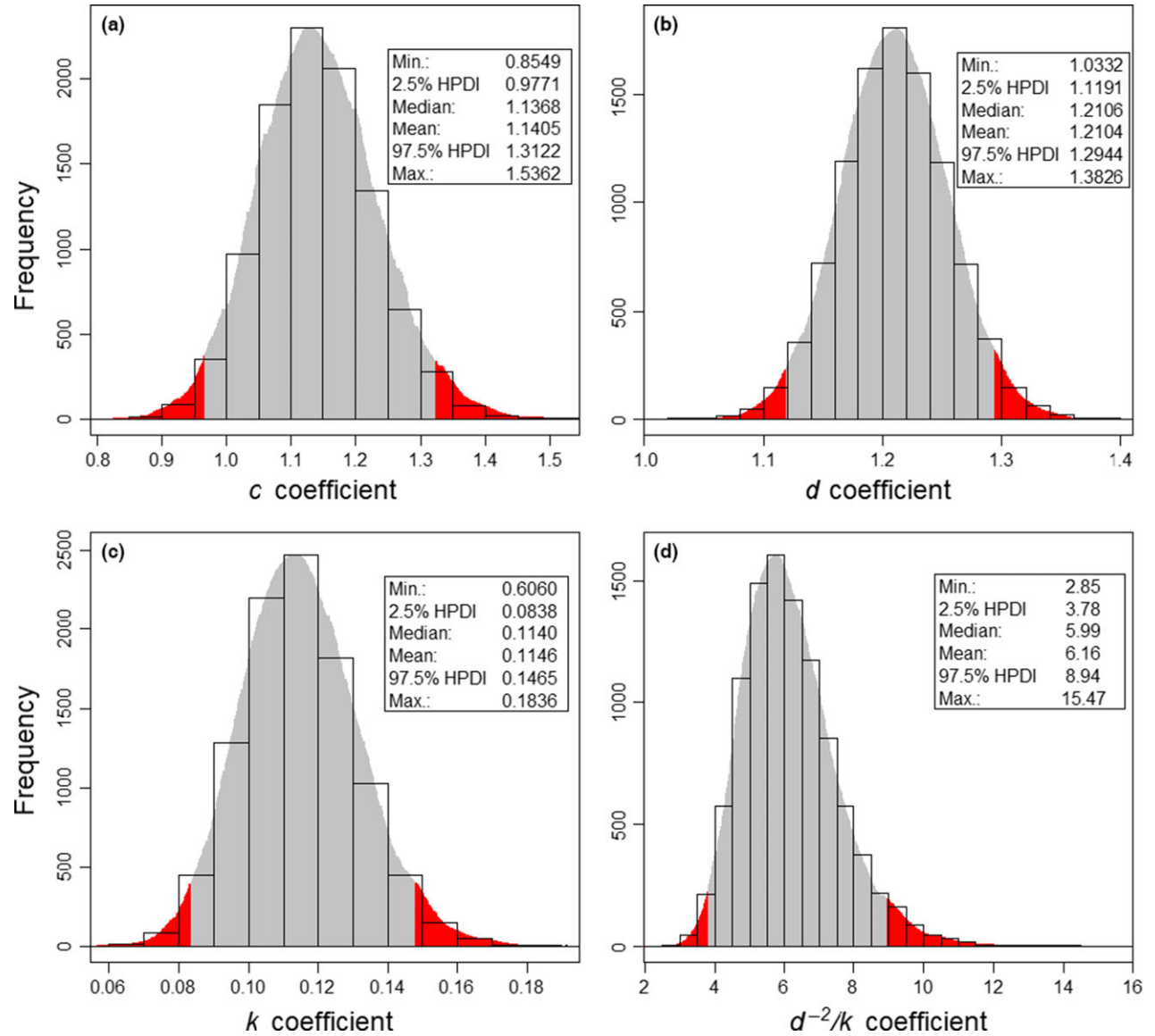


Fig. 6. Frequency and highest posterior density distributions (HPDDs) based on the 10,000 bootstrap estimations of (a)  $c$  coefficient of Eq. 9, (b)  $d$  coefficient of Eq. 9, (c)  $k$  coefficient of Eq. 9 and (d)  $d^{-2}k^{-1}$  which is equivalent to the estimated recruitment of 2011 as ind.  $ha^{-1}$  (the grey zone defines the region of the 95% highest posterior density).

class  $Y_i$  (ind.  $ha^{-1}$ ) according to  $Y_i = G_i/k$  (Fig. 7a). Using Eq. 8b, a respective number of estimations of  $F_i/k$  was derived (abundance of both yellow and silver eels per age class as ind.  $ha^{-1}$ ), and they are given in Fig. 7b, while the recruitment of 2011, before the catch of silver eels, was estimated at 5.99 ind.  $ha^{-1}$  according to the median value of  $d^{-2}/k$  (Figs 6d and 7b).

A respective number of bootstrap survival rates  $RF_i$  (Eq. 7) and metamorphosis rates  $TR_i$  (Eq. 9) per age class were estimated, and they are given in Fig. 7c and d respectively. The survival rate  $RF_i$  of the 0+ age class was calculated using the estimated recruitment, and it was found higher than the survival of 1+, 2+... age classes (Fig. 7c). This result

occurred because the population of 0+ age class, which was sampled during September–October of 2011, is composed by the same specimens which arrived as glass eels through the natural recruitment during spring of 2011. Thus, the survival rate of 0+ age class is a half-year rate and not a full-year rate (as in the case of the rest age classes). The half-year rate corresponds only to the warm season, while it does not include the winter period where frost is an additional factor for mortality increase especially in the case of elvers [mortality because of low water temperature may start to appear even from 12 °C for *A. Anguilla* according to Wu et al. (2010)]. The above fully justify the higher value of half-year survival rate of the 0+ class in comparison

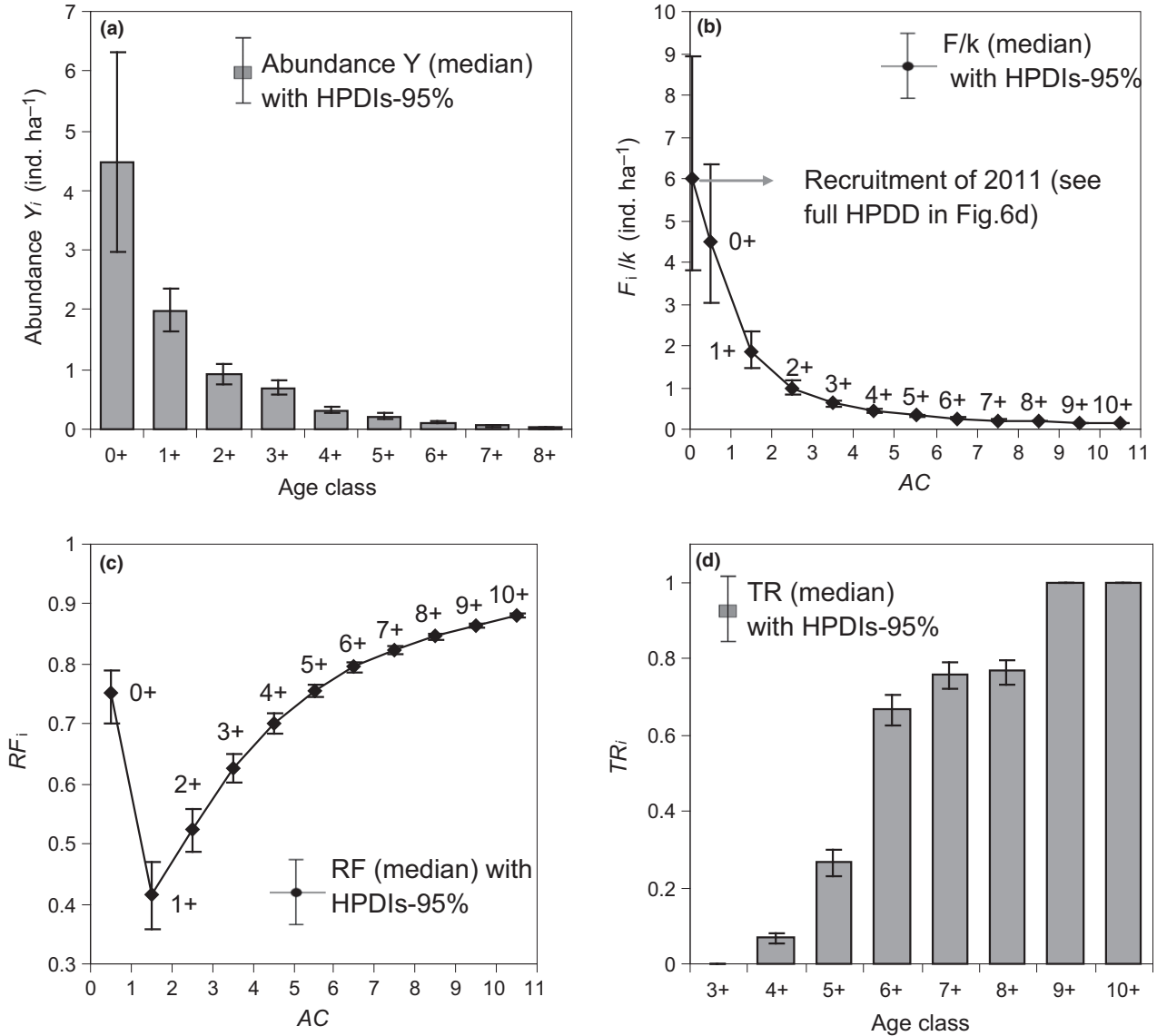


Fig. 7. (a) Abundance per age class  $Y_i$  (ind. ha<sup>-1</sup>) of yellow eels together with their HPDIs-95%, (b) abundance per age class  $F_i/k$  (ind. ha<sup>-1</sup>) of both yellow+silver eels together with their HPDIs-95%, (c) survival rates per age class  $RF_i$  together with their HPDIs-95% and (d) metamorphosis per age class  $TR_i$  to silver eels together with their HPDIs-95%.

with the full-year rates of some of the next age classes (e.g. 1+ to 5+ in Fig. 7c) which are affected by winter effects. The above contradict the assumption of De Leo & Gatto (1995) who assumed that natural mortality during winter is negligible because eels can strongly reduce feeding activities and metabolic rate by entering to a state of torpor. Indeed, eels respond in such way to overcome cold water conditions by moving to deeper waters >5 m (Westerberg & Sjöberg 2014), but the mortality because of low water temperature cannot be considered negligible as high mortality events have been recorded in the lagoon in periods of frost (Rossi & Cataudella 1998). The probability of such phenomena is quite high in Comacchio lagoon because of its shallow water depth (0.5–1.5 m).

The total abundance of yellow eels was estimated at 8.77 ind. ha<sup>-1</sup> (sum of age classes of Fig. 7a), while the total abundance of the population (yellow + silver) before migration was estimated at 9.33 ind. ha<sup>-1</sup> (sum of 8.77 + 0.56 ind. ha<sup>-1</sup>). The stock of yellow eels remaining in the lagoons after silver eel migration in 2011 was estimated at 0.66 g ha<sup>-1</sup> based on the weights of each age class of yellow eels (Table 2), which is equal to a total of 5601 kg after extrapolation for the entire lagoon.

Validation using the silver eel catches of 2012

Equation 11 was used to estimate the abundance  $S_i^{j+1}$  (ind. ha<sup>-1</sup>) per age class of silver eels for 2012

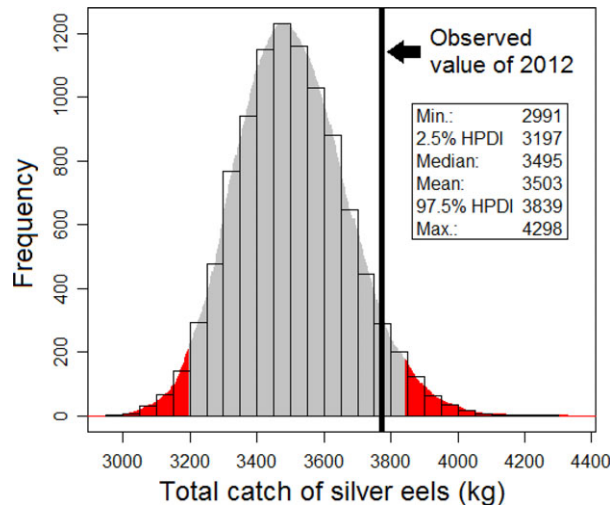


Fig. 8. Predicted values of silver eel catch of 2012 together with their HPDIs-95% and comparison with the respective observed value.

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

## Discussion

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

For example, the preliminary analysis for the derivation of the survival curve and the adoption of the final form of Eq. 6 was based on the corrected  $G_i$  values of the yellow eel age classes in which metamorphosis to silver eels was not observed. As silver eels below the age 4+ were not found in our study, the preliminary analysis for the development of the survival curve was based on four classes (four observations). This number of observations is satisfactory for this type of problem, as in many occasions they

can be fewer because transformation to silver eels may occur even in the 3+ age class (Rossi 1979; Lafaille et al. 2006). If we also consider the fact that some of the initial  $G_i$  values were corrected because of the selectivity of the fyke nets (one was corrected in our case), then the real and correct observations of  $G_i$  can be even fewer. An additional value that could be used is the quantitative measurement of recruitment, but in this case, the  $G_i$  values correspond to frequency while recruitment is considered directly as abundance, and these two parameters are not comparable as the conversion parameter  $k$  is unknown ( $k$  is estimated in the next steps of the mathematical procedure). If recruitment is a known parameter, a prediction correction analysis has to be performed to correct the form of the survival curve. In our case, the proposed survival curve worked well to identify the population dynamics, but its ability to estimate the recruitment must be further investigated as recruitment measurements were not available. Further investigations on the theoretical concept are also required for the validity of the procedures in the section which describes the development of selectivity curve as local environmental conditions and fish behaviour are also likely to affect fyke net selectivity (Naismith & Knights 1990a,b; Desprez et al. 2013).

Semi-closed lagoons (such as Comacchio), which are connected to the sea only through managed canals, facilitate the monitoring of silver eels migration, but a quantitative assessment of recruitment is restricted for various reasons. The recruitment takes place in a 3-month period (for Comacchio, this period is from February to April; unpublished data), and all the possible pathways, which connect the lagoon to the sea, must be blocked on the whole cross section. Blockage is performed with fine mesh nets (2 mm size) connected to fyke nets to capture glass eels. Such attempts for quantitative measurements are impossible in practice because (i) the small size of glass eels allows them to exploit any possible opening to enter in the lagoon increasing the number of nets needed, (ii) it is almost impossible to keep stable, clean and effective a 2-mm barrier net for such a long time in swift waters because their mesh may get obstructed by debris and be washed away by the strong tidal currents and (iii) the use of such structures for a long time may cause implications on ecosystem functioning (e.g. to impede other species recruitment, decrease in the tidal activity etc.). A more detailed description of the factors, which regulate glass eel recruitment, and the techniques that can be used for sampling and abundance estimations are given in the study by Harrison et al. (2014). Drouineau et al. (2016) also proposed the use of recruitment indices to overcome the aforementioned problems. The use of such indices can assist the



evaluation of models like the one of this study, but they require more years of recruitment observations.

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

Additional problem in this study was the low number of observed males (~1%) which is attributed to the low eel population density that favours female dominance (Davey & Jellyman 2005). Sexual dimorphism is usually considered in such models, but in our case, it was not applied because of the low number of male specimens. During the procedure of outliers removal, before the fitting procedure of Eqs 4a and 5, it was observed that almost all of the few observations from male specimens in the data were excluded as outliers. Thus, the modelling approach, which was followed in this study, described the population dynamics of a female dominated population. For eel populations with higher % of males, which allow robust analysis of their morphometric characteristics, the inclusion of sexual dimorphism must be included in the modelling approach (De Leo & Gatto 1995).

The application and validation of the proposed modelling approach can be performed only when the migration of silver eels is fully monitored in such a way to obtain their total population abundance (parameter  $f$ ). During the validation procedure, it was assumed that the  $RF_i$  and  $TR_i$  rates remain the same for the next year. This assumption can be considered

valid when there is no significant variation in the population density between the calibration and validation years. In our case, this assumption was indirectly considered valid by Fig. 2.

The application of the proposed modelling approach and the monitoring data sets of this study provided significant information about the recent conditions of eel population in the Comacchio lagoon allowing the comparison with scientific studies of the past. The data presented in Tables 1 and 2 were used by Castaldelli et al. (2014) to analyse the length-weight, length-age relationships and feminisation of 2011 in comparison with previous studies which were conducted using data from the 1970s and 1980s (Rossi 1979; De Leo & Gatto 1996). The results showed faster maturation rates (fewer age classes) and higher feminisation (reaching 99%), for the population of 2011 in comparison with the past conditions which indicates that the population density was reduced to critical levels (Colombo & Rossi 1978; De Leo & Gatto 1996; Svedäng et al. 1996; Desprez et al. 2013). The critical conditions of the population density are verified by the records of silver eels catches of the period (1960–2013) which show evident collapse of the population during 1990s (Fig. 2). For the period 1998–2013, the migrating population of silver eels is stabilised to the lowest observed values with a mean  $\pm$  SD. equal to  $0.68 \pm 0.36 \text{ kg}\cdot\text{ha}^{-1}$ , while for the period of 1960–1997, it was  $11.8 \pm 8.6 \text{ kg}\cdot\text{ha}^{-1}$  (Fig. 2). The comparison between the two periods indicates a reduction of silver eels approximately to 94%. Further comparison was also performed between the estimated recruitment of 2011 by our modelling approach and the estimated recruitment using data from 1989 (De Leo & Gatto 1995, 1996, 2001; De Leo et al. 2009). Using a bootstrapping procedure, De Leo et al. (2009) showed that the highest probability of recruitment intensity for 1989 is in the range between 50 and  $100 \text{ ind. ha}^{-1}$ , which is more than ten times higher than the estimated value of  $5.99 \text{ ind. ha}^{-1}$  in 2011.

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

European eel population. Decision-makers and scientists, who are responsible for the development of management plans for the recovery of European eel population, can exploit the advantages of such semi-closed lagoons to analyse the potential consequences of different conservation strategies.

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