A global viability assessment of the European eel

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Introduction

Developing effective conservation policies for endangered species requires a solid understanding of how the interaction between multiple threats affects population viability and the ability to foresee the response of population dynamics to alternative management scenarios (e.g. Lawson *et al.*, 2010; Conlisk *et al.*, 2012). This is particularly challenging in the case of migratory species, whose life cycle spans across very different habitats, and whose dynamics are strongly affected by a set of natural and anthropogenic pressures encompassing different time and space scales (e.g. Crozier *et al.*, 2007; Seminoff & Shanker, 2008). An epitomic example in this respect is given by the European eel (*Anguilla anguilla*), a catadromous fish that is distributed all over Europe and North Africa and tolerates a wide range of environmental conditions. Despite the extraordinary adaptability of this fish, the global European eel stock underwent a sharp decline in the last decades, and in 2010, *A. anguilla* was listed as critically endangered by the International Union for the Conservation of Nature and Natural Resources (Jacoby & Gollock, 2014). There are concerns about the conservation status of this species not only at the biological and ecological level, but also for its socio-economic importance, as eels sustained thousands of small-scale fisheries (Dekker, 2003a). To safeguard the global eel stock, the European Council issued a Regulation (EC 1100/2007) with the aim to reduce anthropogenic sources of mortality and increase the abundance of spawners.

Identifying the causes of European eel decline and devising effective measures to support the recovery of the stock are particularly challenging due to the extraordinary life cycle of this fish. *A. anguilla* is a panmictic species (Als *et al.*, 2011): after spawning in the Sargasso Sea, within the North Atlantic gyre, eel larvae follow the Gulf Stream, the North Atlantic Drift and, possibly, the Azores Current towards continental waters of Europe and North Africa, where they

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metamorphose into glass (unpigmented) eels. After reaching coastal waters, estuaries, lagoons, rivers and lakes, they turn into yellow (pigmented) eels and remain in continental waters, in some cases moving across different habitat types (Daverat *et al.*, 2005; Panfili *et al.*, 2012), until the onset of sexual maturation. Maturing eels (silver eels) migrate back to reproductive areas, where they eventually mate and die. Such a complex life cycle exposes eels to a range of stressors, including habitat loss and pollution, parasitic diseases, overexploitation and changes in ocean conditions (Knights, 2003; Dekker, 2004; Lefebvre *et al.*, 2004; Friedland *et al.*, 2007; Kettle *et al.*, 2008a; Bonhommeau *et al.*, 2008a,b; Geeraerts & Belpaire, 2010; Baltazar-Soares *et al.*, 2014). Stress factors act at a very local scale during the continental phase of the life cycle, while the oceanic phase is mainly affected by factors acting at a global scale. The interplay between local and global stressors raises intriguing cross-scale issues, making it difficult to predict the actual effectiveness of conservation plans in the long run.

In recent decades, a number of studies have focused on the main features of the continental phase of the eel's life cycle, such as body growth (Poole & Reynolds, 1996; Melià *et al.*, 2006a,b, 2014; Daverat *et al.*, 2012), density-dependent survival, dispersal and sex determination (Moriarty *et al.*, 1990; De Leo & Gatto, 1996; Lambert & Rochard, 2007; Lobón-Cerviá & Iglesias, 2008; Bevacqua *et al.*, 2011a,b; Schiavina *et al.*, 2015), fishing mortality (Åström & Dekker, 2007; Bevacqua *et al.*, 2007, 2009, 2012), sexual maturation (Vøllestad, 1992; Durif *et al.*, 2005; Bevacqua *et al.*, 2006) and spawner production (Vøllestad & Jonsson, 1988; De Leo & Gatto, 1995; Bevacqua *et al.*, 2007). In contrast, models describing the oceanic phase have been much scarcer until very recently and have mainly analysed the correlation between aggregated indices of recruitment, oceanic circulation and environmental features (Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008a; Kettle *et al.*, 2008a; Durif *et al.*, 2010) or simulated the spatiotemporal dynamics of larval migration (Kettle & Haines, 2006; Bonhommeau *et al.*, 2009a,b; Zenimoto *et al.*, 2011; Melià *et al.*, 2013).

Åström & Dekker (2007) made the first attempt to model the complete life cycle of the European eel, including both the continental and the oceanic phases. However, their model did not account for some key features of European eel biology, such as the variation of vital rates across biogeographic regions, which are critical to determine spawner production at a continental scale. In addition, although their model was parameterized according to reasonable hypotheses on eel life-history traits and in agreement with the established knowledge on eel demography, it was not calibrated against historical data. Recent studies have provided

updated and/or previously not available information for the development of a full life cycle model. Bonhommeau *et al.* (2009b) provided a first estimate of the average number of recruits produced per spawner, while Melià *et al.* (2013) obtained a preliminary estimate of the abundance of the spawning stock. Andrello *et al.* (2011) built, for the first time, a demographic model allowing for spatial variability in vital rates over the entire European eel range, which was used to cast light on the genetic structure of the stock. However, none of these studies investigated the long-term dynamics of the stock.

In this work, we used state-of-the-art knowledge on eel biology and ecology to develop the first age-structured, full life cycle model of the global European eel stock and calibrated it against available historical information. Following Andrello *et al.* (2011), we represented the continental stock as a metapopulation structured into three major subpopulations inhabiting three macro-geographic regions: the Mediterranean basin (MED), the Atlantic region (ATL) and the North and Baltic seas (NB). These regions, which correspond approximately to the Mediterranean, Atlantic and Boreal biogeographic regions as defined by the European Environment Agency (EEA 2002), are characterized by different habitat availability, recruitment abundance, anthropogenic impacts and environmental characteristics. The model explicitly accounts for the main features of the eel's life cycle: density dependence of glass eel settlement, sex determination and survival; large variation in body growth patterns and natural mortality rates across different habitats; and sexual dimorphism in body growth and size at maturity. We performed a rigorous model calibration using a time series of commercial catches reconstructed from historical eel landings statistics and used it to hindcast global catches, standing stock and spawner escapement since the 1970s. Then, we combined the model with a function linking spawner escapement with glass eel recruitment (reproductive success) to project the long-term dynamics of the stock into the current century under different management scenarios. As model projections can be affected by alternative assumptions on the reproductive success, we performed a sensitivity analysis of model outcomes with respect to the key parameter of this function. Finally, we discussed the implications of our results for the conservation of this endangered species.

Materials and methods

Available data

Habitat. Coastal and inland waters of Europe and North Africa, which provide the habitat for the continental phase of

the eel's life cycle, underwent dramatic transformations in the last hundred years (Kettle *et al.*, 2011), and reliable hindcasting of eel population dynamics cannot neglect this phenomenon. Moriarty & Dekker (1997) provided the first, and to date unique, quantitative assessment of the historical distribution of *A. anguilla* across Europe. We used this information, along with that provided in the review of North African wetlands by Hughes & Hughes (1992), to quantify the extent of suitable habitat preceding the major habitat changes occurred during the second half of the twentieth century. From here below, we refer to this reference point as 'baseline' eel habitat (see section S1 in the Supporting information for further details).

A large portion of the suitable eel habitat has likely been lost during the second half of the past century, due to land reclamation, construction of dams and other barriers, deterioration of water quality and anthropogenic changes in the hydrological cycle (Kettle *et al.*, 2011). The exact time horizon over which this loss has taken place is not easy to determine but, on the basis of the available body of information (see Kettle *et al.*, 2011 for a review), we assumed that it occurred mostly between the 1950s and the 1990s in the northernmost parts of the eel distribution range (ATL and NB) and in a narrower time period (between the 1970s and the 1990s) in southern Europe and North Africa (MED). On the contrary, it was not possible to retrieve statistics on the proportion of habitat loss (compared to the baseline extent) in the three regions. Therefore, we assumed it as an unknown parameter to be estimated via the calibration procedure described in the section 'Model calibration'.

Glass eel recruitment. We reconstructed the pattern of eel recruitment over the period 1950–2010 on the basis of the European glass eel recruitment index used by Bonhommeau *et al.* (2008a). The index is based upon the four longest time series of glass eel recruitment available from the ICES Working Group on eel (ICES, 2014), that is from the Ems River (Germany), Den Oever (the Netherlands), Loire River (France) and Nalón River (Spain), and is calculated by averaging the four time series after normalization (i.e. dividing each series by its mean over the whole period). Despite some biases deriving from the absence of data from the MED and NB areas, and from some data gaps in the latest years of the series (the Ems time series ended in 2001 and fishery restrictions truncated the Loire time series after 2008), we decided to rely on this index, which has already been used in previous peer-reviewed work and whose trend is fully consistent with the general pattern emerging from the number of smaller data series available from throughout the distribution range of the species (ICES, 2014).

To transform this index of relative abundance into absolute numbers, we used Dekker's (2000) estimate that the average glass eel recruitment in the early 1990s was ca. 2 billion eels per year (including glass eels subsequently removed by fishing). Therefore, we divided this figure by the average value of the recruitment index over the same period (1990–1994) to derive a proportionality coefficient (=7.57 × 10^9) that was used to reconstruct the time series of recruitment from that of the index. Then, we allocated glass eel recruitment to the three

regions. According to the available information on the latitudinal distribution of glass eel arrivals, fishing pressure and restocking, that is the translocation of glass eels from one region to another (Dekker, 2000, 2003a; Melià *et al.*, 2013), we hypothesized that, between 1950 and 2010, 19%, 4% and 22% of the global glass eel recruitment entered the inland waters of the MED, ATL and NB regions, respectively, while the remaining 55% was removed by glass eel fisheries in the ATL region. Further details on the glass eel allocation procedure are provided in section S2 (Supporting information), along with the reconstructed time series of recruitment to the three regions (Fig. S1).

Adult eel catches. FAO statistics on European eel landings, disaggregated by country, cover the period from 1950 to 2011. However, FAO estimates are considered to be scarcely reliable, due to frequent data gaps. For this reason, Dekker (2003b) reviewed FAO statistics and developed a statistical model to reconstruct a time series of eel catches aggregated over the whole distribution range of the species. Therefore, we used Dekker's reconstructed time series (encompassing the period 1950–2004) to represent global catches, and we used FAO statistics only to determine the proportion of the catch to be allocated to the three regions, assuming that the proportion of nonreported catches is reasonably similar across them. Note that neither FAO landings statistics nor Dekker's (2003b) reconstructed time series report glass eel and adult eel catches separately. However, Dekker (2000) pointed out that while in the MED and NB regions glass eel catches are negligible compared with those of adult eels, in the ATL region, the proportion of glass eel represents 25% (in biomass) of the total catch. For this reason, we corrected the time series for the ATL region ascribing 25% of the reported catches to the glass eel fishery. The reconstructed time series of adult eel catches is shown in Fig. S2 (Supporting information).

Model structure

We described the population dynamics of the global European eel stock with a modified version of Andrello *et al.*'s (2011) model. The model encompasses the two major phases of the eel's life cycle (Fig. 1): the continental phase, extending from the recruitment of glass eels to continental waters until the migration of silver eels to the ocean, and the oceanic phase, during which silver eels congregate in the spawning areas of the Sargasso Sea for reproduction, and eel larvae subsequently disperse across the ocean to eventually reach their settlement places throughout the continental distribution range of the species. For the sake of brevity, we concisely describe in the following the general structure of the model; the reader is referred to section S3 (Supporting information) for model formulae and further details.

The continental phase was described by subdividing the stock into three subpopulations to account for large-scale variation of vital rates across the distribution range of the species. Each subpopulation was further subdivided into five classes, corresponding to sex and development stages: sexually undifferentiated yellow eels (YU), yellow females (YF), yellow
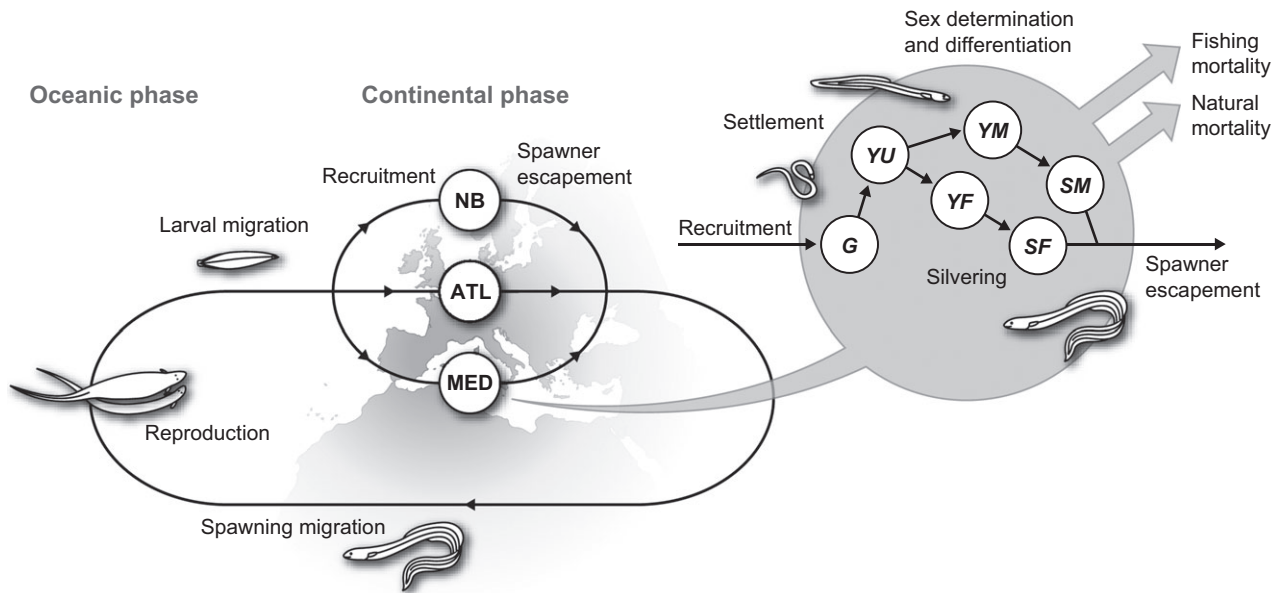
Fig. 1 Full life cycle model of the global European eel stock. During the continental phase, the global stock is subdivided into three subpopulations: Mediterranean basin (MED), Atlantic region (ATL) and North and Baltic seas (NB). Each subpopulation is further subdivided into sex and development stages, as depicted in the balloon on the right side for the MED subpopulation (G: glass; YU: yellow undifferentiated; YF: yellow female; YM: yellow male; SF: silver female; SM: silver male). Further details are provided in section S3 (Supporting information).

males (YM), silver females (SF) and silver males (SM). The dynamics of each subpopulation was described by a set of recursive equations (see section S3.1) incorporating, through specific submodels, the key life-history traits affecting eel demography: glass eel settlement (S3.2), body growth (S3.3), survival (S3.4), sex determination and differentiation (S3.5), and sexual maturation (S3.6). Parameter values for the different submodels, differentiated by region, were derived from published work on eel demography (Dekker, 2000; Bevacqua et al., 2007; Andrello et al., 2011; Schiavina et al., 2015).

As for the oceanic phase, silver eel escapement from continental waters (section S3.7) towards the Sargasso Sea was computed as the sum (across the three regions) of all eels surviving natural and fishing mortality until the onset of sexual maturation. Although the migration success may differ from one region to another, in the absence of empirical evidence and literature data to tune this parameter, we assumed as a first approximation that it was the same for the three subpopulations. The abundance of the spawning stock was eventually linked to glass eel recruitment to continental waters 3 years later (McCleave, 2008; Bonhommeau et al., 2010; Melià et al., 2013) via the stock–recruitment relationship proposed by Andrello et al. (2011), which accounts for size-dependent fecundity and mating success depending on the sex ratio of spawners as follows:

$$G(t+3) = \sigma_S \cdot P_m \cdot f \cdot SB(t) \cdot \sigma_L \qquad (1)$$

where σ_S is the survival of silver eels during the oceanic migration, P_m is the probability of mating (see below), f is the relative fecundity (i.e. the number of eggs produced by a female per unit body mass), SB is the spawning biomass of female eels (calculated via the morphometric relationship described in section S3.1), and σ_L is the survival of eel larvae from egg hatching until metamorphosis to the glass eel stage. We expressed P_m as a function of sex ratio as follows: $P_m = 4\rho(1 - \rho)$, where ρ is the proportion of females (in numbers) in the spawning stock (Andrello et al., 2011). Note that P_m is maximum (and = 1) when $\rho = 1/2$, that is when the sex ratio is balanced (1:1). The product $\sigma_S \cdot f \cdot \sigma_L$ represents the number of recruiting glass eels produced per kg of migrating silver female at the optimal sex ratio and can be considered as a measure of the maximum reproductive success (from now on referred to as MRP). Using the parameter values provided by Andrello et al. (2011), namely $\sigma_S = 13\%$, $f = 1.6 \times 10^6$ eggs kg^{-1} and $\sigma_L = 0.15\%$, one obtains a MRP corresponding to 303 glass eels per kg of spawner. At the end of their oceanic migration, glass eels reaching the European shores disperse over the geographic range of the species. Their settlement success in continental habitats (see section S3.2) is described as a density-dependent function (Bevacqua et al., 2007, 2011a), with settlement potential (i.e. the maximum density of glass eels that can potentially settle in a suitable habitat) differentiated by geographic region (Schiavina et al., 2015).

Model calibration

The majority of model parameters was set according to, or derived from, data and information available from the peer-reviewed literature. However, no information was available to derive reliable estimates for two crucial parameters: the proportion of habitat lost and the settlement potential of glass eels in each of the three geographic regions. Therefore, we esti-

mated these two unknown parameters through the numerical calibration of the model component describing eel dynamics in the continental phase. Specifically, we used the reconstructed time series of glass eel recruitment as an input to the model and produced, as an output, annual catch estimates in the three regions to be contrasted with the observed catches. Therefore, calibration of the unknown parameters was performed without accounting for the oceanic phase of eel dynamics (silver eel migration, reproduction and migration of larvae back to continental waters). The calibration process is summarized in Fig. 2, and further details are provided in section S4 of the Supporting information.

To account for the effect of habitat loss on glass eel settlement, we contrasted two possible mechanisms: the first is that glass eel arriving in sites that have become unsuitable, or that are not accessible any more due to barriers to eel migration, are doomed to die. This is equivalent to assuming that habitat loss does not affect eel density within the residual suitable range, but it determines a reduction of the overall settlement by decreasing the extent of the suitable area. Alternatively, we considered that eels are able to leave unsuitable or inaccessible sites and seek for the next suitable habitat within the same region. This is equivalent to assuming that habitat loss does not affect the abundance of settlement directly, but that it has an indirect effect by increasing eel density within the residual suitable range (thus decreasing the proportion of eels successfully settling in continental waters via density-dependent mechanisms).

To test for the significance of habitat loss trends across regions and geographic variation in settlement potential, we contrasted a full version of the model, with different values of settlement potential and proportion of habitat lost in each geographic region, with a set of reduced models in which one or both parameters were set to the same value for all regions, or habitat loss was set to zero. Overall, we compared the perfor-

mances of 10 models (incorporating different hypotheses about habitat loss and settlement potential; see Table 1) and selected the best model, that is the one providing the best compromise between goodness of fit and parsimony, through a model selection procedure based upon Akaike information criterion. The best model was then used to project the dynamics of the stock into the future, as described in the following section.

Projecting the fate of the European eel

After calibrating and selecting the best demographic model for the continental phase, we coupled it with the oceanic phase and projected the fate of the global European eel stock (and the relevant fishery yield) over the current century (2010–2100) under different management scenarios. The workflow of the analysis is depicted in Fig. 3. We assumed no further loss in eel habitat with respect to 1990 and considered nine possible management scenarios deriving from the factorial combination of (i) three different exploitation rates and restocking strategies for glass eels and (ii) three different exploitation rates for adult eels, as described in Table 2.

Glass eel scenarios are represented by the proportion of total glass eel recruitment that enters each geographic region. In the 'historical' scenario, we considered the reconstructed distribution of glass eel recruitment (which accounts for translocation and restocking from the ATL to the MED and NB regions) and the fishing pressure of the last half of the twentieth century. In the 'unexploited' scenario, we assumed no glass eel fishing and that most (76%) of the glass eels settle in the ATL region (which was likely the case until the first half of the past century, as suggested by demographic and oceanic studies: Dekker, 2000; Kettle *et al.*, 2008b; Bonhommeau *et al.*, 2009a; Melià *et al.*, 2013). In the 'stocking' scenario, we considered the extreme case in which the overall glass eel recruit-
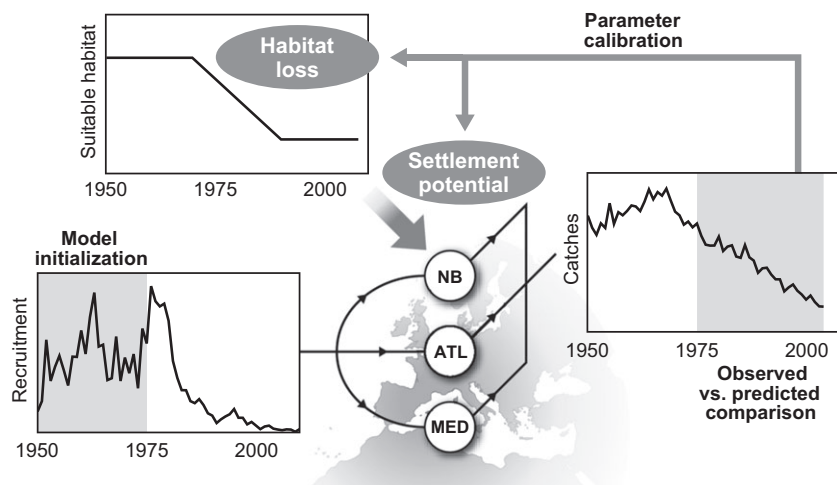

Fig. 2 Model calibration process. The reconstructed time series of glass eel recruitment is used as an input to the model of the continental phase, which produces as an output a time series of eel catches for each geographic region. Model outputs are contrasted with observed catches to estimate the parameter that minimizes the discrepancy between predictions and observations (parameters subject to calibration are highlighted by ellipses). The first 25 years of input data are used to initialize the model, so the corresponding outputs are not considered for the calibration. For further details, see section S4 in the Supporting information.

Table 1 Comparison among candidate models of eel decline across the European eel range. Each model is based on different hypotheses about the geographic variation of settlement potential (different or equal across regions) and habitat loss (different, equal or none), and about the possibility for glass eels to relocate whether habitat becomes inaccessible or unsuitable

Model	Settlement potential	Proportion of habitat lost	Recruitment relocation	RSS	AIC	ΔAIC
M1a	Different	Different	Impossible	0.10×10^9	1261	0
M1b	Different	Different	Possible	0.12×10^9	1278	17
M2a	Equal	Different	Impossible	0.11×10^9	1267	6
M2b	Equal	Different	Possible	0.14×10^9	1291	30
M3a	Different	Equal	Impossible	0.25×10^9	1342	81
M3b	Different	Equal	Possible	0.24×10^9	1338	77
M4a	Equal	Equal	Impossible	0.17×10^9	1512	251
M4b	Equal	Equal	Possible	0.25×10^9	1340	80
M5	Different	None	–	0.45×10^9	1390	130
M6	Equal	None	–	1.17×10^9	1477	216

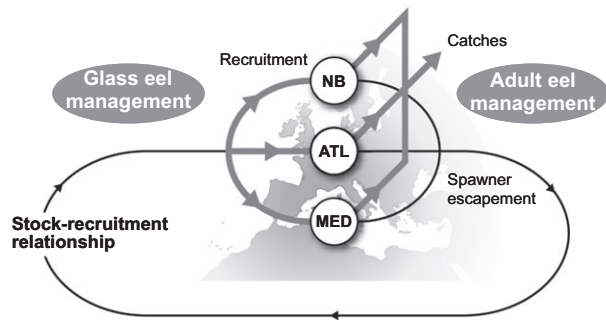RSS, residual sum of squares; AIC, Akaike score; ΔAIC, distance from the best model.

Fig. 3 Model projection. The dynamics of the global European eel stock is projected into the current century (2010–2100) by coupling the model of the continental phase with a stock–recruitment relationship synthesizing the oceanic phase. Nine different scenarios (see Table 1) are considered to show how alternative strategies of glass eel and adult eel management may affect the long-term fate of the stock.

ment is redistributed across the three regions proportionally to the product of the settlement potential of each region and the extent of the residual suitable habitat (see section S5 in the Supporting information). As for adult exploitation, we also considered three management scenarios: a 'historical' one, based on the average rate of fishing mortality experienced by adult eels during the second half of the past century; an 'unexploited' one, in which fishing mortality was set to zero in all regions; and a 'controlled' one, envisaging a 50% reduction of the historical rate of fishing mortality.

Finally, we performed a sensitivity analysis with respect to one of the most critical parameters of the model, namely the maximum reproductive success (*MRS*). By repeating our projections with values of *MRS* varying between 0 and 1000 glass eels per kg of spawner, we assessed how the uncertainty affecting the estimate of this parameter, or its possible variation due to changes in eel fecundity or oceanic conditions, can influence demographic projections. We used the average recruitment between 1950 and 1979 (before the last recruit-

Table 2 Summary of the scenarios used to project the future dynamics (2010–2100) of the European eel stock. Each scenario is the combination of a management scenario for glass eels (defined by the distribution of glass eel recruitment across the three geographic regions) and one for adult eels (defined by the fishing mortality rate of yellow and silver eels beyond 30 cm in length). In the text and following tables and figures, scenarios are identified with a 2-letter abbreviation, with the first letter indicating the settings for glass eel management and the second letter indicating the settings for adult management. For instance, U/C indicates a scenario that envisages the ban of both glass eel fishing and restocking activities (U) and a concurrent control (reduction) of adult fishing mortality (C)

	Glass eel distribution			
Glass eel management	MED	ATL	NB	Fished
Historical (H)	19%	4%	22%	55%
Unexploited (U)	19%	76%	5%	0%
Stocking (S)	34%	22%	44%	0%

	Fishing mortality rate (yr^{-1})	
Adult fishery management	Yellow eels	Silver eels
Historical (H)	0.10	1.43
Unexploited (U)	0	0
Controlled (C)	0.05	0.71

ment decline started in the 1980s) and the average spawner escapement between 1975 and 1984 (the first 10 years of the reconstructed time series) as benchmarks, and set two reference points to compare future levels of recruitment and spawner escapement against those benchmarks: a depletion threshold, corresponding to 1/1000 of the benchmark, and a recovery threshold, equal to 40% of the benchmark (in analogy with the target set by the EC Regulation for spawner escapement). Then, we estimated, for each management sce-

nario, the time needed for recruitment and spawner escapement to fall below the depletion threshold or to recover over the recovery threshold as a function of *MRS*.

Results

Hindcast (1975–2010)

The results of calibrating ten candidate models for the continental phase are summarized in Table 1 and Table S3. Model M1a, considering different values of settlement potential and habitat loss for the three geographic regions, and assuming a direct link between habitat and recruitment loss, is clearly the best according to AIC. The second-best model (M2a, ΔAIC = 6) considers three different proportions of habitat lost, the same link between habitat and recruitment loss, but a unique value for settlement potential. AIC scores show that all the other models are inadequate to reproduce the trend of eel catches observed in the last decades. The best model provides a good fit (R^2 = 0.86, 0.47 and 0.92 for MED, ATL and NB, respectively) to global catches from each region between 1975 and 2004 (Fig. S3). Table 3 compares the baseline habitat extent in the three regions with the residual habitat estimated via the best model (indicated simply as 'the model' in the following). According to our estimates, the most severe loss of suitable habitat has occurred in the North and Baltic seas (–71%); the Mediterranean region has lost 16% of its suitable habitat, while suitable habitat in the Atlantic region has remained essentially unchanged. As for settlement potential, eel habitats of the Mediterranean basin have the highest (472 ind ha^{-1}), while Atlantic habitats have the lowest (314 ind ha^{-1}).

Figure S1 (Supporting information) shows the reconstructed time series of glass eel recruitment, derived from data on glass eel catches over the period 1950–2010. Recruitment ranged, with wide interannual fluctuations, between *ca.* 5 and 20 billion glass eels per year until the early 1980s. Since then, it underwent a sharp decline, and by 2010, it had decreased to 1 billion. Reconstructed trends of continental standing stock, catches and spawner escapement, disaggregated by

sex/maturation stage and geographic region, are shown in Fig. 4. The estimated biomass of the continental standing stock (Fig. 4a) has decreased by almost one order of magnitude, from 200 000 t in 1975 to about 30 000 in 2010. Eel catches (Fig. 4b) and spawner escapement towards the ocean (Fig. 4c) have decreased consequently. In terms of biomass, the standing stock is made up mainly by female eels: the estimated proportion of males in the standing stock (and, consequently, in the spawner escapement) has been decreasing since
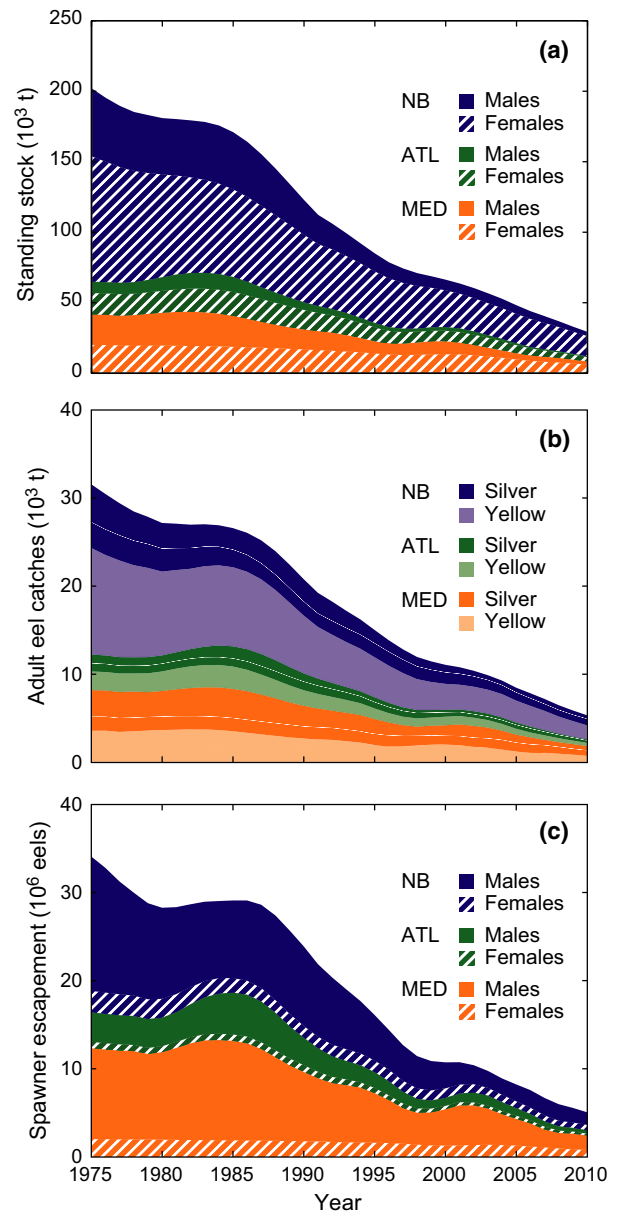

Fig. 4 Reconstructed trends (1975–2010) for the global European eel stock by geographic region. (a) continental standing stock (yellow eels); (b) adult eel catches (yellow and silver eels); (c) spawner escapement (migrating silver eels). MED: Mediterranean basin; ATL: Atlantic region; NB: North and Baltic seas.

Table 3 Baseline European eel habitat (derived from Hughes & Hughes, 1992; Moriarty & Dekker, 1997), habitat loss and residual habitat in 1990 (estimated with the best model, see Table 2) for the three geographic regions

	Mediterranean	Atlantic	North and Baltic
Baseline habitat (km^2)	14 635	11 863	71 173
Habitat loss (km^2)	2342	0	50 533
Residual habitat (km^2)	12 293	11 863	20 640

the mid-1980s, because density-dependent sex determination has caused a shift of sex ratio in favour of females as eel density in the continent decreased. In numbers, however, males still represent the largest fraction of the stock and of the spawners escaping from continental waters. About 50% of the catch is made up by silver eels in the MED and ATL regions, while yellow eel catches are quantitatively more relevant in the NB region, which is characterized by a longer duration of the yellow eel stage.

Projections (2010–2100)

Projected trends of glass eel recruitment, adult eel catches and spawner escapement in the period 2010–2100 are shown in Fig. 5 and summarized in Table S4 (Supporting information). Within the set of management scenarios analysed in this work, only two guarantee a partial recovery of glass eel recruitment (Fig. 5a) up to the level of the early 1990s: both require the complete closure of the adult eel fishery and glass eel restocking from the ATL to the MED and NB regions, either with the same distribution as in the past decades (scenario H/U, maintaining the present level of glass eel exploitation) or proportionally to habitat availability (scenario S/U, in which the glass eel fishery is also closed). The two scenarios that guarantee the partial recovery of recruitment to past levels through a complete closure of the adult eel fishery (H/U and S/U) would also guarantee a full recovery of the standing stock (see Fig. S4a). Besides them, also those envisaging a 50% reduction of adult fishing mortality may allow a partial recovery (S/C), or at least the stabilization of the stock (H/C), provided that glass eel restocking is performed (at least as in the past). The scenarios considering a reduction of adult fishing effort show the first sign of recruitment increase about 3 years after their implementation (Fig. 5a, arrow 1), due to the time lag between silver eel migration and glass eel recruitment; glass eel restocking (scenarios H/U and S/U, and in part also S/C) produces visible effects on recruitment after ca. 20 years (Fig. 5a, arrow 2), that is the time necessary for eels to settle in continental waters, complete their life cycle and give their reproductive contribution to the next generation.

Scenario S/C is the one expected to maximize catches in the future (Fig. 5b). However, the benefits of diminishing the exploitation rate would become apparent only 20 years after the reduction of fishing mortality. On the other hand, 40 years after reducing adult fishing mortality to 50% of the current one, the catch would become 15% higher than in 2010 and almost 15 times larger than that corresponding to present exploitation
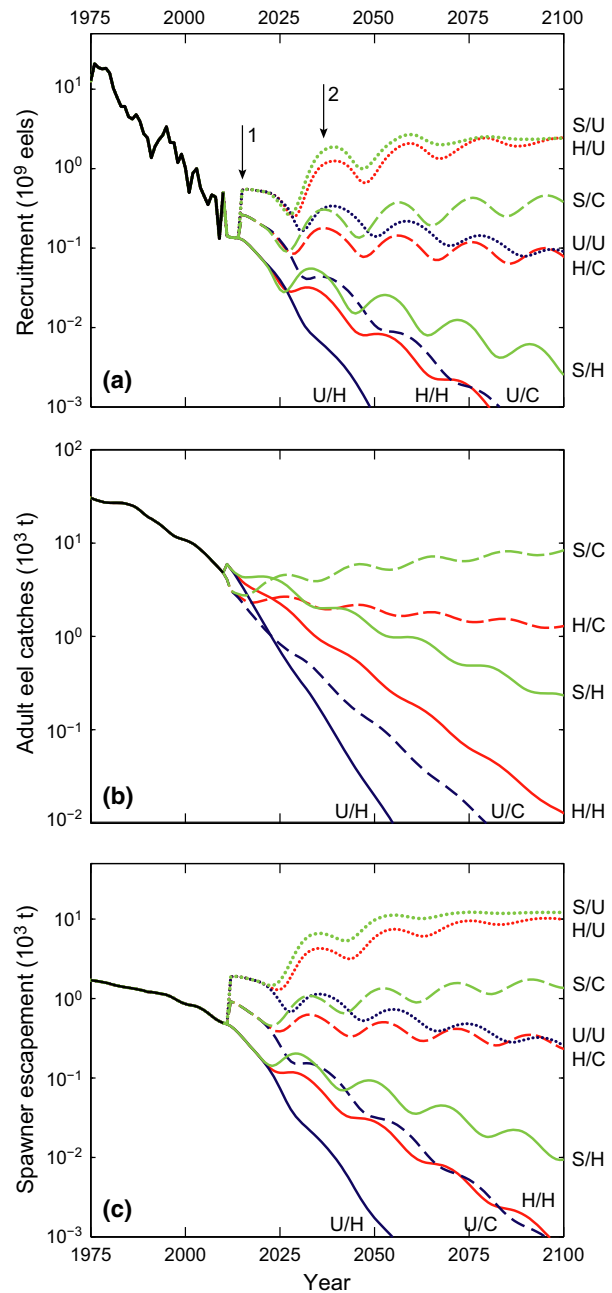

Fig. 5 Projected trends (2010–2100) for the global European eel stock under different management scenarios (see Table 1 for abbreviations). (a) recruitment (glass eels); (b) adult eel catches (yellow and silver eels); (c) spawner escapement (migrating silver eels, females only). Solid black lines show the relevant hindcast. The arrows in panel (a) highlight the short-term (3 years) effect of closing the adult eel fishery (arrow 1) and the midterm (15–20 years) effect of glass eel restocking (arrow 2).

levels (scenario H/H). In the case of an immediate closure of adult eel fishing (scenarios H/U, U/U and S/U), the escapement of migrating eels (Fig. 5c) would rapidly attain the levels of the 1990s, but would

continue to increase after 2020 (*i.e.* 10 years after the implementation of the management policy) only if restocking were implemented (scenarios H/U and S/U). Different management scenarios affect spawner escapement also with respect to sex ratio (see Fig. S4b), as a consequence of the higher probability for undifferentiated eels to develop into males as eel density in continental waters increases (see section S3 in the Supporting information). Scenarios fostering an increase in eel density through a partial or complete closure of the fishery and/or glass eel restocking (such as S/U, H/U and S/C) would increase the relative abundance of males up to 70–80% of the spawner escapement, whereas the scenarios with the most severe impacts on the viability of the stock (U/U, U/C, U/H) would shift the sex ratio of spawners towards a more balanced ratio (ca. 50–60% of males).

With the value of *MRS* used in our simulations (ca. 300 recruits per kg of spawner), a full recovery of glass eel recruitment to the levels of the 1960s would not be feasible even under the most conservative management scenarios. The results of the sensitivity analysis (see Fig. S5 in the Supporting information for a complete graphical summary) indicate that predictions about the time horizon over which the depletion (or the recovery, depending on the specific management scenario considered) of the global eel stock would take place are critically influenced by the reproductive success. For values of *MRS* between 200 and 400, the historical management of the fishery would cause the depletion of glass eel recruitment between 2035 and 2060. The only scenarios that would guarantee to maintain eel recruitment beyond the depletion threshold are those envisaging a complete closure of the fishery (scenarios S/U, H/U and U/U), or a reduction of adult fishing mortality (−50%) accompanied by glass eel restocking (scenarios S/C and H/C). On the other hand, the recovery of eel recruitment to safe levels (i.e. 40% of the 1950–1979 average) is a difficult target to meet. For *MRS* < 600, bringing recruitment over the recovery threshold would be impossible. The recovery might occur around 2030 in the most optimistic hypothesis, that is for *MRS* > 900, a complete closure of the adult fishery and appropriate glass eel restocking, while keeping the adult eel fishery active would impair the recruitment recovery even for higher values (up to 1000) of *MRS*. The effects of *MRS* on projections of future spawner output are similar to those on recruitment, yet slightly less critical, as regards the expected time to depletion. For values of *MRS* between 200 and 400, the historical management of the adult eel fishery would cause the depletion of spawner output by the end of the century. At present levels of reproductive success, spawner output recovery would be immediate if a complete closure of the adult fishery were combined with glass eel restocking (scenarios S/U and H/U). A recovery (by 2050) would be compatible also with a partial (50%) reduction of fishing pressure, if this could be accompanied by the implementation of restocking measures based on habitat availability (S/C).

Discussion

The results of calibrating the model for the continental phase suggest that a considerable proportion of the habitat suitable for eels has been lost in the Mediterranean basin (−16%) and in the North and Baltic seas (−71%) during the last half of the twentieth century. If this is the case, habitat loss might have played a key role in the drop of eel catches between 1975 and 1985: in fact, the observed reduction in catches cannot be ascribed to a decrease of glass eel recruitment, which, on the contrary, reached its maximum in the late 1970s (see Fig. S1). On the other hand, results for the Atlantic region seem to indicate that habitat loss has been negligible in this area. This suggests that the primary driver of the observed decline of adult eel catches along Atlantic coasts may have been glass eel overfishing (Briand *et al.*, 2003; Dekker, 2003a) and that its magnitude may have been so large as to mask the effect of possible habitat loss occurred during the study period. In fact, the second-best model (M2a, which is, however, much less supported than the best model in terms of ΔAIC; see Table 1) indicates an 11% reduction of the suitable habitat in the ATL region. In this case, the best model might have overestimated the residual eel habitat in the ATL region with respect to the actual habitat currently available.

The calibration of the model allowed us to derive also a preliminary estimate of the settlement potential (i.e. the maximum number of glass eels per hectare that can annually settle in a watershed) in the three major geographic regions. Settlement potential varies across the three regions, with Mediterranean habitats supporting the settlement of an eel density 50% higher than that supported in the Atlantic region (472 vs. 314 eels ha^{-1}). This gradient of increasing settlement potential from north to south is consistent with latitudinal gradients in primary productivity and with the scarce evidence available from the literature (Desprez *et al.*, 2013; Schiavina *et al.*, 2015). Density dependence plays an important role in the regulation of the continental dynamics of eel stocks, affecting both glass eel settlement (e.g. Bevacqua *et al.*, 2011a) and yellow eel survival (Vøllestad & Jonsson, 1988; De Leo & Gatto, 1996; Lobón-

Cerviá & Iglesias, 2008; Acou *et al.*, 2011; Bevacqua *et al.*, 2011b).

The EC Regulation encourages the translocation of newly recruited eels to increase spawner production and imposes that an increasing fraction (from 35% in 2009 to 60% in 2013) of juvenile eels is made available for restocking. While eel restocking was widely carried out in the past to improve local fishery yields, its actual contribution to improving the spawning stock is still controversial (e.g. Prigge *et al.*, 2013; ICES, 2014; Couillard *et al.*, 2014; Simon & Dörner, 2014). Appropriately quantifying settlement potential in different environments is therefore a crucial point to understand the consequences of eel fishery management and restocking practices (as already pointed out by previous studies, e.g. Müller, 1975; Moriarty *et al.*, 1990). In particular, if restocking aims to enhance the production of spawners, it may be appropriate to focus it on areas with high productivity, such as Mediterranean lagoons (Desprez *et al.*, 2013; Schiavina *et al.*, 2015).

Interestingly, our assessment of silver eel decline over the last decades (a 90% decrease between 1975 and 2010) is more severe than that provided by the most recent IUCN Red List assessment (50–60% over the last 45 years; Jacoby & Gollock, 2014). Differences may be due to the fact that the analysis conducted by the IUCN was applied to 'an amalgamation of multiple life stages, which may not exactly mirror the mature spawning stock' (Jacoby & Gollock, 2014), while in our hindcast exercise, we modelled separately the dynamics of life stages characterized by different mortality rates, such as yellow and silver eels (Dekker, 2000; Bevacqua *et al.*, 2009).

The results of forecasting eel dynamics over the 21st century suggest that management policies oriented to increasing spawner escapement could effectively contribute to enhancing glass eel recruitment. Proper conservation policies may be able to restore spawner escapement to the levels of the 1970s (although with significant socio-economic impacts) through the complete closure of the adult eel fishery (scenarios S/U and H/U), or to the levels of the early 1990s, through a 50% reduction of fishing mortality (scenario S/C). One of the objectives of the EC Regulation is to increase the spawning stock, according to the belief that the recent collapse of the European eel was mainly caused by a lack of spawners (as suggested, for instance, by Dekker, 2003b). If this were true, there would be still time to save the European eel stock from extinction; also, an appropriate management of the adult eel fishery (e.g. scenario S/C) might guarantee, in the long run, an overall catch similar to the present one (ca. 4000 t yr^{-1}). Although our analysis suggests that it would be difficult (if not impossible) to attain past maxima of glass

eel recruitment, it also suggests that a partial recovery ensuring the conservation of the stock may be feasible. Interestingly, these projections match the most recent data on eel recruitment (ICES, 2014), showing that, after reaching its minimum in 2009, recruitment started to recover, attaining in 2013 the levels of 2005. In fact, recent restrictions to international eel trade and the implementation of eel management plans aimed at limiting fishing mortality, along with a generalized decline of market demand, might have determined exploitation levels similar to those envisaged by our S/C scenario.

Of course, our results are highly dependent on the assumptions we used to close the full life cycle model. In particular, the oceanic phase of European eel's life cycle is still poorly known, and information on eel fecundity and migration success of adults and larvae is very scarce. Determining the stock–recruitment relationship is a fundamental step to understand marine population dynamics (Beverton & Holt, 1957; Walters & Martell, 2004), as its form has crucial consequences for the conservation management of the species under scrutiny. Also, environmental factors (such as climate fluctuations) might affect recruitment success more than the abundance of the parental stock, as suggested by Szuwalski *et al.* (2014) for a number of other marine species. In the case of the European eel, however, the information available to date is not sufficient to speculate about more complex functional forms.

Quantifying the contribution of each spawner to future recruitment is indeed a critical point. Results discussed just above rely on the specific value assigned to *MRS* (ca. 300 recruits per kg of spawner). The average body mass of a female silver eel ranges (depending on the geographic region of origin) between ca. 400 and 600 g, corresponding to a recruitment of ca. 120–190 glass eels per spawner, a range that is consistent with the figure (135) estimated by Bonhommeau *et al.* (2009b). In contrast, Åström & Dekker (2007) derived a value of only 15.2 glass eels per spawner, but their figure may include also mortality during settlement in continental waters. Narrowing the range of uncertainty that affects the estimate of *MRS* is extremely important to predict the actual long-term fate of the eel stock, as shown by the results of our sensitivity analysis. In fact, if the order of magnitude of *MRS* were lower than that of our estimate, none of the management scenarios considered would be able to bring back recruitment into safe biological limits. On the other hand, the reproductive success may also change over time: in particular, in the past it may have been higher than what we assumed in our model. This would explain why we were not able, by assuming a constant value of *MRS*, to reproduce a complete recovery of recruitment, even if considering management policies that would increase

the number of migrating spawners to historical levels. Variation in *MRS* is most likely a major driver of observed historical fluctuations in eel recruitment and, together with habitat loss, of the decline occurred in the last decades. There is a number of factors that may have affected *MRS* in both the continental and the oceanic phases of eel's life cycle. In continental waters, a wide range of pollutants may have contributed to decrease adult viability and fecundity (see Geeraerts & Belpaire, 2010 for a review). Survival of migrating silver eels is also impaired by the infection of the nematode *Anguillicoloides crassus* that damages the eel swim bladder (Palstra *et al.*, 2007; Sjöberg *et al.*, 2009). Finally, changes in the oceanic environment might have decreased the migration success of eel larvae by affecting primary productivity (Bonhommeau *et al.*, 2008b), water temperature (Bonhommeau *et al.*, 2008a) and/or oceanic circulation (Friedland *et al.*, 2007; Baltazar-Soares *et al.*, 2014; but see Bonhommeau *et al.*, 2009a). Another important simplification of our model is that we assumed that reproductive success does not depend on the region of origin. In fact, Kettle *et al.* (2011) suggested that eels leaving from the south-western corner of the continental range may provide the largest contribution to reproduction thanks to the shorter distance of those sites from reproductive grounds. However, the actual reproductive success of spawners coming from different geographic regions is not known, and available information on the migration of adult eels is scant. Also, the actual ability of stocked eels to find their way to the Sargasso Sea is still debated (Limburg *et al.*, 2003; Westin, 2003; Prigge *et al.*, 2013; Westerberg *et al.*, 2014).

To project the dynamics of the eel stock to the end of the current century, we assumed that the environmental and ecological determinants of eel demography, such as habitat availability, life-history traits and larval dispersal, will remain constant over the whole century. The aim of our work is, in fact, to assess the consequences of different management options rather than different environmental scenarios. Further habitat loss would hasten eel extinction and impair conservation policies, while habitat restoration (e.g. by removing barriers to eel migration and improving water quality) would favour the recovery of the stock. Global warming would accelerate body growth but also increase the natural mortality rate (Bevacqua *et al.*, 2011b; Daverat *et al.*, 2012), with differential effects on the different geographic regions. Changes in oceanic circulation might affect patterns of larval migration that in turn would change the geographic distribution of recruitment (Melià *et al.*, 2013).

Despite our efforts to provide a realistic representation of the full European eel's life cycle, we had to introduce a number of simplifying assumptions and to rely on data whose validity is, in some cases, still debated. In considering the demographic structure homogeneous within each of the three macrogeographic regions, we necessarily disregarded a number of particular patterns that can be observed at a finer geographic scale, such as differences across sites with respect to water temperature and quality, eel density in relation to the trophic status of the water body, fishing gear selectivity or extra-mortality induced by the presence of turbines or other infrastructures. Although our results rely on available data on continental eel habitat, recruitment and catches provided by international organizations and/or published on peer-reviewed journals, they are representative of large-scale patterns emerging at the broad geographic scale and cannot reveal locally relevant patterns. Our demographic hindcast and projections should thus be intended as a means to explore general population trends and assess the relative importance of anthropogenic drivers at the scale of the whole distribution range of the species, averaging out heterogeneities that may be observed at the local scale. For instance, while the several existing time series of glass eel recruitment show apparently different patterns from one site to another (see, e.g. ICES, 2014), when they are observed altogether they all show wide fluctuations during the past century and a dramatic decline after the 1980s. It is hoped that future research on eel demography and habitat availability, conducted at the global scale but at a higher spatial resolution, will provide valuable data that may be used to recalibrate the model and further refine the outputs of our analysis.

We recognize that our results should be interpreted with due caution and should be considered as indicative of general average trends and not as precise forecasts of stock abundance and spawner escapement on a fine spatiotemporal scale. In spite of its limitations, we are confident that our modelling exercise provides valuable insights into past and future population dynamics of the European eel at the global scale. Although large historical fluctuations in eel recruitment and stock abundance already occurred in the past and might be part of a natural cycle, our hindcast is consistent with the view that the dramatic decline of the stock observed in the last half century is mainly the result of a synergistic effect of habitat loss (and/or degradation) and overfishing. A decrease of the average recruitment success (possibly caused by changes in the oceanic environment and/or impaired adult fecundity) may also have played a role in the decline. Projections produced under different management policies suggest that the global eel

population may be doomed to extinction within a few decades if effective conservation measures, embracing a global perspective, are not undertaken. The complete closure of eel fisheries would permit to avoid the extinction, but would probably not be enough to get back to historical abundance levels if past levels of reproductive output are not re-established.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods.
Table S1. Baseline eel habitat.
Table S2. Model parameters.
Table S3. Candidate models of eel decline.
Table S4. Projected effect of different management scenarios on the global eel stock.
Figure S1. Reconstructed time series of glass eel recruitment (1950–2010).
Figure S2. Reconstructed time series of adult eel catches (1950–2004).
Figure S3. Fitting performances of the best model.
Figure S4. Projected trends of standing stock and sex ratio under different management scenarios.
Figure S5. Sensitivity of expected depletion/recovery year with respect to reproductive success.