When will the eel recover? A full life-cycle model

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The European eel population has declined over the past decades in most of its distribution area, and the stock is outside safe biological limits. The EU has taken up the challenge to design a management system that ensures the escapement of 40% of spawning-stock biomass, relative to unexploited, unpolluted circumstances in unobstructed rivers. This ultimately aims to restore the spawning stock to a level at which glass eel production is not impaired, i.e. to restore to full historical glass eel recruitment. To explore the trajectory from the current depleted state to full recruitment recovery, we developed a simple model of stock dynamics, based on a simplified stock–recruitment relationship and the conventional dynamic pool assumptions. Recruitment trajectories under different future fishery regimes are explored, for the medium (one generation time) and long time-span (until full recruitment recovery). Reducing fisheries to zero, recovery is expected within ~80 years, whereas under an ultimately sustainable fishing regime of just 10% of the current rate of fishing mortality, recovery may take more than 200 years. Moreover, management regimes, apparently leading to slight recovery of the stock in the coming 5–15 years, might still be unsustainable in the long run.

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Introduction

The European eel (*Anguilla anguilla* L.) desperately needs protection (Anon., 2003; ICES, 2006a). Yields have gradually declined by 75% since the mid-1960s (Dekker, 2003), and the abundance of glass eels (young eels immigrating from the ocean) is now <5% of its pre-1980 level (ICES, 2006a). A European Regulation to recover the stock has been proposed (CEC, 2005), but the time-scale required for recovery, and its dependence on the intensity of management measures, has not been investigated. This study presents a first modelling approach to describing that dependence.

In fishery management, it is generally assumed that density-dependence in the reproductive and young life stages generates a non-linear relationship between spawning-stock biomass (SSB) and recruitment (*R*) (Haddon, 2001; Hilborn and Walters, 2001; ICES, 2003a), and that survival to the reproductive stage is density-independent (Figure 1). Tentative analysis of historical trends in eel recruitment and harvest suggests strong depensation in the stock–recruitment relationship at low SSB (Dekker, 2004), but the processes and parameters are not well known. Rather than choosing between the conventional (concave) stock–recruitment relationship and a depensatory (convex) relationship, we use a simplified local approximation to any general non-linear function, viz. a segmented linear relationship (the hockey stick relationship of Barrowman and Myers, 2000), as in Figure 2, and in practice, we only deal with the dynamics along the left-most, sloped part of the hockey stick. Moreover, we assume that the biomass of females on the spawning ground is determining future recruitment, i.e. we assume that the current scarcity of males is not restrictive. Consequently, biological characteristics of females will determine

the predicted dynamics of the stock, and in particular, female longevity will set the recovery rate of the population.

Here, we develop a model of the stock–recruitment and recruitment–stock relationships. For the latter, parameters are derived from the literature. To our knowledge, the former has not been analysed before, and we derive parameters directly from historical time-series. When the dynamics of both the continental and the oceanic life stages are known, the dynamics of the recovery process can be quantified. Hereafter, we formalize this line of reasoning in a model, estimate crucial parameters, and focus on the time required to recover recruitment to its historical level, i.e. as observed in the mid-20th century, by future restrictions on anthropogenic impacts. In essence, we estimate the time it takes until recruitment is expected to recover to historical levels, and do not consider precautionary management targets, which take uncertainties in our knowledge into account. The latter will be stricter, and in practice mandatory to protect the eel, given our imperfect knowledge. In the current analysis, we disregard the uncertainty in the assessment of the continental life stages, and concentrate on adding the oceanic stages. This addition is a step forward in the analysis of the lifetime dynamics of the stock, which undoubtedly comes with its own uncertainties.

We assume that exploitation targets the last part of the yellow eel stage, and the silver eel stage, i.e. the final continental years of the eel's life cycle. The model formulation can be adapted easily to other situations, but yellow and silver eel exploitation are so widespread (Dekker, 2003) that we considered our approach an appropriate starting point. Owing to the lack of continent-wide estimates of the magnitude of anthropogenic mortalities other than the fishery, we focus on the effects of restricting fishery
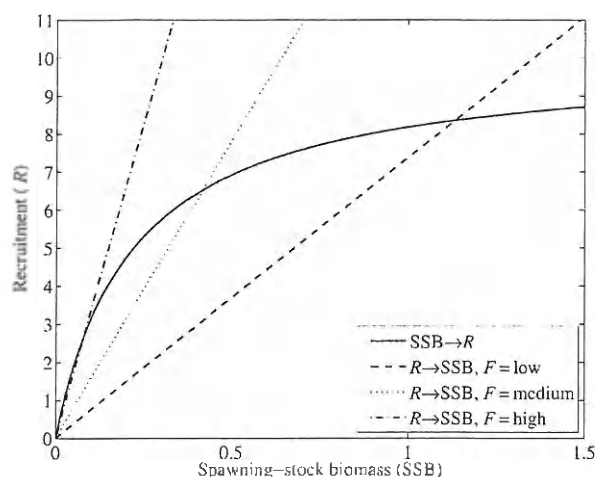
Figure 1. General density-dependent stock–recruitment relation of the Beverton–Holt type (solid curve), and density-independent stock–recruitment relationships (dashed, dotted, and dot-dashed lines for various levels of fishing mortality). The intersections between the two types of curve determine equilibrium conditions. Note that the solid line gives R as a function of SSB, whereas the broken lines give SSB as a function of R, i.e. in the latter ones, the horizontal axis represents the dependent variable. R represents the recruitment of glass eels to continental waters, and F the instantaneous rate of fishing mortality.

mortality only. Other sources of anthropogenic mortality (e.g. habitat loss, downstream migration barriers) have an impact on the same life stages, and reductions of these impacts will have a comparable effect. However, we ignore anthropogenic
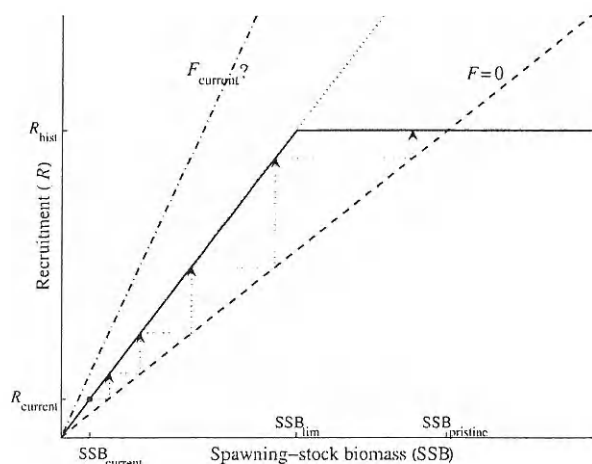
mortality in the early continental phase (notably fisheries targeting glass eels, and upstream migration barriers), because the processes involved are not well understood. Density-dependence is generally assumed to play an important role at this life stage, which would necessitate a model based on local habitat conditions, and we cannot see how such a local approach can be integrated into a simple population-wide model, as presented here.

The eel stock is most likely panmictic (Dannewitz *et al.*, 2005), and it is generally assumed that there is just one spawning stock. Whether eels from the whole distribution area, or from just a restricted part, contribute to the reproduction is not known. Therefore, our model is supposed to represent the whole stock, i.e. parameter values were selected representing the stock-wide averages.

The model
Defining time

We define time t (years) as an arbitrary point in time, i.e. t is absolute. In our numerical analyses, j denotes the number of years since protective management measures were taken, restricting fishing pressure, so a negative value of j represents years before the protective actions. Additionally, we define time-intervals τ for the various life stages of the eel (Figure 3), where τ quantifies the number of years since the onset of a particular life stage. In other words, τ is always relative to a life stage, not to an individual's life. The duration of the full continental life-span is indicated by τ, the duration of exploitation during yellow and silver eel stages by τ_{ex}, the period from the onset of exploitation until spawner escapement by τ_{ee}, and the duration of the full oceanic life stages (including both spawning migration, reproduction and larval migration) by τ_{oc}. We derived values for all time-spans from the literature. As the variation in time-spans is not available, we assume that all eels have the same fixed time-spans. In
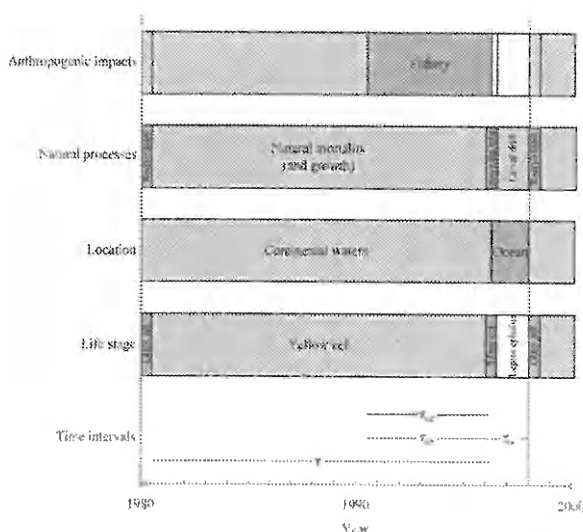

Figure 2. Simplified, segmented linear stock–recruitment relationship (solid line). The average historical recruitment is R_{hist} and the minimum spawning stock that can generate R_{hist} is SSB_{lim}. Recruitment–spawning stock relationships for three fishing mortality levels are indicated (dashed, dotted, and dot-dashed lines). At $F = 0$, the spawning stock will eventually stabilize at the pristine level $SSB_{pristine}$, whereas recovery from the current depleted situation ($SSB_{current}$, $R_{current}$) will follow the path along the dotted arrows. Our analysis focuses on the number of steps (generations) it takes to restore full historical recruitment (five in this graphic example).

Figure 3. The time-line in our model, with indications of life stages, their location (continental or oceanic waters), the main processes included, and their time-spans (see Table 1 for parameter definitions). The horizontal axis indicates the years, as for the 1980 glass eel recruitment.

particular, we assume initially that all female eels become silver eels, spawn and then die at an exact age of 16 years ($\tau = 16$), although this unrealistic assumption is relaxed later.

General model

At time t, certain numbers (R_t) of glass eels recruit to continental waters. Under the assumption that both natural mortality (M) and fishing mortality (F) are independent of population abundance, $R_t e^{(-F\tau_{ex}-M\tau)}$ of the recruits will have survived to the silver eel stage after τ years, and will then return to the spawning grounds. Defining the net reproductive output of a single silver eel as b, which is supposed to be density-independent at the current very low densities, we obtain

$$R_{t+\tau+\tau_{oc}} = R_t e^{(-F\tau_{ex}-M\tau)} b, \qquad (1)$$

where M is the instantaneous rate of natural mortality and F the instantaneous rate of mortality attributable to fishing. Both mortality rates are here expressed per year. All parameters, their meaning, and their values are listed in Table 1.

The assumption of density-independent reproduction corresponds only to the first sloped linear segment of the stock–recruitment relationship in Figure 2, and it is applicable to the current, supposedly depleted, situation of the spawning stock.

The mortality rate of oceanic life stages is essentially unknown. We assume that oceanic mortality for both the adults returning to their spawning grounds, and for the recruits migrating towards the continent, is constant. As the stock–recruitment relationship, represented by b in Equation (1), relates the size of the silver eel run from the continent to the abundance of recruits arriving at the continent, this effectively includes oceanic mortality at both life stages.

Primary effects of fishing restrictions on the present cohorts

For the first $\tau_{oc} - 1$ years after a reduction in fishing mortality by a factor x ($0 \leq x \leq 1$) in year t, spawner escapement will increase, but no change in recruitment is expected yet. In the following τ_{ee} years, a gradual increase of the recruitment is expected, because of an increased spawning stock. At the end of this period, at $t + \tau_{oc} + \tau_{ee} - 1$, recruitment is expected to have increased by a factor

$$k_{t+\tau_{oc}+\tau_{ee}-1} = \frac{R_{t+\tau_{ee}-1-\tau}e^{(-xF\tau_{ex}-M\tau)}b}{R_{t+\tau_{ee}-1-\tau}e^{(-F\tau_{ex}-M\tau)}b} = e^{[F\tau_{ex}(1-x)]}, \qquad (2)$$

from the level recruitment would have been with no reduction in fishing mortality. We call this increase in recruitment the primary effect, because it results from reduced mortality on the year classes already in the population at time t, but not yet from stronger year classes entering the stock after the mortality reduction (the secondary effect, discussed later).

The primary effect of fishery restrictions can be evaluated directly from Equation (2), but future recruitment levels will also be affected by trends in past recruitment. The decline in recruitment observed in the recent past will lead to a decline in the spawning stock in the coming years, and subsequently to a decline in the expected future recruitment, with or without fishery restrictions. Indices of recruitment between 1977 and 2004 presented by ICES (2006a) suggest that recruitment has been

declining at a roughly constant instantaneous rate (D) since 1977 (Figure 4). Assuming that this downward trend will continue if no substantial protection is provided, future recruitment without fishery restrictions can be calculated from present recruitment (at time t) as $R_{x=1,t+\tau_{oc}+\tau_{ee}-1} = R_t e^{[-D(\tau_{oc}+\tau_{ee}-1)]}$. With fishing

Table 1. Overview of parameters and their values.

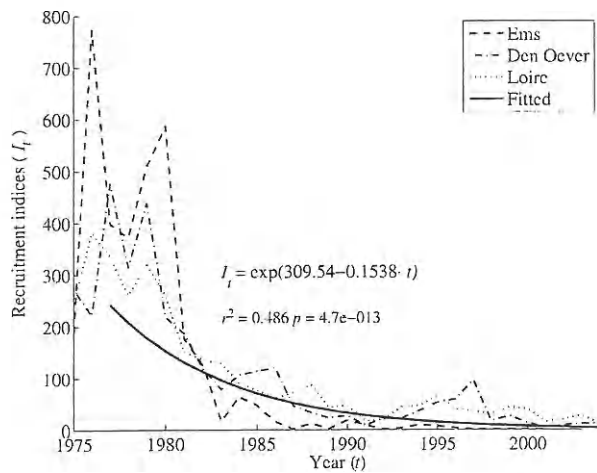| Parameter	Meaning	Value and unit	Source
τ_{oc}	Duration of oceanic life stages	2 years	–
τ	Duration of continental lifespan	16 years	Dekker (2000a)
τ_{ex}	Duration of exploited phases	6 years	Dekker (2000a)
τ_{ee}	Time interval between onset of exploitation and spawner escapement	6 years	–
$F\tau_{ex}$	Lifetime fishing mortality	3.25	Dekker (2000a)
F	Instantaneous fishing mortality rate	0.54 year^{-1}	Dekker (2000a)
M	Instantaneous natural mortality rate	0.14 year^{-1}	Dekker (2000a)
R_t/R_{hist}	Current recruitment strength expressed as a proportion of average historical recruitment	2.5% of the average from 1960 to 1979	ICES (2006a)
D	Instantaneous rate of decline observed in recruitment indices	0.1538 year^{-1}	ICES (2006a); Figure 4
b	Net individual reproductive output, number of glass eels arriving per silver eel leaving the continent	15.2	Equation (4)
x_{max}	Allowed fishing mortality, as a proportion of the current rate, at which future recruitment is stabilized, but without long-term recovery	0.148	Equation (7)
$T_{R_{hist}}$	Number of generations required to restore recruitment to full historical level	4 generations 79 years after fishing restrictions 72 years after the onset of secondary effects	Equation (6), with the assumption that the fishery is stopped completely

Figure 4. Standardized recruitment indices at Ems, Den Oever, and Loire (broken lines) (after ICES, 2006a), and the estimated common trend from 1977 to 2004 (solid line).

restrictions, the full primary effect combined with past recruitment decline becomes

$$R_{t+\tau_{oc}+\tau_{ee}-1} = k_{t+\tau_{oc}+\tau_{ee}-1}R_{x=1,t+\tau_{oc}+\tau_{ee}-1}$$
$$= e^{[F\tau_{ex}(1-x)]}R_t e^{[-D(\tau_{oc}+\tau_{ee}-1)]}, \tag{3}$$

expressing future recruitment in terms of the present.

The primary effect [Equation (2)] is expected to remain at its maximum level until $t + \tau + \tau_{oc}$, but during this interval, the past recruitment trend will superimpose a decline. Recruitment is expected to increase first (primary effect), but then to decrease again (as a hangover from past recruitment decline), despite continuing protection.

Secondary effects of fishing restrictions on future cohorts

Fishing restrictions will increase the survival of the already recruited stock (the primary effect, see above), which in turn will result in higher SSB, stronger future year classes, and subsequently a further increase in the production of spawner biomass (because of both increased survival and the subsequent increased recruitment). We label the production of stronger spawning stocks attributable to the stronger year classes as a secondary effect of the fishing restrictions. The secondary effect is expected when the recruits of the primary effect spawn and their offspring return to the continent, i.e. after an additional $\tau + \tau_{oc}$ years; full secondary effects will start to show at $t + \tau_{oc} + \tau_{ee} - 1 + \tau + \tau_{oc}$.

Quantification of the secondary effect requires estimation of parameter b, the slope of the stock–recruitment relation at current low-stock abundance. The current spawning stock can be derived from historical recruitment $\tau + \tau_{oc}$ years ago, which was $e^{[D(\tau+\tau_{oc})]}$ as high as current recruitment, and the total survival during the continental stages as $e^{(-F\tau_{ex}-M\tau)}$. The reproductive output per spawner, b, is equal to the current number of recruits

divided by the current spawning stock, i.e.

$$b = \frac{R_t}{R_{t-\tau-\tau_{oc}}e^{(-F\tau_{ex}-M\tau)}} = \frac{R_t}{R_t e^{[D(\tau+\tau_{oc})]}e^{(-F\tau_{ex}-M\tau)}}$$
$$= e^{[F\tau_{ex}+M\tau-D(\tau+\tau_{oc})]}. \tag{4}$$

All parameters now being known, we can predict recruitment T generations into the future after the primary effect has taken full effect as

$$R_{t+\tau_{oc}+\tau_{ee}-1+T(\tau+\tau_{oc})} = R_{t+\tau_{oc}+\tau_{ee}-1}e^{(-xF\tau_{ex}-M\tau)T}b^T$$
$$= e^{[F\tau_{ex}(1-x)-D(\tau_{oc}+\tau_{ee}-1)]}R_t e^{[F\tau_{ex}(1-x)-D(\tau+\tau_{oc})]T}. \tag{5}$$

By replacing the left side of Equation (5) with R_{hist} and solving for T, the number of generations $T_{R_{\text{hist}}}$ required to achieve full recovery of historical recruitment is

$$T_{R_{\text{hist}}} = \text{ceiling}\frac{D(\tau_{oc}+\tau_{ee}-1)-F\tau_{ex}(1-x)-\ln(R_t/R_{\text{hist}})}{F\tau_{ex}(1-x)-D(\tau+\tau_{oc})}, \tag{6}$$

where the term "ceiling" indicates a rounding up to the nearest integer. The full time required for recovery is $\tau_{R_{\text{hist}}} = \tau_{oc}+\tau_{ee} - 1 + T_{R_{\text{hist}}}(\tau+\tau_{oc})$.

Finally, a breakpoint reduction in fishing intensity, for which the recruitment decline is expected to stop, can be determined from Equation (5) by setting $e^{(-xF\tau_{ex}-M\tau)T}b^T = 1$ (i.e. recruitment remains constant over time). However, such a decrease will not achieve long-term recovery. This breakpoint is when fishing is reduced to a fraction $x_{\max}$ of the current intensity, viz.

$$x_{\max} = \frac{\ln(b)-M\tau}{F\tau_{ex}} = \frac{F\tau_{ex}-D(\tau+\tau_{oc})}{F\tau_{ex}}. \tag{7}$$

Numerically deriving the expected recruitment

To illustrate the expected development of recruitment over time numerically, we first calculate recruitment for the period before any effects of fishing restrictions can be seen as

$$R_{t-\tau_{oc}-\tau+i} = R_t e^{[D(\tau_{oc}+\tau-i)]}$$
$$\text{for } 0 \le i \le (\tau_{oc}+\tau+\tau_{oc}-1), \tag{8}$$

which is simply a back-calculation of the historical decline from $t - \tau_{oc} - \tau$ to $t + \tau_{oc} - 1$. After fishing restrictions have been implemented at time t, the expected recruitment $\tau_{oc} + j$ time-steps later is expressed as

$$R_{t+\tau_{oc}+j} = R_{t+\tau_{oc}+j-\tau-\tau_{oc}}e^{\{-[F\tau_{ex}-F\min(j+1,\tau_{ee})]-F\min(j+1,\tau_{ee})x-M\tau\}}$$
$$\times e^{[F\tau_{ex}+M\tau-D(\tau+\tau_{oc})]}, \tag{9}$$

where j is the number of years since fishery restrictions ($j = 0$, the year when restrictions are implemented). The function $\min(j+1, \tau_{ex})$ takes the minimum of the two expressions within the parentheses. Equation (9) is based on Equation (1), where total fishing mortality is stepwise changed from $F\tau_{ex}$ to $F\tau_{ex}x$ after fishery

restrictions have been implemented; see Åström (2005) for further discussion of this part of Equation (9). The equation is iterated using estimates of R for the right side of Equation (9), first from Equation (8) and then from Equation (9) itself, in accordance with the time indices.

Parameter values

The parameter values we used are summarized in Table 1. For the most part, they are based on Dekker (2000a), who developed a stock-wide assessment of the eel stock, but parameter values concerning recruitment were derived from recruitment indices presented in ICES (2006a). In general, these parameters represent an average for the whole population, but the estimates for fishing mortality exclude the glass eel fisheries around the Bay of Biscay.

Results
Primary effects of fishing restrictions on the present cohorts

Full primary effects of completely closing the fishery ($x = 0$) combined with past decline in recruitment are expected to result in some 22% of historical recruitment ($0.22R_{hist}$) after 7 years ($\tau_{oc} + \tau_{ee} - 1 = 2 + 6 - 1$). This primary effect will then last for another 12 years ($\tau + \tau_{oc} - \tau_{ee} = 16 + 2 - 6$), although the past recruitment decline will gradually decrease recruitment again to 3.5% of the historical level [the second trough in Figure 7 later, which shows numerically derived recruitment over time, using Equations (8) and (9)]. The first signs of the secondary effect start showing after 19 years ($\tau_{oc} + \tau_{ee} - 1 + \tau + \tau_{oc} - \tau_{ee}$), reaching its maximum 25 years after fishing restrictions have been applied ($\tau_{oc} + \tau_{ee} - 1 + \tau + \tau_{oc}$). The primary effect of different levels of fishery restrictions, expressed as the proportion of the present rate of fishery mortality allowed (x), is shown in Figure 5. A full closure of fishing is expected to result in a recovery of recruitment up to 22% of the historical level in 7 years, because
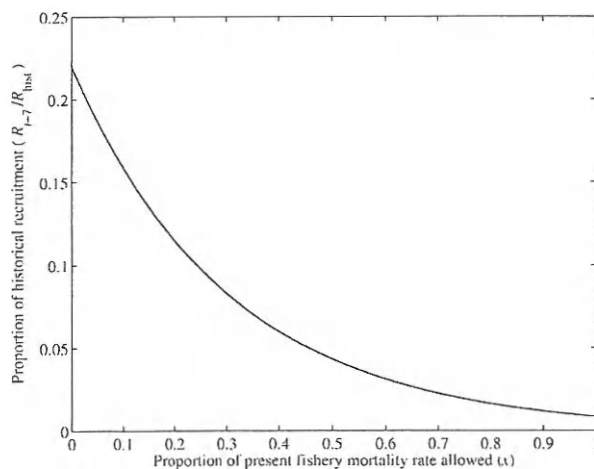
of improved survival of the available, but gradually weakening, year classes. Even if the protection level remains complete, the hangover of the past recruitment decline results in renewed deterioration, until 18 years after the fishery was closed. It is only after this stage that secondary effects come into play.

Secondary effects of fishing restrictions on future cohorts

Following the primary effect in the first 7 years after fishing restrictions, restoring recruitment to 22% of the historical level (at a maximum, if all fishing is banned), further recovery will require that these stronger year classes grow to full maturity and contribute to a recovery of the spawning stock. This secondary effect necessarily takes more than one generation. Figure 6 shows the time required for a full recovery of historical recruitment, as a function of the intensity of fishing reductions. Note that the horizontal axis of this figure ranges from 0 (total ban on fishing) to 0.15, just above $x_{max} = 0.148$, which is the maximal relative fishing intensity at which any long-term recovery is expected.

Following the initial recovery through primary effects, and a subsequent deterioration because of past recruitment decline, future recruitment starts to follow a sawtooth pattern, i.e. up and down (Figure 7). Under a ban on fishing, full recovery is expected in 79 years (7 years for the primary effect + 72 years for the secondary effect), but this is again followed by a deterioration down to 24% of historical recruitment 86 years after fishery restrictions. Only after ~130 years is recruitment expected to remain continually above the historical level. Allowing a moderate fishery of 10% of the current level increases the recovery period to over 200 years (Figure 6), whereas a fishing rate close to $x_{max} = 14.8\%$ of the current level increases the restoration period infinitely.

The sharp sawtooth pattern in Figure 7 is the consequence of our assumption that all female eels mature at a fixed age of 16 years. This is obviously a simplification of reality, and the sharp sawtooth pattern is in part an artefact of that assumption. To overcome this shortcoming, we modelled the maturation frequency as a smooth (arbitrary) distribution around the average age at
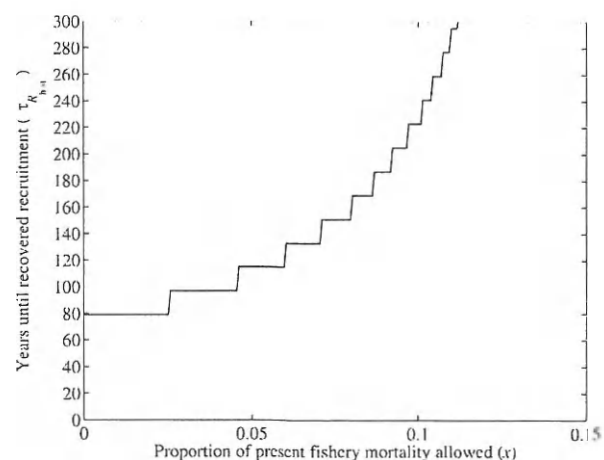
Figure 5. The relation between the allowed proportion (x) of the present rate of fishing mortality and recruitment 7 years later (i.e. full primary effect and past decline), expressed as proportions of historically average recruitment (R_{t+7}/R_{hist}). The long-term goal for the recovery of the European eel is 100% of average historical recruitment ($R = R_{hist} = 1$).

Figure 6. The time required for full recruitment recovery $\tau_{R_{hist}}$ as a function of the allowed proportion of present rate of fishing mortality (x) according to Equation (6). Note that the horizontal axis only reaches 0.15, which already corresponds to a 85% reduction in fishing mortality.
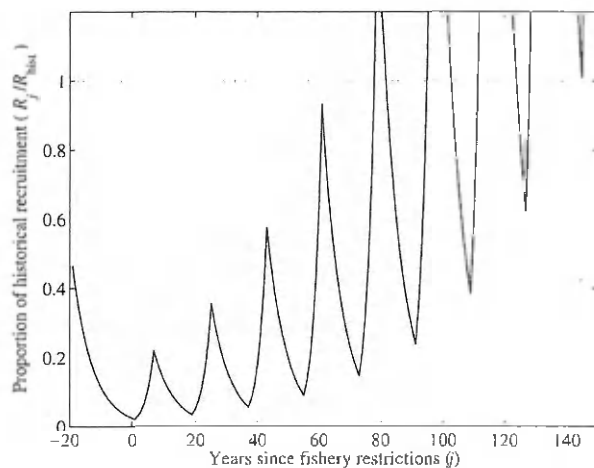
Figure 7. Expected recruitment after a complete closure of fishing at the relative time $j = 0$, numerically derived from Equations (8) and (9). Note that $j < 0$ represents the time before fishing restrictions.
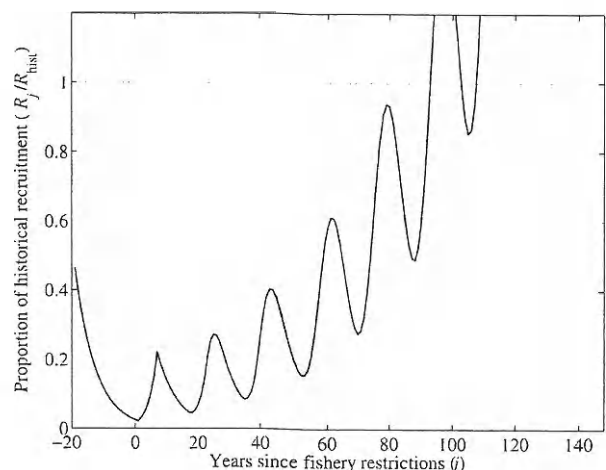

Figure 9. Expected recruitment after a complete closure of fishing at $j = 0$, as in Figure 7, except that eels are now assumed to mature over a range of eight different ages (cf. Figure 8).

maturity of 16, between ages 13 (no maturation) and 21 (all mature). This is shown in Figure 8, and we used a beta distribution with parameters $\alpha = 2.2$, $\beta = 4.8$ to skew the distribution towards older ages, although the exact form of this distribution is of little importance. The result is a much smoother trajectory (Figure 9), but the overall picture and the sawtooth pattern remain the same. Because the sharp "teeth" of Figure 7 are now smoothed out, peak recruitment 79 years after the fishery was closed (the first full recovery without smoothing) no longer reaches the historical level, but the next "tooth" does, at $j = 97$ years (where j represents the number of years since fishing restrictions were implemented). However, the interspersed periods of low recruitment (at $j = 18$, 36, etc.) of the trajectory are now rapidly smoothed, and minimal recruitment levels (the troughs) arise relatively more rapidly.

Finally, we return to the minimally required reduction in fishing x_{max}, and apply the smoothed maturation pattern
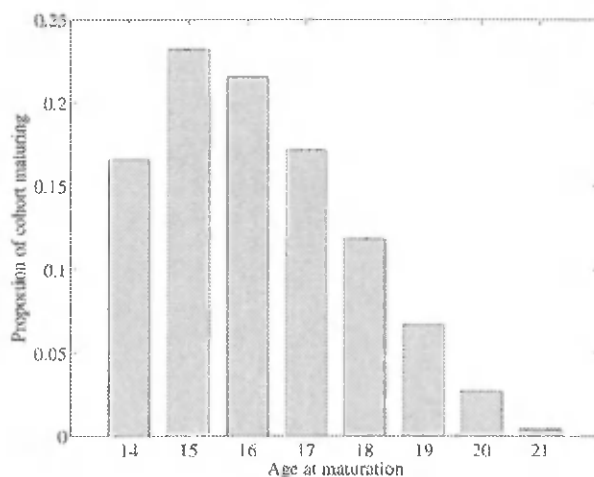
(Figure 10). Under these assumptions, recruitment increases rapidly because of the primary effect, lasting for 7 years. In the long term, however, the inadequate reduction in fishing results in no further recovery through to the secondary effect. In other words, an observable initial success in recovery is no guarantee of ultimate success.

Sensitivity analyses

To evaluate the robustness of the presented results, we present elasticity analyses of x_{max} and $T_{R_{hist}}$ in Tables 2 and 3, respectively. The elasticity values illustrate the relative change of x_{max} or $T_{R_{hist}}$ that a small relative increase of the different parameters induces

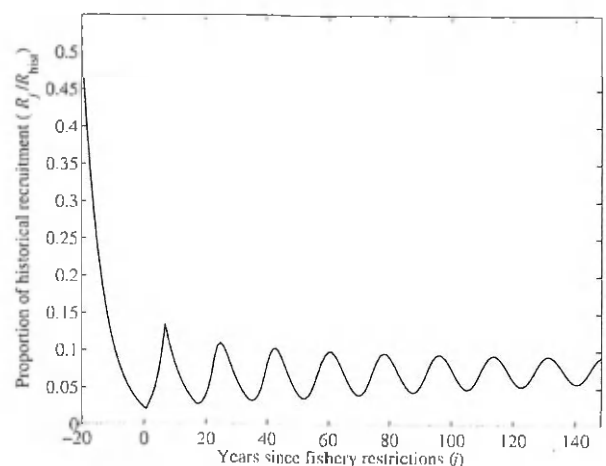**Figure 8.** Proportion of each cohort assumed to mature at eight different ages.

Figure 10. Illustration of the prerequisite on the rate of fishing mortality (x_{max}), according to Equation (7). The proportion of the present rate of fishing mortality (F) allowed is set to $x_{max} = 0.148$ so that we see no long-term recovery in recruitment after the initial increase attributable to the primary effect following a reduction in fishing effort at $j = 0$. Maturation is assumed at eight different ages. Note the change of scale on the y-axis.

Table 2. Sensitivity of x_{max} (the maximal allowable fishing intensity as a fraction of the current, that would bring the decline to a halt) to the parameters that affect x_{max} according to Equation (7).

F	τ_{ex}	D	τ	τ_{oc}
5.7	5.7	-5.7	-5.1	-0.6

(cf. Caswell, 2001), when all other parameters are kept at their standard values (Table 1).

From Table 2, we see that all parameters have a similar effect on x_{max}, although with different signs, except for τ_{oc}. The precise estimate of the time of the oceanic stage τ_{oc} is apparently not that relevant. The other parameters are categorized into two groups: F and τ_{ex} together determine the lifetime fishing mortality, whereas D and τ quantify the historical decline and the generation time, respectively.

The parameters associated with exploitation (F and τ_{ex}) have the greatest effect on the number of generations needed for recovery (Table 3). The parameters τ_{oc}, τ_{ee}, and R_t/R_{hist} have the least effect, and between them come D and τ. Note that if current estimates of the rate of fishing mortality (F) or the time-span of exploitation (τ_{ex}) is too high, recovery time is expected to be even longer and the rate of fishing mortality would have to be reduced even further.

Discussion

Our results show that:

- the eel being slow-growing, recovering the stock will take considerable time, of the order of several decades, even after massive reductions in mortality;
- the length of the recovery period is tightly linked to the level of reduction in fishing (or other anthropogenic) mortality;
- large reductions in mortality are required to achieve long-term recovery;
- an initial increase in recruitment does not guarantee long-term recovery.

Even if eel fisheries were to be banned immediately and completely, recovery of the stock is expected to take several decades or more. None of the current biologists studying the eel resource, nor the stakeholders or politicians influenced by or deciding on protection plans, would likely live to see the recovery. However, for there to be any hope at all for the stock, our analyses indicate that reductions in fishing and all other anthropogenic impacts should be made as soon and as stringently as possible.

The sensitivity of these results to our parameter estimates is considerable. One combination of parameters (F and τ_{ex}) corresponds to the original data sources, used in the parameter

Table 3. Sensitivity of $T_{R_{hist}}$ (the number of generations until full recovery of recruitment) to the relevant parameters according to Equation (6), for three values of x (the fraction of current fishing intensity allowed).

x	F	τ_{ex}	D	τ	τ_{oc}	τ_{ee}	R_t/R_{hist}
0	-8.9	-8.9	6.5	5.1	0.8	0.6	-0.7
0.05	-11.5	-11.5	9.3	7.7	1.1	0.5	-0.6
0.10	-20.3	-20.3	18.3	15.7	2.1	0.5	-0.5

estimation (Dekker, 2000a). The other influential combination (D and τ) effectively quantifies the steepness of the historical decline in recruitment and the generation time. Our perception of the history and the anthropogenic impacts might be wrong, but in the absence of appropriate knowledge, our results provide a precautionary (although not conservative) estimate of expected recovery periods.

It is of some concern that our estimates of stock-wide biological characteristics, such as age at maturity, tend to be typical for the northern parts of the distribution of the eel. If so, recovery periods might be shorter than calculated, but the historical dominance of northern research complicates a more balanced view. However, even if growth rates were twice as high (Yalçin-Özdilek *et al.*, 2006), and age at maturity half as high as we have assumed, recovery would still be a decadal process.

The eel is not the only depleted fish species, although it is one of the worst cases (Dekker, 2004). For fish stocks in general, the effect of management measures following a stock collapse has been well analysed in modelling studies, paralleling ours. In cases where recovery fails at a decadal time-scale, external factors are supposed to be involved. An example is the recent analysis for North Atlantic cod (*Gadus morhua*) stocks (ICES, 2006b), discussing *inter alia* exploitation, climate change, trophic interactions with predators and prey, and depensation in the stock–recruitment relationship. For the eel case, however, the anticipated decadal or centennial recovery period predicted here is related to its longevity, and the extremely low current recruitment that is supposed to indicate an extremely low effective SSB. If external factors other than the fishery are also involved, our model will be inadequate, and recovery periods even longer than we anticipate.

There is tentative evidence that the stock–recruitment relationship of eel might indeed show depensation (Dekker, 2004; ICES, 2005), i.e. that recruitment declines faster than the spawning stock when stock levels are low. Depensation has not been taken into account in the present analyses. If depensation is real, the prospect for recovery is even worse than analysed here. The population might already be below its critical point, where a maximum reduction in (anthropogenic) mortality cannot alone compensate for the depensation. If the past 25 years of decline reflect depensation, this also implies that the estimate of the recruit production per spawner (b) we use here reflects a past situation with higher b than can be expected for the further depleted spawning stock of today. On the other hand, depensation would imply that b depends positively on the size of the spawning stock, and that an initial effect of protective measures would benefit from positive feedback, through increased reproductive output b.

Our model is oversimplistic about the biology of the eel, and the various anthropogenic factors affecting the stock. The model focuses on fishing mortality in the yellow and silver eel stages. Fisheries on other life stages (glass eel) have been ignored, as have other sources of anthropogenic mortality (e.g. habitat loss, migration barriers, pollution). Additionally, potential density-dependent processes in the continental phase (dispersion, growth, mortality, and sex differentiation; see ICES, 2003b, for an overview) have been neglected. These simplifications were deliberately applied, to enable a population-wide approach to be developed and clear and traceable results to be obtained. Long-term trends in the spawning stock will depend primarily on lifetime mortality levels, rather than on what factors impose the mortality. In general, one can replace our fishing mortality

by any other mortality factor, without affecting results significantly. Strong density-dependence of some kind (e.g. in sex differentiation) might reduce the effect of mortality reductions, as modelled here. However, this will only apply locally and be difficult to verify in natural populations, because its effects are hard to separate from other simultaneous processes. So far, the evidence for density-dependence in the European eel is weak, likely because of its current depleted status. For glass eel fisheries, a time-shift could be expected prolonging the time for full primary response to fishery restrictions, because the response time would correspond to the whole continental part of the life cycle. However, the issue of the glass eel fisheries cannot be assessed without considering potential local density-dependence in full, which would clearly go beyond our aim of a simple and tractable model. Moreover, the general decline observed in recruitment since 1980 (Moriarty, 1986; Dekker, 2000b; ICES, 2006a), and the decline observed in yellow and silver eel fishery yields (Dekker, 2003, 2004), makes it increasingly unlikely that density-dependence still plays a key role in stock dynamics (Dekker, in press).

Here, our main focus was on modelling and quantifying the stock–recruitment relationship, for the current depleted situation. To our knowledge, this is the first attempt to model the full life cycle of the European eel. Hopefully, this work will inspire others (and ourselves) to improve the modelling, and to improve the quantification of parameters, i.e. to improve our general understanding of eel biology.

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References

Anon. 2003. Québec declaration of concern: worldwide decline of eel resources necessitates immediate action. Fisheries, 28: 28–30.

Åström, M. 2005. Spawner escapement from yellow and silver eel fishery. Appendix 3.3 in ICES Document CM 2005/I: 01, Report of the ICES/EIFAC Working Group on Eels, Galway (WGEEL), 22–26 November 2004, Galway, Ireland.

Barrowman, N. J., and Myers, R. A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences, 57: 665–676.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, MA.

CEC. 2005. Proposal for a Council Regulation establishing measures for the recovery of the stock of European Eel (presented by the Commission). COM (2005) 472 final.

Dannewitz, J., Maes, G. E., Johansson, L., Wickström, H., Volchaert, F. A. M., and Järvi, T. 2005. Panmixia in the European eel: a matter of time.... Proceedings of the Royal Society of London, 272: 1129–1137.

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

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

Dekker, W. 2003. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? Fisheries Management and Ecology, 10: 365–376.

Dekker, W. 2004. Slipping through our hands—population dynamics of the European eel. PhD thesis, University of Amsterdam. 186 pp.

Dekker, W. A conceptual management framework for the restoration of the declining European eel stock. *In* Eels at the Edge. Ed. by J. M. Casselman, and D. Cairns. American Fisheries Society Symposium, 58 (in press).

Haddon, M. 2001. Modelling and Quantitative Methods in Fisheries. CRC Press, Boca Raton, FL.

Hilborn, R., and Walters, C. J. 2001. Quantitative Fisheries Stock Assessment, Choice, Dynamics and Uncertainty. Kluwer Academic Publishers, Dordrecht.

ICES. 2003a. Report of the ICES study group on Precautionary Reference Points for Advice on Fishery Management (SGPRP). ICES Document CM 2003/ACFM: 15.

ICES. 2003b. Report of the ICES/EIFAC Working Group on Eels. ICES Document CM 2003/ACFM: 06.

ICES. 2005. Report of the ICES/EIFAC Working Group on Eels. ICES Document CM 2005/I: 01.

ICES. 2006a. Report of the joint EIFAC/ICES Working Group Eel (WGEEL), 23–27 January 2006, Rome, Italy. ICES Document CM 2006/ACFM: 16.

ICES. 2006b. Report of the Workshop on the Decline and Recovery of Cod Stocks Throughout the North Atlantic, Including Tropho-Dynamic Effects (WKDRCS), 9–12 May 2006, St John's, Canada. ICES Document CM 2006/OCC: 12. 155 pp.

Moriarty, C. 1986. Riverine migration of young eels *Anguilla anguilla* (L.). Fisheries Research, 4: 43–58.

Yalçin-Ozdilek, Ş., Gümüş, A., and Dekker, W. 2006. Growth of European eel in a Turkish river at the south-eastern limit of its distribution. Electronic Journal of Ichthyology, 2: 55–64. http://ichthyology.tau.ac.il/2006/YALCIN-OZDILEK.pdf.