Effect of management measures on glass eel escapement

Laurent Beaulaton and Cédric Briand

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Stocks of European eel (*Anguilla anguilla*) have declined continuously and steadily, since 1980. A model, GEMAC, namely Glass Eel Model to Assess Compliance, has been developed with the objective of assessing anthropogenic impacts on glass eels in estuaries and evaluating the effects of management measures, to support initiatives aimed at helping the eel stocks recover. The model is described and applied to two estuaries with contrasting anthropogenic pressures: the Vilaine and the Garonne. It assesses the proportion of settled glass eels relative to a non-impacted situation with current ($\%S/R$) or pristine recruitment ($\%S/R_0$). The estimated $\%S/R$ ($\%S/R_0$) is 5.5% (1.1%) for the Vilaine and 78% (19%) for the Garonne, in accord with the different levels of anthropogenic pressure in these two estuaries. A sensitivity analysis shows that the assessment of $\%S/R$ is accurate, and that in a data-poor context, the $\%S/R$ is under-assessed, as required by the precautionary approach. Seven management scenarios are explored all aiming to halve the anthropogenic pressure, but in fact leading to different levels of glass eel escapement, from almost zero to a 13-fold increase. This variation emphasizes the need for the estuarine context of eel stock management to be carefully evaluated for effectiveness when implementing management measures.

Keywords: anthropogenic mortality, fisheries management, GEMAC, glass eel, process-based model.

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L. Beaulaton: CEMAGREF, "Estuarine ecosystems and diadromous fish" Research Unit, 50 avenue de Verdun, 33612 Cestas Cedex, France. C. Briand: Institution d'Aménagement de la Vilaine, Boulevard de Bretagne, 56 130 La Roche Bernard, France. Correspondence to L. Beaulaton: tel: +33 5 57 89 27 17; fax: +33 5 57 89 08 01; e-mail: laurent.beaulaton@bordeaux.cemagref.fr

Introduction

The continuous and steady decline in glass eel (*Anguilla anguilla*) recruitment and more generally in European eels has given rise within ICES, and the worldwide scientific community, to grave concern about the status of eels (ICES, 2000; Dekker *et al.*, 2003; FAO EIFAC and ICES, 2006). Among the reasons suggested for the decline, some apply specifically to the glass eel stage: industrial water intake, habitat modification and reduction, migration barriers such as dams and diversions, and fisheries. The last are concentrated in the Bay of Biscay (87% of European glass eel fisheries), where 76% of recruitment of the species occurs (Dekker, 2000b). The direct mortality factors encountered at the glass eel stage do not decrease with declines in the resource: as prices increase, fisheries remain attractive whereas other mortality factors such as industrial water intake remain constant.

In 1997, the glass eel fisheries employed more than 1200 professional fishers, generated a turnover of €68 million, and ranked as the most important in terms of income of Bay of Biscay fisheries, ahead of sole (*Solea solea*), European hake (*Merluccius merluccius*), European anchovy (*Engraulis encrasicholus*), and langoustine (*Nephrops norvegicus*) fisheries (Castelnaud, 2000). The European Commission has stressed the need to develop management plans for each river basin (as laid out in the EU Water Framework Directive 2000/60/EC) and all life stages (CEC, 2005). Within river basins, the estuary is the practical management unit for the glass eel stage. The objective of the model we have developed is to provide a basic framework with which to assess anthropogenic impacts on the glass eel stage in estuaries.

Here, we describe the GEMAC model, Glass Eel Model to Assess Compliance, and apply it to two river basins, the Vilaine and the Garonne, with different anthropogenic pressure: a dam closes the estuary and an intensive fishery is prosecuted in the Vilaine, and a moderately intensive fishery with industrial water intake only is the situation in the Garonne. A sensitivity analysis of the model is also conducted, and the model is applied to aggregated data derived from administrative sources, which are more readily available than highly detailed data from research projects, to assess the utility of the model in a data-poor context. Finally, management scenarios are tested, their impact on glass eel stock is analysed, and the consequences on spawner output are discussed.

Methods

Model

GEMAC is a spatially explicit, biological process-based model that can be applied on a daily time-scale. It is used to investigate how glass eel fisheries and industrial water intake affects the number of settled glass eels in an estuary with either current or pristine levels of recruitment, under different management regimes. It also helps to derive proxies for management purposes, and can be run in data-poor situations. The processes handled by the model are recruitment, pigmentation, settlement, migration, natural mortality, and fisheries and industrial water intake. The model has been developed in R (R Development Core Team, 2005). An earlier version of the model is described in detail in the SLIME project (Dekker *et al.*, 2006). A full description of GEMAC 2.0, which is used here, is provided in the Appendix, so only the main concepts are given below.

Daily recruitment

Daily recruitment can either be real data or can be fitted to the common trend in recruitment found throughout Europe (Dekker *et al.*, 2006).

Pigmentation

Glass eels are separated into stages according to the classification of Elie *et al.* (1982), by pigmentation. The pigmentation stage structure is calculated from pigmentation time, reflecting a glass eel's experience of environmental conditions (temperature, salinity) in the estuary (Briand *et al.*, 2005a). The movement of glass eels from one pigmentation class to the next requires a transition matrix derived from daily values of temperature and salinity in the estuary.

Settlement

Glass eels settle in an estuary according to their pigmentation time. Settlement means an adoption of a benthic behaviour, typical of yellow eels. From then on, they are assumed to be inaccessible to the fishery and industrial water intake.

Migration

Glass eels migrate upstream in the estuary, from one area to the next. Migration is handled with a transition matrix. The probability of changing area is inversely proportional to the length of the area, and directly proportional to migration speed, which is assumed to be constant over the whole study area. Glass eel migration speed can be determined empirically using the methods described in Beaulaton and Castelnaud (2005), or estimated by the model.

Natural mortality

As natural mortality has an equivalent role in the model as anthropogenic mortality or settlement, this parameter needs to be fixed. Data on natural mortality of eels are scarce. Berg and Jorgensen (1994) found daily mortalities from stocking experiments of 0.31 g 0+ eels ranging from 0.0138 to 0.0233. Bisgaard and Pedersen (1991) assessed a daily mortality of 0.0049 from marking experiments on <15 cm eels. An average value of 0.01 is used for daily instantaneous natural mortality in this study.

Fisheries and industrial water intake

We consider glass eel fishing and losses attibutable to industrial water intake as analogous to filtering particles from a fluid. The filtration rate corresponds to the volume filtered by a fishery or an industrial water intake divided by the volume of the area. Allowing for a concentration factor, the filtration rate is considered to be equivalent to an estimate of instantaneous mortality caused by fishing or the intake of water by industry.

Model output

The main output of the model is a management target, which has been defined in terms of both mortality and biomass (Sissenwine and Shepherd, 1987; Mace, 1994). The model mortality target is the proportion of settled glass eels per recruit relative to non-impacted conditions (%S/R), defined as follows:

$$\%S/R = \frac{(\text{escapement})_{F,F'}}{(\text{escapement})_{F=0,F'=0}}.$$

For each area, the escapement corresponds to the number of settled glass eels added to the number of the glass eels alive on the last day of the simulation (see Appendix). Escapement is computed for given fishing effort and industrial water intake. To calculate escapement in non-impacted conditions (no fishing, no industrial water intake), we fixed the instantaneous rate of anthropogenic mortality (F and F') to zero, ran GEMAC again, and computed the escapement associated with these new conditions.

This target is the easiest to handle because it is defined in relative scale, so does not need absolute recruitment to work. As the historical decrease in recruitment is not considered in the target, it is also less subject to density-dependent processes. However, as the first draft of the proposal of European regulation (CEC, 2005) suggests a target biomass, another output is calculated: the proportion of settled glass eels relative to pristine conditions (%S/R_0). We decided simply to multiply the %S/R by a coefficient (θ_r) representing the decrease in recruitment from a pristine state. Following the recommendations of the EIFAC/ICES working group on eels (FAO EIFAC and ICES, 2006), θ_r is the decrease in recruitment from the level of the current year compared with 100% of the mean level during the period 1950–1979. The recruitment level was calculated with the GEMAC recruitment model (Dekker *et al.*, 2006), which provides indices of recruitment from 1950 to 2004.

Case studies

The model is applied separately to two well-studied and documented watersheds (Figure 1) with contrasting human pressures: the heavily fished and dammed Vilaine estuary, and the large, open estuary of the Garonne basin, which is moderately fished but has a nuclear power plant that extracts water for cooling purposes.

The Vilaine basin

The Vilaine catchment (10 400 km^2, NW France, 47°30′N 2°29′W) has an intensive, small pushnet (2×1.13 m^2) fishery for glass eels located just below an estuarine dam, 12 km from the river mouth, with the maximum number of boats operating at night ranging from 87 to 114 boats between 1999 and 2004. The study is therefore focused on the estuary below the dam. Information on catch and effort per day has been collected from logbook surveys, commercial surveys, and boat censuses (Briand *et al.*, 2003). Point estimates by mark-recapture of estuarine stock sizes are available with data on pigment stage structures in 1999, 2000, and 2002–2004 (Briand *et al.*, 2005b). The estuary is modelled using just one area and data from the fishing seasons 1998/1999 to 2003/2004.

The Garonne basin

The Gironde is the tidal part of the Garonne basin (81 000 km^2, SW France, 45 35′N 1°05′W). It consists of a large brackish estuary (450 km^2) plus the fresh-water tidal part of the Garonne River, the Dordogne River and its tributary, and the Isle River (60 km^2 in all). Fishing for glass eels takes place in both brackish and fresh-water tidal areas. In 1999, in the brackish estuary, 74 fishers caught 40.6 t using large pushnets (maximum 14 m^2). Upstream in the fresh-water tidal river, 75 fishers caught 8.3 t using two kinds of gear: small pushnets (2×1.13 m^2) used by 74 fishers yielding 7.5 t, and scoopnets (1.13 m^2) used by 24 fishers (one of them also using pushnets) yielding 0.8 t (Beaulaton and Castelnaud, 2007). Catch and effort were annually recorded from a group of cooperative fishers (representing 22% of glass

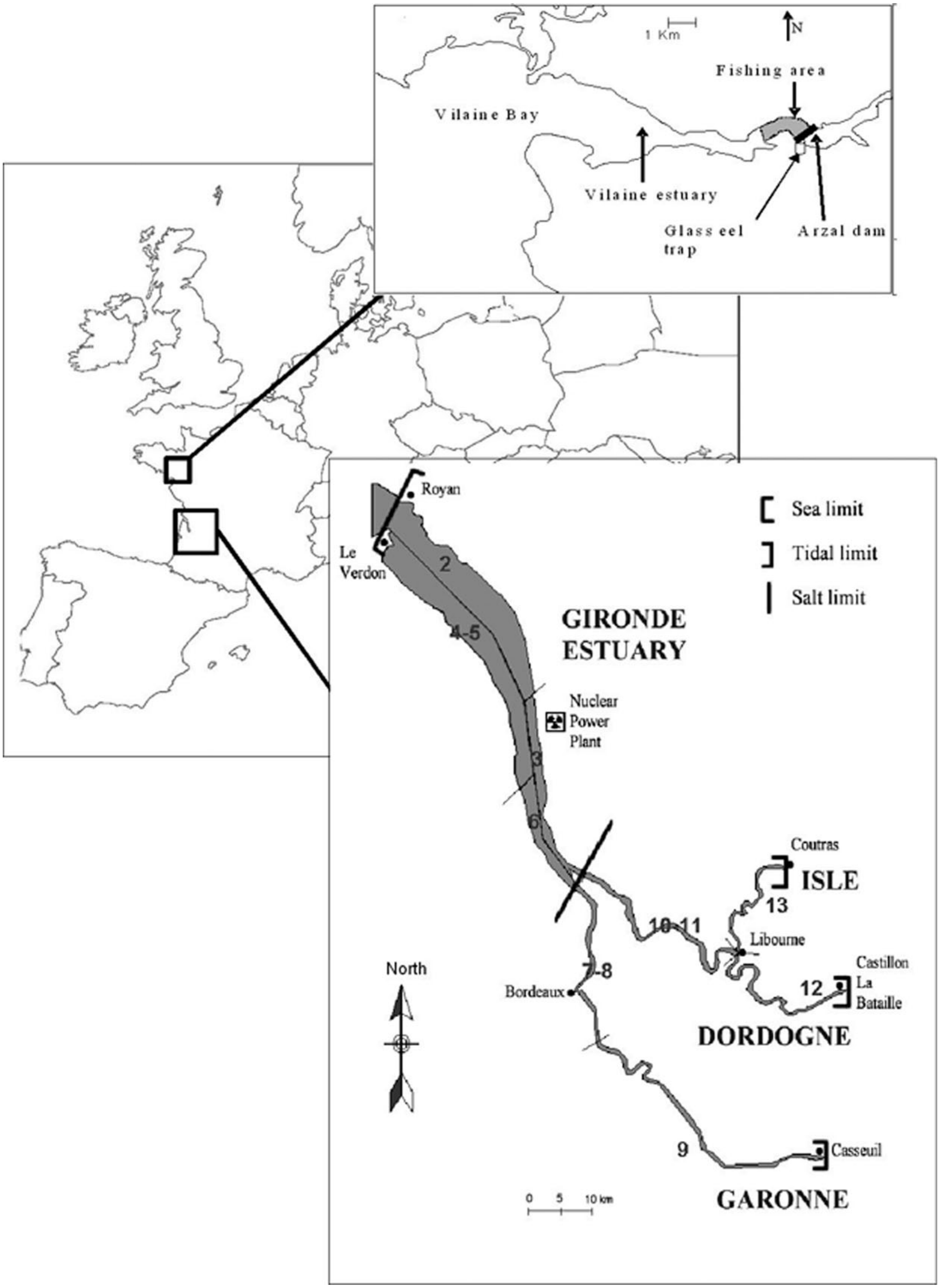

Figure 1. Map showing the areas of the case studies: the Vilaine estuary (upper map) and the Gironde (lower map). The Gironde areas are given by numbers. The Garonne axis consists of areas 4–5, 6, 7–8, and 9 and the Dordogne axis of areas 2, 3, 10–11, 12, and 13.

eel fishers in 1999) and extrapolated to the whole population (Beaulaton and Castelnaud, in press). Independent stock surveys have been conducted in the brackish estuary, giving monthly estimates of density (Girardin *et al.*, 2005). The number of fishers and their spatial distribution is estimated annually from information gathered by fisher associations and the CEMAGREF cooperative fishermen's network. A nuclear power plant (area 3) pumps 12.6×10^6 m^3 of water per day from the brackish estuary for cooling purposes. Roqueplo *et al.* (2000) estimated that 15% of glass eels circulating in the cooling system died during a week. This equates to 1.89×10^6 m^3 per day in which all glass eels are killed. The nuclear power plant is the main industrial water intake and at maximum capacity can pump 168 m^3 s^{-1}, the same order of magnitude as the mean Dordogne river discharge (277 m^3 s^{-1}). It is assumed to be the only significant industrial water intake in the Gironde.

For our study, we used data from the fishing season 1998/1999, but disregarding scoopnet fisheries because such fishing effort has been mainly transferred to small pushnets; the use of small pushnets began in 1996. For the 1998/1999 season, scoopnet catches were <2% of the total (Beaulaton and Castelnaud, in press).

The two banks of the estuary and the corresponding rivers are considered independent in hydrographic terms, leading us to consider the Gironde as two separate estuaries (the Garonne and the Dordogne axes). This assumption is supported by the morphology of the estuary, with one channel per bank and several islands, and by the analysis of glass eel migration speed (Beaulaton and Castelnaud, 2005).

Calibration of the model

GEMAC uses seven groups of parameters, either estimated from external references or calibrated by model optimization:

(i) *Pigmentation*. Seven parameters to convert temperature and salinity into pigmentation time and four parameters to turn pigmentation time into pigmentation stage. Values were estimated from experimental data (Briand *et al.*, 2005a).

(ii) *Filtration*. Daily filtration capacities of a boat or an industry. For the fishery, one parameter for the Vilaine estuary and two for the Gironde, for large and small pushnets, respectively. The concentration factor (see Appendix) is mixed with these parameters, which are calibrated by optimization. The daily instantaneous filtration induced by the nuclear power plant on the Gironde is fixed to the mean volume pumped by the power plant and corrected for glass eel survival (see above and Appendix).

(iii) *Volume*. One parameter for each area, i.e. one for the Vilaine estuary and nine for the Gironde, fixed to the estimated water volume of each area.

(iv) *Settlement*. Two parameters for the gamma cumulative distribution function. These parameters are calibrated by optimization for the Gironde, and the same values are assigned to the Vilaine estuary.

(v) *Recruitment*. A common trend is used for both case studies (Dekker *et al.*, 2006). It uses latitude, basin surface, temperature, discharge, and tide to provide an index of relative abundance. Scale parameters are used to convert this relative abundance into absolute abundance. As six years are explored for the Vilaine basin, six scaling parameters (one for each year) are required. For the Gironde, two scaling parameters are required, one for each bank. In the Vilaine, because of the intensive fishing pressure, escapement is mostly outside the fishing season. The percentage of recruitment in April is modelled with six additional parameters (one for each year) to account for late recruitment variations. Scale and late recruitment parameters are calibrated by optimization.

(vi) *Natural mortality*. One parameter, fixed.

(vii) *Migration*. The length of each area is used as input. One parameter for glass eel speed is calibrated by optimization in the Gironde.

We optimized a weighted error sum of squares with the "L–BFGS–B" method of Byrd *et al.* (1995), which allows variables to be constrained within lower and upper bounds. For the Vilaine estuary, the optimization is therefore conducted on 13 parameters (1 for filtration and 12 for recruitment) in fitting a stock estimate, daily catch, total annual catch, and stage structure. For the Gironde, the optimization is on seven parameters (two for filtration, two for settlement, two for recruitment, and one for migration), fitting daily observed catch, daily observed catch per unit effort (cpue) as an abundance index, and daily density data from a scientific survey.

Sensitivity analysis

The influence of parameters on the main output, i.e. %S/R, is tested using a uniform random sample of parameter values in a range of 15% around their calibrated value. Fishing filtration, volume, settlement, recruitment, mortality, and migration parameters are sampled, and provide 500 combinations of parameters from which to compute %S/R. The value of the parameter is expressed in a relative way, i.e. its value is divided by the calibrated value. The values of %S/R are analysed by GLM with quasi-likelihood, logit link, and a variance equal to $\mu^2/(1-\mu)^2$. This method is adapted for percentages (McCullagh and Nelder, 1989). We used a GLM to predict the effect of an increase of 1% of each parameter on the %S/R scaled by its predicted value in the absence of any change. Results are expressed in terms of relative change in %S/R, and the effect of parameter variations is compared between the Vilaine and the Gironde.

Application of GEMAC in data-poor contexts

A major obstacle to management in this way is that few estuaries are monitored as intensively as the Vilaine and the Gironde. In our case, in the absence of scientific survey data, the only data available would have come from the fishery administration, and at best the effort would have been estimated from the annual number of fishers. Therefore, we tested the effect of using such limited aggregated data on the %S/R. To produce more realistic and better estimates with these aggregated data, effort is set to zero during legal weekly closures. Other parameters were kept to their calibrated value, and %S/R was computed and compared with %S/R values computed with more accurate daily data.

Test of management measures

In the EU's proposed regulation (CEC, 2005), one of the measures suggested is a reduction of 50% of fishing effort. We extended this suggestion to cover industrial water intake too, and used GEMAC to test the effects on glass eel escapement. A reduction of 50% of both fishing effort and industrial water intake might be achieved by the following:

(i) *Licence control*. The number of fishers and the industrial intake are halved.

(ii) *Fortnightly closure*. All anthropogenic impacts are banned either for the first or the second fortnight of a month and authorized for the other. Two scenarios are therefore possible, depending on which fortnight is closed.

(iii) *Daily closure*. All anthropogenic impacts are banned during even days and authorized during odd days.

(iv) *Seasonal closure*. The length of the season is reduced. Fishing is authorized for some 5 months per season from 15 November to 15 April. The fishing season can be reduced by opening later and/or closing earlier. A fishing closure in the middle of a season is unlikely. We tested the following open seasons: November 15 to January 31 (early opening); January 01 to March 15 (middle season opening); February 01 to April 15 (late opening). Industrial water intake is also banned during fishing closure.

Results

GEMAC outputs and goodness-of-fit

In the Vilaine, the Pearson correlation between observed and predicted values can be summarized as follows: 0.5 for the stock estimated by mark and recapture; >0.99 for the total annual catch; 0.32–0.74, depending on year, for pigment stage structures; 0.63 and 0.79 for daily catches in 1998/1999 and 1999/2000, the only two seasons for which daily data are available. From 1998/1999 to 2003/2004, the mean %S/R is 5.5% and varies from 2% to 10% according to the length of the fishing season and the strength of late recruitment. The mean %S/R_0 is 1.1% and ranges from 0.3% (2001/2002) to 2.8% (1998/1999) (Table 1).

For the Gironde, the correlation between observed and predicted catches, cpue, and density range from 0.85 to 0.94, 0.63 to 0.73, and 0.58 to 0.86, respectively, depending on area. The %S/R is estimated as 78%, and %S/R_0 as 19% (Table 1).

Calibrated parameters

For the Vilaine, annual recruitment as estimated by the model decreases from 17.2 to 7.4 t from 1998/1999 to 2004/2005. April recruitment ranges from 0.1% to 11.2% of the seasonal total recruitment and is within the range of values observed from 1987 to 1995. Values are larger for the Gironde in 1998/1999, where the recruitment calculated on the Garonne axis is 84.0 t and on the Dordogne axis is 52.3 t, giving a total recruitment of 136 t for the whole Gironde (Table 1).

The filtration rate is calculated to be 1.4×10^5 m^3 d^{-1} boat^{-1} for the pushnet fishery in the Vilaine, about ten times larger than daily filtration estimates for the similar small pushnet fishery in the Gironde, 1.4×10^4 m^3 d^{-1} boat^{-1}. However, the latter corresponds to a shorter fishing duration: 1.6 h in the Gironde vs. 4.3 h in the Vilaine. The daily filtration of large pushnet boats in the Gironde estuary (Table 1) is estimated to be 2.0×10^6 m^3 d^{-1} boat^{-1}.

The mean pigmentation time of the settlement function was 2.25 and the variance 0.135, corresponding to an intermediate pigmentation time between that necessary for passage from stage VB to VI_{A2} (1.56), and from stage VB to VI_{A3} (3.68). As the two parameters were correlated and other combinations fitted the Vilaine data too, values derived for the Gironde are used for the Vilaine.

The glass eel migration speed in the Gironde is taken as 6.1 km d^{-1}.

Sensitivity analysis

The %S/R distributions obtained with re-sampled parameters are normally distributed and the modes (and ranges) are 5.5 (4.5–7.0)% for the Vilaine and 78 (73–83)% for the Gironde (Figure 2). The associated coefficients of variation are 9.4% and 2.3%, respectively. GLM predicted and observed values agree well for the Vilaine estuary ($r = 0.995$) and the Gironde ($r = 0.998$). GLM analysis provides estimates of the influence of each parameter and classifies them for each basin (Figure 3). The first result (except for the April parameter used in the Vilaine) showed that an increase of 1% of a parameter changed the %S/R by <0.2% of its value.

For the Vilaine estuary, late recruitment had the greatest impact on results. An increase of 1% in this parameter increased the %S/R

Table 1. Comparison of Vilaine estuary and Gironde characteristics, inputs, and results.

Parameter	Vilaine estuary	Gironde
Characteristics		
Basin surface	10 400 km^2	81 000 km^2
Estuary volume	3.5×10^7 m^3	3.9×10^9 m^3
Inputs		
1999 recruitment	17 t	136 t
Official number of fishers	163	149
1999 catch	15.3 t	44.1 t
Fishing filtration (including concentration factor)		
Small pushnet	1.4×10^5 m^3 d^{-1} boat^{-1}	1.4×10^4 m^3 d^{-1} boat^{-1}
Large pushnet		2.0×10^6 m^3 d^{-1} boat^{-1}
Industrial water intake (corrected from glass eel induced mortality)		1.89×10^6 m^3 d^{-1}
Results		
%S/R	5.5%	78%
%S/R_0	1.1%	19%

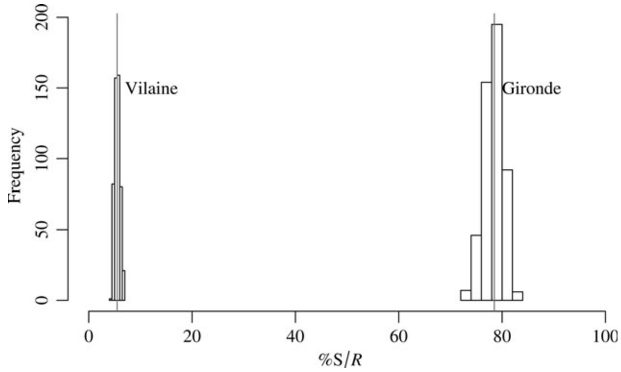

Figure 2. Distribution of %S/R for the 500 parameters randomly sampled in a range of 15% around their calibrated values for the Vilaine estuary and for the Gironde. The vertical lines are the %S/R corresponding to the calibrated parameters, i.e. 5.5% and 78% for the Vilaine and the Gironde, respectively.

from 0.002% to 0.97% of its value, and the response was proportional to the calibrated value. The %S/R sensitivities to variations in total recruitment, natural mortality, and filtration parameters were next, but variation in settlement parameters had little or no influence on the model output. For the Gironde, the large pushnet filtration was the most important parameter, and natural mortality one of the least influential. As expected, in both cases, increasing filtration parameters led to declines in %S/R, whereas increasing the volume and the natural mortality parameters increased the %S/R. In the Gironde, a faster glass eel migration speed parameter increased the %S/R. Scaling recruitment parameters (annual for the Vilaine and by bank for the Gironde) could either increase or decrease the %S/R, depending on the situation.

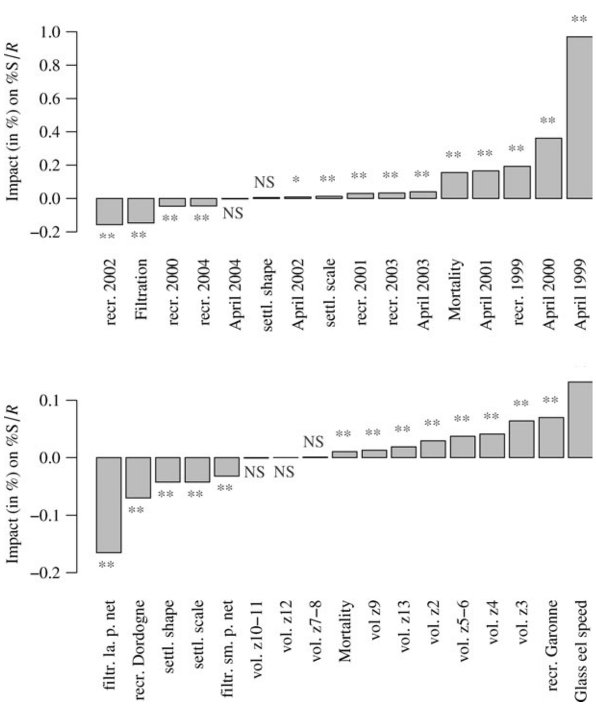

Figure 3. Sensitivity analysis: change (in %) of %S/R when each parameter is in turn increased by 1% as predicted by the GLM for the Vilaine estuary (upper panel) and for the Gironde (lower panel). The label "April 1999" means late recruitment in the 1998/1999 season; "filtr. la. p. net", large pushnet filtration; "filtr. sm. p. net", small pushnet filtration; "vol. Z2", Volume of area 2; "settl.", settlement; NS, non-significant; $*p < 0.05$, $**p < 0.01$.

Application of GEMAC in data-poor contexts

The annual number of fishers in the Vilaine estuary according to official data is 163 (Table 1). Using this figure, %S/R reduces from 5.5% to 3.9%. In the Gironde, the annual numbers of fishers are 74 and 75 for large and small pushnet fisheries, respectively (Table 1). Calculated from these data, the %S/R reduces from 78% to 64%.

Test of management measures

The results of management scenarios clearly showed that all measures halving fishing and industrial effort were not equivalent (Figure 4). This difference was striking for the Vilaine estuary, where only early opening performed well and allowed a %S/R of 73% to be reached. A mid-season opening scenario was the second best performer, allowing %S/R to reach 16%. No other scenario yielded a %S/R > 9%. For the Gironde, licence control, fortnightly closure, daily closure, and early opening were almost equivalent, with a %S/R of around 87%. Late opening provided the greatest increase in %S/R (90%), and mid-season opening yielded the last increase, 83%.

Discussion

Calibration and results of the models

Like many process-based models, GEMAC has a large set of parameters to fit and is difficult to calibrate. For this reason, some parameters have been fixed, decreasing the number of free parameters. The Vilaine estuary and the Gironde model are therefore not fully optimized, so the results should be considered with care. For instance, a different rate of natural mortality could lead to differing results. However, catches, stage structure, and stock for the Vilaine model and catches, cpue, and densities for the Gironde model were well predicted.

For the Vilaine estuary, empirical measurements gave an estimated filtration rate of 49 536 $m^3\ d^{-1}\ boat^{-1}$ (CB, unpublished data). In the Isle River (area 13 of the Gironde), measurements made during four fishing trips in 2005 gave a mean filtration rate of 15 482 $m^3\ d^{-1}\ boat^{-1}$ (N. Susperrégui, pers. comm.). The ratio between the observed and the optimized filtration gives a concentration factor of 2.8 for the Vilaine estuary, and close to 1 for the Isle River.

In the Vilaine, a value of concentration factor of 2.8 seems feasible for the following reasons: (i) the fishery is mostly in the upper part of the fishing area and concentrated near the estuarine dam; (ii) the measurement of filtration rate was made during experimental trips, which are less intensive than commercial fishing. In the open Isle River, the concentration factor being close to 1 indicates that fishers do not fish glass eels in concentrated patches.

No observations of filtration capacity of large pushnets were available. The optimized filtration rate for the large pushnet was 140-fold greater than the filtration of the small pushnet in the Isle River. This is a plausible value, because the gear is six times larger, fishing duration is 3–6 times longer, and boats using large pushnets are more powerful and use tidal currents that can be stronger in the estuary than in the Isle River. Fishers deploying

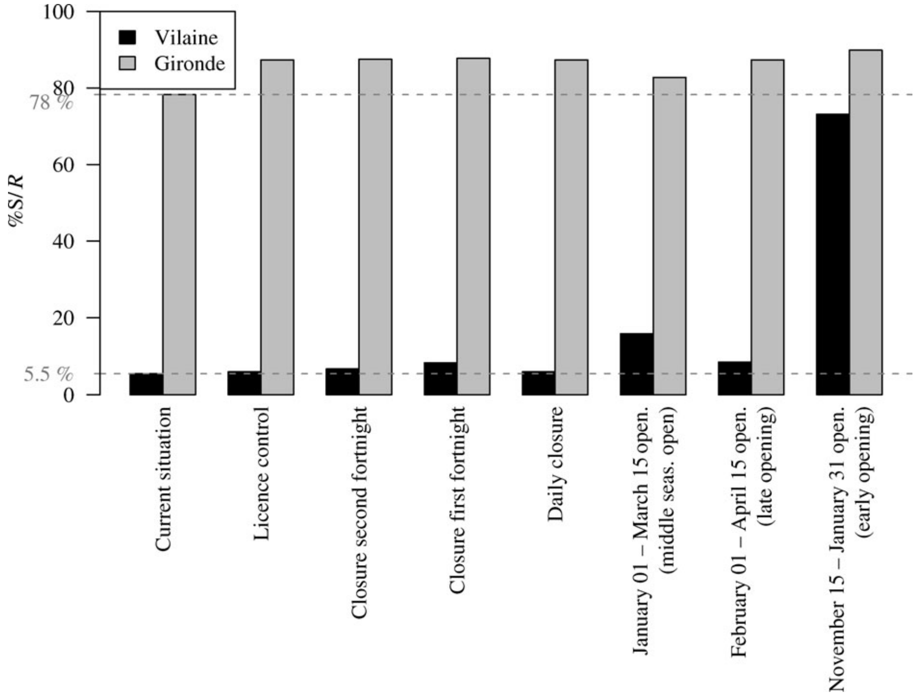

Figure 4. Effect of different management measures on %S/R in the Vilaine estuary and in the Gironde. Dashed horizontal lines are the current level of %SPR for the Vilaine estuary (5.5%) and the Gironde (78%).

large pushnets can also benefit from a small increase in concentration of glass eels near the banks (Lambert, 2005).

Glass eel migration speed has been estimated as 3–4 km d^{-1} in the Gironde (Beaulaton and Castelnaud, 2005), whereas the optimized value was 6.1 km d^{-1}. However, in the model, glass eel speed is not a true migration speed in the sense that it is only a proportionality coefficient to turn distance within a given segment of the estuary into a probability of moving to a different area. This probability is assumed constant from one area to the next and constant over time, irrespective of the time already spent by a glass eel in the departure area. It would be more realistic if this probability were to be drawn from a skewed distribution according to the duration spent by a glass eel in a specific area.

The calibrated settlement parameters led to maximum settlement at the VI_{A2} stage, although in the model, settlement can be observed as early as stage VB, especially in downstream areas in the Gironde where young stages are most abundant. This result is in accord with settlement events believed to occur at the VI_{A2} stage in the Vilaine (Briand *et al.*, 2005b). Settlement at this stage makes sense, because Jegstrup and Rosenkilde (2003) showed that the T4 thyroid hormone level in glass eels begins to decrease from stage VI_{A2}, and Edeline *et al.* (2004, 2005) confirmed that decreasing T4 levels corresponded to reduced migration both in experimental and field data.

Our sensitivity analysis shows that natural mortality has only a minor influence on %S/R. However, the range of values tested was just 15%, at around 0.01, despite the greater uncertainty associated with the value of natural mortality. The value of daily mortality chosen in this model (0.01) corresponds to a medium value compared with literature values, which are as high as 0.0233 (Berg and Jorgensen, 1994) and as low as 0.0049 (Bisgaard and Pedersen, 1991; Adam, 1997).

As expected, the values of %S/R are strikingly different between basins. Consistent with this study, annual exploitation rates >95% have been estimated in the Vilaine estuary, according to glass eel trap monitoring (Briand *et al.*, 2005b). These values can be compared with (1 − %S/R), which is also slightly more than 95%. However, exploitation rate and %S/R are not equivalent, even if they are closely related. In fact, (1 − %S/R) is smaller than the exploitation rate because it accounts for that fraction of fished glass eels that would have died in an unfished environment. Therefore, both values indicate that most of the recruited glass eels are fished in the Vilaine estuary during the fishing season and that the only possible escapement is after fishing season closure in late April and May.

In contrast, in the large, open Gironde estuary, the value of (1 − %S/R) (22%) indicates a less intense fishery, although no independent estimate can confirm this figure. In the Adour estuary, close to the Gironde and also undammed, where a small pushnet fishery operates both in the marine and the fluvial part of the estuary, the mean exploitation rate of the marine fishery for the years 1998–2004 was estimated to be 16.4% (Bouvet *et al.*, 2006), although the exploitation rate of the river fishery was unknown. The exploitation rate in the Gironde would, therefore, be of the same order of magnitude as the Adour marine fishery. For other eel species, rates of exploitation have been estimated at 30–50% for the *Anguilla rostrata* elver fisheries from the East River (Nova Scotia, Canada; Jessop, 2000), 44–75% for the *Anguilla japonica* elver fisheries from Shuang-chi River (Taiwan; Tzeng, 1984). These figures show that glass eel fisheries vary from one place to another. Notwithstanding, we have demonstrated with our model that the ratio between filtered volume and estuary volume is a good proxy of fishing mortality, so a cut in carrying capacity (i.e. estuary volume) will lead to an increase in fishing pressure through the increase in the volume ratio. Moreover, when carrying capacity is reduced by the construction of a dam, the concentration factor may increase, as for the Vilaine estuary.

Sensitivity analysis

Our model does not seem to be too sensitive to parameter uncertainty, as shown by our sensitivity analysis (Figure 3). The predicted distributions of %S/*R* are close to their calibrated values (low coefficients of variation) when the parameters are varied by 15% around the calibrated value (Figure 2). This is further illustrated by the influence of a 1% change in all parameters except April recruitment, which changed %S/*R* by $<0.2\%$ of its fitted value.

April recruitment has a greater influence; an increase of just 1% leads to a relative %S/*R* variation ranging from 0% to nearly 1%. This greater influence is explained by the fact that a glass eel recruited in April will have a better probability of escaping the fishery. As such, the response is directly proportional to the calibrated value.

Settlement parameters are one of the least important factors for the Vilaine estuary, whereas they play a major role in the Gironde (Figure 3). This is a consequence of the difference in fishing pressure in the two estuaries. In the Vilaine, variation in these parameters does not change the fact that glass eels are caught before settling during the fishing season and escape the fishery when it stops. For the Gironde, the volumes of areas 10–11, 12, and 7–8 are not significant because of the absence of (or low) anthropogenic pressure in these areas. Glass eel migration, however, is a key parameter. Its increase leads to faster upstream migration, preventing large pushnets from catching glass eels and explaining its positive influence on %S/*R*. Improved definition (see Appendix) might be possible, and would enhance the precision of our estimate of %S/*R*.

Application of GEMAC in data-poor contexts

For both case studies, replacement of daily counts of fishers by an official annual number leads to underestimating %S/*R*, by 7% and 18% for the Vilaine and Gironde, respectively, as a consequence of the overestimation of fishing effort. In fact, fishers do not fish every day, despite what we consider when using administration data. This smaller %S/*R* is in accord with a precautionary approach. The estimated %S/*R* is, however, not too far from the likely real value. This implies that for most estuaries, knowing the extent of the fishing area, the corresponding volume, the number of licences, and the duration of the fishing season might make it possible to provide a reasonable estimate of %S/*R* at the glass eel stage. The same applies for industrial water intake, for which filtered volumes are generally known. Any improvement from these raw data will permit more refined estimates to be made. For long estuaries, with several fishing areas, for instance the Loire River, an estimation of glass eel migration speed would be needed.

Test of management measures

In both case studies, licence control and fortnightly or daily closure lead to a smaller increase in %S/*R* than a seasonal closure scenario. However, depending on the basin and on the month when fishing is banned, a seasonal scenario can also be the least effective. As expected, if the closed period is during peak migration (the early opening scenario in both basins), %S/*R* increases more, whereas closure outside this peak migration period (late opening scenario for the Vilaine estuary, mid-season opening for the Gironde) can lead to less effective management. The impressive increase in the %S/*R* for the early opening scenario in the Vilaine estuary is a perfect illustration of this fact. However, the cost to the fishery would be a large decrease in landings from a cumulative catch for 6 years of 70 to 22 t, if the early opening scenario were to be invoked. Clearly, the socio-economic consequences of such scenarios need to be evaluated.

General discussion

A dozen European eel population dynamics models exist, from the large scale "procrustean" model of Dekker (2000b) and Åström and Dekker (2007), to a purely theoretical model (Lambert and Rochard, 2007) and case-specific models (Sparre, 1979; Gatto *et al.*, 1982; De Leo and Gatto, 1995; Dekker, 2000a; Lambert *et al.*, 2006; Aprahamian *et al.*, 2007; Bevacqua *et al.*, 2007). Among them, just four (Dekker, 2000b; Aprahamian *et al.*, 2007; Bevacqua *et al.*, 2007; Lambert and Rochard, 2007) address the glass eel stage, and no model estimates glass eel anthropogenic mortality, despite needing it as input. GEMAC, therefore, fills a gap in European eel modelling effort. In its principles, it is similar to other process-based models such as SMEP (Aprahamian *et al.*, 2007) and Globang (Lambert and Rochard, 2007). The processes handled are similar, pigmentation being considered as a growth/ageing process. GEMAC benefits from migration processes developed in models such as the glass eel estuarine migration model SEGPA (Lambert, 2005), because this process is poorly implemented in GEMAC and migration speed seems to be one of the key parameters of our model. Conversely, GEMAC can be used to improve or complement other models that handle the whole glass eel stage poorly, if at all. In the framework of implementation of any management plan for eels, all stages need to be considered.

%S/*R* is the main output of GEMAC and can be related to %SPR (percentage spawner-per-recruit), representing the actual proportion of spawners produced by a basin relative to non-impacted conditions through multiplying similar percentages occurring at other life stages (yellow, silver) and produced by some of the other models cited above. The settlement phase, from settled glass eel to yellow eel, will also have to be considered because it can be seen as a critical phase. However, to our knowledge, no model explicitly considers evaluation of that phase, and GEMAC is the only model that specifically takes into account mortality at the glass eel stage.

Our results show that GEMAC can be used for an initial assessment of the anthropogenic impact at the glass eel stage. It can also help to test management scenarios and develop management proxies (e.g. the number of boats, filtration capacities), so guiding the implementation of initial management measures. Upon reaching these first steps, management will need to evaluate the impact of the measures taken. Either the model is able to produce secondary outputs that can be compared with observations and assess whether observations match predictions, or other indicators should be developed, e.g. monitoring the abundance of 0+ eels. For GEMAC, pigment stage structure could be used as a secondary output. When anthropogenic mortality is high (as in the Vilaine), glass eels are killed before they pigment. Therefore, large relative catches of young, unpigmented glass eels can indicate high pressure on the stock. However, this index is not sufficiently precise for management implementation. Another solution would be to survey glass eel density and fishing effort closely and to run the model again with the new data. Density data would allow more precise fitting of recruitment and daily anthropogenic pressure (e.g. fishing effort) information, so allowing assessment of anthropogenic impacts with greater precision. As GEMAC runs on an annual basis, the assessment can be done from one year to another. However, additional development is needed for the model to be run during the course of a season to permit fine adjustment of management measures, e.g. deciding on earlier closure of the fishery. This implies accurate prediction of recruitment by the end of a season having known the level of recruitment at the start of the season.

The current proposal for management plans (CEC, 2005) only expresses the management target in terms of biomass. However, a target %SPR could be an easier short-term goal to manage (FAO EIFAC and ICES, 2006). The EIFAC/ICES Working Group on eel advocated an %SPR (F_{lim}) limit of 30% and a cautious %SPR (F_{pa}) of 50% (ICES, 2001) based on a target taken from other species. A recent study on European eels suggests that a %SPR $>$ 60% would restore the eel stock (FAO EIFAC and ICES, 2006). Whatever the chosen target, the Vilaine estuary with a %S/R of 5.5% is well below any target suggested, and this is without considering the additional anthropogenic impacts that affect the stock at the yellow and silver eel stages. For the Gironde, the glass eel fisheries and the nuclear power plant alone are not large enough to exceed the target 60%. However, the anthropogenic impact on yellow and silver eel stages should be added to the value calculated here, i.e. yellow eel fisheries, and the effects of turbines and pollution.

Considering the proportion of settled glass eels relative to pristine conditions (%S/R_0), both the Vilaine and Gironde estuaries are far from the biomass target suggested by CEC (2005), and this is without taking into account yellow or silver eel anthropogenic mortality. This is because of the decrease in glass eel recruitment since the start of the 1980s (Moriarty, 1990; Beaulaton and Castelnaud, 2007). The decline in recruitment is so large that it is unlikely that the biomass target will be reached soon. However, we here used a coefficient of decrease in glass eel recruitment to convert %S/R into %S/R_0. As such, we implicitly raised the cautious hypothesis that there was no density-dependent mortality in the past. To our knowledge, there is no evidence for or against this phenomenon for glass eels.

The escapement of settled glass eels is too low to permit the biomass target to be reached in either of the two estuaries. This finding, for estuaries in the central and most heavily recruited part of the distribution of the species (Dekker, 2003), supports a conclusion that immediate and massive increase in silver eel escapement is urgently needed for there to be any chance at all of recovering the European eel stock.

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Appendix

Description of GEMAC 2.0

The model is a process-based model, handling sequentially:

(i) recruitment
(ii) pigmentation
(iii) mortality/settlement
(iv) migration.

The number of glass eels in the estuary is stored in an array of three dimensions, $N_{d,\pi,j}$, d being the day, π the pigmentation time class (see below), and j the area.

Recruitment

Each day, new glass eels recruit into the estuary, and they enter the model within an initial pigmentation time class π_0 and in some area j_0 (R_{d,π_o,j_0}). The daily recruitment has been fitted separately from the model and corrected using a scaling parameter R_0:

$$N_{d,\pi_0,j_0} = N_{d-1,\pi_0,j_0} + R_0 R_{d,\pi_0,j_0} \text{ or}$$
$$N_{d,\pi,j} = N_{d-1,\pi,j} \text{ for } \pi \neq \pi_0 \text{ and } j \neq j_0.$$

Pigmentation

Pigmentation time structure is calculated from gamma cumulative function (Briand *et al.*, 2005a). First, mean daily temperatures and salinities are centred to a range between 0 and 1.

$\theta_{d,j}$ = daily transformed temperature
$d_{d,j}$ = daily transformed salinity

Then, they are beta-transformed and multiplied to calculate the daily pigmentation time in area j ($\phi'_{d,j}$).

$$\Theta_{d,j}(\theta_{d,j}; p_5; p_6) = \text{beta}(\theta_{d,j}; p_5; p_6)$$
beta function of parameters p_5, p_6

$$\Delta_{dj}(d_{d,j}; p_7; p_8) = 1 - \text{beta}(d_{d,j}; p_7; p_8)$$
beta function of parameters p_7, p_8

$$\varphi'_{d,j} = \Theta_{d,j}(d_{d,j}; p_7; p_8)\Delta_d(d_{d,j}; p_7; p_8)$$
daily pigmentation time in area j

Glass eels are separated into 121 0.1 classes (π_n), from class [0,0.1[to class [11.9,12[and a 12+ class. Each day the probability of changing from one class (π_n) to the next (π_{n+i}) $\text{prob}_{\pi n,\ \pi n+i}$ is calculated as follows:

$$\text{prob}_{\pi_n,\pi_{n+i}} = \max\left(0,\ \frac{\min(\pi_{n,e}+\varphi'_{d,j},\ \pi_{n+i,e}) - \max(\pi_{n,b}+\varphi'_{d,j},\ \pi_{n+i,b})}{\pi_{ne}-\pi_{nb}}\right),$$

$\pi_{n,\ b}$ and $\pi_{n,\ e}$ being the beginning and end limits of class π_n.

This formula assumes that glass eels are distributed uniformly within one class. Daily probabilities are computed for all π_n, π_{n+i} classes ($i > 0,\ n+i \leq 121$). They are stored in an array with four dimensions $T_{d,j,\pi,\pi}$. The changes in pigment time are calculated each day.

$$N_{d,\pi,j} = \sum_{\pi}(N_{d,\pi,j} {}^{*}\, T_{d,j,\pi,\pi}).$$

A pigmentation stage structure can be deduced from the population array (N), because it is structured by pigmentation time. Glass eels reaching one pigmentation stage (VI_{A0cum} = glass eels being at or more advanced than stage VI_{A0}) are estimated for one day, one area, and one pigmentation time class using the mid-pigmentation time of this class (φ_π) as input to the gamma cumulated functions (Γ) corresponding to this stage:

$$\text{VI}_{A0\text{cum}} = \Gamma(\varphi_\pi; p_1; 1)N_{d,\pi,j};$$

$$\text{VI}_{A1\text{cum}} = \Gamma(\varphi_\pi; p_2; 1)N_{d,\pi,j};$$

$$\text{VI}_{A2\text{cum}} = \Gamma(\varphi_\pi; p_3; 1)N_{d,\pi,j};$$

$$\text{VI}_{A3\text{cum}} = \Gamma(\varphi_\pi; p_4; 1)N_{d,\pi,j}$$

where p_1–p_4 are shape parameters of each cumulative stage function.

These calculations are repeated over the classes and are used to calculate the pigment stage composition for 1 d and one area. For instance, the number of glass eels at stage VI_{A0} can be computed as follows:

$$\text{VI}_{A0} = \text{VI}_{A0cum} - \text{VI}_{A1cum}.$$

Mortality/settlement

This part of the model is written classically (Beverton and Holt, 1957).

$$N_{d,\pi,j} = N_{d-1,\pi,j}\,\mathrm{e}^{-Zd,\pi,j};\ Z_{d,\pi,j} = M + F_{d,j} + F'_{d,j} + S_{d,\pi,j},$$

where M is the natural mortality, $F_{d,j}$ the fishing mortality, $F'_{d,j}$ the industry water intake mortality, and $S_{d,\pi,j}$ is the settlement. The presence of a dimension in the subscript (e.g. π) indicates that the quantity varies over that dimension (e.g. pigmentation time class).

The fishing mortality or the industrial water intake mortality is calculated from the ratio of the total volume filtered by either fishery ($\Psi_{d,j}$) or industrial water intakes ($\Psi'_{d,j}$) and the volume of the estuarine zone (V_j), corrected by the factor ψ. This factor is a glass eel concentration factor for the fishery and the percentage of glass eels killed by industry water intake.

$$F_{d,j} = \frac{\psi\Psi_{d,j}}{V_j}$$

$$F'_{d,j} = \frac{\psi\Psi'_{d,j}}{V_j}.$$

For fishing mortality, the total volume filtered ($\psi_{d,\ j}$) can be split into the mean volume filtered by each boat and by the total number of boats.

Settlement is calculated from a gamma function (Γ) with parameters p_{10} and p_{11}. The proportion of glass eels settling each day, in each area, for each pigmentation class ($\text{prob}_{d,\pi,j}$) corresponds to the conditional probability of settling between pigmentation time $\varphi_\pi - \varphi'_{d,j}$ and φ_π, φ_π being the mid-pigmentation time of class π and $\varphi'_{d,j}$ the daily pigmentation time in area j (see above):

$$\text{prob}_{d,\pi,j} = 1 - \frac{1-\Gamma(\varphi_\pi, p_{10}, p_{11})}{1-\Gamma(\varphi_\pi - \varphi'_{d,j}, p_{10}, p_{11})}.$$

Settlement rate ($S_{d,\pi,j}$) is deduced from this proportion ($\text{prob}_{d,\pi,j}$).

$$S_{d,\pi,j} = \ln(1 - \text{prob}_{d,\pi,j}).$$

Migration

The migration is handled with a transition matrix T. Each cell $T_{i\to j}$ of this matrix corresponds to the probability of a glass eel moving each day from area i to area j. The proportion $T_{i\to j}$, area j being adjacent to area i, depends on glass eel migration speed (v). and the length of area i (L_i):

$$T_{i\to j} = \frac{v}{L_i}.$$

For an area j not adjacent to area i, $T_{i\to j}$ is zero. When area i has more than one adjacent area (for confluence), $T_{i\to j}$ is weighted according to the relative rate of discharge of each river joining. The special case $j = i$ describes the proportion of glass eels staying in area i each day:

$$T_{i\to i} = 1 - \sum_{j\neq i} T_{i\to j}.$$

Some outputs of the model

The number of glass eels present on day d in area j is assessed by summing the pigment time dimension

$$N_{d,j} = \sum_{\pi} N_{d,\pi,j},\ \text{number of glass eels.}$$

The number caught, pumped, dead, or settled at day *d* in area *j* is computed using the Baranov equation:

$$C_{dj} = \frac{\sum_{\pi} N_{d-1,\pi,j} F_{dj} (- \mathrm{e}^{-Zd,\pi,j})}{Z_{d,\pi,j}},$$

daily catch in area *j*;

$$C_{dj} = \frac{\sum_{\pi} N_{d-1,\pi,j} F'_{dj} (1 - \mathrm{e}^{-Zd,\pi,j})}{Z_{d,\pi,j}},$$

daily pumping mortality in area *j*;

$$\mathrm{CS}_{dj} = \frac{\sum_{\pi} N_{d-1,\pi,j} S_{d,\pi,j} (1 - \mathrm{e}^{-Zd,\pi,j})}{Z_{d,\pi,j}},$$

daily settlement in area *j*;

$$\mathrm{CM}_{dj} = \frac{\sum_{\pi} N_{d-1,\pi,j} M_{d,\pi,j} (1 - e^{-Zd,\pi,j})}{Z_{d,\pi,j}},$$

daily natural mortality in area *j*.

Escapement (E) of glass eels is the number of glass eels settled during all simulations, plus the number alive on the last day (d_∞):

$$E = \sum_{d,j} \mathrm{CS}_{d,j} + \sum_{j} N_{d_\infty,j}.$$

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