German Eel Model (GEM II) for describing eel, *Anguilla anguilla* (L.), stock dynamics in the river Elbe system

Deutsches Aalmodell (GEM II) zur Beschreibung der Bestandsdynamik des Aals, *Anguilla anguilla* (L.), im Elbesystem

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**Abstract**

The eel, *Anguilla anguilla* (L.), stock of the river Elbe severely decreased during the last decades. Detailed knowledge of the stock dynamics in freshwater and especially of the impact factors is necessary to take effective measures for stock conservation and improvement. The dynamics of the eel stock are modelled based on immigration, stocking, natural mortality and mortalities caused by fishing, angling, cormorants and hydropower plants. The model estimates the number of emigrating eel. Moreover, it enables to study the sensitivity of the estimates related to the uncertainty of the source data of the different influencing factors. The model may be used to develop management strategies and to assess the efficiency of different management options.

**Zusammenfassung**


**Introduction**

The recruitment of glass eel to Europe shows a heavy decline in the last 25 years. The historical low levels observed in recent years are an indication that the stock is clearly out of safe biological limits (ICES 2008). In order to fulfil the European Council regulation (EC) No 1100/2007 of 18 September 2007 for establishing measures for the recovery of the eel stock (European Union 2007) a model is required because data to assess the present and former situation are insufficient or not yet available. The challenge for the European Community is to develop a management system that ensures that local measures produce results in a consistent way across the various river basins, member states, and adjacent countries to establish the escape ment to the sea of at least 40 % of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock. As the eel has a catadromous life cycle, only the freshwater phase (including coastal and brackish water) can be studied and managed.
Earlier approaches of eel stock modelling (e.g., Rossi 1979, Sparre 1979) were based on classical fishery modelling by using cohort models or age-structured models. These early modelling approaches provided first insights into certain eel populations but lacked to include some key characteristics of eel population dynamics.

A major step to develop a realistic model was made with SLIME (Study Leading to Informed Management of Eels) (Dekker et al. 2006). Six different models were reviewed and tested, using 10 case study data sets from all over Europe at a river basin level to derive reference points for sustainability, and to model the potential effect of legal and technical measures aimed at stock recovery. Generally, previous modelling approaches can be categorised as stage specific models (e.g., GEMAC in SLIME), cohort models (Sparre 1979, Rossi 1979, Gatto and Rossi 1979), input-output models (Völlestad and Jonsson 1998), size and age-structured models (e.g., De Leo and Gatto 1995, Dekker 1996, Greco et al. 2003, Åström and Wickström 2004, DemCam in SLIME), models enabling an analysis of spatially distributed populations (Lambert and Rochard 2007) and global models (Dekker 2000, Åström and Dekker 2006). Accordingly, the focus and the modelling methods differ, with respect to the main purpose of the model, the availability of data and the accuracy needed.

Most of the models consider eel stocks of certain water bodies, some of them by taking into account spatial aspects. Exceptions are global models, which aim at the assessment of the entire European eel stock (Dekker 2000, Åström and Dekker 2006) and which provide an estimate of the time scale of recovery of recruitment and which may give information about the scale of restrictions necessary to make a recovery likely.

Aspects, which are considered in the recently developed models, include e.g. recruitment, growth, sexual development, density dependence, carrying capacity, migration and simulation of a variety of effects (not just fishing). Most models are built to enable the testing of management options by modelling different scenarios and also to reconstruct former or “pristine” conditions. There are also simplistic models, which are flexible (e.g., SWAM in SLIME).

Different models for estimating the escapement of silver eel were tested and applied during the EU project “Pilot projects to estimate potential and actual escapement of silver eel” (POSE, Walker et al. 2011) which used different basic data for the estimation. The presented model was part of this EU project.

Detailed knowledge of the stock dynamics in freshwater and especially of the impact factors is necessary to take effective measures for stock conservation and improvement. The dynamics of the eel stock in the river Elbe system are modelled based on immigration, stocking, natural mortality and mortalities caused by fishing, angling, cormorants and hydropower plants. This model developed for the Elbe has the general advantages of simple adjustment and extension by being MS-EXCEL based and modular structured and was also applied for Irish and simulated data within the EU project POSE.

The advantage of the used approach is that estimates of the stock size by age groups exist during the entire period for comparing estimates of the model with sampling data to adapt the input data of the model.

The described model is based on the model used for the German management plan of the river system Elbe in 2008 (Anonymous 2008), but, three adaptations were realized based on new data and new knowledge.

The Bertalanffy growth function was estimated based on new age – length data. This change influenced many other model parameters where length based data were transferred into age based data by means of the growth function, like the minimum landing age of fishermen and angler, the proportion of silver eel by age etc. The natural mortality of 13 % for each age group according to Decker (2000) was replaced by the model of Bevaqua et al. (2011) which incorporates the mean water temperature, sex, the weight and the density of eels. In addition, field data have shown that fishermen and angler capture not only yellow eel as assumed in the model for 2008. Therefore, the catch of silver eel was incorporated into the model.

Notations with general implication

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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</thead>
<tbody>
<tr>
<td>a</td>
<td>index of age group defined as years in freshwater</td>
</tr>
<tr>
<td>t</td>
<td>index of year</td>
</tr>
<tr>
<td>ti</td>
<td>year of the model start</td>
</tr>
<tr>
<td>N1,a</td>
<td>eel stock in number of age group a in the year ti</td>
</tr>
<tr>
<td>L1,a</td>
<td>mean length of age group a in the year ti</td>
</tr>
<tr>
<td>W1,a</td>
<td>mean weight of age group a in the year ti</td>
</tr>
<tr>
<td>Cx,t</td>
<td>total weight of eel in year t which leave the system by factor x</td>
</tr>
<tr>
<td>N1,t,x</td>
<td>number of eel which leave the system by factor x</td>
</tr>
<tr>
<td>N1,t,a</td>
<td>number of eel of age group a in the year t</td>
</tr>
<tr>
<td>W1,t,x</td>
<td>mean weight of eel in year t which leave the system by factor x</td>
</tr>
<tr>
<td>P1,t,a</td>
<td>Proportion of silver eel of age group a in the year t</td>
</tr>
<tr>
<td>R1,t,a</td>
<td>Number of immigrating recruits of age group a in the year t</td>
</tr>
<tr>
<td>R1,t,a</td>
<td>Number of restocked recruits of age group a in the year t</td>
</tr>
</tbody>
</table>
Factors which were taken into account for describing the dynamics:
F effects by commercial fishermen
A effects by recreational fishery (anglers)
C effects by cormorants
B effects by the transition from yellow eel to silver eel
M effects by natural mortality

General relations

The model estimates the number of emigrating eel. Moreover, it enables to study the sensitivity of the estimates related to the uncertainty of the source data of the different influencing factors.

The aim of the development was an age based model which describes the dynamics of the eel stock in number by age group and year. The model should incorporate the effects of commercial and recreational fishing together with the influences of the natural mortality, the increasing effect of predation by cormorants, the transformation from the yellow eel to the silver eel stage and the effects of power plants. It was assumed that eel remain in freshwater for a maximum of 20 years (Tesch 1999). The available data for describing the different factors which influence the stock dynamics have different quality. Total catch in kg by year is estimated for the commercial fishermen and angler. The mean weight of the catch and age-length based samples are only available from some areas and short time periods. Length based estimates exist for the transformation of yellow eel to silver eel and for the eel which are taken by cormorants based on stomach samples. To combine the different data types a procedure is necessary for transferring length based data into age based data. The available age-length data (Simon unpublished) are used to estimate the Bertalanffy growth curve of eel.

\[ L_t = L_\infty [1 - e^{-k(t-t_0)}] \]  
with \( L_\infty = 115.04, k = 0.065 \) and \( t_0 = -1.0 \).

The age of a given length was then estimated by

\[ a' = t_0 - LN(1 - \frac{L}{L_\infty})/k \]  
and \( a = \text{round} (a') \).

The procedure was used to estimate the minimum age of capture with 6 years based on the legal size of 45 cm for commercial fishermen and anglers. The procedure was also used to transfer the length frequency of eel fed by cormorants into age frequency and to transfer the length based fraction of silver eel into age based proportions of silver eel. Furthermore, the mean weight by age group was estimated based on the length-weight relation \( W = a L^b \) with \( a = 0.0008 \) and \( b = 3.197 \) in combination of Equation 2 and 3.

The minimum landing age by fishermen was described by delta-function

\[
D_{F,t,a} = \begin{cases} 
0 & \text{for age } < 6 \\
1 & \text{for age } \geq 6 
\end{cases}
\]

The same function was used for anglers because the legal size for fishermen and angler is equal.

In addition, the following assumption was used for estimating the catch in number by age group and year because appropriate data are lacking:

The age frequency of the catches by fishermen and anglers is similar to the age frequency of the stock combined with the requirement that eel younger than 6 years are not landed.

Recruitment

The recruitment of eel is composed of natural immigration of glass/yellow eel, \( R_{N,t,a} \), and stocking with eel of different age groups, \( R_{R,t,a} \). The numbers of stocked eel by age group and year are taken from statistics of fisherman, anglers and fishery authorities. The numbers of immigrating eel are estimated based on monitoring results from immigrating eel at different Elbe tributaries (Simon and Fladung 2006). In addition, the length frequency of immigrating eel was estimated at weir Geesthacht in the lower middle Elbe based on samples taken in different years.

Amount of naturally died eel

The proportion of natural died eel was estimate based on Bevaqua et al. (2011). The model incorporates the weight and sex of eel as well as the mean water temperature to estimate the natural mortality. In addition, the three density levels of the eel stock are taken into account.

In addition, the effects of cormorants are incorporated because the model describes the effects of increasing cormorant population, as separate parameter. Therefore, the fraction of eel which dies by natural reasons defined, \( P_{M,a} \), of mentioned above age groups were reduced to 85-96% dependent on the effects of cormorants in year with low cormorant population. The \( P_{M,a} \) was used to estimate the number of eel by age group and year due to natural reasons with

\[ N_{M,t,a} = N_{t,a} \times P_{M,a} \]
Commercial fishermen

Estimates of total catch of eel by fishermen in year \( t \) which are given in kg, \( C_{F,t} \), are available for the period from 1985 to 2010. The minimum landing length of eel by fishermen is 45 cm which is transformed into the minimum landing age of 6 years as described in Equation 2 and 3. The mean weight of eel captured by fishermen in year \( t \), \( w_{F,t} \), can be estimated by

\[
w_{F,t} = \frac{\sum \limits_a N_{t,a} \cdot w_{t,a} \cdot D_{F,t,a}}{\sum \limits_a N_{t,a} \cdot D_{F,t,a}}
\]

(5)

Because appropriate data are lacking Equation 4 assumes that the age frequency of captured eel is similar to the age frequency of the yellow and silver eel stock. This assumption is supported by field observations that eel catches by fishermen and angler are not selective. The total number of eel captured by fishermen can then be estimated by

\[
N_{F,t} = \frac{C_{F,t}}{w_{F,t}}
\]

(6)

and the catch in number by age group in year \( t \) by

\[
N_{F,t,a} = N_{F,t} \cdot \frac{\sum \limits_a N_{t,a} \cdot D_{F,t,a}}{\sum \limits_a N_{t,a} \cdot D_{F,t,a}}
\]

(7)

Recreational fishery by anglers

The total catch by anglers is estimated based on the number of anglers, \( M_A \), and the mean catch in kg by angler and year, \( w_{A,t} \). The total catch in kg by angler can be estimated by

\[
C_{A,t} = M_A \cdot w_{A,t}
\]

(8)

The mean weight of eel captured by angler in year \( t \), \( w_{A,t} \), can be estimated by

\[
w_{A,t} = \frac{\sum \limits_a N_{t,a} \cdot w_{t,a} \cdot D_{A,t,a}}{\sum \limits_a N_{t,a} \cdot D_{A,t,a}}
\]

(9)

where \( D_{A,t,a} \) is the delta-function which describes the minimum landing age of eel by angler. The Equation 8 is similar to Equation 4 with the possibility of a different minimum landing size/age.

The total number of eel captured by angler can then be estimated by

\[
N_{A,t} = \frac{C_{A,t}}{w_{A,t}}
\]

(10)

and for the catch in number by age group in year \( t \) follows

\[
N_{A,t,a} = N_{A,t} \cdot \frac{\sum \limits_a N_{t,a} \cdot D_{A,t,a}}{\sum \limits_a N_{t,a} \cdot D_{A,t,a}}
\]

(11)

Mortality of eel by cormorants

The mortality of eel by cormorants to the eel population is described by means of different data types which are based on data sampling and assumptions. The feeding pressure of the cormorant population, \( M_C \), was estimated based on the amount of cormorants, their stay duration, the daily food intake and the average eel proportion in their diet (Brämick and Fladung 2006). Samples of cormorant stomachs were used to estimate the fraction of eel in the total diet of cormorants, \( P_{C,t} \). The stomach samples were also used to estimate the relative age distribution of eel, \( P_{C,t,a} \) and the mean weight of eel, \( w_{C,t} \) taken by cormorants.

In addition, it was assumed that the highest proportion of eel in the food of cormorants was observed with 13 % in 2002 (Brämick and Fladung 2002) and that a further decrease of the eel stock of the age groups 2 to 15 which are fed by cormorants results in a decreasing proportion of eel in the food of cormorants. Therefore, the total weight of eel taken by cormorants in the current years after 2002 was related to the eel population of age groups 2 to 15 in 2002.

Statistical analyses of the stomach samples have shown that the relative length distribution of eel fed by cormorants can be described by log-normal distribution. The length frequency was transferred into age frequency by means of Equation 2 and 3 (Figure 1). The total number of eel fed by cormorants in year \( t \) can be estimated by

\[
N_{C,t} = \frac{C_{C,t}}{w_{C,t}}
\]

(12)
The numbers of eel by age group which were fed by cormorants follows by

\[ P_{B,t,L} = \frac{1}{1 + e^{-t(a+bL)}} \]  

(14)

where the index \( L \) denotes the length.

\( P_{B,t,a} \) was estimated based on \( P_{B,t,L} \) by means of Equation 2 and 3. Youngest female silver eel were estimated as 7 years old. Low fraction of silver eel was applied for age groups 4 to 6 to include the effect of male silver eel which presents 5 % to 8 % of the stock. The fraction of silver eel increases with increasing age. \( P_{B,t,a} \) is more than 95 % for eel older than 15 years which corresponds with length of more or equal than 76 cm. This estimate did not correspond with the samples of silver eel more than 90 cm long in different areas. Therefore, a correction factor was added, \( F_B \), which defines the highest proportion of yellow eel which transfers to silver eel in all age groups. An estimate of \( F_B = 0.8 \) was used for the model (Figure 2).

**Fraction of silver eel and mortality by hydropower plants**

Samples of length frequencies of silver eel in the river Elbe were used to describe the transition from yellow eel to silver eel by age. The length data were transformed into age data by Equation 2 and 3. The fraction of silver eel by length, \( P_{B,t,L} \), was described by a logit-function which increases from zero to 1.
The number of silver eel by age group and year was describe by

$$N_{B,J,a} = \frac{N_{I,a} \times P_{B,J,a} \times F_{B}}{\sum_{a} N_{I,a} \times P_{B,J,a} \times F_{B}} \tag{15}$$

The total numbers of silver eel which leave the Elbe river system is reduced by mortalities caused by hydropower plants, cooling water intakes etc. To incorporate the different effects of mortalities by water exploitation in different parts of the Elbe river system the total water area, S, was stratified into 10 parts with relatively equal mortality by the barriers. S0 is the area where the survival of silver eel is not influenced by barriers. S10 is the area where 10% of the silver eel died due to barriers, etc.

The total number of silver eel which leave the Elbe river system can then be estimated by

$$N'_{B,J,a} = N_{B,J,a} \times \frac{\sum_{i=0}^{100} S_i \times (100 - i)}{100} \times S \tag{16}$$

where i increases in steps of 10.

Stock development

The abundance of age group a in year t was calculated by

$$N_{t,a} = N_{t-1,a-1} + R_{M,J,a} + R_{R,J,a} - N_{M,J-1,a-1} - N_{F,J-1,a-1} - N_{A,J,a-1} - N_{C,J-1,a-1} - N_{B,J-1,a-1} \tag{17}$$

Structure and basic assumptions of the presented model are adjusted to the main factors which determine the dynamic of the eel stock in the river Elbe system and the availability of data. In some cases sub models and assumptions were required for describing the effects of the different factors. The stock model was developed to allow an easily extension by additional factors to adapt basic assumptions by empirical data and to take into account the uncertainty of the input data. Moreover, the model can be used to study the effects of different management scenarios, like an increase of cormorants, the decrease of the total catch or the increase of stocking.

The growth curve is an important part of the model because it is used to transfer length based into age based data. The presented model uses one growth
The effects of the commercial and recreational fishery are described based on the minimum landing size and the assumption that the age structure of the landings corresponds with the mean age structure of the stock. This assumption does not incorporate possible effects of gear selectivity as it is described by the model of Bevaqua et al. (2007). Different gear types are used in the river Elbe. In most cases the gear is designed in such a way that eel larger than the minimum landing size is representationally captured. The total catch by commercial and recreational fishery is estimated from catch data respectively from average catch and amount of anglers. However, the model can be adapted if source data are available in more detail.

A logistic-function is used to describe the length/age-specific transformation from yellow to silver eel maturation. This type of function corresponds well with the observations. About 5% males are included in the model by the early onset of emigration with 35 cm length assuming equal growth of both sexes. Another type of sigmoidal function was used by De Leo and Gatto (1995) and Bevaqua et al. (2006), which described the silvering in relation to body size and sex. Despite differences in the exact shape of the function, the use of a logit-function appears to be appropriate to describe the transformation.

One special feature of the model is predation of eel by cormorants. So far, this aspect has not been considered in detail in any of the existing models although the size of the cormorant populations strongly increased during the last decade in many areas (Pivernetz 2007). The effect of cormorant predation on local or regional eel stocks differs appears to be substantial in some cases (Brämick and Fladung 2006). A first, rough estimation of cormorant predation on eel on a European scale revealed a consumption of 4000-6000 t annually, corresponding to about 15-40% of the commercial catches (Carss 2006). This extent justifies special consideration of this factor in the model, in particular as data are available for the river Elbe system. Including this factor is also useful, since it can theoretically be influenced by managing the cormorant population. The effect of cormorant predation under different scenarios may add valuable information to the discussion about a European cormorant management plan. Furthermore, the effect of cormorant predation can be analysed on a regional basis.

The main mortality factors for downstream migrating silver eel are fishery (but see comments above) and technical constructions like hydropower turbines and cooling water intakes. Prey on cormorants is usually restricted to smaller individuals and is assumed to have no direct effect on silver eel. Potential mortalities due to diseases or parasites and such factors were not incorporated into the model due to the absence of data and the probably high variability in space and time. However, these types of mortality are partially included in the natural mortality.

The model assumes that turbines damage only silver eel, although there are also some effects on yellow eel during movements within the rivers. Estimation of the turbine mortalities are based on original data or average mortality of ~30% less a percentage for the protection device.

According to the position of the obstacles and the known or estimated mortality rates at each location, the river Elbe system can be divided into several sub-areas, for each of which the cumulative turbine mortality down to the estuary can be calculated. By using a step size of ten percent, the whole system can be divided into ten sub-areas of similar turbine mortality. This way of modelling makes it easy to study the effect of improvement of the migration capacity of water power stations because the influenced area will be added to another sub-area.

Different approaches for natural mortality of eel have been discussed in the literature. On the one side, Vøllestad and Jonsson (1998) and Dekker (2000) used constant natural mortalities. Such constant natural mortalities are also used in the stock assessment of many marine fish stock by ICES. On the other side, higher mortality rates were estimated for the youngest age classes followed by a decrease down to 0.10 – 0.07 for the older age groups (De Leo and Gatto 1995, Bevaqua et al. 2011). Similar decreasing natural mortality for older age groups was observed in the Elbe river catchment (Simon and Brämick 2012). Therefore, the method of Bevaqua et al. (2011) where applied in the model. Nevertheless both options of natural mortality can be used in the model to study their effects concerning the eel stock dynamics.

In addition, the fraction of eel which dies by natural reasons were reduced to 85-96% as measured by the effects of cormorants in year with low cormorant population because the cormorants were added as additional parameter in the model.

Some remarks are necessary with regard to the sources of mortality included in the model. In case of cormorant predation, the model uses data, which are available from the Elbe system and are therefore re-
garded as rather reliable. For natural mortality literature data had to be used, but in the future data from the Elbe system are required.

In case of turbine mortality, some simplifications were made, which need to be reviewed. The assumption that turbines only act on silver eel, leads to an underestimation of this mortality type for yellow eel. In turn, it overestimates turbine mortality for silver eel.

Recruitment in a river system consists of natural migration of glass eel or elvers and re-stocking. As for many rivers in Europe, natural immigration is hampered by high numbers of artificial obstacles. Whereas in the main river (Elbe) itself only one weir exists in the German part of the catchment (at Geesthacht, with a functioning fish pass), the majority of the tributaries are negatively affected by obstacles like weirs or dams. Consequently, re-stocking accounts for the major part of recruitment in the system (Brämick et al. 2006). Therefore, representative data on re-stocking numbers are of major importance for the modelling of the stock. The size of the stocked eel is categorized in six groups of variable size. For each of the groups the age can be estimated based on length and the growth curve to assign the restocked eel to the different age groups (AG 0-5).

By including the main factors which determine the dynamics of the eel stock in the river Elbe system, the model is an important analytical tool for the preparation of the Eel Management Plan (EMP), which is demanded by the European Commission. It enables estimation of the present condition of the eel stock in the river system as well as a description of the reference situation. By including several mortality factors, it offers the possibility to develop and evaluate different management scenarios and to assess the efficiency of management options. It will therefore aid the development of an efficient management strategy, including the fishery as well as non-fishery factors. This strategy should target on achieving a favourable situation of the eel stock in the river system as well as on enabling a sustainable fishery on eel.

Testing and application of the model within the EU project POSE (Walker et al. 2011) have shown that adaptations of the model can be easy handled. For the Irish data the model was adapted to an age range from 0 to 35 years and two models for male and female eel were combined. The models by sex used different growth functions and input data like the proportion of silver eel by age. In addition, the model was applied for the simulated dataset (CREPE) used in the EU project POSE. The analyses within the EU project further showed that the model results are uncertain if the distribution of eel and thereby the natural mortality is highly patchy as observed in the simulated data set. In this case it seems to be useful to apply spatial separated models.

Even though the model is adjusted to the conditions in the river system and to the availability of data, it also includes several assumptions and uncertainties. Therefore, the results of the model will have to be validated by monitoring the stock, especially by silver eel monitoring, which should be conducted as close as possible to the estuary.

The incorporation of normally distributed errors to describe the uncertainty of the input data makes it possible to study the effects of the uncertainty of single parameters like cormorants or anglers related to the migration of silver eel. The results of these studies can be used to decide where additional investigations and samplings are required in the future.

**Literature**


