



Model prediction vs. reality—testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ* observation of silver eel escapement in compliance with the European eel regulation

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A direct monitoring of European silver eel (*Anguilla anguilla*, L) escapement from rivers and estuaries has been proven to be challenging, and a Europe-wide documentation of escaping silver eel numbers therefore hardly seems realistic. To reinforce management decisions, policy-makers are thus widely reliant on the accuracy of escapement models. A 3-year programme of silver eel escapement monitoring was undertaken to compile model input data and revise an eel population model (German Eel Model II; GEM II) already used in the decision-making process of management authorities. By compiling necessary input data and analysing vital system-specific population characteristics, it was possible to compare the documented silver eel escapement with the modelled potential silver eel escapement. Resulting model predictions were close to actually monitored escapement numbers, which were distinctly lower than reference escapement values for the same freshwater system given in the implementation report of the German Eel Management Plans. Applying different commercial and recreational catch scenarios revealed the sensitivity of the model. The results show the potential of the GEM II and highlight the importance of high-quality input data to use model predictions as the basis for management measures.

Keywords: *Anguilla anguilla*, GEM II, management plan, population dynamics model, silver eel escapement.

Introduction

For centuries, the European eel (*Anguilla anguilla*, L) has been an important target species for fishers all over Europe (Tesch, 2003). However, since the 1980s, the stock has been in a steep decline, and alarmingly low recruitment numbers are documented in virtually every time-series available, as well as reflected in landing numbers all over Europe (Dekker, 2003; ICES, 2010). Nowadays, the European eel stock is considered to be out of safe biological limits and the species is listed in Annex II of the Convention on International Trade in Endangered Species (CITES; ICES, 2010). To stop the downward trend, the European Council (EC) issued regulation No.1100 (European Union, 2007), establishing measures for the recovery of the stock of European eel. One of its

main objectives is to guarantee a minimum of a 40% spawner escapement to the sea in relation to the potential spawner escapement under pristine conditions. Each EU member state was obliged to elaborate Eel Management Plans (EMPs) on a river basin level to reach the given escapement target. A rejection of the EMP would entail strict reductions and eventually the closure of the national eel fisheries.

Therefore, a proper evaluation of any management measure implies the assessment of silver eel spawner escapement, which is methodologically challenging, especially for large river systems. Recent attempts have been largely based on commercial landings (Charrier *et al.*, 2012), sonar-based quantification (Bilotta *et al.*, 2011), mark–recapture studies, or estimations derived from

tagging experiments (Feunteun *et al.*, 2000; Amilhat *et al.*, 2008) as well as the application of stock and escapement models (Aprahamian *et al.*, 2007; Bevacqua *et al.*, 2007; Fenske *et al.*, 2011; reviewed by De Leo *et al.*, 2009).

As a panmictic species, the European eel lacks a well-defined population structure (Als *et al.*, 2011). Fenske *et al.* (2011) pointed out for *Anguilla rostrata* that a common spawning ground and overlapping generations probably lead to a situation where local recruitment is not directly related to overall stock size or local spawner abundance. This also holds true for the closely related European eel. Most common fish population models have been developed for iteroparous species with well-defined population structures. To take this into account, models estimating population dynamics in eel are often trying to cover large geographical scales and are therefore largely dependent on input data compiled from literature sources (Aprahamian *et al.*, 2007; Åström and Dekker, 2007; Lambert and Rochard, 2007). Thus, in the absence of system-specific input data, it is often necessary to convert and generalize vital population characteristics onto a larger scale and/or simplify the model assumptions (Aprahamian *et al.*, 2007; Åström and Dekker, 2007). It has, however, been shown for several Anguillidae species (including the European eel) that vital population characteristics differ with system and/or habitat (Vøllestad, 1992; Poole and Reynolds, 1998; Melia *et al.*, 2006; Lin *et al.*, 2007; Jessop, 2010). Therefore, generalizations can significantly bias the model outcome and limit the conclusiveness of model-based management measures.

Factors influencing the actual number of escaping silver eels from freshwater systems into coastal waters are numerous and widely discussed (Aprahamian *et al.*, 2007; ICES, 2010). They range from commercial and recreational fishing, to predation by birds (e.g. cormorants), to migration barriers (ICES, 2010). Additionally, to evaluate the influence of each factor, initial recruitment numbers, e.g. stocking and/or natural immigration of juveniles to a freshwater system, are of high importance. In order to estimate the dynamics of the European eel stock with respect to immigration, restocking, natural mortality, mortality caused by commercial and recreational fisheries, predators (such as cormorants), and hydropower turbines, Oeberst and Fladung (2012) developed an age-structured eel population model for the River Elbe system (Germany)—the GEM II (German Eel Model II). One of the main output parameters of this model is the number of silver eels that are potentially able to migrate out of a specific system. The main advantage of the model is the possibility to account for uncertainties of the source data, such as, for example, the fact that data on immigrating eels are often of only poor quality.

In order to evaluate models directly used in the decision-making process of management authorities, it is important to ensure detailed and continuous system-specific data time-series. The advantage of the Schwentine River system is the absence of any natural immigration of eels (eliminating an input factor often hard to grasp), the relatively high quality of model input data due to their limited size, and a relatively small number of stakeholders, together with the possibility to directly monitor the actual silver eel escapement, thereby allowing a comparison of different management scenarios.

The study objective was to compare predicted silver eel escapement of the eel population model described by Oeberst and Fladung (2012) with the direct count of escaping silver eels.

Thereby, the potential of eel population modelling in supporting the decision-making process of management authorities could be evaluated.

Material and methods

Study area

The Schwentine River system (part of the Schlei–Trave river basin district) close to Kiel was chosen as an exemplary freshwater system to monitor actual silver eel escapement and collect necessary model input data (Figure 1). The system consists of several freshwater lakes connected by the Schwentine River and has a total area of ~ 7500 ha (total area of lakes: 5984 ha). It discharges into the Kiel Fjord (54°19'39"N, 10°11'11"E), with an average discharge of 3.9 m³ s⁻¹ and ranging from ~ 0.6 to 13.4 m³ s⁻¹. It has been blocked for any upstream fish migration for > 100 years by two consecutive hydropower stations ~ 7 and 9 km upstream of the river mouth. Since 2005, the upper hydropower station ("Raisdorf II") has been equipped with a fish pass combined with trash racks (light spacing: 20 mm) in front of the turbine entries. All silver eels leaving the system are forced to use the fish pass and end up in a fish trap. To date, the lower hydropower station is still not equipped with a fish pass and, thus, no natural ascent of juvenile eels into the system is possible. Therefore, the entire local eel population depends on stocking conducted by commercial fishers, angling societies, and government authorities.

Model description

The GEM II, developed by Oeberst and Fladung (2012), is an age-structured population model describing eel stock dynamics and estimating the potential silver eel escapement both in numbers and in total weight. Escapement is predicted based on vital population characteristics, immigration (including stocking), natural mortality, and mortality caused by recreational/commercial fisheries, cormorants, and hydropower (Oeberst and Fladung, 2012). Cormorant predation was considered separately to better incorporate its highly variable effects in distinct freshwater systems (Oeberst and Fladung, 2012). Even though this model has been developed to document eel stock dynamics in the Elbe river, it is not limited to it and can be transferred to other freshwater systems. Developed in 2008, the model was subsequently adapted according to new data and literature information to meet the requirements of the implementation report of the German EMPs in 2012 (Oeberst and Fladung, 2012), and was part of the EU project "Pilot projects to estimate potential and actual escapement of silver eel" (POSE; Walker *et al.*, 2011).

The GEM II used here was restricted to 20 age classes, because age reading resulted in only a negligible number of eels older than 20 years. Therefore, it was assumed that eels rarely stay longer than 20 years in the Schwentine River system. Availability of data dramatically decreased prior to the early 1990s, and the time horizon for the model had to be set to 17 years (1993–2010). This time frame, however, was considered to minimize sufficiently the bias introduced by using a dummy start population for a comparison calculated with actually monitored escapement in the years 2009 and 2010. It was therefore necessary to compile model input data stretching back to the year 1993. For a detailed description of the GEM II, see Oeberst and Fladung (2012).

The GEM II allows integration of mortality caused by hydropower plants. In the Schwentine River system, two hydropower

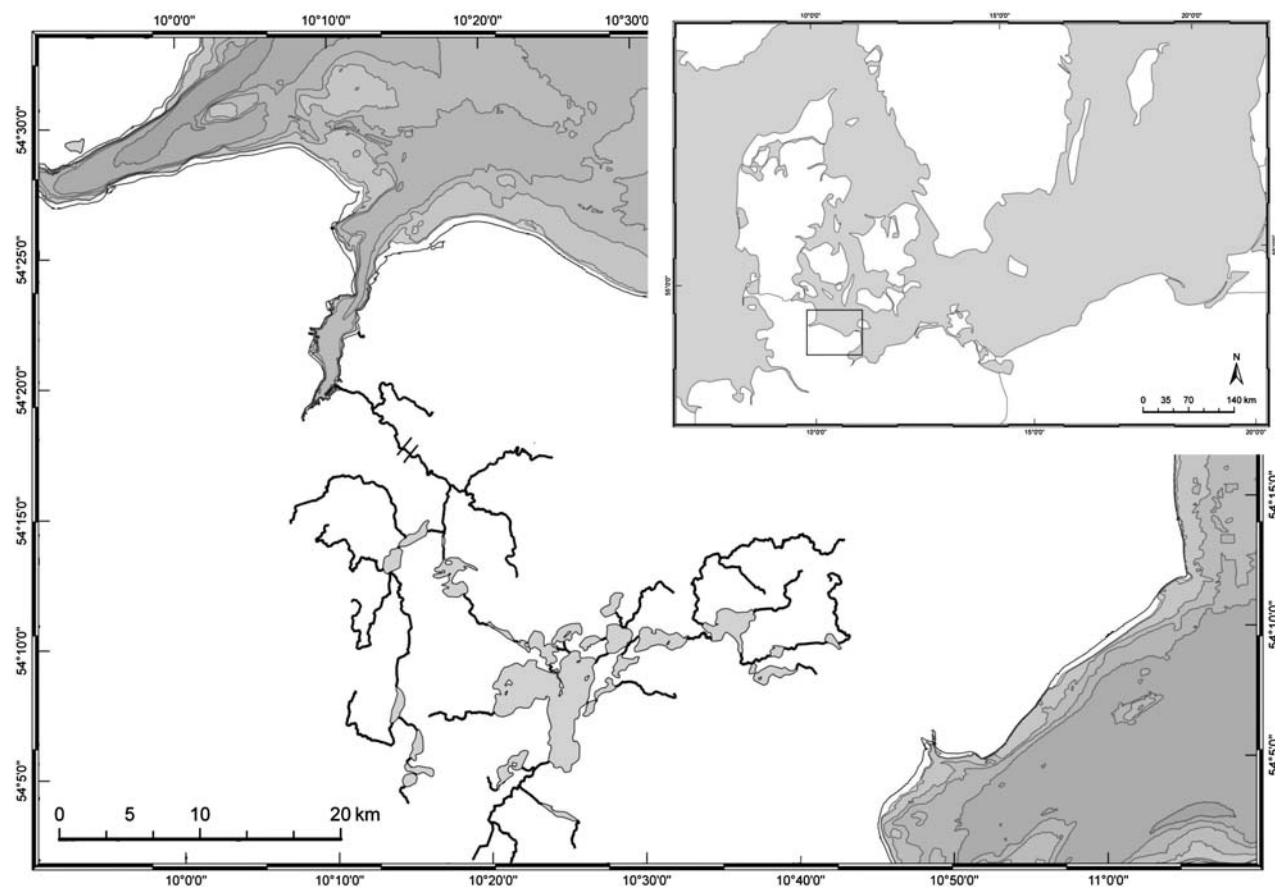


Figure 1. Study area: Schwentine River system in northern Germany, discharging into the Baltic Sea. The inset shows the location of the study area in the Baltic Sea area. Black bars in the main map indicate hydropower stations.

plants impede the escapement of silver eels (Figure 1). However, since escapement numbers were assessed at the upper hydropower plant and trash racks were regularly checked for eels, hydropower mortality was set to be zero in the present study. Furthermore, the model was restricted to a total wetted area of 5984 ha. The often small rivers connecting the systems' lakes were negligible, because fishing as well as stocking activities are mainly restricted to lake habitats.

Data collection

A 3-year silver eel monitoring programme was initiated to collect system-specific model input data and escapement numbers of the Schwentine River system. Monitoring of silver eel escapement out of the Schwentine River in the years 2009 and 2010 was performed by regular inspection of a trap blocking the fish pass that bypasses the upper hydropower station. Total length, wet mass, eye diameter, and pectoral fin length of every single eel caught were documented, and eels were assigned to a maturity stage according to Durif *et al.* (2005). To reinforce data collected at the fish trap and prevent biasing the assessment of system-specific vital population characteristics (e.g. length–weight relationships) towards migrating eels leaving the system, commercial catches were analysed for their length–weight relationship and proportion of silver eels (subsample) once a month in each summer. In total, 147 eels (total length spectrum: 20.2–102.5 cm) were measured to determine the length-at-age relationship for the Schwentine River system. Otoliths were prepared and read according to the

manual published by the “ICES Workshop on Age Reading of European and American Eel” (ICES, 2009).

Since natural recruitment was considered to be zero in the Schwentine River system, recruitment numbers equal stocking numbers. Stocking with eel is decentralized in Germany, and the respective data (1993–2010) were collected from local state authorities (State Agency for Agriculture, Environment and Rural Areas, LLUR) as well as fishers and angling societies operating in the Schwentine River system. The numbers of stocked eels were provided in total weight (kg) per year and respective water body within the system and (when possible) subclassified into “glass eels”, “elvers”, and “yellow eels”. Total stocking in kg was converted into numbers based on the average weight of different estimated age groups, and varied between ~238 000 and 13 500 individuals per year.

Commercial catch data were provided by the LLUR. Data were cross-checked and, if possible, amended by data from the individual fishers. In cases where no catch data were available for individual lakes and single years, gaps were filled according to yearly overall average catch per hectare. Catch data were provided in total weight (kg) per year and respective water body. The minimum legal size of eels in the Schwentine River system is 35 cm for both commercial and recreational fishers. However, local fishers communicated that eels of this size are usually too small to be put on the market, and the actual minimal landing size was assumed to be 50 cm. Since recreational catch data were not collected in a centralized database, historical catch data of

two of the biggest angling societies located in the Schwentine area were analysed to estimate an average catch (kg) of eel per angler and year. The average catch was then multiplied by the total number of recreational fishers in the Schwentine River system per year.

As the cormorant (*Phalacrocorax carbo*) is often regarded as one of the major predators on eel in European freshwater systems, bird predation was assessed separately by stomach content analysis and analysis of regurgitant samples collected in the central colony of the Schwentine River system. Cormorants shot by authorized fishers were collected and stored frozen at -40°C for subsequent stomach content analysis. Stomach contents were screened for otoliths and other remains of *A. anguilla*. Regurgitant samples were collected during the daytime once a month and stored frozen at -20°C prior to analysis. In addition, total cormorant numbers (residents and migrants) were counted. Retrospective cormorant predation on eel was modelled using a time-series of cormorant numbers (2000–2010) for the Schwentine River system and an energetic consumption model according to Tasker and Furness (1996; N. Sonntag, unpublished data). Cormorant predation for the years 2000–2010 was estimated to range between 700 and 1800 kg. Due to a lack of information on the cormorant numbers prior to the year 2000, the cormorant predation assessed by Worthmann and Spratte (1987) for the year 1987 (1187 kg) was used as a constant for 1993–1999.

Vital population characteristics

The GEM II requires several system-specific, age- or size-structured population characteristics to describe the local stock dynamics. Growth rates of European eels are highly variable with habitat and sex (Poole and Reynolds, 1996; Svedäng et al., 1996; Melia et al., 2006). Due to the relatively small size at maturity of male European eels (Tesch, 2003), it was not possible to sample them quantitatively in the fish trap. Monitoring results and model estimations are, therefore, restricted to female European eels in the Schwentine River system. System-specific eel growth of females was described using the von Bertalanffy growth function (VBGF):

$$L_t = L_{\infty}[1 - e^{-k(t-t_0)}] \quad (1)$$

where L_t is the length at time t , L_{∞} the asymptotic length, k the growth coefficient, and t_0 the initial condition parameter when the hypothetical length is zero. Fish growth is commonly described by the VBGF, with all three parameters being based on length-at-age data (Chen et al., 1992). It has, however, been questioned whether the VBGF is actually capable of describing the growth in eels (Sparre, 1979). To account for uncertainties of the VBGF in estimating the growth of semelparous fish species, Froese and Pauly (2013) suggest setting the asymptotic length (L_{∞}) to a fixed value. Semelparous fish are expected to mature at the size and age of the maximum growth rate in weight to maximize their expected reproductive output (Froese and Pauly, 2013), and Froese and Pauly (2013) expect one-time spawners to mature slightly before reaching 0.67 asymptotic length (L_{∞}). Accordingly, and since more precise values are missing for eels, the average length of escaping silver eels (83.1 cm, $n = 357$, subsample of stage F IV and F V eels) was considered to constitute approximately two-thirds (66%) of the system-specific L_{∞} . Therefore, L_{∞} was set to $83.1 \text{ cm} / 0.66 = 124.6 \text{ cm}$. Additionally, t_0 was set to -1 in order for the VBGF to describe the length of age class 0 at between 60 and 75 mm, the length associated with the zero band

in otoliths of glass eels arriving at the European continent and thus entering the continental growth phase (Poole et al., 2004; ICES, 2009; Daverat et al., 2012). Estimation of k based on length-at-age data of 147 eels (silver eels, yellow eels, and juveniles) with L_{∞} and t_0 fixed resulted in a value of 0.0638 and was calculated in STATISTICA 8.0 (StatSoft Inc.). VBGF used in the GEM II and documented length-at-age of sampled eels are given in Figure 2.

The age at a given length was estimated according to (Oeberst and Fladung, 2012):

$$a' = t_0 - \frac{LN\left(1 - \frac{L}{L_{\infty}}\right)}{k} \quad (2)$$

and

$$a = \text{round}(a') \text{ with } a' \text{ rounded to the closest integer} \quad (3)$$

System-specific mean weight by age group was estimated based on the weight-at-length relationship $W = a \times L^b$ ($a = 0.0012$ and $b = 3.1106$) in combination with Equations (2) and (3). The regression parameters a and b were estimated using weight and length data of 518 eels sampled in the fish pass and from commercial catches (length range, 32.5–100.7 cm; weight range, 62.4–2249.7 g). All length-based data were then converted into age-based data by combining Equations (2) and (3).

System-specific sexual maturity (fraction of silver eels) was assessed as the proportion of mature females per age class. The fraction of silver eels per age class was described by fitting a logistic model to maturity data (silver stage according to Durif et al., 2005) from female eels ($n = 640$) collected in the Schwentine River system.

Natural mortality was included according to the model of Bevacqua et al. (2011). The model estimates the proportion of eels that died from natural causes per age class based on the mean water temperature of the system, the density of the eels (three possible density levels), and the system-specific length–weight relationship. As small changes in temperature led to significant changes in natural mortality, a temperature time-series (provided by the LLUR) was used to model natural mortality on a yearly basis retrospective to 1993. With respect to the stocking numbers assessed for the model period, system-specific eel density was considered to be high.

Parameter fitting and model scenarios

While most of the parameters were directly assessed by sampling data on eels in the Schwentine River system (length-at-age, age-at-maturity, etc.), it was necessary to estimate the dummy start population artificially. The age distribution of the start population (1993) was estimated based on the years 2002–2004. It strongly influences the age distribution and stock abundance of the first model years, with decreasing effects during the following model period (Oeberst and Fladung, 2012). The start population can be further adjusted to presumable stocking activities prior to 1993 by introducing an additional factor (“factor for year one”). The “factor for year one” influences the age distribution of the first model year compared with the reference period for the dummy start population. Setting this factor to >1 indicates a higher stocking prior to 1993 compared with the following

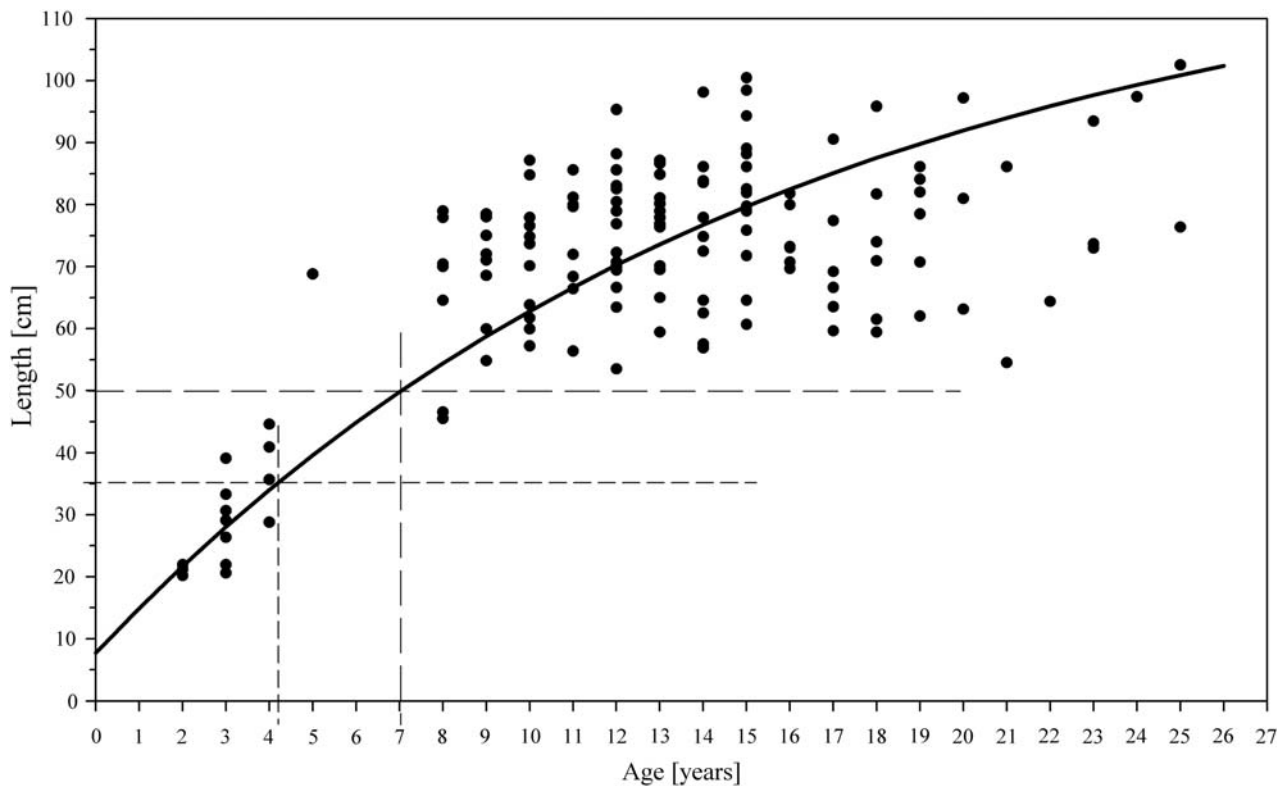


Figure 2. von Bertalanffy growth function (VBGF) for European eel in the Schwentine River system. The horizontal lines indicate the legal minimal landing size (35 cm) of *A. anguilla* for commercial fishers and angling societies, and actual minimal landing size (50 cm) after personal communication with fishers.

years. In contrast, values < 1 indicate lower stocking prior to 1993. In addition, the fraction of silver eels per age class can be corrected for large yellow eels otherwise not accounted for by the logistic model. This can be done by varying the maximum proportion of yellow eels that become silver eels ($F_B \leq 1$). Changing F_B strongly influences the age distribution of potentially emigrating silver eels. Values approaching 1 for F_B will result in relatively young silver eels leaving the system, while decreasing F_B increases the number of older silver eels (Oeberst and Fladung, 2012). These two parameters can be varied to achieve the best possible structural agreement between model outcome and field data, and thereby to identify the best performing model variant. To avoid the unintentional levelling of predicted and documented escapement numbers, parameter fitting was based on the comparison of modelled and documented relative age distribution instead of absolute numbers. To achieve frequencies > 5 necessary for the statistical analysis, the 20 existing age classes were grouped as four age groups. Absolute numbers of potentially escaping silver eels (based on the GEM II) were normalized to monitoring numbers. Goodness-of-fit between observed and predicted relative age distributions of silver eels was tested by χ^2 test (MS EXCEL).

To document the sensitivity of the model, several model scenarios were run, once the best performing model variant was identified. Scenarios included the reduction and increase of commercial and recreational fisheries by 10% and the reduction and increase of stocking by 10%. In all scenarios, only the respective input parameter was changed, while the remaining set of input parameters stayed the same as in the best performing model variant.

Results

Relative age distribution (based on the GEM II) of potentially escaping silver eels from the Schwentine River system was strongly influenced by changes in F_B and “factor for year one”, while resulting changes in absolute numbers were relatively small. It was not possible to adjust the parameters in such a way that relative age distribution of GEM II variant and monitoring results matched beyond doubt. The χ^2 goodness-of-fit analysis resulted in significant differences between the observed and expected relative age distribution of escaping silver eels for 2009 and 2010 in all model variants. The χ^2 test results of varying F_B and “factor for year one” are given in Table 1. Observed and predicted relative age distributions for the years 2009 and 2010 and varying GEM II variants are given in Figure 3a and b. To compare absolute numbers of actually escaping silver eels (monitoring 2009 and 2010) and potentially escaping silver eels estimated by the GEM II, the model variant with the smallest sum of χ^2 test values (variant 3; $F_B = 0.3$ and “factor for year one” = 0.4) was used.

Yearly stocking with *A. anguilla* of different age classes ranged from $\sim 13\,500$ (2008) to $238\,000$ (1993) individuals. The local eel biomass in the Schwentine River system was estimated (GEM II) at $24\,981$ kg ($85\,695$ eels) in 2009 and $21\,123$ kg ($119\,633$ eels) in 2010 (Table 2). Directly assessed commercial landings summed up to a total of 5233 kg in 2009 and 6610 kg in 2010. The GEM II estimated the corresponding absolute numbers to be 9486 eels in 2009 and $13\,690$ eels in 2010 (Table 2). Calculated recreational landings amounted to 830 kg in both 2009 and 2010. Cormorant predation was assessed to be 1100 kg in 2009 and 1200 kg in 2010. The GEM II estimated the corresponding absolute

Table 1. Model variants tested to identify the best performing setting of F_B and “factor for year one”.

	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5	Variant 6
Factor for year one	1	0.5	0.4	0.4	0.4	2
F_B	1	0.5	0.3	0.2	0.1	1
d.f.	3	3	3	3	3	3
χ^2 test (year 2009)	20.40	23.54	14.06	12.54	17.41	109.90
χ^2 test (year 2010)	60.89	38.13	32.26	54.26	96.53	155.64
Critical value χ^2 (d.f. = 3, $p = 0.05$)	7.81	7.81	7.81	7.81	7.81	7.81

All variants were run with the same set of assessed input parameters while changing F_B and “factor for year one” according to the values given here. Goodness-of-fit analysis (χ^2 test) was done comparing the relative age distribution of predicted and documented silver eel escapement. The χ^2 test identified Variant 3 (highlighted) as representing the best fit.

numbers to be 10 680 eels in 2009 and 11 650 eels in 2010 (Table 2).

Silver eel monitoring at the hydropower station (2009 and 2010) resulted in unexpectedly low escapement numbers of female silver eels. In 2009, only 97 silver eels were documented, with a total weight of 105 kg, resulting in $0.02 \text{ kg ha}^{-1} \text{ year}^{-1}$ (total area accounted for = 5984 ha). In 2010, the total number of emigrating silver eels was 683, with a total weight of 691 kg, resulting in $0.12 \text{ kg ha}^{-1} \text{ year}^{-1}$ (total area accounted for = 5984 ha). Potential silver eel escapement numbers estimated by the GEM II differed slightly from monitoring results. The model calculated 728 silver eels (748 kg) for 2009 and 363 silver eels (385 kg) for 2010, corresponding to $0.13 \text{ kg ha}^{-1} \text{ year}^{-1}$ in 2009 and $0.06 \text{ kg ha}^{-1} \text{ year}^{-1}$ in 2010 (Tables 2 and 3).

Reducing the catch numbers of the commercial fisheries by 10% (“fisher minus 10%” scenario) resulted in 1948 potentially escaping silver eels (2044 kg) in 2009 and 1579 silver eels (1709 kg) in 2010 (Figure 4). The “fisher minus 10%” scenario resulted in an $\sim 168\%$ increase in the number of escaping silver eels for 2009 and an $\sim 335\%$ increase for 2010. Increasing the catch numbers of the commercial fisheries by 10% (“fisher plus 10%” scenario) resulted in 72 silver eels (63 kg) in 2009 and 273 silver eels (259 kg) in 2010 (Figure 4). The “fisher plus 10%” scenario resulted in an $\sim 90\%$ decrease in silver eel numbers for 2009 and an $\sim 25\%$ decrease for 2010. Reducing the catch numbers of the recreational fishery by 10% (“angler minus 10%” scenario) resulted in 940 potentially escaping silver eels (970 kg) in 2009 and 562 silver eels (599 kg) in 2010 (Figure 4). The “angler minus 10%” scenario resulted in an $\sim 29\%$ increase in silver eels numbers for 2009 and an $\sim 45\%$ increase for 2010. Increasing the catch numbers of the recreational fishery by 10% (“angler plus 10%” scenario) resulted in 521 silver eels (533 kg) in 2009 and 177 silver eels (188 kg) in 2010 (Figure 4). The “angler plus 10%” scenario resulted in an $\sim 28\%$ decrease in silver eel numbers for 2009 and an $\sim 51\%$ decrease for 2010. Silver eel output for different scenarios is summarized in Table 3.

Discussion

Estimated potential silver eel escapement based on the GEM II output was at about the same level as the directly monitored escapement of silver eels out of the Schwentine River system. However, it has to be highlighted that the GEM II, besides describing the dynamics of the eel stock, estimates the potential silver eel escapement, namely the number of eels that become silver and potentially could start their migration out of the system. It has, however, been shown that the actual number of silver eels starting their migration is strongly influenced by environmental parameters and obstacles (Vøllestad et al., 1986; Feunteun et al.,

2000; Breteler et al., 2007; Acou et al., 2008), indicating that silver eels, despite an advanced maturity stage, might postpone the onset of migration and even revert to the yellow stage when facing unfavourable conditions (Durif et al., 2003, 2005).

The age-structured GEM II requires length-based data to be converted into age-based data. Therefore, the growth function used to convert length-based data into age-based data strongly influenced the necessary input data and thus had a large influence on the model outcome. Eel growth is highly dependent on habitat (Svedäng et al., 1996; Melia et al., 2006), and published growth functions for female *A. anguilla* vary significantly (De Leo and Gatto, 1995; Poole and Reynolds, 1996; Holmgren et al., 1997; Simon, 2007). Describing eel growth, in general, has been proven to be challenging, and Sparre (1979) even suggested abandoning the use of VBGF. Nevertheless, VBGF was used to describe the growth of eels in the original GEM II (Oeberst and Fladung, 2012) and to document the model’s potential also in the present model variant. In the present study, fixing the L_∞ at 1.5 times the average size of escaping silver eels accounted for system-specific maturation patterns. The resulting VBGF closely resembled both the documented system-specific length-at-age relationship and the VBGF ($L_\infty = 114 \text{ cm}$, $k = 0.058$, and $t_0 = -0.81$) for eels in the Schwentine River system previously given by Worthmann and Spratte (1987). The high plasticity of growth in eels causes enormous variation not only between habitats, but also between sexes (Poole and Reynolds, 1996), and a sensible growth description usually requires two individual VBGFs for females and males, respectively (Poole and Reynolds, 1996; Melia et al., 2006). As it was not possible to catch enough males in the Schwentine River system to allow a sound analysis, the present VBGF and the GEM II were restricted to females. Sex determination in freshwater eels is believed to be environmentally induced, and eels enter freshwater as sexually undifferentiated glass eels (Wiberg, 1983; Holmgren and Mosegaard, 1996; Davey and Jellyman, 2005). Besides population density and habitat quality, geographical habitat differences have been proposed to influence the sex ratio of European eels (Tesch, 2003; Kettle et al., 2011). Tesch (2003) and Kettle et al. (2011) described northern European waters to favour predominantly female-dominated populations, while southern European waters may support eel populations strongly skewed towards males. Stocking numbers and available habitat area in the Schwentine River system implicated a relatively high population density, and natural mortality was calculated appropriately. It has been proposed that high population densities relative to available habitat area and quality result in male-dominated sex ratios in *A. rostrata* (Krueger and Oliveira, 1999). Due to the relatively small size of male European eel (Tesch, 2003), the monitoring in the present study was probably biased

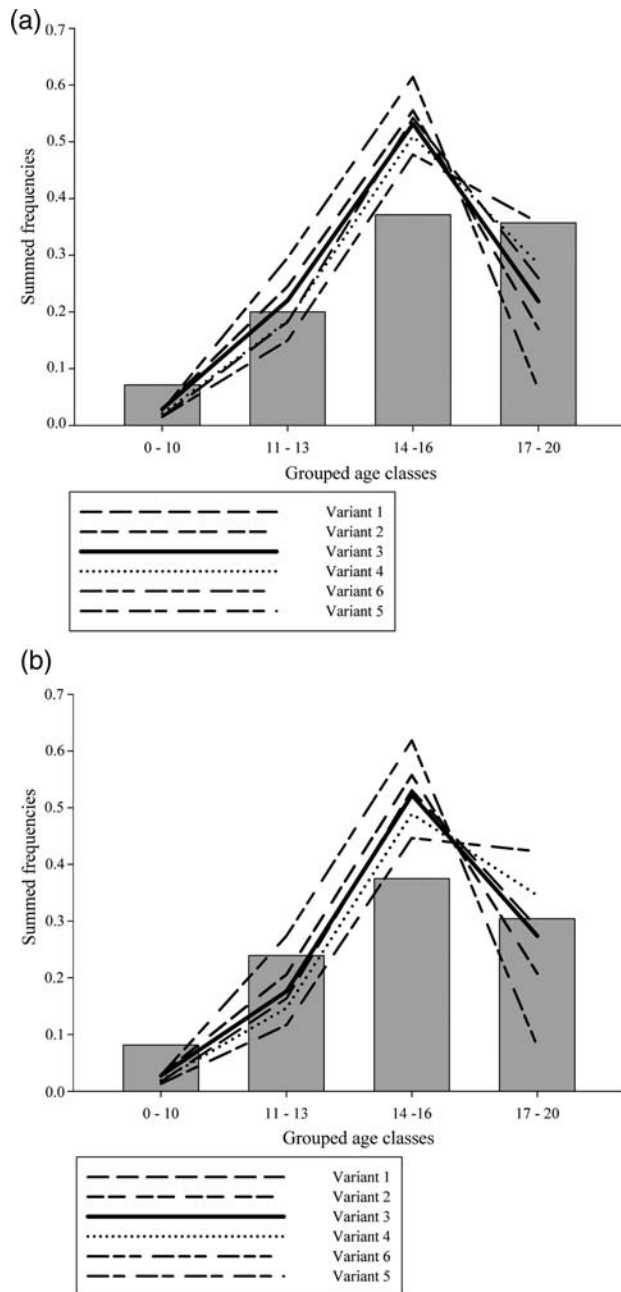


Figure 3. (a) Relative frequency distribution of grouped age classes (2009) of actually escaping silver eels (grey bars) and potentially escaping silver eels from different model variants (lines). (b) Relative frequency distribution of grouped age classes (2010) of actually escaping silver eels (grey bars) and potentially escaping silver eels from different model variants (lines).

towards females. However, the legal minimum catch size for the European eel and corresponding mesh sizes in the commercial fishery should have been able to document a male-dominated population in the Schwentine River system. In addition, Wickström *et al.* (1996) showed that juvenile eels stocked into northern European freshwater systems with limited natural recruitment predominantly develop into females. They estimated that in a lake with even higher stocking densities than in the Schwentine River system, only $\sim 3.4\%$ of stocked elvers and

glass eels developed into males (Wickström *et al.*, 1996). The present catch composition of commercial fishers and escapement monitoring results confirmed an eel population in the Schwentine River system dominated by females, and the male bias was considered to be negligible.

In spite of the absence of a Baltic Sea glass eel time-series, natural glass eel recruitment to Baltic Sea tributaries is commonly believed to be low (Westerberg, 1998; ICES, 2011). Generally, low recruitment combined with the still existent blockage of any upstream migration into the Schwentine River system by two consecutive hydropower stations support the idea of a local occurrence of eel being entirely dependent on stocking. Additionally, Prigge *et al.* (in press) showed that at least 62.5% of silver eels emigrating from the Schwentine River system had otolith strontium to calcium ratio profiles consistent with an individual stocking history. Stocking numbers provided by commercial fishers, recreational angling societies, and state authorities were therefore considered to represent the entire recruitment of juveniles to the Schwentine River eel population.

While the cumulated catch data for the commercial fishery were directly provided by commercial fishers and legal authorities, the effect of recreational fishers had to be estimated from average catch and total number of anglers in the Schwentine River system. The generalization of individual preferences and target species in angling most probably led to a loss in data quality. In addition, it was not possible to account for anglers who are not organized in angling societies in the Schwentine River system, and total recreational catch numbers used in the current GEM II variant are most probably underestimated. It has previously been reported that on average recreational fishers in Germany land ~ 0.65 kg of eel per year (Anonymous, 2012). Calculated average catch in the Schwentine River system was slightly higher (~ 0.9 kg per recreational fisher and year) (L. Marohn, unpublished data).

The milestone report of the implementation of the German EMP estimates the pristine reference silver eel escapement of the Schlei–Trave river basin (discharging into the Baltic Sea) at between 1.5 and 3.8 kg ha⁻¹ year⁻¹. The 40% minimum escapement postulated by the EU (Anonymous, 2012) would therefore require an escapement between 0.6 and 1.52 kg ha⁻¹ year⁻¹. Potential escapement based on the GEM II for 2009 and 2010 was thus at ~ 10 – 21% (0.06 and 0.13 kg ha⁻¹ year⁻¹) of the lower 40% escapement aim.

Connecting rivers in the Schwentine River system are usually rather shallow and fast flowing, whereas Laffaille *et al.* (2003) showed that larger eels tend to prefer deeper freshwater habitats. In addition, stocking and eel fisheries in the Schwentine River system outside the lake habitats are negligible. Consequently, uncertainties in estimated eel population dynamics due to area restriction of the GEM II were also considered to be negligible.

Different eel fishery scenarios showed that estimates of potential escapement are strongly dependent on input data. Changing the number of eels taken by commercial and recreational fisheries by only 10% significantly influenced the number of potentially escaping silver eels. Legal restrictions of the commercial/recreational eel fisheries, however, seem to be one of the possible measures showing instant short-term improvement of escapement numbers, but concurrently are often the subject of great public controversies (Dorow and Arlinghaus, 2012). Due to the retrospective construction of the different scenarios, however, implications for system-specific management decision are limited.

Table 2. *Anguilla anguilla* stock size, mortality, and potentially escaping silver eels for the Schwentine River system for 2009 and 2010, estimated by the GEM II (variant 3). Numbers in parentheses indicate the percentage with respect to the total stock size of the same year.

	2009		2010	
	Weight (kg)	No. of eels	Weight (kg)	No. of eels
Stock size	24 981	85 695	21 123	119 633
Natural mortality	2267 (9.1)	12 193 (14.2)	2120 (10.0)	21 648 (18.1)
Commercial fishers	5233 (20.9)	9486 (11.1)	6610 (31.3)	13 690 (11.4)
Recreational fishers	830 (3.3)	1505 (1.8)	830 (3.9)	1720 (1.4)
Cormorants	1100 (4.4)	10 680 (12.5)	1200 (5.7)	11 650 (9.7)
Silver eels	748 (3.0)	728 (0.8)	385 (1.8)	363 (0.3)
	Weight (kg) ha ⁻¹	No. of eels ha ⁻¹	Weight (kg) ha ⁻¹	No. of eels ha ⁻¹
Commercial fishers	0.9	1.6	1.1	2.3
Recreational fishers	0.1	0.3	0.1	0.3
Cormorants	0.2	1.8	0.2	1.9
Silver eels	0.13	0.12	0.06	0.06

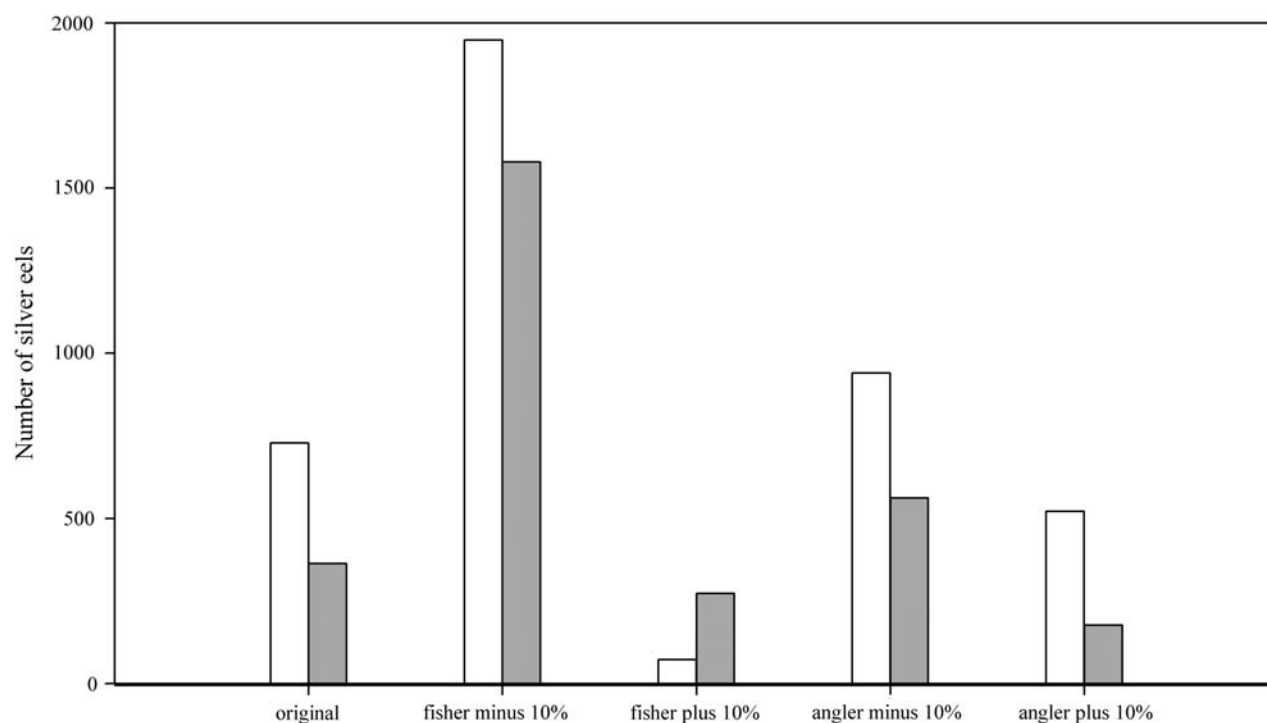


Figure 4. Number of potentially escaping silver eels for 2009 (white bars) and 2010 (grey bars) with different fishery scenarios.

Table 3. Silver eel output for fisher/angler scenarios, reference estimate, and 40% aim for the Schwentine River system.

Scenario	2009		2010	
	kg ha ⁻¹ year ⁻¹	no. of eels ha ⁻¹ year ⁻¹	kg ha ⁻¹ year ⁻¹	no. of eels ha ⁻¹ year ⁻¹
Reference estimate ^a	1.5–3.8 kg ha ⁻¹ year ⁻¹			
40% aim ^b	0.6–1.52 kg ha ⁻¹ year ⁻¹			
Original	0.13	0.12	0.06	0.06
Fisher – 10%	0.34	0.33	0.29	0.26
Fisher + 10%	0.01	0.01	0.04	0.05
Angler – 10%	0.16	0.16	0.10	0.09
Angler + 10%	0.09	0.09	0.03	0.03

^aAnonymous (2012).

^bEscapement aim formulated by the EU.

The present study constitutes one of the first actually to compare the silver eel escapement of a small freshwater system with the potential escapement predicted by an escapement model. Even though the Schwentine River system has to be considered a small to medium freshwater system and the number of involved stakeholders is limited, compiling the necessary input data and characterizing the vital population characteristics was challenging. Nevertheless, results document the potential of the GEM II when estimating escaping silver eels in numbers and weight. At the same time, the present results highlight the importance of high-quality databases to secure a sound model-based management and question the compliance of regional management strategies with the minimum criteria defined by the European eel regulation.

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References

- Acou, A., Laffaille, P., Legault, A., and Feunteun, E. 2008. Migration pattern of silver eel (*Anguilla anguilla*, L.) in an obstructed river system. *Ecology of Freshwater Fish*, 17: 432–442.
- Als, T. D., Hansen, M. M., Maes, G. E., Castonguay, M., Riemann, L., Aarestrup, K., Munk, P., *et al.* 2011. All roads lead to home: panmixia of European eel in the Sargasso Sea. *Molecular Ecology*, 20: 1333–1346.
- Amilhat, E., Farrugio, H., Lecomte-Finiger, R., Simon, G., and Sasal, P. 2008. Silver eel population size and escapement in a Mediterranean lagoon: Bages-Sigean, France. *Knowledge and Management of Aquatic Ecosystems*, 390–391: 5.
- Anonymous. 2012. Umsetzungsbericht 2012 zu den Aalbewirtschaftungsplänen der deutschen Länder 2008. 51 pp.
- Aprahamian, M. W., Walker, A. M., Williams, B., Bark, A., and Knights, B. 2007. On the application of models of European eel (*Anguilla anguilla*) production and escapement to the development of Eel Management plans: the River Severn. *ICES Journal of Marine Science*, 64: 1472–1482.
- Åström, M., and Dekker, W. 2007. When will the eel recover? A full life-cycle model. *ICES Journal of Marine Science*, 64: 1491–1498.
- Breteler, J. K., Vriese, T., Borcherding, J., Breukelaar, A., Jorgensen, L., Staas, S., De Laak, G., *et al.* 2007. Assessment of population size and migration routes of silver eel in the river Rhine based on a 2-year combined mark–recapture and telemetry study. *ICES Journal of Marine Science*, 64: 1450–1456.
- Bevacqua, D., Melia, P., Crivelli, A. J., Gatto, M., and De Leo, G. A. 2007. Multi-objective assessment of conservation measures for the European eel (*Anguilla anguilla*): an application to the Camargue lagoons. *ICES Journal of Marine Science*, 64: 1483–1490.
- Bevacqua, D., Melia, P., De Leo, G. A., and Gatto, M. 2011. Intra-specific scaling of natural mortality in fish: the paradigmatic case of the European eel. *Oecologia*, 165: 333–339.
- Bilotta, G. S., Sibley, P., Hateley, J., and Don, A. 2011. The decline of the European eel *Anguilla anguilla*: quantifying and managing escapement to support conservation. *Journal of Fish Biology*, 78: 23–38.
- Charrier, F., Mazel, V., Caraguel, J. M., Abdallah, Y., Le Gurun, L. L., Legault, A., and Laffaille, P. 2012. Escapement of silver-phase European eels, *Anguilla anguilla*, determined from fishing activities in a Mediterranean lagoon (Or, France). *ICES Journal of Marine Science*, 69: 30–33.
- Chen, Y., Jackson, D. A., and Harvey, H. H. 1992. A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 1228–1235.
- Daverat, F., Beaulaton, L., Poole, R., Lambert, P., Wickström, H., Andersson, J., Aprahamian, M., *et al.* 2012. One century of eel growth: changes and implications. *Ecology of Freshwater Fish*, 21: 325–336.
- Davey, A. J. H., and Jellyman, D. J. 2005. Sex determination in freshwater eels and management options for manipulation of sex. *Reviews in Fish Biology and Fisheries*, 15: 37–52.
- Dekker, W. 2003. On the distribution of the European eel (*Anguilla anguilla*) and its fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 787–799.
- De Leo, G. A., and Gatto, M. 1995. A size and age-structured model of the European eel (*Anguilla anguilla*, L.). *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 1351–1367.
- De Leo, G. A., Melia, P., Gatto, M., and Crivelli, A. J. 2009. Eel population modeling and its application to conservation management. *American Fisheries Society Symposium*, 58: 327–345.
- Dorow, M., and Arlinghaus, R. 2012. The relationship between personal commitment to angling and the opinions and attitudes of German anglers towards the conservation and management of the European eel *Anguilla anguilla*. *North American Journal of Fisheries Management*, 32: 466–479.
- Durif, C., Dufour, S., and Elie, P. 2005. The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, 66: 1025–1043.
- Durif, C., Gosset, C., Rives, J., Travade, F., and Elie, P. 2003. Behavioral study of downstream migrating eels by radio-telemetry at a small hydroelectric power plant. In *Biology, Management, and Protection of Catadromous Eels*, pp. 343–356. Ed. by D.A. Dixon. Symposium 33. American Fisheries Society: Bethesda, MD.
- European Union. 2007. Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel, pp. 17–23. *Official Journal of the European Union*.
- Fenske, K. H., Wilberg, M. J., Secor, D. H., and Fabrizio, M. C. 2011. An age- and sex-structured assessment model for American eels (*Anguilla rostrata*) in the Potomac River, Maryland. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1024–1037.
- Feunteun, E., Acou, A., Laffaille, P., and Legault, A. 2000. European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 1627–1635.
- Froese, R., and Pauly, D. 2013. Fish stocks. In *Encyclopedia of Biodiversity*. Ed. by S. Levin. Available at http://www.fishbase.de/rfroese/FishStocksNew_2.doc
- Holmgren, K., and Mosegaard, H. 1996. Implications of individual growth status on the future sex of the European eel. *Journal of Fish Biology*, 49: 910–925.
- Holmgren, K., Wickström, H., and Clevestam, P. 1997. Sex-related growth of European eel, *Anguilla anguilla*, with focus on median silver eel age. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 2775–2781.

- ICES. 2009. Report of the Workshop on Age Reading of European and American Eel (WKAREA). ICES Document CM 2009/ACOM: 48.
- ICES. 2010. Report of the ICES/EIFAC Working Group on Eels (WGEEL). ICES Document CM 2010/ACFM: 18.
- ICES. 2011. Report of the 2011 Session of the Joint EIFAAC/ICES Working Group on Eels. ICES Document CM 2011/ACOM: 18.
- Jessop, B. M. 2010. Geographic effects on American eel (*Anguilla rostrata*) life history characteristics and strategies. *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 326–346.
- Kettle, A. J., Vollestad, L. A., and Wibig, J. 2011. Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? *Fish and Fisheries*, 12: 380–411.
- Krueger, W. H., and Oliveira, K. 1999. Evidence for environmental sex determination in the American eel (*Anguilla rostrata*). *Environmental Biology of Fishes*, 55: 381–389.
- Laffaille, P., Feunteun, E., Baisez, A., Robinet, T., Acou, A., Legault, A., and Lek, S. 2003. Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecology of Freshwater Fish*, 12: 254–264.
- Lambert, P., and Rochard, E. 2007. Identification of the inland population dynamics of the European eel using pattern-oriented modelling. *Ecological Modelling*, 206: 166–178.
- Lin, Y. J., Lozys, L., Shiao, J. C., Iizuka, Y., and Tzeng, W. N. 2007. Growth differences between naturally recruited and stocked European eel *Anguilla anguilla* from different habitats in Lithuania. *Journal of Fish Biology*, 71: 1773–1787.
- Melia, P., Bevacqua, D., Crivelli, A., Panfili, J., De Leo, G., and Gatto, M. 2006. Sex differentiation of the European eel in brackish and freshwater environments: a comparative analysis. *Journal of Fish Biology*, 69: 1228–1235.
- Oeberst, R., and Fladung, E. 2012. German Eel Model (GEM II) for describing eel, *Anguilla anguilla* (L.), stock dynamics in the river Elbe system. *Information on Fishery Research*, 59: 9–17.
- Poole, W. R., and Reynolds, J. D. 1996. Growth rate and age at migration of *Anguilla anguilla*. *Journal of Fish Biology*, 48: 633–642.
- Poole, W. R., and Reynolds, J. D. 1998. Variability in growth rate in European eel *Anguilla anguilla* (L.) in a western Irish catchment. *Biology and Environment—Proceedings of the Royal Irish Academy*, 98B: 141–145.
- Poole, W. R., Reynolds, J. D., and Moriarty, C. 2004. Early post-larval growth and otolith patterns in the eel *Anguilla anguilla*. *Fisheries Research*, 66: 107–114.
- Simon, J. 2007. Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). *ICES Journal of Marine Science*, 64: 1414–1422.
- Sparré, P. 1979. Some necessary adjustments for using the common methods in eel assessment. In *Eel Research and Management*, pp. 41–44. Ed. by E. Thurow. Papers presented at an ICES/EIFAC Symposium, Helsinki, 9–11 June 1976.
- Svedäng, H., Neuman, E., and Wickström, H. 1996. Maturation patterns in female European eel: age and size at the silver eel stage. *Journal of Fish Biology*, 48: 342–351.
- Tasker, M. L., and Furness, R. W. 1996. Seabird/fish interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report, 216: 6–42.
- Tesch, F. W. 2003. *The Eel*. Blackwell Science, Oxford.
- Vøllestad, L. A. 1992. Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology*, 61: 41–48.
- Vøllestad, L. A., Jonsson, B., Hvidsten, N. A., Næsje, T. F., Haraldstad, Ø., and Ruud-Hansen, J. 1986. Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 1909–1916.
- Walker, A. M., Andonegi, E., Apostolaki, P., Aprahamian, M. W., Beaulaton, L., Bevacqua, D., Briand, C., et al. 2011. Studies and Pilot Projects for Carrying Out the Common Fisheries Policy. LOT 2: Pilot Projects to Estimate Potential and Actual Escapement of Silver Eel (POSE). Final Report. 542 pp.
- Westerberg, H. 1998. Oceanographic aspects of the recruitment of eels to the Baltic Sea. *Bulletin Francais de la Peche et de la Pisciculture*: 177–185.
- Wiberg, U. H. 1983. Sex determination in the European eel (*Anguilla anguilla*, L.)—a hypothesis based on cytogenetic results, correlated with the findings of skewed sex-ratios in eel culture ponds. *Cytogenetics and Cell Genetics*, 36: 589–598.
- Wickström, H., Westin, L., and Clevestam, P. 1996. The biological and economic yield from a long-term eel-stocking experiment. *Ecology of Freshwater Fish*, 5: 140–147.
- Worthmann, H., and Spratte, S. 1987. Nahrungsuntersuchungen am Kormoran (*Phalacrocorax carbo*): Die Auswirkungen der Kormorane auf die schleswig-holsteinische Binnenfischerei, Schleswig-Holstein, Fischereiamt.

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