Fisheries Management and Ecology

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ARTICLE OPEN ACCESS

Sensitivity of the German Eel Model to Key Inputs and Uncertainties

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Received: 25 January 2024 | **Revised:** 6 November 2024 | **Accepted:** 8 November 2024

Funding: Financial support was provided to TW, JS, EF, and UB for advancements in the GEM III by the Fishery Ministries of the Federal States of Brandenburg, Saxony-Anhalt, Schleswig-Holstein, and Thuringia (Grant MLUL-34-1400/925+1#164109/2021). The analysis was commissioned and financed by German Federal States departments of fisheries.

Keywords: European eel | German Eel Model | model sensitivity | model uncertainty

ABSTRACT

Informed recovery of the European eel (*Anguilla anguilla*) requires reliable information on stock dynamics and effects of management. No global European eel stock model is presently available, so demographic or extrapolation models are used to estimate eel production at local sub-stock levels. Model inputs are often difficult to estimate and highly uncertain, which can affect accuracy of predictions. A sensitivity analysis was thus applied to the German Eel Model for the River Weser to evaluate how uncertainties in ten key input variables affected predicted eel escapement biomass. Uncertainty in the proportion of female eels and their age-specific natural mortality, hydropower-related mortality, and restocking had the largest influence on overall uncertainty. Conversely, uncertainty in eel predation by cormorants and age composition of immigrating male eels had small effects on outcome uncertainty. Based on expert judgment about the difficulty of parameter estimation, number of restocked eels, the proportion of females among outmigrants, and losses due to hydropower are the most feasible variables to address through monitoring. Better estimation of input variables and their uncertainties is crucial to improve eel stock assessment and management.

1 | Introduction

The European eel (*Anguilla anguilla*, eel hereafter) is among the most iconic fish species of large economic value in coastal and inland fisheries (Kuroki, Righton, and Walker 2014; Dekker 2019). This panmictic species has a facultative catadromous life cycle and it is assumed to spawn in the Sargasso Sea (Tsukamoto, Nakai, and Tesch 1998; Tesch 2003; Als et al. 2011, Wright et al. 2022). Eels arrive at the European continent as juvenile glass eels, after which some colonize coastal waters and others migrate upstream to inland waters (Tesch 2003). In inland waters, eels grow to metamorphose from the pre-pubescent yellow eel stage to the pubescent silver eel stage prior to their seaward spawning migration. During this time, eels show extreme phenotypic plasticity that depends on environmental factors, with variability in life history traits such as growth to silver eel stage ranging 2–57 years (Rossi and Villani 1980; Poole and Reynolds 1996; Panfili et al. 2022). Furthermore, the European eel is sexually dimorphic in growth and maturity, with male silver eels growing to 29–54 cm, while female silver eels grow to 40 to over 100 cm (Dekker 2004). Sex ratio of eels is site-specific and depends on environmental characteristics of the catchment (Tesch 2003; Davey and Jellyman 2005) and population density (Vøllestad and Jonsson 1988; Roncarati et al. 1997; Tesch 2003; Davey and Jellyman 2005; Laffaille et al. 2006). The role of genetics on sexual phenotype is not fully understood, while size and social stress influence sex determination (Davey and Jellyman 2005; Geffroy et al. 2016). Male silver eels are often more abundant in areas of high population density, whereas females are more abundant in areas of low density (Davey and Jellyman 2005; Laffaille et al. 2006).

Catches of juvenile and marketable sized eels have declined sharply throughout Europe over past decades (Moriarty and Dekker 1997; Dekker 2004). As a consequence, the panmictic eel stock has been considered outside safe biological limits since 1999 (ICES 1999) and has been listed as critically endangered on the red list of the International Union for Conservation of Nature since 2008 (Freyhof and Kottelat 2008; Pike, Crook, and Gollock 2020). The International Council for the Exploration of the Sea (ICES) currently advises that all fishery and non-fishery anthropogenic mortality should be zero, in accordance with a precautionary approach (ICES 2022a). Consequently, a management framework for eel in the European Union was established in 2007 (Council Regulation (EC) No. 1100/2007; EU 2007). Under this regulation, member states are required to implement management measures tailored to specifics of each river basin where eel would naturally occur (Eel Management Unit, EMU). The goal is to aid stock recovery by reducing anthropogenic mortality to achieve a silver eel escapement target of at least 40% of silver eel biomass relative to the best estimate of pristine escapement before 1980. Evaluation of management progress and reporting to the EU Commission is triennial (EU 2007; Fladung and Brämick 2021; ICES 2022b). To fulfill these obligations, modeling local stock dynamics under different scenarios is imperative.

Different modeling approaches have been deployed in EU member states for stock assessment and management progress across 81 European EMUs (ICES 2022b), such as the German Eel Model (GEM; Oeberst and Fladung 2012), the DemCam model used in France (Bevacqua et al. 2007), the Scenario-based Model for Eel Population (SMEPII) used in the United Kingdom (Aprahamian et al. 2007; Walker et al. 2011), and Eel Density Analysis (EDA) used in France, Spain, and Portugal (Mateo et al. 2022). Although these models differ, nearly all rely on information gathered by habitat-specific sampling to estimate parameters, and numbers and biomass of out-migrating silver eels. Statistical models such as EDA extrapolate from a limited number of sampling sites to estimate yellow eel density at a catchment level, which introduces uncertainty due to habitat heterogeneity and restricted sampling (Mateo et al. 2022). Such models do not require estimating many demographic parameters but are limited in their ability to provide a mechanistic understanding of how management actions might affect eel stocks. Demographic models build on a life-cycle approach to estimate effects of alternative management actions on silver eel escapement based on estimates of recruitment, mortality, and life history traits, but do not typically account for spatial heterogeneity that may be important in large watersheds. Input factors for such models vary over time, habitats, and between sexes (Tesch 2003; Boulenger, Crivelli, et al. 2016; Geffroy and Bardonnet 2016; Teichert et al. 2023). As a consequence, high sampling effort is required to accurately quantify parameters for each of the EMUs.

For nine EMUs defined in Germany, stock assessment, management planning, and reporting are conducted using the German Eel Model, version IIIc (GEM, Oeberst and Fladung 2012; Appendix S1). To assess accuracy of model outputs for silver eel escapement, mark-recapture studies have been performed in three German EMUs (Fladung, Simon, Hannemann et al. 2012; Prigge, Marohn, and Hanel 2013; Brämick, Fladung, and Simon 2016; Höhne et al. 2023). In all cases, modeled silver eel escapement was considerably higher than mark-recapture estimates (Höhne et al. 2023), thereby calling for testing and refining model assumptions and input parameters. Given their temporal and spatial variability, acquiring better input parameter estimates across EMUs requires substantial resources for sampling programs that may only slightly reduce uncertainty of output parameters. Thus, identifying parameters whose uncertainty exerts a large influence on expected silver eel outmigration can help to guide future studies, especially if difficulty of reducing uncertainty is also included. In addition, accurate estimates of uncertainty are important to better understand and communicate how management actions likely affect outmigrating eel biomass.

Sensitivity analysis is a central method to identify influential parameters and key uncertainties (Saltelli, Chan, and Scott 2001; Helton et al. 2006) that has frequently been applied in population modeling (Ginot et al. 2006; Cariboni et al. 2007; Radinger, Hölker, and Wolter 2017). Therefore, we used a sensitivity analysis to evaluate sensitivity of GEM-predicted eel escapement biomass to uncertainty in selected input variables using a case study of the River Weser. In addition, we used expert knowledge to rank the effort likely required to reduce uncertainty in key parameters. Our primary objective was to identify key input variables and parameters that should be the subject of future studies to most improve the accuracy of silver eel escapement estimates and thereby better inform management.

2 | Methods

2.1 | German Eel Model Description and Case-Study EMU

The GEM (Fladung, Simon, Brämick, et al. 2012; Oeberst and Fladung 2012) is a modular, age- and sex-specific population model (Figure 1, described in detail in Appendix S1) initially developed in 2007 in cooperation between the Potsdam Institute of Inland Fisheries and the Thünen Institute for Baltic Sea Fisheries Rostock. Since 2015, the GEM has been used for development and progress evaluation of eel management plans for all nine German EMUs (Brämick et al. 2023) and has been extended and revised throughout its use. Sensitivity of the GEM to uncertainty of input variables was assessed based on GEM IIIc adapted to the River Weser catchment as a case-study EMU. With a total eel catchment area of 55,472 ha, the Weser catchment is among the largest German river basins with an implemented eel management plan. The yearly target for out-migrating eels from the Weser catchment was 331 t during 2020–2022, or 40% of the estimated reference state (Fladung and Brämick 2024). During 2005–2019, the model-estimated percentage of annual outmigration in relation to the estimated reference state ranged 17%–46%.

2.2 | Sensitivity Analysis

For the sensitivity analysis, the Excel-based GEM was converted into a format suitable for efficient, repeated model runs using R

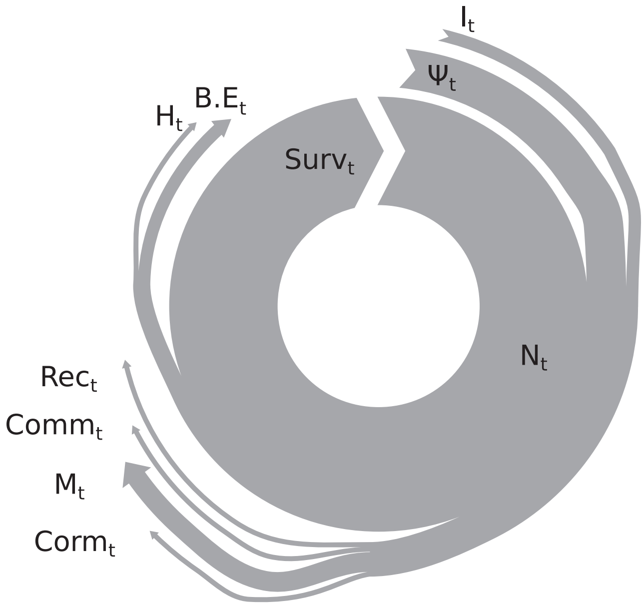

FIGURE 1 | Conceptual representation of the German Eel model (GEM) and its main compartments. The number of European eels (*Anguilla anguilla*) in the freshwater system per year N_t depends upon the number of surviving eels from last year $Surv_t$ and recruitment comprising natural immigration I_t and restocking Ψ_t as inputs and several important removals. Removals are due to cormorant predation $Corm_t$, natural mortality M_t, commercial fishing $Comm_t$, and recreational fishing Rec_t. The key target variable is the annual biomass of silver eels successfully out-migrating to the sea $B.E_t$ that is corrected for additional losses due to hydropower H_t. Note that the GEM considers number of fish grouped per age-class and sex, but this level of detail is omitted for simplicity.

version 4.1.2 (R Core Team 2021). Individual calculation steps and the structural design of the Excel-based model were reproduced in R for consistency. Sensitivity of the GEM was evaluated using a widely used sampling-based approach (Saltelli, Chan, and Scott 2001; Helton et al. 2006) that is effective for determining contributions of individual uncertain input variables to overall uncertainty in model results (Helton et al. 2006). The sensitivity analysis included five steps: (1) defining probability distributions to describe uncertainty of individual input variables; (2) generating a large sample of combinations of input variables from probability distributions using Latin Hypercube Sampling (LHS) (Mckay, Beckman, and Conover 1979; Helton and Davis 2003); (3) running and calculating the GEM model for each sample combination of input variables; (4) graphically evaluating model uncertainty by examining scatterplots of input versus output values; and (5) quantifying the contribution of each individual model input variable to output uncertainty.

2.3 | Uncertainty of Input Variables

Ten input variables were preselected for sensitivity analysis (Table 1) that were considered relatively uncertain or likely to have large effects on uncertainty in biomass of silver eels out-migrating each year $B.E_t$. Preselection of variables was based on expert judgment to cover all main compartments of the GEM (Figure 1), including natural recruitment and mortality, anthropogenic mortality sources, and restocking. The model was run annually with variable inputs. The mean predicted annual biomass of out-migrating eels (kg) between 2005 and 2019, $\overline{B.E}_{2005-2019}$ (*B.E* hereafter), was used as the response variable in the sensitivity analysis to minimize influences of individual years, including temporal confounding, trends, and error propagation.

Uncertainty of input variables that entered the model as single (yearly) values was described using triangular probability distributions (Table 1) that are commonly used in simulation studies (Johnson 1997) and described by a lower limit a, an upper limit b, and a peak c, with $a < b$ and $a \leq c \leq b$ (Forbes et al. 2011). The specific yearly value of each input variable from the current model application for the Weser catchment was used to define the parameter c for each year. Due to a lack of sensible information on the uncertainty of input variables, upper and lower limits a and b for input variables were generally set 10% above and below c, based on expert judgment (Table 1). Input variables that entered the model as age-specific frequency distributions were varied by modifying their shape (Table 1; Appendix S2).

2.4 | Sampling-Based Model Runs and Evaluation

Latin Hypercube Sampling (LHS, Mckay, Beckman, and Conover 1979) was used to examine how simultaneously varied input variables affected the model output. LHS is a time-effective, stratified sampling approach frequently applied in sensitivity analyses of complex biological systems to generate a sample of variable values from a multidimensional distribution. The distributional range of each input variable was divided into intervals of equal probability that were randomly sampled without replacement, to ensure full coverage of the range of each input variable and comprehensive sampling of combinations of multiple variables (Saltelli, Chan, and Scott 2001; Marino et al. 2008). An LHS matrix of combinations of input variable values was generated using the R-function randomLHS{lhs} (Carnell 2012). The LHS matrix consisted of 1000 rows (number of combinations of variable values for simulation runs) and 13 columns corresponding to uncertain input variables (Table 1; including $\pi_{a,s}$, $M_{t,a,s}$, $S.Corm_{t,a,s}$ which were defined separately for male and female eels). Based on the LHS matrix, 1000 repeated model runs were calculated with an LHS-based randomly selected combination of input variables, with run-specific values drawn from distributions (Table 1).

Scatterplots were used for a visual, qualitative assessment of relationships between variation in input and output variables and to identify non-linear patterns or thresholds. The influence of each uncertain input variable on *B.E* was quantified using partial correlation coefficients (PCC, R-function pcc) and 95% bootstrapped ($n = 1000$ runs) confidence intervals (CI). Partial correlation is a commonly used quantitative approach to sensitivity analysis (Hamby 1994; Gomero 2012) that allows correction for potential cross-correlations between input variables that would otherwise distort results (Hamby 1994). The PCC can take values between a strong negative (−1), strong positive (+1), or uncorrelated (0) relationship between model input and output variables (Fahrmeier et al. 2007). Input variables were classified into four groups

TABLE 1 | Overview of input variables and associated uncertainties related to European eel (*Anguilla anguilla*) dynamics evaluated in a sensitivity analysis of the German eel model (GEM) in the River Weser, Germany, during 2005–2019.

Input variable		Mean value for $2005 \leq t \leq 2019$	Variable uncertainty	
			Lower limit a	Upper limit b
I_t	Total number of naturally immigrating eels in year t	388,387 Ind.	$I_t * 0.I$	$I_t * 1.1$
Ψ_t	Total number of restocked eels in year t	1,900,179 Ind.	$\Psi_t * 0.9$	$\Psi_t * 1.1$
$B.Comm_t$	Total biomass/catch of eels by commercial fishery in year t [kg]	23,175 kg	$B.Comm_t * 0.9$	$B.Comm_t * 1.1$
$B.Rec_t$	Total biomass/catch of eels by recreational fishery in year t [kg]	42,177 kg	$B.Rec_t * 0.9$	$B.Rec_t * 1.1$
$B.Corm_t$	Total biomass removed by cormorants in year t [kg]	11,441 kg	$B.Corm_t * 0.9$	$B.Corm_t * 1.1$
$\pi_{a,s}$	Age- and sex-specific composition of naturally immigrating eels		Proportions in length classes from empirical study 1 (Brümmer 2008; I. Brümmer, pers. comm.)	Proportions in length classes from empirical study 2 (Schubert 1997; H.-J. Schubert, pers. comm.)
$M_{t,a,s}$	Age- and sex-specific natural mortality in year t		$M_{t,a,s}$ calculated for a temperature of 10.44°C (=11.6°C * 0.9)	$M_{t,a,s}$ calculated for a temperature of 12.76°C (=11.6°C * 1.1)
$S.Corm_{t,a,s}$	Age- and sex-specific distribution of eels in cormorant diets		$S.Corm_{t,a,s}$ calculated from a Lognormal (μ, σ^2) with $\sigma = 0.250$	$S.Corm_{t,a,s}$ calculated from a Lognormal (μ, σ^2) with $\sigma = 0.204$
$1 - H_t$	Mean survival from hydropower mortality across the system	0.82	$(1-H_t) * 0.9$	$(1-H_t) * 1.1$
Π	Proportion of females in the population	96%	80%	99%

Note: The lower and upper limits a and b refer to the parameters of the triangular distributions used to describe variable uncertainty. A detailed mathematical description of the GEM is provided in Appendix S1.
Abbreviations: a, age; s, sex; t, year.

with respect to their influence on the uncertainty of $B.E$, including (1) highly correlated (|PCC| > 0.9), (2) moderately correlated (|PCC| 0.5–0.9), (3) weakly correlated (|PCC| < 0.5), or (4) uncorrelated (|PCC| ~0) variables.

To complement PCC-based sensitivity analysis, regression was used to estimate effect sizes (ordinary regression coefficients, b_i, quantifying the magnitude of the relationship between $B.E$ and each model input variable). Specifically, b_i was considered an absolute sensitivity measure (Helton et al. 2006; Manache and Melching 2008) that quantified the change in the model output, $B.E$, as a function of one unit change in a specific input variable i, with other variables constant. For example, b_i measures the change in biomass of silver eels successfully out-migrating when the number of restocked eels increased (or decreased) by one individual per year. Thus, b_i was a measure of model responsiveness, rather than of sensitivity. While regression analysis included simultaneous variation in all input variables, only variables that entered the GEM as eel quantities (kg or individuals) were considered for final representation of regression coefficients. Whether a specific b_i referred to a change in kilograms or individuals depends on how the quantity was originally provided in the GEM. Specifically, for removals by fisheries and cormorants b_i refers to a change in kilograms, whereas for natural immigration and restocking b_i refers to a change in the number of individuals.

2.5 | Expert-Based Assessment

In Autumn 2022, an online survey of experts working in German eel management, and specifically with the GEM, was used to identify difficulty and effort required to obtain accurate estimates of input variables. A simple online Google form was sent to 11 experts (Table S4.1). All interviewed participants had expertise in eel management or eel research, were familiar with the current version of GEM III, and were not involved in the current study (Figure S4.1). Each expert was asked to assess the perceived ease and relative effort needed to estimate a given variable of the GEM accurately or realistically (separate questions for 10 variables, Table S4.1). Experts were allowed to provide their response on a 5-point Likert scale ranging from 1 (very easy or very little effort) to 5 (very difficult or very high effort), with the possibility of a "Cannot judge" response to each question. The median response to each question was used as the measure of central tendency of responses among experts. Subsequently, expert-based scores of estimation difficulty and effort were plotted against sensitivity PCC scores, to allow a relative, comparative assessment of GEM input variables along a gradient from generally easy to estimate and relatively uninfluential to difficult to estimate and highly influential.

3 | Results

Input variables varied greatly in their influence on uncertainty of the overall model result (Figures 2 and 3). The most influential input variables, with highest correlations ($|PCC|>0.9$, Figure 3) with uncertainty of biomass of successfully outmigrating eels, $B.E$, were the proportion of female eels in the population Π, age-specific natural mortality of female eels, $M_{t,a,s=female}$, survival from hydropower mortality, $1-H_t$, and total number of restocked eels, Ψ_t. The variables Π, $1-H_t$, and Ψ_t were highly positively correlated with $B.E$. By contrast, mortality rate in females, $M_{t,a,s=female}$ was highly negatively correlated with $B.E$.

Moderately influential input variables (with $0.5<|PCC|<0.9$) included the number of naturally immigrating eels, I_t, the age-specific composition of naturally immigrating female eels, $\pi_{a,s=female}$, and the total biomass of eels removed (catch) by commercial, $B.Comm_t$, and recreational fishers, $B.Rec_t$ (Figure 3). Less influential input variables ($0<|PCC|<0.5$) were total biomass removed by cormorants, $B.Comm_t$, and the age-specific natural mortality of male eels, $M_{t,a,s=male}$. Variation in age-specific composition of naturally immigrating male eels, $\pi_{a,s=male}$, and the age-specific distribution of eels in cormorant diets, $S.Corm_{t,a,s}$ (for both males and females), were not significantly related to the overall model output uncertainty (CI of PCCs included 0; Figure 3).

The regression analysis revealed that removing one extra 1 kg of eels through fisheries (equivalent to appr. 3 female or 7 male eels) or cormorants (equivalent to appr. 10 female or 17 male eels) per year reduced the predicted mean annual biomass of successfully out-migrating silver eels during 2005–2019, $B.E$, by 1.3–1.4 kg. Increasing the number of eels entering the system by 1 eel through natural immigration or restocking per year increased $B.E$ by 0.16–0.17 kg (Table S3.1).

Eight experts who responded to the survey varied in their answers but provided a clear gradient of estimation difficulty among input variables (Figure 4, Figures S4.2 and S4.3). Variables that were considered easiest to determine and are highly influential to variation on the uncertainty of the model output included the number of restocked eels and the proportion of female outmigrants (Figure S4.2). Little to intermediate difficulty and effort was associated with accurately quantifying total annual catch by commercial fisheries. In contrast, natural mortality was assessed as the most difficult to estimate accurately, and likely demanded the most

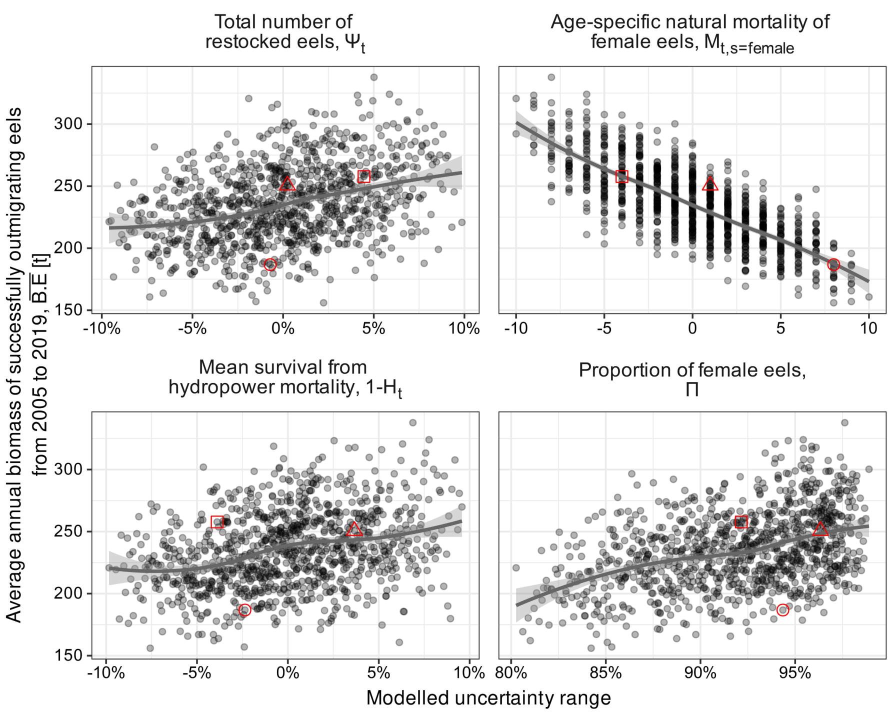

FIGURE 2 | Relationships between the four most influential input variables and predicted mean annual biomass of successfully out-migrating silver eels in the River Weser, Germany, during 2005–2019. $B.E$ is combined for male and female eels. X-axes show the modeled uncertainty range of each input variable (as relative change [Ψ_t, $1-H_t$, Π] or choice of distribution [$M_{t,s=female}$]), Y-axes show resulting model output. Gray lines and bands show the moving local average (LOESS) and the respective 95% CI. The triangle, circle, and square symbols exemplarily show combinations of input variable values from three independent model runs. Scatter plots for additional variables are displayed in Figure S2.4.

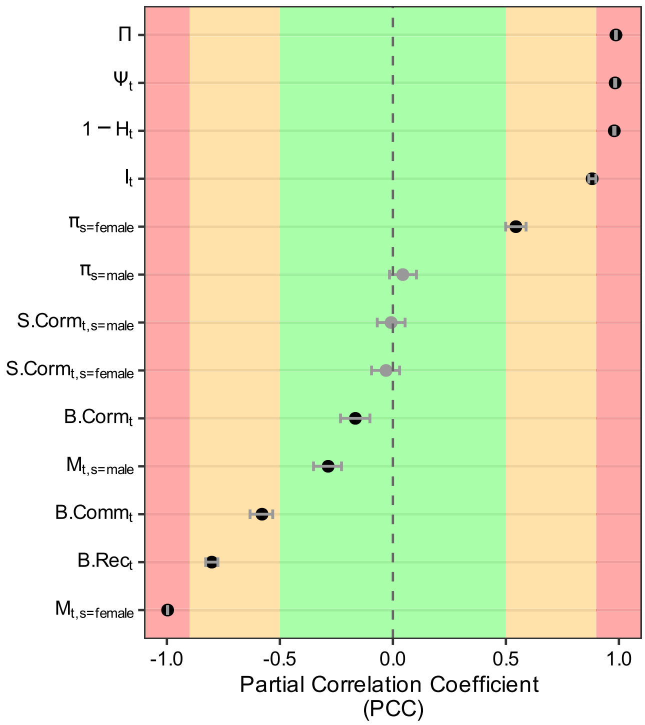

FIGURE 3 | Partial correlation coefficients (PCC) of modeled input variables with 95% CI error bars for the German Eel Model (GEM) in the River Weser, Germany. The PCC quantifies the contributions of uncertainty in model input variables to the overall uncertainty of the model output variable, i.e., mean annual biomass of successfully out-migrating silver eels between 2005 and 2019. PCCs close to +1 (−1) indicate strong positive (negative) correlations between uncertainties in model input and output. Colors refer to groups of highly (|PCC| > 0.9, red), moderately (|PCC| = 0.5–0.9, orange), and weakly influential (|PCC| < 0.5, green) variables. Non-significant variables in gray. Symbolic notation corresponding to individual variables is given in Table 1.

resources, followed by natural recruitment and eel predation by cormorants (Figure S4.2).

4 | Discussion

Deriving meaningful advice for sustainable management of eels based on population models requires reliable, accurate estimates of input parameters and their uncertainty. To improve the accuracy and uncertainties of silver eel escapement estimated by the German Eel Model, and thus to better inform management, a focus on three types of highly influential variables was indicated by our sensitivity analysis: (1) sex-related variables such as the share of females in the population and their specific natural mortality; (2) hydropower-related mortality; and (3) restocking measures.

The sex ratio was a highly influential variable in the GEM, likely because sex determines the age at which eels become vulnerable to length-dependent fishing mortality (Pohlmann, Freese, and Hanel 2016), natural morality (Bevacqua et al. 2011), and length-dependent cormorant predation (Östman et al. 2013; Figure S2.3). Intraspecific density in the first years of the yellow eel phase until approximately 20 cm body length is thought to be a driver of eel sex determination (Vøllestad and Jonsson 1988; Roncarati et al. 1997; Tesch 2003; Davey and Jellyman 2005; Laffaille et al. 2006). The ratio of males to females may vary through time and space, with large differences in sex ratios in rivers of even close proximity (Boulenger, Acou, et al. 2016) or the same river in different periods (Parsons, Vickers, and Warden 1977; Laffaille et al. 2006). This spatial and temporal variability makes it necessary to closely monitor the sex ratio across time in each EMU to improve the sex ratio as GEM input parameter, a task the expert survey identified as relatively straightforward (Figure 4). Molecular technological advancements (Geffroy et al. 2016) might provide particularly useful tools to determine the sex ratio and especially its temporal variability.

The GEM-estimated biomass of out-migrating silver eels was highly sensitive to the estimate of natural mortality, particularly in females. This finding is in accordance with previous studies emphasizing natural mortality as highly influential on fish stock demographics (Punt et al. 2021). While sex-specific differences in natural mortality are generally recognized (Punt et al. 2021; Lindström 1998), natural mortality is frequently considered constant over sexes in fishery stock assessment models (Punt et al. 2021; but see Wilderbuer and Turnock 2009; Bevacqua et al. 2011). For the Pacific herring (*Clupea pallasii*) in Alaska, for example, it has been shown that wrongly estimating the sex ratio can lead to biases in inferred age composition of the population, vulnerability to fisheries mortality, and ultimately spawning biomass (Ward et al. 2019). The sensitivity of the GEM to natural mortality in females must be viewed alongside the high proportion of female eels (96%) in the River Weser study system. The pronounced sexual dimorphism in growth leading to larger female size (Dekker 2004), together with the high female proportion, caused the high observed influence of natural mortality of female eels on predicted outmigrant biomass. Due to the GEM model structure (Figure 1), influence of model variables related to male eels would be somewhat higher in basins with higher proportions of males. However, the GEM's sensitivity to sex-specific natural mortality is considered representative of other German EMUs where similarly high proportions of female eels have been observed (e.g., River Ems, Höhne et al. 2023).

We suggest that targeted and sustained biological investigations of sex-specific mortality, and estimates of its uncertainty are likely to increase reliability of the eel model. Punt et al. (2021) pointed out that natural mortality is among the most difficult parameters in stock assessment models to estimate. Accordingly, our expert survey suggests that natural mortality and related predation mortality by cormorants are particularly challenging to estimate accurately. Natural mortality in the GEM is estimated from a model that uses water temperature, sex, and body mass based on empirical data from 15 European eel stocks (Bevacqua et al. 2011) but does not consider catchment specifics of natural mortality or potential differences between restocked eels and natural recruits (ICES 2010). Such a generalization (at the cost of precision; Levins 1966) could result in a systematic bias in the number of out-migrating silver eels estimated for specific rivers and

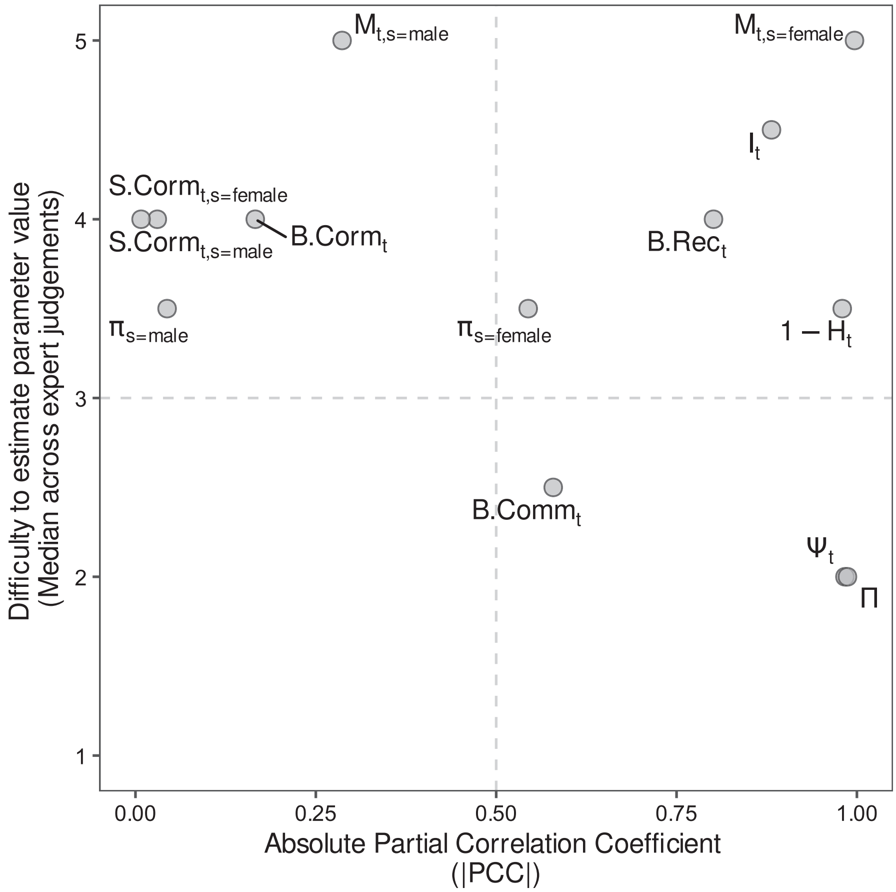

FIGURE 4 | Relationship between the influence of modeled input variables and expert-based judgments of estimation difficulty for the German Eel Model (GEM) in the River Weser, Germany. The influence of each model variable is quantified by its absolute Partial Correlation Coefficient (PCC) score (*x*-axis), wherein larger values denote more pronounced effects on the GEM output, *B.E* (see Figure 3). The *y*-axis pertains to experts' judgment of the overall difficulty in precisely estimating an individual variable. Data points located in the upper-left corner identify GEM variables that may pose challenges for precise estimation, while simultaneously exerting less impact on the model's outcome. Conversely, data points in the lower-right corner indicate highly influential variables that are comparatively easier to estimate. Symbolic notation corresponding to individual variables is explained in Table 1.

periods. Transferring average model predictions to specific systems requires quantifying impacts of potential prediction uncertainty, and true validation is possible only through independent (empirical) data within that specific system (Yates et al. 2018). While being methodologically demanding, empirical assessments of age- and sex-specific natural mortalities, for example, through system-specific tagging studies (Maunder et al. 2023), would allow for validation, likely reduce uncertainty and help provide more accurate silver eel escapement estimates in specific rivers or catchments. Natural mortality might also be estimated from silver eel outmigration and yellow eel abundance informed by fisheries harvest data. For example, models such as the EDA (Mateo et al. 2022) could be used to estimate sub-basin and basin-wide yellow eel abundance through time, to inform, refine, or validate components of the GEM. This would be a major shift away from the current form of the GEM, where parameters are fixed externally, toward an integrated age-structured population modeling approach that is increasingly used for fisheries management (Maunder and Punt 2013; Aprahamian et al. 2021).

Our study showed that hydropower mortality, which averaged 18% in the River Weser EMU, is a highly influential GEM variable, with even small increases in mortality greatly reducing biomass of successfully out-migrating silver eels. Similarly, hydropower turbines have been identified as the largest cause of eel mortality in other countries such as Sweden (Dekker 2021). Investigations of mortality and damage of eels during the passage of hydropower turbines have a long history (e.g., von Raben 1955; Montén 1985), and eels are among the most-studied species worldwide (Winter, Jansen, and Bruijs 2006; Calles et al. 2010; Radinger, van Treeck, and Wolter 2022), including in the River Weser (Schwevers, Adam, and Engler 2011). Their elongated body shape allows even large eels to pass through fish protection screens to be entrained, injured, or killed (Carr and Whoriskey, 2008; Calles et al. 2010; Ebel 2013; Radinger, van Treeck, and Wolter 2022). A global, empirically based estimate of turbine-related mortality of eels across many different types of hydropower plants (95% CI = 11%–21%; Radinger, van Treeck, and Wolter 2022) included the 18% mean hydropower-related mortality of eels in the River Weser. Hydropower-induced mortality of out-migrating silver eels in other German EMUs ranges between 0.2% in the River Oder and 46% in the River Rhine (Fladung and Brämick 2024). In the GEM, hydropower impacts are limited to mortality during downstream migration of silver eels, although yellow eels may also be impacted by hydropower during movements within a river system (Feunteun et al. 2003; Fladung 2019; Riley et al. 2011). Additionally, the GEM uses a gross area-weighted average for hydropower-related mortality, disregarding spatial or temporal variability and its uncertainty. This generalization sacrifices precision (Levins 1966), assuming mortality at plants without empirical estimates can be imputed from an average cross-basin estimate, a common practice in ecological modeling (Nakagawa 2015). However, both construction and aspects such as discharge conditions, operation modes, and fish behavior affect mortality at any particular hydropower station (van Treeck et al. 2021, van Treeck, Radinger et al. 2022). Within- and among-site variability and the spatial arrangement of hydropower plants and eels within a river system (van Treeck, Radinger et al. 2022, van Treeck, Wolter et al. 2022) cause uncertainty associated with any system-wide, aggregated mortality estimate. We recommend that basin-wide hydropower-related mortality estimates be improved by considering specifics of single hydropower sites, their arrangement in relation to density and movement of eels, and their spatial distribution within a river network (i.e., cumulative effects) using spatial modeling (van Treeck, Wolter et al. 2022).

The 10% uncertainty in the number of restocked eels had comparably large effects on GEM-estimated biomass of outmigrating eels, whereas the 10% uncertainty in eels removed by cormorants had less strong effects. This is rather unsurprising, as the GEM is a forward simulation population model, where in- and output quantities deterministically define the standing stock and the number of out-migrating eels (Oeberst and Fladung 2012; Appendix S1) and uncertainties in input variables translate directly into uncertainties in predictions. Eel restocking majorly drives inland silver eel production in German and other European inland waters (Brämick, Fladung, and Simon 2016; Dekker 2021), making it a key quantity for meaningful and reliable predictions. Based on our expert survey, which identified annual restocking quantities of eels (Figure 4) as relatively easy to estimate accurately, prioritizing this variable could significantly enhance eel stock modeling and management.

Other studies found discrepancies between GEM estimates of outmigration and field estimates of outmigration. For example, GEM estimates were 541%–733% higher than estimates from mark-recapture studies on the River Ems during 2020–2022 (Höhne et al. 2023), 8%–87% higher in the River Elbe (Fladung, Simon, Hannemann, et al. 2012), and 60%–254% higher in the River Havel (Brämick, Fladung, and Simon 2016). Such discrepancies between model-based estimates (which are currently used for assessing management success and outmigration; Fladung and Brämick 2024) and mark-recapture studies should be resolved (Höhne et al. 2023) but were beyond the scope of our study aiming at a GEM sensitivity analysis. Furthermore, in addition to the GEM input parameters tested in this study (Table 1), other factors are impacting eel stock dynamics and thereby the amount of outmigrants. Examples include diseases, changes in food webs, contaminants, barriers, water management, fisheries management, and handling stress during stocking operations (Tesch 2003), which were not considered quantifiable in context of eel growth, survival, maturation, and outmigration and not included in the GEM. We cannot exclude that such factors and the spatial variability of parameters within a basin impact the number (and quality) of silver eels and also contribute to observed discrepancies between model results and mark-recapture studies.

We emphasize that future data collection and research efforts should not only aim at accurate mean estimates but also at appropriate uncertainty quantification (Simmonds et al. 2024). Uncertainties considered in this study were based on expert judgment (Drescher et al. 2013) due to the lack of empirical knowledge and likely deviate from actual uncertainty which may be even higher (e.g., for cormorant predation). Uncertainties in model quantities can be generally classified into aleatory (stochastic) and epistemic uncertainty (Kiureghian and Ditlevsen 2009), and the latter can be reduced or refined by gathering more data. For example, cormorant predation and its uncertainty could be estimated through a combination of diet studies using morphological and genetic analyses (Thalinger, Oehm, and Traugott 2022) and tagging studies (e.g., Jepsen et al. 2010) across multiple locations and years. Moreover, estimates of hydropower-induced losses and their uncertainty could be improved by accurately describing all hydropower plants within an EMU, determining ranges of site-specific eel mortality through empirical studies (Heisey et al. 2019; Mueller, Pander, and Geist 2017), and (spatial) modeling that considers variable distribution patterns of fish densities in relation to locations of hydropower schemes (van Treeck et al. 2022). Improved data and uncertainty estimates with regard to recreational fisheries removals could be achieved through qualified extrapolation models of anglers' eel catches (Baisez and Laffaille 2008; Pollock, Jones, and Brown 1994), or empirical efforts such as mark-recapture designs to estimate recreational catches and its spatio-temporal variability (e.g., Bacheler et al. 2009). Accurate estimates of commercial catches and uncertainty, identified as comparably easy to determine by our expert survey (Figure 4), could be attained systematically by collecting data with fishers by combining logbooks, which are currently used and assumed without error, with on-site measurements of landings (Cotter and Pilling 2007).

Joint efforts to refine models and improve understanding of eel biology and population dynamics are key to pave the way for more sustainable and effective eel management. Our sensitivity analysis work might be considered a starting point that provided important insights on where to focus to improve the GEM. This is an important step toward increasing accuracy of model outputs and to assess the model fit with empirical measurements within a specific EMU through validation (Rykiel 1996; Trijoulet et al. 2023; Hale et al. 2023). From our findings, we recommend a future research focus on (i) annual number of restocked eels and their spatial distribution, (ii) the proportion of female eels among outmigrants, and (iii) the spatially distributed losses of eels due to hydropower, which offers relatively feasible avenues for improving mean and especially uncertainty estimates and could significantly bolster the reliability of GEM's predictions in the future. Improving the accuracy of input factors through quality checks of data sources (McCord et al. 2021), validation (Rykiel 1996), and development of future enhancements of the GEM (e.g., consideration of spatial variability; DeAngelis and Yurek 2017) can provide meaningful improvements of model-based estimates of the number of out-migrating silver eels. Such improvements may also help reduce discrepancies between model estimates and mark-recapture studies. Although more difficult, delving into comprehensive scientific investigations to quantify natural mortality and eel immigration rates, and to uncover their intricate ties to environmental factors, assumes a parallel significance to enhance not only the reliability of the GEM but also the understanding of eel demographics in general.

Acknowledgments

Financial support was provided to TW, JS, EF, and UB for advancements in GEM III by the Fishery Ministries of the Federal States of Brandenburg, Saxony-Anhalt, Schleswig-Holstein, and Thuringia (Grant MLUL-34-1400/925+1#164109/2021). The analysis was commissioned and financed by German Federal States departments of fisheries. We are grateful for the contributions of the Eel experts participating in our online survey. Markus Diekmann provided input data to run the GEM for River Weser.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and analysis scripts underlying this study are openly available via figshare at http://doi.org/10.6084/m9.figshare.25768635, Radinger et al. (2024).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.