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Original Article

Overestimating management progress—modelled vs. monitored silver eel escapement in a North Sea draining river

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The success of European efforts towards the recovery of the European eel (*Anguilla anguilla*) population will rely on accurate assessments of local stock status for the implementation of conservation measures. Yet, direct and continuous monitoring of the escapement of potential spawners ("silver eels") is unfeasible in most habitats. Therefore, population models are widely used to estimate local silver eel escapement, but require input information on recruitment, demographic characteristics, and mortalities that are often estimated with great uncertainties. We conducted a combined mark–recapture and acoustic telemetry study across two migration seasons to quantify the actual silver eel escapement in a sub-catchment of the German river Ems. Results were compared with predictions from the demographic model used to provide stock parameters in Germany according to the EU eel-regulation. Mark–recapture results suggested an annual female silver eel escapement of ∼15–17 tons, while the demographic model predicted 90–98 tons, indicating a considerable overestimation. Our results suggest that realistic prediction of silver eel escapement is hardly feasible without high-quality input information and highlight the need for site-specific model calibrations against monitoring data. Overestimations of local stock sizes are problematic if they obscure the necessity for adequate conservation measures, hindering their implementation.

Keywords: acoustic telemetry, *Anguilla anguilla*, demographic models, European eel, management plans, mark–recapture, stock assessment.

Introduction

Accurate estimation of stock status is a central component of reference-point-based conservation management, as it informs the necessity for and identification of appropriate management actions (Hilborn and Walters, 1992; Kuparinen *et al.*, 2012). Obtaining direct counts or estimates of local stock size, however, is elaborate and rarely feasible for species that dwell in complex environments such as rivers, lakes, estuaries, and coastal areas (Dekker, 2003b). Under these circumstances, population models constitute the only alternative to project past, present, and future stock development but are subject to many different levels of uncertainty that can lead to bias in obtained estimates (Francis and Shotton, 1997). In the case of the European eel, uncertainty and bias arise from its complex, yet incompletely understood life history (e.g. density-dependent sex differentiation; Tesch, 2003), the lack of a stock-recruitment relationship for local stocks (De Leo *et al.*, 2009), requiring site-specific recruitment estimates that rarely exist, and the diverse mortality factors that are often estimated at low precision (Walker *et al.*, 2011). Erroneous stock size assessments resulting from uncertainty in input data and model structure may lead to inappropriate management decisions (Schnute and Richards, 2001). Overestimations of stock size are perilous, as they may imply insufficient conservation measures and overexploitation, thereby increasing the risk of stock collapse (Walters and Maguire, 1996; Myers *et al.*, 1997). Underestimations of stock sizes might, for example, imply unnecessary reductions in harvest and thus low stakeholder support for the decision, or the implementation of inefficient, yet costly habitat restoration measures. Hence, to ensure reliability of stock status indicators obtained from a chosen population model, its output should be rigorously validated against *in-situ* observations wherever possible (De Leo *et al.*, 2009; Walker *et al.*, 2011).

The European eel is a semelparous species with a facultatively catadromous life-cycle, reproducing in the Sargasso Sea, within the North Atlantic gyre (Miller *et al.*, 2019; Hanel *et al.*, 2022; Wright *et al.*, 2022). Their larvae cross the Atlantic Ocean and recruit to the coastal and continental waters of Europe and North Africa after metamorphosis to so-called "glass eels". After a growth phase of typically 5–20 years (up to 50 years in rare occasions), premature "silver eels" have to escape their growth habitats to undertake a second migration across the Atlantic, to mature, spawn, and then die (Tesch, 2003; Daverat *et al.*, 2012). Assessing and monitoring local eel stock dynamics has become common practice in European Union Member States through the establishment of recovery measures [Council Regulation (EC) No. 1100/2007;

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Table 1. Results of previous validation studies of the GEM.

Study	Site	Area (ha)	Year	Monitoring method	Model result (no. of individuals)	Monitoring result (no. of individuals)	Modelled/ Monitored escapement
Fladung *et al.* (2012)	Elbe	131 800	2011/2012	Mark–recapture*	215 000–280 000	150 000–200 000	1.08–1.87
Prigge *et al.* (2013)	Schwentine	~7 500	2009	Direct counts at HPP	728	97	7.51
			2010	Direct counts at HPP	363	683	0.53
Brämick *et al.* (2016)	Havel	56 300	2010	Mark–recapture	64 541	25 360	2.54
			2011	Mark–recapture	31 970	19 950	1.6
			2012	Mark–recapture	38 117	10 757	3.54

*Results from the mark–recapture study were extrapolated to ca. one-third of the catchment's wetted area, whereby these were reported as a range.
HPP = Hydropower plant.

European Commission, 2007] to counteract the dramatic decline in recruitment of the panmictic eel population in recent decades (ICES, 2022a). Since a lack of spawner biomass likely preceded the observed collapse in recruitment (Dekker, 2003a), the "Eel regulation" intended to ensure a sufficient annual escapement of silver eels from national eel habitats of each member state every year. The target reference point to be achieved in the long term is a silver eel escapement of 40% relative to the biomass that existed without anthropogenic impacts (or in a reference period before 1980) in any river catchment or otherwise defined geographical unit (= Eel Management Unit, EMU). In order to meet this target, member states had to develop Eel Management Plans (EMPs) for each EMU, and have been reporting about their implementation progress on a triannual basis.

In line with this, EU countries apply different stock assessment approaches adapted to the local conditions and obtainable data, with all of the methods relying on modelling or extrapolation to varying degrees (ICES, 2022b). With few exceptions, the modelling approaches can basically be classified in two categories following ICES (2022b): extrapolation models and demographic models. Extrapolation models typically incorporate distributed monitoring efforts (e.g. electrofishing surveys within the Water Framework Directive) to estimate a habitat-specific production that is then extrapolated to the EMU's total surface area and converted to silver eel output under inclusion of (assumed) cumulative mortalities (e.g. Van De Wolfshaar *et al.*, 2014; Briand *et al.*, 2022). Demographic models are typically age-, stage-, or size-structured, and require quantifications of recruitment and mortalities originating from different natural or anthropogenic sources as input information. Known or assumed relationships of demographic characteristics (growth functions, silvering rates, etc.) are then applied to estimate production and annual escapement from the virtual stock (e.g. Oeberst and Fladung, 2012; Bevacqua *et al.*, 2019).

Germany employs an age-structured demographic model (German Eel Model; GEM) to generate EMU-specific estimates of the actual silver eel escapement in biomass (B_{current}), and the potential biomass in absence of anthropogenic factors at current (B_{best}) and pristine recruitment levels (B_0). The model projects the development of cohorts in a forward direction, beginning with an estimated initial dummy population in a past year (Walker *et al.*, 2011; Oeberst and Fladung, 2012). Similar approaches have also been adopted in other countries, such as Poland or Italy (ICES, 2022b).

The large distribution area and geographic variability in life-history traits of eels require models and their input to be adapted to the local stocks and conditions, while a generalization of patterns across local stocks drives error in the resulting assessment (ICES, 2022b). Although this prerequisite has been stressed by developers of eel population models in early pilot studies (Walker *et al.*, 2011), the lack of precision and local adaptation in model input parameters remains a critical shortcoming in local assessments (e.g. Fladung and Brämick, 2018). Moreover, demographic models in particular treat the whole stock across the considered system as a single unit, thus ignoring the spatial distribution and variation in life-history traits on a smaller scale (Walker *et al.*, 2011; ICES, 2022b).

Following development of the GEM for compliance with the EU eel regulation a few studies have been conducted to test its predictions against *in-situ* observations of silver eel escapement. In these studies, the model-estimated escapement was generally within the same dimension as direct counts or estimations, but overoptimistic in most cases (Table 1). The study sites have in common that for most model parameters, site-specific, and directly measured input data were available or collected within the projects. These studies can thus be seen as a useful reference for the potential of the model under the availability of good-quality input data, in not too complex systems (e. g., with natural recruitment as an influential, but hardly measurable parameter being absent or negligible in two of the three case studies). Although adaptation of GEM is recommended to better represent local conditions, in practice of the EMP implementation input parameters often lack direct and system-specific measurement, as they are difficult or costly to collect.

The overarching aim of this study was to test predictions of the demographic model used in German eel management at the *de facto* available level of precision of input parameters. Therefore, the model input parameters were calculated or estimated based on assumptions underlying implementation of the management plan for the Ems EMU (Table 2) (LAVES and Bezirksregierung Arnsberg, 2008; Fladung and Brämick, 2021). For comparison, the actual annual silver eel escapement was estimated via a mark–recapture and acoustic telemetry study conducted in the tidal river Ems during a continuous period encompassing two migration seasons.

Table 2. Overview of required input parameters for the GEM III with a description of their estimation procedure.

	Parameter	Type	Unit	Origin	Period
1.1	Natural recruitment	Quantity	Number	Calculated using mean annual recruitment before 1980 (B_0) as given in LAVES and Bezirksregierung Arnsberg (2008, p. 8)	1985–2007
1.1	Natural recruitment	Quantity	Number	Calculated using B_0 recruitment and the median B_{current}/B_0 ratio of all ICES recruitment series (ICES, 2022a)	2008–2021
1.2	LFD of natural recruits	Demographic characteristic	%/Age-class	Based on length–frequency distribution from recruitment monitoring in River Elbe (Brämick *et al.*, 2008)	1985–2021
2.1	Stocking	Quantity	Number	Expert judgement estimations based on available data rows for 1985–2007, surveys at fishing clubs and associations for 2008–2019, and supplemented with detailed information on reported or on funded stocking measures since 2011	1985–2019
2.1	Stocking	Quantity	Number	Data for funded stocking measures in NDS and reported stocking quantities in NRW	2020–2021
2.2	LFD of stocked recruits	Demographic characteristic	%/Age-class	Derived from reported numbers and average weights of stocking (LAVES, unpublished data)	1985–2021
3	Growth	Demographic characteristic	Function parameters	Von-Bertalanffy function parameters derived from length-at-age back-calculation from otoliths as described in Supplementary Material S1	1985–2021
4	Natural mortality	Demographic characteristic	%/Age-class	Calculated after Bevacqua *et al.* (2011) using the mean water temperature and assuming a *medium* stock density	1985–2021
5.1	Commercial fishery mortality	Quantity	kg	Expert judgment estimations based on available data series	1985–2007
5.1	Commercial fishery mortality	Quantity	kg	Logbook information according to the Eel regulation. Catches of fishers that fished in areas both upstream and downstream of the monitoring site were corrected following personal communication	2008–2021
5.2	Recreational fishery mortality	Quantity	kg	Expert judgment estimations for NRW and based on multiannual surveys at fishing clubs and associations for NDS, both for the inland part of the EMU Ems	1985–2007
5.2	Recreational fishery mortality	Quantity	kg	Based on the number of fishing licenses and a mean yield for NRW, and annual surveys at fishing clubs and associations for NDS, both for the inland part of the EMU Ems	2008–2019
5.2	Recreational fishery mortality	Quantity	kg	Based on the number of fishing licenses and a mean yield for North Rhine-Westphalia, while Lower Saxonian catches were taken to be the average harvest of 2018–2019 in the absence of survey data	2020–2021
5.3	Predation by cormorants	Quantity	kg	Based on official bird count statistics (breeding pairs + wintering birds) and an assumed average weight and proportion of eels in the cormorant forage (following Brämick and Fladung, 2006)	1985–2021
5.3	LFD of eel in cormorant forage	Demographic characteristic	kg	Based on a log-normal function fitted to stomach sample data from River Elbe as presented in Oeberst and Fladung (2012)	1985–2021
5.4	Mortality at hydropower and pumping stations	Quantity	%	Projection in GEM III based on area shares upstream of a facility with an assumed mortality rate of the respective facility as described in the EMU Weser (LAVES *et al.*, 2008, p. 16)	1985–2021
6.1	LFD of silver eels	Demographic characteristic	%/Age-class	Monitoring in the present study	2020–2022
6.2	Fraction of silver eels	Demographic characteristic	%/Age-class	Logit-function fitted to length–frequency distribution (converted to age-frequencies) derived from the silver eel monitoring (see Oeberst and Fladung, 2012)	2020–2022

Table 2. Continued

	Parameter	Type	Unit	Origin	Period
7	Length-weight relation	Demographic characteristic	Function parameters	Based on our monitoring and data from the EU-Data Collection Framework (DCF) recorded at a similar capture location. All life-stages were used if the morphological discrimination following Durif *et al.* (2005) or macroscopic examination of gonads allowed sexing	2020–2022 (monitoring) 2014–2022 (DCF)
8	Proportion of females	Demographic characteristic	%	Calibrated in the model to match the observed fraction of females according to our monitoring in recent years	1985–2021
9	Silver eel escapement	Quantity	Number, kg	Projection based on GEM III	1985–2021

Parameter indices in the left column were assigned similar to Brämick *et al.* (2016). EMU = Eel Management Unit; NDS = Lower Saxony; NRW = North Rhine-Westphalia; LFD = length–frequency–distribution.

Methods

Study area

The Ems River is located in northwestern Germany and parts of the Netherlands, draining into the North Sea (Figure 1a). Constituting one of nine national Eel Management Units (EMUs), the German part of the Ems catchment covers a water surface of ~44000 ha, with a main stream length of ca. 370 km (LAVES and Bezirksregierung Arnsberg, 2008). The River Ems represents an important eel habitat in Germany with historically exceptional high natural glass eel recruitment, exceeding 5 t or 20 million glass eels in some years (Diekmann *et al.*, 2019). Likewise, the river is assumed to have the highest historical silver eel production per hectare (B_0) across German catchments, estimated at 21 kg ha^{-1} (Fladung and Brämick, 2021). However, current silver eel biomass is estimated at only 11% of pristine levels without anthropogenic impacts (Fladung and Brämick, 2021). Eels in the tidal section of the Ems are fished commercially (by seven fishermen) using stow nets and fyke nets and, to an unknown extent, by recreational fisheries. In contrast, the upper, inland part of the river is exclusively stocked and exploited by anglers (LAVES and Bezirksregierung Arnsberg, 2008; Fladung and Brämick, 2021). In recent years, stocking accounted for 61% of the estimated total recruitment to River Ems in numbers (Ø 2010–2019; LAVES, unpublished data). Five weirs and no hydropower plants are located in the main channel of the Ems within our study area between the cities of Meppen and Emden. The sub-catchment upstream of our monitoring location (described below) covers 5777 ha and thus ~66% of the total river length, but given the large estuarine region, only ca. 13% of the total EMU Ems wetted area. Importantly, the study area upstream of the capture gear is assumed to receive the vast majority of the system-wide natural recruitment and ~80% of all stocked individuals (LAVES and Bezirksregierung Arnsberg, 2008).

Silver eel monitoring

The total number of silver eels escaping annually from the Ems was estimated by a mark–recapture study that integrated information from acoustic telemetry. The mark–recapture study consisted of a continuous monitoring using stow nets and tagging of subsamples of caught eels (described below). As silver eel escapement could be underestimated if only the assumed migration season (usually autumn) was sampled (Reckordt *et al.*, 2014), monitoring of eels was conducted continuously from 1 September 2020 to 31 May 2022 using stow nets that were deployed in the tidal river at a fixed position (53°14′49.7″N, 7°23′47.5″E; Figure 1).

The gear consisted of five adjacent nets with a maximum aperture of 3.5 m height × 7 m width and a mesh size of 10–12 mm in the cod-end, resulting in full selectivity for eels >30 cm (Bevacqua *et al.*, 2009) and therefore complete coverage of migrating silver eels, including the smaller-sized males. Nets were emptied daily by a local fisherman, and captured eels of all life stages were stored in a holding tank in river water near the capture site. On a weekly basis, the collected eels were measured for length (rounded down to the nearest cm), weight (in grammes), horizontal and vertical eye diameter, and pectoral fin length (to the nearest 0.1 mm). Measurements were usually performed on live eels, using a customized tray for body length measurements and by digitally measuring eyes and fins from photographs with a reference scale as described and validated in Höhne *et al.* (2023). If eels were sacrificed (e.g. for growth analysis) or anesthetized for tagging, measurements of eyes and pectoral fin were taken with a calliper. Maturation stages according to Durif *et al.* (2005, 2009) were calculated for all captured eels.

In 2021, the stow nets had to be removed from 7 February 2021 to 18 February 2021 due to ice drift on the river. Only two eels had been caught in the week before and none in the week after the ice, thus any correction of catches for the named period was deemed redundant. Nets were reinstalled gradually following repair between 19 February 2021 (starting with two of five nets) and 19 March 2021. Eel catches within this period were corrected for the number of nets in place. Moreover, catches of four days in December 2020 were lost, as seals apparently cracked the flap of the holding box. While the number of captured eels for that period was recorded by the fisher, their unknown maturation stages were inferred from the stage compositions of the catches in the previous and subsequent catch weeks.

Tagging and mark–recapture study

In total, 304 female silver eels (stages F-III, F-IV, and F-V), representative of the size distribution and migration seasonality in the catch, were marked and released in batches between 15 October 2020 and 28 December 2020 ($N = 120$), 27 April 2021 and 27 May 2021 ($N = 31$), and 29 September 2021 and 15 December 2021 ($N = 153$) (Figure 2). Eels were tagged

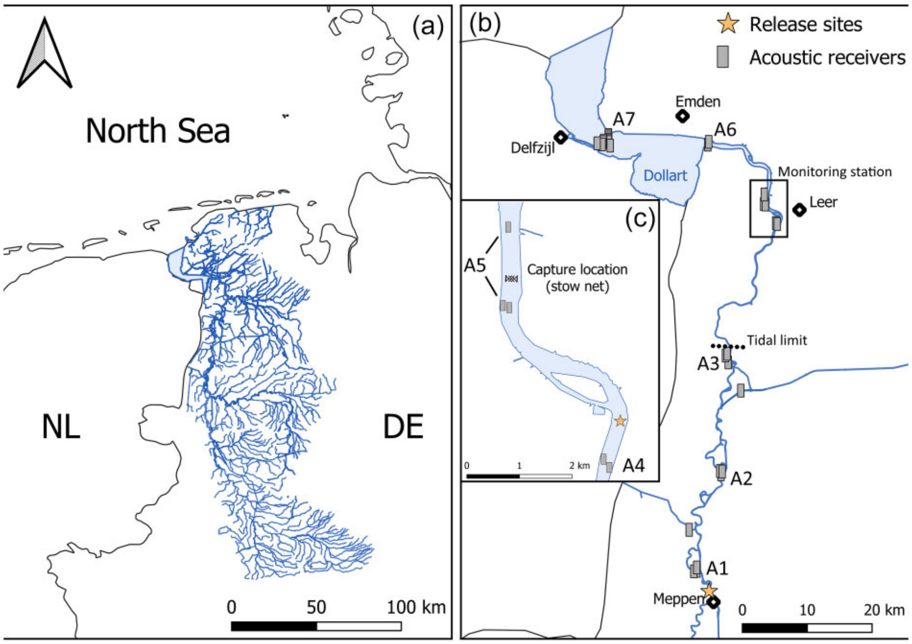

Figure 1. Location and catchment area of the River Ems (German side) (a), the acoustic receiver network consisting of 28 listening stations placed in the main stream and two units in the major canals (b), and the setup of the monitoring station including the location of the capture gear (c).

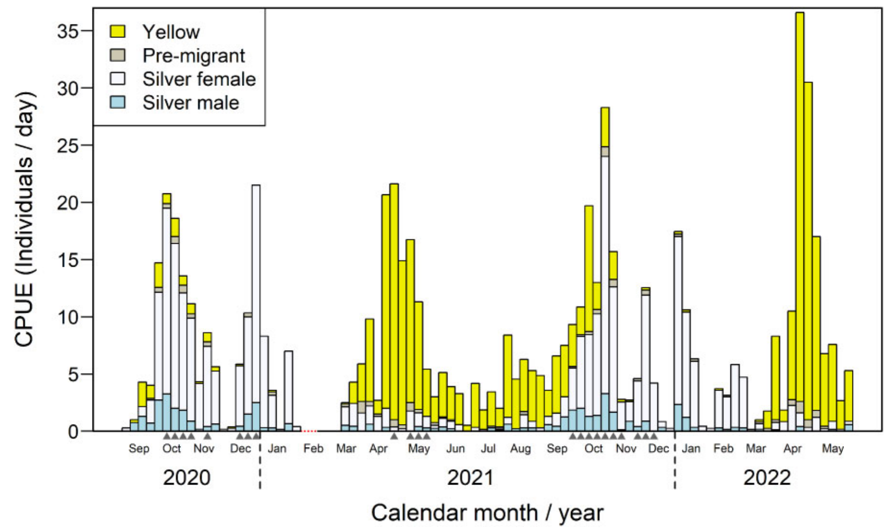

Figure 2. Catch-per-unit-effort of European eels (*Anguilla anguilla*) across the sampling period as the mean number of individuals caught per day within a given calendar week. The fill of bars is categorized according to maturation stage and sex (yellow = Durif-stages I and F-II; pre-migrant = stage F-III; silver female = stages F-IV and F-V; silver male = stage M-II). Grey triangles on the *x*-axis indicate release events of tagged eels. Monitoring was interrupted for two weeks in February 2021 (see red dashed line on *x*-axis) due to ice drift.

externally with T-Bar tags (TBA, Hallprint, Hindmarsh Valley, Australia). In addition, an acoustic transmitter was inserted into the body cavity [V9-2 L ($N = 271$), estimated battery life of 495 days, or V9P-2 L ($N = 33$), estimated battery life of 409 days, with a nominal delay of 60 ± 20 s, Innovasea, Halifax, Canada]. Weight of the tags in water was 2.7–2.8 g, whereby the tag weighed at maximum of 1.24% of the body weight. As prolonged holding times between capture and release of tagged eels might reduce the probability to continue migration within the same season (Stein *et al.*, 2016), we aimed to minimize holding time. Therefore, when daily catches were rather low, we occasionally tagged additional eels that were captured in a second stow net located some hundred metres downstream of our main monitoring gear. The average holding time of eels between capture and tagging was 1.1 ± 1.2 days (mean ± *SD*).

Before tagging, eels were anaesthetized in a clove oil solution (concentration depended on the temperature and salinity of the river water) for several minutes until narcotic immobility was reached (Walsh and Pease, 2002). The disinfected acoustic transmitter was surgically implanted into the body cavity, and the incision was subsequently closed with two stitches, using a slowly absorbable monofilament suture (Surgicryl monofilament DS 24, 3.0 (2/0), SMI AG, St. Vith, Belgium) (Thorstad *et al.*, 2013). The T-Bar tag was anchored in the epaxial musculature, ~5 cm posterior to the origin of the dorsal fin (MacNamara and McCarthy, 2014). Eels were subsequently placed in a dark, aerated recovery tank filled with river water from the catch location, and allowed to recover for ~1–8 h (mean: 3.96 h). Tagged eels were released at two different sites, with 200 eels being released 4 km upstream of the capture location in the tidal region and another 104 eels being released 4 km upstream of acoustic array one in the inland reaches (Figure 1). The latter group was primarily intended to study silver eel's downstream migration behaviour in the system (Höhne et al., *in prep*.), but was included in the escapement quantification to increase statistical power. Eels detected at the capture site (A5) had similar recapture probabilities for both release locations [Bernoulli GLM, χ^2 (1, $N = 253$) = 1.77, $p = 0.184$]. During transportation to the inland release site, fresh river water was added to the tank in order to acclimatize eels to freshwater conditions. It was ensured individually that eels had regained active swimming before release. The described tagging procedures adhered to an animal experimentation permit (33.19-42502-04-20/3436) issued by the Lower Saxony State Office for Consumer Protection and Food Safety (Oldenburg, Germany).

Weekly catches of eels from the monitoring station were carefully screened for the presence of marked eels by looking for external tags and listening for acoustic tag signals with a hydrophone (VR100 and VHTx-69k, Innovasea, Halifax, Canada). To obtain an estimate of the overall fishing mortality of silver eels within the studied river stretch, both the external tag and internal acoustic transmitter were clearly labelled with contact details and the warrant of a reward for reporting (set at €25). The mark-recapture study was announced in various ways, and project flyers were sent to all stakeholders (e.g. local fishers and angling clubs).

We estimated the local population size of annually escaping female silver eels (stages F-III, F-IV, and F-V) using the unbiased modified Lincoln-Petersen method (Ricker, 1975; Pollock *et al*., 1990), consistent with previous silver eel quantification studies (e.g. Klein Breteler *et al*., 2007; Winter *et al*., 2007; MacNamara and McCarthy, 2014; Brämick *et al*., 2016). The number of silver eels (N) was estimated according to the formula:

$$N = \frac{(M+1) \times (C+1)}{(R+1)} - 1,$$

which assumes that the ratio of marked and migrating individuals (M) to population size (N) is equal to the ratio of recaptured, marked fish (R) to the catch taken for census (C), i.e. the total silver eel catch at the monitoring site within a given period (Ricker, 1975; Pollock *et al*., 1990). Only individuals detected on array A5, surrounding the capture site, and/or further downstream were counted as migrating eels (M) in the Lincoln-Petersen estimation procedure. Limits of the 95% confidence interval around the obtained population size estimate were calculated based on a Poisson distribution following Krebs (1999).

As the whole sampling period covered 21 months, silver eel escapement was estimated separately for the first sampling year (September 2020–August 2021), and for the second season from September 2021 to May 2022. As the GEM model predicts silver eel migration on an annual basis, the second (incomplete) sampling year had to be corrected for the missing three months to constitute a complete annual estimate for comparison with the model results. In the first year, 1015 female silver eels were captured between September and May, and 41 (i.e. 4% as many as in the remaining year) were captured between June and August. Therefore, the estimated silver eel escapement for the second sampling season was multiplied by 1.04 to represent a complete annual cycle in the assessment (but in fact, migration timing may vary from year to year, depending on environmental conditions). Calculated numbers of escaping silver eels were then converted to biomass by multiplying with the average weight across all silver eel catches (Klein Breteler *et al*., 2007).

Acoustic tracking

To track the progression of released eels and to determine the fraction of eels that migrated past the monitoring station, i.e. could have been recaptured therein, an acoustic telemetry setup was installed. Thirty acoustic receivers (VR2Tx, Innovasea, Halifax, Canada), forming seven arrays, were installed in the Ems main stream and major canals branching off (Figure 1). In the inland river section, receivers were attached to various fixed structures, such as sheet pilings, dolphins, bridge posts, or level gauges. Receivers in the tidal region were attached to the anchor chains of navigation buoys in consistent depths of 2–3 metres, with the two exceptions of a customized mooring using a concrete anchor block and a floating buoy in shallow, nearshore areas.

A detection efficiency was calculated for each array upstream of the final array A7 following Perry *et al*. (2012) as

$$p_{A1,\ \ldots,\ A6} = \frac{r_i}{r_i + z},$$

with r_i being the number of individuals detected at array i and downstream of it, and z being the number of individuals *not* detected at array i but detected further downstream. The detection range of the final array A7 was determined by analysing the detection data of the sync tags integrated in the VR2Tx receivers of the receiver chain as described in Merk *et al*. (2023). Efficiency of A7 was estimated at 98.3% for an eel passing the array at the observed mean estuarine swimming speed at the shortest transect between receivers. Array A5, which surrounded the monitoring site and thus was used to determine the number of migrants for the Lincoln-Petersen estimation, had a detection efficiency of 98.2%. Given this high detection efficiency (and the inclusion of the individuals that were not detected on A5 but further downstream into the count of "migrants" for the mark-recapture analysis), any correction of the number of migrants was deemed as redundant. The other arrays had detection efficiencies of 93% (A6), 98.4% (A4), and 100% (A1–A3). Data from acoustic receivers was downloaded in November and December 2022.

Application of the German Eel Model

The German Eel Model (GEM) was developed according to data availability at its development site, the River Elbe, as a user-friendly tool implemented in Microsoft Excel, capturing the main aspects of the eel's continental life-phase with intermediate complexity (Oeberst and Fladung, 2012; schematic overview in ICES, 2022b). GEM is an age-structured demographic model that requires quantifications of immigration (= natural recruitment and stocking), growth, mortalities, and emigration (= escapement) to project the development of each cohort sex-specifically in a forward direction. An overview of the required model parameters and a description of how

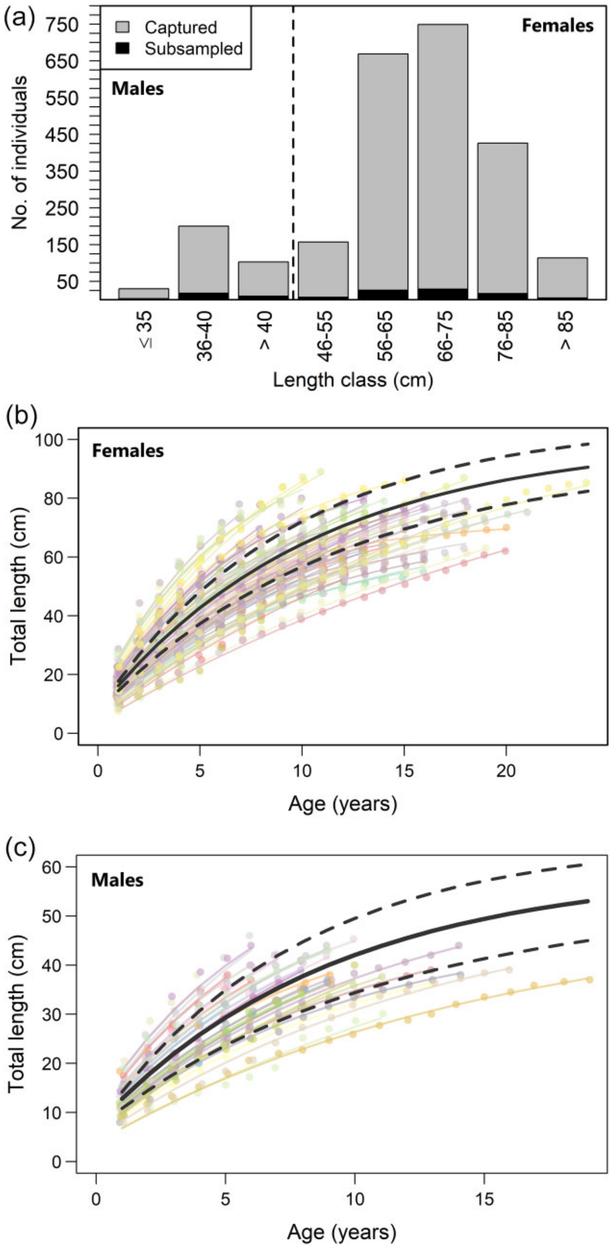

Figure 3. Length class-frequency distribution of silver European eels (*Anguilla anguilla*; stages F-III–F-V, and MII) caught within our monitoring programme and numbers of individuals sampled for growth analysis (a). Individual- and population-average growth curves (solid line) with 95% *CI* (dashed lines) for female (b) and male (c) silver eels.

they were obtained are given in Table 2. In brief, the GEM model requires absolute quantities of natural and stocked recruits, commercial and recreational fisheries landings, cormorant predation, length–frequency distributions for all these parameters, and natural mortality rates (Table 2). Length frequencies are converted to age classes based on a sex-specific von Bertalanffy growth function, for which the estimation procedure within our application is described in detail in Supplementary Material S1. For fishing mortalities, GEM does not take gear types and their selectivity into account, but instead assumes fisheries harvest to be representative of the age-class composition in the virtual stock within a given year. Minimum length limits are converted to minimum age classes harvested, while the harvest of age classes below the limit is assumed to be 0. For a given year, GEM provides the number or biomass of individuals in any age class that constitutes the standing stock of the virtual population. From this standing stock, a fraction of individuals per any age-class is assumed to silver and thus escape within the given year. The silvering proportion by age follows a logistic function that was calibrated based on the age distribution of silver eels observed in the above-described monitoring. From the silver eel production, assumed hydropower mortalities are subtracted by specifying the proportion of wetted area that is assumed to underlie a given mortality level (in 10% categories). As suggested in previous applications of the GEM model, we restricted the modelled age classes to a maximum age of 20, because older individuals were rarely observed in our sampling (Figure 3b and c) (Oeberst and Fladung, 2012; Prigge *et al.*, 2013; Brämick *et al.*, 2016).

The model requires a dummy starting population to be estimated for the beginning of the first modelled year (chosen to be 1985 in our application for conformity with the approach used in the Ems EMP). This starting population was calibrated based on the stock size and age composition in years 1990–1995 (see details of the procedure in Prigge *et al.*, 2013). This reference period was chosen to be some years away from the initial year to reduce the dummy population's impact, but not too far away as eel stock sizes are generally assumed to have changed strongly between the 1980s and today. However, the influence of the starting population on silver eel output in recent years is considered negligible given the maximum residence time of eels in the virtual system of 20 years (Oeberst and Fladung, 2012).

Model input parameters related to natural recruitment, stocking, recreational, and commercial fishing mortality, cormorant predation, proportion of areas exposed to different degrees of hydropower mortality, and average water temperature and stock density level to estimate natural mortality after Bevacqua *et al.* (2011), were provided for the study area by the federal authority responsible for the implementation of the EU eel regulation in the River Ems. Growth functions, length–frequency distributions, and length–weight relationships of male and female silver eels were derived from the herein described monitoring programme.

Numerical implementation

Except for the application of the German Eel Model, which is based on Microsoft Excel, all of the described analyses, including generation of model input parameters from our monitoring, were performed in R version 4.2.0 (R Core Team, 2022). Package "RFishBC" (Ogle, 2022) was used for back-calculation of otolith radius-at-age data; package "nlme" (Pinheiro *et al.*, 2022) was used to compute mixed-effects models, package "ggeffects" (Lüdecke, 2018) was used to create Figure 4; and package "actel" (Flávio and Baktoft, 2021) was used to calculate distances in river km between receiver arrays and river mouth, based on a shapefile of the river.

Results

Capture monitoring

Across the study period from 1 September 2020 to 31 May 2022, 4630 eels were captured at the monitoring site, with

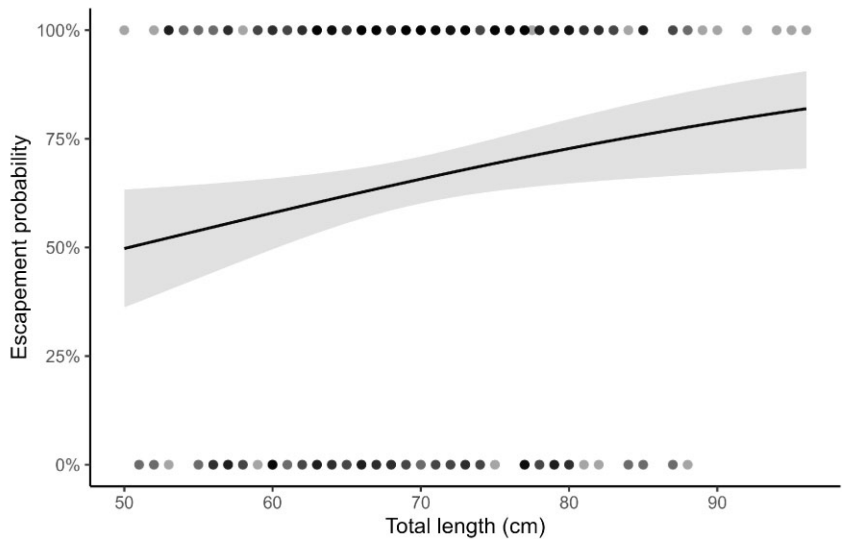

Figure 4. Relationship between body size and escapement success of tagged female silver European eels (*Anguilla anguilla*). The grey ribbon around the regression line represents to 95% *CI*. Raw data points of individual escapement success (0% = not escaped, 100% = escaped) are darker if several data points overlap.

2143 (46.3%) being silver (or pre-migrant) females of stages F-III–F-V, 2148 (46.4%) being yellow eels of stages I and F-II, and 339 (7.3%) being silver males (stage M-II). The proportion of silver male individuals in the silver eel catch within the monitoring programme was 13.6%. The main season of silver eel migration in the Ems was found to extend from late September to January/February, whereas only a minor proportion of silver eels were captured during the spring or summer (Figure 2). Yellow eels were most abundant during spring months (mainly April and May; Figure 2).

Fishing mortality and relative escapement

No catches of tagged female silver eels were reported in the inland part of the studied river stretch, where only recreational fishery is operating. In the tidal region, where commercial fishery is taking place, 19 individuals were reported as recaptured using either stow nets (17) or fyke nets (2). This corresponds to 7.2% of all individuals that were detected at array A4 and/or further downstream ($N = 265$), and accounts for 29% of the observed signal disappearances in the tidal region. Of the 200 eels released in the tidal region, 191 (95.5%) migrated downstream (i.e. were detected on the first array downstream of release site), and 157 (78.5%) successfully escaped (i.e. were last detected on final array A7, ca. 16 km upstream of the river mouth). Of the 104 eels released at the inland site, 94 (90.4%) migrated downstream, and 43 (41.4%) successfully escaped (Figure 5). Of those inland-released eels, 72 (69.2%) successfully progressed to the tidal section (detected ≥ array A3), i.e. the signal of 0.65% of individuals was lost per river km in the inland section. Signal loss rate in the tidal reaches (downstream of array A4) was very similar to the inland section, with 0.66% being lost per river km (including both inland- and tidal-released fish). A generalized linear model with binomial error structure and logit link function indicated that escapement success (i.e. whether an eel reached the final array A7 or not) was positively related to the total length of the fish, not accounting for other covariates [χ^2 (1, $N = 303$) = 6.25, $p = 0.014$)] (Figure 4).

Growth pattern

Back-calculated lengths-at-age, individual-level, and population-level von Bertalanffy growth functions of female and male silver eels are shown in Figure 3. The average growth of female eels from the study area was best described by the von Bertalanffy parameters $L_\infty = 99.9$ cm (95% *CI*-limits: 93.7 cm; 106.2 cm), $k = 0.095$ (0.085; 0.106), and $t_0 = -0.857$ (−0.985; −0.729). Estimates for the population-average growth function of male eels were $L_\infty = 59.6$ cm (53.6 cm; 65.5 cm), $k = 0.109$ (0.089; 0.130), and $t_0 = -1.208$ (−1.537; −0.880). Confidence intervals of von Bertalanffy parameter estimates are reported here to indicate the variation in growth, but GEM is a deterministic model and therefore assumes the average sex-specific growth for each individual in the virtual population.

Silver eel escapement estimates from the mark–recapture vs. modelling approach

For the first study year (September 2020–August 2021), silver eel escapement from the study area was estimated at 25790 individuals (95% *CI* limits: 12167; 54502 individuals), corresponding to 17125 kg (8079; 36191 kg) (Table 2). Silver eel escapement for the period from September 2021–August 2022 was estimated at 22153 individuals (10787; 41254 individuals) or 14710 kg (7163; 27395 kg). The estimates correspond to a silver eel production of 2.55–2.96 kg ha^{-1}. By contrast, application of the GEM to the study area resulted in a predicted female silver eel escapement for the study area of 165330 individuals (in 2020) and 184752 individuals (in 2021), corresponding to an estimated biomass of 90850–97504 kg. These estimates would correspond to an annual silver eel production of 15.73–16.88 kg ha^{-1} from the area monitored.

Discussion

Using a combined mark–recapture and acoustic telemetry approach, we assessed the biomass of female silver eels

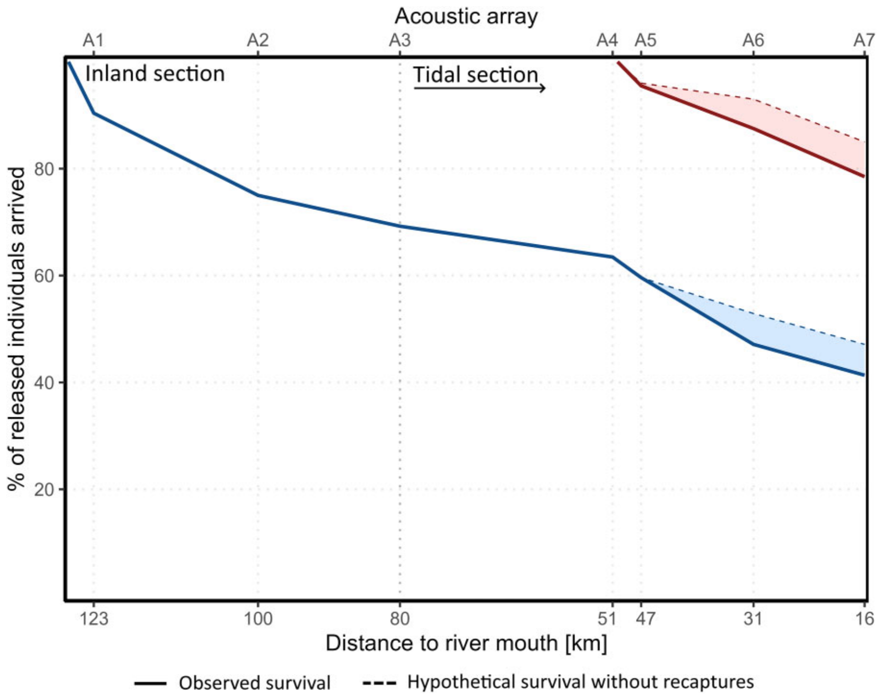

Figure 5. Survival curves (solid lines) indicating the percentage of female silver European eels (*Anguilla anguilla*) that arrived at the given acoustic array (indicated as distance to the river mouth). Blue lines represent the individuals that were released in the inland section ($N = 104$) and red lines represent the eels released in the tidal section ($N = 200$). The amount and location of reported recaptures is indicated through the coloured dashed lines that depict hypothetical survival if recaptured eels had escaped successfully.

Table 3. Results of the mark–recapture study: number of marked and released female silver eels (M_{rel}), marked eels that actually migrated past the capture gear (M), recaptured marked eels (R), and total catch of female silver eels (C).

Year	M_{rel}	M	R	C	Escapement (N), 95% *CI* limits			Biomass (in t), 95% *CI* limits			GEM III result	
					Lower	Estimate	Upper	Lower	Estimate	Upper	N	t
2020/21	151	121	4	1 056	12 167	**25 790**	54 502	8 079	**17 125**	36 191	**165 330**	**90 850**
2021/22[a]	153	136	6	1 087	10 787	**22 153**[b]	41 254	7 163	**14 710**[b]	27 395	**184 752**	**97 504**

[a]Values for M, R, and C apply to the period from 1 September 2021 to 31 May 2022.
[b]Estimate was corrected for relative escapement within three unsampled months (June–August 2022) to represent the assessment for a complete year.
Lincoln-Petersen estimates for female silver eel escapement in numbers and biomass. Model-estimated silver eel escapement numbers and biomass following the application of the GEM III.

annually escaping from the inland and upper tidal sections of the River Ems to currently range between 14.7 and 17.1 tons. The estimated annual silver eel production from the inland and upper tidal sections of the River Ems, corresponding to 2.55–2.96 kg ha^{-1} year^{-1}, is considerably higher than reported estimates from other German river systems. Monitored silver eel production was 0.02–0.09 kg ha^{-1} year^{-1} in the River Schwentine (Prigge *et al.*, 2013; Marohn *et al.*, 2014), 0.032–0.097 kg ha^{-1} year^{-1} in the River Rhine (Klein Breteler *et al.*, 2007), 0.09–0.26 kg ha^{-1} year^{-1} in the River Havel (Brämick *et al.*, 2016), and 0.4–0.8 ind. ha^{-1} year^{-1} in large parts of the River Elbe (Fladung *et al.*, 2012; Table 1). The estimated production of the River Ems is more similar to the reported median silver eel production of 3.87 kg ha^{-1} across 18 European open systems (i.e. no lagoons, etc.) listed in Aprahamian *et al.* (2021), taking into account that many of the reported estimates therein date back to before 2000, when the European eel stock status was better.

In comparison to our monitoring results, the silver eel biomass predicted by the currently deployed demographic model for stock assessment in national eel management (GEM III) for the same area was considerably higher. The model estimated a female silver eel biomass of 90.9 (= 15.73 kg ha^{-1} in 2020)–97.5 t (= 16.88 kg ha^{-1} in 2021), implying an approximately sixfold overestimation of the actual escapement. Mark–recapture studies inevitably rely on assumptions of a closed population, equal capture probability between marked and unmarked individuals, and no tag losses (Pollock *et al.*, 1990). Incorporating these uncertainties, the 95% *CI* around our monitoring estimates ranged from 7.2 to 36.2 t, whereby we conclude that uncertainty in our field study cannot explain the discrepancy between monitored and modelled escapement. The result of an optimistic assessment by the GEM chiefly aligns with previous studies that found an overestimation of actual escapement in five out of six annual estimates from different German river systems (Table 1), but it constitutes the severest, consistent overestimation of GEM reported so far.

There are two potential explanations for the overestimation of actual silver eel escapement observed in this study. Either the quality and accuracy of the available input information was too low, or the structure and assumptions of the model itself needed revision or extension. Previous validation studies of GEM were conducted on systems where many input parameters were measured directly and site-specifically, with the resulting silver eel escapement estimates being less biassed, compared to our study (Fladung *et al*., 2012; Prigge *et al*., 2013; Brämick *et al*., 2016). The larger discrepancy between the modelled estimate and the monitoring results in our case might thus arise from the lack of precision and/or bias in certain input parameters.

Particularly likely to contribute to the overestimation by the model are input parameters that have a strong influence on the escapement output or that are likely biassed in a certain direction. For example, herein (and in the practical use of GEM for EMP implementation in light of the EU eel regulation), natural recruitment is estimated as given in the EMP Ems (LAVES and Bezirksregierung Arnsberg, 2008; see description in Table 2). However, insights from a glass eel mark–recapture study in 2016 (Diekmann *et al*., 2019) suggest that the estimated natural recruitment might be overestimated. According to a running sensitivity analysis of GEM, natural mortality is among the most influential parameters (Radinger *et al*., in prep.). However, the parameter is only estimated indirectly using the average water temperature and a classification of stock density into one of three levels (following Bevacqua *et al*., 2011). Besides, fishing mortality could be misestimated by a lack of information for recreational harvest in the tidal region or underreporting of catches (Deelder, 1984; Moriarty and Dekker, 1997; Correia *et al*., 2018), which is known as a potential cause of stock overestimations (Myers *et al*., 1997). Less relevant mortality factors in the EMU Ems, such as cormorant predation or hydropower mortality, are unlikely to explain the large discrepancy between model and monitoring results.

Our study evaluated the accuracy of the escapement estimation approach by using input data of the same quality as available for the EMP implementation. Therefore, our results underline that an accurate prediction of silver eel escapement is hardly feasible without system-specific and precisely estimated input parameters, as previously emphasized (Prigge *et al*., 2013). On that account, we highlight the urgent need to increase resources and sampling effort for model input parameters.

The almost consistent pattern of overestimation across all of the validation studies might also suggest inadequate assumptions in the demographic model structure, causing overly optimistic outcomes. For example, stocking is a substantial source of eel recruitment in Germany (ICES, 2021), but the assumption of similar natural mortality rates between natural and stocked recruits might be incorrect. Stocked eels might experience post-release mortalities through handling and transport effects, or through lacking adaptation to the wild in case of farmed eels, as indicated by differing rates in survival or growth by some studies (e.g. Bisgaard and Pedersen, 1991; Pedersen, 2000; Simon and Dörner, 2014; Josset *et al*., 2016; but see Pedersen *et al*., 2017; Nzau Matondo *et al*., 2021). Besides, although the limited complexity of GEM facilitates its application, additional features contained in comparable eel demographic models, such as density-dependent sex determination or a fishing effort partition by gear type, including their selectivity, might be necessary (Bevacqua *et al*., 2019).

A first step towards the improvement of the GEM model is running a sensitivity analysis to identify the most influential model parameters and enable data providers to set priorities in the allocation of sampling efforts, which is currently ongoing. Additionally, we suggest testing different model modifications as exemplified above on sites with available direct silver eel quantifications (aforementioned German case studies, this study, and foreign sites with available input data for GEM), to identify and incorporate revisions that improve the model output accuracy across sites.

Individual escapement success

In our telemetry study, ca. 82% of migrating female silver eels released in the tidal region (∼50 km upstream of the river mouth), and only ca. 46% of migrating eels released in the inland section (∼123 km upstream of the river mouth) successfully escaped from the Ems River within the observation period. The observed rates of signal losses were very similar between the inland and tidal river regions, with ca. 0.65% of individuals disappearing per river km in both sections. About 7% of all tagged eels that were released in or migrated to the tidal region (where a commercial fishery operates) were reported recaptured by local fishers. Although much effort was made to make local fishers aware of the presence of tagged eels, five out of 19 recaptures were reported by clients who found the labelled tag inside the eel after purchasing them from the fisheries. Therefore, our observed fishing mortality on tagged eels is likely to represent a minimum estimation of the actual *F*, possibly through (inadvertent) underreporting if external tags were lost or overseen by fishers. This insight highlights the importance of labelling internal transmitters in addition to external tags, if both tag types are used in a mark–recapture study. Subsequent to our study, the closed season for commercial and recreational eel fishery in the tidal area was changed in 2022 and again in 2023, extending beyond the protected season that applied during our study period. This has unknown implications for the representativeness of our estimated *F* under the current policy. No recaptures of silver eels were reported by anglers (mainly operating in the inland river), which might be due to the fasting and dependence on stored energy reserves of migrating silver eels (Tesch, 2003; Freese *et al*., 2019).

In this study, the fate of a substantial proportion of eels that have not escaped, especially in the inland fraction of the study area, remains speculative. As escapement probability of an eel increased with body size (Figure 4), predation might be a plausible explanation for mortality as it often selects against smaller-sized individuals. Cormorants (*Phalacrocorax carbo*), Wels catfish (*Silurus glanis*), and large-sized northern pike (*Esox lucius*), all wide-spread across central Europe, are among the potential predators in the inland river section (Knösche, 2003; Boulêtreau *et al*., 2020). In the tidal river, besides cormorants, harbour seals (*Phoca vitulina*), and grey seals (*Halichoerus grypus*) are likely predators, as their population sizes in the Wadden Sea area have increased substantially throughout the past decades (Brasseur *et al*., 2021; Galatius *et al*., 2022). The external, yellow T-Bar-anchor tag with which eels were tagged in this study, however, might have increased the vulnerability to predators, potentially inflating the frequency of predation events. Another reason for the disappearance of tagged eels could be adverse post-handling effects. While post-tagging mortalities after surgery were estimated to be ≤10% in previously conducted controlled experiments (Winter *et al*., 2005; Thorstad *et al*., 2013), actual mortalities might be higher under natural conditions, as in our study. In addition, handling effects, unsuitable environmental conditions, or upstream transport in the case of inland-released eels could have caused eels to revert to a sedentary stage (Durif *et al.*, 2005). This would imply that these specimens might (have) migrate(d) at a later season than the one following tagging and release, when transmitter batteries were no longer active. The higher frequency of disappearances between release sites and the respective first subsequent array downstream (A1–A5), as compared to other sections (Figure 5), might corroborate this assumption.

Conclusion

Our validation study of the demographic model suggests that the currently estimated silver eel escapement (B_{current}) of 101 tons for the complete EMU Ems (Fladung and Brämick, 2021) is likely an overestimation. An accurate assessment of local stock status, however, is crucial for an efficient biomass target-based fisheries management, as applied for the European eel. Stock size overestimation is known as a potential cause of overexploitation and stock collapse (Walters and Maguire, 1996; Myers *et al.*, 1997) or, in the case of the European eel, might hinder the implementation of sufficient conservation measures and thus slow the recovery of local stocks. To ensure reliable assessments and efficiency of the current European management framework for eel, the various approaches to model local eel stock dynamics across countries must be exposed to regular validation against quantitative silver eel monitoring.

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Supplementary data

Supplementary material is available at the *ICESJMS Journal* online version of the manuscript.

Author contributions

LH, MF, JDP, RH, and LM conceptualized the study. MF, JDP, RH, and LM acquired funding. LH, MF, JDP, JBJH, and LM conducted the field work. LH curated and analysed the data. MD provided input parameters for the GEM model application. EF supervised and validated the GEM model application. JBJH contributed telemetry detection data. LH wrote the original manuscript draft. MF, JDP, MD, EF, JBJH, RH, and LM reviewed and edited the manuscript.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author. Telemetry detection data were uploaded to the European Tracking Network (ETN) data management platform (http://lifewatch.be/etn/) and will be publicly available after the expiration of the moratorium period (https://lifewatch.be/etn/assets/docs/ETN-DataPolicy.pdf).

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