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Original Article

Stocking is essential to meet the silver eel escapement target in a river system with currently low natural recruitment

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Under the European Eel Regulation EG 1100/2007, Member States exhibiting natural habitats for the European eel (*Anguilla anguilla*) on their territory are obliged to prepare Eel Management Plans (EMP) containing appropriate measures to safeguard the escapement of a river system specific silver eel target biomass. Stocking is one management option to reach this target. We used various methodical approaches to study population parameters in a large lowland river under the application of a multi-annual intense stocking programme. The approaches were used to further enhance modelling of stock dynamics and silver eel escapement, in particular. Parameterizing the German Eel Model III (GEM III) with values and functions obtained for recruitment, growth, and mortality resulted in an annual escapement estimate of roughly 32 000–64 000 silver eels from 2010 to 2012. Escapement estimates based on a mark-recapture study conducted in parallel revealed somewhat lower values (11 000–25 000) for the same years. In view of the small number of natural recruits, such values are only contingent if stocking had a profound effect on silver eel production. Results from modelling annual silver eel escapement values indicate that escapement targets set in the EMP for this tributary cannot be reached without stocking. This constellation is likely to apply to other Eel Management Units with low current natural immigration values as well, and might be considered a key dilemma in eel management in such catchments due to the current confusion whether translocation of recruits yields a net benefit to the panmictic stock of the European eel.

Keywords: *Anguilla anguilla*, eel model, Havel river, management, population parameters, recruitment.

Introduction

For >100 years, the vast most European rivers have experienced morphological modulation, fragmentation, and a degradation of water quality. These pressures have hampered, in particular, their suitability and function for long-distance migrating fish species, and resulted in severe yield depressions of commercial inland fisheries. To compensate for this human-induced impact on fish stocks and fishery, stocking of lakes and rivers with young European eels (*Anguilla anguilla*) was conducted in Germany as early as the 19th century (Deutscher Fischerei-Verein, 1894; Walter, 1910) and was followed by other European countries (Moriarty and McCarthy, 1982; Wickström, 1984; Wickström and Dekker, 2012).

The distinct decline in European eel stocks has raised the attention of anglers, managers, and scientists for more than a decade. In this respect, stocking, which is exclusively aimed at sustaining fishery yields, has increasingly been questioned. Today, stocking must also support the production and escapement of silver eel (a migratory phase eel with an advanced maturation status), which has increasingly been prioritized due to declining stock abundance indicators (Moriarty and Dekker, 1997; Dekker, 2004; ICES, 2011).

Moreover, in September 2007, the Council of the European Union (EU) adopted a regulation (EU, 2007) establishing measures for the recovery of European eel stocks. This regulation aims to ensure that 40% of the pristine silver eel biomass of each river system can migrate to sea. Pristine silver eel biomass (defined as B_0 in ICES terminology) is similar to the best estimate of escapement biomass in the absence of any human-induced impacts (EU, 2007). Stocking is one of several potential measures (e.g. a reduction of anthropogenic mortalities, an improvement of river passage and habitats, the transportation of silver eels to waters with no escapement obstacles, and combating predators) to fulfil the requirements of the regulation. Indeed, 14 EU Member States have reported on stocking activities in 49 of 81 Eel Management Units

(EMU) with the implementation of an Eel Management Plan (EMP) (ICES, 2013).

However, the benefit of translocation of early life-stage eels from coastal areas with high natural recruitment to inland freshwater habitats with low or no natural recruitment to increase the spawning stock is under discussion. While stocking aiming to achieve higher fishing yields of predominantly yellow eels has been proven successful in fishery practice (reviews in Tesch, 2003; Knösche *et al.*, 2004; Pawson, 2012), studies on the quantitative effects of stocking on silver eel escapement from larger tributaries with intense stocking over longer periods are rather scarce. Available studies mainly address systems with predominantly natural immigration (Feunteun *et al.*, 2000; MacNamara and McCarthy, 2013; McCarthy *et al.*, 2014), smaller tributaries (Bilotta *et al.*, 2010; Prigge *et al.*, 2013b), or different ecoregions (Desprez *et al.*, 2013). Additionally, stocking inland waters requires various interventions into the natural life cycle of young eels: for example, catching, transporting, temporarily farming, and releasing glass eels into different environments. All listed interventions are hypothesized to impose additional stress and have the potential to negatively impact eels' performance and survival (ICES, 2011; Briand *et al.*, 2012; Simon *et al.*, 2013; Simon and Dörner, 2014). Furthermore, it is assumed that translocated eels experience problems in terms of orientation after silvering when leaving the guiding current of rivers (Westin, 2003; Durif *et al.*, 2013; Prigge *et al.*, 2013a). However, the most comprehensive study in this respect did not find any differences in migration behaviour and orientation between formerly translocated and naturally immigrated silver eels beginning their spawning run from inland waters along the Swedish west coast (Westerberg *et al.*, 2014).

Therefore, the rationale of stocking as a precautionary approach is increasingly being questioned. Thus, the joint EIFAAC/ICES Working Group on Eels has concluded that stocking can only be considered a suitable tool for stock recovery if it generates a net benefit to the stock as a whole (ICES, 2012). To study this notion, certain population parameters (e.g. population size, age structure, growth rate, natural and anthropogenic mortality, and age at silvering) from stocks consisting of translocated individuals must be considered. Furthermore, careful selection of an appropriate study site and design is important. To account for both the high diversity of habitats inhabited by eels and the species' phenotypic plasticity, it is essential to study systems large and diverse enough to mirror this variability, but that are still small and "closed" enough to foster representative sampling. Inspired by the re-launch of a large-scale stocking programme in 2006 in a large lowland river catchment, we applied and combined various methodical approaches to determine parameters imperative for modelling silver eel escapement (e.g. stocking and natural recruitment numbers, sex ratio, growth, age at silvering, and mortality induced by fishery, cormorants, and hydropower turbines). Further, we challenged the results with a mark-recapture study. From modelling results, we aimed to examine the contribution of stocking in a lowland river with intense fishing to reach silver eel escapement targets.

Material and methods

Study area

The Havel River provides a lowland tributary to the Elbe River system, which is the second largest river in Germany, and drains into the North Sea (Figure 1). Our study area covered >80% of the Havel drainage system and is composed of 56 300 ha of a unique combination of riverine stretches and lakes. The area not included in our study consists of a number of lakes in the uppermost stretch of the Havel River. Due to the presence of a weir impassable to upstream migrating eel and a stationary eel trap filtering water discharge at this location, the impact of the excluded area on the eel stock dynamic in the study area was anticipated to be negligible. The mean discharge of the Havel River amounts to 103 $m^3 s^{-1}$ at its confluence with the Elbe River and is associated with a slow current velocity of 0.1 $m s^{-1}$. The main Elbe channel from the North Sea estuary to the Havel River's confluence (distance of 300 km) holds just one weir, which is equipped with Europe's largest fish ladder (http://corporate.vattenfall.de/uber-uns/geschaftsfelder/erzeugung/neubauprojekte/Moorburg/Europas_groesste_Fischtreppe/). In contrast, there are >250 weirs in the Havel River and its tributaries. Upstream migrating fish, such as young eel, face the first weir with a fish ladder just 560 m after having entered the Havel River system.

Natural recruitment

For quantitative monitoring of the natural immigration into the Havel River system, a stainless steel trap (1.8 × 1.5 × 4.3 m) with a mesh size of 4 mm was placed in a fish ladder at the first weir encountered by ascending eel. The trap was operated from May to October from 2005 to 2009. The frame of the trap was mounted on the ceiling of the uppermost Denil-pass chamber and calked to avoid the bypassing of ascending eel. Number and total body length (L_T) of trapped eel were recorded every 2–3 days.

For the subsequent modelling of the stock, however, only eels ≤400 mm L_T were considered natural immigrants entering the system upstream at this point. The very small proportion of larger eels was constituted as resident yellow phase eels. Such eels may display restricted movements for foraging, as indicated by studies on the American eel (*Anguilla rostrata*, Lesueur) (Gunning and Shoop, 1962) and analyses of otolith Sr : Ca ratios of *A. anguilla* (Daverat *et al.*, 2006; Shiao *et al.*, 2006). Therefore, we hypothesized that eels in this phase move up and downstream with the same probability, and excluded those from the modelling.

Stocking

Records of stocking events in the Havel River date back to the early 20th century (Lübbert, 1910). In the present study, quantity and mean length of stocked eels were derived from official statistics beginning in 1985, and were crosschecked with samples taken at stocking events regularly from 2006 to 2012.

Growth

Estimation of age and growth of eels inhabiting the study area was conducted using methods employed by Simon (2015) in a study of eels from the Elbe River's main channel. One hundred and thirty-four silver eels (76 females and 58 males), grouped by 100 mm size classes (length range: 348–975 mm), were sampled at random from a commercial fykenet fishery also used for silver eel mark-recapture studies (Figure 1) throughout the fishing period (July 2010–November 2011). Individual L_T and associated wet weight were recorded before storing eels at −20°C. After thawing, all eels were visually sexed (Frost, 1945). Sagittal otoliths were extracted and stored in 96% ethanol until preparation for age reading by burning and cracking. Age estimation was based on counts of annuli as described by Simon (2007b) and ICES (2009b).

Natural mortality

Natural mortality of yellow eels in the Havel River tributary had been estimated in a previous mark-recapture study conducted in five

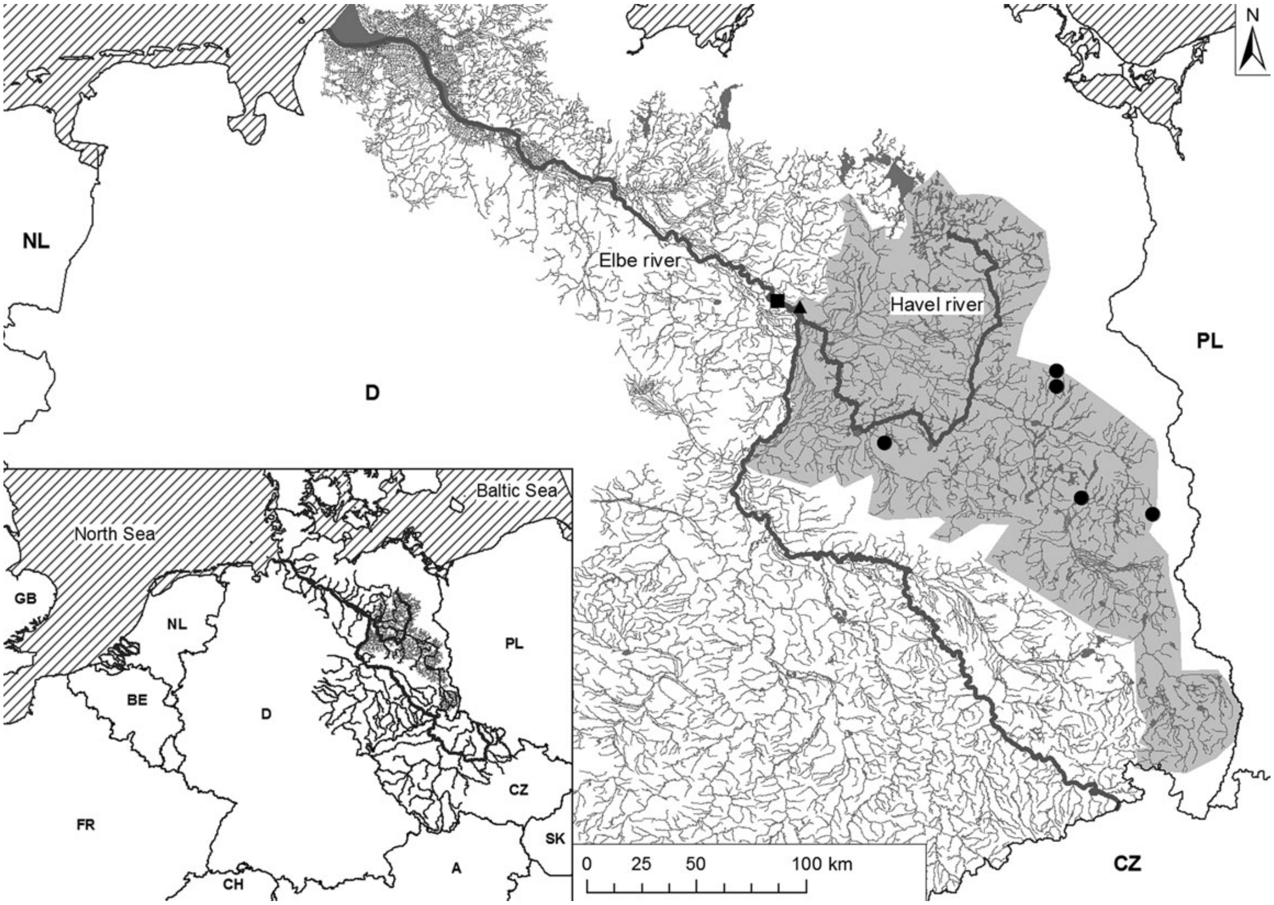

Figure 1. Map of the Elbe River including Havel tributary, the study area (shaded in grey), recruitment monitoring station (filled square), silver eel escapement monitoring station (filled triangle), and isolated lakes stocked to study growth and natural mortality (filled circle).

isolated lakes (Simon *et al.*, 2013; Simon and Dörner, 2014). Since neither extraordinary natural (e.g. cormorant predation: no roosting places exist around study lakes as opposed to the Havel River's main channel) nor human-induced mortality affected eel stocks in these lakes, estimates mirror survival under natural conditions. For modelling survivorship in the present study, however, the results obtained in the previous investigation were impaired by restricted coverage of age classes. Therefore, we applied mortality functions based on data from >30 European waters published by Bevacqua *et al.* (2011). To choose the function most appropriate for the specific conditions in the Havel River tributary, we aligned the mortality estimates obtained from the five lakes (Simon and Dörner, 2014) with Bevaqua's mortality functions for different eel densities. The best fit was gained when using the function for low-density stocks (Figure 2).

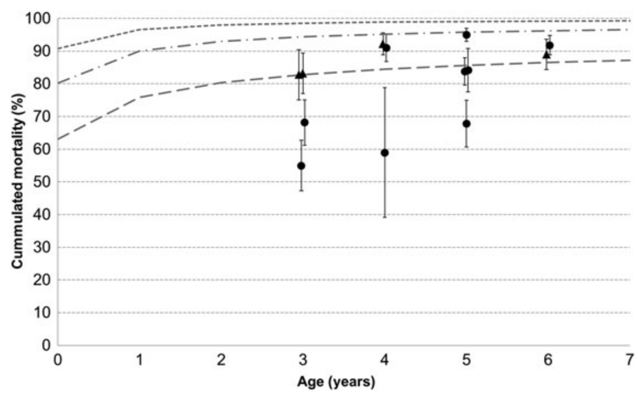

Figure 2. Comparison of estimates of cumulated mortality of stocked eels (filled circle, glass eels and filled triangle, farm eels) in lakes based on a mark-recapture experiment in 2010 (Simon and Dörner, 2014) and calculated cumulated mortality percentage (graphs) from Bevacqua *et al.* (2011) for the Havel tributary. The comparison is based on mean growth rate of female eels, a mean water temperature of 11.7°C and on dot dot dot—low, dash dot dash—mean, and dash dash dash—high eel stock densities. Horizontal point offset within same years was inserted for better visual discrimination.

Fishery mortality

At the time of the study, 89 commercial fishing companies were operating in the study area. The majority fished for eel using fykes, while some also used electrofishing. Companies are obliged to submit species-specific catch statistics to their local fishery authorities yearly. These statistics, from 1985 to 2012, were made accessible for this study. To verify the size and age frequency of catches, samples totalling 1592 eels were taken from catches of four companies situated in different parts of the Havel River system at 15 dates in 2010.

From roughly 90 000 recreational fishery license holders living in the Havel River catchment, 1044 had been randomly chosen to receive logbooks for documentation of eel catches, including individual length, between January and December 2010. The return rate of the logbooks reached 48% at the end of the recording period.

Instantaneous annual fishery mortality rates were estimated according to Beverton and Holt (1957). In contrast, anthropogenic lifetime mortality ($\sum A$) was estimated from the ratio of the current silver eel escapement (B_{current} in ICES terminology) and B_{best} + stocking as described in ICES, 2012.

Additional mortality factors

Besides natural mortality and fishery, eels are exposed to various other local or temporal factors that may cause additional mortalities during their phase of life in the Havel River system. To aid a realistic modelling of stock dynamics, two of such mortality factors of supposedly higher relevance were included in subsequent modelling. Losses due to predation by cormorants near breeding colonies were roughly estimated based on bird counts, average time spent in the study area, daily feed consumption, and the results of a study aimed at quantifying the average proportion of eels in the cormorant forage (Brämick and Fladung, 2006). The latter was linked to the eel stock size in a way that eel proportion values decreased with declining eel stock size. Cumulative mortality experienced by silver eels passing hydropower stations and major cooling water pumping stations when migrating downstream was roughly estimated based on modelled numbers of silver eels starting their migration upstream. For these eels, overall mortality rates of 30 and 0.5% at each hydropower station and pumping station, respectively, were assumed (Rauck, 1980; ICES, 2003). In the presence of protective installations (e.g. racks), mortality rates were reduced for water power stations to 7–26%.

German eel model

For modelling of silver eel escapement, an advanced version (version III) of the German Eel Model (GEM) was applied. As a step forward relating to version II of the GEM (Oeberst and Fladung, 2012), cohort development was calculated separately for both sexes. Therefore, sex-specific differences in, e.g. growth, mortality, and age at silvering, could be accounted for. For the calculation of silver eel escapement for a defined set of years (in our study, 2006–2016), GEM was parameterized for a period starting in 1985. Resident time in the Havel River system was set at 20 years for both sexes in the model. This value was chosen in light of results obtained from length distributions and age estimations of silver eels on their downstream migration (maximum values of 16 years for males and 19 years for females were observed in this study, while Simon (2015) documented 23 years for males and 19 years for females). For parameters with data not covering these periods, such as growth or natural mortality, in all but one case, we performed this parametrization by expanding observed values to the entire modelling period (Table 1). To estimate natural recruitment before our monitoring period (2005–2009), however, we used data from the present study (Table 2) for a backward projection based on the glass eel and small yellow eel recruitment series published in ICES reports (ICES, 2012).

Silver eel escapement monitoring

The number of silver eels leaving the Havel River system was estimated by a mark-recapture study conducted 10 km upstream of the confluence of the Havel and Elbe Rivers (Figure 1). At this location, a special fykenet system with wings spanning about half of the total river width, an opening of 3 × 6 m and a codend mesh size of 15 mm was operated by a commercial fishery throughout the study period, except during periods of ice cover. Catch samples were taken randomly from July to January each season from 2009 to 2011 (Table 3). Individual L_T, weight, eye diameter, and length of the pectoral fin were taken to assess the degree of silvering according to Durif *et al.* (2009). In total, 330 silver eels assigned to silver eel stages FIII to FV and MII, respectively, were selected for marking fish with orange visible implant elastomer tags (Table 3), as described in Simon (2007a). All marked silver eels were included in our mark-recapture estimates, irrespective of their silvering stage. After full recovery, marked eels were released 2 km upstream 1–6 h after marking. Subsequently, recapture in the same gear was registered. In combination with total eel catch statistics of that gear, a Lincoln-Petersen estimate (Bailey, 1951, 1952) was performed to quantify silver eel numbers passing this location. For calculation, the following equation was applied (Krebs, 1999):

$$N = M\left(\frac{C+1}{R+1}\right), \tag{1}$$

where N is the estimated number of downstream migrating silver eels at this location, M is the number of marked silver eels released upstream, C is the total number of silver eels captured in this gear within 1 year irrespective of marks, and R is the number of recaptured marked silver eels.

The sex ratio of migrating silver eels was determined using the length distribution of all captured silver eels over the entire monitoring season. Discrimination between sex-specific length intervals was based on a subsample of 134 silver eels, for which length and sex were determined. From this, all silver eels >465 mm were assigned as females, while smaller individuals were assigned as males.

Eel handling

All eels sampled were anaesthetized by exposure to sodium hydrogen carbonate-buffered tricaine methanesulphonate (MS-222, 0.012% aqueous solution) before further handling. Eels sacrificed for determination of age and sex were overdosed with MS-222 (0.015% aqueous solution for 10 min). The German legislation concerning the care and use of laboratory animals was followed, and ethical permission for the investigation was given by the Ministry for Rural Development, Environment and Consumer Protection of the German Federal State of Brandenburg.

Statistics

Statistical analyses were performed using SPSS 9.0 (SPSS Inc., Chicago, IL, USA). The assumptions of normality and homogeneity of variances of the residuals were not met for many analyses. Therefore, to test for significant differences between sexes for mean age and average length increment in L_T, a Mann–Whitney U test was applied. The level of significance was set at $P < 0.05$.

Results

Natural recruitment in relation to stocking

Recorded L_T of upstream migrating eels at the monitoring location varied from 110 to 640 mm. The vast majority (99.4%) of those eels displayed $L_T \leq 400$ mm (mean value: 271 mm ± 4.6 SD) and were considered in our study as natural recruits. Significant catches of recruits started not before the second half of July and continued with decreasing numbers until November (Figure 3).

Table 1. Parameter employed to run GEM III in the present study, including information on unit, origin of data, and period

	Parameter	Unit	Origin	Period
1.1	Natural recruitment	Number	Monitoring in the present study	2005–2009
1.2	Natural recruitment	Number	Projection based on 1.1 using ICES recruitment dataseries (ICES, 2012)	1985–2004 and 2010–2013
2	Stocking	Number	Official statistics evaluated in the present study	1985–2013
3	Growth	mm	Length-at-age back-calculation from otoliths in the present study	2011
4	Natural mortality	%	Bevacqua *et al.* (2011) after adjustment to experimental data from Simon and Dörner (2014)	1985–2013
5.1	Commercial fishery mortality	kg	Official statistics evaluated in the present study	1985–2013
5.2	Angling fishery mortality	kg	Logbook survey in the present study	2010
5.3	Angling fishery mortality	kg	Projection based on number of licenses issued	1985–2009 and 2011–2013
5.4	Predation by cormorants	kg	Projection based on official bird count statistics and data from Brämick and Fladung (2006)	1985–2013
5.5	Mortality at hydropower and pumping stations	%	Projection based on overall mortality rates from ICES (2003) and Rauck (1980)	1985–2013
6	Length frequency in the catch of fishery	%	Monitoring in the present study	2010
7.1	Silver eel escapement	Number, kg	Mark-recapture experiment in the present study	2009–2011
7.2	Silver eel escapement	Number, kg	Projection based on GEM III	1985–2013

The column on period displays the modelling period for which data of the respective origin were applied.

Table 2. Monitoring season of natural eel immigration at the most downstream weir in the Havel tributary, number of monitoring days, total number and size (average and range) of documented eels, average catch per day of operation, and number and size (average and range) of stocked eels in the period 2005–2009

	2005	2006	2007	2008	2009	Mean
Natural eel immigration						
Monitoring season	03.05.–04.12.	16.05.–01.11.	13.04.–31.10.	15.05.–06.11.	05.05.–17.11.	
Monitoring days (number)	152	143	163	156	176	158
Ascending eels (number)	43 232	35 448	38 010	20 784	27 520	32 999
Average (range) size (mm)	255 (110–400)	277 (160–400)	282 (170–400)	274 (170–390)	274 (150–400)	271 (110–400)
Average catch per day (number)	284	248	233	133	156	211
Stocking						
Eels stocked in total (numbers in mill.)	1.13	3.72	2.97	4.14	4.17	3.22
Average size (range) glass eels (mm)			64 (51–76)		66 (54–77)	66 (51–77)
Average size (range) farmed eels (mm)	185 (80–240)	159 (80–250	167 (80–250)	150 (80–270)	155 (70–250)	159 (70–250)
Average size (range) yellow eels (mm)	356	342	345	352	380	358 (310–470)

Table 3. Year, sampling period, number, mean (range) total length (L_T), and proportion of silvering stages of marked silver eels (FIII–FV; MII)

				Proportion of silvering stages (%)[a]			
Year	Sampling period	Number	Mean (range) L_T (mm)	Stage FIII	Stage FIV	Stage FV	Stage MII
2009	15–23 September	50	654 (569–920)	58	8	34	0
	01–14 December	30	520 (342–834)	0	7	37	56
2010	14–16 July	50	666 (432–842)	90	2	6	2
	28 September–05 October	53	644 (365–954)	21	11	57	11
	02–03 November	45	490 (326–686)	24	0	27	49
2011	23–27 October	102	536 (334–890)	7	4	49	40

[a]Eels were grouped based on the degree of silvering following the methodology of Durif *et al.* (2009).

From 2005 to 2009, ~165 000 natural recruits entering the Havel River were registered at the monitoring location (Table 2). Annual numbers declined during the study period from >40 000 to <30 000. This decline was also apparent on a number-per-day basis. The average number of natural immigrants per year was equivalent to values of roughly 0.5–1 young eel per hectare up-stream water surface area.

From 1985 to 1995, there was intense annual stocking of 3 to >12 million glass eels. In the following years, a shift to farm-sourced and yellow eel stocking along with a reduction of annual intensity to 1–2 million individuals was observed. Following the re-launch of an intense stocking programme in 2006, figures have been increasing to an annual average sum of 3.2 million farm-sourced and glass eels (Table 2). This is equivalent to roughly 50–60 individuals per

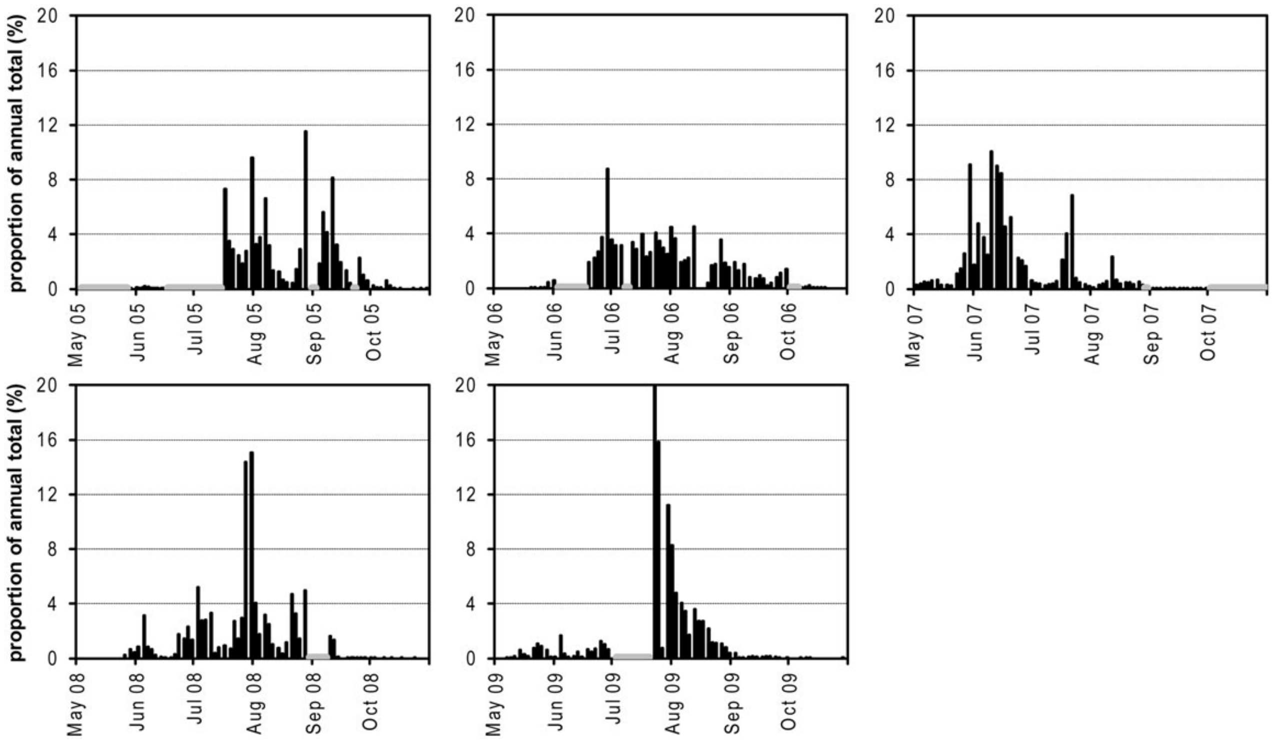

Figure 3. Frequency of natural *A. anguilla* recruits documented per day at the most downstream weir of the Havel River (in percentage of annual total) from 2005 to 2009 (from upper left to right). Grey horizontal lines on the *x*-axis indicate periods without monitoring due to flooding.

hectare. Compared with natural recruitment, stocking accounted for 96–98% of the respective total annual recruitment from 2005 to 2009. When comparing these numbers, it has to be kept in mind that natural recruits entering the Havel River each year were older and larger than restocked counterparts of the same year (Table 2), and were likely to reach silvering age and size earlier.

Growth pattern

The variable L_T of silver eels in our samples ranged from 348 to 485 mm for males ($n = 58$) and from 387 to 975 mm for females ($n = 76$). Age readings revealed estimates from 8 to 16 years for males and 7 to 19 years for females. Across all size classes at capture, mean age, and annual length increments were significantly higher for females with 13 years and 54 mm year^{-1} when compared with males with 12 years and 37 mm year^{-1} (*U* test, *d.f.* 1, $P < 0.01$ for age and $P < 0.001$ for annual length increment; Table 4). The current growth of eels in the Havel River system is reflected by *von Bertalanffy* values of $L_\infty = 1110$ mm, $k = 0.0641$, and $t_0 = -1.149$ for females and $L_\infty = 473$ mm, $k = 0.143$, and $t_0 = -0.931$ for males.

Anthropogenic mortality

Data in logbooks received from anglers showed that, in 2010, only 12% had caught eels in the study area. The average catch per successful eel angler reached 2289 g (range 216–12 713 g). From this, annual total eel catch by anglers was estimated as 0.5 kg ha^{-1} (31 t). In comparison, commercial fishery yielded 2.0 kg ha^{-1} (115 t) in the same year. Considering the length-frequencies of catches as well as growth rates (Table 4), instantaneous annual fishery mortality reached a value of $F = 0.035$. To facilitate an evaluation of the effects of stocking on the total European eel stock, lifetime anthropogenic mortality rates ($\sum A$) are decisive. Based on the data of our study in the year 2010, this rate was estimated to reach a value of 2.03 in the Havel River.

Table 4. Sample size (*n*) and mean ($\pm$ SD) total length (L_T, mm) at age of continental life back calculated from otoliths of female and male silver eels from the Havel River system

	Female		Male	
Age	***n***	**L_T**	***n***	**L_T**
0	76	75 ± 8	58	63 ± 6
1	76	146 ± 18	58	116 ± 14
2	76	207 ± 27	58	160 ± 21
3	76	262 ± 35	58	198 ± 29
4	76	312 ± 43	58	232 ± 34
5	76	360 ± 50	58	264 ± 39
6	76	406 ± 57	58	295 ± 43
7	76	451 ± 62	58	324 ± 46
8	75	493 ± 67	58	350 ± 48
9	73	532 ± 74	56	371 ± 47
10	69	570 ± 80	50	383 ± 42
11	65	601 ± 86	40	388 ± 39
12	49	628 ± 93	27	391 ± 33
13	33	663 ± 97	18	390 ± 26
14	29	684 ± 98	7	401 ± 31
15	17	712 ± 108	5	397 ± 21
16	11	745 ± 114	2	382 ± 13
17	8	771 ± 102	0	
18	6	813 ± 89	0	
19	1	770	0	

Age 0 = glass eel size.

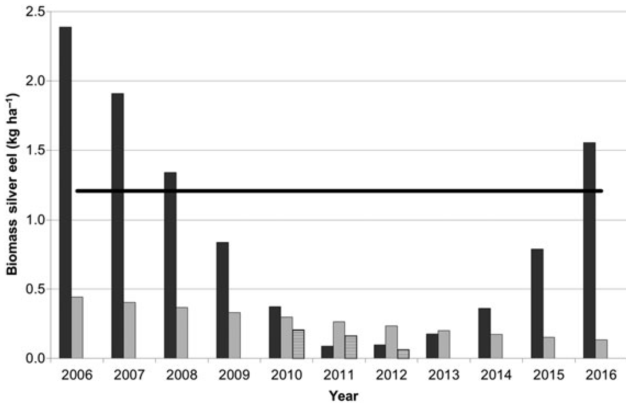

Figure 4. Modelled biomass values of the silver eel (kg ha^{-1}) leaving the Havel tributary at present (black columns, $B_{current}$), and without anthropogenic caused mortalities and stocking (grey columns, B_{best}) in relation to a silver eel escapement target defined in the European eel regulation (black horizontal line) for 2006–2016. Striped columns indicate a silver eel escapement biomass estimate from mark-recapture studies from 2010 to 2012.

Silver eel escapement estimates

Modelling approach

Estimates based on the GEM III showed a high variation in the biomass of silver eels annually leaving the study area (Figure 4). While minimum values of 0.09–0.17 kg ha^{-1} (equivalent to 4900–9800 kg and 32 000–55 000 individuals) were modelled for the period 2011–2013, values exceeding the escapement target (1.2 kg ha^{-1}) were obtained for the period before 2008 and for 2016. At the same time, B_{best} (defined as silver eel escapement corresponding to recent natural recruitment if there were only natural mortality and no stocking) is calculated to reach decreasing values of 0.4–0.1 kg ha^{-1} (35 000–16 000 individuals) between 2011 and 2016.

Mark-recapture approach

Of 330 silver eels marked (Table 3), 17 were recaptured within 1-year post release. Combined with catch statistics of the fykenet, estimates of successfully emigrating silver eels reached values of 25 360 (95% confidence interval = 28 652), 19 950 (15 904), and 10 757 (5608) individuals for 2010–2012, respectively. These numbers correspond to annual biomass estimates of 14 591 kg (95% confidence interval = 16 485), 9811 kg (7821), and 5186 kg (2704), respectively.

Discussion

The results of our study quantify the effect of stocking on silver eel escapement for a large lowland freshwater tributary. According to model estimates, 32 000–64 000 silver eels left the Havel River on their spawning run from 2010 to 2012 (Figure 4). This value will increase to roughly 260 000 silver eels by 2016 due to the effects of the re-launched stocking programme. To evaluate the importance of stocking for silver eel escapement from the Havel River system, a comparison with B_{best} is reasonable. This parameter currently reaches roughly 30 000 individuals, but values will decrease until 2016 to 16 000 individuals due to the decreasing natural recruitment during past years. This means that if recruitment would entirely be based on natural immigration, and these recruits only experienced natural mortality, the estimated number of silver eels would remain distinctively lower when compared with current and future escapement estimates. Therefore, we conclude that, compared with B_{best}, stocking can become a suitable tool to increase silver eel escapement even in EMU with intense eel fishery and other human-induced mortalities.

It cannot be excluded though that the quantity of naturally immigrating recruits was underestimated in our study. Monitoring of natural immigrants had to be stopped for 19–63 days each season (equivalent to 10–30% of the respective monitoring season) within the study period due to occasional trap malfunctions caused by flooding. Within these monitoring gaps, an unknown quantity of migrants entered the Havel River system. Furthermore, a number of individuals might have entered the Havel River system outside the monitoring period. Nevertheless, at these times, water temperatures were <8°C, which is known to inhibit eel movement considerably (Vøllestad *et al.*, 1986; Tesch, 2003). In addition, as no study on the catch rate of upstream migrants was conducted, it cannot be excluded that some individuals might have bypassed the trap by climbing up the lateral walls of the uppermost chamber of the ladder or the weir shutter itself. Due to the very closely fitted ceiling of the trap, and the water level difference at the weir during monitoring periods of >1 m, these eel numbers should have been low. In fact, such bypassers were never observed during daily routine controls. In conclusion, the supposed quantity of eels that may have entered the Havel River system unrecorded would not significantly change either the absolute quantity of natural immigrants and associated B_{best} estimates, or their minor proportion compared with the number of young eels stocked into the system.

As demonstrated by our study, the Havel River is hosting an eel assemblage almost exclusively composed of stocked individuals. Although stocked eels could not be distinguished from natural migrants on an individual basis in our study, population parameters currently recorded for eels in this system can be considered exemplary for stocked eels in a productive natural eel habitat.

There are a number of indications that high eel stock densities may impact demographic population parameters, such as growth, survival, or sex ratios (ICES, 2009a). This may negatively affect (female) silver eel production. For example, data by Rosell (ICES, 2008) demonstrated density-dependent mortality in Lough Neagh for glass eel stocking of >200 equivalents/ha. Acou *et al.* (2011) interpreted male dominated populations as an indication for stock densities reaching carrying capacity in a small coastal catchment in France. In our study, we did not observe such signs when annual stocking and natural recruitment summed to >50 individuals ha^{-1} on average (maximum up to 95 individuals) in the Havel River. The proportion of males in the silver eel monitoring was 24%, and growth estimates based on length-at-age back-calculation using otoliths of silver eels were well within the range observed in neighbouring lowland rivers (Simon *et al.*, 2011; Reckordt *et al.*, 2014) and in isolated lakes (Simon and Dörner, 2014; Figure 5). In parallel, if absolute numbers in natural recruitment observed in our study (10 000–40 000 individuals per year) were used for a backward projection based on glass and small yellow eel recruitment series (ICES, 2012), natural recruitment in the Havel River system from 1960 to 1979 is estimated in a magnitude order of 20–70 individuals ha^{-1}. This is not exceeded by the average sum of today's stocking intensity and natural recruitment. Therefore, our results should be largely unbiased by effects associated with threshold values of stock density.

Silver eel escapement values derived from our mark-recapture study were about half as high as those estimated using GEM III. Differences may be attributed to variations causal factors triggering silver eel escapement, as well as general uncertainties associated with

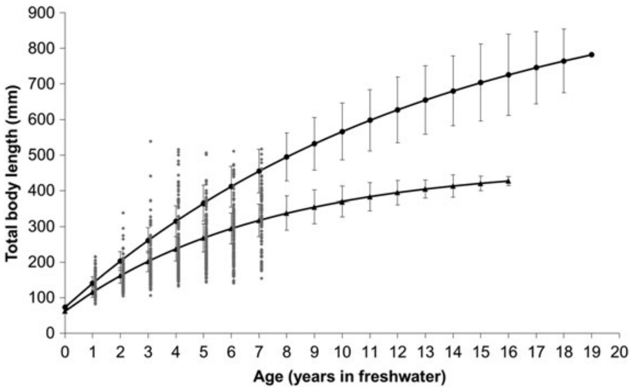

Figure 5. Comparison of mean ($\pm$SD) total length (L_T, mm) at age of continental life back calculated from otoliths of (filled triangle) male and (filled circle) female silver eels in the Havel River, and measured for (grey filled circle) stocked eels of known age in isolated lakes (Simon and Dörner, 2014).

the determination of catch efficiencies by mark-recapture studies (Robson and Regier, 1964; Heimbuch *et al.*, 1990; Krebs, 1999). In addition, the mark-recapture study conducted is likely to partially underestimate the number of males in particular. This is due to their small body size at silvering and the fykenet displaying mesh sizes between 15 mm in the codend and up to 35 mm on the wings. As opposed to larger growing females, male silver eels escaping from waters in northern Europe are known to not exceed 46 cm L_T (Tesch, 2003). Likewise, the number of males up to 450 mm L_T in our modelled annual silver eel escapement values amounts to roughly 28 000 individuals (99% of all silver males). From our own studies (unpublished data), it is known that eels of this size are capable of passing screens with a mesh size of 16 mm. Therefore, we conclude that the results of both approaches, despite the differences, are in the same order of magnitude and support (not question) each other. Therefore, GEM III can be considered giving plausible silver eel escapement estimates when parameterized with tributary-specific data. This is in line with the result of an application of the previous version (GEM II) in a smaller Baltic river catchment (Prigge *et al.*, 2013b). Nevertheless, a number of parameters used for modelling were estimates based on relatively small sample sizes or obtained by extrapolation. Therefore, they display a lower level of confidence than hard data, which impacted the accuracy of our model estimates.

As mentioned before, stocking of young eels in the Havel River has resulted in increased silver eel escapement. In conclusion, stocking displayed an additive effect in a self-recruiting eel stock. For self-recruiting stocks of other species, this is not necessarily the case. As an example, Hühn *et al.* (2014) demonstrated the lack of additive effects in a stock enhancement study on northern pike (*Esox lucius*). The authors concluded that stocking in self-recruiting populations might fail to elevate stock size due to competition of stocked fish with natural recruits. Natural eel recruitment in the Havel River could be demonstrated in our study as well. In contrast to species spawning within a colonized water body, eel recruitment success in inland waters is not driven by internal factors. In such situations, stocking has the potential to add to self-recruiting stocks.

According to our modelling results, silver eel escapement recently declined from 0.5 to $<$0.2 kg ha^{-1}, but will recover in coming years due to the time-lag until restocked eel have matured and become migrant. The target escapement given in the European eel regulation is likely to be reached within the next few years. Challenging this perspective with modelled B_{best} values makes the key dilemma of eel management in the Havel River very clear. Without stocking, the target of the eel regulation will not be met due to low natural immigration numbers, even if all anthropogenic mortality factors could be stopped completely. On the other hand, uncertainties regarding stocking and its net effects on this panmictic species at the species level have been raised (ICES, 2012). Our results are not sufficient to demonstrate whether such a net benefit for the European eel stock as a whole has been achieved under the Havel River stocking programme. However, they provide an estimate of mortality experienced by stocked eel in a freshwater tributary until spawning migration. In a next step, mortality rates during glass eel fisheries for stocking material, transport, and silver eel downstream migration to sea need to be quantified. These accompaniments will allow for a comparison with total mortality rates experienced by natural recruits left untouched in areas where glass eel fishing for stocking material is commenced.

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