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Escapement success of silver eels from a German river system is low compared to management-based estimates

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SUMMARY

1. The European eel (*Anguilla anguilla*) stock experienced a sharp decline during the last decades and is suffering from massive anthropogenic impacts on inland waters. To evaluate the benefit of management measures and to better understand the contribution of single drainage systems to spawner production, knowledge of the respective silver eel escapement is required. Furthermore, a better understanding of environmental conditions that potentially trigger the onset of spawning migration is needed to reduce anthropogenic mortalities during riverine eel migration. Investigations are also necessary to clarify whether fish protecting devices and bypasses at barriers are functional and truly increase eel survival and escapement rates.
2. In this study, total female silver eel escapement from a northern German drainage system (Schwentine River) was assessed over a period of three consecutive years, and downstream migration patterns were compared to potential environmental triggers. Furthermore, the benefit of two fish bypasses (surface and deep) and a trash rack at the hydropower station for the survival of migrating eels was examined, and the spawner quality of escaping silver eels was determined by analysing lipid content and infection intensities with the swimbladder parasite *Anguillicoloides crassus*.
3. The results indicate that silver eel escapement from the Schwentine drainage system is far below the estimated values underlying the respective eel management plan, highlighting the necessity of direct migration assessments to validate indirect estimations that include multiple assumptions and uncertainties. Major downstream migration events took place during short time periods in autumn and appear to be influenced by river discharge and water temperatures, suggesting that a precise prediction of escapement events is possible. Regarding spawner quality, fat reserves appear sufficient for escaping silver eels to migrate and spawn. However, high *A. crassus* prevalence and infection intensities are assumed to further reduce the number of potential spawners. Another matter of concern is the high trash rack mortality at the hydropower station that illustrates the need of fish protecting devices that fulfil eel-specific requirements.

Keywords: *Anguilla anguilla*, eel quality, management, silver eel escapement, trash rack mortality

Introduction

Human impacts on European river systems have increased during the 20th century and reached levels that threaten many riverine species and fisheries. Diadromous species such as European eel (*Anguilla anguilla*, Linnaeus 1758) are specifically affected by the severe modification, deterioration and fragmentation of habitats. The strong decline in eel recruitment since the 1980s and the currently observed low stock size (ICES, 2012) are considered to be caused by a combination of reduced habitat quality, river discontinuity, high fishing mortality and possible climatic changes (Knights, 2003; ICES, 2006; Belpaire *et al.*, 2009). The European Commission recognised the increase in silver eel escapement from fresh waters as essential for a stock recovery and

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changed its legislation accordingly. European member states must now implement management measures that guarantee the escapement of silver eels from river basins to 40% of the best estimated number of eels that would have escaped under pristine conditions (EU, 2007).

To evaluate the benefit of specific management measures, a quantitative assessment of silver eel escapement from inland waters is crucial. Since a direct monitoring of migrating eels is methodologically challenging, silver eel escapement is usually assessed by modelling (e.g. Aprahamian *et al.*, 2007) or by semi-quantitative estimations based on mark–recapture studies (e.g. Feunteun *et al.*, 2000; Verbiest *et al.*, 2012). However, such methods include multiple assumptions and uncertainties. For example, model approaches depend on the quality of input parameters and are prone to differences of river-specific characteristics (e.g. growth rate, fraction of silver eels per length class), while mark–recapture studies include a handling procedure, which might influence the behaviour and catchability of tagged eels and therefore bias the results. Therefore, direct escapement monitoring, despite being labour intensive, provides the only fully reliable way to at least periodically validate the output of indirect estimations.

To improve the escapement success of potential spawners, it is recommended by the International Council for the Exploitation of the Sea (ICES) to reduce all anthropogenic mortalities during silver eel migration to as close to zero as possible (ICES, 2012). This could be facilitated by a precise prediction of downstream migration events, which in most European rivers are severely impacted by migration barriers, especially hydropower stations, causing high mortalities for downstream migrating eels (ICES, 2011). Better knowledge about the timing of escapement events would allow the temporal shutdown of turbines and the closure of silver eel fisheries during well-defined migration periods. A characterisation of environmental conditions that trigger the onset of eel spawning migration could therefore increase silver eel escapement from inland waters considerably and help to accomplish management goals.

Once silver eels have successfully escaped from rivers, they must migrate another 5000–7000 km to reach their spawning ground in the Sargasso Sea. This migration requires the ability for long-term swimming, which is assumed to be impaired by the disturbance of fat accumulation (Van den Thillart, Palstra & van Ginneken, 2007; Belpaire *et al.*, 2009) and the infection with the introduced swimbladder nematode *Anguillicoloides crassus*, Kuwahara, Niimi & Itagaki 1974. *A. crassus* was shown to increase the energy demand of migrating eels, adversely affecting long-term swimming ability (Sprengel & Lüchtenberg, 1991; Palstra *et al.*, 2007). The parasite is thought to be one of the major threats for the European eel stock by further reducing its effective spawning size. Fat content and *A. crassus* load should therefore be considered when estimating the spawner production of a river system.

In this study, the total number of escaping female silver eels from a northern German river system (Schwentine River) was directly assessed during three consecutive years in order to (i) determine the total production of potential spawners within this exemplary drainage system, (ii) compare these empirical data with the estimated escapement numbers that underlie the respective management plan and (iii) detect the environmental parameters triggering the onset of silver eel runs. In addition, the passability of a hydropower station was determined and migrating silver eels were investigated for individual fitness parameters to evaluate the quality of the drainage system for eel spawner production.

Methods

Study area and sampling station

The Schwentine River has a length of 62 km from the source to the mouth and drains into the western Baltic Sea (Fig. 1). The river system consists of two mayor river arms including a lake district and has a water surface of approximately 7500 ha. Two hydropower stations have operated in the lower reaches of the river since the beginning of the 20th century. The uppermost hydropower station (HPS 2) is located approximately 9 km upstream the river mouth and was made passable for up- and downstream migrating fish by the installation of bypasses (Figs 1 & 2). Downstream migrating fish can only pass the HPS 2 via a helix bypass with a surface entrance or a deep bypass at bottom level with a 300-mm-diameter opening. In front of the turbines, a trash rack is mounted to prevent fish and debris from entering. It has a light spacing of 20 mm and is equipped with an automatic debris cleaner that transports attached debris into a container. To ensure the catch of all downstream migrating silver eels, both bypasses were completely blocked by traps. Traps and the container were checked for eels on a regular basis, but at least twice per week.

The HPS 2 is further equipped with a flap gate that can be opened to regulate the water level in the reservoir and downstream the HPS 2 (Fig. 2). During spillage periods, a complete detection of downstream migrating

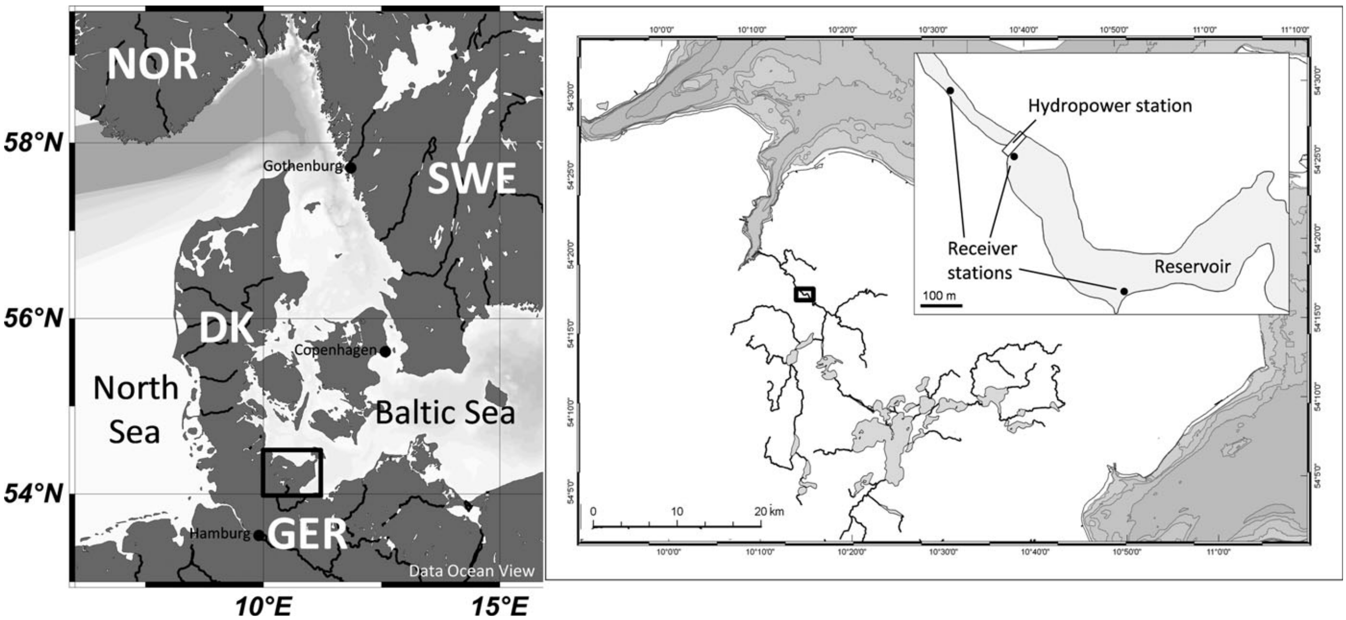

Fig. 1 Large scale map of the sampling area (left) and an overview of the Schwentine River system (right). The detailed map (top right) indicates the positions of the hydropower station and receivers.

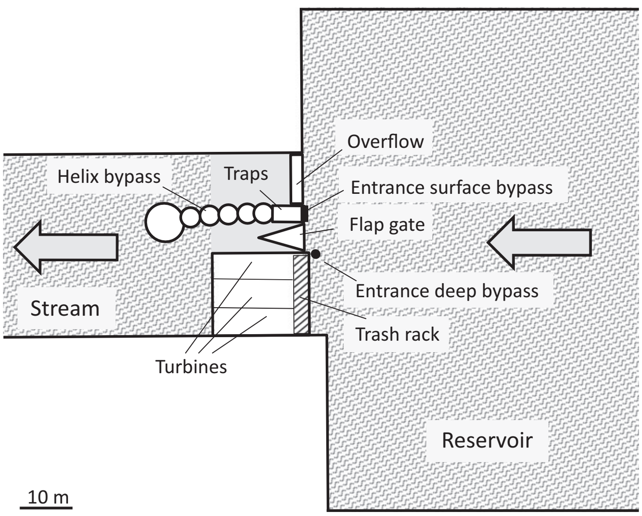

Fig. 2 Schematic overview of the hydropower station. The helix bypass is entered through the surface entrance and completely blocked at its upper end by a fish trap. Eels that entered the deep bypass were caught in an additional trap (not indicated). The trash rack is mounted in front of the turbines and prevents fish and debris from inflowing. Arrows indicate river flow.

eels was not possible. To correct for the number of eels that were able to pass through the open flap gate and to estimate the escapement numbers accordingly, 36 migrating female silver eels (length 70.6–97.5 cm; weight 586–1595 g) caught in the bypass at HPS 2 were tagged between September 2011 and January 2012 with implanted active transponders [Acoustic Transmitter Tags (V9; VEMCO, Canada)] and released the day after catch directly upstream of HPS 2. Three VR2W monitoring receivers (VEMCO, Canada) were installed to detect the movements of tagged individuals. Two receivers were placed in the water reservoir upstream the HPS 2 and one approximately 200 m downstream the hydropower dam (Fig. 1). Receivers were active for 271 days, while the minimum battery life of the transmitters as indicated by the manufacturer was 153 days. During a 26-day period of uncontrolled water spillage through the open flag gate, seven tagged individuals escaped via the flap gate, while only one tagged specimen was caught in the fish pass traps. Accordingly, the number of eels caught in periods of open flap gate was multiplied by seven. All other tagged specimens moved upstream after being tagged ($N = 12$), remained in the reservoir ($N = 7$) or were caught in the bypass while the flap gate was closed ($N = 7$). Only the fate of two individuals is unknown.

Silver eel sampling

Downstream migrating female silver eels were sampled throughout three consecutive years at the HPS 2. Escapement was defined as the sum of all silver eels that were either caught in the bypass-traps or that were killed at the trash rack. Each eel caught was weighed and photographed for subsequent length measurements using Image Tool 3.0 (UT Health Science Center, San Antonio, TX, U.S.A.). If eels were frozen prior to measurements, lengths and weights were corrected for reduction according to Wickström (1986). Eye diameter and pectoral fin lengths were measured to the nearest 0.1 mm to assign individuals to one of the six maturity stages according to the classification of Durif, Dufour & Elie (2005). Female eels assigned to the maturity stages IV and V were considered to be migrating and were therefore included in the escapement census. A total of 228 female silver eels (16.8% of all escapees) was sacrificed for further analyses.

Analysis of environmental factors

Surface water temperatures were measured by a TidbiT v2 data logger (Onset, Bourne, MA, U.S.A.) in the bypass of HPS 2. Temperature records started on 20 February 2009. Therefore, only mean annual temperatures between 20 February and 31 December were compared between years. Durif & Elie (2008) and Vøllestad *et al.* (1986) reported that summer temperatures influence the onset of migration. Therefore, average temperatures from 1 July until 31 August were also compared between years.

River discharge was assessed on a daily basis at a discharge site approximately 9 km upstream the HPS 2 and was compared between years. According to Vøllestad *et al.* (1986), increased river discharge between August and October results in an earlier onset of migration. Therefore, average river discharge from 1 August until 31 October was also compared between years.

Individual spawner quality parameters

Fat analysis. Total lipid content of 79 silver eels was determined following the slightly modified protocol of Smedes (1999). Approximately 50 g of bone free white muscle tissue and skin from a cross section in front of the anus was homogenised. A subsample of 5 g of the homogenate was taken and further shred for two minutes by an ultra turrax (IKA, Staufen, Germany) in an isopropanol/cyclohexan (16 : 20) solution (Carl Roth; Karlsruhe, Germany) and distilled water (20 mL). After centrifugation (at 760 *g* for 5 min), the organic phase was removed. The procedure was repeated with the aqueous phase using a 13% solution of isopropanol in cyclohexan, and the supernatant was added to the organic phase from the first centrifuge process and reduced in a rotary evaporator. After one hour in a drying cabinet at 105 °C and another 24 h in a desiccator, the lipid content was determined gravimetrically and expressed as per cent of tissue weight.

Anguillicoloides crassus infestation. *Anguillicoloides crassus* infection intensities were determined in swimbladders of 118 silver eels. *A. crassus* specimens were counted macroscopically in a sodium chloride solution. Swimbladder damage of 96 silver eels was assessed following the classification key of Hartmann (1993), which ranges from no visible damage (class 1) to heavily thickened walls, reduced lumina and no gas content (class 5).

Species identification. The uncontrolled trade with eels for aquaculture and restocking purposes caused the introduction of considerable numbers of American eels (*Anguilla rostrata*, Le Sueur 1817) into European waters (Frankowski *et al.*, 2009). In order to assess the amount of *A. rostrata* in the Schwentine River and estimate its potential influence on the results of this study, genetic species identification was conducted on mitochondrial cytochrome b and 18S rDNA gene fragments of 142 silver eels. The method of Frankowski & Bastrop (2010) was modified as described by Prigge, Marohn & Hanel (2013a).

Statistical analysis

Statistica 8.0 (StatSoft Inc., Tulsa, OK, U.S.A.) and R statistical language (version 2.15.1) were used for statistical analysis. Cumulative numbers of escaping silver eels per calendar week were used, and regression analyses were performed to test for correlations between silver eel escapement and date and weekly means of water discharge and water temperature. Analysis of variances (ANOVA) and Kruskal–Wallis test were used to test for differences in downstream migration between four moon phases and for yearly differences in water temperature (daily mean) and in river discharge (daily mean). Furthermore, a Kruskal–Wallis test tested for differences in summer temperatures (July–August) and in early autumn river discharges (August–October) between years. A significance level of $P = 0.05$ was applied to all tests.

Results

Silver eel escapement

The flap gate was open for 50 days in 2009, 61 days in 2010 and 27 days in 2011 (Fig. 3). As a result of the telemetry study (see Methods), observed escapement numbers during these periods were multiplied by seven in order to prevent an underestimation of annual silver eel migration. After this correction, annual female silver eel downstream migration accounted for 133 specimens

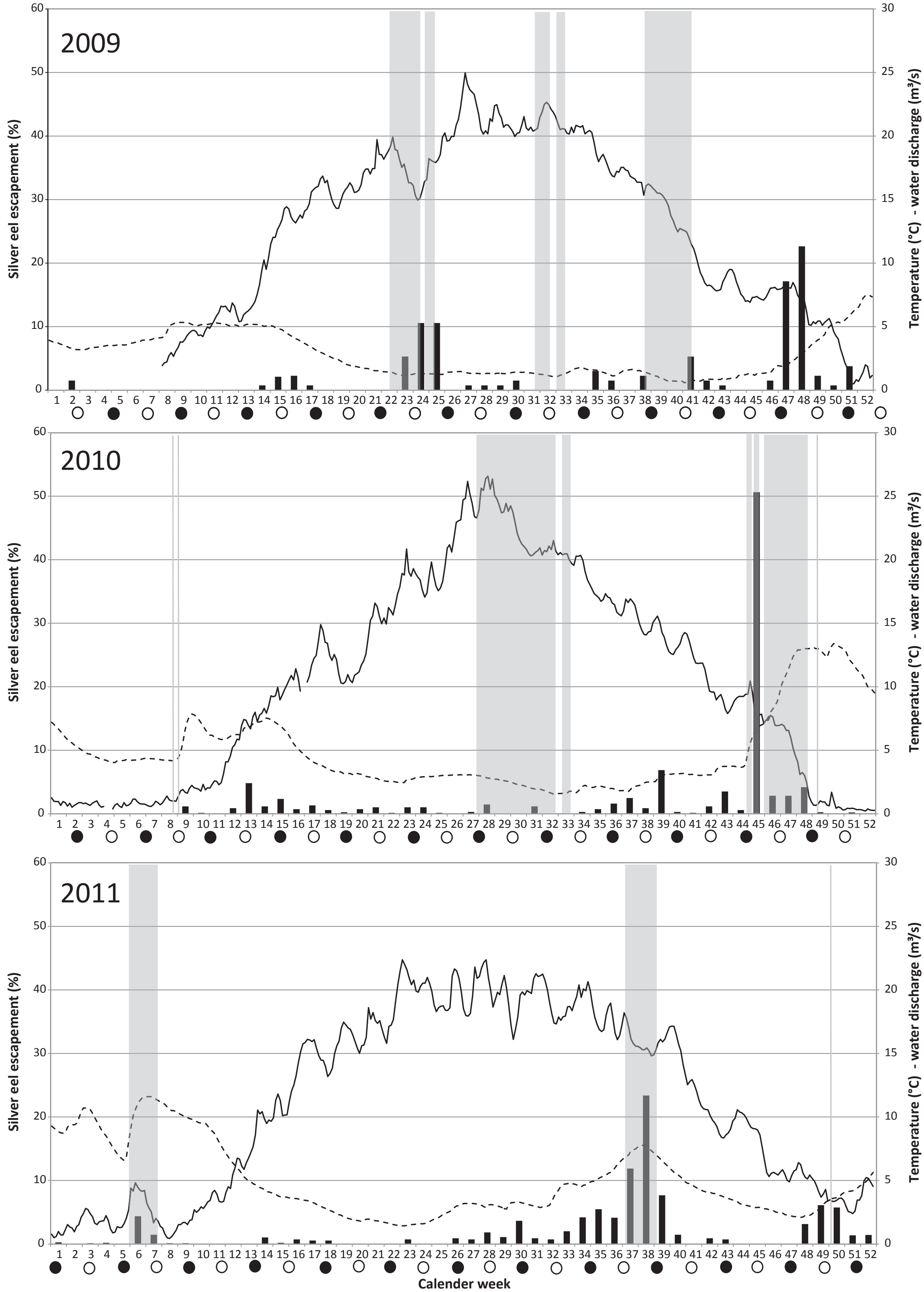

Fig. 3 Corrected silver eel escapement during the years 2009–2011. Black bars represent per cent of the annual silver eel escapement. Solid lines depict water temperature and dashed lines river discharge. Grey areas and vertical lines represent time periods when the flap gate was open. Moon phase is indicated by symbols (● = new moon and ○ = full moon).

in 2009 (144 kg; 0.02 kg ha^{-1} year^{-1}), 683 in 2010 (691 kg; 0.09 kg ha^{-1} year^{-1}) and 544 in 2011 (577 kg; 0.08 kg ha^{-1} year^{-1}; Table 1).

67.1% of these eels used the deep bypass, while only 0.7% entered the surface bypass (Table 1). The remaining 32.2% were impinged on the trash rack at the turbine entrance and either died through the high pressure caused by the strong water current or after being captured by the automatic debris cleaner. The high fraction of trash rack mortality was mainly caused by two rather confined escapement events in November 2010 and December 2011 during which the majority of all escaping silver eels was impinged on the trash rack (77% and 70%, respectively). During the remaining sampling period, trash rack mortality remained low.

Analysis of environmental factors

Silver eel escapement was highest during autumn, but varied widely in strength and timing among years. Regression analysis revealed a seasonal influence (calendar week) on silver eel downstream migration ($P = 0.011$) with an increase in escapement over the year (Table 1, Fig. 3). However, higher numbers later in the year were caused by temporally confined, single migration events in autumn, but not by a steady increase during the year. In 2009, 39.8% of all escaping silver eels migrated during two weeks at the end of November, and in 2010 50.6% of the annual silver eel run migrated during one week in mid-November. In 2011, migration peaks were less distinct. 56.8% of annual escapement happened during a six weeks period from end of August until the end of September, while 15.8% escaped during a second migration peak from November until early December (Table 1, Fig. 3).

River discharge from the Schwentine River varied significantly between years, with values in 2009 being significantly lower than in 2010 and 2011 [H (2,156) = 25.99; $P = 0.000$]. Early autumn runoff was increased in 2011 compared with 2009 and 2010 [H (2,276) = 230.5; $P = 0.000$]. River discharge had a significant effect on silver eel escapement ($P = 0.047$), with highest migration numbers during times of increased water discharge.

In contrast, no significant correlation of escapement and water temperature was detected ($P = 0.852$) and mean annual water temperatures did not differ among years [F (2,851) = 1.216, $P = 0.297$]. However, temperatures from 1 July to 31 August varied significantly between years (H (2,186) = 47.6; $P = 0.000$) and averaged 21.2 °C (SD ± 1.2), 21.8 °C (SD ± 2.6) and 19.3 °C (SD ± 1.4) from 2009 to 2011, respectively.

The four moon phases had no detectable influence on silver eel migration ($P = 0.913$).

Individual silver eel fitness

Fat content ranged from 21.6% to 36.1% and averaged 27.3% (SD ± 3.0). Prevalence of *A. crassus* infection was 79.9% and 21.4% of all analysed eels had infection intensities above ten nematodes per host and were considered to be severely infected. Most specimens showed visible but moderate swimbladder damages (Hartmann class 2 and 3; 89.2%), whereas 4.3% were classified as severely damaged (Hartmann class 4; Hartmann, 1993). Only 6.5% were unaffected (Hartmann class 1). 73.3% of all nematode-free swimbladders showed signs of earlier infections.

Seven of the 142 silver eels analysed were identified as the American eel *A. rostrata* (4.9%). Projecting this proportion to the annual silver eel escapement levels from the Schwentine River produces estimates of 7, 33 and 27 *A. rostrata* in 2009, 2010 and 2011, respectively. These numbers are assumed to be too low to bias the results presented here.

Table 1 Silver eel escapement from the Schwentine River per year and quarter and the fraction of eels that used the provided bypasses or were impinged on the trash rack. The numbers of eels from total escapement that are estimated to have passed via the open spill gate are given in parenthesis

	2009	2010	2011	Mean (±SD)	Total
Total escapement (*N*)	133 (36)	683 (171)	544 (225)	453 ± 286	1360
Total escapement (kg)	144	691	577	471 ± 288	1412
Total escapement (kg ha^{-1})	0.02	0.09	0.08	0.06 ± 0.04	–
1st quarter (% of annual escapement)	1.5	7.0	6.7	5.1 ± 3.1	–
2nd quarter (% of annual escapement)	32.3	10.5	4.7	15.8 ± 14.6	–
3rd quarter (% of annual escapement)	10.6	15.8	67.7	31.4 ± 31.6	–
4th quarter (% of annual escapement)	55.6	66.7	20.9	47.7 ± 23.9	–
Surface bypass	–	–	–	–	0.7%
Bottom bypass	–	–	–	–	67.1%
Trash rack	–	–	–	–	32.2%

Discussion

This study provides a precise assessment of the Schwentine River's contribution to spawner production and highlights the importance of direct escapement assessments for the validation of indirect estimations. Observed annual silver eel escapement from the Schwentine River system is far below values underlying the German Eel Management Plan (EMP). The EMP estimates the annual escapement from all fresh waters of the entire river basin district Schlei/Trave (which includes also the Schwentine River system) to account for 66 t (Anonymous, 2008). Given a water surface area of 23 029 ha, this results in an estimated annual escapement of 2.87 kg ha^{-1}. The observed escapement levels for the Schwentine system range from 0.02 to 0.09 kg ha^{-1} year^{-1} corresponding to about 1–3% of the values estimated in the EMP.

The escapement calculation in the EMP is based on catch and restocking data and includes estimations of turbine mortality and cormorant predation. Since the availability of eel data is usually poor, it must be considered that some estimates in the EMP are rather rough and might have caused an overestimation of escapement numbers. Only if river-specific biological parameters (e.g. growth rate, age at maturity), mortality factors and recruitment numbers are carefully assessed the use of adequate models can result in realistic escapement estimations (Prigge *et al.*, 2013b).

This study highlights the urgent need for carefully assessed river-specific data to improve the quality of estimations. Obviously, such an effort is hardly being put throughout the entire distribution area of *A. anguilla*, and the use of generalised data and their transfer between rivers raises concern. Therefore, in future assessments, the direct monitoring of migrating silver eels should at least sporadically be considered to validate the order of magnitude of escapement estimations. This would help to avoid false interpretations, which might overestimate the current stock situation and counteract efforts for the restoration of the European eel stock.

This study also indicates that an enforcement of temporal closures of fisheries and shutdowns of hydropower stations during well-defined periods in autumn could reduce silver eel mortality during downstream migration considerably. River discharge and water temperature seem to provide feasible indicators to determine the onset of migration and could help to predict periods of increased silver eel migration. Highest migration activity was detected between August and December which corresponds to the general observation of main silver eel downstream migration in autumn (Vøllestad *et al.*, 1986; Tesch, 1999; Haro, 2003). However, timing and intensities of escapement events differed between years. Such inter-annual variations were also observed by Durif & Elie (2008) and Vøllestad *et al.* (1986), suggesting variations in the onset of downstream migration being explained with differences in summer temperatures and river discharge. These assumptions are supported by the results presented for the Schwentine River, where early downstream migration activity coincides with lower water temperatures in summer and higher river discharge in early autumn. Although a direct relationship of water temperature and silver eel escapement was not detectable over the years, these findings suggest that temperature is among the factors influencing eel migration. Nevertheless, the most important trigger for the onset of migration appears to be river discharge. Every observed migration event during the three-year monitoring period was accompanied by an increase in river discharge and indicates its importance as a trigger for the onset of silver eel migration. In contrast, no influence of moon phase on migration activity was observed. Although light conditions might be of interest when predicting eel downstream migration (Tesch, 1999; Haro, 2003; Davidsen *et al.*, 2011), lunar periodicity alone seems to be of minor importance. The results presented here indicate that a careful observation of summer water temperatures and autumn river discharge could suffice to determine periods of high downstream migration activity of silver eels and help reduce anthropogenic mortalities during this crucial life phase.

It was previously reported from experimental and field studies that eels with a total length below 70 cm are able to pass 20 mm trash racks (Adam, 1998; Calles *et al.*, 2010). Hence, in the present study, a non-detection of small silver eels could have caused an underestimation of the number of migrating eels. However, in representative landing data of fishers from the Schwentine River only about 13% of eels are below 70 cm and catch data from the German Data Collection Framework indicate that only 23% of eels with a body length below 70 cm are silver (J.D. Pohlmann & M. Freese, unpublished data). It can therefore be assumed that the quantitative assessment of small female silver eels would not have increased the monitored escapement numbers considerably. In any case, trash rack spacings were too wide for a quantitative monitoring of male silver eels, which only reach maximum sizes of about 46 cm (Tesch, 1999). But as only 25% of all sampled eels from the Schwentine River with a total length below 47 cm were identified as males, the system appears to be female dominated. This assumption is supported by the observation that temperate latitudes support the development of female eels (Wickström, Westin & Clevestam, 1996; ICES, 2010). The non-detection of downstream migrating male eels is therefore considered to only moderately bias the results.

It was striking that despite the provision of bypasses a significant number of migrating eels was impinged on the trash rack and died. However, high trash rack mortalities exclusively occurred in autumn and seem to be caused by a combination of low water temperatures, increased river discharge and large amounts of incoming floating debris, which predominantly consisted of foliage. The foliage covered large areas of the trash rack and might have substantially increased contact pressure at debris free areas. The combination of low water temperature and high contact pressure could have reduced the ability of eels to elude the trash rack and led to high mortalities. Accordingly, European eel stock management should ensure that fish protecting devices at barriers are adjusted to eel-specific requirements to minimise mortalities and migration disturbances at barriers. As already reported by Calles *et al.* (2010), the repulsive effect of trash racks does not prevent eels from being impinged. Trash racks need to be modified in order to divert eels to suitable alternative routes such as bottom bypasses, which must be installed in sufficient numbers to reduce eel mortality at river barriers.

According to literature values (Palstra *et al.*, 2007; Van den Thillart *et al.*, 2007) silver eels from the Schwentine River have sufficient fat reserves for successful migration and reproduction. Nonetheless, high *A. crassus* prevalence is a matter of concern; in almost 80% of all analysed silver eels, the nematode was detected and it can be assumed that the total fraction of infected eels is even higher as a considerable number of empty swimbladders showed effects of previous infections. Severe infection intensities (>10 *A. crassus* per host) were detected in every fifth analysed eel, and it must be considered that these individuals might fail to migrate and reproduce. This is also true for eels that were identified as *A. rostrata* (4.9%). Hence, a considerable fraction of the already low number of escaping eels appears not to be able to successfully participate in reproduction, further reducing the production of spawners in the Schwentine River.

In conclusion, this study clearly demonstrates the discrepancy between aspiration and reality with regard to the estimation of silver eel escapement from the Schwentine river basin. Since the increase in eel escapement is defined as the major target for the European eel regulation, a quantitative assessment is crucial to evaluate the success of implemented management measures, while estimates should be conducted with special diligence. The findings of this study further support the view that the appropriate modification of fish protecting devices and the prediction of the likely timing of large escapement events in relation to environmental conditions such as river discharge and temperature would help to considerably reduce anthropogenic mortalities during downstream migration of silver eels.

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References

Adam B. (1998) Aalabwanderung – Ergebnisse von Versuchen in Modellgerinnen. In: *Durchgängigkeit von Fließgewässern für stromabwärts wandernde Fische* (Ed. M. Lukowski), pp. 37–68. Deutscher Fischerei-Verband E. V., Hamburg.

Anonymous (2008) Aalbewirtschaftungspläne der deutschen Länder zur Umsetzung der EG -Verordnung Nr. 1100/2007 des Rates vom 18. September 2007 mit Maßnahmen zur Wiederauffüllung des Bestands des Europäischen Aals für die Flusseinzugsgebiete Eider, Elbe, Ems, Maas, Oder, Rhein, Schlei/Trave, Warnow/Peene und Weser. www.portal-fischerei.de.

Aprahamian M.W., Walker A.M., Williams B., Bark A. & Knights B. (2007) On the application of models of European eel (*Anguilla anguilla*) production and escapement to the development of Eel Management Plans: the River Severn. *ICES Journal of Marine Science*, **64**, 1472–1482.

Belpaire C.G.J., Goemans G., Geeraerts C., Quataert P., Parmentier K., Hagel P. *et al.* (2009) Decreasing eel stocks: survival of the fattest? *Ecology of Freshwater Fish*, **18**, 197–214.

Calles O., Olsson I.C., Comoglio C., Kemp P.S., Blunden L., Schmitz M. *et al.* (2010) Size-dependent mortality of migratory silver eels at a hydropower plant, and implications for escapement to the sea. *Freshwater Biology*, **55**, 2167–2180.

Davidsen J.G., Finstad B., Økland F., Thorstad E.B., Mo T.A. & Rikardsen A.H. (2011) Early marine migration of European silver eel *Anguilla anguilla* in northern Norway. *Journal of Fish Biology*, **78**, 1390–1404.

Durif C., Dufour S. & Elie P. (2005) The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, **66**, 1025–1043.

Durif C. & Elie P. (2008) Predicting downstream migration of silver eels in a large river catchment based on commercial fishery data Fisheries Management and Ecology. *Fisheries Management and Ecology*, **15**, 127–137.

EU (2007) Council Regulation (EC) No 1100 / 2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official Journal of the European Union L*, **248**, 17–22.

Feunteun E., Acou A., Laffaille P. & Legault A. (2000) European eel (*Anguilla anguilla*): prediction of spawner escapement from continental population parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1627–1635.

Frankowski J. & Bastrop R. (2010) Identification of *Anguilla anguilla* (L.) and *Anguilla rostrata* (Le Sueur) and their hybrids based on a diagnostic single nucleotide polymorphism in nuclear 18S rDNA. *Molecular Ecology Resources*, **10**, 173–176.

Frankowski J., Jennerich S., Schaarschmidt T., Ubl C., Jürss K. & Bastrop R. (2009) Validation of the occurrence of the American eel *Anguilla rostrata* (Le Sueur, 1817) in free-draining European inland waters. *Biological Invasions*, **11**, 1301–1309.

Haro A. (2003) Downstream migration of silver-phase anguillid eels. In: *Eel Biology* (Eds K. Aida, K. Tsukamoto & K. Yamauchi), pp. 215–221. Springer-Verlag, Tokyo.

Hartmann F. (1993) *Untersuchungen zur Biologie, Epidemiologie und Schadwirkung von* Anguillicola crassus *Kuwahara, Niimi und Itagaki 1974* (*Nematoda*)*, einem blutsaugenden Parasiten in der Schwimmblase des europäischen Aals* (Anguilla anguilla *L.*). 1st edn. Shaker Verlag, Aachen.

ICES (2006) Report of the 2006 session of the Joint EIFAC/ ICES Working Group on Eels. CM2006/ACFM, 16, 352pp.

ICES (2010) Report of the Workshop on Baltic Eel (WKBALTEEL), 2–4 November 2010, Stockholm, Sweden. ICES CM 2010/ACOM:59.

ICES (2011) Report of the 2011 session of the Joint EIFAC/ ICES Working Group on Eels. CM2011/ACOM, 18, 246pp.

ICES (2012) Report of the 2012 session of the Joint EIFAC/ ICES Working Group on Eels. CM2012/ACOM, 18, 824pp.

Knights B. (2003) A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. *Science of the Total Environment*, **310**, 237–244.

Palstra A.P., Heppener D.F.M., van Ginneken V.J.T., Szekely C. & van den Thillart G.E.E.J.M. (2007) Swimming performance of silver eels is severely impaired by the swimbladder parasite *Anguillicola crassus*. *Journal of Experimental Marine Biology and Ecology*, **352**, 244–256.

Prigge E., Marohn L. & Hanel R. (2013a) Tracking the migration success of stocked European eels (*Anguilla anguilla*) in the Baltic Sea. *Journal of Fish Biology* **82**, 686–699.

Prigge E., Marohn L., Oeberst R. & Hanel R. (2013b) Model prediction vs. reality—testing the predictions of a European eel (*Anguilla anguilla*) stock dynamics model against the *in situ* observation of silver eel escapement in compliance with the European eel regulation. *ICES Journal of Marine Science* **70**, 309–318.

Smedes F. (1999) Determination of total lipid using non-chlorinated solvents. *Analyst*, **124**, 1711–1718.

Sprengel G. & Lüchtenberg H. (1991) Infection by endoparasites reduces maximum swimming speed of European smelt *Osmerus eperlanus* and European eel *Anguilla anguilla*. *Diseases of Aquatic Organisms*, **11**, 31–35.

Tesch F.W. (1999) *Der Aal*, 3rd edn. Blackwell Wissenschaftsverlag, Berlin.

Van den Thillart G., Palstra A.P. & van Ginneken V. (2007) Simulated migration of European silver eel; swim capacity and cost of transport. *Journal of Marine Science and Technology*, **15**, 1–16.

Verbiest H., Breukelaar A., Ovidio M., Philippart J.C. & Belpaire C. (2012) Escapement success and patterns of downstream migration of female silver eel *Anguilla anguilla* in the *River Meuse*. *Ecology of Freshwater Fish*, **21**, 395–403.

Vøllestad L.A., Jonsson B., Hvidsten N.A., Næsje T.F., Haraldstad Ø. & Ruud-Hansen J. (1986) Environmental factors regulation the seaward migration of European silver eels (*Anguilla anguilla*). *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1909–1916.

Wickström H. (1986) Studies on the European eel by the Institute of Freshwater Research 1977–85. Information fran Soetvattenslaboratoriet, Drottningholm 13

Wickström H., Westin L. & Clevestam P. (1996) The biological and economic yield from a long-term eel-stocking experiment. *Ecology of Freshwater Fish*, **5**, 140–147.

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