Just go with the flow? Route selection and mortality during downstream migration of silver eels in relation to river discharge

Henrice M. Jansen, Hendrik V. Winter, Maarten C. M. Bruijs, and Harry J. G. Polman

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The European eel (*Anguilla anguilla*) has been in steep decline for several decades. Fisheries and hydropower-induced mortality presumably play an important role during the downstream migration of silver eels, and downstream-migrating silver eels must make various navigation and route-selection decisions to reach the sea. We examined the influence of river discharge on route selection of silver eels. To quantify the impact of hydropower and fisheries on silver eel mortality, radio-telemetry experiments were performed in the River Meuse in 2002 and 2004, surgically implanting 300 silver eels with Nedap-transponders. Route selection and passage behaviour near detection stations was assessed. Silver eels were distributed over the alternative migration routes in the river in proportion to the discharge until the silver eels reached the entrance to the turbines. The eels altered their behaviour when approaching the turbines of hydropower plants and showed stationary and recurrent behaviour. We discuss the consequences of this on route selection and mortality rates caused by hydropower facilities and fisheries.

Keywords: fisheries, hydropower, individual eel behaviour, migration, radio telemetry, river discharge, route selection, silver eels.

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H. M. Jansen and H. V. Winter: Institute for Marine Resources and Ecosystem Studies (IMARES), Wageningen UR, PO Box 68, 1970AB IJmuiden, The Netherlands. M. C. M. Bruijs and H. J. G. Polman: KEMA Technical and Operational Services, Utrechtseweg 310, 6812 AR Arnhem, The Netherlands. Correspondence to H. M. Jansen: tel: +31 255 45646; fax: +31 255 56644; e-mail: henrice.jansen@wur.nl

Introduction

The European eel (*Anguilla anguilla*) has been in steep decline for several decades (Dekker, 2004). Many candidate factors affecting different life stages have been proposed, but the relative contribution of each to this decline remains unclear (Feunteun, 2002; Wirth and Bernatchez, 2003; Dekker, 2004). Fisheries and hydropower may cause substantial mortality during the downstream migration of silver eels (Winter *et al.*, 2006, 2007), reducing the number of spawners returning to the sea and hence to the spawning grounds.

The downstream migration of silver eels is time-dependent and generally takes places during autumn, although the exact onset of migration varies between years, depending on the environmental triggers (Vollestad *et al.*, 1986; Boubee *et al.*, 2001; Okamura *et al.*, 2002; Durif *et al.*, 2003; Cullen and McCarthy, 2005; Boubee and Williams, 2006). When migrating downstream, silver eels may opt for different pathways or routes to sea, especially in rivers containing man-made structures such as dams, sluices, shipping locks, fishways, and canals, and mortality rates may differ between the alternative routes. This is most obvious at hydropower stations (HPSs), where silver eels can pass through turbines, overspill water at dams or weirs, or through a fishway. The factors affecting route selection of downstream-migrating silver eels are poorly known. We hypothesize that river discharge may determine the choice of silver eels for alternative migration routes, as has been demonstrated for salmonid smolts (Kemp *et al.*, 2005). By radio telemetry, we investigated whether route selection of downstream-migrating silver eels in the River Meuse is proportional to the discharge through each alternative route, and what the consequences of route selection would be for overall rates of mortality attributable to HPSs and fishing.

Fish confronted with man-made obstructions might change their behaviour. Salmon smolts move back and forth as they approach dams, apparently searching for a surface outlet (Giorgi *et al.*, 1988), and Behrmann-Godel and Echmann (2003) observed circling behaviour of silver eels approaching a hydroelectric power dam. The latter may lead to more complex route selection by downstream-migrating silver eels near man-made obstructions. We examined silver eel behaviour near hydropower stations (HPSs) and its consequences for route selection.

Material and methods

Study area and telemetry

Two HPSs are located in the Dutch part of the River Meuse (HPS1 and HPS2; Figure 1). The river splits into two major branches in the downstream area: Haringvliet and Nieuwe Waterweg. Water discharge by the river is characterized by high annual variability in timing and amplitude, typical of a rain-fed river. The river level is much influenced by the amount of discharge in the drainage area, increasing quickly after heavy rain and water flow being severely restricted during dry periods. Downstream-migrating silver eels originating from the River Meuse must make various navigation and route-selection choices to reach the North Sea: (i) at the two HPSs, eels can migrate through the turbines, over the weir, or through the fishway; and (ii) in the downstream part of the river, eels can take two routes to the North Sea. Commercial fisheries for eels in the river operate mainly during the

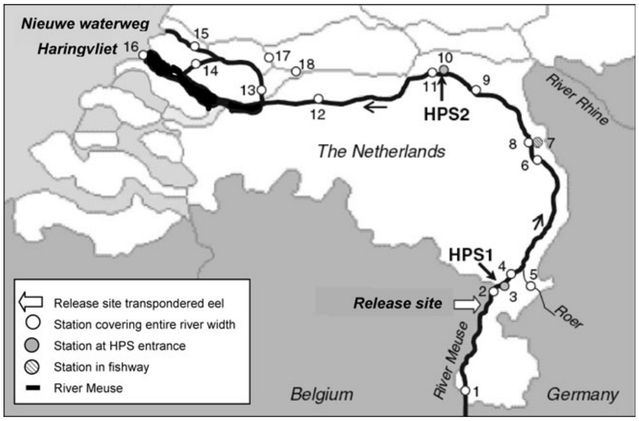

Figure 1. Study area, with the locations of the different detection stations along the course of the Dutch section of River Meuse. The locations of the two HPSs are shown (HPS1 and 2). The small arrows indicate direction of river flow.

period June–November, where in the Dutch part upstream from telemetry detection station 12, electrofishing is common along with a few small fykenets of mesh size 20 mm. At the two locations downstream from HPS1 and HPS2, anchored stownets are used to fish eels, and downstream from detection station 12, large fykenets of mesh size 20 mm are deployed.

Radio-telemetry experiments were performed in the River Meuse in 2002 and 2004 (Winter *et al.*, 2007), when 300 silver eels (76 ± 6.2 cm long) were surgically implanted with Nedap-transponders; 150 in 2002 and 150 in 2004 (for further details on the surgical procedures see Winter *et al.*, 2006). The effects of implanting these transponders in silver eels were tested in a tank experiment during 2001 during the autumn migration period (Winter *et al.*, 2005). There was no significant difference in the mortality or the timing of activity between the group with implanted transponders and the control group, and there was no tag loss. Activity level, though, was somewhat lower than in the control group.

A total of 18 detection stations (Nedap Trail-System®) in the river was used to provide information on the timing of migration and passage behaviour. Time of migration was matched to contemporary river discharge, and 15 of the fixed detection stations covered the entire river width, including the two outlets to the North Sea (Figure 1). In addition, detection stations covered the entrance to the turbines at both HPS1 and HPS2, detecting eels that approached the turbines. Directly downstream of each HPS, a detection station covered the full width of the river. Those eels that were detected at these downstream stations, but not at the station covering the entrance of the turbines, were assumed to have bypassed the HPS over the weir or through the fishway. From telemetry, the mean percentage of misdetections, i.e. eels passing undetected, for all stations was 8.5%, mainly associated with short periods of malfunction that were recorded automatically by the system (Winter *et al.*, 2006). For the four stations downstream and at the entrance of HPS1 and HPS2 during the periods that the timing of passage of silver eels was matched with hydrological conditions, there was no period of malfunction, thus seemingly corroborating our assumption of weir or fishway passage.

Discharge through the different routes

Daily river discharge data were available for the entire period at several locations along the Dutch section of the River Meuse and for both routes to the North Sea (Haringvliet and Nieuwe Waterweg; Figure 1).

Flow rates through the turbines are dependent on HPS management protocols. HPS1 has four, horizontal, Kaplan-bulb turbines, which are switched on/off automatically at certain levels of river discharge (Table 1; Bruijs, 2004). The river flow is distributed equally over the total number of turbines running. Such river flow control rules were used to calculate the division of total river flow between each HPS and its weir per day (Figure 2).

For the period October–December 2004, the actual flow through each turbine of HPS1 was measured, making it possible to validate in practice how accurately the management protocols were carried out. The correlation between the flow measured and calculated through each HPS and its individual turbines is shown in Figure 3. It appears that, using the management protocols, the flow through an HPS on any given day can be predicted accurately from the river discharge ($r^2 = 0.93$, CV = 0.17), whereas the predictive value of river discharge for individual turbine flow is less accurate ($r^2 = 0.48$, CV = 0.28). The distribution of the flow through each HPS over several turbines appears less equal than indicated in the management protocol.

Route selection at hydropower sites and downstream

To examine the hypothesis that the distribution of total river flow over the alternative routes available at a HPS–weir–fishway complex is equal to the distribution of downstream-migrating silver eels over the various routes (i.e. whether they actually go with the flow), we used the timing of passing silver eels and matched this to the flow division over the different routes at that particular time. Because measured flow through the turbines in combination to river discharge was only available for HPS1

Table 1. Management of HPS1 in relation to river discharge (after Bruijs, 2004).

Number of turbines running	River discharge while switching on turbines ($m^3 s^{-1}$)	River discharge while switching off turbines ($m^3 s^{-1}$)	Turbine flow ($m^3 s^{-1}$)	Flow over weir ($m^3 s^{-1}$)	Flow through fishway ($m^3 s^{-1}$)
0	0–30	0–30	0	River flow	0–5
1	30–69.5	30–62.4	River flow/1	0	5
2	69.5–144.4	62.4–102	River flow/2	0	5
3	144.4–158.4	102–144	River flow/3	0	5
4	158.4–500	144–500	River flow/4	0	5
4	500–800	500–800	500/4	River flow–500	5
0	>800	>800	0	River flow	5

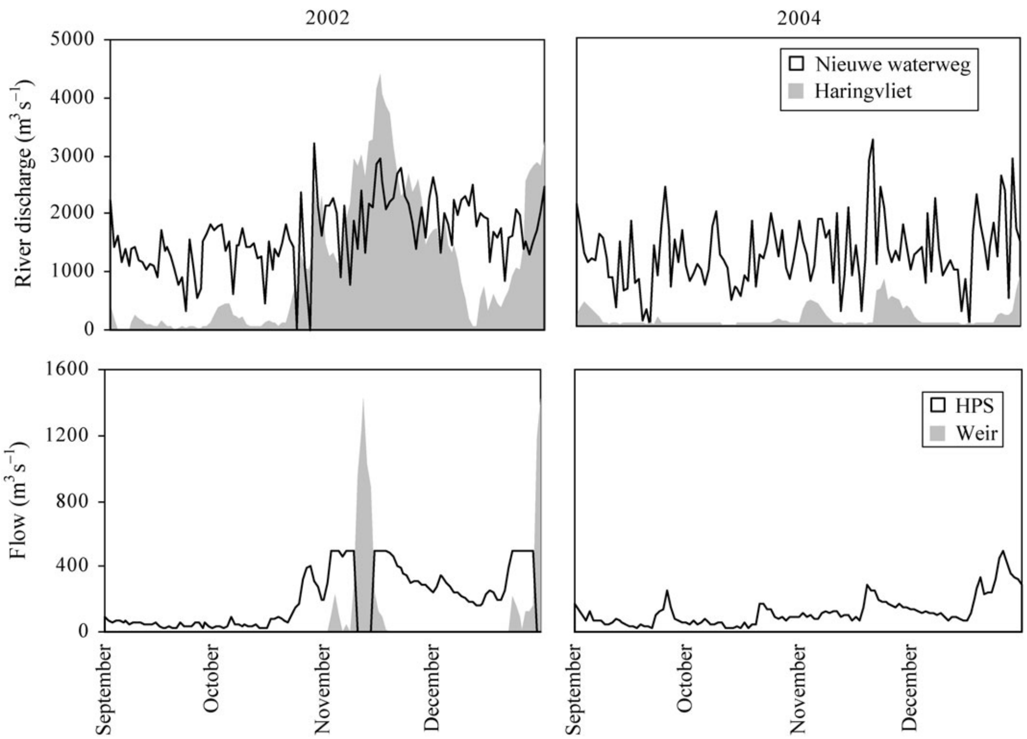

Figure 2. Daily water discharge through the two main migration routes in the downstream area (above) and the daily flow through the HPS1 and over the weir (below) for autumn 2002 and 2004.

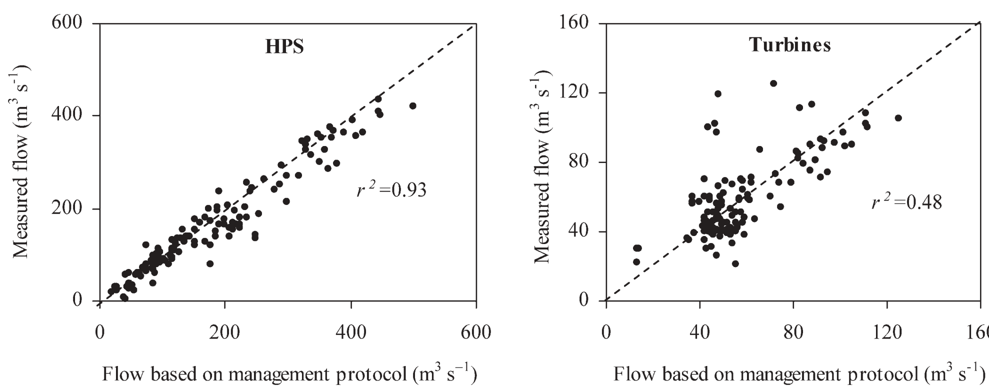

Figure 3. Relationships between flow rates based on river discharge and management protocols and measured flow data through the whole HPS (left) and the average through each turbine (right).

during the period October–December 2004, we used that period and location to match the observed route selection by an eel to the distribution of the flow. From the number of eels detected approaching HPS1 and the number of eels detected directly downstream of the HPS–weir–fishway complex but not at the entrance of HPS1, we calculated the fraction of eels selecting the HPS route and the fractions that must have passed over the weir or through the fishway. This information was then compared with the average fraction of flow through the turbines and that over/through the weir/fishway, as calculated from all flow divisions (the fraction of flow through the HPS and the weir/fishway at the time that each eel was first detected) combined.

The infrastructure of detection stations downstream in the River Meuse allowed us to distinguish between different migration routes used by the silver eels to reach the sea (Figure 1). Because the timing of migration of individual silver eels was not known exactly for the important decision points downstream, flow information could not be linked directly to route selection in the lower section of the river. Comparison between discharge patterns and route selection of silver eels in the downstream area is therefore restricted to a comparison between autumn migration periods in different years.

Fishing and HPS turbine mortality

In the downstream section of the River Meuse, fisheries are mainly performed with large fykenets. In the Dutch section of the river upstream, it is mainly electrofishing, but with fykenets and anchored stownets at two locations, directly downstream of

HPS1 and HPS2. Fishing mortality was estimated from the number of transponders returned by (commercial and recreational) fishers (Winter *et al.*, 2006).

Mortality caused by passage through the HPS was determined in two ways: (i) by radio telemetry, and (ii) by modelling the predicted mortality from turbine flow rates for different lengths of eel (see below). HPS mortality in the Dutch section of the River Meuse is discussed for HPS1, because the required data on turbine flows was available only for that HPS. HPS mortality was assumed for eels detected at the entrance station just upstream from the HPS, but not at the first downstream detection station after the HPS, and that were not recovered by the anchored stownets. It was assumed that all eels detected at the entrance of the HPS would try to pass the turbines. Therefore, only direct mortality by the HPS was recorded.

HPS mortality can also be approximated by a "water-flow-model" based on the number of eels entering the HPS and the mortality rate within the HPS. Hadderingh and Bakker (1998) investigated turbine-related mortality at HPS1 and demonstrated that turbine flow rates correlate with HPS mortality. This is probably because of the relatively small openings between the blades of the guide vanes and the runner blades at low rates of discharge. Bruijs *et al.* (2003) found an inverse relationship between mortality of eels that pass the turbine and turbine flow at HPS1 (Figure 4). Within this relationship, mortality is characterized by:

$$M = 2.8l^{-0.6888}, \quad (1)$$

where M is the percentage of eel losses attributable to HPS mortality, and l the turbine flow, expressed in $m^3\ s^{-1}$ (see Figure 4: 2002 for an average eel length of 64 cm). On the basis of this model, the actual number of eels killed at the HPS is estimated from the relationship between the number detected just in front of the HPS and the approximate rate of mortality based on daily turbine flow rates estimated using the management rules and river discharge time-series. Individual turbine flow, however, was less accurately predicted from river discharge than total HPS flow, which may influence the precision of the mortality rates modelled.

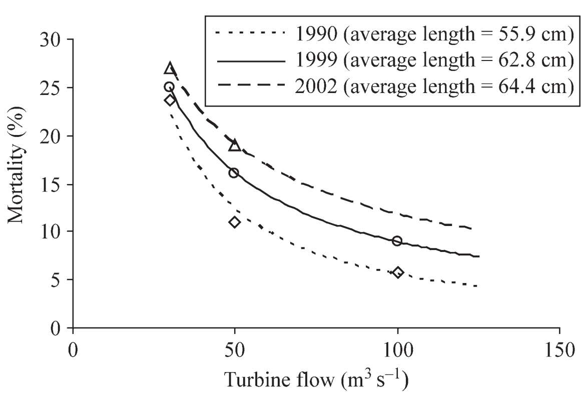

Figure 4. Observed percentage of eel mortality at different turbine flows at Linne HPS, HPS1 (open symbols and the corresponding fitted lines; after Hadderingh and Bakker, 1998; Bruijs *et al.*, 2003).

Eel behaviour

The behaviour of eels was characterized by the number of detections and the time interval between successive detections. In general, detection stations send out interrogation signals, which activate each transponder that passes. The transponder then sends a unique code, which is received by the station. After each signal, the transponder battery switches off automatically for 2 min, to increase the lifetime of the battery. Therefore, the shortest time interval between two successive detections was 2 min. Behavioural patterns of all eels at all detection stations were evaluated. On the basis of the 2-min intervals, we distinguished three types of eel behaviour (see also Figure 5): (i) immediate passage indicated by one or two detections only; (ii) the eel staying near a detection station, yielding a series of detections at 2-min intervals (this pattern is subsequently referred to as "stationary behaviour"); (iii) the eel approaching the turbines, returning upstream and then descending to pass through the turbines, exemplified by a series of detections with intervals exceeding 2 min (this pattern is subsequently referred to as "recurrence behaviour").

Results

Route selection and river discharge at HPS1

During the downstream migration, eels selected both the route via the turbines and that via the weir/fishway to pass the hydropower site. Over the 2 years combined, 181 eels were detected at the entrance of HPS1. Of those, eight were recaptured by fisheries directly downstream and 12 were not recorded again and assumed to have been killed at the HPS. During the 2 years, 205 eels were detected directly downstream of HPS1, meaning that 45 of the 205 eels detected directly downstream of HPS1 were not detected at its entrance. We assumed that these eels should have passed via the weir or fishway (Table 2). Relatively more eels passed via the weir/fishway at both HPSs in 2002 than in 2004. In all, 85% of the eels passed the turbines of HPS1 during the period for which flow data for both turbines and weir were available (October–December 2004). During that period, 84% of the total river flow passed the turbines and 16% was discharged over the weir (Figure 6).

Route selection and river discharge downstream

The distribution of river discharge through the two branches of the downstream section of the River Meuse is dependent on water management. When the rates of river discharge are high, flow is mainly through Haringvliet, whereas during periods of low river discharge, most water tends to be guided via the Nieuwe Waterweg (Figure 2). Discharge during 2002 was high and water was guided through the Haringvliet, whereas 2004 was a fairly dry year and the Haringvliet sluices were closed most of the time, resulting in most of the water passing through the Nieuwe Waterweg. During 2002, 66% of all escaping eels migrated via the Haringvliet, but in 2004, just 20% migrated to the North Sea via the Haringvliet (Table 2).

Fishing and HPS turbine mortality

In 2002, eight radio-tagged eels were caught by fykenet fishers downstream, whereas in 2004, no tagged eels were caught there (Table 2). Upstream, the anchored stownets in the tailrace of the two HPSs and small fykenets are the dominant fishery. In both 2002 and 2004, four eels were caught by anchored stownets just

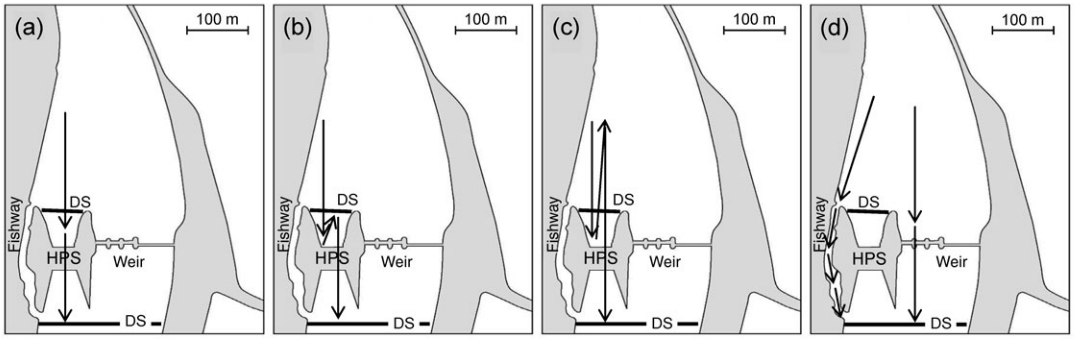

Figure 5. Overview of the HPS1–weir–fishway complex including behavioural patterns (view from above). The location of the detection station in front of the intake of the turbines and downstream across the entire river width is shown as heavy black lines labelled DS. Arrows indicate eel behaviour patterns observed near a hydropower site. (a) Direct passage through the HPS, (b) stationary behaviour, (c) recurrent behaviour, and (d) passage through fishway or over the weir.

downstream from HPS1, whereas five eels in 2002 and eight in 2004 were caught just downstream from HPS2.

As mentioned earlier, 181 eels were detected in front of the HPS1 intake, 12 of which were presumed to have died as a consequence of passage through the turbines. On the basis of mortality rates in the HPS (water-flow model), it was estimated that only 145 individuals would survive. Recalculating mortality rates [Equation (1)] and taking into account the uncertainty in predicting the turbine flow from the river discharge ($CV = 0.28$), the upper 95% confidence limit for the number of surviving eels predicted by the model was 151, well below the 161 eels observed surviving, as measured by telemetry.

Behaviour at HPS sites

Eels repeatedly approached the entrance to the HPS. The average number of detections per eel per detection station was higher for HPS1 than for the river stations (8.1 vs. 2.6 detections per eel per detection station), and the same applied to both study years. Of the 181 eels detected by the station at the entrance of HPS1, 50% were detected there once, 25% were recurrent with intervals >2 min, varying from several hours to several weeks, and 25% showed stationary behaviour, indicated by a series of detections at 2-min intervals.

Discussion

The role of river discharge in route selection

Silver eels approaching a HPS appear to be distributed among the potential migration routes in proportion to the relative river discharge over each, as derived from the timing of first detection per eel (Figure 6). However, near the vicinity of the turbines, eels alter their behaviour and hesitate and even adopt recurrent behaviour. Similar observations of recurrent behaviour were

Table 2. Distribution of downstream-migrating silver eels with transponders over the different alternative routes at three locations; the HPS1–weir–fishway complex, the HPS2–weir–fishway complex, and the downstream area with the two exits to sea.

Year and parameter	HPS1–weir–fishway complex		HPS2–weir–fishway complex		Downstream area
	Number approaching entire complex (HPS vs. weir/fishway)	Number observed directly downstream of complex	Number approaching entire complex (HPS vs. weir/fishway)	Number observed directly downstream of complex	Number passing to sea (Haringvliet vs. Nieuwe Waterweg exits)
2002					
Number of eels passing	*121* (**90** vs. *31*)	**111**	*74* (**46** vs. *28*)	**66**	**41** (**27** vs.**14**)
Fishing mortality	–	**4**	–	**5**	**8**[a]
HPS mortality	–	*6*	–	*3*	–
2004					
Number of eels passing	*105* (**91** vs. *14*)	**95**	*76* (**59** vs. *17*)	**53**	**20** (**6** vs. **24**)
Fishing mortality	–	**4**	–	**8**	**0**[a]
HPS mortality	–	*6*	–	*15*	–

Direct observations of the numbers of eels that were either detected by stations or recaptured by fisheries are given in bold. The numbers of eels that were derived from other observed numbers and transponder identifications are given in italics.
[a]Number of recaptures by fisheries in the downstream stretch between stations 12 and 15/16 combined.

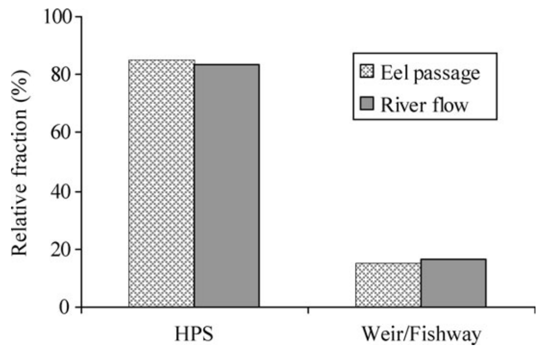

Figure 6. Relative fraction of eel passage and the total river flow over the weir/fishway and through the turbines at the HPS1–weir–fishway complex.

found for silver eels approaching a hydropower barrier in the River Mosel in Germany (Behrmann-Godel and Eckmann, 2003), and for stationary behaviour in the River Nive in France (Gosset *et al.*, 2005). Perhaps changes in patterns of water flow at the intakes of HPSs (e.g. rapid acceleration) are perceived as an obstacle, and may initiate avoidance behaviour (Coutant and Whitney, 2000) or perhaps it is in direct response to being confronted with the trashracks. Eels altering behaviour might search for alternative routes to pass the HPS, for example by migration through the fishway or over the weir after having selected the turbine route. However, we could not test this directly with our experimental set-up because there were no detection stations covering the adjacent weir or fishway. Therefore, the possibility cannot be excluded that the routes actually used for passage deviate from that initially selected, the change in choice being made on the basis of the discharge through each route.

Downstream, the direction of water flow of the River Meuse is strongly influenced by that of the River Rhine. When discharge from the Rhine is low, the Haringvliet sluices remain closed and all river discharge is channelled through the Nieuwe Waterweg. In 2004, when this was the case, the main seaward migration route for eels was via the Nieuwe Waterweg. In years with high river discharge when the Haringvliet sluices are open, eels migrate mainly via the Haringvliet. This is in accordance with the known distribution of eels over alternative routes when river discharges change. Eels clearly adjust their migration route according to the volumes of river flow, a situation known too for salmon smolts (Kemp *et al.*, 2005).

Consequences of route selection on mortality

HPS mortality is indirectly affected by rates of river flow influencing the fraction of eels that will pass the HPS–weir–fishway complex. At low rates of flow, all water is guided through the turbines and eels can only use the fishway to bypass the HPS. At high rates of flow, water spills over the weir, giving eels an alternative bypass. The distribution of eels over each of these routes is related to the rates of water flow (Figure 6). Eels passing HPSs run the risk of ending up in stownets anchored in the tailrace, an additional mortality risk, whereas eels passing the weir avoid being caught by that fishery. At greater river discharges, water spills over the weir and eels can escape from both the HPS turbines and the fisheries. In years with low river discharge, fishing mortality by the stownet fishery was greater than in years with high river discharge.

Mortality caused by HPSs is also directly affected by river flow rates. Several investigations have demonstrated that mortality rates caused by turbines are greater at low flow rates though the turbines (Schoeneman *et al.*, 1961; Cramer and Oligher, 1964; Berg, 1986; Hadderingh and Bakker, 1998). On the basis of known relationships between mortality risk and turbine flow rates, we estimated the total number of eels surviving. Our results suggest that eels have a lesser survival rate than actually observed by the results of radio telemetry. As HPS mortality is positively related to eel length (Haddering and Bakker, 1998; Figure 4), and the experimental eels were larger than the lengths on which the model was based, the model will underestimate total mortality. This means an even greater difference between the observed and the modelled HPS mortality, suggesting that the number of eels actually passing the turbines might have been substantially fewer than the number of eels detected approaching them. This lends more support to the possibility that more eels pass via the weir or fishway after altering their behaviour when they encounter the turbines than predicted from flow rates. If this is true, than eels really do go with the flow, until their behaviour alters close to the turbines, presumably either by encountering the trashracks or in response to the accelerating water.

Comparison of the fishing mortality of the two cohorts in the downstream area reveals that mortality was less for the 2004 cohort. As described earlier, the main migration route of the 2002-cohort was via the Haringvliet, whereas the 2004 cohort was most abundant in Nieuwe Waterweg. Apparently, fishing pressure along the Haringvliet route is greater than along the Nieuwe Waterweg. As route selection appears to be dependent on river discharge, it can be concluded that river discharge indirectly affects fishing mortality by influencing the migration route in downstream area.

Implications for management

Most eel migration in the River Meuse is compressed into a few weeks in autumn (Winter *et al.*, 2006). Fishing and hydropower mortality are influential in determining the fraction of silver eels that migrate successfully through the Dutch section of the River Meuse into the North Sea (Winter *et al.*, 2006, 2007). Therefore, to protect eels effectively, management measures should be implemented as a matter of urgency.

The results of this study clearly indicate that eels do go with the flow and that mortality rates of downstream-migrating silver eels are influenced by the rates of river discharge. Water flow in the downstream area of the River Meuse is dependent on the discharge from the River Rhine and management protocols for sharing river discharge through each of the alternative routes. As fishing mortality is affected by the route selected by the eels, water management might play a role in reducing the number of silver eels ending up caught by fisheries.

Most studies on the impact of HPSs on eels focus only on mortality rates (Berg, 1986; Hadderingh and Bakker, 1998). Current efforts to reduce HPS mortality are concentrated on designing trashracks, so optimize the distance between trashracks and water velocity patterns that enable eels to escape from the trashracks (Behrmann-Godel and Eckmann, 2003). However, the total mortality from HPSs depends on the fraction of eels that pass through turbines relative to the fraction that passes over adjacent weirs or through fishways. Knowledge of fish behaviour around barriers may lead to the successful design of guidance systems (Hadderingh and Bakker, 1989; Durif *et al.*, 2003), helping eels to find an alternative way to pass the HPS site and reducing mortality. This study has shown that eels behave differently (recurrent and stationary behaviour) when close to HPSs, providing possibilities for implementing fish guiding systems. There are several examples of successful bypass systems that have taken account of fish behaviour in their design. For downstream-migrating juvenile salmonids, spill from the water surface is more effective than spill from the seabed because juvenile salmonids are surface-orientated (Johnson and Dauble, 2006). Silver eels, on the other hand, would gain more from downstream-migrating facilities being located near the riverbed, because they are bottom-orientated during their migration (Jonsson, 1991; Tesch, 1994). Indeed, Gosset *et al.* (2005) confirmed the preference of migrating silver eels for riverbed rather than surface bypasses.

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