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Attraction of migrating glass eel (*Anguilla anguilla*) by freshwater flows from water pumping stations in an urbanized delta system

R. Kroes [a,*], E.E. Van Loon [a], E. Goverse [a,b], M.E. Schiphouwer [b], H.G. Van der Geest [a]

[a] *Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, the Netherlands*
[b] *Reptile, Amphibian & Fish Conservation Netherlands (RAVON), Nijmegen, the Netherlands*

HIGHLIGHTS

- In natural systems, river flows play a major role in attracting and directing migrating eels.
- Coastal areas get urbanized more and more and characterized by anthropogenic barriers and hampered or artificial water flows.
- In this study glass eel were sampled at water pumping stations in a constructed part of the Rhine delta in the Netherlands.
- A mixed linear-effect model was used to determine effects of freshwater flows from water pumping stations on glass eel catch.
- Freshwater flows from water pumping stations had a significant but small effect on glass eel catch.

GRAPHICAL ABSTRACT
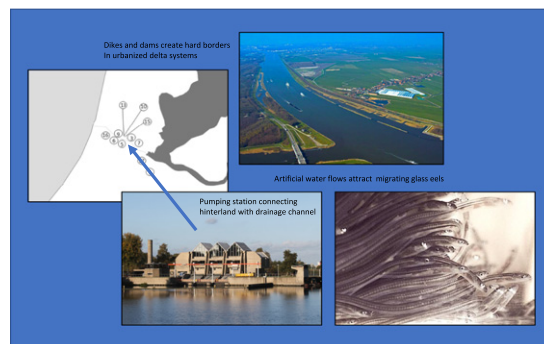
ABSTRACT

Most studies on glass eel (*Anguilla anguilla*) migration are performed in natural estuaries, where they enter freshwater systems to live there for a period of years before they swim back again to the sea to reproduce. In these natural systems, river flows play a major role in attracting and directing migrating eels. However, coastal areas get urbanized more and more and characterized by anthropogenic barriers and hampered or artificial water flows. The effects of these flows on glass eel migration are poorly understood. Therefore, in this study glass eel were sampled at water pumping stations in a constructed part of the Rhine delta in the Netherlands. A mixed linear-effect model was used to determine effects of freshwater flows from water pumping stations on glass eel catch. We found that freshwater flows from water pumping stations had a significant but small effect on glass eel catch. Pumping activity had no significant effect on glass eel catch at sample locations with a continuous freshwater flow from fish passages. However, a low predictive value of the model and low numbers of individuals per sample prohibited strong conclusions on effects of anthropogenic freshwater flows on glass eel migration. More individual tracking techniques should be used to improve understanding migratory behavior of glass eel.

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1. Introduction

River deltas around the globe are often densely populated areas (Syvitski and Saito, 2007). Water storage and flood protection in such areas is regulated by dams and dykes, resulting in the obstruction of fish migration between freshwater and marine ecosystems. These anthropogenic barriers can physically block dispersal movements but also affect natural salt- to freshwater gradients which fish need to during migration.

The European eel (*Anguilla anguilla*) is a catadromous species that suffers from such obstructed migration. According to IUCN Red List of Threatened Species, *A. anguilla* is critically endangered (Jacoby and Gollock, 2014). The species is semelparous and panmictic which makes conservation challenging. Individuals migrate over great distances inhabiting both marine and fresh waters during multiple life stages. Mature eels are proposed to spawn in the Sargasso Sea. After hatching, eel larvae migrate to the European coast within 2 years (Lecomte-Finger, 1992; Zenimoto et al., 2011). In the coastal waters, larvae metamorphose into transparent glass eels of 60–100 mm in size. Although some glass eels stay in the coastal areas, many try to enter the freshwater systems to live there for a period of years before they swim back to the sea to reproduce (Van Ginneken and Maes, 2005).

In natural estuarine systems, river flows play a major role in glass eel migration. When entering river deltas, salinity gradients and flow rate attract and direct migrating glass eels (Arribas et al., 2012; Boivin et al., 2015; Bolliet and Labonne, 2008; Bureau Du Colombier et al., 2007; Creutzberg, 1961; Crivelli et al., 2008; Edeline et al., 2005; Lucas and Baras, 2002; Sola, 1995). And although not intensively studied, earthy and conspecific odorants from freshwater systems may facilitate orientation as well (Creutzberg, 1961; Schmucker et al., 2016; Tosi and Sola, 1993). The estuaria of the main rivers Rhine, Meuse and Schelde are highly regulated. Therefore, natural river flows are absent in many of the urbanized river delta's in The Netherlands. Roughly one third of the country lies below sea level and an elaborate network of pumping stations, dams, dikes, sluices and drainage canals keeps the land from flooding. Since the Netherlands have a precipitation surplus, water pumping station are used to pump excessive water from the low-lying land to the sea, creating freshwater flows. The flow patterns that are created by these pumping stations, however, are completely artificial and follow highly variable on/off patterns that are very different from natural water flow patterns in undisturbed river systems. Still, these non-riverine freshwater flows are expected to attract migrating glass eels. Anecdotic literature and field observations support this theory with increased visual observations of swimming glass eels during active pumping periods. However, so far a quantitative analysis of such data is not available. Hence, the goal of this study is to analyse the effects of non-riverine freshwater flows from water pumping stations in a regulated delta system on migrating glass eels.

To this purpose, sampling data from a long-term glass eel monitoring project in The Netherlands was used. In this study:

1) the characteristics of glass eel catch at water pumping stations in the Dutch delta are described;
2) the temporal dynamics of freshwater flows from water pumping stations are described; and
3) the effects of freshwater flows from water pumping stations on glass eel catch are evaluated.

2. Materials and methods

2.1. Sample locations

Twenty water pumping stations were selected for glass eel sampling by local Dutch authorities (Fig. 1). The water pumping stations were located 1.7 to 58.3 km land inwards from the seashore (swimming distance through the water body, measured with GoogleMaps) and pumped freshwater from the low-lying surrounding lands either into freshwater and brackish drainage canals or into sea directly. All sample locations were spatially distributed along known migratory routes of glass eels and were first or second barriers for eels to migrate further inland. Eight locations were sampled in 2014, 2015 and 2016. Sampling at other locations started in 2015. Four sample locations had a fish passage system during their sampling period with a continuous attraction flow from the freshwater hinterland. Additional fish passages were built at three other locations during our sampling period in 2014 and 2015 (see Supplementary S1 for all sample location characteristics).

2.2. Flow patterns created by water pumping stations

Pumping activity from activated water pumping station was recorded with time intervals of 5 to 20 min by the Dutch water boards responsible for the daily operation of these pumping stations. Water boards recorded discharge data in different ways that are not directly comparable. Discharge data was therefore transformed to a binary structure, indicating either a pumping station was active or not and uniformed to 15 min intervals for each station for the years 2014, 2015 and 2016. To give insight in temporal dynamics of the activity of the 20 water pumping stations that were selected for glass eel sampling, first the total number of days per month with pumping activity was calculated for each location per year. In addition, frequency distributions were made to describe the duration of discrete pumping periods (bin size 1 h) for each location per year.

2.3. Glass eel sampling

Lift nets are commonly used for sampling at locations were glass eels aggregate (Dekker, 1998; Harrison et al., 2014). Locations were sampled by volunteers with 1 square meter hand-held lift nets from the shore from. All volunteers were trained on lift net handling, lift speed and fish taxonomy and handling by the same glass eel expert from RAVON in order to minimize potential sampling effects. Locations were sampled from March to June, the period in which glass eel migration in the Netherlands peaks (Dekker, 1986; Dekker, 1998). Locations were sampled 2 times a week starting half an hour after sunset. Per night, 5 samples were taken with a 5 min recuperation interval. Caught glass eels were stored in fish tanks before release at the end of each nocturnal sampling session according to prescribed legislation. Individual glass eel length was measured, eels longer than 10 cm were considered 'elvers' and were excluded in the analyses of this study. The total number of individual glass eels was recorded per sample per location by date and time. Empirical cumulative distribution functions of the catches were made per sampling location to describe the relative catch distribution per location over the year.

2.4. Sampling moment

To assess the sensitivity of the sampling moment relative to the time after sunset one location (GEOV, Gemaal Overtoom) was sampled continuously for 84 h with 15 min interval in April 2017, using the same catching procedure as for the long term monitoring. All glass eels passing a glass eel passage facility near the sample location were collected with a lift net at the exit of the passage and counted each hour as well. The number of individuals caught was plotted against time with local day-night cycle. An indication for best moment of sampling was visually inspected from the plot and compared to the chosen time in the monitoring program. In addition, CPUE was calculated using local time of sunrise and sunset as discrimination between day and night.

2.5. Data analysis: modeling glass eel catch and attractive freshwater flows

The start and end of the glass eel catch season was determined by first and last catch for each sample location per year. Samples with

Fig. 1. Locations of the 20 sampled water pumping stations in The Netherlands. For coordinates and names, see Table S1.

zero values outside the glass eel season were excluded from the analysis. Also samples for which the time to last pumping activity was longer than 7 days were excluded from the analyses.

The response variable in our analysis represents glass eel catch. The catches in their raw form are characterized by large variations between years (2014, 2015 and 2016) as well as sample locations. Therefore, numbers of caught glass eel were transformed to relative numbers by calculating relative catch in a sample as a fraction of the total catch at that location over that year. The resulting variable (the relative catch fraction) had many small values and zeros. In order to stretch the lower end of this range and make any differences easier to detect, a square-root transformation was applied to the response variable. Ultimately, this also made the model residuals more normally distributed.

Besides several potentially relevant covariates (like distance to sea or time after sunset) that might influence glass eel catch, the monitoring data contained variation with respect to the pumping activity in combination with presence of fish passage, leading to freshwater traces being highly variable (pumping activity only) or less variable (pumping activity with presence of a fish passage). This property was exploited to evaluate if artificial freshwater flows created by water pumping stations acted as a navigation cue for glass eel, using linear mixed-effects models (R package lme4, Bates et al., 2015) as the modeling framework. The analysis comprised two steps: first a variable selection step to identify a model containing all relevant predictor variables besides the presence of a fish passage; and secondly a model testing step where the effect of freshwater traces on glass eel catch (null-model) and effects of fish passage presence (alternative model) was evaluated using the best model (or models) identified in the first step.

Sampling took place at fixed locations, hence the measurements over time were not independent. We took this into account by including a random intercept for the sampling location in the mixed-effects model in both analysis steps.

In the variable selection step, the following six variables were included: 1) time after sunset (tas), 2) sample number (samplenr; 1 to 5, i.e. an ordinal representation of time after sunset), 3) day of year (doy), 4) shortest distance from sampling location to sea (disttosea), 5) the number of barriers between sampling location and sea (nrbarrier), and 6) the time since last pumping activity of the pumping station nearest to the sampling location and sampling moment (pumptdif). All relevant combinations of these variables were made, resulting in a set of 35 models (see supplementary material S1 for a full list of these models). The models were fitted on the data and ranked according to the AICc criterium. The models with AICc values ≤4 from the lowest AICc value in this list, with significant predictors (significance level, <0.05) were used for the model testing step.

In the variable selection step, three models met the AICc criterion:

$$\text{sqrt(fracyr)} \sim \text{samplenr} + \text{doy} + \text{pumptdif} + (1|\text{location}) \tag{1}$$

$$\text{sqrt(fracyr)} \sim \text{samplenr} + \text{doy} + \text{disttosea} + \text{pumptdif} + (1|\text{location}) \tag{2}$$

$$\text{sqrt(fracyr)} \sim \text{samplenr} + \text{doy} + \text{nrbarrier} + \text{pumptdif} + (1|\text{location}) \tag{3}$$

However, both the variables disttosea and nrbarrier were not significant (see the details in supplementary material S1). Therefore, the first model (including samplenr, doy and pumptdif as predictors) was used as the null-model in the model testing step.

The alternative model included an interaction-term between time after last pump activity (pumptdif) and the presence of a fish passage

(passage). The hypothesis underlying this alternative model was that the permanent freshwater flow from the fish passage would remove any impact from the variable freshwater input from pumping activity.

The formula representing the alternative hypothesis was:

$$\text{sqrt(fracyr)} \sim \text{samplenr} + \text{doy} + \text{pumptdif} * \text{passage} + (1|\text{location}) \quad (4)$$

If the interaction effect in the alternative model was significant (in the right direction, i.e. presence of a passage should make the effect of time to last pumping activity insignificant) this would lead to rejection of the null-hypothesis. A likelihood-ratio test was used with a 0.05 significance level to test whether the null model would be rejected in favor of the alternative model. Model-coefficients of the null or alternative model were interpreted, depending on which was best supported by the data (as appears from the likelihood ratio test). Finally, the marginal R-squared value, as a metric of overall explanatory power by the model, was interpreted.

3. Results

3.1. Water flow patterns created by water pumping stations

The water pumping activity of the different pumping stations varies widely between as well as within locations and years (Figs. 2 and 3). Most pumping stations show a frequent pumping activity, resulting in an average number of 27 days of activity per month. However, at some locations also low activities (e.c. with only 2 days of pumping per month) are recorded (Fig. 2). There is also a large variation in the duration of the pumping events. For example, location GEZP is daily active (Fig. 2), but pumping activity is always 1 h or less (Fig. 3). Other locations like GEAO have less days with activity, but with longer pumping periods, occasionally exceeding 24 h. The combination of the number of days with pumping activity and the duration of the pumping events result in a highly variable and irregular freshwater flow pattern created by these pumping stations.

3.2. Glass eel catch

79 glass eels were caught by lift net sampling during the 84-hour continuous sampling period and during the same period 47 glass eels were caught in the fish passage. The majority (94%) of all glass eels was caught between sunset en sunrise and catch was evenly distributed over the night (Fig. 4). At night, 0.64 N/sample and 1.42 N/sample were caught with lift net and at the exit of the fish passage respectively. At daytime, 0.02 N/sample and 0.06 N/sample were caught with lift net and in fish passage respectively (Supplementary table S2).

In the monitoring program, 5174 samples were taken and 4501 glass eels were caught over the years 2014, 2015 and 2016. The average number of eels per sample was 0.87, ranging from 0 to 160. The in-season average catch was 1.22/sample. Fig. 5 shows the variation in glass eel catch between and within locations and years. Locations with low catch numbers show large discrete steps in the distribution (e.g. GEGO and SPRO) whereas locations with high catch show a smoother cumulative catch distribution (e.g. GENA and GEOV). Many locations had multiple successive sampling moments without glass eel catch, as indicated by the elongated horizontal periods in the frequency distribution.

3.3. Effects from freshwater flows on glass eel catch

Our null-model (Eq. (1)) as well as the alternative model (Eq. (4)) contained only significant predictors (see details in Supplementary material S3). When applying the likelihood-ratio test to these models, this
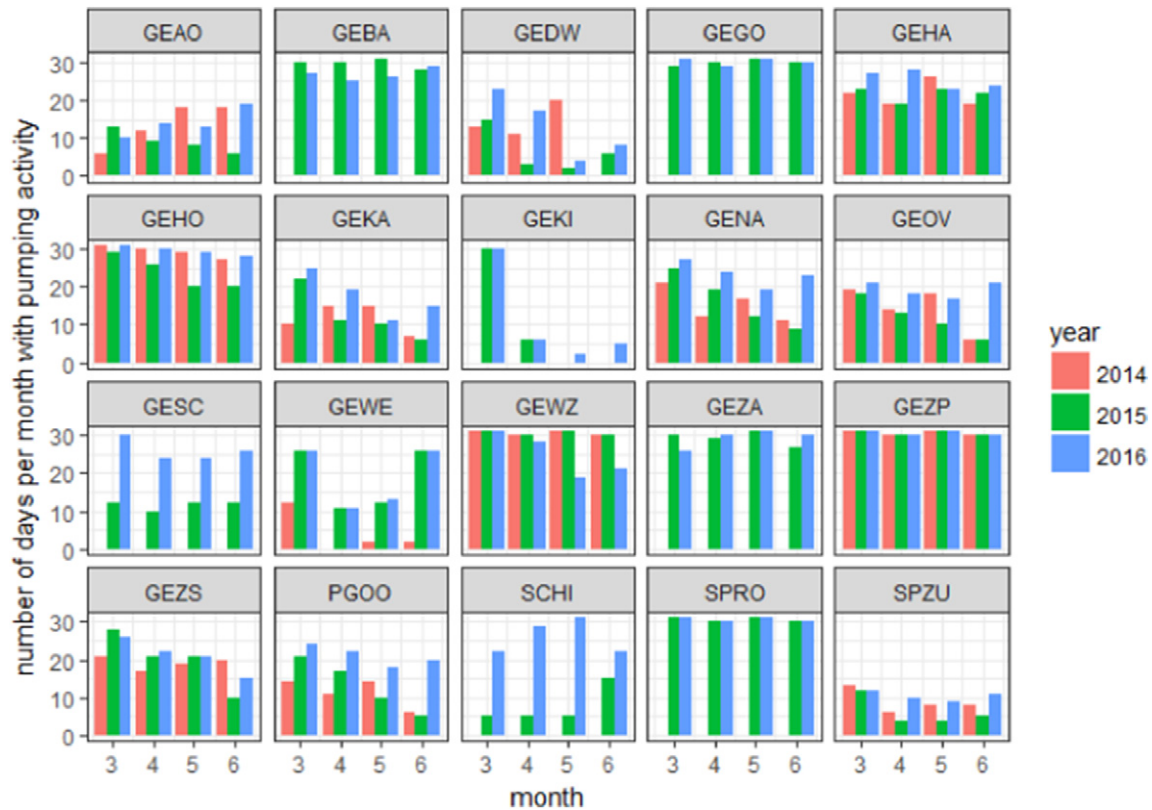
Fig. 2. Average number of days per month with pumping activity per sampling location for each year (2014–2016). Discharge data from water boards was used for sampled periods only. Locations GEDW, GEHA, GEHO, GEKA, GENA, GEOV, GEWZ and GEZP were sampled in all three sample years. GEZS was only sampled in March and April 2015. GEKI, GESC and GEBA were sampled in 2016. GEAO, GEGO, GEWE, GEZA, PGOO, SPRO and SPZU were sampled in 2015 and 2016. Pumping station GEZP was daily active in each month and year. Pumping station GEAO was active for 10 days per month on average.

Fig. 3. Frequency distribution of single event duration of continuous pumping (bin width 1 h) per sampling location per year. Discharge data from water boards was used for sampled periods only.

led to the rejection of the null-model in favor of the alternative model ($P = 0.035$; see details in Supplementary material S3). The alternative model seemed to be valid: the direction of the coefficients for the alternative model (positive for sample number and negative for pumptdiff in the absence of a fish passage) made sense biologically, and the residuals did not show deviations from normality (see Supplementary material S3). Overall, freshwater flows from water pumping stations had a significant but small effect on glass eel catch: more glass eels were caught shortly after pumping activity ($P = 0.0008$). At locations with a fish passage, this effect did disappear (Fig. 6). However,
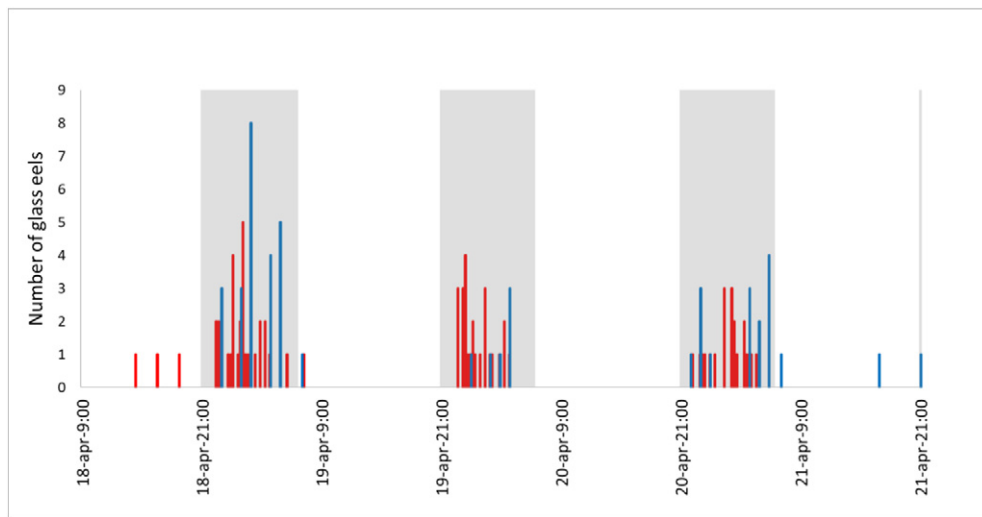

Fig. 4. Catch per sample during the 84 h monitoring session at location GEOV in 2017. Lift net samples were taken every 15 min. Lift net catch is indicated by red bars. Glass eels that successfully passed the fish passage were counted every hour. Fish passage catch is indicated by blue bars. The grey fields represent night-time and are limited by local time between sunset and sunrise.
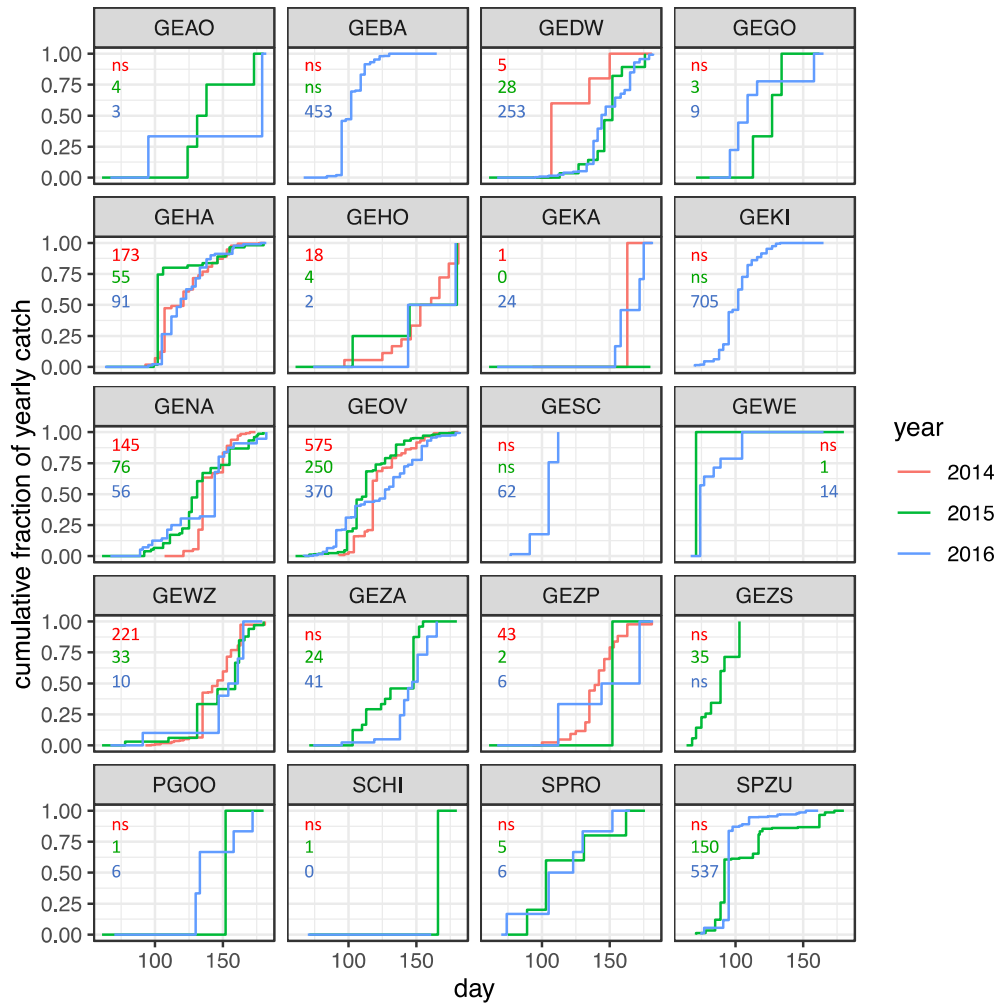
Fig. 5. Cumulative fraction of yearly catch for each location per year. Total yearly catch is indicated by the colored numbers inside the panels (ns is sot sampled). The sampling period is indicated by start and end of each cumulative line. First catch generally started around the end of March. Highest catch was in April–May and decreased at the end of the sampling period in June.

the model with most support (the alternative model) still had a very small value of the marginal R-squared, 0.02. Hence, even though significant and (in terms of both direction and magnitude) meaningful effects were found by the presence of freshwater traces and time after pump activity, these don't explain an important part of the variation in the relative catch.
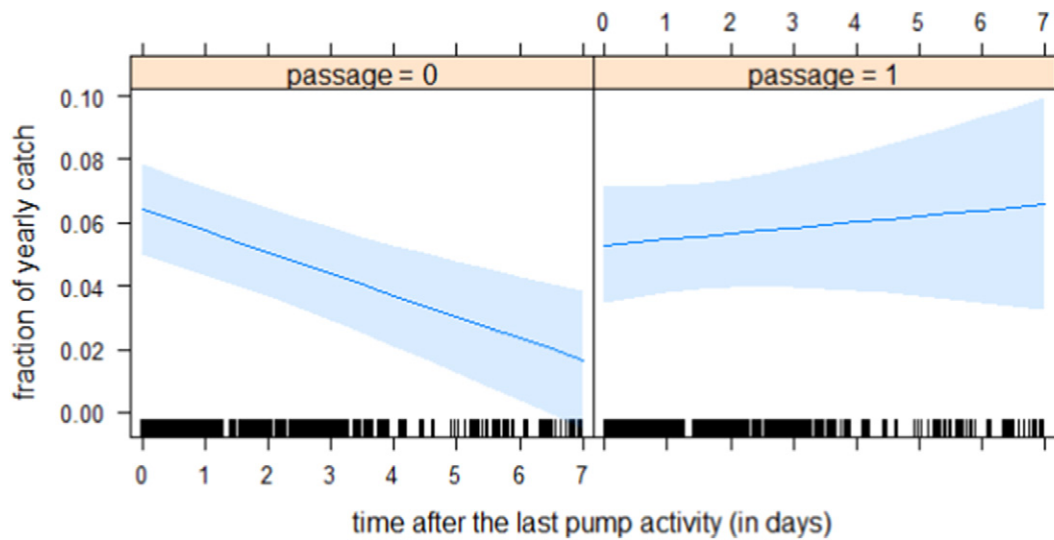

Fig. 6. Marginal effect of time after last pump activity on fraction of yearly catch for locations without fish passage (left) and with fish passage (right), predicted by a linear mixed model. The light-blue areas give the 95% confidence interval around the mean. The black lines on the x-axis specify time after last pump activity for each sample.

4. Discussion

With increasing global human population and more people living in coastal areas, more and more river deltas are regulated which negatively affect migration of fish (Van Puijenbroek et al., 2019). The results of this study indicate that anthropogenic freshwater flows in such areas disturb glass eel migration. Data from water pumping stations show high fluctuations in activity, producing a scatter of discontinuous freshwater traces on the migration routes of glass eels. The statistical analysis shows that pumping activity did have an effect on glass eel catch at locations without fish passage: on average more glass eels were caught short after pumping activity. At locations with fish passages however, pumping activity had no effect on glass eel catch. Based on these results we propose that freshwater flows from both pumping activity and fish passages acts as orienting stimuli for glass eels, and that the continuous flows form the dominant stimulus if present. The attractive effect of freshwater flows found in this study corresponds with results from studies on both *A. anguilla* and other Anguillid species (Edeline et al., 2005; Harrison et al., 2014; Boivin et al., 2015). Even though the effects found in this study were significant, the effect sizes were small and the used model had low predictive value. Our main explanation for this low effect size is the relatively low frequency of pumping station activity, relative to the dynamics of glass eel density and residence time. In the Netherlands, glass eels swim along multiple water pumping stations during their migration. Some water pumping stations can be active when passing by, others can be inactive. Attractive effects can only be expected when higher densities of glass eels are present near a location with an active water pumping station and this particular combination can only be expected to occur occasionally.

In natural conditions, salinity gradients and flow rate attract and direct glass eels to upstream freshwater residence habitat. Hydrology of freshwater flows from pumping stations differs from these natural conditions. Apart from the discontinuous character, salinity gradients produced by water pumping stations are probably less pronounced than in natural conditions. Many water pumping stations pump freshwater from the hinterland directly into salt or brackish waters or even freshwater systems with comparable salinity. Because of differences in density between salt- and freshwater, strong separation between the waters may occur without mixing and hence without producing clear traces for migrating glass eels. This is expected to happen along the North Sea Canal for example, one of the main sampled water bodies in this study (Swinkels et al., 2015). Several authors state that saline gradients from freshwater flows are not always the main key for diadromous species to enter freshwater systems. Arribas et al. (2012) performed a multi-variate analysis on glass eel recruitment in a Spanish estuary. They concluded that recruitment depends on a combination of local turbidity, water temperature and salinity conditions. Edeline et al. (2006) showed that the glass eel migratory behavior, through locomotor activity and salinity preference, may be controlled by interacting physiological and environmental factors. Light intensity, water temperature, lunar cycle, tidal amplitude, body weight and food abundance are also indicated to trigger glass eel migration (Harrison et al., 2014). Furthermore, strong currents from water pumping activity might inhibit glass eel migration as well (Martin, 1995). Sampling during or shortly after pumping activity can therefore also be less effective. Experimental studies from Tosi and Sola (1993), Sola (1995) and Briand et al. (2002) suggest that earthy odours and odours from adult eels attract glass eels as well. If present, water pumping stations are expected to produce attractive gradients of these odours. Since eels have excellent sense of smell, odours can have attractive effects on much greater time-scale than used in this study. Apart from environmental conditions, Podgorniak et al. (2016) showed that individualism in glass eels also influences migration behavior. They suggested that social interactions explain why well-known abiotic factors like weather, temperature and water discharge sometimes fail in predicting the migration waves of glass eels.

Reconstruction of exact hatching site and migration routes of the larvae and glass eel have been discussed from the early 20th century (Boetius and Harding, 1985; Van Ginneken and Maes, 2005; Westerberg et al., 2018) but still depend on analysis of recruitment and sampling data (Dekker, 1998; Lecomte-Finger, 1992). Unfortunately, density and residence time of glass eel at individual sampling locations was not known in this study and may vary by recruitment and local conditions other than freshwater flows. Reliable densities could not be derived from multi-decennial monitoring programs as well (Westerberg et al., 2018). The sample method used in this study traditionally shows high variation (Dekker, 1998; Jessop, 2000). However, alternatives for more effective sampling or individual tracking are lacking to date. Results from the 84-hour monitoring session did however confirm that timing of sampling was effective. To compensate for the disadvantages of the sampling method, a large number of samples was taken at multiple locations in this study. Still, in 2630 of 3672 samples within the glass eel season (i.e. between first and last catch within a year), no individuals were caught. These low catch numbers may be caused by the dramatically decreased population of *A. anguilla* from the early 80s (Dekker, 2003).

5. Conclusion

This study suggests that anthropogenic water flows attract and direct glass eels. Migration can only be successful if preparation, timing, ability to perform an ongoing and precise movement and stopping at the right time and place are present (Smith, 1985). Since many water pumping stations in the Netherlands have no facilities for glass eels to pass, these barriers do not only obstruct migration, but can also delay further swimming to other locations were migration to the hinterland is possible. It is unknown how these anthropogenic barriers influence migration of glass eels at the individual level. For adult eels, telemetry techniques are increasingly used to track migrating eel from freshwater to sea and are providing a wealth of new insights about its movement (Bultel et al., 2014; Righton et al., 2016; Trancart et al., 2018; Verhelst et al., 2018). Tracking individual juvenile eel is the next challenge, but we need it to unravel the characteristics of this life stage and to protect the European eel for extinction.

Declaration of competing interest

The authors declare that there are no conflicts of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.136818.

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