Understanding downstream migration timing of European eel (*Anguilla anguilla*)

– Analysis and modelling of environmental triggers

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Preface

This study was carried out by Florian Stein, University of Potsdam in collaboration with Karlstad university. Main participants in this study and authors of this report are listed on the front page.

The project was performed within Krafttag ål which is a program for eel preservation between seven hydropower companies and the Swedish Agency for Marine and Water Management.

The program is managed by a steering group:

Erik Sparrevik	Vattenfall Vattenkraft AB (chair)
Niklas Egriell	Swedish Agency for Marine and Water Management
Johan Tielman	E.ON Vattenkraft Sverige AB
Marco Blixt	Fortum Generation AB
Jan Lidström	Holmen Energi AB
Ola Palmquist/Katarina Ingvarsson	Tekniska Verken i Linköping AB
Angela Odelberg	Statkraft Sverige AB
Sara Sandberg (adj.)	Elforsk

Krafttag ål runs between 2011-2013 and consists of measures for the eel as well as research and development (R&D) projects. (*Krafttag* is a Swedish word for effort. *Kraft* also means power.) In order to carry out cost-effective measures for spawning migrating eel from freshwater habitats, more knowledge and facts are needed. The R&D part of the program was funded by Swedish Agency for Marine and Water Management, Vattenfall Vattenkraft AB, E.ON Vattenkraft Sverige AB, Fortum Generation, Sollefteåforsen AB, Statkraft Sverige AB, Tekniska Verken i Linköping AB, Holmen Energi and Karlstad Energi.

Stockholm, October 2014

Sara Sandberg
Program area Hydro power
Elforsk

Sammanfattning

Ålbeståndet i Europa har varit på tillbakagång under en längre tid. En av anledningarna till detta är dödlighet orsakad av turbiner i vattenkraftverk. För att undvika att ålar skadas vid turbinpassage kan driften av kraftverk anpassas till när ålen vandrar. Denna studie på fem platser i södra Sverige syftade till att öka kunskapen om vandringsbeteende av Europeisk blankål genom att använda avancerade statistiska modeller för att studera hur olika miljöförhållanden påverkar ålens vandringsbeteende.

Resultaten från studien visade att ålarnas vandring kunde förklaras med hjälp av s.k. ”triggers” eller miljöparametrar som triggar vandringen. De viktigaste var hydrologiska variabler (t.ex. vattenflöde), vattentemperatur och månfas. Ålarna vandrade företrädesvis på natten (98,5%) och när vattentemperaturen på hösten var högre än 5 °C. Under våren startade vandringen när vattentemperaturen översteg 6,5 °C. Vår- och höstvandring skiljde sig åt. På våren verkade ökad vattentemperatur vara den huvudsakliga triggern, oberoende av hydrologiska variabler och månen. Under hösten var även månfas och hydrologiska variabler viktiga. Det fanns en skillnad i viktiga triggers mellan vattendragstorlek och/eller geografisk placering. I mindre, uppströms belägna biflöden tycktes hydrologiska variabler vara viktigast. På större/nedströms belägna platser var vikten av vattentemperatur och månfas betydligt större.

Vi testade även modellernas överförbarhet. Överförbarhet bland tidsserier för samma plats gav några tillförlitliga resultat, medan överförbarheten mellan platser var begränsat till platser som låg inom samma avrinningsområde. Eftersom denna studie hade en begränsad datainsamling på våren, rekommenderas att den delen utökas i kommande studier för att ytterligare undersöka vårutvandring samt för fler valideringar av modellers förmåga till överförbarhet mellan säsonger. Vid kommande studier bör även ålars vandringsbeteende vid fångstfällor verifieras med andra tekniker (t. ex. telemetri eller sonar-system), eftersom vi i denna studie inte med säkerhet kunde säga att fångade ålar betedde sig exakt likadant som andra ålar.

Våra resultat visar tydligt att den turbinducerade dödligheten för ål minimeras om turbiner körs dagtid, vid vattentemperaturer under 5 °C och vid minskande eller stabila flöden. En mer detaljerad styrning av turbindrift bör anpassas efter lokala förhållanden, och helst föregås av enskilda studier och mätningar av vattentemperatur och hydrologiska variabler. Dessutom är det viktigt att anpassningar (t.ex. turbindrift, “early warning” system etc.) tar hänsyn till den temporala dynamiken av vattentemperatur och hydrologiska variabler.

Summary

The European eel stock has long been in decline. Consequently, the species has been added to the IUCN Red List of Threatened Species. One threat that has been identified as one possibly having an impact on the stock is mortality caused by hydroelectric power plant turbines. Turbine management, which is adapted to preferable migration conditions, might reduce the risk of this threat. Our study, conducted at five locations in southern Sweden, aimed at learning about the migratory behaviour of European silver eels paying special attention to preferable environmental conditions for migration by using advanced statistical modelling.

Results indicated that downstream migration triggers can be reliably described using hydrological variables (discharge, precipitation or one of their dynamic derivations), water temperature and moon. Spring and autumn migrations seemed to be triggered differently. In spring, rising water temperatures seemed to be the key trigger, quite independently of hydrological variables and the moon. In the autumn, the importance of the moon and hydrological variables on downstream migration increased. In addition, migration triggers differed depending upon the size of the body of water and/or its location in the river system. In smaller/upstream tributaries, hydrological variables seemed to be the key trigger. In larger/downstream waters, the importance of water temperature and the moon increased.

The transferability of models was limited. Moreover, models indicated that in some cases, the dynamics of water temperature and hydrological variables (precipitation, discharge) provided more explanatory power than the measured, absolute values. Transferability among time series from the same location delivered some reliable results. Success of transferability between locations was limited to sites which originated from the same river catchment. In spring, migration activity did not occur until water temperatures exceeded 6.5 °C in a tributary and 9 °C in the Kävlingeån River. Eels showed significant nocturnal migration behaviour (98.5 %; n = 205) and migration activity became very unlikely in autumn if water temperatures dropped below 5 °C.

Our data on spring migration is limited to one site in a tributary and one site in a lower mainstream. Furthermore, spatial transferability among catchments has not been tested in previous studies. Therefore, we recommend that future studies be performed during the spring and autumn migrations in tributaries as well as lower mainstreams.

Moreover, previous studies indicate that some eels hesitate for several days or even reverse upstream instead of entering the traps the same night that they arrive. Additional visual techniques such as hydroacoustic cameras should be applied upstream of catch facilities in order monitor eel migration

activity of unharmed eels. This enables the validation of trap catchability and consequently the response of our models.

Our results clearly show that turbine induced mortality could be minimized if turbine operation focuses on daytime periods, when water temperature is below 5 ° C and when the discharge not is stable or decreasing. Moreover, local adaptive turbine management should be accompanied by studies to determine the local constellation of environmental triggers. In addition, it will be crucial, that later applications (e.g. turbine management, early warning systems etc.) consider the temporal dynamic of water temperature and hydrological variables.

Content

1 Background

The recruitment of European eel has been in steep decline and is currently only 1-5 % of what it was in the 1970s (Åstrom and Dekker, 2007). Consequently, the species was added to the IUCN Red List of Threatened Species as *critically endangered* (Freyhof and Kottelat, 2010) and is characterized as *outside of safe biological limits* (ICES, 1999). The European Union is demanding that measures be taken to ensure that stocks recover through the implementation of national Eel Management Plans intending to allow at least 40 % escapement of reference silver eel biomass (EU, 2007).

The downstream migration of anguillid species has been the subject of several studies and much speculation. Timing of migration is believed to peak in autumn and spring (Tesch, 2003). In the northern hemisphere, autumn migration is earlier at higher latitudes (August-September) than at lower latitudes (October–January) (Haro, 2003). Permanent monitoring in the German Warnow River, however, revealed continuous migration activity throughout the year with high temporal variation (Reckordt et al., 2014). Downstream migration activity of anguillids has been associated with numerous potential environmental predictors. These include hydrological variables (e.g. discharge, flow velocity, water temperature) as well as climatic variables (e.g. barometric pressure, precipitation, air temperature) and lunar cycle.

Increased migration activity is often understood to occur during less illuminated phases of the lunar cycle, but alternative explanations have been offered: Boëtius (1967) and Deelder (1970) assume an internal rhythm related to the lunar cycle but independent from moonlight, while earlier studies concluded that the absence of moonlight itself is the driving factor (Lowe, 1952; Petersen, 1906). Experimental studies have also concluded that they avoid direct artificial light (Cullen and McCarthy, 2000; Hadderingh et al., 1999) and prefer distinct nocturnal behaviour (Petersen, 1906; Riley et al., 2011). In contrast, two recent studies reported no significant influence of moon phase on silver eel migration (Marohn et al., 2014; Reckordt et al., 2014).

Migration is often associated with increased discharge events (Hadderingh et al., 1999; Lowe, 1952), from both natural and artificial sources (Acou et al., 2005; Cullen and McCarthy, 2003). Additionally, it is postulated that discharge regulation might obscure the underlying periodicity of the lunar cycle in regulated river systems (Cullen and McCarthy, 2003).

The relationship between migration and water temperature seems to be expressed by preferable ranges or threshold values which differ between geographical locations. In Brittany, Acou et al. (2008) observed migration peaks at water temperatures between 6 and 10 °C. Vøllestad et al (1986) identified an optimal temperature around 9 °C in Norwegian waters. In the German Warnow River, Reckordt et al. (2014) identified higher weekly migration rates at temperatures greater than 10.4 °C in combination with increased discharge and wind speed. Haro (1991) identified a range from 10 to 18 °C through experimental laboratory studies for Atlantic eels (genus *Anguilla*).

With this study, we aimed to obtain general and site-specific knowledge on the migratory behaviour of European silver eels in terms of preferable environmental conditions. Such knowledge is considered to be pivotal for the management of an endangered species (Jeltsch et al., 2013). Knowledge of preferable migration conditions enables adaptive management and reduction in mortality caused by turbines. By using advanced statistical modelling approaches, we tested the importance of environmental variables in triggering migration. Furthermore, analysis of model transferability in space (among sites) and time (among time series) will generate crucial background knowledge for the implementation of early warning systems. Therefore, this knowledge could contribute to achieve the goals of national eel management plans, including the Swedish Eel Management Plan (Anonymous, 2008).

2 Material and Methods

2.1 Study sites

We worked in five river catchments in southern Sweden in order to collect reliable data on eel migration that enables testing temporal and spatial model transferability. Three of the selected rivers (Kävlingeån (3), Mörrumsån (4), Rönne å (5) are parts of prioritized rivers in the Swedish eel management plan (Anonymous, 2008; Dekker et al., 2011). Mörrumsån drains into the Baltic Sea, Kävlingeån into Öresund and Rönne å into the Kattegat as well as Ätran (sites Skärhult (1) and Ätrafors (2)).

Figure 1: Study sites in southern Sweden

2.1.1 Skärhult (1) – Skärhultaån

Skärhultaån (57°10'15.35"N, 12°47'8.98"E) is a small creek that drains several lakes (catchment area ca. 3.2 km²; including the lakes Skärsjön and Tjärnesjön) into Högvadsån River, a tributary to Ätran River (Hallands län). The stationary eel trap (ålkista) has been used by the Andersson family for generations until Sweden prohibited eel landing for non-commercial fishery in 2007 (Dekker et al., 2011). Since 2007, Karlstads university used the trap for several eel projects (Calles and Bergdahl, 2009; Calles et al., 2012). The advantage of the trap is its extraordinary setting. The trap covers the width of the entire creek and consequently is expected to have a very high catchability.

In fall 2011 and 2012 we were forced to take the trap out of service and open it up for several days due to heavy discharge which threatened to burst the small dam. In spring 2013, ice cover (Figure 2) prevented the operation of the trap until late April. The analysis in the report also includes data from Skärhultaån which were collected in the frame work of the project *`Ål i Ätran - En fallstudie för svensk ålförvaltning*' in 2010 and2011 (Calles et al., 2012).

Figure 2: The Skärhultaån trap during non operational conditions due to ice in spring 2013 (upper left); very low discharge inside the trap in summer 2013 (upper right). Trap operating under heavy discharge conditions in fall 2012 (lower left); high discharge conditions inside trap in fall 2012 (lower right).

2.1.2 Ätrafors (2) – Ätran

Ätrafors (57° 2'1.82"N, 12°40'3.87"E) is the second hydroelectric plant in the mainstream of the Ätran River (catchment area: 3342.2 km), located about 27 km from the sea (Hallands län). The intake channel is 290 m long and 5 m deep. At the turbine intake, the water is diverted into three intake gates, equipped with tubes that lead to three twin-Francis turbines.

Since 2008, the intake channel is equipped with a 35° angled low slope rack (Calles et al., 2013) from which pipes lead into four cages (collection facility; Figure 3). After malfunction in 2010 and 2011, the traps were modified and daily catch data from 2012 and 2013 were provided by E.ON. The data series from 2013 is comparably short as a result of a dry year with low discharge and non-operable facilities caused by the theft of equipment. Morphological parameters of eels caught in Ätrafors were not measured, but eels were transported downstream and released below the last hydroelectric power plant (Herting).

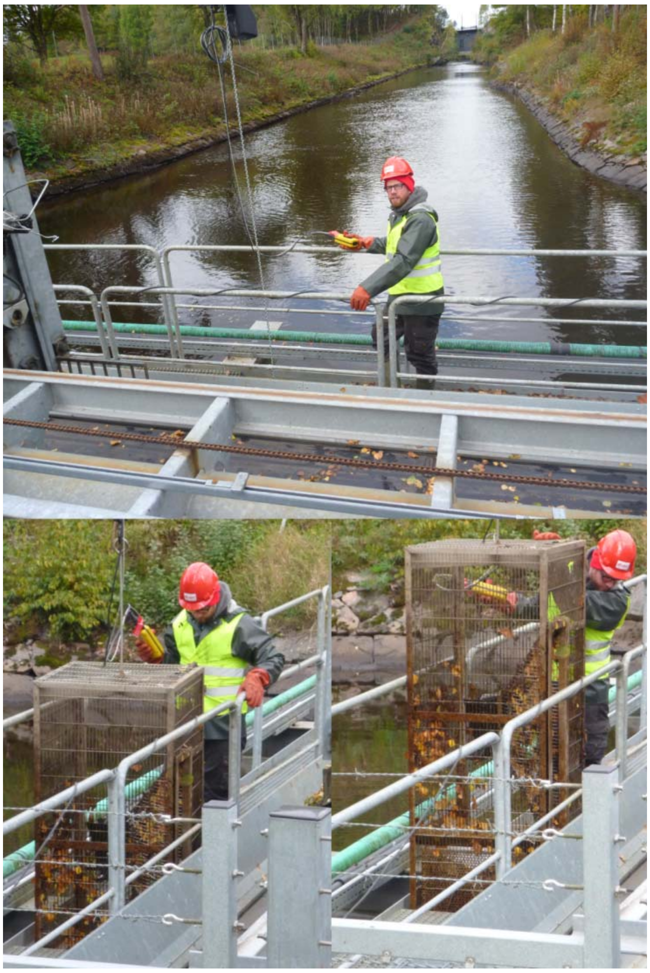


Figure 3: Collection facility in Ätrafors in the Ätran River. The four cages were lifted by an electric operated winch that had to be replaced twice in 2013.

2.1.3 Håstad Mölla (3) – Kävlingeån

Håstad Mölla (55°46'41.49"N, 13°13'53.00"E) is an old water mill by the Kävlingeån River (catchment area: 1203.8 km²) in Skåne län (Thoms-Hjärpe et al., 2002). Upstream of the mill, the river is split into two arms of which one arm flows towards the mill and through the temporarily used 'original' Wolf trap (Wolf, 1951; Figure 4). The trap is usually operated by the consultancy Eklövs fiskevård in spring in order to monitor salmon migration and trap eels for trap and transport.

Figure 4: Wolf trap in Håstad Mölla in the Kävlingeån River. View from downstream with closed gates (left); View from upstream with opened gates (right).

2.1.4 Granö (4) - Mörrumsån

Granö (56°25'58.71"N, 14°41'6.52"E) is located at the outlet of Hönshyltefjorden, Blekinges Län. The out flowing Mörrumsån River (catchment area: 3369.1 km²) passes a low sloping rack, equipped with an advanced collection facility (Figure 5).

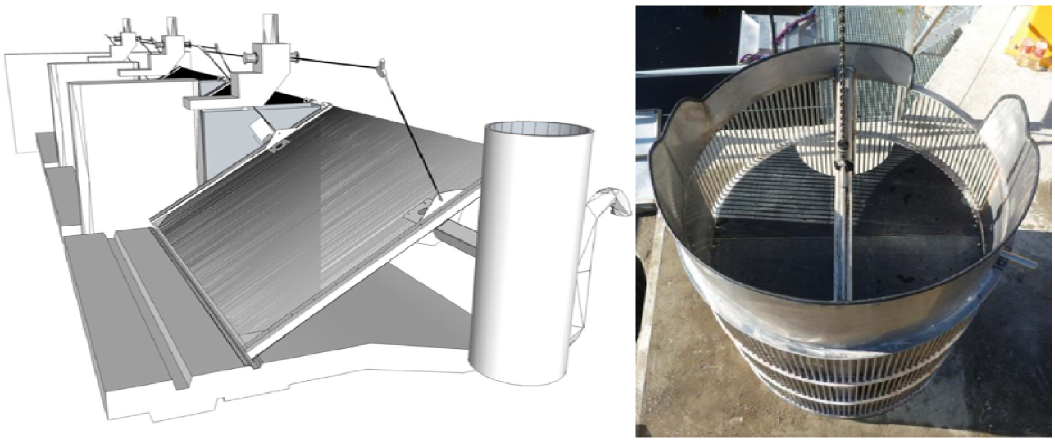


Figure 5: Granö Fiskavledare. Sketch of the low sloping rack (left) and the collection facility (right) (Karlsson et al., 2014).

2.1.5 Rönnemölla (5) – Rönne å

Rönnemölla (55°56'40.69"N, 13°22'37.44"E) is a mill including a small hydroelectric power plant, located in Rönne å River (catchment area: 1896.6 km^2), 6.5 km downstream of the outflow of lake Ringsjön (origin). Upstream from the turbine intake, the river water is dammed forming a reservoir. The dam is equipped with two small spill gates which can be opened to temporarily supply the stationary eel trap with river water (Figure 6). Problems occurred from unexpectedly heavy discharge regulation at the outlet of the drinking water reservoir lake Ringsjön (Figure 7). Resulting low water levels in the mill lake forced the trap and turbine owner to prohibit the use of the trap for most of the study period (Autumn 2012). In 2013, we were not allowed to run the trap at all.

Figure 6: Stationary eel trap at Rönnemölla in the Rönne å River (left) and gates regulating the outlet of lake Ringsjön (right).

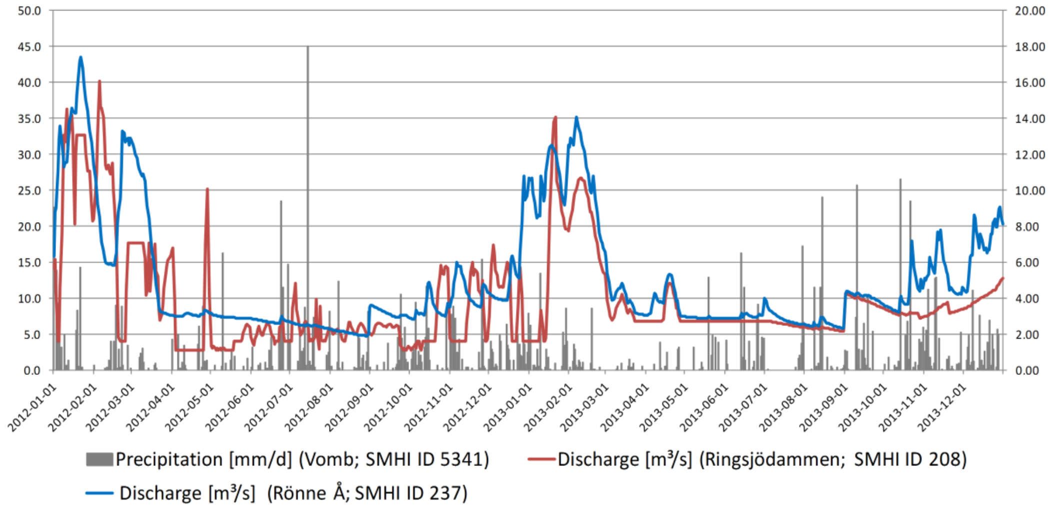


Figure 7: Discharge and precipitation in the Rönne å River (2012 & 2013). Data from SMHI.

2.2 Data collection and sample design

We counted migrating eels and sampled environmental factors at the five sites in southern Sweden (mentioned above) in order to identify preferable *migration windows*.

In Skärhult, Håstad Mölla, Granö and Rönnemölla eels were anaesthetised using benzocaine (2 g in 10 L water) and the following morphometric parameters were measured: Target length in mm (L_T), Body mass in g (M), horizontal eye diameter in mm (D_h), vertical eye diameter (D_v) and Pectoral fin length in mm (L_F). When recovered, eels were released downstream of the trap (Skärhult, Rönnemölla) or transported further downstream to avoid turbine passage (Håstad Mölla, Ätrafors).

At the sites in Skärhult (1) and Rönnemölla (5), we set up Infrared video cameras (8.5 mm CCD, Conrad electronics, Germany) linked to a digital video recorders (TVVR30003, ABUS, Germany) equipped with 2 TB hard discs (Figure 8). The view of interest (VOI) was focussed on the area where eels accumulated after they were caught. This was gained by sloping, smooth boards that led the eels to and kept them in the VOI. The IR camera and recorder were supplied by 12 V car batteries that had to be replaced every third day. The illumination in the VOI was reinforced by IR emitters. In the field, a small LCD monitor was attached to the recorder to enable the identification of the arrival time of the eels. Arrival time was later used as response in the 5 min resolved generalized linear models (GLM). Additionally, we used the arrivals times to calculate time-lags between preceding sunset and arrivals as well as following sunrise and arrival.

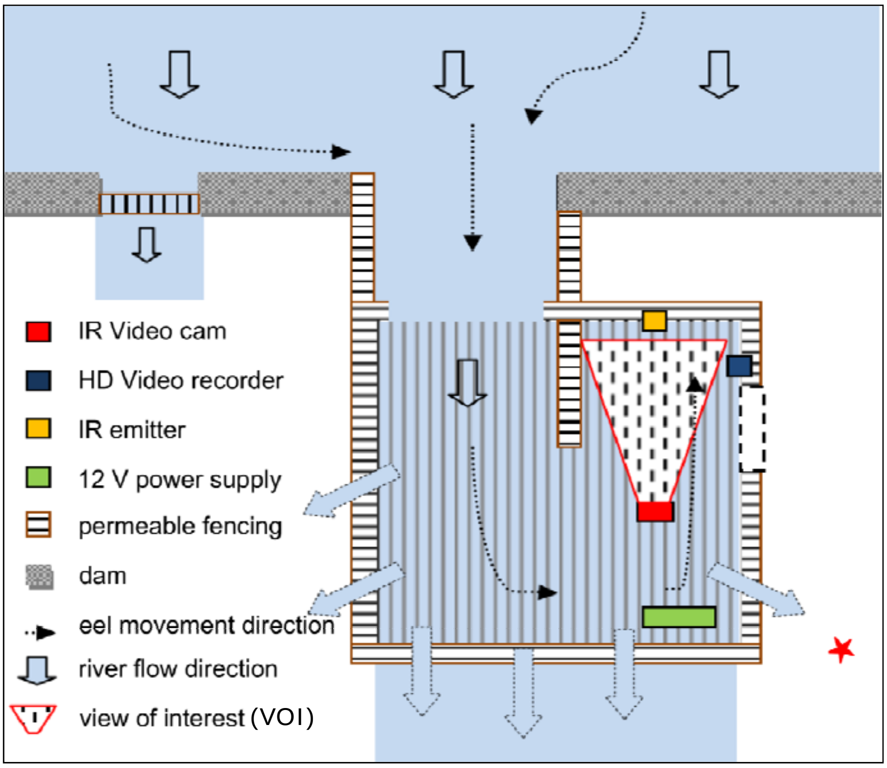


Figure 8: Sketch of the stationary eel trap in Skähultaån, the Ätran River. All electric units were stored in waterproof boxes and supplied by 12 V car batteries (Stein et al., 2013)

In Håstad Mölla (3) we made several attempts to set up an IR video installation. Unfortunately, all attempts failed due to the risk of harming other migrating fish species. Consequently, we estimated models using daily mean data for Håstad Mölla.

Data from Ätrafors (2) were provided by E.ON. Traps were checked ones per day during expected migration seasons in 2012 and 2013. In combination with environmental variables we estimated models on daily mean data for Ätrafors.

For Granö (4), we used telemetry data from the Granö Fiskavledare Project. In the framework of this project, eels were caught, radio-tagged and released in the upstream lake area (Karlsson et al., 2014). Whenever an eel arrived at a receiver's detection range, i.e. arrived at the site of the automatic receiver, we interpreted that as migration activity. We derived the number of eels per day that showed migration activity and used this as the response variable in our model for Granö.

In 2011 we carried out a small-scale mark and recapture study (*n*=29) in Skärhult. All eels that were marked and released at two different locations upstream (distance from trap; 500 m e.g. 7 km) were recaptured, except three individuals. High catchabilty (89.7 %) as well as perfect preconditions for the IR video equipment made Skärhult an excellent location to study eel migration timing.

We set up a small weather station (HOBO micro station, Onset Computer Corp., USA) equipped with sensors to measure air temperature, precipitation, solar radiation, wind speed, wind direction, and barometric pressure in Skärhult. Furthermore, we provided every site with water level loggers (HOBO U20, Onset Computer Corp., USA) and pendant temperature/light data loggers (HOBO 64K-UA-002-64, Onset Computer Corp., USA), set to 5 minute resolution (Figure 9). For the data download we used two different couplers (BASE-U-4 and ONS-BASE-U-1, Onset Computer Corp., USA).

Figure 9: Equipment. Video box including recorder, screen and power supply (upper left); One eel enters the trap in Skärhult (upper right); Water level logger (lower left); Pendant temperature/light data loggers (lower right).

Water level was measured by pressure loggers. In order to convert the pressure data into water level data they have to be referenced by barometric pressure. As an alternative, we tested modelled discharge data and gained comparable results. Moreover, this data is freely available via “Sveriges meteorologiska och hydrologiska institute” (SMHI, 2014; http://vattenwebb.smhi.se). Data on the fraction of the moon illuminated were downloaded from US Naval Observatory Astronomical Applications Department (2012).

External validation requires the same predictor variables in every model/data set. In order to enable validation among all data sets, we only included variables that were available for all sites (Table 1).

2.3 Statistical Analyses

2.3.1 Temporal data resolution and modelling approaches

According to the equipment of our study sites, we had two types of data with differing temporal resolution: two data sets with 5 min-resolution and nine data sets containing daily data. Both data types were analysed separately: $models_{5min}$ and $models_{daily}$. For analysis we estimated generalized linear models (GLM) in order to relate the response variable to a set of environmental predictor variables. Depending on our data sets, the response is probability (binomial distribution) or count data (poisson distribution).

Variable groups	Variable specification	Variable names	Number of variables
Lunar cycle	Fraction of the moon illuminated [0..1]	moon	1
Hydrological variables	Discharge [m^3/s]	Q, Q_{dif1}, Q_{dif2}, Q_{dif3}, Q_{dif4}, Q_{dif5}, Q_{dif6}, Q_{dif7}	8
	Precipitation [mm/day]	P, P_{cum1}, P_{cum2}, P_{cum3}, P_{cum4}, P_{cum5}, P_{cum6}, P_{cum7}	8
Water temperature variables	Water temperature [°C]	T_{water}, $T_{water.dif1}$, $T_{water.dif2}$, $T_{water.dif3}$, $T_{water.dif4}$, $T_{water.dif5}$, $T_{water.dif6}$, $T_{water.dif7}$	8

Table 1: List of variables that were tested as potential predictors for eel migration. $_{difx}$ indicates the time period from the present day to the preceding x days that was used for the calculation of the differences (discharge and water temperature). $_{cumx}$ indicates the time period from the present day to the preceding x days that was used for the calculation of the cumulative precipitation.

The $models_{5min}$ use a binary response variable (0 or 1). They estimate the probability that eels are present (1) or absent (0). We used the $models_{5min}$ to predict the probability of detecting migrating eels with the 25 environmental predictors.

The $models_{daily}$ use the daily sum of caught eels as response variable and the 25 environmental predictors. They were applied to predict the number of migrating eels using the 25 environmental predictors. The response in the Granö data set differed from the other eight data sets. Here, we used the number of tagged eels per day that showed migration activity.

2.3.2 Variable selection

An integral part of model building is the identification of the most important environmental predictor variables. In the first step, the predictors were checked for bivariate (Spearman) correlation. Only variables with a correlation coefficient less than 0.7 were used in the same model to avoid multicollinearity (Dormann et al., 2013). In the case of water temperature, we modelled a unimodal relationship by additionally including the squared term. For variable selection, we used backward stepwise variable selection based on Akaike Information Criterion (AIC) (Schröder et al., 2008)

We selected the variables out of a pool which contained moonlight measured on the scale from 0 to 1 and the environmental predictors discharge [m^3 s^{-1}], precipitation [mm d^{-1}] and water temperature [°C], which were averaged over a one day period. In addition, we generated variables for cumulative precipitation (from the present day to the preceding one to seven days) and also the differences between the present and the preceding one to seven days for the environmental predictors. These additional variables were added to the data set as independent potential predictors. Consequently, all data sets included the same 25 variables (Table 1). Measured and generated variables that describe the same predictor variable are termed as variable group.

2.3.3 Model validation

To assess the models' performance (i.e. model quality), we calculated three different performance criteria for the models in daily resolution. The Spearman's rank correlation coefficient (r_s) is calculated between the observed number of eels and the number of eels predicted by the model (r_s = negative or 0: no correlation between observations and predictions, r_s = 1: perfect correlation). Nash-Sutcliffe efficiency (NSE) is a common measure for the comparison of time series in hydrology. Positives values (NSE > 0 to 1) indicate that the model is better than the mean of the observed data (NSE = 0); negative values indicate that the mean yields better predictions. Explained deviance (*D*) expresses the deviance (a variance measure calculated for GLM) in the data set that is represented by the model variables. If the value is greater 0, the models predicts better than a model that is estimated on the mean number of observed eels (i.e. the so-called null model).

For the models in five minute resolution, we calculated two different performance criteria that are common measures for models estimated for binary response variables (presence or absence). The area under the receiver operating characteristic curve (AUC) asses the discriminatory power of the models (Fielding and Bell, 1997) and the value ranges from 0.5 to 1 (1 = perfect model). The values for pseudo R^2 after Nagelkerke (1991) range from 0 to 1 (1 = model explains all variability in the data set).

Internal model validation was performed by bootstrapping with 10.000 iterations (Schröder et al., 2008; Verbyla and Litvaitis, 1989). For external validation, each model was applied on every other data set and the performance criteria were calculated for these model transfers. The internal validation indicates if the model performs well (values close to 1) or not (values close to 0). On the same scale, the external validation indicates if model transferability makes any sense.

In general, external validation considers: a) temporal validation where models are transferred to different time periods but the same location, b) spatial validation, where models are transferred to data from different locations but the same time period, as well as c) model transfers in space and time. We applied all types of validation for all daily data sets.

In order to gather information on the importance of the predictors, we calculated reduced models where one of the predictors was excluded. The discrepancy between the explained deviances of the complete and the reduced models indicates the importance of the excluded variable: if the difference is large, the predictor is important. Additionally, we applied a likelihood-ratio test comparing the complete model and the reduced models to evaluate the significance of the detected difference.

Statistical calculations were performed using the free statistical software R (R Development Core Team, 2013) with packages, `fmsb` (Nakazawa, 2011), `plotmo` (Milborrow, 2011), `dismo` (Hijmans et al., 2013), `rms` (Harrel, 2013) and `epicalc` (Chongsuvivatwong, 2012), `lattice` (Sarkar, 2014), and `hydroGOF` (Bigiarini, 2014). Additionally, we applied LR-Mesh (Rudner, 2004) for visualizing response surfaces of the binary models in high resolution.

Figures that illustrate the model surfaces contain the same elements (Figure 10). In order to visualize the model content, we generated model surfaces in three dimensions (3D). The model prediction function was applied on a matrix that was formed by the ranges of the model variables. Subsequently, this matrix was plotted as a surface. X and Y axis represent one variable each. Model elevation represents the number of predicted eels. If moon is one of three significant model variables, it is set to constant 0 or 1; representing the minimum or maximum of the variable range. In that case, the model surfaces for new moon (0) and full moon (1) conditions were plotted on top of each other. In most cases, more eels are predicted under new moon conditions and consequently the elevation of the black mash surface (new moon) tops the surface that represents full moon conditions (solid gray surface). If moon was not significant, only one black mash surface was plotted.

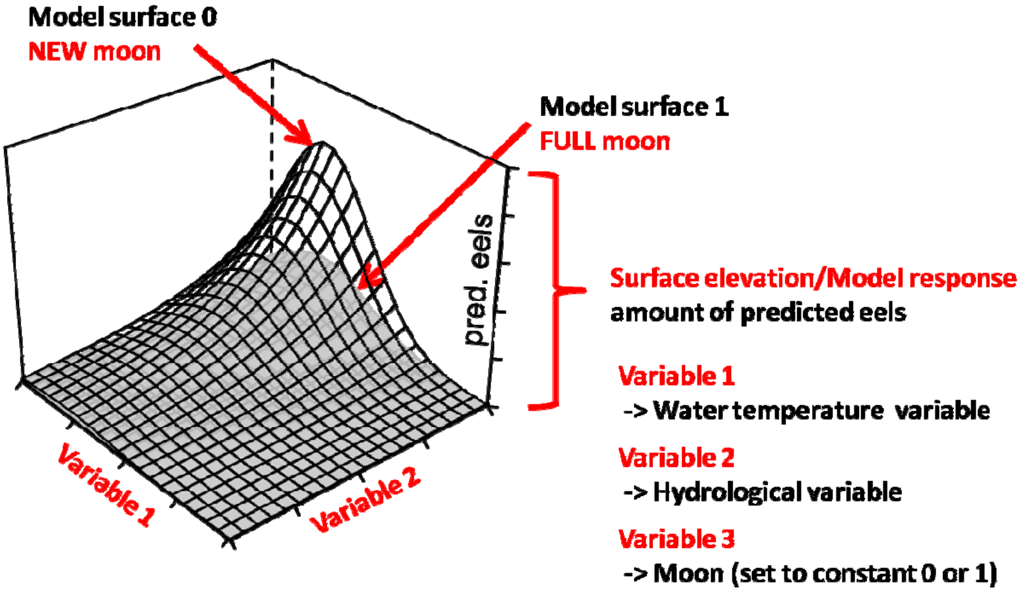


Figure 10: Elements of the model surface figures

3 Results

3.1 Models per site

Models were estimated for the single seasons of the five sites. On the one hand, the results indicate that downstream migration triggers can reliably be described by one of the hydrological variables (discharge, precipitation or one of their dynamic derivations) and water temperature. On the other hand, moon seems to have a relative low or even no influence on the migration. One exception is Ätrafors autumn 2013 $model_{daily}$ where moon covers the major part of the model deviance.

The models for Håstad autumn 2012 and Ätrafors autumn 2013 dramatically over-estimate the number of predicted eels at certain combinations of model parameters: For Håstad autumn 2012 the observations were over-estimated by factor 10 while for Ätrafors autumn 2013 prediction over-estimated the observations by factor 200. Since the models were trained on comparable short field data sets with only limited number of variable combinations, extrapolations to unmeasured parameter combinations are quite uncertain (Dormann, 2007). If parameter combinations are underrepresented in the model train data, predictions get very inaccurate and should hence not be performed. For plotting the model surfaces, we therefore excluded areas of non-measured parameter combinations (Figures 17 and 20).

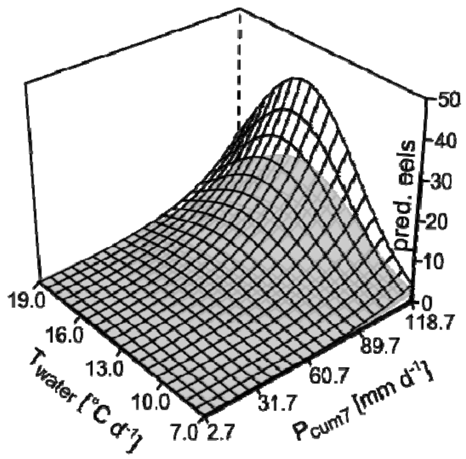
3.1.1 Skärhult

The $model_{daily}$ surfaces for the three autumn seasons from Skärhult (2011-2013) indicate highest amounts of eels if the respective hydrological variable is maximal (Figures 11-13; Tables 2-4). In 2011, the model considers cumulative precipitation of the preceding seven days (P_{cum7}), in 2012 the discharge dynamic of the preceding three days (Q_{dif3}) and in 2013 the daily mean discharge (Q).

In contrast, water temperature is described by a range of preferable degrees Celsius that shifts in between the three autumn seasons. The $model_{daily}$ autumn 2011 predicts eel for the entire range between 7 and 19 °C with much lower numbers at minimum and maximum T_{water}. $Model_{daily}$ autumn 2012 does not predict eels at the lowest water temperatures between 4 and 8 °C while the prediction for $model_{daily}$ autumn 2013 peaks on a relative low water temperature level and does not predict eels when water temperature exceeds 16 °C. Year 2013 was a comparably dry year. Late in the season when the water temperature was already low, increased precipitation resulted in increasing discharge that triggered migration even though the water temperature was already out of the optimal temperature window. This was confirmed by the higher loss of deviance and the p-values of the likelihood-ratio test (Table 4). In 2013, moon was not significant and consequently not considered in the model estimation.

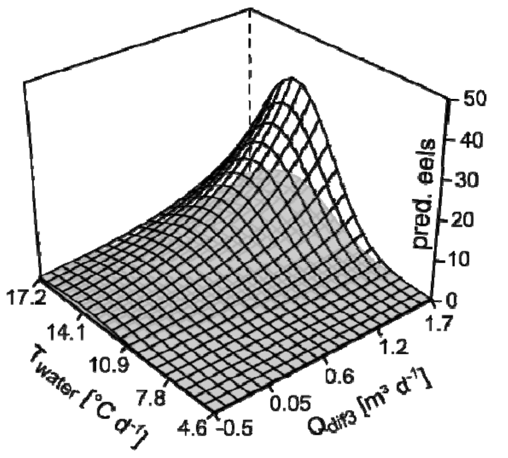
The importance of the variables is indicated by explained deviance (*D*) of the reduced models and the p-value of the likelihood-ratio test (significance of detected model difference). $Model_{daily}$ autumn 2011 looses 38 % of its deviance if precipitation (P_{cum7}) is excluded. The exclusion of moon has almost no effect on the deviance (loss = 2 %) as well as the exclusion of T_{water} (loss = 8 %). The same pattern is reflected by the p-value of the likelihood-ratio test. The reduced model from autumn 2012 shows a slightly different pattern. The loss in deviance is almost the same as for autumn 2011 if the hydrological variable is excluded (39 %), but the exclusion of water temperature results in a higher loss in deviance (27 %) as well as the exclusion of moon (8 %). In autumn 2013, moon was not considered in the model estimation and the deviance loss by exclusion of T_{water} (36 %) and Q (38 %) are almost identical.

Model performance of the three models is good. Values for explained deviance (*D*) range from 0.49 to 0.72 and Spearman correlations (r_s) from 0.54 to 0.60. In contrast, Nash-Sutcliffe efficiency performs badly for the 2012 and 2013 models (-0.64 and 0.04).



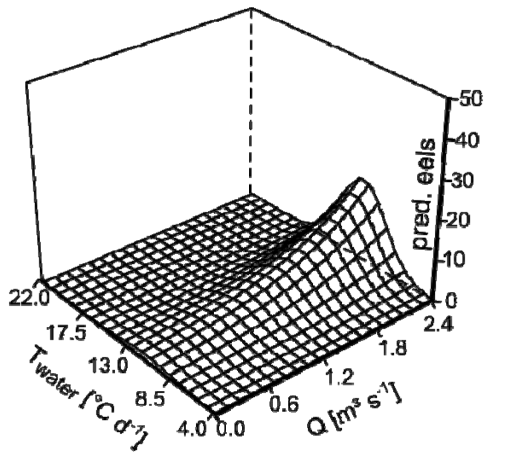
Validated model performance: *D* = 0.72, NSE = 0.80, r_s = 0.60

Figure 11: Model surface for Skärhult $model_{daily}$ autumn 2011



Validated model performance: ***D*** **= 0.52, NSE = -0.64,** r_s **= 0.64**

Figure 12: Model surface for Skärhult model$_{daily}$ autumn 2012



Validated model performance: ***D*** **= 0.49, NSE = 0.04,** r_s **= 0.54**

Figure 13: Model surface for Skärhult model$_{daily}$ autumn 2013

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-8.42	1.68	-5.00	5.60E-07	***
T_{water}	1.17	0.24	4.85	1.20E-06	***
T_{water}^2	-0.04	0.01	-4.89	9.90E-07	***
P_{cum7}	0.03	0.00	11.10	<20e-16	***
Moon	-0.75	0.27	-2.80	5.20E-03	**

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.73	100	
model.no.P_{cum7}	0.45	62	1.00E-36
model.no.T_{water}	0.67	92	9.00E-08
model.no.moon	0.72	98	5.00E-03

Table 2: Details for Skärhult $model_{daily}$ autumn 2011

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-12.48	3.60	-3.47	5.20E-04	***
Q_{dif3}	1.38	0.16	8.44	< 2e-16	***
Moon	-1.14	0.32	-3.63	2.90E-04	***
T_{water}	1.99	0.57	3.48	5.10E-04	***
T_{water}^2	-0.07	0.02	-3.18	1.49E-03	**

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.66	100	
model.no.Q_{dif3}	0.40	61	5.69E-16
model.no.T_{water}	0.48	73	1.87E-10
model.no.moon	0.61	92	2.57E-04

Table 3: Details for Skärhult $model_{daily}$ autumn 2012

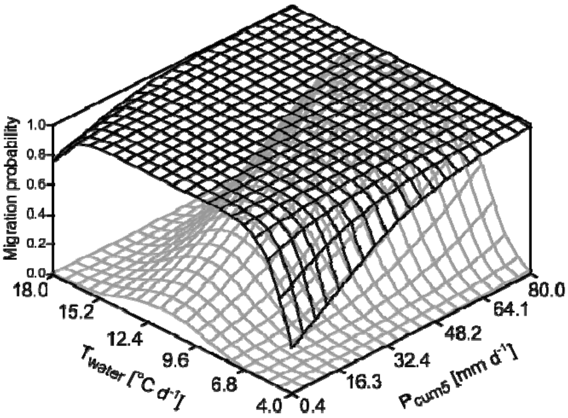
Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-12.54	1.94	-6.48	9.50E-11	***
T_{water}	2.38	0.37	6.37	1.90E-10	***
T_{water}^2	-0.11	0.02	-6.12	9.40E-10	***
Q	1.15	0.11	10.16	< 2e-16	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.59	100	
model.no.Q	0.36	64	2.74E-22
model.no.T_{water}	0.35	62	2.60E-22

Table 4: Details for Skärhult $model_{daily}$ autumn 2013

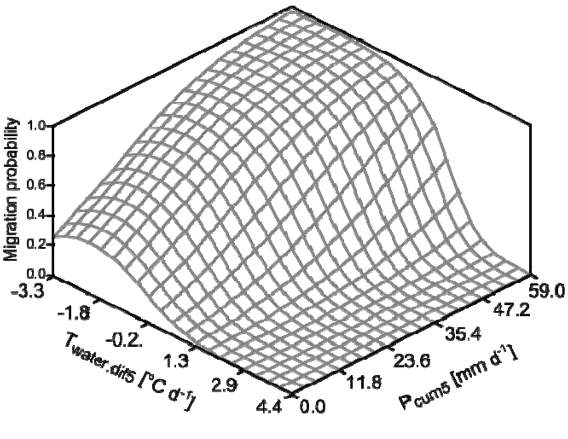
The surfaces for the data sets in 5 minute resolution ($models_{5min;}$ Skärhult autumn 2012 and 2013) draw a slightly different picture (Figures 14 and 15; Tables 5 and 6). For autumn 2012, model surfaces indicate a much higher migration probability under new moon conditions compared to the full moon conditions even though moon is much less significant than precipitation and water temperature (Figure 14; Table 5). Furthermore, the loss of deviance is higher, if water temperature is excluded (34 %) compared to the loss of the $model_{daily}$ of 2012. Exclusion of cumulative precipitation (P_{cum5}) results only in a loss of 18 %. Water temperature is described by a range of preferable degrees Celsius (between 7 and 15 °C) if precipitation is minimal. But analogue to increasing precipitation, the water temperature range expands towards its minimum and maximum.

The model surface of $model_{5min}$ autumn 2013 has a different appearance due to a different water temperature variable (Figure 15). $T_{water.dif5}$ describes the water temperature dynamic within the preceding five days. Consequently, the variable does not indicate a preferable water temperature range as the preceding models do. In contrast, the values reach from 4.4 to -3.3 and indicate most suitable migration conditions if water temperature decreased by about 2 °C within the preceding five days while the cumulative precipitation of the last five days is maximal. Model deviance looses 30 % if $T_{water.dif5}$ is excluded and 22 % if P_{cum5} is excluded.



Validated model performance: ***AUC*** **= 0.65,** R^2 **= 0.63**

Figure 14: Model surface for Skärhult $model_{5min}$ **autumn 2012**



Validated model performance: ***AUC*** **= 0.90,** R^2 **= 0.63**

Figure 15: Model surface for Skärhult $model_{5min}$ **autumn 2013**

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-9.90	7.99	-1.24	2.15E-01	
P_{cum5}	0.06	0.02	3.75	1.76E-04	***
T_{water}	2.73	0.82	3.32	9.14E-04	***
T_{water}^2	-0.12	0.03	-3.90	9.71E-05	***
moon	-7.77	4.12	-1.89	5.92E-02	.
Model	***D***	***D* [%]**	**LR-test p-value**		
model.complete	0.28	100			
model.no.T_{water}	0.19	68	4.70E-03		
model.no.P_{cum5}	0.23	82	8.70E-02		
model.no.moon	0.27	96	2.20E-03		

Table 5: Details for Skärhult model$_{5min}$ autumn 2012

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.81	0.52	-3.50	4.67E-04	***
P_{cum5}	0.07	0.02	4.42	9.68E-06	***
$T_{water.dif5}$	-1.07	0.27	-3.90	9.57E-05	***
$T_{water.dif5}^2$	-0.26	0.13	-1.98	4.78E-02	*

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.46	100	
model.no.$T_{water.dif5}$	0.32	70	2.85-05
model.no.P_{cum5}	0.36	78	1.50E-03

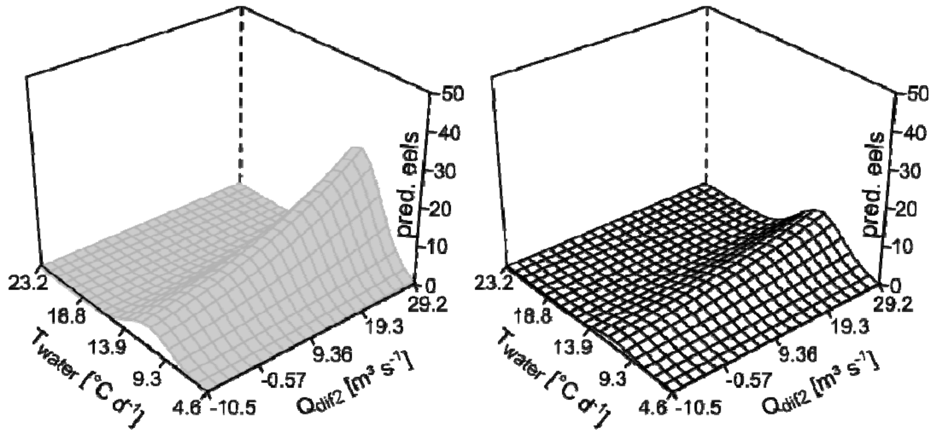
Table 6: Details for Skärhult model$_{5min}$ autumn 2013

3.1.2 Ätrafors

The model$_{daily}$ for autumn 2012 indicates highest amounts of eels if water temperature ranges between 9 and 14 °C while the discharge dynamic of the preceding two days (Q_{dif2}) is maximal (Figure 16). The importance of water temperature is indicated by the loss in deviance if T_{water} is excluded (Table 7). No eels are predicted if the water temperature exceeds 16 °C. Unlike all other models, this model indicated one basic difference. The model predicted greater numbers of eels under full moon conditions than for new moon conditions (Figure 16).

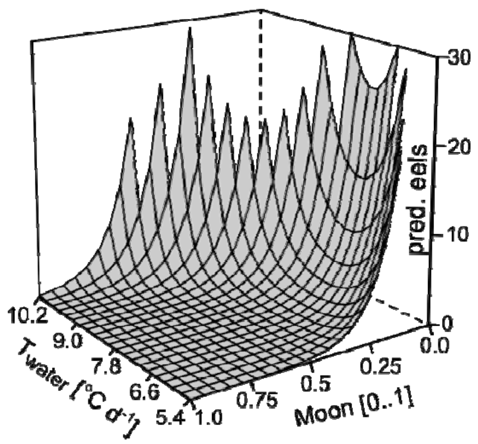
The model daily for autumn 2013 considers moon and water temperature (Figure 17; Table 8). Nevertheless, due to the limited data set and resulting limited variable combinations, the model's validity is limited, as well.

Model performance of the model autumn 2012 is ok, while the performance of model$_{daily}$ autumn 2013 is the best among the study results, but its validity is limited.



Validated model performance: *D* = 0.23, NSE = 0.28, r_s = 0.41

Figure 16: Model surfaces for Ätrafors model$_{daily}$ autumn 2012



Validated model performance: *D* = 0.88, NSE = 0.82, r_s = 0.77

Figure 17: Model surfaces for Ätrafors model$_{daily}$ autumn 2013

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-8.95	0.81	-11.03	< 2e-16	***
moon	1.03	0.21	4.90	6.00E-07	***
P_{cum5}	0.02	0.00	7.80	6.40E-15	***
T_{water}	1.85	0.16	11.33	< 2E-16	***
T_{water}^2	-0.09	0.01	-11.33	< 2E-16	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.59	100	
model.no.T_{water}	0.38	64	1.40E-74
model.no.P_{cum5}	0.56	95	7.10E-15
model.no.moon	0.58	98	3.80E-07

Table 7: Details for Ätrafors model$_{daily}$ autumn 2012

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	46.66	12.72	3.67	2.40E-04	***
moon	-10.58	1.35	-7.85	4.00E-15	***
T_{water}	-10.08	2.92	-3.45	5.60E-04	***
T_{water}^2	0.58	0.17	3.47	5.20E-04	***

Model	*D*	*D* [%]	LR-test p-value	
model.complete	0.92	100		-
model.no.T_{water}	0.9	98	1.40E-02	
model.no.moon	0.32	35	4.30E-52	

Table 8: Details for Ätrafors model$_{daily}$ autumn 2013

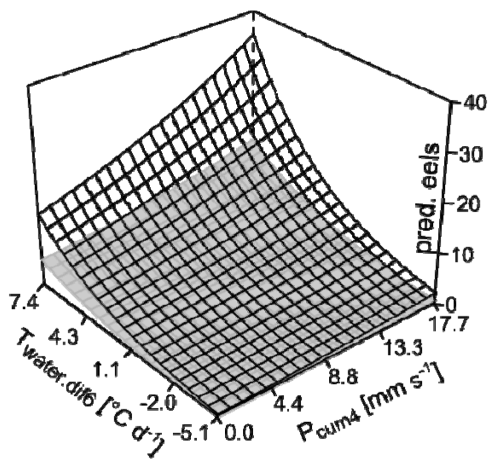
3.1.3 Håstad Mölla

The model$_{daily}$ for spring 2012 considers the dynamic of water temperature during the preceding six days ($T_{water.dif6}$), cumulative precipitation of the preceding four days (P_{cum4}) and moon (Figure 18; Table 9). Most eels are predicted if $T_{water.dif6}$ and P_{cum4} are maximal, but the higher elevation at the end of the y axis ($T_{water.dif6}$) indicates, that water temperature's contribution to the model deviance is stronger. This is also expressed by the deviances of the reduced models. If $T_{water.dif6}$ is excluded, the model deviance covers only 57 % of the complete model. In contrast, the exclusion of P_{cum4} results in coverage of 90 % of the complete model. The contribution of moon is indicated by the interspace between the two model surfaces and a loss in deviance of 4 %.

The model$_{daily}$ for spring 2013 considers only water temperature and moon (Figure 19; Table 10). Predicted migration activity starts when water temperature exceeds 5.5 °C and peaks between 13 and 15 °C and moon illumination is minimal. Excluding moon from the complete model, results in a loss of 9 % deviance. Contrary, the exclusion of T_{water} results in loss greater 99 %.

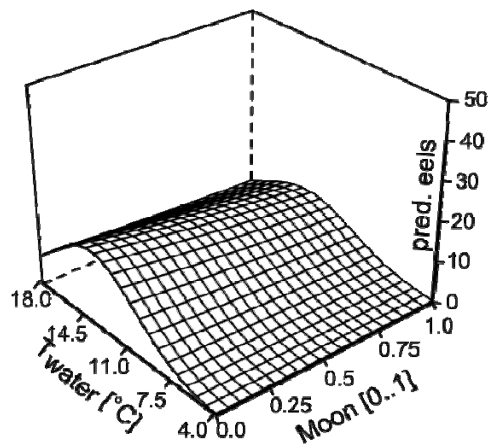
First estimations also considered a negative model coefficient for discharge as a significant variable. But when discharge was actually slightly higher after snow melt in spring and no eels were caught - water temperature was still below 5 °C. All other models as well as recent studies (e.g. Stein et al., in revision) indicate that there is no migration activity below 5 °C. Consequently, we extracted the first days from the data set and discharge was no longer significant.

The model$_{daily}$ for autumn 2012 considers water temperature (T_{water}), daily mean discharge (Q) and moon (Figure 20; Table 11). Most eels are predicted if Q is maximal while T_{water} ranges from about 9 to 16 °C. Highest loss in deviance results if discharge is excluded from the model estimation (65 %). Models with excluded T_{water} and moon cover 89 % and 81 %, respectively, of the complete model deviance.



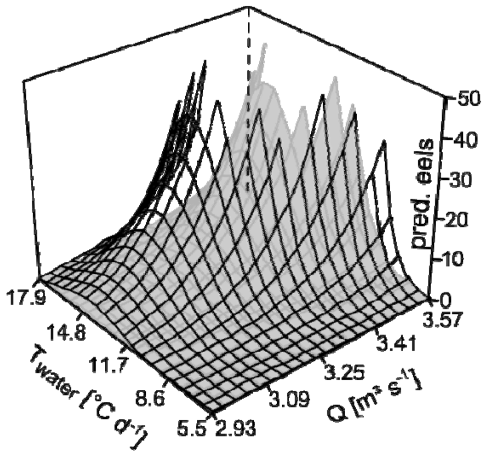
Validated model performance: *D* = 0.55, NSE = 0.55, r_s = 0.75

Figure 18: Model surface for Håstad Mölla $model_{daily}$ spring 2012



Validated model performance: *D* = 0.43, NSE = 0.26, r_s = 0.69

Figure 19: Model surface for Håstad Mölla $model_{daily}$ spring 2013



Validated model performance: *D* = 0.54, NSE = 0.59, r_s = 0.72

Figure 20: Model surface for Håstad Mölla $model_{daily}$ autumn 2012

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.30	0.21	6.25	4.10E-10	***
P_{cum4}	0.05	0.02	2.98	2.88E-03	**
$T_{water.dif6}$	0.20	0.03	6.01	1.90E-09	***
moon	-0.99	0.27	-3.59	3.30E-04	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.63	100	
model.no.$T_{water.dif6}$	0.36	57	2.00E-10
model.no.P_{cum4}	0.57	90	3.80E-03
model.no.moon	0.54	86	2.40E-04

Table 9: Details for Håstad Mölla $model_{daily}$ spring 2012

Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-5.62	0.87	-6.46	1.10E-10	***
T_{water}	1.21	0.13	9.22	<2E-16	***
T_{water}^2	-0.04	0.00	-8.90	<2E-16	***
moon	-0.58	0.14	-4.23	2.30E-05	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.44	100	
model.no.T_{water}	6.40E-06	1.50E-03	9.70E-43
model.no.moon	0.4	91	2.10E-05

Table 10: Details for Håstad Mölla $model_{daily}$ spring 2013

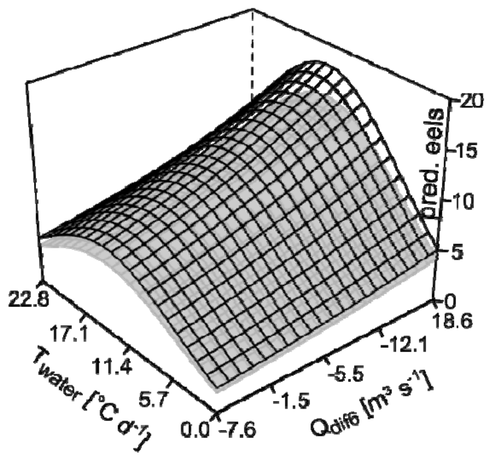
Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-41.35	7.46	-5.55	2.90E-08	***
Q	7.08	0.94	7.52	5.50E-14	***
T_{water}	3.35	0.72	4.68	2.80E-06	***
T_{water}^2	-0.13	0.03	-4.67	3.00E-06	***
moon	-1.59	0.20	-7.90	2.70E-15	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.63	100	
model.no.T_{water}	0.56	89	6.80E-10
model.no.Q	0.41	65	3.10E-28
model.no.moon	0.51	81	2.70E-16

Table 11: Details for Håstad Mölla $model_{daily}$ autumn 2012

3.1.4 Granö

The model which was estimated on the telemetry data from Granö considers discharge dynamic of the preceding six days (Q_{dif6}), water temperature and moon. A model that is estimated without water temperature covers only 11 % of the deviance. If Q_{dif6} or moon is excluded, the model covers 96 and 97 %, respectively, of the deviance. Both variables contribute little to the deviance which is additionally reflected by the large difference of the p-values compared to the value for T_{water} (Table 12). Both model surfaces are mainly shaped convex by the water temperature while the slope resulting from Q_{dif6} is less distinctive (Figure 21). Additionally, the small surface interspace shows the low influence of moon. Model performance of the $model_{daily}$ from Granö is the lowest among the study results.



Validated model performance: D = 0.08, NSE = 0.06, rs = 0.24

Figure 21: Model surface for Granö $model_{daily}$ (2012 -2013)

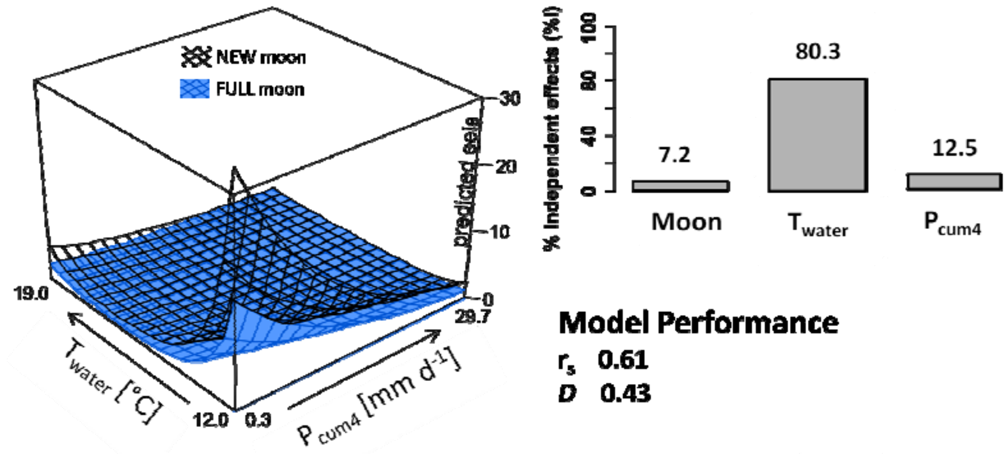
Coefficients	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.27	0.05	25.80	< 2E-16	***
Q_{dif6}	0.04	0.01	5.15	3.70E-08	***
T_{water}	0.18	0.01	20.03	<2E-16	***
T_{water}^2	-0.01	0.00	-17.10	<2E-16	***
moon	-0.20	0.04	-4.57	4.80E-06	***

Model	*D*	*D* [%]	LR-test p-value
model.complete	0.097	100	
model.no.T_{water}	0.011	11	1.60E-123
model.no.Q_{dif6}	0.093	96	4.70E-06
model.no.moon	0.094	97	6.70E-08

Table 12: Details for Granö $model_{daily}$ (2012 -2013)

3.1.5 Rönnemölla

Due to described problems (see 2.1.5) and the resulting short study period, we gained only 31 days of trap operation and caught only 40 eels. Estimated models failed by insufficient data (Figure 22). Even though the model performance seems to be reliable (r_s = 0.61, D = 0.43), model surfaces imply the problems which occurred by the limited study period. The surfaces indicate maximum number of eels if water temperature and precipitation (P_{cum4}) are minimal. The data set contains only a narrow range of water temperature (12.0 – 18.8 °C) and a relative even number of eels per day (ø 1.3 ±1.2 SD). In combination with the heavily regulated discharge (2.1.5), model output cannot be considered as useful.



Model Coefficients	Estimate	Std. Error	t value	Pr (>|z|)
(Intercept)	44.37	15.22	2.92	0.004**
moon	-0.75	0.86	-0.87	0.382
T_{water}	-5.38	1.97	-2.73	0.006**
T_{water}^2	0.17	0.06	2.58	0.010**
P_{cum4}	-0.09	0.04	-2.46	0.013*

Figure 22: Results for Rönnemölla extracted from KTÅ talk in 2013. Surfaces represent the model response for full moon and new moon conditions. Bars show the independent effects of the variables. Table summarizes the model output.

3.2 Model transferability

Knowledge on model transferability in space and time is crucial in terms of eel migration predictions and future early warning systems. Transferability in time aims for predicting eel migration with models that were trained on data from the same site but preceding or following years. In contrast, model transferability in space aims for predicting eel migration among sites with models that where trained with data from a different site.

In the first step, we calculated correlations (r_s) between the observed number of eels and the model-predicted number of eels. Surprisingly, plotted graphs were sometimes contrary to sufficient values (Figure 23; Example 1). In the second step, we calculated the Nash-Sutcliffe efficiency which is a common measure for the comparison of time series in hydrology. This criterion seemed to be more adequate for our validation as the values were low when the plots indicated low model transferability (Figure 23; Example 1). Finally, we calculated the Explained deviance (*D*) which occurred to be an adequate measure compared to the overoptimistic r_s and the rigorous NSE.

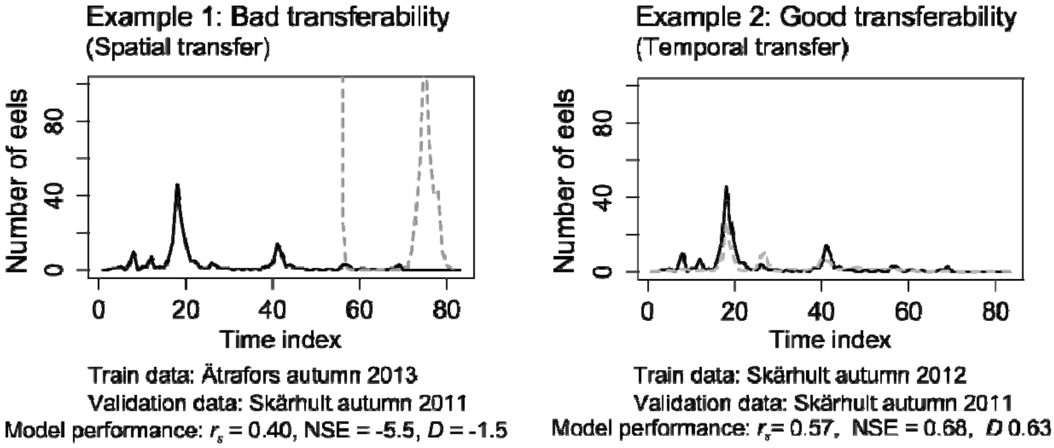


Figure 23: Examples for bad and good model transferability in space and time

3.2.1 Model transferability in time

In our study, we tested the transferability in time between different seasons from the same site. This indicated that model transfer works in 33 % and 50 % for the data from Skärhult and Ätrafors. These data sets contained autumn seasons only. For the data sets from Håstad Mölla, temporal transferability failed. Surprisingly, the only case where the validation delivered positive but weak values, the model from spring 2012 was transferred to the autumn data set of the same year.

In Skärhult, out of the six temporal validations that were executed for the three seasons, two gained positive values for all three performance criteria (D, NSE, r_s) (Table 13). One temporal validation achieved two positive values (D, r_s) and three only one positive value (r_s). The temporal validation which were executed for the $model_{5min}$, failed (Train 2012, Validation 2013: D = -7.23, NSE = -87.63, r_s = 0.07; Train 2013, Validation 2012: D = -19.88, NSE = -21.84, r_s = 0.05).

Temporal validation between the two seasons from Ätrafors produced three positive values (D, NSE, r_s) when the model Ätrafors autumn 2012 predicted on the data set Ätrafors autumn 2013. If the direction was reversed (model 2013 predicts on data 2012), only negative value were produced (Table 13).

In difference to Skärhult and Ätrafors, Håstad Mölla contains two spring and one autumn data sets. Temporal validation between the three seasons from Håstad Mölla was successful only in one case and reached positive, but very low values (Table 13). Data from Granö were only used as one data set without seasonal subsets. Consequently, temporal validation was not applied.

3.2.2 Model transferability in space

Transferability in space was tested by external spatial model validation. In total, model transfer worked moderate. Best transferability was between Skärhult and Ätrafors where 33 % of the cases worked well. Between Kävlingeån and Ätran 13 % worked poorly, while the model from Mörrumsån was not transferrable to and any other catchment.

Four out of twelve spatial validations that were executed between Skärhult and Ätrafors gained positive values for all three performance criteria (*D*, NSE, r_s) (Table 13). One additional validation gained positive values for two criteria (*D*, r_s). Validations among Kävlingeån catchment and Ätran catchment gained positive values in two cases, but values were too low to consider reasonable transferability. The remaining 13 validations gained one (only r_s) or no positive value and consequently failed, as well. Validation among Mörrumsån catchment and the other two catchments failed in all cases.

Furthermore, migration started earlier in the tributary (Skärhultaån) than it did in the mainstream (Ätran) (Figure 24).

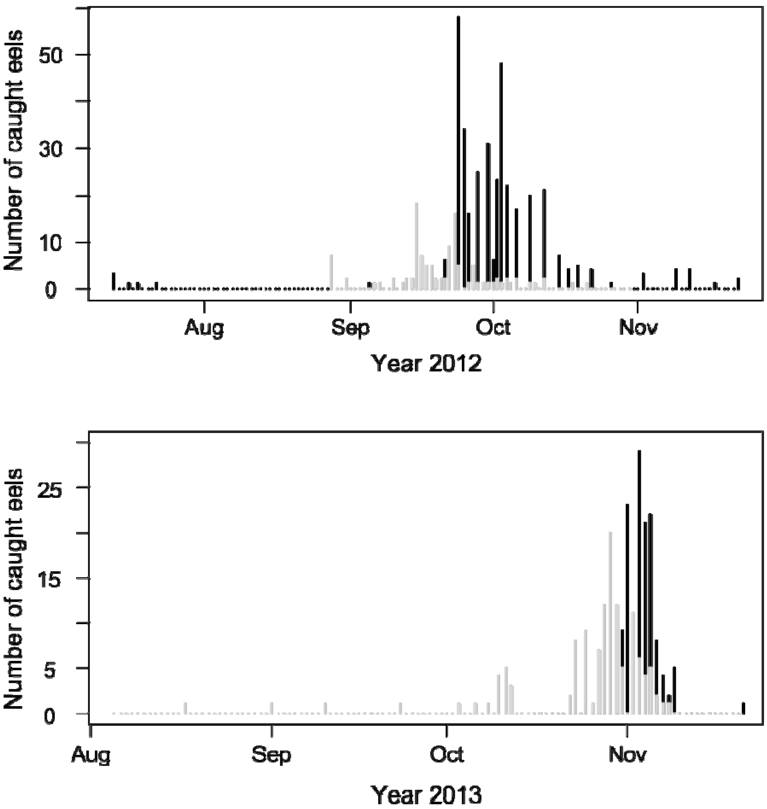


Figure 24: Number of caught eels for the years 2012 and 2013 within the Ätran catchment. Light gray bars represent the catches from Skärhult (tributary). Black bars represent the catches from Ätrafors (mainstream).

Train Data		Validation Data																										
		Ätran catchment															Kävlingeån catchment									Mörrumsån catchment		
		Skärhult autumn 2011			Skärhult autumn 2012			Skärhult autumn 2013			Ätrafors autumn 2012			Ätrafors autumn 2013			Håstadmölla spring 2012			Håstadmölla autumn 2012			Håstadmölla spring 2013			Granö 2012-2013		
	Quality criteria	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s	*D*	NSE	r_s
Ätran catchment	Skärhult autumn 2011	0.72	0.80	0.60	0.07	-0.83	0.64	-0.43	-0.09	0.01	0.35	0.21	0.28	0.65	0.48	0.68	-3-37	-0.98	0.02	-1.82	-0.41	0.17	-4.06	-1.06	0.51	-4.14	-0.70	0.25
Ätran catchment	Skärhult autumn 2012	0.63	0.68	0.57	0.52	-0.64	0.64	0.12	0.27	0.14	-7.64	-9.19	0.23	-4.14	-3.09	0.44	-2.93	-0.79	-0.13	-0.89	-0.30	0.51	-3.79	-0.97	0.32	-5.20	-22.5	0.27
Ätran catchment	Skärhult autumn 2013	-1.01	-0.09	0.06	-0.73	-1.42	0.32	0.49	0.04	0.54	0.32	0.12	0.43	0.18	0.09	0.50	-10.57	-1.08	-0.14	-2.64	-0.41	-0.06	-6.84	-1.02	0.12	-7.92	-0.7	0.34
Ätran catchment	Ätrafors autumn 2012	-0.98	-0.21	-0.13	-1.28	-5.39	0.30	0.23	-5.39	0.34	0.54	0.28	0.41	0.20	0.18	0.28	-8.35	-0.91	0.26	-1.85	-0.32	-0.33	-4.92	-0.77	0.04	-5.7	-0.58	0.3
Ätran catchment	Ätrafors autumn 2013	-1.53	-5.5	0.40	-1.62	-5.02	0.08	-5.11	-7.25	-0.30	-5.63	-1.03	-0.41	0.88	0.82	0.77	-5.19	-2.04	0.29	-1.67	-3.67	0.44	-3.24	-1.33	0.08	-1.6 +47	-5.1e +96	-0.18
Kävlingeån catchment	Håstadmölla spring 2012	-1.39	-14.5	0.37	-3.78	-28.6	0.55	0.03	0.01	0.38	-0.32	-1.18	0.29	-1.1	-19.9	0.64	0.55	0.55	0.75	0.003	0.06	0.46	-0.33	-0.14	0.23	NA	-0.61	-0.07
Kävlingeån catchment	Håstadmölla autumn 2012	-6.20	-0.18	0.42	-8.57	-0.27	0.32	-6.11	-0.14	0.46	NaN	-Inf	0.42	-6.43	-Inf	0.16	-202.0	-95839	-0.00	0.54	0.59	0.72	-5.34	-1.01	-0.26	- 8.9e+1 57	-Inf	-0.33
Kävlingeån catchment	Håstadmölla spring 2013	-0.67	-1.17	0.28	-1.78	-4.79	0.49	-1.73	-4.93	-0.15	-0.11	-0.19	-0.10	0.29	0.03	0.16	-1.90	-4.79	-0.38	-0.06	-0.24	0.18	0.43	0.26	0.69	-1.17	-0.31	0.25
Mörrumsån catchment	Granö 2012-2013	-0.96	-1.1	0.52	-2.39	-5.41	0.62	-2.63	-6.86	0.28	-0.55	-1.99	0.25	-0.70	-2.55	0.68	-1.06	-2.15	0.03	-0.00	-0.00	0.66	0.04	0.05	0.41	0.08	0.06	0.24

Table 13: Model transferability in space and time. Table summarizes the model performance for internal bootstrap validation (black cells, white letter) and external temporal and spatial model validation. Dark gray cells mark validations where all three performance criteria are positive. Light gray cells mark validations where two criteria are positive. White cells mark validations where one or no criteria is positive. Quality criteria: *D* = Explained deviance; NSE = Nash-Sutcliffe model efficiency coefficient; r_s = Spearman's rank correlation coefficient.

3.3 Morphometric fish data and nocturnal behaviour

The morphometry of the measured eels varied between the sites (Table 14). Eels from Skärhult (*n* = 414) were the largest (802 mm ± 89 mm; 984 g ± 350 g) while eels from Håstad Mölla (*n* = 1027) were medium sized (726 mm ± 75; 738 g ± 258 g). Eels from Rönnemölla (*n* = 39) were the smallest (682 mm ± 69 mm; 686 g ± 286 g). Eels that were tagged with radio transmitters were selected by size. Consequently, length and mass of these individuals cannot be compared with the other sites.

Site	*n*	L_T [mm]	M [g]	D_h [mm]	D_v [mm]	L_F [mm]	Response in Model	Data Resolution	Study period (d)
Skärhult Autumn 2011	196	805 (± 100)	1005 (± 391)	9.5 (± 1.1)	8.8 (± 1.0)	40 (± 5.9)	222	Daily	83
Skärhult Autumn 2012	129	798 (± 85)	982 (± 338)	8.1 (± 1.0)	9.2 (± 1.1)	41 (± 5.1)	113	Daily / 5 min	64
Skärhult Spring 2013	5	813 (± 61)	973 (± 180)	8.9 (± 1.5)	8.5 (± 1.8)	40 (± 4.6)	-	-	108
Skärhult Autumn 2013	89	800 (± 67)	939 (± 260)	9.3 (± 0.9)	9.2 (± 0.9)	42 (± 4.7)	125	Daily / 5 min	108
Håstad Mölla Spring 2012	176	743 (± 86)	802 (± 305)	8.2 (± 1.4)	8.4 (± 1.6)	37 (± 5.4)	175	Daily	40
Håstad Mölla Autumn 2012	375	713 (± 68)	715 (± 243)	8.2 (± 1.0)	8.2 (± 1.0)	36 (± 4.3)	360	Daily	54
Håstad Mölla Spring 2013	476	731 (± 74)	734 (± 247)	8.2 (± 1.3)	8.0 (± 1.0)	36 (± 4.5)	473	Daily	59
Rönnemölla Autumn 2012	39	682 (± 69)	686 (± 286)	7.6 (±1-5)	7.8 (± 1.5)	33 (± 6.3)	40	Daily	31
Ätrafors Autumn 2012	-	-	-	-	-	-	369	Daily	133
Ätrafors Autumn 2013	-	-	-	-	-	-	128	Daily	36
Granö 2012-2013	87	863 (± 70)	1290 (302)	-	-	-	75	Daily	594

Table 14: Morphometric fish data and model data resolution. L_T = Target length, M = Mass, D_h = Horizontal eye diameter, D_v = Vertical eye diameter, LF = Pectoral fin length, (±) = Standard deviation; SD

Arrival times of the eels (Skärhult, Rönnemölla) were set in relation to preceding sunset and following sunrise (Figure 25). In average, eels arrived in the trap 4.8 hours (± 3 h SD) after sunset and 7.5 hours before sunrise (± 3.5 h SD). Only 3 of 205 eels (1.5 %) arrived in the trap during daylight.

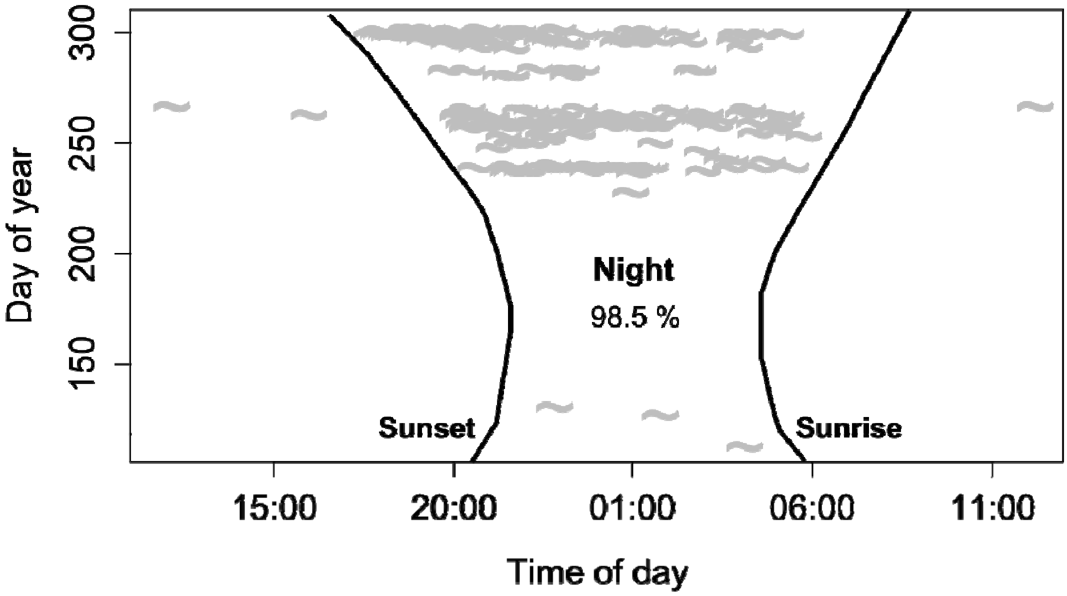


Figure 25: Eel arrivals in relation to Time of day and Day of year. Black bars represent sunset and sunrise. Gray symbols represent eel arrivals.

4 Discussion

With our study, we obtained knowledge about the migratory behaviour of European silver eels focusing on preferable environmental conditions. The identification of preferable migration conditions enables the turbine operation management to be adapted to predicted migration peaks in order to reduce eel mortality caused by turbines. By using advanced statistical modelling approaches, we tested the importance of environmental variables in the triggering of migration. Furthermore, analysis of model transferability in space (among sites) and time (among time series) generated first background knowledge for the implementation of early warning systems.

4.1 Triggering environmental variables

Our results showed that up to 88 % of the eel's migration could be reliably described using one hydrological variable (discharge, precipitation or one of their dynamic derivations), water temperature and moon. Consequently, in order to gain reliable results, it would be adequate to only measure these variables or even simply obtain them from free available sources (e.g. SMHI). The number of variables necessary for the reliable prediction of eel migration varied in previous studies. Model estimations by Trancart et al (2013) considered only weekly sums of precipitation in order to save up to 90 % from turbine induced mortality, while Durif and Elie (2008) consider photoperiod, discharge, temperature and sunshine hours to be relevant predictors in order to reach a prediction efficiency of 58-95 %.

Moreover, our results indicated differences in trigger importance depending on the location within the catchment (upper tributary vs. lower mainstream). In smaller tributaries, discharge seems to play a more important role, which also was noted by (Trancart et al., 2013). Usually, tributaries are smaller in terms of depth, width and mean discharge. Consequently, they are more sensitive to precipitation and the resulting increase in discharge. Increased discharge and associated increased water level enables the overflow of narrow areas that previously functioned as obstacles (e.g. rocks, small dams, reconnection of previously isolated meander). Most of the caught eels will originate from the upstream lake area rather than from the tributary itself. If or how they recognize the increasing discharge conditions in the outflow, cannot be determined by our study. It is possible that they move towards the outflow along with rising water levels or the recognition of continuing precipitation on the water surface. Earlier migration in upper tributaries does make sense in terms of the eel's ecology. In order to reach the sea before preferable migration conditions disappear, migration timing has to happen earlier in the upper regions.

Unlike all other models, $model_{daily}$ for Ätrafors autumn 2012 indicated one basic difference. The model predicted greater numbers of eels under full moon conditions than for new moon conditions. For regulated river systems it has been postulated that discharge regulation is able to obscure the underlying periodicity of the lunar cycle (Cullen and McCarthy, 2003). In our case, migration was mainly triggered by water temperature and discharge. The positive effect of the full moon might be a coincidence which is superimposed by the strong effect of water temperature.

Our data on spring migration were limited to one site in a tributary (Skärhultaån) and one site in a lower mainstream (Kävlingeån). In the tributary we caught only 5 eels while the numbers for the lower mainstream were greater 170 and 470, respectively in two seasons.

Firstly, this indicates that spring migration is less distinctive in the upper river system than it is in the lower system. It has been proposed that spring migration is a delay of eels that were obstructed by adverse conditions in late autumn (Durif et al., 2006; Durif et al., 2003). Due to the earlier migration period in the upstream region it is very unlikely that these eels are interrupted before they reach the lower mainstream.

Secondly, the models for the spring data from Håstad Mölla indicate that water temperature has a much larger triggering effect in spring than it has in autumn. In order to confirm or contradict those findings; we recommend additional studies on spring migration in tributaries as well as lower mainstreams. The biggest challenge for future studies will be the identification of appropriate locations that are already equipped or could be equipped with traps that deliver sufficient catch data (Calles et al., 2012; Wolf, 1951). Water temperature loggers are available from previous studies and data on the fraction of the moon illuminated (US Naval Observatory Astronomical Applications Departement, 2012) precipitation and discharge are freely available (http://vattenwebb.smhi.se).

4.2 Model transferability

We used generalized linear models to predict the numbers of migrating eels in time and space. One crucial aspect of this modelling approach is the model validation. This enables the exploration of their general applicability. If the model performs well using the same predictors independent of spatial or temporal set up, it can be used to predict when eels are going to arrive at different power plants using only a few monitoring data sets.

The models performed moderately well in temporal transferability if autumn season were validated among each other. For the two ‘autumn only’ sites transferability was good for 33 % and 50 % of the validations. At another site that included spring and autumn seasons, temporal transferability failed. For this site, only one validation returned positive values, but values were so low that they have to be regarded as coincidence rather than positive transferability. Trancart et al. (2013) applied a SAMIRAX model to predict turbine shutdown in order to save eels. Their approach required long time series (7 years) of catch data and environmental parameters for temporal validation, but as a result, it delivers sufficient predictions based only on weekly precipitation. From their perspective, precipitation is an adequate proxy that reflects almost all exogenous cues affecting migration. At an earlier stage in our analyses we had a similar idea and used only precipitation as a proxy for the hydrological conditions. But when we implemented the modelled discharge data (SMHI, 2014) model deviance increased and moon simultaneously lost explanatory power.

The environmental conditions varied between years. In 2013 frost conditions remained longer than usual and discharge conditions were low at all sites until late autumn. That might be one reason for the different considerations of absolute and dynamic variables. For example, after a long dry period a relative low increase in discharge might have a stronger effect on triggering migration than it would have in a wet year with high mean discharge.

Even though we had limited spring data, the bad transferability may be explained by the strong trigger effect of water temperature in spring. Due to a lack of comparable studies that distinguish between triggering predictors in spring and autumn, we have no reference that could prove or disprove our finding.

The sites Ätrafors and Skärhult are located within the same river catchment (Ätran). Transferability among these two sites performs reliably while transferability between the Ätran, Kävlingeån and Mörrumsån catchments fails. To our knowledge, spatial transferability among catchments has not been tested in previous studies. Therefore, it is difficult to assess the validity of our findings. However, it indicates that the model approach used here might need catchment specific models.

We were able to improve the information on model transferability with the aforementioned stepwise calculation of model quality criteria (3.2). But still, we might face the problem of temporal autocorrelation that has not been sufficiently considered. Therefore, we recommend that later studies take a two-step approach. The intended validation method would contain (1) a validation of randomly picked points and (2) a subsequent validation of time series. The combination of these two independent validation approaches might deliver more precise results wherein temporal autocorrelation is eliminated.

4.3 Recommendations and outlook

Our study provides new general and site-specific knowledge on the downstream migration of eels. It contains detailed information describing the varying effects of environmental triggers as well as model transferability in time and space. In terms of reducing turbine induced mortality, this knowledge might be used as a base for the improvement of turbine management and future early warning systems.

The following recommendations might be considered in terms of future applications:

1. Distinct nocturnal migration and very limited migration activity below 5 °C can be generalized for all study sites. Thus, this should be considered in terms of adaptive turbine management (e.g. focus on daytime turbine operation when water temperature is below 5 °C, while discharge is increased).
2. Prior to adaptive turbine management, studies should determine the local constellation of environmental triggers. This can be determined using GLMs that are estimated for daily catch data and free available environmental data (discharge, precipitation and moon) plus monitored water temperature.
3. It will be crucial, that prospective applications (e.g. turbine management, early warning systems etc.) consider the temporal dynamic of water temperature and the hydrological variables and that the possible effects of temporal autocorrelation are investigated.
4. To the best of our knowledge, spatial transferability among catchments has not been tested in previous studies. Therefore, we encourage future studies which enable testing spatial transferability within catchments as well as among different catchments.

Our results are based on catch data from stationary eel traps. We have no proof that the traps catch all of the eels that are willing to migrate downstream. Previous studies indicate that some eels hesitate for several days or even reverse upstream instead of entering the traps on the same night they arrive (Calles et al., 2013; Calles et al., 2010; Karlsson et al., 2014). Additional visual techniques such as hydroacoustic cameras (Dual-frequency identification Sonar; DIDSON) should be applied upstream of catch facilities in order to monitor the migration activity of unharmed eels. This assists in the validation of trap catchability and consequently the response of our models. Furthermore, the technique would potentially enable a behavioural comparison of tagged and untagged eels in later tagging studies.

In order to improve the modelling approach, several changes are possible. In contrast to use the number of eels per day as the response variable, it might be beneficial to use the fraction of the captured eels, instead. This would be done by using the fraction of the captured eels out of all remaining eels to be captured at that specific site during the same season. These fractions will give information on the size of the proportion of the population that responded to the triggers each day. This approach might deliver more accurate information about the probability of a single eel to get captured (migrate) given a specific set of environmental conditions.

Furthermore, models might be improved by adding the ‘number of dark hours’ as an additional variable. The number of dark hours per day differs considerably from the beginning to the end of the migration period in dependence of the latitude. In combination with the different response (fraction of captured eels) this would probably generate different results that might have a larger potential of being transferable between sites.

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