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Towards transferability in fish migration models: a generic operational tool for predicting silver eel migration in rivers

Nils Teichert^{1,2}, Stéphane Tétard³, Thomas Trancart^{1,2}, Eric de Oliveira³, Anthony Acou^{4,5}, Alexandre Carpentier⁶, Bastien Bourillon^{1,2} & Eric Feunteun^{1,2}

¹ Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, Paris, France.

² MNHN, Station Marine de Dinard, CRESCO, Dinard, France.

³ EDF R&D LNHE - Laboratoire National d'Hydraulique et Environnement, Chatou, France.

⁴ Office Français pour la Biodiversité - UMS OFB-CNRS-MNHN PatriNat, Station marine du MNHN, Dinard, France.

⁵ Pôle R&D OFB-INRAE-Agrocampus Ouest-UPPA pour la gestion des migrateurs amphihalins dans leur environnement, Rennes, France.

⁶ Université de Rennes 1 - Unité BOREA (Museum national d'histoire Naturelle, Sorbonne Université, CNRS, UCN, IRD, UA), Rennes, France.

Corresponding author: nils.teichert@mnhn.fr

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Abstract

In the global context of river fragmentation, predicting fish migration is urgent to implement management actions aimed at protecting and promoting the free movement of diadromous fish. However, large-scale applicability of conservation measures requires transferable models that enable prediction of migration even in data-poor regions. Here, we surveyed 12 contrasted European river sites to predict the activity peaks of silver eels (*Anguilla anguilla*) during river migration towards spawning areas through an ensemble modelling approach. Site-specific Boosted Regression Tree (BRT) models were adjusted using standardized hydrological variables to predict migration probability, which were aggregated in consensus predictions. Results of independent cross-validations demonstrated that silver eel migration runs were accurately predicted in response to changes in river discharge. Transferability and predictive performance were improved by considering catchment-size dissimilarity between river sites (85 to 109 930 km²) when combining the site-specific predictions. Nevertheless, we provided two examples for which the effects of human actions on flow conditions were so high that they prevented reliable predictions of migration runs. Further contributions should thus take advantage of the flexibility of our approach for updating model collection with new sites to extend the predictive performance under a larger range of ecological conditions. Our transferable hydrological-based modelling framework offers an opportunity to implement large-scale management strategies for eel conservation, even in rivers where eel monitoring data lack. The BRT models and prediction functions were compiled in an R package named 'silvRpeak' to facilitate operational implementation by end-user managers, which can determine when mitigation measures should be implemented to improve river continuity (e.g. turbine shutdown and sluice gate opening) and balance their economic activity towards eel conservation. The only input required is discharge records that are widely available across European hydrological stations.

Keywords: fish migration; river obstacle; European eel management; eel runs prediction; ensemble modelling; model transferability.

1. Introduction

The growing societal demand for predictive science remains a challenge for ecologists who are solicited to develop accurate and realistic models for informing managers and policy makers within the context of environmental change (Coreau et al., 2009). The implication of predictive models for supporting decision-making therefore assigns important responsibility for ensuring the relevance of models, providing correct outcome interpretation, and underlining application limits (Mouquet et al., 2015). Given the ecological and societal consequences of management decisions, prediction performance and accuracy are crucial components that require addressing for the acceptance of predictive models (Addison et al., 2013), along with transferability potential to different contexts or locations (Yates et al., 2018). Predictive models are thus regularly developed to inform stakeholders on numerous ecological concerns, such as spatial changes in biodiversity components or modifications in migration timing of organisms (Lenoir and Svenning, 2015).

Migration forecasts are particularly relevant to promote the free movement of diadromous fish in fragmented river networks (Barbarossa et al., 2020) for which migration between freshwater and marine environments are mandatory (van Puijenbroek et al., 2019). While river obstruction affects accessibility of catchments during upstream migration, dams and hydropower turbines are also sources of mortality during downstream movement (Eyler et al., 2016; Feunteun et al., 2000; Song et al., 2019). Even without power plants, reservoir dams can temporarily or permanently stop fish migration (Acou et al., 2008; Besson et al., 2016; Trancart et al., 2020). By accounting for the influence of environmental cues or behavioural settings, several predictive models have been developed to predict migration events for several diadromous species, including white sturgeon (e.g. Paragamian & Kruse, 2001), American eel (e.g. Smith, Fackler, Eyler, Villegas Ortiz, & Welsh, 2017), European eel (e.g. Durif & Elie, 2008; Trancart et al., 2013), or Atlantic salmon (Teichert et al., 2020a). Although providing accurate operational predictions, these models are data consuming and remain largely site specific so they cannot be generalized to other locations. This transferability issue is often due to the statistical

associations between response variables (i.e. migration estimate) and environmental predictors that are exclusively estimated for a given location but diverge in strength or do not occur under other conditions (Wenger and Olden, 2012). However, the large-scale applicability of conservation measures needs generic operational models enabling the prediction of migration even in data-poor regions (McCarthy et al., 2008) because economical constraints prevent the biological monitoring of each river obstacle.

To offset its decline, the critically endangered European eel *Anguilla anguilla* (L., 1758) was listed in Appendix II of the CITES convention, and the European Union enforced an Eel Management Plan targeting escapement of at least 40% of silver eels that should be produced under pristine conditions (European Council, 2007). Among a range of conservation measures, this plan was recommended to reduce turbine mortality, and a number of fish passage facilities were built for that purpose (Nieminen et al., 2017). However, numerous river obstacles remain without fish passage facilities because of structural impossibilities or economic constraints, and thus continue to limit escapement of silver eels to their reproduction areas (Acou et al., 2008; Trancart et al., 2020). In these locations, active solutions can be implemented without modifying the dam structure, e.g. trapping and transporting eels downstream of the dam, shutting down turbines during migration peaks, or increasing bypass attractiveness by regulating discharge (McCarthy et al., 2008; Smith et al., 2017). These measures provide effective outcomes, but they require accurate predictions of migration runs for limiting the socio-economic costs of mitigation actions (e.g. water storage reduction or hydropower generation loss; Drouineau et al., 2018; Song et al., 2019; Teichert et al., 2020b).

In Europe, eel migration typically occurs in several discontinuous runs during autumn and early winter (Durif and Elie, 2008) but occurs earlier and over a prolonged time period with increasing distance to the putative Sargasso spawning grounds (ICES, 2020; Righton et al., 2016). Therefore, fluctuation in migration timing are reported across European ecoregions, notably in the Baltic region, and between growing habitats, i.e. marine, brackish or freshwaters (ICES, 2020). Silver eel downstream migration is

initiated by endogenous and exogenous signals that coincide with optimal conditions for successful migration (Sandlund et al., 2017). Although multiple exogenous factors have been associated with eel movement (e.g. lunar phase, rainfall, water turbidity, pH, wind, and temperature), the migration peaks in rivers typically occur with rainfall events associated with sharp flow pulses, which in turn affect water velocity, turbidity, and conductivity (Cullen and McCarthy, 2003; Drouineau et al., 2017; Vøllestad et al., 1986). Runs generally occur at night, beginning during rising river flow phases (Behrmann-Godel and Eckmann, 2003; Vøllestad et al., 1986), which promotes protection against predation and reduces the swimming energy cost (Sandlund et al., 2017). Since river discharge is highly correlated with climatic and river physicochemical parameters, and widely monitored in real time across European river networks (notably near the river dams), this synthetic proxy provides a great opportunity to develop large-scale conservation measures based on generic hydrological-based models (Drouineau et al., 2018; Teichert et al., 2020b).

Here, we hypothesized that hydrological settings can be used to produce transferable models for predicting silver eel migration in rivers, with the operational aim of extending the application of conservation measures in data-poor locations. We thus developed a flexible and replicable modelling framework to provide operational decision criteria for end-user managers to implement mitigation strategies supporting the objectives of European eel management plans.

2. Materials and methods

2.1. Data collection of silver eels

2.1.1. General context of study sites

Eel migration was investigated in France and Belgium across 12 river sites (Fig. 1). Hydrological conditions were selected to ensure the representativeness of a range of river systems inhabited by eels. Although the river sites are essentially located along the Atlantic region of Europe, their

catchments extend between 85 and 109 930 km² (Table 1). The rivers flow throughout the year (perennial rivers) with an average river discharge ranging from 1 to 840 m³.s⁻¹. These rivers are subjected to pluvial or pluvio–nival regimes that are featured by high water periods during autumn and winter due to rainfalls, which can be extended in spring when the snow melts. Among the 12 sites, 10 were selected as reference sites where the natural flow regime are either not at all or only moderately modified by human activities during high-flow conditions, i.e. supporting limited or absent water storage. Conversely, the two remaining sites, the Somme and Vilaine Rivers, were used to test the transferability of migration models in highly disturbed hydrological contexts. Somme River is severely impaired by flow regulation, intensive channelling, and successive damming, which contribute to the buffering of seasonal hydrological variation and induce hydropeaking (i.e. frequent and short duration artificial releasing pulses). In the Vilaine River, a dam (500 m long) was built in the estuarine zone to regulate the river flow for flood protection and navigation purposes, which contribute to the delaying of eel migration.

2.1.2. *Field monitoring surveys*

Silver eel migration was described at a daily scale from four different monitoring techniques depending on sites, i.e. video counting data (five sites), fish trap data (three sites), fishery data collection (three sites), and telemetry data (one site; Fig. 1). The length of the time series ranged from 1 to 20 consecutive years (Supporting Information, Appendix A). Eel monitoring was largely conducted during the main migration period between September and March. Although this temporal window was slightly reduced in some locations (e.g. Dordogne, Loire, and Somme), the main migration runs were included in the sampled period (Durif and Elie, 2008).

For each river site, the monitoring data were used to produce qualitative estimates of daily migration reflecting the most important migration peaks within the season (Durif and Elie, 2008). The beginning of the migration season was fixed at 1 September in accordance with the majority of monitoring surveys. We defined P50, P75, and P95 as the main migration days required to cumulatively reach

50%, 75%, and 95% of the annual numbers of migrating silver eels. Although P50 and P75 days mechanically focused on the intensive migration runs, the P95 days usually included moderate- and low-migration events.

2.2. Modelling approach

To develop a modelling framework that can be subsequently incremented with new sites, we adopted an ensemble modelling approach to predict the migration peaks of silver eels. Site-specific models were firstly adjusted separately using Boosted Regression Trees (BRTs), then the ensemble model aggregates each single-model predictions to produce the final predictions. BRTs provide a flexible approach for modelling a response variable according to mixed types of predictors (continuous and categorical). It notably enables the modelling of non-linear relationships between the migration probability and a set of correlated predictor variables without any assumptions (Elith et al., 2008).

2.2.1. Environmental predictors

The downstream migration of silver eels was assumed to be primarily triggered by changes in river flow (e.g. Cullen & McCarthy, 2003; Drouineau et al., 2017). However, hydrological metrics have to be standardized to ensure the transferability of predictors between rivers featured by different flow conditions. Thus, this standardization uses quantile values of the frequency distribution of discharge, which reflect flow characteristics throughout the discharge range of rivers. Specific to river sites, these flow values are generally widely available or can be easily computed based on hydrological time series. Five hydrological metrics were selected as predictors of silver eel migration:

- Q_class is a class estimate of daily flow conditions denoted as numeric values between 0 and 10, where class bounds correspond to the discharge quantiles 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 0.99 of the river;

- *delta_1d* is the daily flow change standardized by the river flow amplitude. It was calculated as the discharge difference compared to the previous day divided by the difference between discharge quantiles 0.1 and 0.9, which provided a broad estimate of river flow amplitude;
- *delta_3d* and *delta_7d* are the sums of daily flow change over 3 and 7 days, respectively, standardized by the river flow amplitude. They were calculated as the sums of daily discharge differences divided by the difference between discharge quantiles 0.1 and 0.9;
- *N_above* is the cumulative number of days on which discharge exceeded the river discharge quantile 0.7 since the beginning of the migration season, i.e. 1 September. Other quantile values were tested but rejected because they were associated with lower model performance.

While *delta_1d* reflected the daily intensity of flow pulse, *delta_3d* and *delta_7d* captured the flow trends over a longer period. Standardization by the river flow amplitude enabled us to produce a comparable range of values for each river, even when absolute discharge records were distinct. Overall, the *delta* variables were expected to stimulate the downstream migration of silver eels, whereas *N_above* should have been negatively related to the migration probability. As this incremented variable reflected the amount of hydrological opportunities for migration since the season beginning (i.e. flow pulses greater than 70% of discharge records), the probability of migration peak should progressively decrease in response to the reduction in available stocks of silver eels in rivers.

In addition, the moon phase (new, waxing, full, and waning) was also considered as a predictor because eel activity is expected to increase on dark and moonless nights (Sandlund et al., 2017). A categorical approach was preferred to a continuous index of moon illumination to limit site-specific overfitting that can restrict the performance of aggregated models.

2.2.2. Adjustment of site-specific models

For each river, the occurrence probability of the three migration classes (P50, P75, and P95) was modelled separately using the hydrological variables and lunar phase as predictors. The tuning

parameters of BRTs were selected after a preliminary exploration of models' predictive performance. The best outcomes were obtained for BRT models adjusted with a Bernoulli error distribution, learning rate of 0.005, bag fraction of 0.5, and tree complexity of one, which denotes an additive model with simple trees. While complex model structures tended to increase the accuracy of site-specific predictions, the use of simple trees enhanced the transferability across river sites. For a similar purpose, we specified in our model structure that *delta_1d*, *delta_3d*, and *delta_7d* had monotone increasing relationships with eel migration, whereas *N_above* induced a decreasing effect. A class weighting method was applied to address the imbalanced distribution between the number of days with (n_1) and without (n_0) migration, which differed within and between sites. For each observation (x_i), a weight (w_i) was applied to assign a higher weight to a minority class than to a majority class, according to the following equation:

$$w_i = \begin{cases} 1/n_1 * 0.5 & \text{if } x_i = 1 \\ 1/n_0 * 0.5 & \text{if } x_i = 0 \end{cases}$$

The class weighting fixed a common class probability threshold at 0.5 to discriminate days with and without migration for each model, which also enabled the aggregation of predictions. Finally, the best number of boosting iterations in BRTs was selected based on the out-of-bag estimate of the improvement in predictive performance (Elith et al., 2008).

2.2.3. Ensemble model aggregation

For the three migration classes (P50, P75, and P95), the predictions of site-specific models were then aggregated following two different methods: averaging and weighted averaging. In the averaging method, the predicted probabilities were basically averaged considering an equal contribution of all river sites to the final prediction. However, it can be assumed that the cross-prediction performances were better between river systems with comparable hydrological conditions and catchment structure. This assumption was tested in the weighted averaging approach by assigning different weights for each site-specific model depending on their dissimilarity in catchment sizes. The dissimilarity between

two river sites (s_{ij}) was calculated as the absolute difference in log-transformed catchment size, where the log-transformation contributed to the buffering of large size differences between catchments (85–109 930 km²). Accordingly, the weight (w_{ij}) of the model j for predicting migration in site i was defined as follows:

$$w_{ij} = \frac{\min(S_i) - s_{ij}}{\max(S_i) - \min(S_i)} + 2$$

where S_i is a vector of the pairwise dissimilarity values between the site i and the sites associated with the models used for predictions. By construction, this weighting formula provided twice as much importance to the most similar site as to the most different site for providing predictions in the ensemble model.

2.2.4. *Description and evaluation of models' transferability*

The importance of the six predictors was assessed for site-specific models following Friedman (2001), which produced relative scaled values between 0% and 100%. A general overview of predictors' influence on the migration probability was then produced by averaging the importance values across river sites. In addition, the effects of predictors on the migration probability were described using partial dependence plots (Elith et al., 2008). This method provided a visualization of the fitted functions in the BRTs by showing the effect of a variable after accounting for the average effects of all others.

The performance of site-specific and ensemble models was assessed with two metrics: 1) the area under the curve (AUC) of the receiver operating characteristics (Hanley and McNeil, 1982), and 2) the accuracy, which indicated the percentage of correct classification. Contrary to the AUC metric, the accuracy requires the definition of a probability threshold to discriminate migration days from those without migration. This threshold was set to 0.5 in accordance with the weighting method used for fitting the site-specific models. To obtain a direct measure of transferability (Wenger and Olden, 2012), the pairwise predictive performance of site-specific models was calculated using each model

for predicting migration in other sites (i.e. fully independent cross-validation). Similarly, the performance of ensemble models was assessed on independent data by excluding the self-predictions for each site. Finally, we used paired *t*-tests to determine whether the performance (accuracy and AUC) of ensemble models weighted by catchment size was significantly higher than considering an equal contribution of all river sites. To illustrate the relationships between the catchment size weight and pairwise performance of site-specific models, generalized linear mixed models (GLMMs) with a Gaussian distribution were fitted using the reference model and training site as random effects. These random terms enabled an account of the non-independence of cross-predictions when assessing the significance the linear relationships between the model weights and pairwise performance (based on *F*-tests).

The analyses were conducted using R (R Core Team 2018, version 3.5.1), specifically the packages '*gbm*' (Greenwell et al., 2019) and '*nlme*' (Pistocchi et al., 2017). To ensure model operational transferability, all the adjusted BRT models, as well as model aggregation and prediction functions, were compiled in the R package '*silvRpeak*' (Supporting Information, Appendix C).

3. Results

3.1. Influence of hydrological predictors

A total of 30 BRTs was adjusted for predicting the three abundance classes of migrant silver eels (P50, P75, and P95) in the 10 reference river sites. For all classes, *N_above*, *delta_3d*, and *delta_7d* were the three most important variables with a predominant effect of flow changes over 3 and 7 days for P50 and P75 models (Fig. 2). Although the other predictors expressed more limited influences, the importance of daily flow change (*delta_1d*) tended to increase with migration class intensity, whereas the effect of daily flow conditions (*Q_class*) decreased. The moon phase appeared as the less influential variable.

In every migration class, the partial response of *delta* variables revealed non-linear relationships with migration probability, generally with threshold effects (Fig. 3; Appendix B). The migration probability abruptly increased when the flow changes became positive, indicating that eel migration was clearly related to discharge pulses. In contrast, the partial effects of *Q_class* were slighter and unbalanced between sites, but they were usually optimal for middle to high daily flow conditions. As expected, the migration probability decreased in response to the amount of discharge pulses (*N_above*) for all migration classes, suggesting a depletion in the silver eel stocks throughout the season. Finally, the migration probability was lower during the full moon phase and maximal during the new and waning moon phases.

3.2. Performance of migration models

For the three migration classes, the site-specific models revealed high adjustment performances with accuracy ranging from 74% to 97% of correct classification and AUC values between 0.85 and 0.99. When the predictive performance was evaluated by cross-validation between sites, the range of accuracy (between 0.50 and 0.97) and AUC (between 0.48 and 0.99) values extended, specifically for the minimum values (Table 2). This result suggests that outputs of some site-specific models were poorly transferable to other sites (Fig. 4a; Appendix B). Nevertheless, the aggregation of predictions in ensemble models revealed high predictive performance with accuracy ranging from 71% to 94% of correct classification and AUC values between 0.74 and 0.98 (Table 2). Although at least one site-specific model over-performed the ensemble model for each site, the range of accuracy and AUC values clearly increased towards higher predictive performance. Overall, predictive performance was better for P50 and P75 than for P95, reflecting a higher ability to detect the major migration runs than low-migration events.

The cross-prediction performance of site-specific models was generally higher between sites with similar catchment sizes (Fig. 4b). For the three migration classes, the mixed linear models revealed that the catchment size weights used for aggregating models were significantly related to accuracy (*F*-

values between 6.4 and 34.0, p -values between < 0.001 and 0.012) and AUC (F -values between 13.0 and 35.6, all p -values < 0.001). As a result, the predictive performance of ensemble models was slightly improved by weighting the site-specific predictions with the similarity in catchment size (Table 2).

3.3. Overview of migration predictions

In accordance with the high performance of ensemble models, the predicted migration probability efficiently reflected the migration runs in small and large river systems (Fig. 5a-b). Although the hydrological characteristics greatly differed, the peaks of eel activity recorded during pulses of river discharge were correctly identified. The sensitivity to flow pulses tended to decrease as the season progressed because hydrological opportunities for downstream migration had already occurred. On the contrary, predictions for the disturbed rivers were more inconsistent, notably because peaks of eel migration did not co-occur with increased river flow. For example, eel movement in the Vilaine River was sometimes observed to be out of phase with flow pulses (Fig. 5c), probably due to migration delays induced by flow regulation actions. Similarly, the silver eel migration runs in the Somme River were desynchronised with hydrological cues because river flows are subjected to intensive hydropeaking (Fig. 5d).

4. Discussion

4.1. Modelling approach and environmental predictors

Although several studies have previously emphasized the relevance of site-specific models for managing silver eel migration (Smith et al., 2017; Teichert et al., 2020b; Trancart et al., 2013), our findings demonstrated how forecasting approaches can be transferred across multiple river systems. Although there was generally at least one site-specific model that over-performed the ensemble model, selecting the best model *a priori* can be challenging. Therefore, building consensus predictions

avoids the risk of model mis-selection and provides an efficient way to reduce discrepancies and uncertainties (Marmion et al., 2009) while upgrading cross-river transferability. As previously emphasized by Durif & Elie (2008), the major migration peaks (P50 and P75) are usually more efficiently predicted than the lower one (P95). Nevertheless, the transferability of ensemble models remained high for the three migrations classes, and predictive performance was improved by weighting predictions depending on the similarity in catchment size. Such findings indicate that models are more transferable between rivers with comparable hydrological and catchment features. It can be expected that the repartition of silver eel stocks across river networks influences migration patterns (Brujls and Durif, 2009). In small rivers, the annual number of silver eels is usually low, and most eels rapidly migrate to the sea during the first hydrological opportunity (Teichert et al., 2020b). Contrarily, migration peaks and seasons are generally extended in large rivers because growing habitats are more largely disseminated along tributaries (Costa et al., 2008). The ensemble modelling approach enabled us to gather this diversity of settings by learning from the differences between site-specific models. Increasing model collection can improve the chance of obtaining reliable predictions for a larger spectrum of hydrological or ecological contexts. Here, we used a simple catchment size weighting, but future studies should consider increasing the number of site-specific models and then combining them with other similar criteria (e.g. distance to the sea, altitude, river fragmentation, or hydrological regime disturbance) to refine the predictions depending on local contexts. For example, the sensitivity of silver eel to hydrological conditions can be different in intermittent streams, such as Mediterranean rivers, or across river reaches subjected to loss of longitudinal connectivity (Acou et al., 2008). Similarly, the use of hydrological predictors only should appear restrictive for predicting migration in lagoons, reservoirs, or lakes, where other environmental factors are involved (e.g. water level, wind, coastal current, or atmospheric pressure; Acou et al., 2008; Cullen and McCarthy, 2003; Trancart et al., 2018a; Verbiest et al., 2012). In these contexts, knowledge on migration controls of silver eels should still be deepened through local monitoring surveys before implementing generic and transferable approaches.

Site-specific approaches generally use a mix of temporal (e.g. day of the year) and environmental (e.g. rainfall, river flows, temperature, and lunar phase) information for predicting eel movements (Durif and Elie, 2008; Sandlund et al., 2017; Smith et al., 2017), but the transposition of model outcomes between multiple catchments requires the selection and standardisation of a set of common predictors (Wenger and Olden, 2012). For operational purposes, the selected predictors should also induce similar behavioural responses among sites, and they must be widely available in real time across river networks (Teichert et al., 2020b). In flowing rivers, hydrological conditions fulfil these conditions as silver eel downstream migration usually peaked with rising river flow phases (Cullen and McCarthy, 2003; Drouineau et al., 2017; Durif and Elie, 2008). In accordance with these observations, our results revealed that migration probability was more influenced by flow changes (especially over 3 and 7 days) than daily flow conditions. However, the sensitivity of eels to absolute discharge values is expected to be shaped by the hydrological regimes experienced during their growth period (Trancart et al., 2018b).

To enable cross-site transferability, the hydrological variables were thus standardized according to flow values representative of each river site. Therefore, the correction by flow amplitude enabled us to produce predictors with common variation ranges, whereas the amplitude of flooding peaks was highly contrasted between sites. Despite its lower contribution, moon phase also accounted for the inhibitor effect of light conditions on eel activity (Sandlund et al., 2017; Vøllestad et al., 1986). In contrast, the physico-chemical conditions were not retained to ensure the large-scale transferability of our models. Indeed, real-time information on these parameters (e.g. turbidity, conductivity, and temperature) are more challenging to obtain because monitoring networks are scarce. Although temperature has been described as a key factor influencing the silvering process and beginning of migration season (Sandlund et al., 2017), the temperature ranges associated with physiological and behavioural processes are expected to vary across areas (Bruijs and Durif, 2009), which limits the possibility of transposition between sites (Wenger and Olden, 2012). Nevertheless, further investigations should develop bioclimatic models to predict spatiotemporal variation in the initiation

of eel migration. Such development can efficiently complement our approach by providing information on the calendar date on which the hydrological model should be applied for predicting migration peaks.

4.2. Management implication and transferability

Given the extent of hydrological stations in European river networks, hydrological-based models can potentially be applied to flowing rivers distributed across the whole continental repartition area of eels. In Europe alone, more than 21 300 hydropower dams have been recorded, and more than 8 700 additional plants are planned or under construction (WWF et al., 2019). However, the triggering and control of silver eels migration are certainly different in lagoons, highly regulated rivers, reservoirs, and lakes where the water level and its variation, together with atmospheric conditions overrule flow regimes (Acou et al., 2008; Feunteun et al., 2000; Trancart et al., 2018a). To ensure the transferability of our models to end-user stakeholders, we compiled the BRT models and prediction functions in an R package named '*silvRpeak*', available in Appendix C. Accordingly, information on river flow characteristics (i.e. quantile discharge values) and real-time monitoring of river discharge are the only two requirements for producing daily predictions in a river site where eel surveys are lacking. The model predictions, focusing on the main migration runs, provide operational indications as to when mitigation measures should be implemented to improve silver eels migration (Trancart et al., 2013). Nevertheless, the definition of a management policy generally results from negotiations between multiple stakeholders, which can lead to the selection of more or less conservative actions depending on local ecological and socio-economic factors. In such situations, the qualitative approach based on migration class provides flexibility either to focus on the major migration runs (P50) or to extend predictions to moderate (P75) and low-migration events (P95). In the same way, the cut-off value in model predictions (i.e. occurrence probability threshold) can be modulated by stakeholders to determine when mitigation actions should be taken or ceased (Smith et al., 2017). As detailed in others studies, several management actions can be planned in hydropower plants, such as turbine

shutdowns (Smith et al., 2017; Teichert et al., 2020b; Trancart et al., 2013), fish capture and release downstream (McCarthy et al., 2008), or reducing the flow passing through the turbine (Jansen et al., 2007). Similarly, the migration delays or failures induced by reservoir dams can be efficiently reduced by opening sluice gates to re-establish ecological continuity or by organising trap and transport operations when silver eels migrate downstream (Besson et al., 2016; Feunteun et al., 2000; Trancart et al., 2018a). In heavily affected rivers where downstream migration is essentially controlled by management decisions of water reservoirs, such as in the Frémur River (Acou et al., 2008), forecasts of eel migration from upstream discharge records can provide decisive information for planning the opening of sluice gates.

Although our approach implements the first steps towards a generic model, the method principally focuses on movements triggered by hydrological cues. The migration events that do not co-occur with changes in river flow are thus not detected. Such occasional migration can happen in large rivers, such as the Loire River, in which eel movement can be related to heavy rainfall or contrasted flow conditions across river tributaries (Bruijs and Durif, 2009). A gap between predicted and actual migration can also occur when migration delays are induced by obstacles and management actions (e.g. sluice gate operations, dams, and water reservoirs; Trancart et al., 2020), e.g. in the Vilaine River (dam generating an abrupt discontinuity in the estuarine–fluvial gradient) or in the Somme River (recurrent artificial discharge peaks). Accordingly, the model should be applied with caution when hydrological conditions or ecological continuity is highly modified. Further investigations should thus consider identifying quantitative metrics (e.g. hydrological variation thresholds) to quantify uncertainty in model predictions depending on local configurations, and investigating migration control in lentic water bodies, such as large lakes, lagoons, and marshes.

5. Conclusion

In summary, we demonstrated that a generic and transferable model for predicting silver eel migration can be developed based on hydrological predictors. The method was successfully applied to

a range of independent river systems and can be used as an operational tool to implement real-time management strategies. This study thus offers an opportunity to improve silver eel survival at large scales because model output provided accurate indications of when mitigation measures should be implemented, even in rivers where monitoring data are lacking. Although applicability is currently limited to running rivers or river reaches where hydrological regimes are not at all or only weakly modified, the model collection can thereafter be updated with new sites to extend prediction ability to a larger range of ecological contexts. We consider that the ensemble modelling framework proposed here can be extended to other global geographical areas or for other biological models, e.g. American eel (*Anguilla rostrata*) and Japanese eel (*Anguilla japonica*), to support the effective management of fish migration in data-poor regions.

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Figure captions

Figure 1: Location of the 12 monitored rivers in France and Belgium, using four sampling methods.

Figure 2: Relative importance of predictors for the three migration classes of silver eel. The number of models where predictors have a non-zero influence are indicated in parentheses.

Figure 3: Partial dependence plots for the six predictors used for predicting eel migration (P75) in the ten reference river sites.

Figure 4: Predictive performances of site-specific and ensemble models for the 75% migration class. a) Cross-validation AUC values for river sites sorted by catchment size (in columns) according to the models used for predictions (in row). b) Linear relationship between pairwise AUC values of site-specific models and weights used in the ensemble models.

Figure 5: Examples of migration probabilities predicted from the weighted models (P50, P75, P95) using daily river discharge ($\text{m}^3 \cdot \text{s}^{-1}$) of two reference (a and b) and two disturbed river sites (c and d). Class predictions (probability > 0.5) are indicated by upper dots. Grey bars reflect the relative observed migrations, where the main peak was fixed to one.

CRedit author statement

Nils Teichert: Conceptualization, Methodology, Data curation, Formal analysis, Software, Writing-Original draft preparation. Stéphane Tétard: Conceptualization, Data curation, Writing - Review & Editing. Thomas Trancart: Conceptualization, Supervision, Writing - Review & Editing. Eric de Oliveira: Conceptualization, Supervision, Data curation, Writing - Review & Editing. Anthony Acou: Conceptualization, Data curation, Writing - Review & Editing. Alexandre Carpentier: Conceptualization, Writing - Review & Editing. Bastien Bourillon: Conceptualization, Writing - Review & Editing. Eric Feunteun: Conceptualization, Supervision, Writing - Review & Editing.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Table 1: Hydrological features of the river sites monitored for silver eel migration. The names of nearest cities are indicated, as well as the surfaces of river catchments upper the hydrological stations. Q10, Q50 and Q90 correspond to the discharge quantiles 0.1, 0.5 and 0.9 of the rivers.

River	City	Catchment area (km ²)	River discharge (m ³ .s ⁻¹)			
			Mean	Q10	Q50	Q90
Aulne	Chateauneuf	1 224	21.9	1.73	11.5	56.4
Dordogne	Bergerac	14 040	278	58.5	220	585
Elorn	Plouedern	260	5.57	1.31	3.52	12.7
Loire	Montjean	109 930	840	177	570	1870
Meuse	Amay	16 416	202.4	44.5	133.8	478.8
Oir	Ducey	85.4	1.06	0.26	0.67	2.6
Orne	May-sur-Orne	2 516	22.3	3.04	12	55.2
Scorff	Plouay	300	5.01	0.92	3.29	11.2
Sèvre Niortaise	Niort	1 074	11.2	1.79	6.16	25.7
Somme	Bray-sur-Somme	1 543	7.59	3.44	7.13	12.7
Touques	Lisieux	632	5.32	3.21	4.47	8.07
Vilaine	Rieux	10 100	71.9	6.68	33.3	193

Table 2: Predictive performances of site-specific and ensemble models for the three migration classes. The asterisks indicate whether the performances of weighted models are significantly higher comparatively to averaged models. ns $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$.

Migration class	Site-specific models		Ensemble models - Averaged		Ensemble models - Weighted		
	Accuracy	AUC	Accuracy	AUC	Accuracy		AUC
P50	0.66 - 0.97	0.48 - 0.97	0.87 - 0.93	0.84 - 0.97	0.86 - 0.94	*	0.84 - 0.97
P75	0.55 - 0.97	0.68 - 0.99	0.81 - 0.93	0.82 - 0.98	0.81 - 0.94	ns	0.82 - 0.98
P95	0.50 - 0.89	0.61 - 0.93	0.71 - 0.88	0.74 - 0.88	0.72 - 0.88	*	0.75 - 0.88

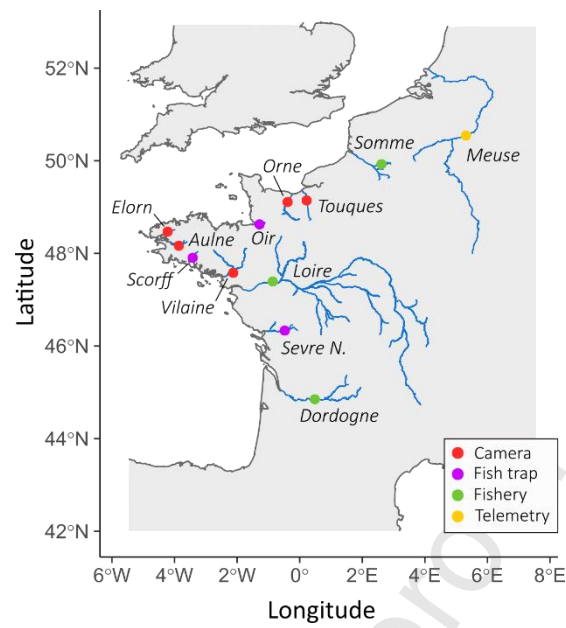


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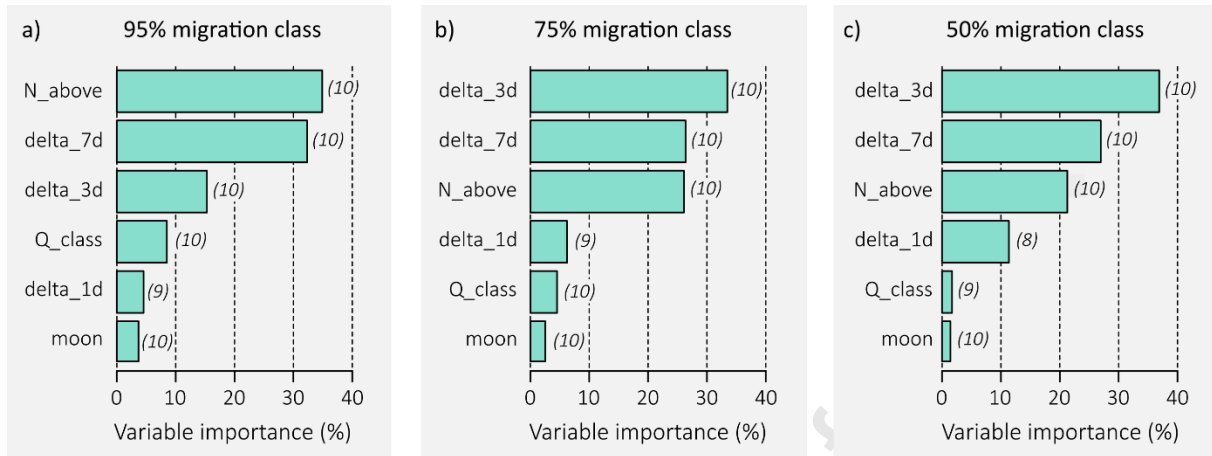


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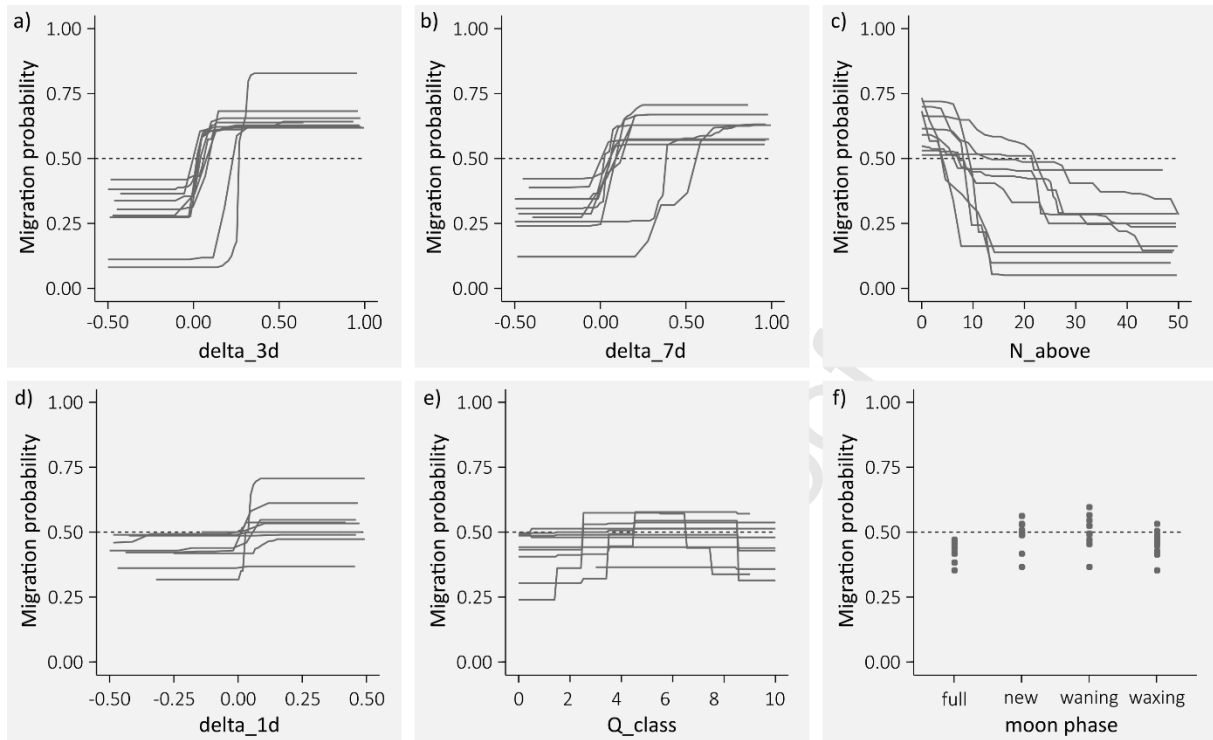


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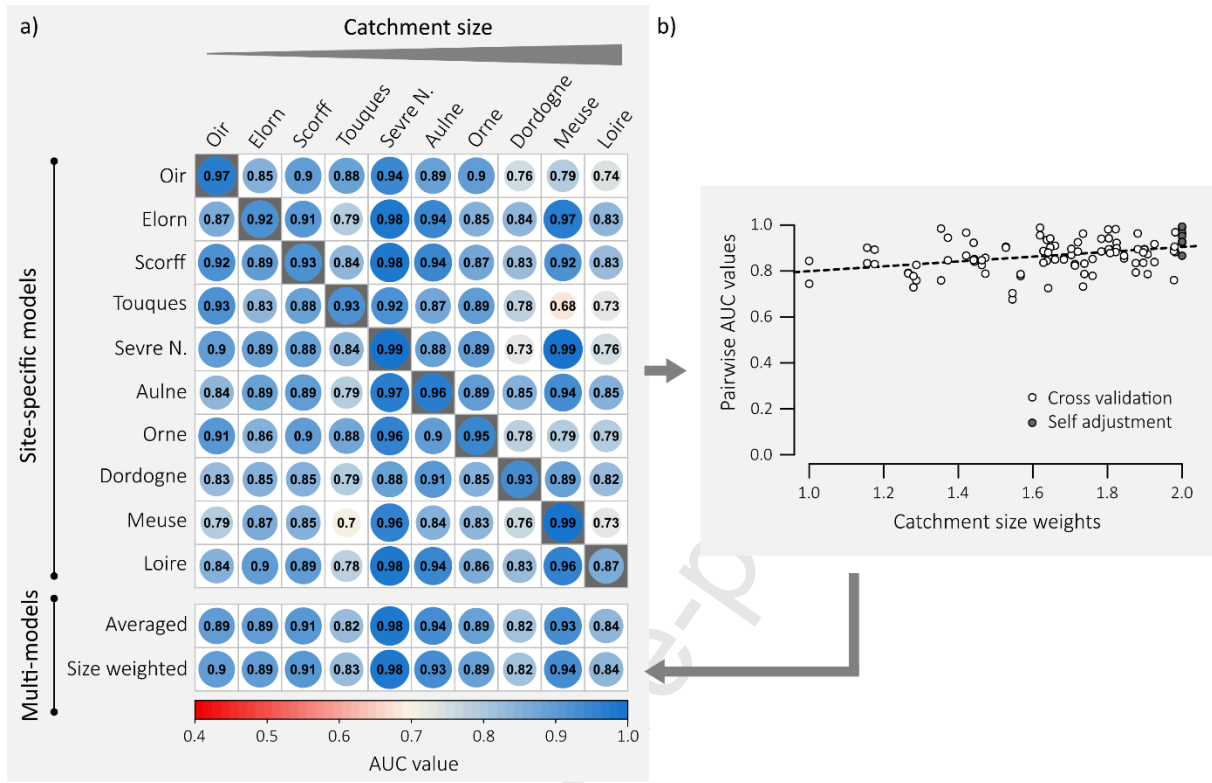


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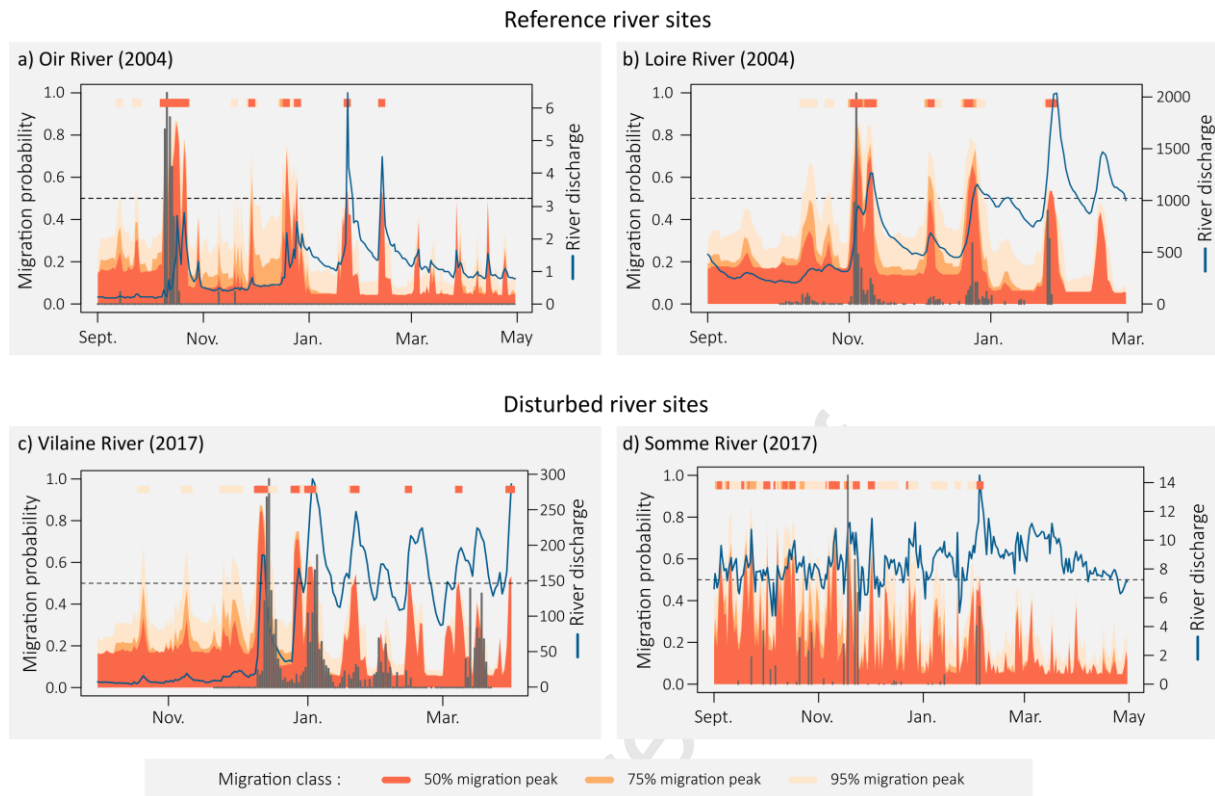
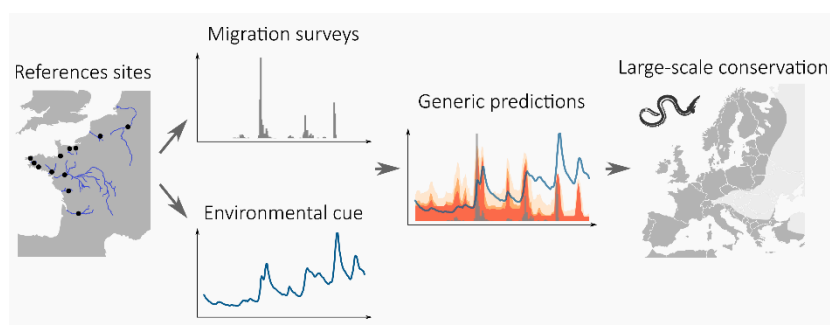


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Graphical abstract

Highlights

- Transferable tools for predicting migration are required to protect diadromous fish
- A generic hydrological-based model was developed to predict silver eel migration
- European silver eel migration was accurately predicted in response to river discharge
- Cross-validations demonstrated the model transferability in 10 river sites in Europe
- This study offers an opportunity to implement large-scale conservation measures