Received: 13 June 2019 | Revised: 17 February 2020 | Accepted: 24 April 2020
DOI: 10.1002/aqc.3382

RESEARCH ARTICLE

WILEY

# Development of an accurate model to predict the phenology of Atlantic salmon smolt spring migration

Nils Teichert[1] | Jean-Philippe Benitez[2] | Arnaud Dierckx[2] | Stéphane Tétard[3] | Eric de Oliveira[3] | Thomas Trancart[1] | Eric Feunteun[1] | Michaël Ovidio[2]

[1]Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, Station Marine de Dinard, Dinard, France

[2]UR-FOCUS, Biology of Behaviour Unit, Laboratory of Fish Demography and Hydroecology, University of Liège, Liège, Belgium

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

**Correspondence**
Nils Teichert, Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, Station Marine de Dinard, Dinard, France.
Email: nils.teichert@mnhn.fr

**Funding information**
European Union; Public Service of Wallonia, General Operational Direction of Agriculture, Natural Resources and Environment, Nature and Forest Department

## Abstract

1. Changes in migration timing, resulting from the alteration in river continuity or the effect of climate change, can have major consequences on the population dynamics of diadromous fish. Forecasting the phenology of fish migration is thus critically important to implement management actions aimed at protecting fish during their migration.
2. In this study, an 11-year monitoring survey of Atlantic salmon smolts (*Salmo salar*) from the Ourthe River, Belgium, was analysed within a European Special Area of Conservation to improve the understanding of environment-induced spring migration. A logistic model was fitted to forecast smolt migration and to calculate phenological indicators for management, i.e. the onset, end, and duration of migration, while accounting for the influence of photoperiod, water temperature, and hydrological conditions.
3. The results indicated that the photo-thermal units accumulated by smolts above a 7°C temperature threshold was a relevant proxy to reflect the synergistic effect between temperature and photoperiod on smolt migration. After integrating the effect of river flow pulses, the model accurately explained the inter-annual changes in migration timing ($R^2$ = 0.95). The model predictions provide decisive management information to identify sensitive periods during which mitigation measures (e.g. hydropower turbine shutdown, river discharge management) should be conducted to promote smolt survival.
4. The model was used to predict phenological characteristics under future scenarios of climate change. The results suggest a joint effect of hydrological alterations and water warming. Temperature increases of 1–4°C were associated with earlier initiation of migration, 6–51 days earlier, and spring flood events greatly influenced the duration of the migration period. Accordingly, the combined effects of human-induced modifications of the hydrological regimes and increasing temperatures could result in a mismatch between the smolt and favourable survival conditions in the marine environment.

KEYWORDS
climate change, disturbance, engineering, fish, hydroecology, hydropower, migration, river

## 1 | INTRODUCTION

For many organisms, the timing of key life-history transitions is controlled by external cues that coincide with favourable environmental windows for promoting individual fitness (McNamara, Barta, Klaassen, & Bauer, 2011). Such mechanisms are involved in fish migration, allowing fish populations to take advantage of the spatial and temporal heterogeneity of aquatic habitats for foraging, resting, or spawning (Dingle & Drake, 2007; Gross, Coleman, & McDowall, 1988). The initiation of fish migration is usually triggered by endogenous and exogenous signals that coincide with optimal conditions for successful migration and biological functions in the new environment (Jonsson & Jonsson, 2009; McCormick, Hansen, Quinn, & Saunders, 1998). For example, the migration of silver eels toward reproductive areas is synchronized by environmental factors (i.e. temperature, hydrology, or light intensity) that provide favourable conditions to avoid predators (Sandlund et al., 2017). Disturbances in river continuity and/or the effects of climate change, however, can influence the timing of migration and have major consequences on population dynamics and species interactions (Kuczynski, Chevalier, Laffaille, Legrand, & Grenouillet, 2017; Miller-Rushing, Høye, Inouye, & Post, 2010).

The Atlantic salmon (*Salmo salar*) is a diadromous species that migrates between nursery habitats in rivers and feeding areas in marine water or lakes (Bardonnet & Baglinière, 2000). These complex life-history transitions, associated with drastic changes in habitat conditions, make salmon populations vulnerable to human-induced disturbances (McCormick et al., 2009). Among other threats, climate change and the loss of river network connectivity have been reported as major drivers in the global decline of salmon populations (Jonsson & Jonsson, 2009; Otero et al., 2014; Thorstad, Økland, Aarestrup, & Heggberget, 2008). During the migration to the marine feeding areas, the smolt and post-smolt stages are particularly vulnerable, as changes in the migration timing can result in a mismatch with favourable survival conditions when the juveniles reach the sea (Thorstad et al., 2012). Aside from climate warming, the presence of physical obstacles in the river, such as dams or weirs, can also contribute to increased migration time to the coastal areas (Marschall, Mather, Parrish, Allison, & McMenemy, 2011). Moreover, migrating smolts may pass through the turbines of hydropower plants, resulting in direct or delayed mortality (Bickford & Skalski, 2000; Thorstad et al., 2017). Thus, to restore wild salmon populations, it is crucial to develop management strategies to promote the survival of migrating smolts. To facilitate smolt movement, several measures have been implemented in hydropower plants (Larinier, 2008), e.g. passage solutions with physical or behavioural barriers to divert or guide the fish to bypasses (Gosset, Travade, Durif, Rives, & Elie, 2005; Larinier & Travade, 2002). Effective downstream passage solutions can be complex, however, depending on the size and configuration of the site (Larinier & Travade, 2002). At some locations, active solutions may consist of the trap and transport of fish past the turbine or turbine shutdowns during migration peaks (Stich, Bailey, Holbrook, Kinnison, & Zydlewski, 2015; Thorstad et al., 2012). These measures require precise migration forecasts (based on calendar dates or using environmental records) to limit the impact on hydropower generation. Thus, predictive models to forecast the phenology of smolt migration are valuable management tools to assess phenological shifts in response to environmental changes.

The migration of juvenile Atlantic salmon typically occurs during the spring and early summer (Otero et al., 2014), but downstream movement during other months is possible (Jonsson & Jonsson, 2014). Indeed autumn migrations have been reported in some locations – these are considered pre-smolt migrations because the fish are not yet physiologically adapted to saline water (Ibbotson et al., 2013; Riley et al., 2008; Taal et al., 2014) – but autumn migrants may also contribute to the reproducing population as some adults have been detected returning from marine waters (Riley, Ibbotson, & Beaumont, 2009). During the spring smolt migration, fish undergo substantial behavioural, morphological, and physiological changes to cope with the marine conditions (McCormick et al., 1998). The smolts progressively aggregate in schools and exhibit a negative rheotactic behaviour before beginning their downstream migration (Martin et al., 2012). In the early season, the smolts are generally nocturnal but in the late season, with increased migration activity, light responsivity changes, and they tend to be balanced between day and night (Tétard et al., 2019). The parr–smolt transformation, smoltification, is partly regulated by photoperiod and temperature (Zydlewski, Stich, & McCormick, 2014). Experimental studies reported that successful smoltification requires short day length, followed by a phase of photoperiodic rise (Ebbesson, Ebbesson, Nilsen, Stefansson, & Holmqvist, 2007; Stefansson et al., 2007; Strand, Hazlerigg, & Jørgensen, 2018). Inter-annual variations in water temperature are partly responsible for variability in the onset and end of smolt migration between years (Dolotov, 2006; Jonsson & Jonsson, 2014; Otero et al., 2014). Some authors identified 8°C or 10°C as the determinant water temperature thresholds for migration initiation (Haraldstad, Kroglund, Kristensen, Jonsson, & Haugen, 2017; Hvidsten, Heggberget, & Jensen, 1998; Otero et al., 2014), whereas others found that the accumulated daily thermal units (e.g. degree-days) provide more accurate predictions (Jonsson & Ruud-Hansen, 1985; Zydlewski, Haro, & McCormick, 2005). No consensus has yet emerged to determine which component (temperature threshold vs. thermal time) is most relevant to migration phenology. Stich, Kinnison, Kocik, Zydlewski, and Krkošek (2015) suggested that both components may be involved, which is consistent with the degree-day concept measured as the time integral of daily temperature recorded above a given temperature threshold (Bonhomme, 2000; Neuheimer & Taggart, 2007). Although photoperiod and water temperature appear to be the primary triggers of smolt migration, spring floods can also play a decisive role (Aldvén, Degerman, & Höjesjö, 2015; Hvidsten, Jensen, Vivås, Bakke, & Heggberget, 1995). In Icelandic rivers, smolts from different areas vary in their response to flow changes, suggesting that the sensitivity to environmental cues may vary across geographical areas (Antonsson & Gudjonsson, 2002). Monitoring surveys also commonly report substantial inter-annual fluctuations in migration timing under field conditions (Aldvén et al., 2015; Jonsson & Jonsson, 2014). Therefore, modelling the combined effects of multiple environmental factors is essential for the accurate phenology forecast of smolt migration in river ecosystems.

Historically, Atlantic salmon were widely distributed in tributaries of the Meuse River, but since the 1930s they have declined throughout the hydrographic region (Philippart et al., 1994). In 1987, an ambitious conservation project (Meuse Saumon 2000) was initiated to restore salmon and sea trout (*Salmo trutta*) populations in the Meuse basin. This project was notably motivated by the framework of the European Habitats Directive (Council of the European Communities, 1992), which enjoins the Member States to ensure the restoration or maintenance of natural habitats and species listed in Annex I and II, respectively. Annex II provides a list of species (about 900), including *Salmo salar*, for which Special Areas of Conservation should be designated to manage and restore favourable conditions to ensure the long-term survival of species and their habitats. The presence of Atlantic salmon and other listed threatened species (e.g. sculpin *Cottus gobio*, brook lamprey *Lampetra planeri*) in the lower Meuse River and its tributaries has encouraged the Walloon authorities to propose several areas to be included in the Natura 2000 network. In such context, several steps have been taken to improve the water quality and river connectivity along the Meuse river basin (e.g. fishway, bypass), and restocking actions are conducted every year in the main tributaries, using eggs and juvenile salmon from Scottish, Irish, and French strains. The Ourthe River is a major tributary of the Belgian Meuse and is currently the focus of restocking operations owing to its high water quality and the availability of suitable salmonid habitats (Ovidio et al., 2017). Since 2007, 100,000–500,000 Atlantic salmon juveniles have been released annually within the Ourthe River basin. The first positive outcome of the restoration project was obtained when an adult salmon in reproductive migration was caught in the lower Belgian Meuse. Although the number of spawners increases each year (Ovidio et al., 2019), the salmon population in the lower Belgian Meuse currently remains supported by the stocking management strategy (Ovidio et al., 2017); the project's success is hampered by the low smolt escapement during their passage through the canalized Meuse. River fragmentation by dams alters the flow velocity regime and causes shifts in water temperature, which disorients the migrating smolts and reduces their survival. In addition, the presence of hydroelectric power plants results in direct mortality when the fish cross through the hydropower turbines. Several fishways were built to allow adult salmon migration in upper areas of the river, but the smolts remain susceptible to turbine-induced injuries during their downstream migration. Thus, measures aiming to increase the survival of smolts are essential to improve the outcome of the restoration programme in the Meuse River Basin.

The objective of this study was to improve the understanding of the relationship between environmental factors and smolt spring migration by investigating an 11-year survey of Atlantic salmon at a hydroelectric power plant in the Ourthe River, Belgium.

## 2 | STUDY AREA

Atlantic salmon smolts were collected at the Méry hydropower plant (50°33′04.9”N 5°35′07.3″E), in the lower Ourthe River (mean interannual discharge: 44 $m^3 s^{-1}$) and 12.7 km upstream of the confluence with the Meuse River (Figure 1). The upstream part of the Ourthe basin includes 3,273 km of river length and 32.8% are included in the Natura 2000 network. The hydropower site consists of an intake weir (length: 100 m, maximum height: 1.8 m) that diverts water towards two turbines (Kaplan turbine, diameter: 1.8 m, speed: 250 revolutions $min^{-1}$). The maximum diverted water flow is 10 $m^3 s^{-1}$. The minimum ecological flow is maintained at 3–5 $m^3 s^{-1}$ and continuously spills over the dam. A slightly inclined trash rack (length: 10 m, height: 3 m, 67° angle) with 5-cm spaced bars is positioned before the water intake and helps to guide the migrating fish toward a bypass (mean flow in the bypass: 0.25 $m^3 s^{-1}$). A mercury power lamp was installed at the bypass entrance to improve its attractiveness to smolts. Fish using the bypass are collected in a trap (length: 1 m, width: 0.8 m, height: 0.8 m) for scientific monitoring. Preliminary telemetry surveys conducted at the Méry site estimated that, depending on hydrological conditions, 45–64% of the migrating smolts used the bypass (Renardy et al., 2020). The trap efficiency is expected to decrease at higher river flow, and trap monitoring cannot be conducted when the river flow exceeds 100 $m^3 s^{-1}$. In 2018, a third hydropower turbine (Archimedes screw, with a rotational speed of 22.8 revolutions $min^{-1}$, maximum flow: 7 $m^3 s^{-1}$) was installed on the right bank of the river (Figure 1). The attractiveness of this

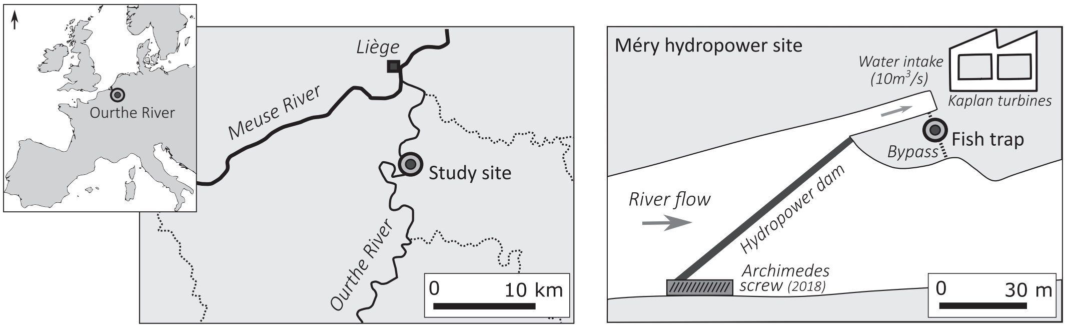

**FIGURE 1** Geographical location of the study site on the downstream Ourthe River, a tributary of the Meuse River in Wallonia, Belgium. Atlantic salmon smolts were caught using a fish trap located in a bypass of the Méry hydropower plant

pathway was estimated to be low (from 1 to 12% of migrating smolts) owing to the hydraulic configuration (Renardy et al., 2020). Therefore, the repartition of smolts between the migration pathways was presumed to be comparable with those observed before installation of the third turbine installation.

Water temperature (°C) and river discharge ($m^3\ s^{-1}$) were continuously monitored during the study period. Hourly water temperature was recorded using data loggers (Onset TidBit) located at Méry site, and hourly flow data ($m^3\ s^{-1}$) were provided by the Wallonia Public Service of Hydrological Studies (SETHY, Walloon Region).

# 3 | METHODS

## 3.1 | Monitoring phenology of smolt migration

Atlantic salmon smolts were monitored in the fish trap during the spring migration, i.e. generally from mid-March to June of 2007–2018. However, for the 2008 season, sampling occurred later (22 April), so numerous smolts may have already migrated downstream. Consequently, smolts caught in 2008 were excluded from the analyses. The number of smolts in the trap was recorded approximately every 2 days (mean ± SD, 2.3 ± 1.4 days), depending on the hydrological conditions and the number of smolts previously caught. Accordingly, the time between counts was extended when the fish catch numbers were low. These fluctuations in sampling efforts prevent accurate daily estimates, but the data can be used as cumulative proportions to investigate the phenology of smolt migration. Indeed, the cumulative proportion analysis considers the total number of individuals that have already migrated on each sampling date but does not require daily estimates of smolts abundance during the whole migration season.

The river flow (mean ± SD) was 31.9 ± 21.3 $m^3\ s^{-1}$ during the study period. The fish trap efficiency varied with the hydrological conditions owing to its location on the side of a power channel where the maximum discharge is fixed at 10 $m^3\ s^{-1}$. The catch rate is thus expected to decrease when river discharge increases because of the higher proportion of fish passing over the submerged dam. This effect was accounted for by correcting the number of smolts by assuming that the catch rate was linearly related to the river flow. In the absence of specific study site details, this assumption is based on telemetry experiments of Atlantic salmon smolts in other rivers (Thorstad et al., 2017). The corrected number of smolts ($N_{cor}$) was calculated as: $N_{cor} = N_{trap} * Q_{river}/Q_{channel}$, where $N_{trap}$ is the number of smolts collected in the trap, $Q_{river}$ is the mean river discharge during the monitoring interval, and $Q_{channel}$ is the channel discharge, reaching a maximum value of 10 $m^3\ s^{-1}$.

The cumulative proportion of smolts was calculated over the sampling years to model the timing of migration and the phenological indicators. The onset of migration was defined as the day when 10% of smolts have migrated, and the end of migration was defined as the day when 90% of the smolts have been caught in the trap. Subsequently, the duration of the migration season was calculated as the time interval between the onset and end of migration, during which 80% of the spring smolts migrated.

## 3.2 | Phenological model of smolt migration

The smolt migration phenology was assumed to be shaped primarily by the environmental conditions experienced by fish over time, rather than by the instantaneous conditions or calendar time units. This approach is analogous to the developmental threshold model, which assumes that the developmental transitions in plants or animals can be predicted once a given level of developmental units has accumulated (Donohue, Burghardt, Runcie, Bradford, & Schmitt, 2015). Here, the accumulated thermal time (degree-days to migrate) and photo-thermal time were used as the developmental units, to account for the critical role of water temperature and photoperiod in regulating smolt migration (McCormick et al., 1998; Zydlewski et al., 2005, 2014).

### 3.2.1 | Degree-day

For each date, the degree-day ($DD$, °C day) was estimated as: $DD = \sum DTT$, where $DTT$ is the daily thermal time, using the winter solstice as the starting date of the cumulative function. This starting point was selected for consistency with experimental results showing that exposure to an increase in photoperiod is required to induce the parr–smolt transformation (Stefansson et al., 2007; Strand et al., 2018). According to the classic formula (Chezik, Lester, Venturelli, & Tierney, 2014), the daily thermal time was calculated as: $DTT = T_{avg} - T_{thr}$, *if* $T_{avg} > T_{thr}$, where $T_{avg}$ is the daily average temperature estimated as $T_{avg} = (T_{min}+T_{max})/2$. $T_{min}$ is the minimum temperature, $T_{max}$ is the maximum temperature, and $T_{thr}$ is a temperature threshold – the temperature below which smolt migration is expected to be effectively zero. When $T_{avg} > T_{thr}$ the daily thermal time is set to zero. No prior assumption was formulated for $T_{thr}$, so the degree-days were calculated at five different temperature thresholds: $T_{thr}$ = 5,6,7,8,9 °C, to determine which best explains the variability in smolt migration. This thermal range was based on previous studies examining the temperature thresholds that initiate smolt spring migration (Haraldstad et al., 2017; Otero et al., 2014; Whalen, Parrish, & McCormick, 1999).

### 3.2.2 | Photo-thermal unit

The photo-thermal units ($PTU$, °C day hour) accumulated between the winter solstice and the sampling date were calculated as $PTU = \sum (DTT * D_{light})$,where $D_{light}$ is the day length (in hours). This metric is commonly used in plant ecology (McMaster et al., 2008) because it integrates the role of photoperiod within the predictions of phenology by multiplying the thermal time by day length. Therefore, the photo-thermal approach assumes an interactive effect between temperature and photoperiod, which has been demonstrated in the timing of smolt development (McCormick, Shrimpton, Moriyama, & Björnsson, 2002; Zydlewski et al., 2014).

### 3.2.3 | River discharge peak

A sharp increase in river discharge is expected to increase the daily proportion of migrating smolts (Aldvén et al., 2015; McCormick et al., 1998), which can also influence migration timing, i.e. onset, end, and duration. To account for this effect, a simple binary metric was generated to indicate whether smolts had experienced a discharge peak since the spring equinox. A value of 0 was assigned to the sampling dates before the first discharge peak and a value of 1 was assigned to the dates after the peak. The values were all 0 if no discharge peak was experienced during the year. Discharge peaks ($Q_{peak}$) were defined as the days when the river discharge was more than twice those recorded during the 5 previous days (selected empirically based on a visual exploration of data). Similarly, the spring equinox was used as the starting date because smolts did not appear responsive to a change in river flow before this photoperiod threshold, according to the results (see Results section).

### 3.2.4 | Phenological model

Logistic models were adjusted to model the cumulative proportion of migrating smolts as a function of the environmental conditions experienced by fish: photoperiod ($PP$), degree-days (from $DD_{5^\circ C}$ to $DD_{9^\circ C}$), photo-thermal units (from $PTU_{5^\circ C}$ to $PTU_{9^\circ C}$), and discharge peaks ($Q_{peak}$). Except for the discharge peaks, all of these factors were highly inter-correlated (Pearson correlation coefficients, all $r > 0.8$), so to avoid multicollinearity, they could not be included in the same model (Dormann et al., 2013). Thus, a model selection procedure was conducted to compare the performances of the 34 possible models lacking correlated variables. Explicitly, these models included one ($Q_{peak}$, $PP$, $DD_{5^\circ C\ to\ 9^\circ C}$, or $PTU_{5^\circ C\ to\ 9^\circ C}$) or two predictors when the effect of discharge peaks was analysed in combination with the photoperiod ($PP$), degree-days (from $DD_{5^\circ C}$ to $DD_{9^\circ C}$), or photo-thermal units (from $PTU_{5^\circ C}$ to $PTU_{9^\circ C}$). Models with interaction terms were also tested when two predictors were included. The Akaike Information Criterion (AIC) was used to determine the most parsimonious phenological model for smolt migration. The logistics models were fitted using the data collected between 2007 and 2017, and the 2018 migration season was used to assess the model's predictive performance. Parametric bootstrapping was conducted with 1,000 replicates to generate 95% confidence intervals of the selected model parameters, including model coefficients and performance criteria (pseudo-$R^2$). The estimated coefficients were assumed significant when the 95% confidence intervals did not overlap zero. The model coefficients derived from the bootstrap simulations were then used to estimate uncertainty in the predictions of the phenological indicators.

### 3.2.5 | Warming scenarios

The most parsimonious model for smolt migration was used to explore potential phenological variation under scenarios of increased water temperature. By 2030, global climate projections predict an air temperature increase of up to 2.5°C across Europe. By 2060, the most pessimistic scenarios suggest that temperatures may increase by 4.3°C, but with significant differences between the regions (Mack et al., 2019). Thus, the phenological indicators (the onset, end, and duration of migration) were calculated for climatic scenarios where the water temperature increases by +1°, +2°, +3°, and +4° compared with the mean temperatures during the study period (2007–2018). No seasonal variation in water warming was assumed, so the temperature increase was applied uniformly throughout the year. To assess the combined influence of river temperature and hydrology, the phenological indicators of warming were estimated without river discharge peaks during the migration period or with a flow pulse in the early season (1 April). Indeed, the peaks in river discharge can act in combination with temperature to synchronize the initiation of fish migration; therefore, the projections with and without discharge peaks can illustrate the influence of river flow on the smolt migration under scenarios of future climate change.

All computations and statistical analyses were performed in R (R Core Team, 2018), using the package '*boot*' for the bootstrap procedure (Canty & Ripley, 2017) and the package 'vioplot' for the graphical outcomes (Adler & Kelly, 2018).

## 4 | RESULTS

### 4.1 | Annual patterns of monitored smolt migration

During the study period, the fish trap was monitored 385 times (24–40 surveys per migration season) and 15,695 migrating smolts were collected, with large inter-annual variation (97–4,496 fish per season). The spring migration generally occurred between early April and mid-May, but there was variability in seasonal patterns (Figure 2). The seasonal distributions of smolt catches were usually uni- or bi-modal, but the migration events were sometimes evenly distributed throughout the season (e.g. 2017). Nevertheless, migration runs were commonly observed within the seasonal survey period (Figure 2), suggesting synchronicity in downstream movements in response to environmental or social cues. Several migration pulses coincided with sharp increases in river flow (e.g. 2009, 2015, and 2016). Interestingly, the peaks in river discharge recorded before the spring equinox did not trigger migration events. Conversely, the flow peaks experienced by fish in late March were associated with early smolt migration in 2015 and 2016.

### 4.2 | Phenology of smolt spring migration

The most parsimonious phenological model selected from AIC values was also the one that provides the highest adjustment value (DATA

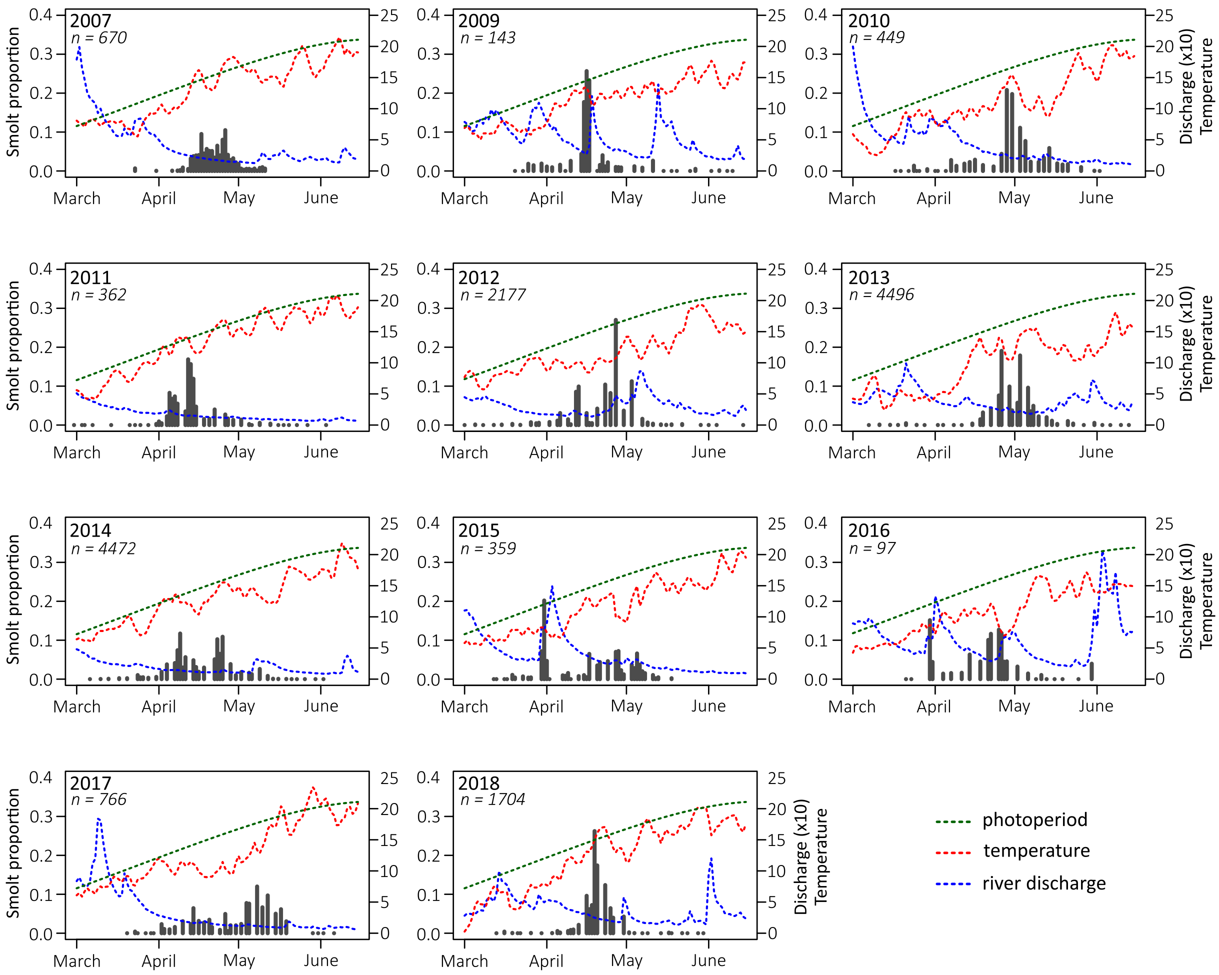

**FIGURE 2** Seasonal patterns of smolt migration observed at the Méry hydropower site (50°33′04.9″N 5°35′07.3″E) between March 2007 and June 2018. The grey bars represent the proportion of migrating smolts collected in the fish trap after adjusting the catch rate by the river discharge (see Methods). The daily variation in water temperature (°C, red dotted lines), river discharge ($m^3 s^{-1}$, blue dotted lines), and day length (hours, green dotted lines) are provided for each sampling year. Note that the y-scale is not indicated for the photoperiod, but the day length ranges from 10.9 to 16.4 h between 1 March and 15 June

S1 APPENDIX A), with a pseudo-$R^2$ of 0.956 (95% confidence interval: 0.945–0.966). This model included the photo-thermal units accumulated above 7°C ($PTU_{7^\circ C}$), the peak discharge ($Q_{peak}$) experienced after the spring equinox, and the interaction of the two factors. The effects of all of the environmental variables were statistically significant – none of the 95% confidence intervals overlapped zero (Table 1). The cumulative proportion of migrating smolts progressively increased with the photo-thermal units, and the river discharge peaks induced discrete pulses of downstream migration. The negative interaction term between these two variables suggests that the influence of discharge peaks tended to decrease throughout the season. Overall, the seasonal patterns of smolt migration were accurately forecasted even for the 2018 season that was not used to adjust the model (Figure 3). For this independent period, the predictive performances remained high, with a pseudo-$R^2$ of 0.960 (95% confidence interval: 0.948–0.968).

The phenological indicators derived from the model predictions were close to the actual observations (Figure 4). Indeed, the average errors for predicting the onset and the end of migration were 3.8 days (95% confidence interval: 0.9–6.6 days) and 3.7 days (95% confidence interval: 1.6–5.7 days), respectively. The prediction error for the

**TABLE 1** Estimated coefficients of the logistic phenological model of smolt migration in the Ourthe River, Wallonia, Belgium. The 95% confidence intervals generated from 1,000 bootstrap replicates are provided. Model coefficients are assumed significant when the confidence intervals do not overlap zero. $PTU_{7^\circ C}$ is the photo-thermal units above the 7°C temperature threshold and $Q_{peak}$ is the discharge peaks

| | | 95% confidence interval | |
|---|---|---|---|
| Coefficients | Estimate | Lower | Upper |
| *Intercept* | −3.96419 | −4.17684 | −3.7707 |
| $PTU_{7^\circ C}$ | 0.00245 | 0.00231 | 0.00261 |
| $Q_{peak}$ | 2.88322 | 2.60857 | 3.14343 |
| $PTU_{7^\circ C} : Q_{peak}$ | −0.00083 | −0.00106 | −0.00061 |

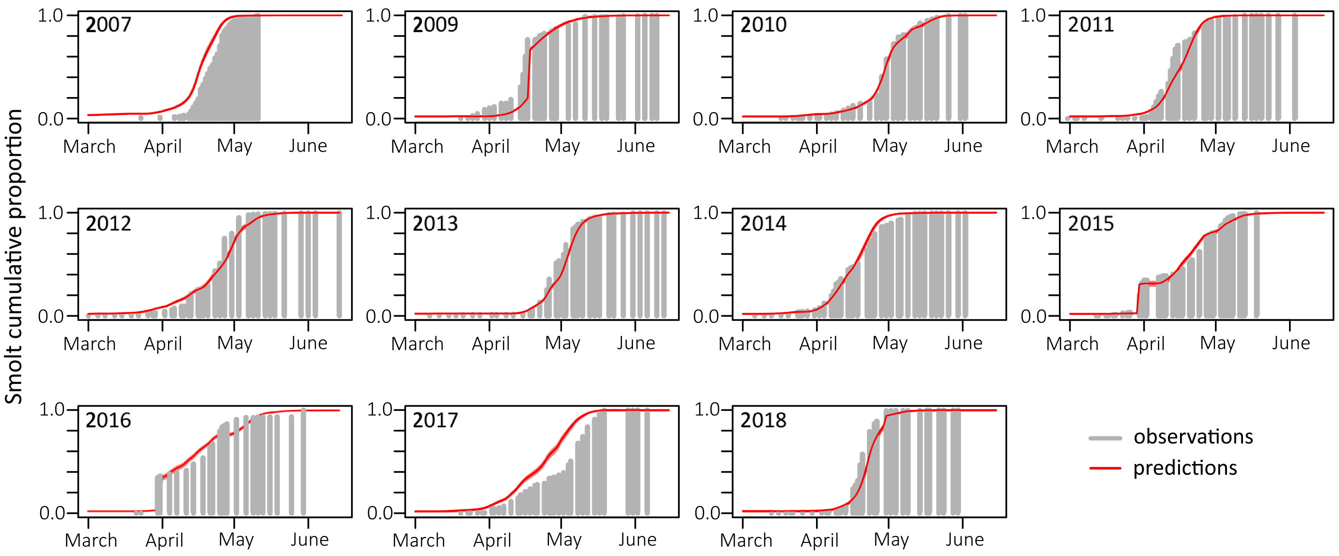

**FIGURE 3** Cumulative proportion of migrating smolts (grey bars) caught at the Méry hydropower site for each migration season, between March 2007 and June 2018. The red lines indicate the predictions of the phenological model using two environmental predictors: the photothermal units ($PTU_{7^{\circ}C}$) and peaks in river discharge ($Q_{peak}$). The 2018 migration season was used as an independent period for assessing the model's predictive performance

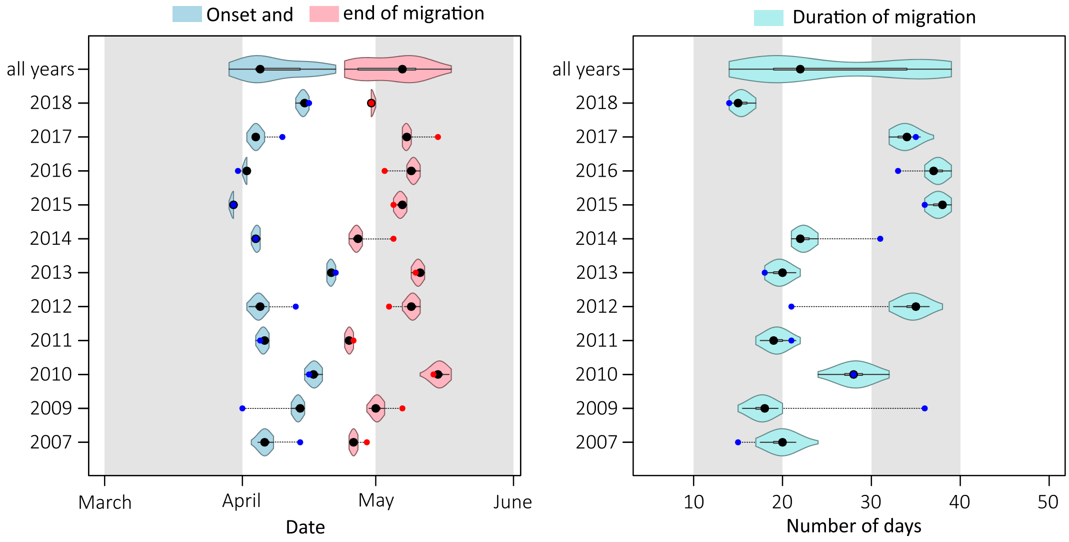

**FIGURE 4** The phenological indicators of the smolt migration in the Ourthe River between March 2007 and June 2018, as estimated from the predictive model. The violins show the uncertainty in estimates of the onset (left panel, light blue), the end (left panel, light red), and the duration (right panel, light green) of migration from 1,000 bootstrap replicates, whereas the linked colour points indicate the actual observations. The duration of migration represents the time interval between the onset and the end of migration, when 80% of the smolts migrated

duration of migration was 5.2 days (95% confidence interval: 1.3–9.2 days), even so, three seasons slightly deviate from the trapping observations (i.e. 2009, 2012, and 2014). The timing of spring migration, as estimated by the predictive model, varied greatly among years in the Ourthe River (Figure 4). The beginning of the spring migration varied from 30 March to 21 April, whereas the end of migration occurred between 25 April and 15 May. Likewise, the duration of migration ranged from 15 to 38 days, depending on the year. The extended migration periods generally occurred when a discharge peak was experienced in the early season (e.g. 2015 or 2016) or when the river temperature remained low (e.g. 2017). Conversely, short migration periods generally occurred when the water temperature increased in phase with the photoperiod (e.g. 2007 or 2011) or when a pulse in river flow occurred during a migration run (e.g. 2009).

### 4.3 | Projection of warming scenarios

The phenological model was used to evaluate the impact of warming water temperature on the phenological indicators of spring smolt

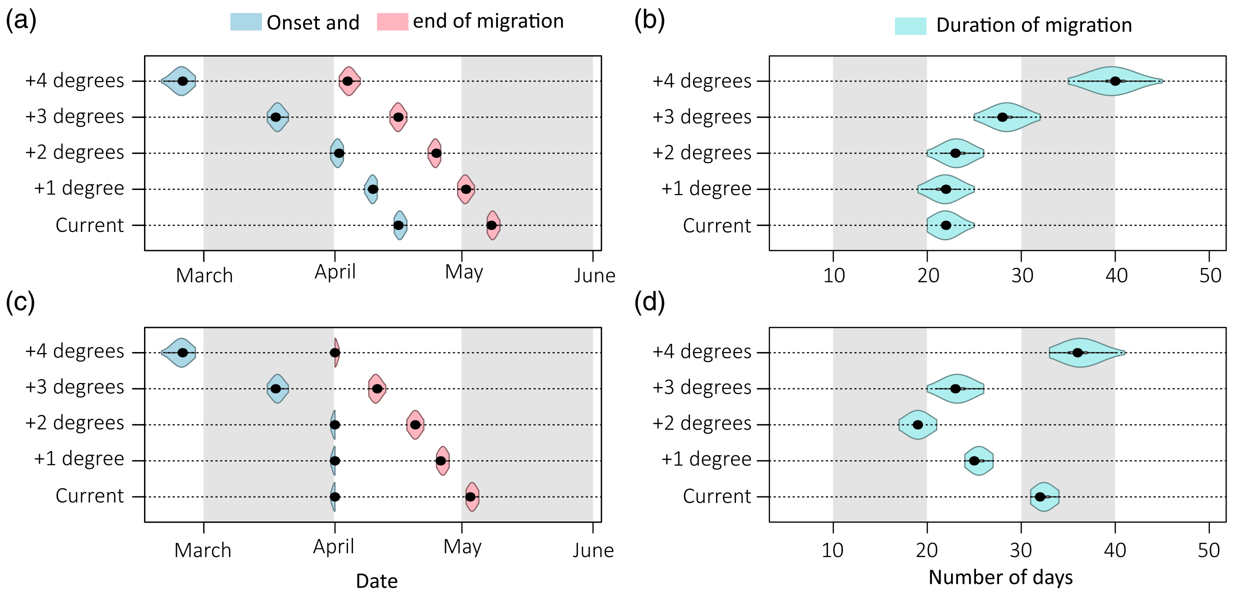

**FIGURE 5** Changes in phenological indicators of the smolt migration under scenarios of water temperature increase (+1°, +2°, +3°, and +4°) without a peak in river discharge (a and b) and when a flow pulse occurs on 1 April (c and d). The baseline conditions, i.e. ‘current’, corresponds to the daily mean temperatures recorded during the study period (2007–2018). The violins show the uncertainty in estimates of the onset (a and c, light blue), the end (a and c, light red), and the duration (b and d, light green) of migration from 1,000 bootstrap replicates. The duration of migration represents the time interval between the onset and the end of migration, when 80% of the smolts migrated

migration (Figure 5). With a temperature increase of 1–4°C, and without river flow, the onset of migration advanced 6–51 days. This shift in migration timing is associated with a change in the end of migration ranging from 6 to 34 days. An increase in water temperature <2°C weakly affected the duration of migration, while the migration period was extended when temperature changes were >3°C. River hydrological conditions are also expected to influence the timing of migration. Indeed, when a peak in river discharge occurs on 1 April, the smolt migration is triggered earlier at low temperatures (i.e. current, +1°, and +2° scenarios), and generally results in longer migration periods. Conversely, the discharge peak tended to reduce the migration duration for higher temperature scenarios (Figure 5), highlighting the cumulative influence of temperature and river hydrology on the phenology of smolt migration.

## 5 | DISCUSSION

### 5.1 | Environmental cues and the phenology of smolt migration

During the study period, the total number of smolts collected in the trap was highly variable between years, suggesting an important effect of restocking actions. Indeed, the number of Atlantic salmon juveniles released in upstream regions of the river strongly differed between years. By contrast, the annual differences in river conditions (e.g. temperature, food availability or competition) can also affect the survival between year classes and induce inter-annual variations in the number of migrating fish. Accordingly, investigating the annual proportions of migrating smolts appears more relevant than considering the absolute number of fish. In the Ourthe River, the duration of spring migration can vary from 15 to 38 days, depending on the external cues that the smolts experience. Photoperiod, water temperature, and flow rates have all been recognized as key environmental cues for regulating the onset and end of smolt migration (Jonsson & Jonsson, 2009; McCormick et al., 1998; Otero et al., 2014; Thorstad et al., 2012; Whalen et al., 1999). Whereas these previous studies directly explored the relationship between phenological indicators and environmental conditions (Jonsson & Jonsson, 2014; Jonsson & Ruud-Hansen, 1985), the seasonal cumulative distributions of migrating smolts were modelled using a logistic function in the present study. This phenological model accurately forecasts the general trends of smolt spring migration in the Ourthe River ($R^2$ = 0.945–0.966), with comparable predictive performances to those obtained for forecasting migration probabilities in Chinook salmon (Sykes, Johnson, & Shrimpton, 2009). Although the smolts caught in the Ourthe River were hatchery fish released at the pre-smolt stage, they remained highly sensitive to the environmental cues triggering fish migration. This corresponds with previous reports of hatchery-reared smolts (Karppinen, Jounela, Huusko, & Erkinaro, 2014). However, the lack of wild populations means that it is difficult to investigate whether the behavioural responses and migration timing highlighted in the present study are unique to hatchery-reared fish. Interestingly, even though the released smolts were from different origins, the model still fits the data well. This suggests that the origin of restocked fish had a small influence compared with the local environmental conditions. Nevertheless, further investigations are required to determine the relative importance of phenotypic plasticity and local stock adaptation in the migratory responses of smolts (Otero et al., 2014).

Overall, the phenological model of smolt spring migration in the Ourthe River explicitly accounted for the combined effects of temperature, photoperiod, and river discharge. These external cues greatly influenced the phenological indicators, so that the migration season can be advanced, delayed, shortened, or prolonged, depending on the conditions experienced by fish. Several studies have indicated that the thermal time metrics (e.g. accumulated daily temperature) are better predictors of smolt migration than daily records of water temperature (Jonsson & Ruud-Hansen, 1985; Sykes et al., 2009; Zydlewski et al., 2005). For example, Zydlewski et al. (2005) proposed that the initiation and termination of the downstream movement can be predicted from the cumulative mean daily temperature experienced by the fish since 1 January. This approach provides encouraging outcomes, but several authors reported inconstancies due to the noise induced when winter temperatures are included when the smolting process is not yet initiated (Haraldstad et al., 2017; Jonsson & Jonsson, 2014). As proposed in the phenological model, the strict application of the thermal time or degree-day concept can help to solve this problem. The degree-day concept requires the definition of a temperature threshold above which temperature is relevant for inducing physiological, developmental, or behavioural processes (Bonhomme, 2000). Here, a range of thresholds (5–9°C) was tested to identify the best fit for the observed data. The results suggest that the daily thermal time for smolt migration in the Ourthe River basin can be estimated accurately using a 7°C temperature threshold ($PTU_{7^\circ C}$). This value also corresponds to the temperature below which migration events are extremely rare in the study river. This threshold-based, thermal time approach complies with other studies suggesting that the timing of smolt migration is regulated by the combination of actual river temperature and fish heat accumulation (Haraldstad et al., 2017; Jonsson & Jonsson, 2014; Stich, Kinnison, et al., 2015). Interestingly, several studies reported that a large proportion of smolt migration occurs when the river temperature exceeded 8°C (Haraldstad et al., 2017; Whalen et al., 1999), which is very close to the threshold defined in the present study. Estimating the thermal units above a temperature threshold appears to be more relevant than using simple cumulative daily records. This approach helps to remove the noise induced by winter temperature variability by focusing on the thermal time that influences the initiation of migration.

The results revealed that the photo-thermal units were better predictors than degree-days for forecasting the smolt spring migration in the Ourthe River. The proposed photo-thermal metric is a relevant variable to predict the combined effects of temperature and photoperiod while avoiding multicollinearity in phenological models (Sykes et al., 2009). The influence of photoperiod is not surprising, as this factor is commonly reported as the primary driver of the parr–smolt transformation before migration (Stefansson et al., 1991; Zydlewski et al., 2014) and as a regulator of smolt swimming activity (Martin et al., 2012). Experimental studies have also demonstrated that exposure to short photoperiod, followed by an increase in day length, is required to stimulate the physiological processes of smoltification (Ebbesson et al., 2007; Stefansson et al., 2007; Strand et al., 2018). Although geographical variation in photoperiod can explain large-scale fluctuations in smolt phenology, local inter-annual variations are most likely controlled by temperature and river flow (Otero et al., 2014). Nevertheless, Zydlewski et al. (2014) showed that photoperiod and temperature can act in combination to regulate the downstream movement of Atlantic salmon smolts under experimentally controlled conditions. The results support this finding based on field monitoring surveys: the photo-thermal units were decisive predictors in the phenological model. The photo-thermal units reflect a synergistic relationship between day length and thermal time, suggesting that the smolt migration occurs earlier when the temperature increases quickly and in phase with the photoperiod cycle. Conversely, the smolt migration may be delayed by low temperatures, even if favourable photoperiodic cues are encountered. Interactions among external cues are important processes for regulating the physiological and behavioural responses of organisms (Helm et al., 2017), as they are expected to promote reliability to meet advantageous environmental windows for life-history transitions (McNamara et al., 2011).

The results also suggest an effect of the hydrological conditions on smolt spring migration. Similar observations have been reported in field studies, where a sharp increase in river flow can stimulate smolt migration activity (Aldvén et al., 2015; Antonsson & Gudjonsson, 2002; Hvidsten et al., 1995; Jonsson & Jonsson, 2011; Karppinen et al., 2014; Persson, Kagervall, Leonardsson, Royan, & Alanärä, 2019). In the West River basin, Whalen et al. (1999) found variability in the influence of river discharge peaks throughout the migration season; responsivity was highest during the mid-season until the physiological status of smolts declined. This result is supported by the negative interaction between the photo-thermal time and discharge peak in the phenological model, which reflects a decreasing influence of hydrology over the course of the migration season. The lower effect of discharge peak in the late season may also be explained by the fact that a large proportion of smolts have already migrated. Conversely, the discharge peaks in the early season can induce large pulses of smolt migration (Otero et al., 2014), even though the photo-thermal conditions are not yet optimal. Such early downstream movement events contribute to extended migration periods, as observed in 2015 and 2016. Whereas photoperiod and temperature are related to smoltification, river hydrology appears more involved in triggering migration runs and may help to synchronize smolt movements. Thus, the discharge peaks are not indispensable for initiating fish migration, but they can promote massive downstream movements during increased river flow. Moving in a group can provide protection against predation (Berdahl, Westley, & Quinn, 2017) and migration during high flow is energetically beneficial (Persson et al., 2019), as also proposed for silver eels *Anguilla anguilla* (Barry et al., 2016). Nevertheless, smolt activity was not affected by discharge peaks before the spring equinox, suggesting that the sensitivity to hydrological change occurred only after the photoperiod cue had been received. However, the starting date and flow rate (twice the discharge of the 5 previous days) were defined subjectively, based on data exploration. Therefore, further investigations are required to refine these estimations and to improve the understanding of joint effects of river discharge and photoperiod on smolt downstream movements. Future studies may benefit from using telemetry surveys to overcome the limits associated with fish trap monitoring, such as the relationship between catch rate and river flow and the inability to check the trap during high flow peaks.

## 5.2 | Management issues

Forecasting migration periods is a crucial concern for the implementation of conservation measures during key periods of fish life-history (Trancart, Acou, De Oliveira, & Feunteun, 2013). Indeed, forecasts of migratory activity represent decisive management information to identify sensitive periods when downstream passage solutions need to be fully operational. Various management alternatives have been developed to promote river connectivity and smolt survival (Larinier, 2001; Tétard et al., 2019; Tomanova et al., 2018), but the active solutions require accurate predictions of migration timing to limit the technical constraints and economic costs (Stich, Kinnison, et al., 2015). This is particularly relevant for hydropower turbine shutdown or flow management policies, which serve to reduce smolt mortality by modulating the attractiveness and harmfulness of turbines (Fjeldstad, Alfredsen, & Boissy, 2014; Thorstad et al., 2012). To achieve the conservation objectives, the turbines can be stopped during migration peaks or the bypass discharge can be increased to guide the smolts toward safe ways (Fjeldstad et al., 2012). Thus, from a management perspective, the timing of migration should be accurately forecasted (from calendar dates or environmental records) so that the conservation measures are conducted only when the migration events are expected to occur (Smith, Fackler, Eyler, Villegas Ortiz, & Welsh, 2017). Minimizing the impact on hydropower generation is essential to the long-term acceptance and sustainability of conservation policies (Teichert, Trancart, Feunteun, Acou, & Oliveira, 2020). The phenological model proposed in the present study does this: it provides a flexible management tool for determining when conservation measures should begin and end to meet a conservation objective, defined by a proportion of migrating smolts. For the Ourthe River basin, the phenological indicators were calculated to determine the time interval that encompassed 80% of the spring migrants. In agreement with the high model predictive power, 77.5% of the smolts would have been affected by the conservation actions if the dates of migration onset and end had been used. Local managers can apply this by using real-time temperature and flow discharge measurements to calculate daily estimates of cumulative smolt migration, and then decide when management actions are required (e.g. hydropower turbine shutdown, discharge management).

Migration forecasts also provide crucial information to determine when the fishway functionalities should be restored and revised (Lagarde, Teichert, Boussarie, Grondin, & Valade, 2015). Although bypasses have been built on many dams (hydropower or not), these devices should be carefully maintained (removal of clogging, structure reparation, flow management) to ensure their effectiveness. The phenological model was adjusted for the Meuse River basin, but the analytical approach and model structure can be extended to other river systems because the method involves simple environmental parameters that are routinely monitored across river networks. This may involve a simple, location-based adjustment of the temperature threshold ($T_{thr}$), as water temperature generally fluctuates with altitude and between river basins. Thus, the temperature threshold associated with the first smolt movements is expected to be site-dependent (Martin et al., 2012). If this is true (confirmation will come from future complementary studies), the model could apply to locations lacking long-term smolt migration data. Moreover, the absence of calendar information in the prediction process is also advantageous for transferring the method to other areas, while yielding reliable outcomes in a context of global change. Nevertheless, the model proposed in this study is designed to predict the phenological fluctuations in smolt spring migration. Autumn downstream movements of juvenile salmon were not considered as previous bypass monitoring in the Ourthe (1 year) and Amblève rivers (2 years; a tributary of the Ourthe) yielded no evidence of autumn smolt migration (Ovidio et al., unpublished data). Although most fish migrations occur in the spring and early summer (Otero et al., 2014), individuals migrating outside of the peak season should also be considered when assessing river productivity (Birnie-Gauvin & Aarestrup, 2019). For example, downstream movements of juvenile Atlantic salmon have been reported in Norway (Jonsson & Jonsson, 2014), England (Pinder, Riley, Ibbotson, & Beaumont, 2007; Riley et al., 2008), Finland (Taal et al., 2014), and Canada (Cunjak, 1992). However, the proportion of autumn migrants varies between river basins (Jonsson & Jonsson, 2014), so more in-depth sampling is required to determine whether autumn migrations may sometimes occur in the Meuse River basin. Future studies should also determine if the model structure and triggering factors can be extended into the autumn period.

## 5.3 | Influence of climatic scenarios

Previous field studies and the present results suggest that water warming can affect the timing of smolt migration (Jonsson & Jonsson, 2014; Otero et al., 2014). Thus, a mismatch between smolt migration and conservation actions can occur if mitigation measures are based on calendar dates fixed each year. With these operational rules, the migration window should be regularly re-evaluated to account for potential temporal shifts in smolt migration. Similarly, management policies based on a fixed number of days per year may provide irregular outcomes owing to the strong inter-annual variability in the duration of migration. On the contrary, the phenological model proposed here intrinsically overcomes this by moderating the migration period according to the thermal time experienced by the fish. Therefore, fish thermal history provides an interesting approach to estimate phenological changes under future climate regimes, as evidenced by a study of spawning time in Atlantic cod (Neuheimer & Mackenzie, 2014). For a temperature increase of between 1 and 4°C, the results indicate that the migration may start 6–51 days earlier than observed for average present conditions. This estimate is consistent with the trends reported in the Imsa River, where the smolt migration has advanced 2 weeks since the 1970s (Jonsson & Jonsson, 2014). Similarly, Otero et al. (2014) demonstrated that the smolt seaward migration has occurred 2.5 days earlier per decade throughout the North Atlantic basin. The phenological model also predicts that the duration of migration can be extended when the river temperature rises more than 2°C because the temporal shift is expected to be lower for the end than for the onset of migration. For the +4°C scenario, the migration duration could reach 40 days, which suggests that the mitigation measures should be twice as long to target an efficiently large proportion of the migrating smolts.

River flow also plays an important role in smolt migrations, so projections under future climate conditions should incorporate the combined effects of temperature and hydrology. The duration of migration is generally extended when discharge peaks occur early in the season because downstream movements are triggered before the beginning of the photo-thermal-induced migrations. Conversely, the duration of migration is reduced when the discharge peaks occur during the migration season because high flow synchronizes fish movements and a large proportion of smolts migrate together over a short period. The loss of seasonal flow peaks that result from the alteration of natural hydrological regimes and river flow management (Zeiringer, Seliger, Greimel, & Schmutz, 2018) may act in combination with warming temperatures to reduce the connection between external cues and favourable environmental conditions for smolt survival (Otero et al., 2014). Thus, measures aimed at restoring natural flow regimes (e.g. reduced abstractions, release from reservoirs) and spring flushes are critically important to improve the synchronicity of smolt migration. The timing of migration also plays a decisive role in smolt survival in the marine environment (Hvidsten et al., 1998; McCormick et al., 1998), as delayed or early entry into the ocean may result in physiological stress and sub-optimal growth conditions (Thorstad et al., 2012).

To conclude, this study proposed a simple and operational model to forecast the spring migration phenology of Atlantic salmon smolt in the Meuse River basin, based on the environmental conditions experienced by fish. While the smoltification and the timing of migration are influenced by endogenous factors (e.g. body or physiological conditions; Handeland, Imsland, Björnsson, & Stefansson, 2013), the implementation of these individual effects is difficult to apply in an operational model. Findings of this study highlight a combined influence of photoperiod, river temperature, and hydrological conditions, which were used to predict the cumulative distributions of migrating smolts. The results indicate that the photo-thermal units accumulated by smolts above a 7°C temperature threshold was a relevant proxy to reflect the synergistic effect between temperature and photoperiod. The phenological model can be used to identify the key period during which mitigation measures should be implemented to promote smolt survival. This operational tool is notably relevant to Special Areas of Conservation involving migratory fish, where management strategies should be applied to ensure the ecological needs of the species are met whereas the restoration of river conditions benefits all freshwater fish species, the re-establishment of ecological continuity throughout the river continuum is essential for ensuring recovery of diadromous species. For the Atlantic salmon, the success of management efforts in conservation areas is thus conditioned by the migration success between the river sites and the marine environment. Indeed, the mortality of early life stages during the downstream migration cannot be compensated for by increasing growth and survival of adults (Thorstad et al., 2017). In large rivers, such as the Meuse, numerous obstacles are reported along the smolt migration route, and coordinated international actions are required to limit the cumulative impacts of dams. The phenological model can be used to find the best balance between hydroelectric production and smolt migration activity from the tributaries to the sea. Several solutions can be applied depending on the local configuration of sites, such as operating turbine shutdowns or increasing the proportion of smolts using bypasses. Given the nocturnal migration of smolts, the turbine shutdowns can preferentially be operated during the night, but should be extended during the day in the late migration season when the nocturnal behaviour is generally buffered (Tétard et al., 2019). By contrast, the attractiveness of bypasses and thus the proportion of smolts using safe-ways can be enhanced by increasing the discharge into the bypass (Fjeldstad et al., 2012) or by using artificial lighting strategies (Tétard et al., 2019). The duration of mitigation periods can also be modulated depending on the annual proportion of smolts targeted in conservation objectives. For example, in the Ourthe River the survival of 80% of the migrating smolts can be improved by conducting management measures during the sensitive window, ranging from 15 to 38 days. Since calendar information is not required, the phenological model can be used to forecast migration patterns in scenarios of climate change, where both river flow and water temperature regimes are expected to vary. Such conservation measures are expected to promote the survival of smolts during their downstream migration and, a few years later, increase the number of adult salmon reaching the spawning grounds in the tributaries of the River Meuse.

## ACKNOWLEDGEMENTS

Financial support for the monitoring of the bypass trap of Méry during the 11-year study by the University of Liège was provided by the Public Service of Wallonia, General Operational Direction of Agriculture, Natural Resources and Environment, Nature and Forest Department, thanks to the Meuse Salmon program. The European Union financially supported the scientific treatment of the monitoring data through the LIFE Nature and Biodiversity programme, as part of the LIFE4FISH project (LIFE16 NAT/BE/000807). We are very grateful to Kim Birnie-Gauvin (DTU Aqua, Silkeborg, Denmark) and Matthew Newton (University of Glasgow, UK) for their comments and suggestions that have improved the relevance of the manuscript. We thank Niels Duchesne for authorizing access to the hydroelectric site during the study and the SPW-SETHYMET for the water flow data. We thank Gilles Rimbaud (University of Liège) and the team of Dr Xavier Rollin and Yvan Neus (Walloon Fisheries Service) for their help in the monitoring process.

## ORCID

*Nils Teichert* https://orcid.org/0000-0002-8873-9613
*Jean-Philippe Benitez* https://orcid.org/0000-0002-5643-070X
*Eric de Oliveira* https://orcid.org/0000-0002-6812-0100
*Thomas Trancart* https://orcid.org/0000-0002-1426-7895
*Michaël Ovidio* https://orcid.org/0000-0002-0136-5840

## REFERENCES

Adler, D. & Kelly, S. T. (2018). vioplot: Violin plot. *R package version 0.3.0*.

Aldvén, D., Degerman, E., & Höjesjö, J. (2015). Environmental cues and downstream migration of anadromous brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts. *Boreal Environment Research*, *20*, 35–44.

Antonsson, T., & Gudjonsson, S. (2002). Variability in timing and characteristics of Atlantic salmon smolt in Icelandic Rivers. *Transactions of the American Fisheries Society*, *131*, 643–655.

Bardonnet, A., & Baglinière, J.-L. (2000). Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 497–506. https://doi.org/10.1139/f99-226

Barry, J., Newton, M., Dodd, J. A., Lucas, M. C., Boylan, P., & Adams, C. E. (2016). Freshwater and coastal migration patterns in the silver-stage eel *Anguilla anguilla*. *Journal of Fish Biology*, *88*, 676–689.

Berdahl, A., Westley, P. A. H., & Quinn, T. P. (2017). Social interactions shape the timing of spawning migrations in an anadromous fish. *Animal Behaviour*, *126*, 221–229.

Bickford, S. A., & Skalski, J. R. (2000). Reanalysis and interpretation of 25 years of Snake–Columbia River juvenile salmonid survival studies. *North American Journal of Fisheries Management*, *20*, 53–68. https://doi.org/10.1577/1548-8675(2000)020<0053:RAIOYO>2.0.CO;2

Birnie-Gauvin, K., & Aarestrup, K. (2019). A call for a paradigm shift: Assumed-to-be premature migrants actually yield good returns. *Ecology of Freshwater Fish*, *28*, 62–68. https://doi.org/10.1111/eff.12431

Bonhomme, R. (2000). Bases and limits to using "degree day" units. *European Journal of Agronomy*, *13*, 1–10.

Canty, A. & Ripley, B. (2017). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-20. R Package Version 1.*3–20*.

Chezik, K. A., Lester, N. P., Venturelli, P. A., & Tierney, K. (2014). Fish growth and degree-days II: Selecting a base temperature for an among-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 1303–1311. https://doi.org/10.1139/cjfas-2013-0615

Council of the European Communities. (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal of the European Communities*, *L206*, 7–50.

Cunjak, R. A. (1992). Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. *Ecology of Freshwater Fish*, *1*, 26–34. https://doi.org/10.1111/j.1600-0633.1992.tb00004.x

Dingle, H., & Drake, V. A. (2007). What is migration history? *Bioscience*, *57*, 113–121.

Dolotov, S. I. (2006). The effects of water temperature on the migration of smolts of the Atlantic salmon *Salmo salar* L. *Journal of Ichthyology*, *46*, S194–S203. https://doi.org/10.1134/s0032945206110099

Donohue, K., Burghardt, L. T., Runcie, D., Bradford, K. J., & Schmitt, J. (2015). Applying developmental threshold models to evolutionary ecology. *Trends in Ecology and Evolution*, *30*, 66–77. https://doi.org/10.1016/j.tree.2014.11.008

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Ebbesson, L. O. E., Ebbesson, S. O. E., Nilsen, T. O., Stefansson, S. O., & Holmqvist, B. (2007). Exposure to continuous light disrupts retinal innervation of the preoptic nucleus during parr-smolt transformation in Atlantic salmon. *Aquaculture*, *273*, 345–349. https://doi.org/10.1016/j.aquaculture.2007.10.016

Fjeldstad, H. P., Alfredsen, K., & Boissy, T. (2014). Optimising Atlantic salmon smolt survival by use of hydropower simulation modelling in a regulated river. *Fisheries Management and Ecology*, *21*, 22–31. https://doi.org/10.1111/fme.12044

Fjeldstad, H. P., Uglem, I., Diserud, O. H., Fiske, P., Forseth, T., Kvingedal, E., … Järnegren, J. (2012). A concept for improving Atlantic salmon *Salmo salar* smolt migration past hydro power intakes. *Journal of Fish Biology*, *81*, 642–663. https://doi.org/10.1111/j.1095-8649.2012.03363.x

Gosset, C., Travade, F., Durif, C., Rives, J., & Elie, P. (2005). Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications*, *21*, 1095–1105. https://doi.org/10.1002/rra.871

Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, *239*, 1291–1293. https://doi.org/10.1126/science.239.4845.1291

Handeland, S. O., Imsland, A. K., Björnsson, B. T., & Stefansson, S. O. (2013). Long-term effects of photoperiod, temperature and their interaction on growth, gill Na+, K+-ATPase activity, seawater tolerance and plasma growth-hormone levels in Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *83*, 1197–1209. https://doi.org/10.1111/jfb.12215

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B., & Haugen, T. O. (2017). Diel migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: An assessment of environmental cues. *Ecology of Freshwater Fish*, *26*, 541–551. https://doi.org/10.1111/eff.12298

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., & Bloch, G. (2017). Two sides of a coin: Ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*, 20160246. https://doi.org/10.1098/rstb.2016.0246

Hvidsten, N. A., Heggberget, T. G., & Jensen, A. J. (1998). Sea water temperatures at Atlantic salmon smolt entrance. *Nordic Journal of Freshwater Research*, *74*, 79–86.

Hvidsten, N. A., Jensen, A. J., Vivås, H., Bakke, Ø., & Heggberget, T. G. (1995). Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic Journal of Freshwater Research*, *70*, 38–48.

Ibbotson, A. T., Riley, W. D., Beaumont, W. R. C., Cook, A. C., Ives, M. J., Pinder, A. C., … Scott, L. J. (2013). The source of autumn and spring downstream migrating juvenile Atlantic salmon in a small lowland river. *Ecology of Freshwater Fish*, *22*, 73–81. https://doi.org/10.1111/eff.12003

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, *75*, 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories*. Dordrecht, The Netherlands: Springer.

Jonsson, B., & Ruud-Hansen, J. (1985). Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 593–595. https://doi.org/10.1139/f85-076

Jonsson, N., & Jonsson, B. (2014). Time and size at seaward migration influence the sea survival of *Salmo salar*. *Journal of Fish Biology*, *84*, 1457–1473. https://doi.org/10.1111/jfb.12370

Karppinen, P., Jounela, P., Huusko, R., & Erkinaro, J. (2014). Effects of release timing on migration behaviour and survival of hatchery-reared

Atlantic salmon smolts in a regulated river. *Ecology of Freshwater Fish*, *23*, 438–452. https://doi.org/10.1111/eff.12097

Kuczynski, L., Chevalier, M., Laffaille, P., Legrand, M., & Grenouillet, G. (2017). Indirect effect of temperature on fish population abundances through phenological changes. *PLoS ONE*, *12*, e0175735. https://doi.org/10.1371/journal.pone.0175735

Lagarde, R., Teichert, N., Boussarie, G., Grondin, H., & Valade, P. (2015). Upstream migration of amphidromous gobies of La Réunion Island: Implication for management. *Fisheries Management and Ecology*, *22*, 437–449. https://doi.org/10.1111/fme.12142

Larinier, M. (2001). Environmental issues, dams and fish migration. *FAO Fisheries Technical Paper*, *419*, 45–89.

Larinier, M. (2008). Fish passage experience at small-scale hydro-electric power plants in France. *Hydrobiologia*, *609*, 97–108. https://doi.org/10.1007/s10750-008-9398-9

Larinier, M., & Travade, F. (2002). Downstream migration: Problems and facilities. *Bulletin Français de la Pêche et de la Pisciculture*, *364*, 181–207. https://doi.org/10.1051/kmae/2002102

Mack, L., Andersen, H. E., Beklioğlu, M., Bucak, T., Couture, R.-M., Cremona, F., … Birk, S. (2019). The future depends on what we do today – Projecting Europe's surface water quality into three different future scenarios. *Science of the Total Environment*, *668*, 470–484. https://doi.org/10.1016/j.scitotenv.2019.02.251

Marschall, E. A., Mather, M. E., Parrish, D. L., Allison, G. W., & McMenemy, J. R. (2011). Migration delays caused by anthropogenic barriers: Modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications*, *21*, 3014–3031. https://doi.org/10.1890/10-0593.1

Martin, P., Rancon, J., Segura, G., Laffont, J., Boeuf, G., & Dufour, S. (2012). Experimental study of the influence of photoperiod and temperature on the swimming behaviour of hatchery-reared Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture*, *362–363*, 200–208. https://doi.org/10.1016/j.aquaculture.2011.11.047

McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 77–92. https://doi.org/10.1139/d98-011

McCormick, S. D., Lerner, D. T., Monette, M. Y., Nieves-Puigdoller, K., Kelly, J. T., & Björnsson, B. T. (2009). Taking it with you when you go: How perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. *American Fisheries Society Symposium*, *69*, 195–214.

McCormick, S. D., Shrimpton, J. M., Moriyama, S., & Björnsson, B. T. (2002). Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. *The Journal of Experimental Biology*, *205*, 3553–3560.

McMaster, G. S., White, J. W., Hunt, L. A., Jamieson, P. D., Dhillon, S. S., & Ortiz-Monasterio, J. I. (2008). Simulating the influence of vernalization, photoperiod and optimum temperature on wheat developmental rates. *Annals of Botany*, *102*, 561–569. https://doi.org/10.1093/aob/mcn115

McNamara, J. M., Barta, Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, *14*, 1183–1190. https://doi.org/10.1111/j.1461-0248.2011.01686.x

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Neuheimer, A. B., & Mackenzie, B. R. (2014). Explaining life history variation in a changing climate across a species' range. *Ecology*, *95*, 3364–3375. https://doi.org/10.1890/13-2370.1

Neuheimer, A. B., & Taggart, C. T. (2007). The growing degree-day and fish size-at-age: The overlooked metric. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 375–385. https://doi.org/10.1139/f07-003

Otero, J., L'Abée-Lund, J. H., Castro-Santos, T., Leonardsson, K., Storvik, G. O., Jonsson, B., … Vøllestad, L. A. (2014). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, *20*, 61–75. https://doi.org/10.1111/gcb.12363

Ovidio, M., Dierckx, A., Bunel, S., Grandry, L., Spronck, C., & Benitez, J. P. (2017). Poor performance of a retrofitted downstream bypass revealed by the analysis of approaching behaviour in combination with a trapping system. *River Research and Applications*, *33*, 27–36. https://doi.org/10.1002/rra.3062

Ovidio, M., Kestemont, P., Dierckx, A., Benitez, J.-P., Mandiki, R., Neus, Y., … Rollin, X. (2019). Rehabilitation effort for anadromous salmonids in the river Meuse basin. Achievements and new challenges. *Advances in the populations ecology of stream salmonids*, 20-25 may 2019, Granada University, Spain.

Persson, L., Kagervall, A., Leonardsson, K., Royan, M., & Alanärä, A. (2019). The effect of physiological and environmental conditions on smolt migration in Atlantic salmon *Salmo salar*. *Ecology of Freshwater Fish*, *28*, 190–199.

Philippart, J. C., Micha, J. C., Baras, E., Prignon, C., Gillet, A., & Joris, S. (1994). The Belgian project "Meuse Salmon 2000". First results, problems and future prospects. *Water Science and Technology*, *29*, 315–317. https://doi.org/10.2166/wst.1994.0128

Pinder, A. C., Riley, W. D., Ibbotson, A. T., & Beaumont, W. R. C. (2007). Evidence for an autumn downstream migration and the subsequent estuarine residence of 0+ year juvenile Atlantic salmon *Salmo salar* L., in England. *Journal of Fish Biology*, *71*, 260–264. https://doi.org/10.1111/j.1095-8649.2007.01470.x

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/

Renardy, S., Benitez, J. P., Tauzin, A., Dierckx, A., Matondo, B. N., & Ovidio, M. (2020). How and where to pass? Atlantic salmon smolt's behaviour at a hydropower station offering multiple migration routes. *Hydrobiologia*, *847*, 469–485. https://doi.org/10.1007/s10750-019-04108-w

Riley, W. D., Ibbotson, A. T., & Beaumont, W. R. C. (2009). Adult returns from Atlantic salmon, *Salmo salar*, parr autumn migrants. *Fisheries Management and Ecology*, *16*, 75–76. https://doi.org/10.1111/j.1365-2400.2008.00643.x

Riley, W. D., Ibbotson, A. T., Lower, N., Cook, A. C., Moore, A., Mizuno, S., … Privitera, L. (2008). Physiological seawater adaptation in juvenile Atlantic salmon (*Salmo salar*) autumn migrants. *Freshwater Biology*, *53*, 745–755. https://doi.org/10.1111/j.1365-2427.2007.01933.x

Sandlund, O. T., Diserud, O. H., Poole, R., Bergesen, K., Dillane, M., Rogan, G., … Vøllestad, L. A. (2017). Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues. *Ecology and Evolution*, *7*, 5956–5966. https://doi.org/10.1002/ece3.3099

Smith, D. R., Fackler, P. L., Eyler, S. M., Villegas Ortiz, L., & Welsh, S. A. (2017). Optimization of decision rules for hydroelectric operation to reduce both eel mortality and unnecessary turbine shutdown: A search for a win–win solution. *River Research and Applications*, *33*, 1279–1285. https://doi.org/10.1002/rra.3182

Stefansson, S. O., Bjömsson, B. T., Hansen, T., Haux, C., Taranger, G. L., & Saunders, R. L. (1991). Growth, parr–smolt transformation, and changes in growth hormone of Atlantic salmon (*Salmo salar*) reared under different photoperiods. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 2100–2108. https://doi.org/10.1139/f91-249

Stefansson, S. O., Nilsen, T. O., Ebbesson, L. O. E., Wargelius, A., Madsen, S. S., Björnsson, B. T., … McCormick, S. D. (2007). Molecular mechanisms of continuous light inhibition of Atlantic salmon parr-smolt transformation. *Aquaculture*, *273*, 235–245. https://doi.org/10.1016/j.aquaculture.2007.10.005

Stich, D. S., Bailey, M. M., Holbrook, C. M., Kinnison, M. T., & Zydlewski, J. D. (2015). Catchment-wide survival of wild- and hatchery-reared Atlantic salmon smolts in a changing system. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1352–1365. https://doi.org/10.1139/cjfas-2014-0573

Stich, D. S., Kinnison, M. T., Kocik, J. F., Zydlewski, J. D., & Krkošek, M. (2015). Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1339–1351. https://doi.org/10.1139/cjfas-2014-0570

Strand, J. E. T., Hazlerigg, D., & Jørgensen, E. H. (2018). Photoperiod revisited: Is there a critical day length for triggering a complete parr–smolt transformation in Atlantic salmon *Salmo salar*? *Journal of Fish Biology*, *93*, 440–448. https://doi.org/10.1111/jfb.1376010.1111/jfb.13760

Sykes, G. E., Johnson, C. J., & Shrimpton, J. M. (2009). Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society*, *138*, 1252–1265. https://doi.org/10.1577/t08-180.1

Taal, I., Kesler, M., Saks, L., Rohtla, M., Verliin, A., Svirgsden, R., … Saat, S. (2014). Evidence for an autumn downstream migration of Atlantic salmon *Salmo salar* (Linnaeus) and brown trout *Salmo trutta* (Linnaeus) parr to the Baltic Sea. *Helgoland Marine Research*, *68*, 373–377. https://doi.org/10.1007/s10152-014-0395-2

Teichert, N., Trancart, T., Feunteun, E., Acou, A., & Oliveira, E. D. (2020). Resolving the trade-off between silver eel escapement and hydropower generation with simple decision rules for turbine shutdown. *Journal of Environmental Management*, *261*, 110212. https://doi.org/10.1016/j.jenvman.2020.110212

Tétard, S., Maire, A., Lemaire, M., De Oliveira, E., Martin, P., & Courret, D. (2019). Behaviour of Atlantic salmon smolts approaching a bypass under light and dark conditions: Importance of fish development. *Ecological Engineering*, *131*, 39–52. https://doi.org/10.1016/j.ecoleng.2019.02.021

Thorstad, E. B., Havn, T. B., Sæther, S. A., Heermann, L., Teichert, M. A. K., Diserud, O. H., … Økland, F. (2017). Survival and behaviour of Atlantic salmon smolts passing a run-of-river hydropower facility with a movable bulb turbine. *Fisheries Management and Ecology*, *24*, 199–207. https://doi.org/10.1111/fme.12216

Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, *18*, 345–371. https://doi.org/10.1007/s11160-007-9076-4

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*, 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x

Tomanova, S., Courret, D., Alric, A., De Oliveira, E., Tétard, S., & Lagarrigue, T. (2018). Protecting efficiently sea-migrating salmon smolts from entering hydropower plant turbines with inclined or oriented low bar spacing racks. *Ecological Engineering*, *122*, 143–152. https://doi.org/10.1016/j.ecoleng.2018.07.034

Trancart, T., Acou, A., De Oliveira, E., & Feunteun, E. (2013). Forecasting animal migration using SARIMAX: An efficient means of reducing silver eel mortality caused by turbines. *Endangered Species Research*, *21*, 181–190. https://doi.org/10.3354/esr00517

Whalen, K. G., Parrish, D. L., & McCormick, S. D. (1999). Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. *Transactions of the American Fisheries Society*, *128*, 289–301. https://doi.org/10.1577/1548-8659(1999)128<0289:mtoass>2.0.co;2

Zeiringer, B., Seliger, C., Greimel, F., & Schmutz, S. (2018). River hydrology, flow alteration, and environmental flow. In S. Schmutz & J. Sendzimir (Eds.), *Riverine ecosystem management* (pp. 67–89). Amsterdam, The Netherlands: Springer International Publishing.

Zydlewski, G. B., Haro, A., & McCormick, S. D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 68–78. https://doi.org/10.1139/f04-179

Zydlewski, G. B., Stich, D. S., & McCormick, S. D. (2014). Photoperiod control of downstream movements of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, *85*, 1023–1041. https://doi.org/10.1111/jfb.12509

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Teichert N, Benitez J-P, Dierckx A, et al. Development of an accurate model to predict the phenology of Atlantic salmon smolt spring migration. *Aquatic Conserv: Mar Freshw Ecosyst*. 2020;30:1552–1565. https://doi.org/10.1002/aqc.3382