

ARTICLE

Freshwater Ecology

Near-term lake water temperature forecasts can be used to anticipate the ecological dynamics of freshwater species

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Abstract

Near-term ecological forecasting can be used to improve operational resource management in freshwater ecosystems. Here, we developed a framework that uses water temperature forecasting as a tool to predict the migrations of Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*) between freshwater and the sea. We used historical observations of lake water temperature and fish migrations from an internationally important long-term monitoring site (the Burrishoole catchment, Ireland) to generate daily probabilistic predictions (0%–100%) of when relatively large numbers of fish migrate. For this, we produced daily lake water temperature forecasts that extended up to 34 days into the future using Forecasting Lake and Reservoir Ecosystems (FLARE), an open-source ensemble-based forecasting system. We used this system to forecast lake water temperature conditions associated with percentile-based fish migrations. Two metrics, P66 and P95, were used to indicate days with migrations in excess of 66% and 95%, respectively, of the historical daily fish counts. The results were first validated against water temperature observations, with an overall root mean squared error (RMSE) of 0.97°C. Our forecasts outperformed two other possible water temperature forecasting approaches, using site climatology (1.36°C) and site persistence (1.19°C). The predictions for fish migrations performed better for the P66 metric than for the more extreme P95 metric based on the continuous ranked probability score (CRPS), and the best results were obtained for the salmon downstream migration. This forecasting approach with quantified uncertainty levels has the potential to assist decision making, especially in the face of increased risks for these species. We conclude by discussing the scalability of the framework to other settings as a tool aimed at supporting management practices in real time.

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KEYWORDS

diadromous fish, ecological forecasting, lake modeling, probabilistic prediction, water management

INTRODUCTION

The biota of freshwater ecosystems is responding to an increasing range of human and climatic pressures (Priya et al., 2023), resulting in changes in behavior and ecology (Mishra et al., 2021; Staudinger et al., 2021). Such changes represent a challenge for environmental management because they are often unforeseen and straightforward mitigation or conservation measures cannot always be applied (Abbass et al., 2022; IPCC et al., 2023). Basing management actions on past conditions is becoming less reliable (Diffenbaugh, 2020; Nissan et al., 2019), especially as ecosystem dynamics become more variable, leaving managers with limited time to react (Foley et al., 2015). However, anticipating some of these alterations in ecosystem function is becoming possible through the application of near-term ecological forecasting systems (Bradford et al., 2020; Dietze et al., 2018). These types of systems generate forecasts (i.e., predictions of future environmental conditions with quantified uncertainty; Lewis et al., 2022) in operational time frames (e.g., monthly, weekly, daily, or sub-daily) and generally integrate data into workflows in near real time (i.e., as new data are collected through the use of automated sensors, wireless data transfer, and cyberinfrastructure), allowing for quick iterative generation of information (Carey et al., 2022).

Recent deployments of near-term ecological forecasting systems for predicting specific environmental variables, including water temperature, have successfully supported water management in a range of applications (e.g., drinking water supply, hydropower, and agriculture) (Kim & Ahn, 2022; Lofton et al., 2023; Saeed et al., 2024; Zwart et al., 2023). Water temperature is a key controller of many processes in the freshwater environment (Bonacina et al., 2023; Maberly et al., 2020) and one of the most monitored parameters in lakes and reservoirs worldwide (Peñas et al., 2023; Piccolroaz et al., 2024). This makes it a useful parameter for forecasting change in aquatic systems (Gumpinger et al., 2010; St-Hilaire et al., 2021). For example, water column mixing (turnover), the occurrence of algal blooms, and the sediment nutrient release in lakes/reservoirs are often associated with water temperature changes (Cai et al., 2023; Liu et al., 2023; Yin et al., 2023) and hence have been the focus of near-term forecasting in aquatic systems (e.g., Rousso et al., 2020; Schaeffer et al., 2024; Thomas et al., 2020). To date, however, there has been less focus

on forecasting the dynamics of other, equally important, components of freshwater ecology, such as the biology of fishes (Slingsby et al., 2023).

Fishes are an important component of freshwater ecosystems globally (Tamario et al., 2019), and migratory species are of intrinsic social, cultural, and economic value to many societies (Gende et al., 2002; Oke et al., 2020). The life cycle timing (phenology) of fish migrating from freshwaters to the sea and vice versa (i.e., diadromous fish) has a direct impact on aquatic food webs (Dias et al., 2019; Ouellet et al., 2022), nutrient cycling (Oke & Hendry, 2019; Weaver et al., 2018), aquaculture (Ouellet et al., 2022; Vladic & Petersson, 2016), and hydropower (Carter et al., 2023; Knott et al., 2023). In general, diadromous fish migrations are driven by a combination of environmental factors, including temperature, flow conditions, photoperiod, and moonlight exposure (Lin, 2017; Sparks et al., 2019; Valiente et al., 2011). In particular, water temperature influences the metabolism and other physiological processes of fish directly (Seebacher & Post, 2015), resulting in pronounced effects on the timing and extent of migrations (Riley et al., 2012; Zydlewski et al., 2014). It, therefore, has potential as an explanatory variable on which to build a near-term migration forecast, especially in the face of an increasingly variable climate, which can induce shifts in the phenology of (but not limited to) diadromous fish (Legrand et al., 2021; Lowerre-Barbieri et al., 2019; Rinaldo et al., 2024).

Previous work on predicting or hindcasting diadromous fish migrations (e.g., Battin et al., 2007; Durif & Elie, 2008; Hobday et al., 2016; Jacox et al., 2020; Sykes et al., 2009; Teichert, Benitez, et al., 2020) has centered on recreating catchment flow conditions in specific settings with modeling approaches (e.g., statistical, process-based), often using long-term climate projections and incorporating multiple variables besides water temperature. However, most of those predictions are measured on a seasonal to annual scale, while management applications and conservation measures for these species could benefit from near-term forecasts (Roberts et al., 2023; Welch et al., 2019), which could be deployed using a lower number of variables (King et al., 2023; Teichert, Tétard, et al., 2020). Such an approach could be particularly applicable in sites with limited monitoring and/or in settings where fish migrations could be significantly impacted by human activities (e.g., dam and turbine operations) (Barbarossa et al., 2020; Carter et al., 2023).

Here, we present a near-real-time framework that uses water temperature as a determinant of diadromous fish migrations. A daily automated ensemble-based forecasting system was developed to provide probabilistic predictions of fish migrations. This system was applied to Lough Feeagh (Burrishoole catchment, western Ireland), a site with long-term observation datasets of water temperature and daily diadromous fish migrations. Historical data (January 2004 to November 2020) were used to determine the lake temperature conditions associated with percentile-based migration regimes of two diadromous species: Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*). We then combined the ensemble lake temperature forecasts and the percentile-based migration conditions to generate daily probabilistic predictions of future migrations, and we evaluated the prediction skill against the most recent fish monitoring records (November 2020 to November 2023).

Our study aimed to address the gap in near-real time forecasting of daily fish migrations by building a forecast for fish migration using a single explanatory variable that is both readily available in near real time and relatively straightforward to model (i.e., water temperature). We assessed this approach by first evaluating the water temperature forecasting system performance at our study site and second by quantifying forecast performance for the probabilistic predictions of the different fish migrations. We discuss the implications of the results within a freshwater resource management context. We highlight the potential benefits and limitations of the forecasting framework for real-world operational applications and how it might be a scalable tool in those settings.

METHODS

The framework of this study consisted of three main phases graphically presented in Figure 1, which also outlines the study site monitoring arrangement.

Study site

Lough Feeagh is a monomictic lake located in the Burrishoole catchment in western Ireland (53°56' N, 9°35' W). It is the largest water body (~3.95 km²) in a system of lakes interconnected by river networks that discharge into the Atlantic Ocean (Figure 2). It holds a volume of ~6.0 × 10⁷ m³, with mean and maximum depths of 14.5 and 46.8 m, respectively. The Black and the Glenamong rivers are its primary inflows, and the Salmon Leap and the Mill Race water channels are its outflows. The climate in the area is temperate oceanic,

with an average annual rainfall of 1700 mm year⁻¹ and mean air temperature of 11°C (2004–2023).

Atlantic salmon (*S. salar*) and European eel (*A. anguilla*) fish species are endemic to the Burrishoole catchment and are key constituents of its aquatic food web (de Eyto et al., 2020). The migrations of these species to and from freshwater and the ocean are well documented (e.g., Byrne et al., 2003; de Eyto et al., 2022; Poole et al., 2018; Reed et al., 2017; Sandlund et al., 2017). In brief, salmon spawn in the Burrishoole catchment in winter, and juveniles spend a little over two years in freshwater. They migrate to the Atlantic Ocean as smolts in late spring, and after spending one winter at sea, they return to freshwater in the summer as mature adults to spawn. Current evidence supports the view that European eel spawn as a single spawning stock in the Atlantic Ocean in the area of the Sargasso Sea (Als et al., 2011). Juveniles arrive off the Irish coast in autumn and enter estuaries from November to February. As temperatures rise, many commence active migration into freshwaters as elvers. Once in freshwater, elvers grow into yellow eel, which is the life stage in which they spend most of their life (7–58 years in the west of Ireland). Eels mature only once when they undergo a process known as silvering before returning to the Atlantic Ocean to spawn, after which they die.

Water temperature monitoring

As part of an Automatic Water Quality Monitoring System (AWQMS) deployed in Feeagh, the water temperature has been measured at 13 different depths (0.9, 2.5, 5, 8, 11, 14, 16, 18, 20, 22, 27, 32, and 42 m) at a high frequency (2-min intervals) since 2004. The surface water temperature (0.9 m) is measured via a Hach Environmental Hydrolab Data Sonde X5 with an accuracy of ±0.1°C (UK OTT Hydrometry Ltd.; <https://www.otthydromet.com>), while the other 12 depths are measured via platinum resistance thermometers with an accuracy of ±0.2°C (UK Labfacility Ltd. PT100 1/10DIN 4 wire sensor; <http://labfacility.com>), enabling a complete vertical profile reading. The sensors are cleaned monthly, and the multiparameter probe is calibrated once per month (de Eyto et al., 2016).

Water temperature data from the AWQMS that had undergone appropriate quality assurance/quality control (QA/QC) were obtained from the Marine Institute monitoring web services (<http://marine.ie>). Data from 2004 to 2023 were used in this study, together with the volumetric percentage of lake water corresponding to each depth (Marine Institute, 2017). Lake thermal stratification in Feeagh was defined as the difference

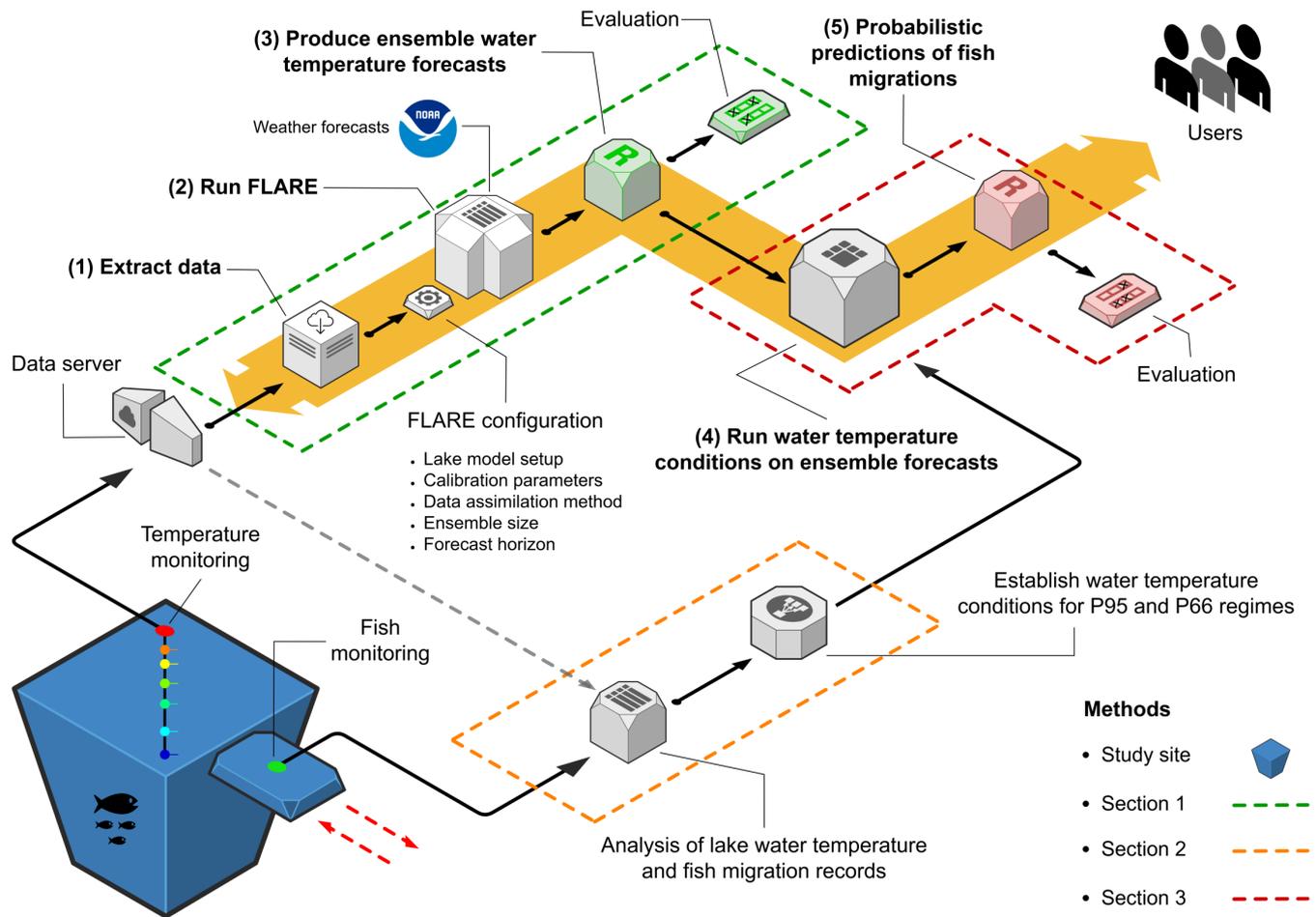


FIGURE 1 Flow diagram of the forecasting framework structure. The framework contains three main phases indicated by dashed lines (see key). The automated components of the framework are indicated by five iterative steps denoted in boldface alongside a continuous solid yellow arrow. Illustration credit: Ricardo Paíz. FLARE, Forecasting Lake and Reservoir Ecosystems.

of $>1^{\circ}\text{C}$ between the surface (0.9 m) and bottom (42 m) lake temperatures (Woolway et al., 2020).

Fish monitoring

Three fish migration datasets from 2004 to 2023 (matching the water temperature monitoring data period) were used in this study: (1) daily downstream (juvenile smolt) and (2) daily upstream movements (adults) of Atlantic salmon; and (3) daily downstream movements of maturing adult European “silver” eel.

All fish moving into and out of the catchment were counted at two sites, the Salmon Leap and the Mill Race, the two water channels connecting freshwater Feeagh with the downstream brackish lagoon, Lough Furnace, which leads directly to the Atlantic Ocean through Clew Bay (Figure 2). The daily counts were performed manually using permanent whole river upstream and downstream fish traps and are part of long-term monitoring

efforts that record the transition of fish migrations between the freshwater and marine domains (de Eyto et al., 2022; Long et al., 2023). The fish traps follow a Wolf type trap design employing horizontal grids with 10-mm gaps on a 1:10 inclination (Poole et al., 2018; Wolf, 1951). Trapping at the catchment involves a fish fence and wolf trap on the Mill Race outflow installed in 1958 and a full flow controlled Wolf trap on the Salmon Leap outflow installed in 1970 (see Poole et al., 2018 for more details).

Water temperature forecasting

We deployed the Forecasting Lake And Reservoir Ecosystems system (FLARE) to generate daily water temperature forecasts in Feeagh for three years (1 November 2020 to 1 November 2023; 1095 days). FLARE is an open-source system for lake and reservoir water quality forecasting aimed at supporting management (Carey

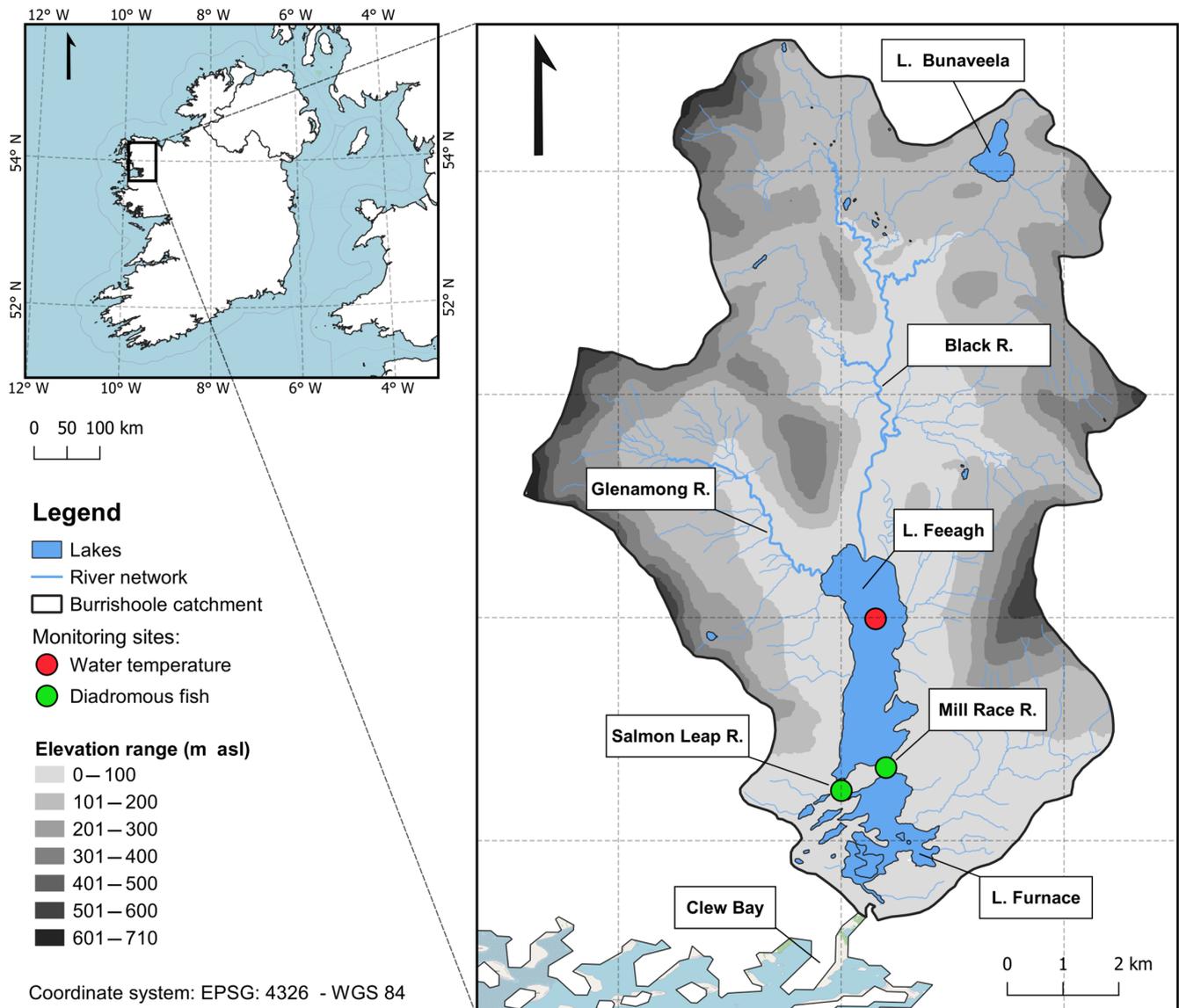


FIGURE 2 Location of Lough Feeagh and the Burrishoole catchment in western Ireland, including main water bodies and topographic elevation in meters above sea level (m asl). The monitoring sites for water temperature and fish are indicated by red and green dots, respectively.

et al., 2022; Thomas et al., 2020). By integrating real-time monitoring, hydrodynamic modeling with data assimilation, and an ensemble-based forecasting algorithm, FLARE provides daily water quality forecasts for multiple lake/reservoir depths with a forecast horizon of up to 35 days with quantified uncertainty (Thomas et al., 2020, 2023; Wander et al., 2024). To date, several FLARE-based forecasting systems have been deployed to provide predictions of different water quality variables, for example, water temperature, dissolved oxygen, and chlorophyll *a* (Carey et al., 2022; Thomas et al., 2023; Wander et al., 2024; Woelmer et al., 2022, 2024).

FLARE uses the General Lake Model (GLM) (Hipsey et al., 2019), a widely used one-dimensional (1-D) model, as the process model to generate

predictions for each ensemble member. GLM has been previously applied to Feeagh in non-forecasting studies (Bruce et al., 2018; Mesman et al., 2020). We used the 31-member National Oceanic and Atmospheric Administration Global Ensemble Forecasting System (NOAA GEFS) (<https://www.ncei.noaa.gov>) (Hamill et al., 2022) output for the grid cell that contains Feeagh as the forcing weather forecast ensemble. FLARE quantifies uncertainty by adding random noise to each FLARE ensemble member (process uncertainty), assigning one of the 31 members of the weather forecast ensemble to each FLARE ensemble member (driver uncertainty) and having different parameter values for each FLARE ensemble member (see Wander et al., 2024, for more details). FLARE uses data

assimilation (specifically the Ensemble Kalman Filter with state augmentation) to calibrate the parameter values and set the spread of the ensemble when each forecast was initiated (day 0 of the forecast).

Configuration

FLARE was configured based on previous applications of the system (Thomas et al., 2020, 2023; Wander et al., 2024). First, we configured GLM for Feeagh with the bathymetry used in previous model applications at the site (Mesman et al., 2020). Second, we configured FLARE-specific settings for water temperature forecasting. The number of FLARE forecast ensemble members was set to 248 to avoid erroneous data correlations that can arise when using smaller ensembles (Wander et al., 2024); so that each of the 31 weather forecast ensemble members was used eight times to drive the lake model, with each having slightly different process noise, parameters, and initial conditions (following Thomas et al., 2020). Details on the GLM configuration and FLARE water temperature forecasting configuration for Feeagh can be found in Appendix S1.

Infrastructure

To make FLARE functional in real time at Feeagh, we developed an infrastructure that runs in the cloud and interconnects the framework system with the extraction of field observations to generate forecasts (see Figure 1).

For each day that a forecast is generated, first, we extracted the most recent water temperature monitoring data from a local data server using an R script (see Appendix S1). This script was automatically run in a public GitHub repository via a scheduled GitHub Action (.yml file). These data were collated into daily mean water temperature values for each monitoring sensor and stored in a single target file in the same repository. This target file was updated every time the action ran. The FLARE workflow was then run in the same repository using an R script with the “FLAREr” R package via a scheduled GitHub Action (.yml file). The target file with the new observations was acquired within the workflow before a forecast generation, allowing FLARE to perform data assimilation as specified in the configuration. The resulting water temperature forecasts were collated by several filters, including depth, ensemble member, date, and forecast horizon, and were allocated into columnar storage data format files (.parquet) (see Appendix S1).

Evaluation

We evaluated the performance of the lake water temperature forecasts against observations based on root mean square error (RMSE; see Appendix S1). RMSE is commonly used to assess the accuracy of water temperature predictions in many forecasting applications (Feigl et al., 2021; Qiu et al., 2021), including other FLARE deployments (Thomas et al., 2023; Wander et al., 2024). The evaluation was carried out for the volume-averaged lake water temperature calculated using the 13 monitoring depths (hereafter referred to as average lake water temperature) and for each monitored depth. RMSE values were computed for all 1–34 forecast horizon days over the entire forecasting period (excluding the time from 1 January to 9 May 2021 when no observations were available). The results were averaged for each forecast horizon day and for FLARE (overall performance calculated by aggregating all FLARE forecasts produced, i.e., all average lake water temperature forecasts and all individual depth forecasts).

We compared the performance of FLARE to (1) site persistence and (2) site climatology. Predictions based on both persistence and climatology have been widely used in environmental science as they are relatively easy to generate (Murphy, 1992) and provide an important baseline that enables the performance of new forecasting systems to be contextualized (Bento et al., 2022; Brown et al., 2018; Thomas et al., 2020; Yang, 2019; Zachow et al., 2023). Persistence predictions were based on the assumption that future water temperature conditions will be the same as the recent past (Wilks, 2019), that is, they would vary depending on the forecast horizon. For example, a persistence forecast set with a 16-day forecast horizon and produced on date d will use the observed water temperature on date $d - 1$ as a prediction, extending that value over the next 16 days. Climatology predictions were based on long-term average conditions of lake water temperature so that the historical average of a specific day in a year is indicative of the water temperature for the same day in the future. A climatology forecast produced for 18 March 2021 will, for example, be equal to the average water temperature of Feeagh on that same day (18 March) in the historical records (2004–2020).

Lastly, we generated a reliability diagram to evaluate how well the uncertainty was characterized for the water temperature forecasts (Thomas et al., 2020; Zwart et al., 2023) by quantifying proportions of observations within different confidence intervals (CIs) (10th, 25th, 50th, 75th, and 90th) for different forecast horizons (1, 7, 14, 21, 28, and 34 days ahead). An ideally calibrated forecasting system would have 10% observations

within the 10% forecast CI (the range containing the middle 10% of the ensemble distribution), 25% observations in the 25% forecast CI (the range containing the middle 25% values of the ensemble distribution), etc. If the percentage of observations within its given CI is higher or lower, the forecasting would be considered underconfident or overconfident, respectively (Bröcker & Smith, 2007).

Historical analysis: Fish migrations and water temperature

To relate the fish migrations with lake water temperature, we consulted research on which water temperatures have been linked to diadromous fish migrations. This indicated that (1) ambient water temperatures and (2) cumulative water temperature values have a strong role in triggering the timing and extent of diadromous migrations (e.g., Riley et al., 2012; Sparks et al., 2019; Sykes et al., 2009; Zydlewski et al., 2005, 2014). Therefore, we used both temperature metrics as hydrologic controls of daily fish runs of Atlantic salmon and European eel migrations. Note that daily fish runs refer to fish migrations occurring in a day.

Cumulative lake water temperature is a function of the start date chosen and is calculated by integrating the daily average temperatures over time during an annual cycle, starting from 0°C. In contrast to related metrics such as degree days and growing degree days, cumulative water temperature simply accumulates daily temperature magnitudes, rather than considering differences from a baseline value (which can be a specific threshold or 0°C) or between daily values. Zydlewski et al. (2005, 2014) defined the start of cumulative temperatures on 1st January. By contrast, Riley et al. (2012) defined the start using two dates, 21 December (winter solstice) and 15 February, and found a better correlation for the latter date which was attributed to the proximity of their migrations to that time (15 March). Similarly, Sykes et al. (2009) defined the start on 9 March and found a strong correlation with salmon smolt migrations (which started in April). Here, we defined 1 March as the start of the cumulative temperatures for Feeagh, as this date indicates the beginning of spring in Ireland, the season when temperatures start to rise and when salmonids start to manifest strong migratory behavior (de Eyto et al., 2022).

Daily observed values of average lake water temperature in degrees Celsius and average lake cumulative temperature in degrees Celsius-days were computed for Feeagh. These were compared with datasets for all three diadromous fish migrations, matching daily fish counts from January 2004 to November 2020. Then, two sub-datasets were created by extracting values based on

two daily fish count percentiles, respectively: 95th (P95) and 66th (P66). These metrics were selected to represent two different regimes for the number of fish going through the traps each day for each species. P66 and P95, therefore, indicate days when daily counts are in excess of 66% and 95%, respectively, of the historical daily fish count records. With these two metrics, we aimed to identify two distinct regimes where the number of fish migrating was likely to be high (P66) and very high (P95; indicative of extreme events). Both P66 and P95 indicate meaningful regimes of migration intensities with implications for applied management that could require important resources to ensure safe fish passage.

On each of these sub-datasets, we performed a symmetric outlier reduction (5% trim) on the driver data (i.e., the lake water temperatures and cumulative lake water temperatures) to focus on the central tendency of the migrations (Benhadi-Marin, 2018; Osborne & Overbay, 2004; Xu, Mazur, et al., 2020). Then, for each sub-dataset, we extracted the minimum and maximum values of the two water temperature metrics, respectively. As a result, we obtained (1) a range of daily lake water temperatures and (2) a range of daily lake cumulative water temperatures for each fish migration regime. These ranges were then used as the start and end points for the specific lake water temperature conditions necessary for the different fish migrations to occur, notwithstanding that we recognize that other controlling factors, including photoperiod, moon phase and water flow, also play a role (Byrne et al., 2003; Sandlund et al., 2017).

Probabilistic forecasting of fish migrations

Using both the lake water temperature forecasts produced and the lake water temperature ranges established, we generated daily probabilistic predictions for each fish migration regime for the period 1 November 2020 to 1 November 2023. For the generation of each fish migration prediction, we used the nowcasted lake average water temperature instead of using temperature observations from individual sensors. We used this approach for simplicity and also to support future scaling to other lake ecosystems.

First, we calculated a daily value for forecasted lake cumulative water temperatures from the daily forecasted lake water temperatures (both collated by forecast horizon, 1–34 days ahead; and ensemble member, 1–248). Then, to generate the probabilistic predictions for a specific fish migration regime (e.g., P66 salmon downstream), we assessed when both water temperature conditions were met. For each day, the percentage of the 248 ensemble members that (1) fell within the maximum–minimum

range for the lake water temperature condition and (2) also fell within the maximum–minimum range for the cumulative lake water temperature condition represented the daily probability of that fish migration regime occurring. Consequently, we were able to obtain daily probabilistic predictions, in the order of 0%–100%, for each forecast horizon (i.e., 1- to 34-day-ahead probabilistic predictions per fish migration regime). Our modeling approach, therefore, predicts fish migrations based solely on lake water temperature variation. Similar to other models (e.g., Sykes et al., 2009; Teichert, Tétard, et al., 2020), our forecasting framework does not account for any fish stock number in the catchment before and after a model prediction. An illustrative example of a daily output of the forecasting framework showing an average lake water temperature forecast, an average cumulative lake water temperature forecast, and probabilistic predictions for the P66 and P95 regimes of the Atlantic Salmon downstream migration are presented in Figure 3.

Evaluation

We evaluated the performance of the probabilistic predictions for the fish migrations against the most recent fish monitoring data based on the continuous ranked probability score (CRPS). CRPS measures both the precision and accuracy of our probabilistic forecasts by comparing them to observations (Bröcker, 2012; Taillardat et al., 2023). A lower CRPS value indicates a higher performing forecast with a smaller error margin (see Appendix S1 for more details). The evaluation was carried out for all 1–34 forecast horizon days over the entire forecasting period (November 2020 to November 2023), and the results were averaged for each forecast horizon day. Only the observed daily fish runs equal to or exceeding historical P66 and P95 runs were used for the P66 and P95 regime CRPS evaluations, respectively, and represented percentage values of 100% against the probabilistic predictions (the rest were treated as 0%).

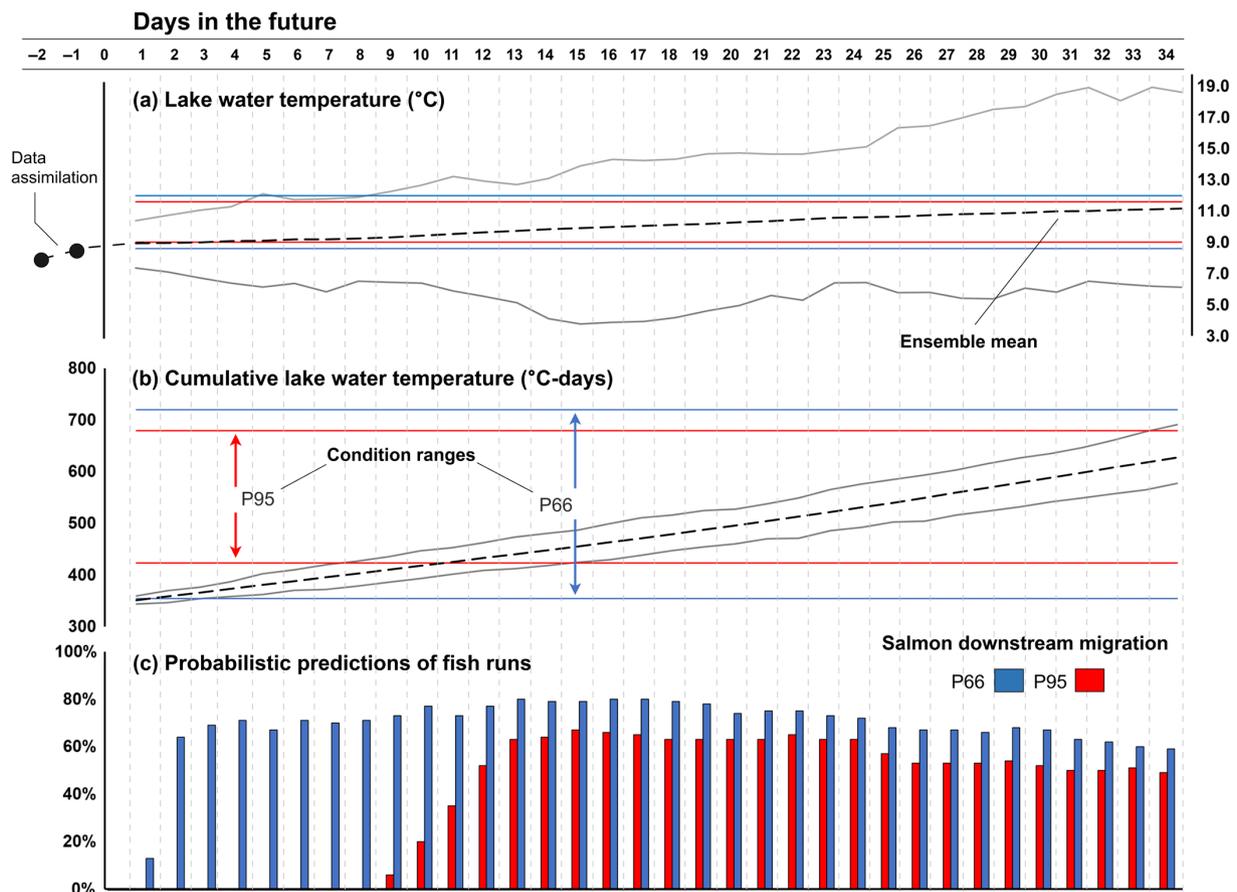


FIGURE 3 Illustrative example of a daily output of the forecasting framework containing (a) an average lake water temperature forecast, (b) an average cumulative lake water temperature forecast, and (c) probabilistic predictions of the P66 and P95 regimes for the Atlantic salmon downstream migration. The red and blue bands in panels (a) and (b) indicate the lake water temperature conditions necessary for the P66 and P95 regimes to occur, respectively. The two black dots in panel (a) represent measured water temperature observations used for data assimilation. The continuous gray lines around the ensemble mean (dotted black line) in panels (a) and (b) denote the 95% CI uncertainty of the temperature forecasts. Illustration credit: Ricardo Paiz.

RESULTS

Water temperature observations

The observed average lake temperatures in Feeagh exhibited relatively stable dynamics during both the historical period (January 2004 to November 2020) and the forecasting period (November 2020 to November 2023), ranging from 3.5 to 16.5°C (average of 10.7°C) (Figure 4). Peak temperatures and thermal stratification were observed typically from April to September (spring and summer). Conversely, mixed lake conditions presenting the lowest water temperatures prevailed from October to March (autumn and winter) (see Appendix S2: Figure S1 for water temperature measurements at each monitoring depth). Throughout the forecasting period, the lake exhibited thermal stratification

44% of the time (486/1095 days) and mixed conditions 56% of the time (609/1095 days).

Water temperature forecasts

The overall RMSE performance for all forecasts produced using FLARE (for all 13 individual depths and the average lake water temperature aggregated across all 1- to 34-day-ahead horizons) over the three-year forecasting period was 0.94°C. The climatology and persistence forecasts performed worse than FLARE, with overall values of 1.36 and 1.19°C RMSE, respectively.

For the surface temperature only, the RMSE values of the FLARE temperature forecasts consistently increased as the forecast horizon became longer (indicating a

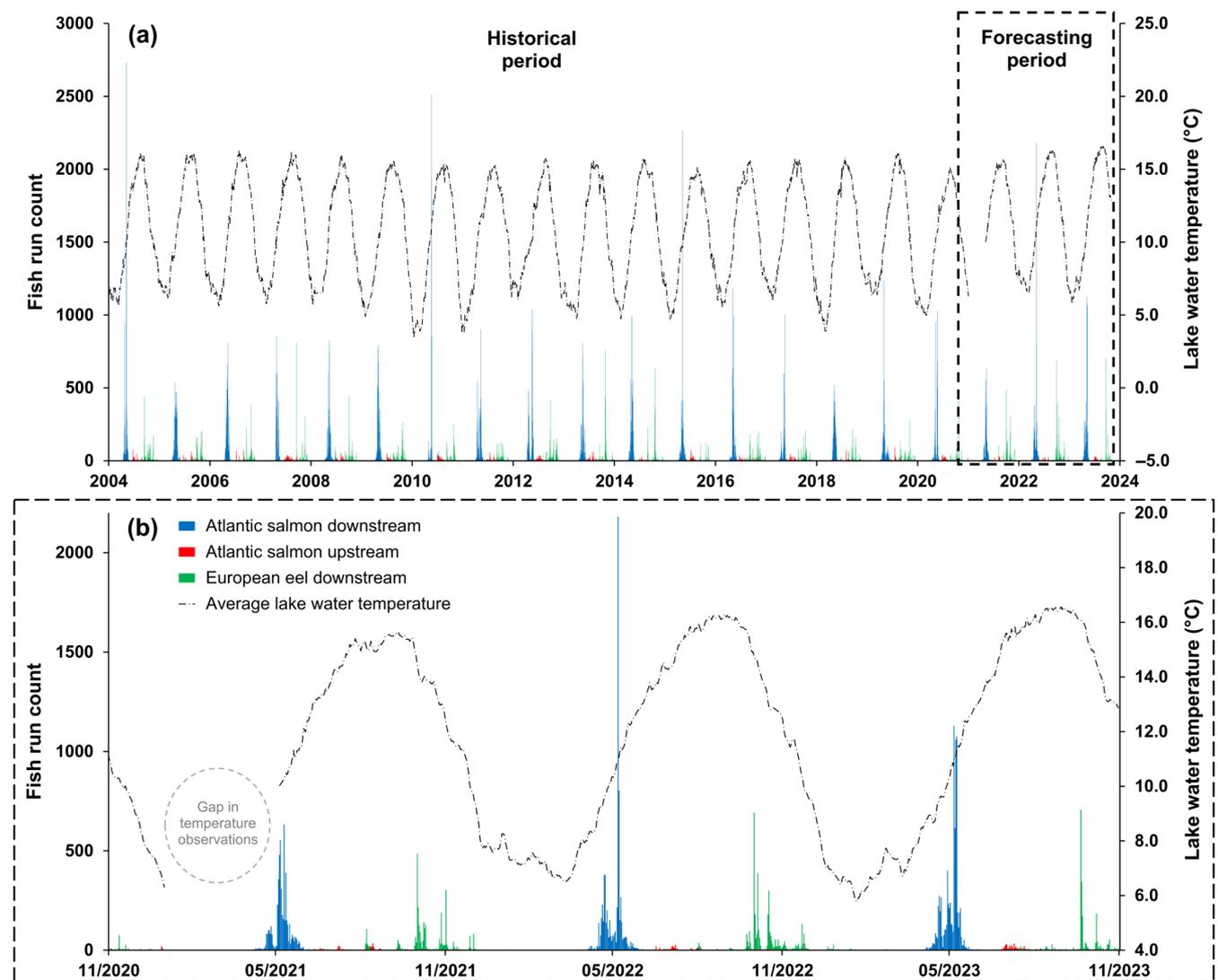


FIGURE 4 Measured average water temperature observations in Lough Feeagh and daily fish counts of Atlantic salmon downstream, Atlantic salmon upstream, and European eel downstream migrations in the Burrishoole catchment. The observed data within the forecasting period (black dashed box) in (a) is highlighted in greater detail in (b).

decrease in performance), from 0.30 to 1.58°C (Figure 5a). Climatology surface temperature forecasts, with an RMSE of 1.41°C, were outperformed by FLARE on the first 28 of 34 forecast horizon days. Persistence forecasts for the surface temperature ranged from 0.34 to 1.96°C and were consistently outperformed by FLARE on all forecast horizon days. The average lake water temperature forecasts using FLARE performed slightly better than the surface temperature forecasts, with RMSE values ranging from 0.20 to 1.34°C (Figure 5b). Climatology average lake water temperature forecasts, with an RMSE of 1.10°C, were outperformed by FLARE on the first 21 of 34 forecast horizon days. Persistence

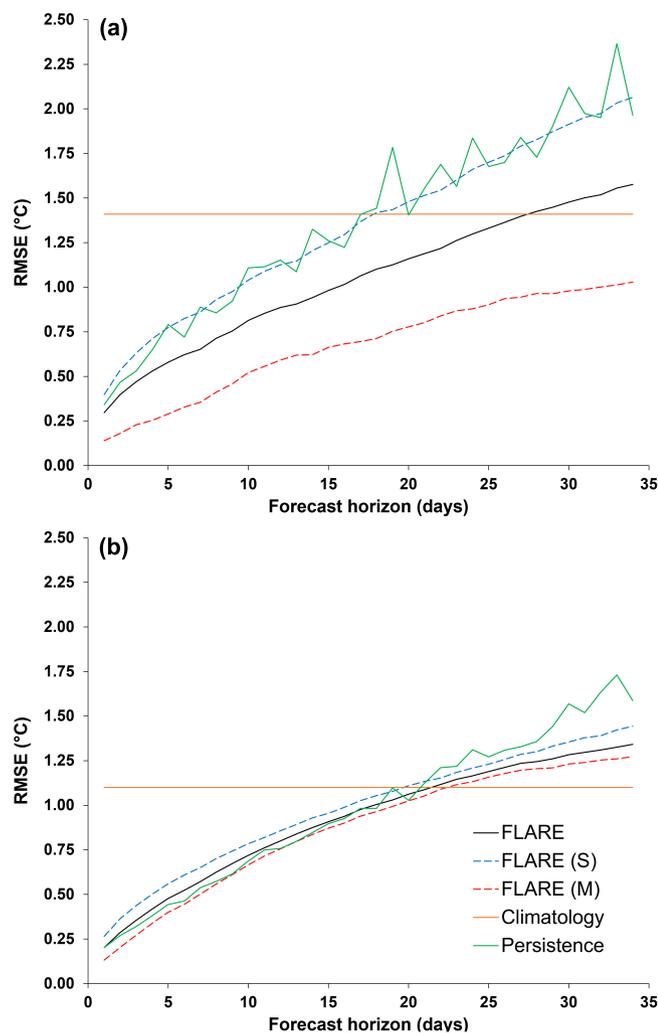


FIGURE 5 Root mean square error (RMSE) of the (a) surface lake water temperature (0.9 m) and (b) average lake water temperature forecasts produced over the entire forecasting period. Forecasting Lake and Reservoir Ecosystems (FLARE) (S) and FLARE (M) represent FLARE RMSE values for forecasts produced under stratified and mixed lake conditions, respectively. Climatology and persistence indicate RMSE performance for forecasts produced using their respective approaches.

forecasts for the average lake water temperature ranged from 0.20 to 1.59°C and performed similarly to FLARE on the first 21 forecast horizon days, but then, they were outperformed by FLARE on days 21–34. Typically, FLARE predictions produced during lake mixed conditions were more accurate than those produced during stratified conditions (Figure 5).

Moreover, forecast uncertainty was well characterized by FLARE for all forecasts produced in Feeagh (forecasts for average lake water temperature and each monitoring depth). Relatively small variations in confidence from an ideal forecast were observed, although these varied depending on the forecast horizon length (Figure 6). On short to intermediate forecast horizons (<21 days ahead), FLARE predictions were mostly underconfident by up to 16%. In longer forecast horizons (>28 days ahead), the uncertainty estimates fluctuated from more confidence (up to −9%) to less confidence (up to 6%).

Fish migration dynamics

The fish migrations during the historical period (January 2004 to November 2020) exhibited a day-sensitive phenological behavior with substantial differences in magnitudes and regime timings (Figure 4; Table 1). On average, 90 juvenile smolt Atlantic salmon moved downstream per day during fish runs (median of 14), with a maximum count of 2733 observed in a single day (7 May 2004). The P66 and P95 numbers of salmon migrating downstream were 39 and 431 fish, respectively. Salmon began to go downstream around April, coinciding with rising lake water temperatures (Figure 4). Their migratory behavior decreased in mid-May and generally ceased after June. The maximum count of adult salmon migrating upstream was 92 individuals (18 July 2019), with an average of 7 fish (median of 3). The P66 and P95 for the daily upstream migration of salmon were 6 and 27 fish. The counts were more sporadic than daily counts of downstream migrating salmon. Salmon started to migrate upstream in June, sometimes overlapping with the end of the downstream migration movements. The fish runs of salmon going upstream decreased usually around October, but some counts extended till December.

In contrast to Atlantic salmon, the core of European eel migrations took place when there was a decreasing trend in lake water temperatures (Figure 4). The daily average for the number of adult eel migrating was 18 individuals (median of 5). The maximum count was 813 (17 September 2007). The P66 and P95 daily downstream migrations were 9 and 80 eels, respectively. Downstream migrations of eel were recorded all year round. However, the highest numbers (in the order of the P95) were recorded between

August and November. The P66 and P95 metrics established for all three fish migrations were representative of all annual cycles of the 17 years of the historical period of this study (Appendix S2: Figure S2).

Water temperature conditions for fish migrations

In general, all six fish migration regimes (P66 and P95 for all three migrations) required the lake water temperatures to be temperate to warm (8.8–15.9°C), with the ranges for the P95 regimes generally being narrower than those for the P66 regimes (Table 2). The widest ranges were for eel downstream, reflecting the longer period over which that migration occurred. The salmon upstream migration coincided with the warmest lake water temperatures. By contrast, colder temperatures were associated with the two downstream migrations, with lower range limits in the order of 9.0°C (Table 2). These low temperatures aligned with the onset and end of winter, when eel migration terminated and salmon downstream migration started, respectively.

The cumulative lake water temperature conditions differed for the three different fish migrations. The salmon downstream migration occurred over small and well-constrained ranges of cumulative lake water temperatures for both regimes. By contrast, much larger and

broader ranges of cumulative lake water temperatures were associated with the salmon upstream and eel downstream migrations (Table 2).

Probabilistic predictions of fish migrations

Using predictions of Atlantic salmon downstream migration for 2021 as an example, the P95 regime predictions generally extended before and after the observed P95 fish runs; however, the observed P66 fish runs were well captured by the forecasts (Figure 7; Appendix S2: Figures S3–S8). Predictions for shorter horizons displayed relatively large fluctuations in value before and after observed fish run counts reflecting that not only the general block of migrations could be captured but also a degree of day-to-day variations. For instance, European eel predictions for short horizons (<8 days ahead) displayed much lower probabilities prior to observed events than during events (Appendix S2: Figures S7–S8). Another clear difference among the probabilistic predictions for the different forecast horizons was the order of percentage magnitude, which decreased on average with the horizon (Appendix S2: Figure S9).

In general, the P66 regime probabilistic predictions for all three fish migrations performed better, with lower CRPS values, than those for the P95 regimes (Figure 8).

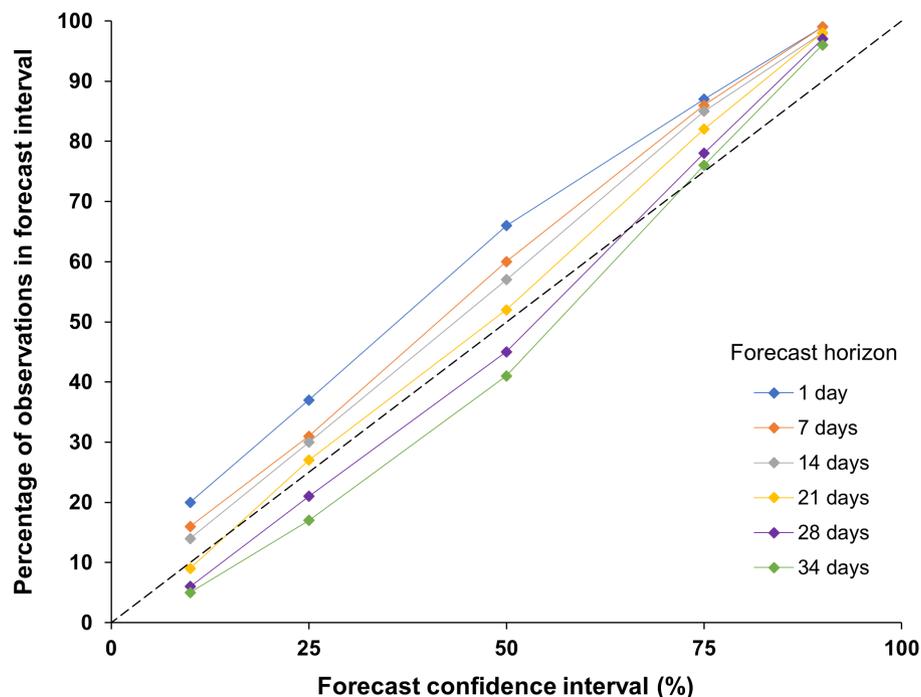


FIGURE 6 Reliability diagram for all lake water temperature forecasts produced by Forecasting Lake and Reservoir Ecosystems over the entire forecasting period. The percentage of lake water temperature observations within different forecast CIs is indicated for different forecast horizons. The continuous black dotted line represents ideal forecast confidence calibration (i.e., a forecasting system that perfectly characterizes uncertainty; 1:1 relationship between forecast CI and the percentage of observations within it).

The predictions for the salmon downstream migration performed best, starting at a CRPS of 5% followed by a generally linear trend (Figure 8a). However, the score was still under 11% at the end of the forecast. The upstream migration for salmon had the widest range of CRPS values, increasing from 9% to 18% over the forecast. The P66 predictions for eel performed more stably, with CRPS starting at 8% but then remaining at about 12% from 5 days ahead. By contrast, the performance of the P95 regime predictions across the forecast horizon was not as good. Higher CRPS values were obtained of up to 31% (Figure 8b). The predictions for eel were the best in this regime, with a narrow CRPS range of values from 13% to 16%. The CRPS values for the two salmon migrations increased steeply in very short horizons (<5 days ahead) and then continuously decreased.

DISCUSSION

Accurate ecological forecasts and associated uncertainty have the potential to aid management in an increasingly uncertain world, including decisions on the allocation of resources for fish monitoring programs. Our study shows that the FLARE system accurately replicated lake temperature dynamics in our study lake, which we used to produce reasonable probabilistic predictions for three fish

TABLE 1 Average, median, maximum, P66, and P95 regime fish run counts for the Atlantic salmon downstream, Atlantic salmon upstream, and European eel downstream migrations in the Burrishoole catchment during the historical period of this study, January 2004 to November 2020 ($n = 6150$).

Metric	Atlantic salmon		European eel, downstream
	Downstream	Upstream	
Average fish run count	90	7	18
Median fish run count	14	3	5
Maximum fish run count	2733	92	813
P66 fish run count	39	6	9
P66 time frame	April to July	June to December	January to December
P95 fish run count	431	27	80
P95 time frame	April to May	June to September	August to November

Note: The P66 and P95 time frames indicate the earliest and latest months in a year when the P66 and P95 fish runs have been counted, respectively.

migrations up to 34 days into the future, with the best results being for the P66 regime of Atlantic salmon downstream migration (Figure 7; Appendix S2: Figure S3). Enhancing decision making in freshwater management with such forecasts has the potential to yield not only environmental but also economic benefits as it can allow more appropriate allocation of human and economic resources (Baker et al., 2020; Franklin et al., 2024; Xu, Yang, et al., 2020). A forecast of fish migration with associated probability produced today for the subsequent 7- to 10-day period, for example, could allow an operator to plan resource allocation in advance. This could be particularly relevant for lakes and reservoirs that provide different services (e.g., navigation, drinking water supply, flood control, hydropower, aquaculture), where more informed daily or sub-daily scale operations could enhance the protection of diadromous fish (Carter et al., 2023; Harris et al., 2016; Norman et al., 2023).

Although our example was for a catchment with a relatively low degree of human intervention, the approach is transferable to catchments where daily management of fish migrations is considered crucial to their survival (Bolstad et al., 2021; Ouellet et al., 2022). With informed fish migration regime forecasts, various mitigation measures can be evaluated for improved conservation of diadromous fish. Forecasts for relatively short horizons (e.g., <14 days ahead) could enhance daily-scale actions, such as the operation of fish bypass structures in drinking water reservoirs (Piper et al., 2013; Song et al., 2019), scheduling of dam releasing in flood control (Katopodis & Williams, 2012; Trancart et al., 2020), and periodic pumping and turbine shutdowns in hydropower (Carter et al., 2023; Nyqvist et al., 2017), all of which could enable safer passages for fish. Forecasts for longer horizons (e.g., >14 days ahead) could be more relevant for (but not limited to) the control of nature-like fishways (Steffensen et al., 2013), planning of fishing timing in aquaculture (Gargan et al., 2015; Harringmeyer et al., 2021), and routine operation of fish traps/racks in monitoring and research (Piper et al., 2020; Ruokonen et al., 2022). In addition, having future predictions of fish moving in and/or out of the systems could enable the estimation of fish counts in situations and periods where direct counting is not feasible due to restrictions on environmental factors (e.g., flow conditions) and other limitations (e.g., staff, funds).

While many studies have simulated diadromous fish migrations, there are few that have developed true forecasts with quantified uncertainty, especially on a daily time scale. By using lake water temperature as a core variable, our study expands the available pool of near-term ecological forecasting tools for predicting fish migrations (e.g., King et al., 2023; Teichert, Tétard, et al., 2020; two previous frameworks that were developed using river

TABLE 2 Lake water temperature conditions established for the different regimes (P95 and P66) of the Atlantic salmon downstream, Atlantic salmon upstream, and European eel downstream migrations in Lough Feagh, Burrishoole catchment.

Metric	Atlantic salmon				European eel, downstream	
	Downstream		Upstream		P95	P66
	P95	P66	P95	P66		
Lake water temperature (°C)	9.2–11.8	8.8–12.2	13.4–15.9	12.8–15.8	10.0–15.3	8.9–15.6
Cumulative lake water temperature (°C-days)	423–679	354–720	1078–2122	1053–2475	2151–3132	1746–3247

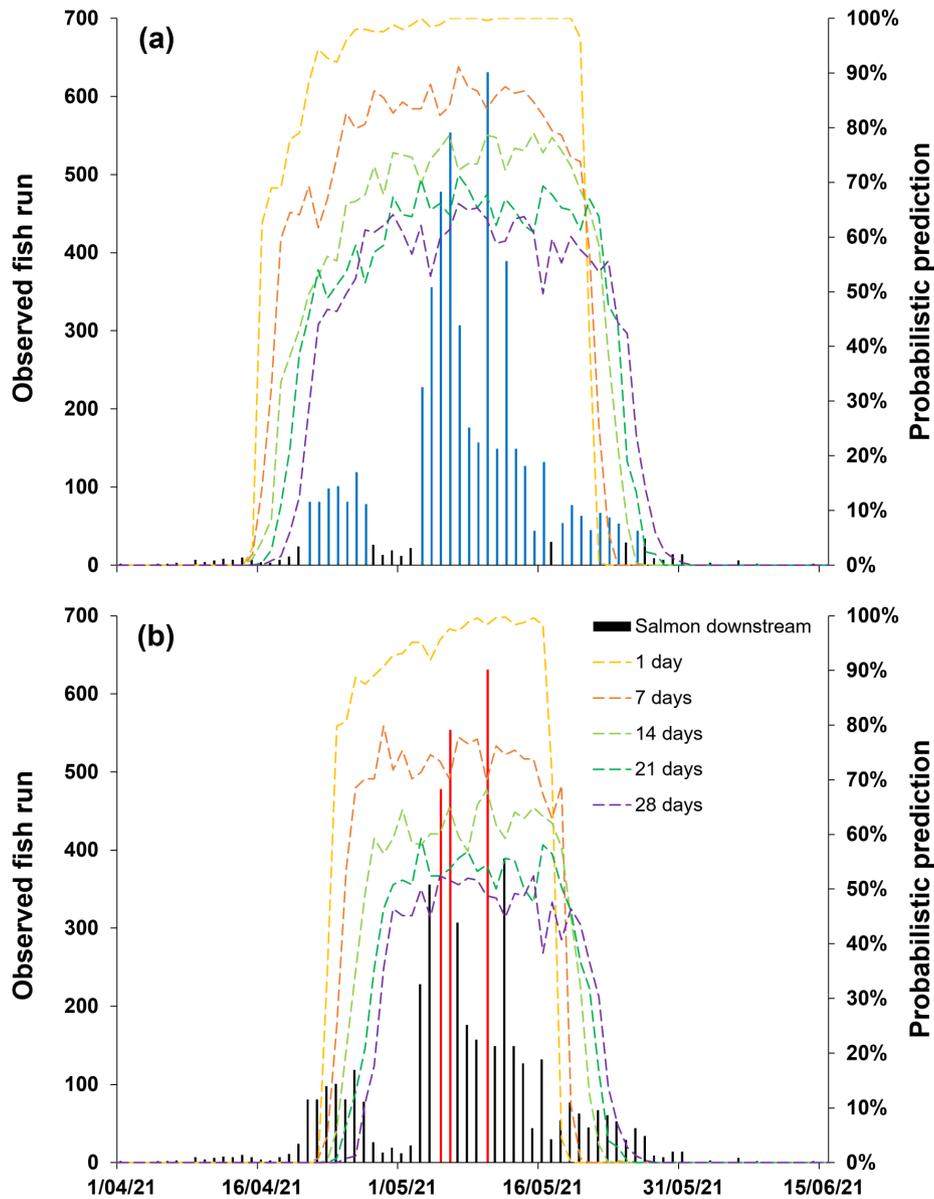


FIGURE 7 Daily probabilistic predictions of Atlantic salmon downstream migration for different forecast horizons (1, 7, 14, 21, and 28 days ahead) against observed fish runs during 2021: (a) the P66 regime predictions and (b) the P95 regime predictions. The observed fish run counts equal to or exceeding historical P66 and P95 fish run counts are highlighted in blue and red, respectively.

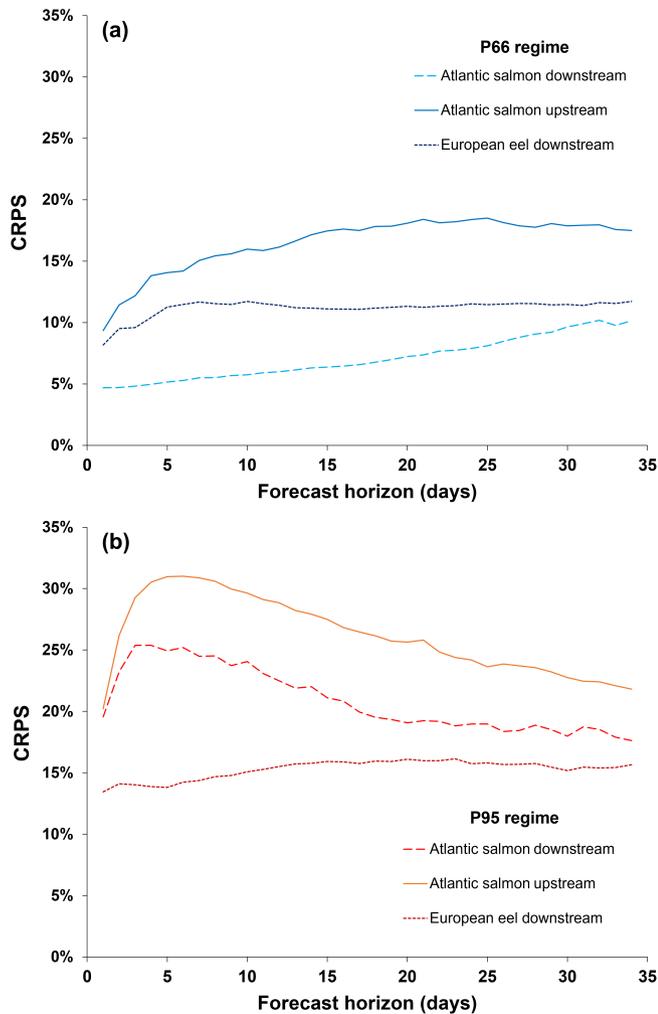


FIGURE 8 Continuous ranked probability score (CRPS) of the (a) P66 and (b) P95 probabilistic predictions of Atlantic salmon downstream, Atlantic salmon upstream, and European eel downstream migrations produced over the entire forecasting period.

hydrologic connectivity data). Importantly, our forecasting framework is flexible. It can be adapted with site-specific information to anticipate local fish migration regimes and therefore inform decisions as to when mitigation measures should be applied. An optimal approach to implement and adapt it would be with a human-centered design to supply context-dependent management needs (Carey et al., 2022; Lofton et al., 2023). Mitigation measures for migrating fish will differ between sites depending on many factors, for example, management concerns, ecological status, infrastructure, financial options, socioeconomic conditions, and regulatory frameworks (Tamario et al., 2019). Although we forecast two regimes in this study, P66 and P95, other tailored solutions could be explored as appropriate. Such a modeling framework could also allow scenario testing to be undertaken for the upcoming management period. For example, trade-offs between the requirements of different

stakeholders and sectors could be evaluated, aiming to achieve sustainability in management practices and production systems (Franklin et al., 2024).

Uncertainty in the predictions

Including uncertainty in forecasts and communicating that uncertainty to stakeholders is a critical aspect of successful ecological forecasting (Dietze et al., 2018; Lewis et al., 2022). Our forecasts will have uncertainty related to both aspects of the workflow: water temperature and fish migration. In general, the water temperature forecasts performed very well at our study site (with a low RMSE), although uncertainty estimates tended to be slightly underconfident, especially in shorter horizons (Figure 6). This is likely due to overfitting observations during data assimilation, a factor that is relatively common in model-based forecasting frameworks (Wander et al., 2024; Zwart et al., 2023). Water temperature forecast uncertainty also increased for longer time horizons (Figure 3), again a common feature of ecological forecasting. A partitioning of uncertainty could be used in future work to quantify the relative contribution of different sources to total uncertainty so that key areas for improvement could be identified (Wander et al., 2024). Previous studies have reported that the ability of FLARE to reproduce water temperatures (i.e., model process) and the error related to the meteorological driver data contributed most to total uncertainty, especially in longer horizons (Thomas et al., 2020). The results presented here performed similarly to other deployments of FLARE for surface water temperature forecasting (Thomas et al., 2020, 2023; Wander et al., 2024), which is reassuring, as this was the first application of FLARE for forecasting volume-averaged lake water temperature and cumulative water temperature.

The uncertainty associated with our water temperature forecasts will feed into the fish migration forecasts, while additional uncertainty will be related to how well water temperature acts as a control of fish movements. Although water temperature is a key driver of diadromous fish migrations, we recognize that it is only one of a suite of variables that act together (Sandlund et al., 2017; Tamario et al., 2019; Teichert, Benitez, et al., 2020). The degree to which a change in water temperatures will trigger fish run events is difficult to quantify even under completely controlled conditions (Sparks et al., 2019) because of its intrinsic interactions with other triggering variables (Zydlewski et al., 2014) and because of the complexity of fish life histories, especially for migratory species. Despite these complexities, our framework was still able to (1) represent historical fish migrations through the use of the P66 and P95 metrics, as these accounted for events in all 17 years of migration

data (Appendix S2: Figure S2), and (2) hindcast migration extent and timing relatively well, especially for the P66 regime. We do note that the temporal distribution of the probabilistic predictions for all three migrations was somewhat restricted by the cumulative lake water temperature condition. However, relying solely on ambient lake water temperature as a condition would have been problematic. Predictions for the salmon downstream migration, for example, would then have extended not only from April to July for this site but also included November to January, a period with no observed fish runs. The use of a combination of both lake water temperature metrics as conditions to trigger the diadromous fish migrations was therefore more prudent.

The probabilistic predictions for all three fish migrations based on P66 regimes performed best, again with a decrease in performance for longer forecast horizons. By contrast, a different pattern was observed for the more extreme P95 regimes, where the performance of the salmon migration predictions increased for longer horizons. While this may appear counterintuitive, the improved CRPS performance at longer horizons reflects a reduction in overestimation, as the magnitude of the predictions decreased with the forecast horizon. This occurred because the P95 daily probabilistic predictions tended to overextend around P95 fish run observations throughout the forecasting period (see Figure 7; Appendix S2: Figures S3–S8), and higher probabilities are penalized more on days with no observed P95 fish run than lower probabilities in the CRPS metric. The absolute magnitude difference between 0% (no observed P95 fish run) and 55% (longer horizon daily probability) is smaller than with 82% (shorter horizon daily probability), for example, favoring the CRPS metric.

There were also differences in performance across our selected migrations, with a lower performance for the salmon upstream migration, especially for the P95 regimes. This may have reflected stochasticity in fish migration dynamics (Baldursson, 1991; Lewy & Nielsen, 2003). For instance, during the forecasting period, a limited number of salmon upstream runs (five in total) fell within the range of the historical P95 runs. Consequently, there was a clear overestimation of our P95 for salmon migrating upstream. For example, P95 events were predicted from June to September 2022 when no P95 upstream runs were observed (Appendix S2: Figure S6). It is likely that runs with very large numbers migrating upstream are more controlled by factors other than temperature (e.g., increased water flow enabling catchment upstream accessibility) (Milner et al., 2012). Moreover, adult salmon going upstream will have experienced marine temperatures before migrating (Jonsson & Jonsson, 2009). This may induce different phenotypical

responses than in fish undertaking downstream migration, which will have been regulated by temperatures in the freshwater environment.

Scalability and further development

Our framework provides an initial step that can be built on not only at our study site but also potentially at other sites. It has several advantages that increase its potential to be scalable to other settings. First, a large number of lakes and reservoirs globally already monitor water temperature with a range of different methods (e.g., point measurements, profilers, thermistor chains) (Piccolroaz et al., 2024). This includes sites that are important for diadromous fish (Ouellet et al., 2022; Tickner et al., 2020) and where available data for fish runs could provide points of reference for testing the framework (Nygqvist et al., 2017; Piper et al., 2020; Teichert, Benitez, et al., 2020; Teichert, Tétard, et al., 2020). Furthermore, data-poor sites could implement the necessary water temperature monitoring relatively easily, as temperature is one of the initial and least resource-consuming parameters included in monitoring programs (Peñas et al., 2023). A critical point in other settings would be to investigate site-specific temperature conditions for fish migration at other sites. Indeed, by undertaking a comparison with other lakes with fish migration data, it could be possible to identify general conditions so that the approach could be applied even in locations which do not monitor fish counts but have water temperature monitoring.

A second aspect that facilitates the application of the framework at other sites is its use of cyberinfrastructure. Having the framework set up in the cloud provides additional flexibility and utility, especially as more advanced modeling techniques and forecasting approaches emerge. For instance, other lake water temperature models than GLM could be tested within FLARE (Olsson et al., 2024), or other weather forecast products could be used as driver data. Having the framework online also allows remote management and troubleshooting which may lead to lower maintenance efforts than on more traditional systems (Fer et al., 2021; Recknagel, 2023). Additionally, the forecasting framework can operate iteratively and automatically. The production of forecasts does not require manually triggered actions unless wanted, rather it can work with scheduled actions in online repositories. This feature is particularly relevant because, once the system is set up and its accuracy assessed, its automation can facilitate the dissemination of both water temperature and, in our framework example, fish migration forecasts to operators and managers. This also enables forecasts to be easily reproduced, archived, and used in the future for research and to facilitate collaboration (Carey et al., 2022; Lofton et al., 2023).

CONCLUSIONS

This study provides an investigative example of near-term (daily-scale) ecological forecasting of freshwater species (here, Atlantic salmon and European eel) using water temperature as an environmental driver. Our example showed that daily lake water temperature forecasts could be translated into fish migration predictions extending up to 34 days ahead. While such predictions and their associated uncertainty would need to be put in context for local users, we propose that a similar approach could assist ecological forecasting and management applications at other sites, where understanding the dynamics of fish migration has management implications. It, therefore, has the potential to contribute to adaptation in freshwater management in a time of increasing global change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Paíz, 2024a, 2024b) are available on Zenodo: <https://doi.org/10.5281/zenodo.15364329> and <https://doi.org/10.5281/zenodo.13627954>, respectively.

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SUPPORTING INFORMATION

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

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