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Coastal to Riverine Entry Timing During the Spawning Migration of the European Shads (*Alosa* spp.): Drivers and Phenological Trends for the French Atlantic Coast Populations

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ABSTRACT

During the spawning migration of the anadromous allis *Alosa alosa* and twaite *Alosa fallax* shads, timing of river entry is decisive to ensure that arrival in the spawning grounds matches with favourable conditions for reproductive success. Identifying the environmental cues that drive the timing of river entry is therefore crucial to understanding the implications of climate change for shad populations and to implementing management measures for these threatened species. In this study, data from fisheries and fish counting stations located in the estuaries or low reaches of 10 rivers were combined to investigate the effects of coastal, river conditions and abundance on the timing of migration. Phenological trends were quantified at five sites with more than 20 years' monitoring, and we analysed whether these trends aligned with the period when river temperatures were in the most favourable range for offspring survival. The results indicated that the temporality of spring warming in coastal habitats and photoperiod were key drivers influencing river entry timing. Their relative influence varied between models predicting migration initiation, median and end dates. Significant shifts toward earlier and longer migration periods were quantified. At the site with the longest monitoring time series, the shift in migration timing increased the time lag between early shad arrival and the period of most favourable breeding temperatures. Therefore, further studies should assess the repercussions of earlier spawning migration on the phenology and success of reproduction and juvenile stages.

1 | Introduction

Anadromous fish, born in freshwater, migrate to the ocean where they grow before returning to freshwater to reproduce (McDowall 1997). They make an energetically costly and difficult seasonal migration to the freshwater spawning grounds, during which fish mobilize previously accumulated energy reserves to fuel migration and reproduction (McBride et al. 2015). Anadromous life history is present in multiple families, particularly among Salmonidae and Clupeidae (Delgado and Ruzzante 2020). Two anadromous clupeid species inhabit the Eastern Atlantic coasts: the allis shad *Alosa alosa* (Linnaeus, 1758) and the twaite shad *Alosa fallax* (Lacépède, 1803), which are closely related and hybridize (Baglinière 2000). The allis

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shad is generally semelparous, and the twaite shad is iteroparous, but the proportion of repeat breeders varies across populations and years for both species (Mennesson-Boisneau et al. 2000a). Adults migrate to rivers at the end of the winter and during the spring. The allis shad can migrate upstream over distances exceeding 800km in some rivers, whereas the twaite shad spawns in lower river reaches (Mennesson-Boisneau et al. 2000b).

The timing of upstream migration is decisive to ensure arrival at breeding grounds when conditions are favourable for spawning and offspring survival, particularly for species such as shads that migrate and reproduce in rapid succession (Quinn and Adams 1996; Poulet et al. 2021; Tillotson et al. 2021). Migration timing also determines the hydrological and thermal conditions that fish will encounter in freshwater and the resulting energy expenditure (Leonard et al. 1999; Lennox et al. 2018). As shads rely primarily on stored energy reserves to fuel migration and breeding phases, reproductive success depends on their ability to manage the rate of energy expenditure and the timing of migration and breeding acts (Tentelier et al. 2021). Optimally, fish will deplete their gamete stock in the most favourable location and conditions for offspring prospects, before their energy reserves are depleted to a critical threshold that is either lethal for semelparous individuals or might trigger a return to the sea for iteroparous shads (Castro-Santos and Letcher 2010; Tentelier et al. 2021). Anthropogenic pressures can hamper these tradeoffs, particularly physical obstacles through migration delays and the additional energy costs they entail (Castro-Santos and Letcher 2010).

Migration timing is guided by environmental cues perceptible within the local environment, along with internal cues (e.g., level of energy reserves or stage of gonad maturity) and social interactions for schooling species (Winkler et al. 2014; Shaw 2016; Berdahl et al. 2017). Evolution must have selected the environmental cues that allow migratory fish to anticipate, with some reliability, conditions in spatially distant breeding sites at later times (Winkler et al. 2014). Environmental cues triggering anadromous fish migration vary between species and even populations and often include photoperiod, coastal conditions, river temperature and hydrology (Quinn and Adams 1996; Keefer et al. 2008; Ellis and Vokoun 2009; Legrand et al. 2021; Yeldham et al. 2023). For the allis shad, river temperature has been identified as a strong driver of fluvial migration dynamics, which is inhibited below 10°C to 11°C, whereas discharge has less influence (Rochard 2001; Acolas et al. 2006). Identification of migration cues enables predictive tools to be developed to forecast migration and implement management measures (Teichert et al. 2020).

Climate change is modifying marine and freshwater conditions, but trends in temperature and hydrology are temporally and spatially contrasted (Costoya et al. 2015; L'Hélvéder et al. 2017; Arevalo et al. 2020). One of the major responses of organisms to climate change is to change the timing of life events, along with physiological modifications, distributional changes and microevolutionary genome adaptations (Hughes 2000; Walther et al. 2002). However, when migration is initiated in an environment distinct from the fitness-decisive breeding areas, different trends between both environments may cause a mismatch between ancestrally selected migration cues and optimal timing under current conditions (Winkler et al. 2014; Shaw 2016; Walker et al. 2019). Shifts in the timing of migration and reproduction have been documented for several fish species (Crozier and Hutchings 2014; Chust et al. 2023). In France, shad migration period has been advancing over the period 1984–2016, at a faster rate than for other anadromous species (Legrand et al. 2021). Once in the spawning grounds, shads behaviorally adjust the timing of breeding acts to maximize offspring survival, but in some years, reproduction occurred at suboptimal—mainly colder—temperatures, with no clearly identified reasons for these failures (Lambert et al. 2018).

The present study investigated factors that drive the timing of shad river entry and the implications of climate change on this process, using fish counts and fishery monitoring data collected in the fluvial estuaries and lower fluvial reaches of 10 rivers. These data provided a broad sample in terms of geographical location, catchment size, shad abundance and recent demographic trends. The first objective was to assess the relative influence of coastal and fluvial conditions on the timing of river entry and the effects of abundance and basin characteristics. Based on five rivers with more than 20 years' data, we then quantified sitespecific trends in migration phenology and assessed whether the synchrony between spawner river entry and the period with the most favourable breeding temperatures had shifted over time.

2 | Material and Methods

2.1 | Study Area: Status of Shad Populations and Monitoring Sites

The allis and twaite shads were originally distributed along the west European and Moroccan coasts of the Atlantic Ocean (Baglinière 2000). Populations, particularly of allis shad, suffered severe declines and distribution contraction during the late 19th and the 20th centuries, mainly due to river fragmentation, habitat degradation, pollution and overfishing (Baglinière et al. 2003; Merg et al. 2020; Nachón et al. 2020; Antognazza et al. 2022). Along the French Atlantic coast, populations are still present in numerous catchments (Martin et al. 2015; André et al. 2018; Taillebois et al. 2020), but abundance has declined in most rivers, particularly in the Garonne and Dordogne rivers where the allis shad was still relatively abundant until the late 1990s (Rougier et al. 2012; Legrand et al. 2020). The allis shad has been classified as critically endangered in France since 2019, whereas the twaite shad is classified as least concern. Shad populations in Brittany and Normandy, although less abundant, may result from the long-ignored persistence of small populations or from recolonization in recent decades (Baglinière et al. 2003; Belliard et al. 2009; Taillebois et al. 2020). Genetic and otolith microchemical studies suggest that fidelity to the natal basin prevails in both species but that there is a significant flow of strayers for allis shad, mainly between nearby rivers, resulting in a weak genetic structure in populations (Martin et al. 2015; Randon et al. 2018; Nachón et al. 2020; Rougemont et al. 2022).

Rivers in France that host shad populations and have migration monitoring data collected in upper estuaries or lower fluvial reaches were included in this study. We gathered data from fishery monitoring programs in four rivers and fish counting stations in six rivers (Figure 1; Table 1). Studied counting stations are the first monitoring stations from the sea, located in dams constituting the limit of tidal estuary in the Seine and Vilaine rivers or located close to the tidal limit (3–21 km), in the second (Nivelle, Aulne and Orne) or third (Vire) obstacle from the sea, although in the latter case, the first obstacle is fully open during ebb tides. Monitoring sites located further upstream were not included, as the factors triggering coastal to riverine entry timing differ from those affecting migration dynamics as shad migrate further upstream (Mennesson-Boisneau et al. 2000b).

Because of their phenotypic similarity, the two shad species are not distinguished in video monitoring stations nor systematically separated in catch declarations. Fish counts and fisheries data may include allis, twaite and hybrid shads in varying proportions across rivers and years, but some information on composition can be available. In the Nivelle River, where fish are handled and identified after trapping (Lange et al. 2015), and in fishery data from the Garonne and Dordogne rivers (Castelnaud et al. 2001), it is assumed that the data relate almost entirely to allis shad, but there is more uncertainty in the other sites. Therefore, the generic term European shad *Alosa* spp. was used in this work.

2.2 | Migration Monitoring Data

Fish counting stations consist of video counting devices or cage traps located on dam fishways, which count all or a substantial part of upstream migrating shads (Legrand et al. 2020). The six stations from which data was gathered are located on pool fishways with vertical slots, equipping dams ranging in height between 1.3 (Aulne) and 5.4m (Seine). Some shads may escape counting stations under particular tide and high discharge conditions, by migrating through navigation locks in the Vilaine, Aulne and Seine dams or during punctual non-monitoring days in the Nivelle River. It is nevertheless assumed that these data provide a representative image of migration phenology. Years with significant monitoring interruptions during the migration period, due to technical issues with the counting devices or fishway closure, were excluded.

Shad populations support commercial net fisheries in the Loire and Adour estuaries and formerly in the Garonne–Dordogne estuaries where a moratorium was implemented in 2008 due to the collapse of the allis shad population (Rougier et al. 2012). Fishery data, albeit subject to substantial biases, can provide valuable indications of migration phenology. In the Loire and Adour estuaries, data from 2009 onwards were obtained from



FIGURE 1 | Locations of the 10 migration monitoring sites, discharge and river temperature monitoring stations. The oceanic distribution of the allis shad during the December–April period and the upstream extent of its fluvial distribution are represented. The 50-km radius around each river mouth includes oceanic habitats where sea surface temperature metrics were calculated.

TABLE 1 | Study river data. The number of analysed years distinguishes years with reliable phenological indicators, used to characterize migration phenology and quantify trends, and years with both reliable phenological indicators and complete environmental data, used to assess the drivers of migration phenology. The trend in shad counts was studied at monitoring stations located upstream of the fishing areas in the Adour, Garonne, Dordogne and Loire rivers (Legrand et al. 2020).

						Number of analy	ysed years	Trend in
						Penology	Drivers of	annual shad counts
River	Drainage area (km²)	Monitoring site	Monitoring type	Distance from the river mouth (km)	Monitoring period	characterization and trends	migration phenology	(Legrand et al. 2020)
Seine	76,674	Poses-Amfreville Dam	Video counting	160	2018-2022	4	4	Not studied
Orne	2971	May sur Orne Dam	Video counting	24	2010-2021	11	11	Nonsignificant
Vire	1239	Claies de Vire Dam	Video counting	29	2002-2021	20	17	7
Aulne	1799	Châteaulin Dam	Video counting and trapping	35	2000-2022	20	20	Nonsignificant
Vilaine	10,532	Arzal Dam	Video counting	12	1996–2021	19	15	Nonsignificant
Loire	118,073	Cordemais to Thouaré	Fishery monitoring	25-65	2009–2019	9	9	7
Dordogne	24,066	Bec d'Ambès to Castillon	Fishery monitoring	80-153	1986–2007	22	22	7
Garonne	56,210	Bec d'Ambès to Casseuil	Fishery monitoring	80-159	1986–2007	22	17	7
Adour	16,915	Urt to Bec du Gave	Fishery monitoring	22–32	2010-2019	10	œ	Nonsignificant
Nivelle	242	Uxondoa Dam	Trapping	12	1984–2022	39	32	Nonsignificant

the 'Suivi National de la Pêche aux Engins et aux filets' (SNPE) program (https://professionnels.ofb.fr/fr/node/356). SNPE compiles mandatory catch declarations from professional and recreational inland fishermen who use nets and traps. We used reports from professional fishermen. In the upper Garonne and Dordogne estuaries, the Girpech database was used for the period 1986–2007. Girpech compiles shad capture declarations from cooperative fishers until the 2008 moratorium (Castelnaud et al. 2001; Beaulaton 2008).

Daily catch records were extracted from both the SNPE and Girpech databases. Data were selected from the most assiduous fishermen, who recorded at least 9 days with shad catches using trammel or gillnets within the year considered (between 2 and 18 fishermen, depending on the year and the river; mean = 8.9). In the SNPE, daily reports include the total number of shads caught, the total captured weight or both values. In each estuary, the most complete variable was selected: total shad weight in Loire and total shad number in Adour. There were records (<2%) in which the selected variable was not reported but where information was reported for the other variable (total number of captured shads in Loire and total shad weight in Adour). For these records, shad number and weight values were converted using the mean individual body weight calculated from records where both the number of captured shad and the total weight were reported (2.0 kg in the Loire and 1.9 kg in the Adour estuary). In the Girpech database, the total number of shads caught is recorded. The average catch per unit effort (CPUE) was calculated for each day and estuary, corresponding to the mean weight (Loire) or number (Adour, Garonne and Dordogne) caught by active fishermen. In the Loire estuary, we removed 5 years with major gaps in the CPUE series, either due to the absence of fishing activity or the nondeclaration of catches, in order to limit the bias of the phenological indicators (Figure S1).

2.3 | Migration Phenology and Abundance Indicators

Four annual indicators of migration timing were calculated from the cumulative daily fish counts and CPUE series: (1) run initiation; (2) median; (3) end dates, corresponding to the days of the year when 5%, 50% and 95% of the cumulative annual run were reached; and (4) migration period duration, which is the number of days between run initiation and end dates. Percentile-based indicators are commonly used (Boisneau et al. 2008; Legrand et al. 2021; Dalton et al. 2022), being more accurate and less biased than estimators based on the occurrence of a specific number of individuals (Moussus et al. 2010). Mean values and standard deviations were calculated to characterize the migration period in each river. A paired-sample Student *t*-test was used to determine whether initiation-to-median and median-to-end times differed.

To account for the potential effect of abundance on migration timing, a within-site *z*-score standardized abundance indicator (*Ab*) was estimated from the cumulated annual shad counts or mean annual CPUEs, according to the type of data. Mean annual CPUE was calculated using the formula:

$$m_{y,r} = \frac{C_{y,r}}{f_{y,r}}$$

where *C* is the total number or weight of shad catches and *f* is the total fishing effort in year *y* and river *r*. This formula does not take account of the fact that daily abundance and catchability of migrating shad vary throughout the season, but did correlate with fishery-independent abundance indicators in the Garonne and Dordogne rivers (Beaulaton 2008).

2.4 | Environmental Variables

Two mechanisms by which environmental conditions may trigger migration timing were considered: reaching threshold photoperiod and temperature values, which could indicate the most favourable time to enter freshwater, and seasonal conditions prior to migration, which could affect the internal state of fish (Winkler et al. 2014; Shaw 2016).

2.4.1 | Photoperiod

Daily photoperiod was calculated at the latitude of each estuary using the method of Forsythe et al. (1995) implemented in the *meteor* package (Hijmans 2023) on R software (R Core Team 2024). The first days of the year with daytime lengths exceeding 13, 14 and 15 h were selected as predictors (P_{13} , P_{14} and P_{15}). In the absence of prior assumptions, these thresholds were in the range of the mean values at the initiation, median and end dates of the migration period.

2.4.2 | Sea Temperature

At sea, shads are mainly distributed in shallow coastal areas close to the plume of the main rivers (Taverny and Elie 2001; Trancart et al. 2014; Elliott et al. 2023), either their natal river plume or distant ones, as some individuals disperse over large distances (Nachón et al. 2020). Seasonal displacements suggest that shad schools move closer to the coasts and estuaries in winter, which may be related to the onset of the spawning migration (Trancart et al. 2014; Nachón et al. 2015; Dambrine 2017). Consequently, sea surface temperatures (SST) were extracted for coastal habitats modelled as favourable for shad within a 50-km radius around each estuary (Dambrine 2017). SST data from the Copernicus program were used (Copernicus Climate Change Service C3S 2019; Good et al. 2019; Merchant et al. 2019), following the process detailed in Appendix A. The mean SST during winter (SST_winter), from 21 December to 20 March, was calculated to assess the effect of seasonal temperatures on migration timing. We also considered whether the rate and phenology of SST warming during the late winter and spring could act as a migration cue. The first days of the year when SST values reached $\Delta 3^{\circ}$ C, $\Delta 4^{\circ}$ C and $\Delta 6^{\circ}$ C above the minimum SST experienced during winter were calculated (SST_{Δ_3} , SST_{Δ_4} and SST_{Δ_6}). These thresholds were defined after preliminary analysis of the average SST changes during the migration period.

2.4.3 | River Temperature

River temperature was recorded at migration monitoring sites, or measurements were available at close reaches in the 'Naïades' repository (www.naiades.eaufrance.fr). As datasets did not cover the entire study period for most sites, site-specific general additive models (GAMs) were fitted to predict temperatures in years without measurements (Appendix B). Temperature series were smoothed with a 5-day moving average, and the first days of the year when temperatures were above 11°C, 15°C and 18°C were extracted (RT_{11} , RT_{15} and RT_{18}). 11°C was identified as a threshold below which migration is inhibited (Rochard 2001; Acolas et al. 2006), and preliminary analysis showed that 15°C and 18°C were close to the mean temperatures found during the median and end dates of migration.

2.4.4 | River Discharge

Daily discharge rates were extracted from the 'Hydroportail' repository (https://www.hydro.eaufrance.fr). In each catchment, hydrometric stations that were located close to the estuary and had data covering the entire migration monitoring period were selected. Stations in the Nivelle, Adour, Garonne, Vilaine, Vire and Orne basins had periods of missing values; series were interpolated linearly if missing periods were less than seven consecutive days. Two metrics were calculated: mean discharge from the onset of winter to the phenological indicator date (Q_winter), to test whether higher outflow at the river mouth prior to migration influenced migration timing, and mean discharge over the 30 days preceding indicator (Q_{30d}) . The 30-day period roughly corresponds to the average number of days between migration initiation and median date indicators and between the median and end dates. Because of variations in catchment size, discharge metrics were standardized within each site.

2.4.5 | Monitoring Site and Catchment Characteristics

The distance from the monitoring site to the upstream limit of the allis shad migration range (D_mig) , which is greater than the twaite shad migration range in the studied rivers, was measured from distribution maps based on observations made over the 2006–2015 period (André et al. 2018). The upstream migration limit was used as a proxy for spawning distribution, as breeding grounds are not identified in some of the study rivers. In catchments where shad migrate up more than one river, the axis with the greatest distance was selected. The distance from the river mouth to the monitoring site (D_sea) and the number of dams to pass (n_dams) were also measured, as migration delays to reach the monitoring site could contribute to explaining intersite variability. Catchment area (c_area) was measured to test whether it contributed to the intersite differences. Spatial analyses used QGIS software (QGIS Development Team 2023).

2.5 | Data Analysis

2.5.1 | Influence of Coastal, River Conditions and Abundance on Migration Phenology

The effect of environmental variables and abundance on phenological indicators was assessed using a multimodel inference approach (Harrison et al. 2018). Separate linear mixed-effects models (LMMs) were fitted for migration initiation, median and end indicators using the lme4 (Bates et al. 2015) and lmerTest packages (Kuznetsova et al. 2017). LMMs were structured with a random intercept by site and 11 fixed effect predictors:

- Initiation date model: P₁₃, SST_winter, SST_Δ₃, RT₁₁, Q_winter, Q_30d, Ab, D_mig, D_sea, n_dams and c_area
- Median date model: P₁₄, SST_winter, SST_A₄, RT₁₅, Q_winter, Q_30d, Ab, D_mig, D_sea, n_dams and c_area
- End date model: *P*₁₅, *SST_winter*, *SST_*Δ₆, *RT*₁₈, *Q_winter*, *Q_30d*, *Ab*, *D_mig*, *D_sea*, *n_dams* and *c_area*

Predictors were *z*-score standardized, except for discharge and abundance metrics, which were initially standardized within each site. To check for collinearity, variance inflation factors (VIF) were calculated and predictors with VIF > 3 were excluded. From the full LMMs, models with all possible combinations of fixed-effect predictors were fitted and ranked using the small-sample-corrected Akaike's information criterion (AICc). Models with Δ AICc < 6 relative to the best fitting model were selected, and weighted coefficients were calculated. Ranking and model averaging were performed using the MuMIn v1.48.4 package (Bartoń 2024). Marginal and conditional explained variance (R^2) were calculated to measure goodness of fit (Nakagawa and Schielzeth 2013).

2.5.2 | Trends in Migration Phenology

To quantify the temporal trends in phenology in the five sites with more than 20 years' monitoring data (Table 1), site-specific linear models were fitted with year as predictor. The evolution of SST metrics along the study area (latitude 43° N to 51° N, longitude 6° W to 1° E) was quantified over the period 1985–2022 using the Theil–Sen slope, and trend significance was assessed using a Mann–Kendall test modified for autocorrelated data, implemented in the *spatialEco* v2.0-2 package (Zhang et al. 2000; Evans et al. 2023).

2.5.3 | Match Between River Entry Timing and the Period With Optimal Breeding Temperatures

Assessment of whether the time lag between spawner river entry and the period with the most favourable breeding temperatures had changed was based on an experimental study by Jatteau et al. (2017), which defined the optimal temperature range for allis shad embryo survival: >80% survival between 15.7°C and 25.6°C. Egg incubation lasted 7.6 days at 15°C, and the duration decreased at warmer temperatures (Jatteau et al. 2017). Hence, the first day of the year after which the river temperature was above 15.7°C for seven consecutive days was defined as the first day with optimal breeding temperature. The trend of this metric was assessed in each river using a linear model with year as predictor. The time gap between the migration timing indicators and the metric was calculated:

$$G_{y,r} = M_{y,r} - R_{y,r}$$

where M is the migration timing indicator and R is the first day with optimal breeding temperatures in year y and river r. Temperature data from the counting stations were used in the Nivelle, Aulne and Vire due to the proximity of spawning grounds. As shad migrate further upstream in the Garonne and Dordogne, temperatures measured at the Golfech and Tuilières dams, close to the main spawning grounds, were used.

3 | Results

The core migration period extended from March to early July across the study area (Figure 2). Phenology broadly followed a latitudinal gradient, with migration occurring earlier in southern rivers, although there were notable variations as the earliest and latest occurrences were found in the Loire and Nivelle rivers, respectively. The difference between sites could reach up to 50–60 days for each indicator in a given year. In terms of interannual variability, the mean interval between the earliest and

latest indicators was 34 ± 12 days for the five sites with more than 20 years of data, with similar variability for the migration initiation, median and end dates. The mean duration of the migration period was 51 ± 11 days; it ranged from 37 ± 9 days in Vire to 78 ± 11 days in Adour. Shad abundance tended to be higher in the first part of the migration period; the number of days between run initiation and median dates (22 ± 8 days) was significantly shorter than between median and end dates (29 ± 5 days; Student *t*-test, p = 0.006).

3.1 | Influence of Coastal, River Conditions and Abundance on Migration Phenology

Two predictors were excluded from the full models due to collinearity: catchment area and number of dams downstream of the



FIGURE 2 | Indicators of migration initiation (left edge of blue lines), median (circle) and end (right edge) dates by site and monitoring year, expressed as days of the year (since the first day of the civil year, 1 January). The size of the median date indicator is proportional to the annual run abundance (within-site standardized metric). Sites are ordered according to their position along the coastline, from the Nivelle River (south) to the Seine River (north). Light-grey 10-day bands and dashed lines (100th and 150th days of the year) are depicted in the background to facilitate visual comparisons.

monitoring site. Eighty-four of the 512 models including all potential predictor combinations were selected for the initiation date, 19 for the median date and 57 for the end date (Tables S1, S2 and S3). Selected models had marginal R^2 values of 0.26 ± 0.09 , 0.50 ± 0.01 and 0.42 ± 0.05 for each phenological indicator, respectively, and conditional R^2 values of 0.66 ± 0.01 , 0.56 ± 0.01 and 0.55 ± 0.02 .

The averaged parameters indicated a significant effect of spring warming SST on initiation and median date indicators: migration occurred earlier when $\Delta 3^{\circ}$ C and $\Delta 4^{\circ}$ C warming thresholds were reached earlier in the year, whereas mean winter SST had less effect (Figure 3). Over 1985–2022, the $\Delta 3^{\circ}$ C and $\Delta 4^{\circ}$ C warming thresholds tended to be reached earlier along the Bay of Biscay estuaries (Figure 4) because of seasonally contrasting trends in SST. In contrast, there was no significant trend around

the northern estuaries, where winter and spring SST warmed at similar rates (Figures S2 and S3).

There was a significant effect of river temperature on the median date, which occurred earlier when the 15°C threshold was reached earlier. The effect of photoperiod was greater on models predicting median and end dates than on the initiation date model, although confidence intervals were wide. Migration ended slightly earlier when abundance was high. Metrics describing the position of the monitoring site along the migration axis made a strong contribution to intersite differences. Firstly, shad tended to migrate earlier in rivers where the upstream distribution limit was further from the sea. Secondly, migration occurred later as the distance from the sea to the monitoring site increased, despite the selection of sites located in upper estuaries and low fluvial reaches.

Predictor	Estimate ± 95% CI	<i>p</i> value	SW
a) Initiation			
Photoperiod (P13)	H	0.990	0.20
Mean winter SST (SST_winter)	⊢	0.525	0.24
SST warming temporality (SST_D3)		0.001 ·	1.00
River temperature (RTI)	⊢ ∔ -1	0.771	0.20
Winter discharge (Q_winter)	⊧ ∎	0.203	0.42
Discharge 30 days (<i>Q_30d</i>)	F	0.986	0.20
Abundance (Ab)	⊢ ∔-1	0.638	0.22
Distance to the upper migration limit (D_mig)	L	0.010 ·	0.90
Distance to the river mouth (D_sea)	F	0.151	0.43
b) Median			
Photoperiod (P14)		0.001 ·	1.00
Mean winter SST (SST_winter)		0.210	0.41
SST warming temporality (SST_D4)	1	0.009 ·	0.98
River temperature (RT15)		0.007 ·	0.97
Winter discharge (Q_winter)	⊢ _	0.448	0.28
Discharge 30 days (<i>Q_30d</i>)		0.455	0.29
Abundance (Ab)	⊢-∎	0.058	0.67
Distance to the upper migration limit (D_mig)	F	0.001 ·	1.00
Distance to the river mouth (D_sea)	F	0.001 ·	1.00
c) End			
Photoperiod (P15)		0.007 ·	0.87
Mean winter SST (SST_winter)		0.287	0.40
SST warming temporality (SST_De)	P <mark>₩</mark> ₩	0.113	0.54
River temperature (RT_{IB})		0.078	0.61
Winter discharge (Q_winter)		0.127	0.51
Discharge 30 days (Q 30d)		0.708	0.24
Abundance (Ab)	F	0.001 ·	1.00
Distance to the upper migration limit (<i>D_mig</i>)		0.001 ·	1.00

FIGURE 3 | Model coefficients from the averaged models of the effects of environmental conditions, abundance and monitoring site position on migration (a) initiation, (b) median and (c) end dates. Coefficients are averaged form the models that include the considered predictor. SW represents the sum of the Akaike weights of the models including the predictor. To facilitate visual interpretation, significant effects and SW \geq 0.5 are in bold, and bars are coloured by predictor group: photoperiod, SST, river temperature, discharge, abundance and monitoring site position.

3.2 | Trends in Migration Phenology

Significant shifts toward earlier initiation were detected in the Nivelle, Dordogne and Aulne rivers and earlier median dates in the Nivelle, Garonne and Dordogne (Figure 5). Although non-significant, trends were also directed toward earlier phenology in the Vire River. The mean trend across the five sites was -5.5 days per decade for migration initiation and -4.6 days per

decade for median date; confidence intervals were, however, relatively wide in all sites. Dordogne was the only river where the end indicator advanced significantly; the average trend across the five sites was -0.8 day per decade. These contrasting trends between initiation and end indicators resulted in an average increase in migration duration of +4.7 days per decade, significant increases being recorded in the Nivelle, Garonne and Aulne rivers.



FIGURE 4 | The 1985–2022 trend of the day of the year when (a) $\Delta 3^{\circ}$ C, (b) $\Delta 4^{\circ}$ C and (c) $\Delta 6^{\circ}$ C above the minimum winter SST were reached.



FIGURE 5 | Trends in migration initiation, median and end date indicators in the five rivers with more than 20 years' data. Prediction lines for significant trends ($p \le 0.05$) are solid, and 95% confidence intervals are dashed. Estimates are indicated for significant trends; complete results are provided in Table S4.

3.3 | Match Between River Entry Timing and the Period With Optimal Breeding Temperatures

On the other hand, the first day of the year as of which river temperatures were in the optimal range for embryo survival, characterized by strong interannual variability, did not significantly shift in these five rivers (Figure S4 and Table S5). As migration initiation dates advanced, the time lag between river entry and the first day of the year with optimal breeding temperatures significantly increased in the Nivelle River (Figure 6). In the other sites, confidence intervals were wide and no significant trend was detected (Table S6).

4 | Discussion

The present study combined data collected over the period 1984–2022 from fish counting stations and commercial fisheries located in the estuaries or lower reaches of 10 rivers along the French Atlantic coast. This large spatiotemporal dataset, associated with fine-scale environmental data, provided new insights into the drivers of coastal to riverine entry timing and the variations in their relative effects throughout the migration period. Important site-specific shifts in migration phenology were quantified, with estimates in the range of the average trends observed at the national scale by Legrand et al. (2021). However, this trend did not align with changes in the periods of optimal river temperatures for embryo survival, which could have implications for reproductive success.

There are potential biases in the migration monitoring data used. Fishery records suffer from variations in fishing effort and shad catchability (Beaulaton 2008), whereas fish count data depend not only on the time at which shad arrive below the dams but also on the degree of passability, which varies with fishway quality and environmental conditions (Belo et al. 2021). Indeed, the time lag between when individuals enter estuaries and when they are monitored varies between the rivers studied, depending on the location of the monitoring site along the estuary-river continuum (fluvial estuary or low fluvial reaches), the distance from the river mouth and the presence and passability of dams. The random effect 'site' and the inclusion of distance from the sea as a site-level descriptor partially accounted for this variability in the LMMs, but interannual variations within each site might introduce noise into the data. To reduce bias in phenological indicators, the stations were carefully selected, and despite limitations, our results revealed consistent trends between rivers with both types of data. In addition, abundance was very low in some years, particularly in the Nivelle River (4 years with fewer than 10 shads), making the phenological indicators dependent on the migratory behaviour of a few particular individuals.

The temporality of SST warming and photoperiod were the main environmental predictors of migration timing. Their relative effects varied over the migration period, tending to decrease for STT and to increase for photoperiod, albeit confidence intervals were wide. This suggests that early and late migrants may rely on both cues at different levels. Early migration and long freshwater residence allow higher reproductive success in alewife (Alosa pseudoharangus); individuals can cope with a wider range of conditions and meet more potential mates, and early hatched juveniles may face less trophic competition (Marjadi et al. 2019, 2023). However, the probability of encountering unfavourable breeding conditions is high in early spring and varies greatly between years (Paumier et al. 2020). To avoid entering rivers long before optimal breeding conditions arise, it may be adaptative for early migrating shad to rely primarily on temperature cues. Consistently, early migrating shad generally have greater mass (Beaulaton 2008), which may allow them to spend more time in freshwater. As spring progresses, the probability of encountering favourable breeding conditions increases (Paumier et al. 2020). Hence, later migrants may rely primarily on photoperiod, providing reliable information on seasonal advancement independently of short-term weather fluctuations (Winkler et al. 2014). Accordingly, a telemetric study found that



FIGURE 6 | Trend in the time lag between migration initiation, median and end indicators and the first day of the year as of which river temperatures were in the optimal range for embryo survival in the Nivelle River. The blue line represents the first day with optimal spawning temperatures; points are below when the phenological indicator occurred earlier than this day.

the timing of twaite shad river entry was cued by photoperiod (Yeldham et al. 2023).

River temperature has long been identified as a driver of shad migration (Menesson-Boisneau et al. 2000b). Focusing on estuaries and low river reaches, our results suggest that SST may be the main factor triggering river entry of early-migrating individuals, as SST is directly perceptible in shad coastal habitats. The rate and phenology of SST warming during late winter and spring appeared to influence the timing of migration in our models. The underlying mechanisms require further research. Gametogenesis is already at an advanced stage when shads enter freshwater (Bengen 1992; Mouchlianitis et al. 2019). In American shad (Alosa sapidissima), gonadal development gradually increases as the temperature rises within the 2months preceding the onset of spawning (Liu et al. 2021). Shads possibly migrate after reaching a critical level of gonad development (Yeldham et al. 2023), the timing of which may depend on the temporality and rate of SST warming.

Favourable migration timing might be anticipated to a certain extent by shads, but river conditions are inherently stochastic. The period on which optimal breeding temperatures arise varies greatly from year to year. Thus, timing variation among individuals, resulting in a relatively long migration period, may ensure a basal rate of reproductive success at the population level, despite certain timings resulting in poor success in some years (Reed et al. 2010; Freshwater et al. 2018). Likewise, the degree of predictability of river conditions explains latitudinal variation in the proportion of iteroparity in American shad populations, with repeated reproduction acting as a bet-hedging strategy in northern populations, which face less predictable environments (Glebe and Leggett 1981).

Our results indicated an earlier river entry in large catchments, where shads migrate further from the sea. Because of collinearity, the effect of catchment size and distance to the upstream migration limit could not be disentangled. Two hypotheses could explain these differences. Larger catchments, with outflow that is more perceptible at sea, may attract shad earlier than smaller ones. Alternatively, populations at greater distances from the spawning grounds may enter rivers earlier, ensuring a longer migration time before favourable breeding conditions arise. For example, the distance from the sea to the spawning grounds and the thermal regime of the natal rivers influence the timing of migration in sockeye salmon populations (Hodgson and Quinn 2002; Crossin et al. 2004). Compared to salmonids, shad populations show substantial straying rates and less genetic differentiation, particularly for the allis shad (Rougemont et al. 2022), which may limit local adaptation. However, shads are gregarious at sea (Taverny and Elie 2001; Nachón et al. 2020) and fidelity to the natal basin prevails (Martin et al. 2015; Randon et al. 2018). Therefore, mechanisms such as juvenile imprinting during the seaward migration (Keefer and Caudill 2014) and collective decision-making (Sumpter et al. 2008) in schools composed mainly of homing shads and possibly a proportion of iteroparous individuals that have already migrated in previous years could promote local timing adaptation. However, Nachón et al. (2020) suggested that the straying rates may have been higher in the 1980s, when populations were more abundant, as dispersal at sea would potentially be density-dependent. In addition, the distance metric used in this study is limited, as the migration time required to access breeding grounds also depends on other factors, in particular the obstacles encountered along the rivers. It could be replaced by a functional distance metric (Roy and Le Pichon 2017).

Along with climate-driven environmental changes, demographic processes may also contribute to temporal variations in migration phenology (Tillotson et al. 2021). Our results indicate that migration ended slightly later when abundance was low, suggesting an influence of social cues. The influence of social facilitation on the synchronization of breeding activity has also been suggested at the endpoint of the spawning migration (Lambert et al. 2018; Tentelier et al. 2021). When abundance is low, there may be longer periods of group build-up prior to river entry (Berdahl et al. 2017), particularly toward the end of the migration period, when most adults are already in freshwater. However an opposite effect has been observed for alewife, that is, longer migration at higher abundance (Dalton et al. 2022). Our results may be affected by biases in our abundance metric, particularly for fishery data, as the mean annual CPUE also depends on shad catchability, which is subject to variations (Beaulaton 2008). In addition, the timing of migration varies with sex, size and age: males, larger and older shads tend to enter rivers earlier (Mennesson-Boisneau et al. 2000a). Thus, changes in population structure might affect phenology, but to our knowledge, no study corroborates this hypothesis with sufficient spatio-temporal coverage in the studied rivers. For example, no trends in age, size or mass structure were detected in a 1980-2005 fishery survey in the median Loire (Boisneau et al. 2011), but these results should not be generalized. Further research on this topic would be of interest, as the age and size of allis shad at maturity have been related to thermal conditions at sea and may be affected by climate change (Lassalle et al. 2008). Changes in the rate of hybridization between the allis and twaite shads may also have an effect on phenology, but information on the interannual variations in hybridization rates is lacking. These hypotheses would need to be tested and remain to be corroborated. However, in light of the results of this study, demographic processes do not seem to be a key driver of river entry phenology.

The site-specific trends in migration phenology quantified in this study are in the range of the average values calculated from 16 French monitoring stations (Legrand et al. 2021). Overall, migration initiation and median dates are advancing faster than end dates, lengthening the migration period. These trends are consistent with a stronger relative effect of temperature cues on early migrants and photoperiod on later ones and are in accordance with the trends in coastal temperature along the study area. Because of contrasting seasonal trends, the rate of spring SST warming increased in the coastal areas of the Bay of Biscay, whereas it remained stable in the English Channel, where SST showed similar trends during winter and spring. This contrast is consistent with previous studies conducted in the two areas (Costoya et al. 2015; L'Hélvéder et al. 2017).

Phenological trends were consistent in sites monitored during the periods 1984–2022 (Nivelle), 1986–2007 (Garonne and Dordogne) and 2001–2022 (Aulne), indicating a continuous advancement pattern over the last four decades throughout the

Bay of Biscay rivers, at a rather homogeneous rate across basins as suggested by Legrand et al. (2021). This phenological shift might influence reproductive success and ultimately population dynamics through different mechanisms. First, the Allee effect or depensation, consisting of a reduction of individual fitness when population size or density decreases, is a possible cause of the collapse of shad populations (Rougier et al. 2012; Poulet et al. 2023). As most of the studied populations are declining (Legrand et al. 2020), the dispersal of fewer individuals over a longer migration period might exacerbate this process. Low abundance, through less social facilitation, might limit the ability of shad to anticipate the most favourable breeding conditions (Lambert et al. 2018). In addition, different trends between SST, which triggers migration, and river temperature, which is decisive for reproductive success, could increase the risk of temporal mismatch between the timing of river entry and the period with optimal breeding conditions. Our results indicated such pattern in the Nivelle. It may also be the case in the Garonne and Dordogne if the trend toward earlier migration observed from 1986 to 2007 has continued since then, as the period with the most favourable breeding conditions did not shift between 2003 and 2016 (Paumier et al. 2020). Too early migration could increase the risk of spawning at suboptimal temperatures and limit offspring production, although the effects would be mitigated by the relatively wide thermal tolerance range of embryos and larvae (Jatteau et al. 2017). Shads that arrive too early could delay reproduction and wait for better conditions, optimizing offspring prospects (Lambert et al. 2018; Poulet et al. 2023). However, this delay might increase the risk of exhausting energy reserves and of predation before fully completing reproduction.

Assuming that the timing of river entry and spawning correlate, as partially observed for river herring (Rosset et al. 2017), the phenology of juvenile life stages might also change. Thirtyday-old juveniles are more sensitive to high temperatures and low oxygen conditions than 60- to 85-day-old ones (Baumann et al. 2021). Under climate change, advances in reproduction timing could be adaptative, as older juveniles would be exposed to peak summer conditions. However, the expected benefits would be greater for late-breeding shads, and the trends observed here suggest that the initiation of the breeding period is more likely to have advanced than its end. Accordingly, in a study carried out in the Loire from 1995 to 2004, the day on which 5% of juveniles were caught advanced from late to mid-July, whereas the days with 50% and 95% of cumulative catches did not change significantly (Boisneau et al. 2008). In addition, 1-month-old juveniles' diet appears to be restricted to cladocerans, and recruitment could be impacted if earlier hatching does not match a period of good prey availability (Tommasi et al. 2015; Baumann et al. 2023). Subsequently, an advancement in the period when juveniles reside in the estuary, as documented in the Gironde estuary between 1985 and 2010, could lead to a mismatch with prey availability (Chevillot et al. 2017) and affect the risk of exposure to summer hypoxia events (Boussinet et al. 2023).

To conclude, the timing of shad river entry was mainly driven by the phenology of spring sea surface temperature warming and photoperiod in this study, whereas the relative influence of these cues varied over the migration period. Distance to spawning sites or catchment size also contributed to variation in timing between sites, potentially reflecting local adaptations, although this question requires further investigation. Significant phenological shifts were found, increasing the time that early migrating shads must spend in freshwater before reaching optimal breeding temperatures in certain rivers. Further studies would be required to assess whether earlier spawning migration, which is the first step in the freshwater life cycle, has led to changes in the phenology and success of reproduction and juvenile stages. As regional climate continues to change, this would shed light on the implications for shad population dynamics.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The migration datasets used in this study are available upon reasonable request from the organizations that carry out monitoring in the different rivers (see the 'Acknowledgements' section). Sea surface temperature data are available at https://cds.climate.copernicus.eu/, discharge data at https://www.hydro.eaufrance.fr/ and river temperature data at https://naiades.eaufrance.fr/, 10.15454/8IL3LJ, https://magest.oasu.ubordeaux.fr/, https://doi.org/10.57745/7DT6QC and https://www.seine -available at https://ponapomi.ofb.fr/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.