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Local reflects global: Life stage-dependent changes in the phenology of coastal habitat use by North Sea herring

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Abstract

Climate warming is affecting the suitability and utilization of coastal habitats by marine fishes around the world. Phenological changes are an important indicator of population responses to climate-induced changes but remain difficult to detect in marine fish populations. The design of large-scale monitoring surveys does not allow fine-grained temporal inference of population responses, while the responses of ecologically and economically important species groups such as small pelagic fish are particularly sensitive to temporal resolution. Here, we use the longest, highest resolution time series of species composition and abundance of marine fishes in northern Europe to detect possible phenological shifts in the small pelagic North Sea herring. We detect a clear forward temporal shift in the phenology of nearshore habitat use by small juvenile North Sea herring. This forward shift might be linked to changes in water temperatures in the North Sea. We next assessed the robustness of the effects we found with respect to monitoring design. We find that reducing the temporal resolution of our data to reflect the resolution typical of larger surveys makes it difficult to detect phenological shifts and drastically reduces the effect sizes of environmental covariates such as seawater temperature. Our study therefore shows how local, long-term, high-resolution time series of fish catches are essential to understand the general phenological responses of marine fishes to climate warming and to define ecological indicators of system-level changes.

KEYWORDS
climate change, fisheries, population ecology, small pelagics

1 | INTRODUCTION

Climate warming has caused well-documented shifts in the distribution of species in terrestrial and aquatic ecosystems (Pecl et al., 2017) including changes in the dynamics of fish populations across the globe (Perry et al., 2005; Rijnsdorp et al., 2009; Sydeman et al., 2015). In several coastal zones, phenological shifts in the occurrence of adult and larval fish have also been observed (Asch, 2015; Langan et al., 2021). In parallel, industrial fishing has altered the abundance, structure, and reproductive characteristics of marine fish populations (Grift et al., 2003; Jackson et al., 2001; Pauly et al., 1998, 2002). As opposed to large-scale effects on populations that may be readily detectable, understanding the role of external environmental processes on local or regional population

dynamics is more challenging (Heath et al., 2012). Small pelagic fish species pose an especially complex case, as their populations can exhibit both "volatile" short-term dynamics in response to local or regional conditions, and long-term "stable" cyclicity due to larger scale climate events (Schwartzlose & Alheit, 1999; Tourre et al., 2007). Furthermore, many species exhibit ontogenetic shifts in habitats, spending part of their life cycle in coastal or estuarine zones, which may constrain the ability of species to cope with warming (Petitgas et al., 2013). The importance of external environmental processes can, therefore, be life stage-specific (Dahlke et al., 2020; Peck et al., 2013). The local dynamics of small pelagic fish are an essential component to better understand potential changes in areas historically important to the life cycle dynamics of species, and to examine whether the phenology in the use of important habitats may have shifted over time.

The Atlantic herring (*Clupea harengus*) is a common, ecologically and commercially important small pelagic fish species in areas of the North Atlantic (Dahle & Eriksen, 1990; Whitehead et al., 1984) where the species is composed of separate autumn- and winter-spawning stocks with life stage-specific distributions (Dickey-Collas et al., 2010). In the southern North Sea, Atlantic herring is also commonly observed in the Wadden Sea, a shallow coastal system serving as a spawning, nursery, and feeding ground for many North Sea fish species (Tulp et al., 2017). Unlike other small pelagic fishes that release batches of eggs, Atlantic herring is a single-batch spawner laying benthic eggs on gravel substrate. Autumn-spawning North Sea herring has different subcomponents that spawn in specific regions at specific times; spawning in Orkney-Shetland, Buchan/Banks and Downs areas occurs in September, October/November, and December/January, respectively (Maathuis et al., 2023; Payne, 2010). The larvae drift eastward across the North Sea and develop slowly during winter, with older (younger) larvae from higher (lower) latitude spawning grounds reaching sizes of ~25 (<20) mm in the first quarter of the next year (Hufnagl et al., 2015).

The results of biophysical modelling studies suggest that herring larvae produced by the Downs spawning subcomponent drift north-eastward from the English Channel and enter the Wadden Sea around mid-April (Dickey-Collas et al., 2009). A recent empirical study by Maathuis et al. (2023) observed multiple cohorts of differently sized juveniles entering the Wadden Sea from March until June, indicating that these small juveniles originate from different spawning subcomponents. Gaps in knowledge exist on the habitat utilization of the Wadden Sea by early juvenile Atlantic herring and other small pelagic fish since these young life stages cannot be properly sampled in the demersal trawl surveys used to annually monitor fish populations in these near-shore waters (Maathuis et al., 2023). Furthermore, the coarse temporal resolution of these large-scale surveys does not allow inferences on seasonally important factors. Limited temporal resolution also prevents the detection of potential phenological shifts that might have occurred during the past few decades. This limits our understanding of the external processes governing the local dynamics of herring and other fish moving between shallow coastal nursery and feeding grounds of the Wadden Sea and offshore waters of the North Sea. Local survey efforts conducted at high temporal resolution are needed to help fill such important gaps in knowledge on potential climate-driven changes in phenology and habitat utilization.

Survey efforts with sufficiently high temporal resolution to examine climate-driven changes in phenology are rare in the marine environment, particularly those with a historical coverage allowing comparisons over multiple decades. Although long-term high temporal resolution time series exist for lower trophic levels such as plankton (Hosie et al., 2003), they are particularly rare for higher trophic levels such as fish. However, the Royal Netherlands Institute for Sea Research (NIOZ) has consistently used a kom-fyke to collect standardized catch data of marine fishes moving between the North Sea and Western Wadden Sea through the Marsdiep tidal race since the 1960s (van der Veer et al., 2015) (Figure 1). This survey is unique in northern Europe due to its high temporal resolution, with daily sampling occurring during two annual sampling campaigns in spring and autumn. Previous analyses of these data have identified phenological shifts such as changes in the day of first occurrence, peak occurrence, and last occurrence of members of the Wadden Sea fish community over the past five decades (Van Walraven et al., 2017). Given its daily resolution, this time series allows a finer scale exploration of changes in the phenology of species such as Atlantic herring. From
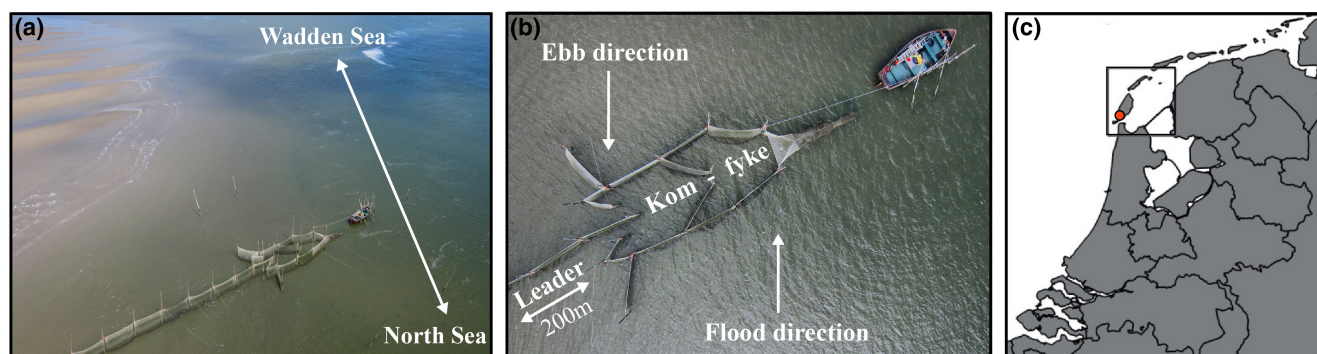

FIGURE 1 Setup of the NIOZ kom-fyke (a, b) and its geographic position on the border between the North Sea and Wadden Sea (c). Images (a) and (b) used with permission from van Walraven (personal communication).

a methodological standpoint, the preselection of specific days (first occurrence, peak occurrence, and last occurrence) as a phenological yardstick for peak migration may obscure shifts in species such as herring that, due to their schooling and flexible foraging behavior, exhibit marked daily variation in habitat use or occupancy. Furthermore, it remains unknown if and how potential shifts in phenology differ among juvenile and adult herring. More detailed phenological analysis would reveal if local dynamics in coastal habitat use by North Sea herring align with the larger regional and global population responses to climate-driven warming observed in marine fish.

Here, we examined potential life stage-specific changes in the population dynamics of Atlantic herring moving between the North Sea and Wadden Sea using long-term time series of weekly standardized herring catches (1981–2021) collected by the NIOZ kom-fyke. We used a generalized additive modelling (GAM) approach to decompose the overall trend in weekly standardized herring catches into distinct annual, seasonal, and environmental signals. These results allowed us to identify temporal trends in herring abundance, body size, and reproductive status in the Western Dutch Wadden Sea. We also examined potential changes in the seasonal trends in herring abundance over the past four decades, that is, phenological shifts. Finally, we checked the sensitivity of our outcomes with respect to changes in the sampling design of the kom-fyke by re-running our analysis with different sampling frequencies. Our analyses on the longest, most high-resolution time series for marine fish in Northern Europe will advance understanding of the factors determining the movement and phenological shifts of herring and potentially other temperate small pelagic fishes from offshore to nearshore waters. Our work underscores the importance of maintaining highly temporally resolved, long-term ecological time series for examining the dynamics of climate-driven phenological shifts.

2 | MATERIALS AND METHODS

To examine phenological changes in North Sea herring and the factors contributing to potential changes in these dynamics, we analyzed the number of herring in daily spring and autumn catches from 1982 to 2021. We also included information on fish life stage, based on dissections of herring captured in the same program. Below, we describe the source of the data and steps in data preparation and analysis in detail.

2.1 | Data sampling

2.1.1 | Fish catches

We used catches in the long-term time series data from the NIOZ kom-fyke program. The leader net of the kom-fyke extends 200 m from the shoreline into the subtidal zone where two chambers with a mesh-size of 10×10 mm collect fishes (van der Veer et al., 2015). Additional details on the kom-fyke netting and other

gear and program specifications are provided by van der Van Der Veer et al. (1992). The kom-fyke is emptied daily during two annual sampling periods that run approximately from the end of March through the end of June, and from the start of September through the beginning of November (see Figure S1 for the exact distribution of sampling effort). The timing of this monitoring coincides with the well-known seasonal ingress of fish from the North Sea into the Wadden Sea in spring, and the emigration of young-of-the-year fish from the Wadden Sea to the North Sea in autumn. Kom-fyke sampling is discontinued in high summer due to net fouling by macro-algae blooms. Sampling does not occur in winter due to increased risks to equipment and personnel posed by storms and ice floes. Catches were sorted according to species and the total length (TL) of each individual was measured based on 1 cm size bins, for example herring between 5.00 and 5.99 cm would enter the dataset as 5 cm herring. If herring catches were too large to count all specimens individually, a well-mixed, volume-based subsample was taken, to ensure all different size classes remained proportionally represented. For the historical developments of the fyke program and sample counting, see van der Veer et al. (2015).

2.1.2 | Abiotic factors

We collected data on local Wadden Sea surface water temperature, regional North Sea surface water temperatures, lunar illumination, and local tidal range as abiotic explanatory variables. Local Wadden Sea surface water temperatures have been measured continuously by the NIOZ Jetty monitoring setup (NIOZ, 2023), located approximately 500 m from the fyke (Figure 1). Regional North Sea surface water temperatures and tidal ranges near the fyke (Den Helder) were collected from publicly accessible weather buoy and acoustic sensor data (Rijkswaterstaat, 2023). We calculated the maximum possible lunar illumination received for each sampling date using the Lunar package in R (Lazaridis, 2022).

2.2 | Data preparation

2.2.1 | Phenology data

We defined a time window when daily sampling data were available from both the fyke sampling and abiotic factors for a 39-year period (1982–2021). We performed additional filter operations on the dataset to minimize any bias due to data measurement or entry errors, as well as potential overestimation of catches due to weather events preventing the daily emptying of the fyke. We only included samples with >12 and <48 h of fishing effort, and samples with reported body sizes falling within the species limits known from the literature. The catch data were standardized by taking the weekly summed catch per unit effort (CPUE, with effort measured in days), and the weekly mean of the abiotic factors. We chose weekly over daily CPUE to correct for a lack of fishing on some days. The final

time series consisted of 939 sampled weeks of log-transformed herring catches and abiotic factors spread over 39 years. Resolution in the time series varied slightly during two periods. First, there were no catch data from early 2020 when the covid pandemic prohibited fieldwork. Second, the temporal resolution in regional North Sea water temperatures was lower for certain weeks in the 1980s compared to 1990–2021. Therefore, we ran our model multiple times, excluding and including these parts of the time series, to examine qualitative and quantitative changes in model outcomes. We found that only the effect of tidal range changed depending on the inclusion of these time periods, but the effect of all other covariates remained the same. We therefore chose to include these periods in the time series and excluded the tidal range effect from detailed interpretation.

2.2.2 | Dissection data

We used data from dissections performed on a subset of weekly catches from 2005 to 2021 to assess trends in the reproductive status of herring in the kom-fyke ($N = 480$). The reproductive status of individuals was determined based on a 6-point scale of gonadal ripening (Table S1). We used this information to determine the length at which 50% of individuals had reached maturity using logistic regression (L_m50) (Figure S2). The abundance data were then divided into juvenile ($TL < L_m50$) and adult ($TL > L_m50$) categories to examine how the relative contribution of these two life stages to catches might have shifted over time.

2.3 | Data analysis

We used generalized additive models (GAMs; Wood, 2006) to examine temporal changes in the local population dynamics of herring moving between the Wadden Sea and North Sea in relation to abiotic factors. We fitted our additive models using the function gam from the package mgcv (Wood, 2015). Our base model included North Sea and Wadden Sea water temperatures, lunar illumination, tidal range, week, year, and the interaction between week and year as covariates, next to a first-order autoregressive error structure (AR(1)) (Equation 1).

$$E(y_i) = \alpha + f_1(Year_i) + f_2(NS\,temp_i) + f_3(WS\,temp_i) + f_4(Lunar_i)$$
$$+ f_5(Tidal\,range_i) + f_6(Week_i) + f_7(Week_i, Year_i) + (\rho\varepsilon_{t-1} + \omega_t).$$
(1)

where the AR(1) error term is comprised of autocorrelation parameter ρ, ranging between $-1 < \rho < 1$, and ω is a random error term following the standard assumptions for normally distributed errors, $\omega_t \sim_{iid} N(0, \sigma^2)$. In Equation (1), smooths $f_1 - f_6$ represent the main effects of year, North Sea and Wadden Sea water temperatures, lunar illumination, tidal ranges, and week, respectively. The smooth f_7 is a tensor interaction product that models how the seasonal effect of week on herring catches varies over the years. A tensor interaction

allows assessment of the separate singular effects of two variables versus their interaction effect, which is why we chose this type of interaction term. We used the automated variable selection procedure developed by Marra and Wood to identify significant model terms (Marra & Wood, 2011), and we additionally report the contribution of each covariate based on AIC and BIC scores (Table S2). Next to this, we checked for model fit by examining model convergence and residual diagnostic tables and plots (Quantile–Quantile, density distribution, response vs fitted values, and autocorrelation) using the *gam.check()* and *resid.check()* functionalities in the R packages mgcv and itsadug (van Rij et al., 2020; Wood, 2015). The base model converged, explained 43.5% of variation, 45% of null deviance, and had good residual fit diagnostics (Table 1; Figures S3 and S4). We checked for potential extrapolation artifacts in seasonal trends due to the temporal gap between fishing seasons within a year by running the same model on subsets of spring data only ($R^2 = 29.2\%$; Deviance = 31.2%) and fall data only ($R^2 = 33.1\%$; Deviance = 34.8%). The predicted week trend remained qualitatively similar between these models and the full-data model (compare Figure S5 to Figure 3a), whereas the interaction between week and year was still found in the fall data only model (Figure S6), but absent in the spring data only model (Figure S5).

Next, we attempted to expand our base model to examine the role of body size in driving the phenological trends by including herring size as an additional covariate. The expanded model with continuous body size converged, and explained 47% of variation, implying that body sizes carry additional relevant information. However, the model also suffered from considerably worse fit, especially heteroskedasticity. Residual plots indicated that the model could not adequately predict small catch numbers close to zero, systematically overestimating them. This is due to zero-inflation when accounting for continuous size classes, that is, for most size classes catches are zero. To address this issue, we first tried fitting a zero-inflated negative binomial, and a zero-inflated Poisson distribution to untransformed catch data. However, due to the large range and variation in catches (0–5000), choosing a zero-inflated Poisson or negative

TABLE 1 Smoother fit diagnostics.

Smooth	Spline	Knots	Edf.	*k*-index	*p*-value
S(Year)	Thin plate	9	2.326	0.60	<.001
S(NS temp)	Thin plate	9	0.747	0.96	.13
S(WS temp)	Thin plate	9	1.286	1.01	.56
S(Tidal range)	Thin plate	9	0.403	1.05	.89
S(Lunar)	Thin plate	9	2.038	1.02	.69
S(Week)	Cyclic cubic	8	6.102	1.06	.93
ti(Week, Year)	Cyclic cubic, Thin plate	12	2.12	1.04	<.001

Note: Low *p*-values (*k*-index <1) can indicate the number of knots used in constructing the smoother is too low. Except for S(Year), all smoothing terms in the model had good fit. We varied the number of knots in S(Year), but found no difference in smoother shape or fit, and therefore, kept the automatically selected smooth with nine knots in the model.

binomial distributions on untransformed catches did not improve fit. Fit could be improved when outlier catches were excluded. However, the high outlier catches are of particular interest in this study as they represent peak migration points. We therefore chose to examine how the role of body size and life stage have shifted over time by visually inspecting ridgeline plots, rather than including size class as a covariate in the model.

Finally, we examined how the modelled effects change with respect to monitoring design by rerunning the model with lower sampling frequencies (single fishing day per week, single fishing day per 2 weeks, and single fishing day per month). We used these frequencies to have an approximate qualitative comparison to the outcomes expected in large fisheries surveys with limited temporal resolution. For the single sample per week case, we used the first fishing day of every week; for the biweekly case, we used the first fishing day of every odd week; and for the monthly sample, we used the first fishing day of the month. We examined model fit and summary statistics and extracted the predicted partial effects for each covariate to examine how both the significance and the effect size changed under each sampling regime.

3 | RESULTS

The abundance of herring fluctuated strongly during the 1982–2021 period (Figure 2a; Mean weekly standardized catch: 3198 individuals, Median: 356 individuals, 5th percentile: 12 individuals, 95th percentile: 14,269 individuals). Our additive model reflected these fluctuations, predicting a large seasonal component that matched the peak-to-peak periodicity, but not the amplitude, of observed herring abundance. The model, therefore, underestimated the absolute values of the minima and maxima in herring catches. The fitted trend could be decomposed into significant partial smoother effects

of year, week, lunar illumination, tidal range, and regional North Sea water temperatures (Table 2).

3.1 | Partial effects

The partial effect of year identified strong periods of increase and decrease in predicted herring catches during the past four decades (Figure 2b). Weekly standardized catches were predicted to be lowest at the start of the time series in 1982 with 169 individuals [95% CI (38, 738)]. Subsequently, there was a period of gradual increase in catches, up to 803 individuals, 95% CI (383, 1684) in 2001. However, this period was followed by a strong decrease back to low levels of 183 individuals, 95% CI (86, 391) in 2015, and 298 individuals, 95% CI (73, 1219) in 2021. The narrowing and decrease in upper and lower confidence bounds during the period of decline in the last two decades indicate a general decrease in peak weekly standardized catches in individual years during this time period.

We find a strong seasonal signal in herring catches depending on the week sampled within the year (Figure 3a). Predicted catches differed by up to two orders of magnitude between weeks 15–25 (~25 individuals, 95% CI (6, 110)) and weeks 35–45 (~1186 individuals, 95% CI (261, 5379)). We also observed a forward temporal shift in the seasonal trend over time (Figure 3b), with a relative increase in predicted catches in spring and summer (~ weeks 15–25), and a relative decrease in predicted catches in late fall (~ weeks 35–45).

We found regional water temperatures in the North Sea to be important for changes in the abundance of herring. Relatively cold North Sea water temperature (5–10°C) lead to approximately fivefold increases on average, but with substantial uncertainty, in predicted catches (~1554 individuals, 95% CI (267, 9023)) compared to those expected under the long-term mean annual water
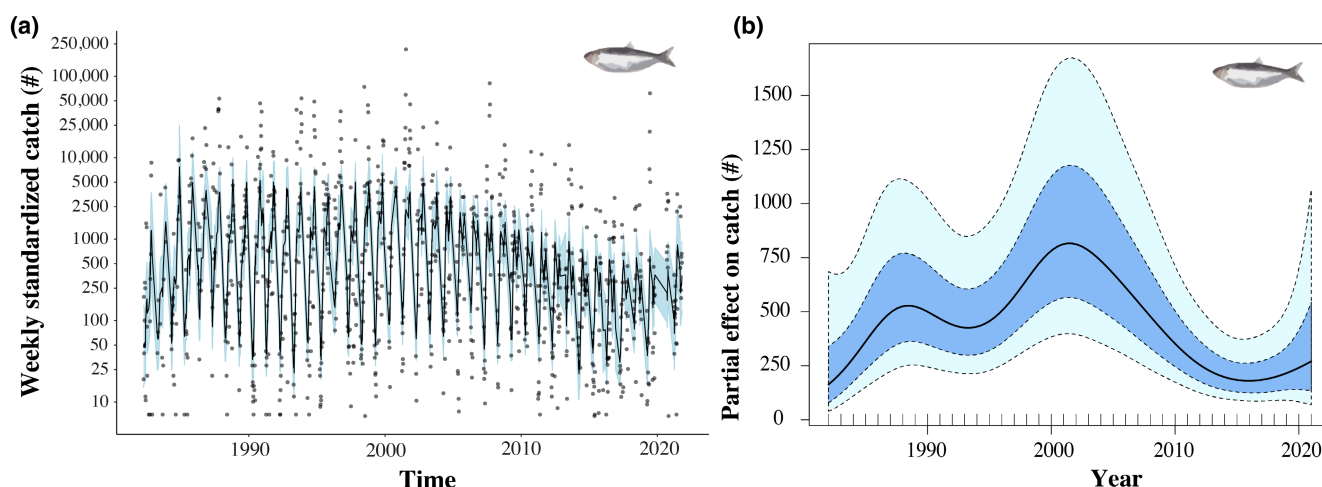

FIGURE 2 (a) Fitted additive model predictions of weekly standardized herring catches ±95% CI in the NIOZ kom-fyke from 1982 to 2021, with a logarithmic y-axis scaling. Gray dots represent the observed values. The gap in early 2020 is due to covid restrictions prohibiting fieldwork. Rerunning the model, excluding the gap, did not alter the shape or significance of individual smooth terms in the generalized additive model. (b) Partial effect of year on weekly standardized herring catches. The shaded dark blue area represents the point-wise standard errors and the shaded light blue area the point-wise 95% CI.

temperature of 12.8°C (348, 95% CI (171, 697)) (Figure 4a). Lunar illumination had a much smaller effect on changes in herring abundance. Periods of full moon and the change to new moon increased weekly standardized catches by ~200 individuals compared to catches outside these periods (~ 513 vs 319 individuals; Figure 4b). The effect of tidal range varied between periods of high and low tidal ranges, but we found this effect to be inconsistent

with respect to time series resolution, whereas all other partial effects were consistent. We, therefore, exclude tidal range from detailed interpretation.

3.2 | Sampling frequency

We find that moving from weekly standardized catches based on daily sampling to standardized catches based on a single fishing day every week, biweekly, or per month, significantly reduced effect sizes (Table 3). Furthermore, the reduced sampling frequency models suffered from heteroskedasticity (Figures S8–S10). The effects of lunar illumination and North Sea water temperature were no longer significant when sampling frequency was decreased to a biweekly or monthly sample. Similarly, no significant change in the seasonal trend over time could be detected when sampling frequency was reduced to a monthly sample. In contrast, the significant effect of year, and season remained present for all sampling frequencies. However, the effect sizes were reduced by over a tenfold with decreased sampling frequency. Visual inspection indicated that the resulting smoother plots were qualitatively similar in the year and seasonal trend between sampling frequency designs (Figures S13 and S14). However, the plots of changing
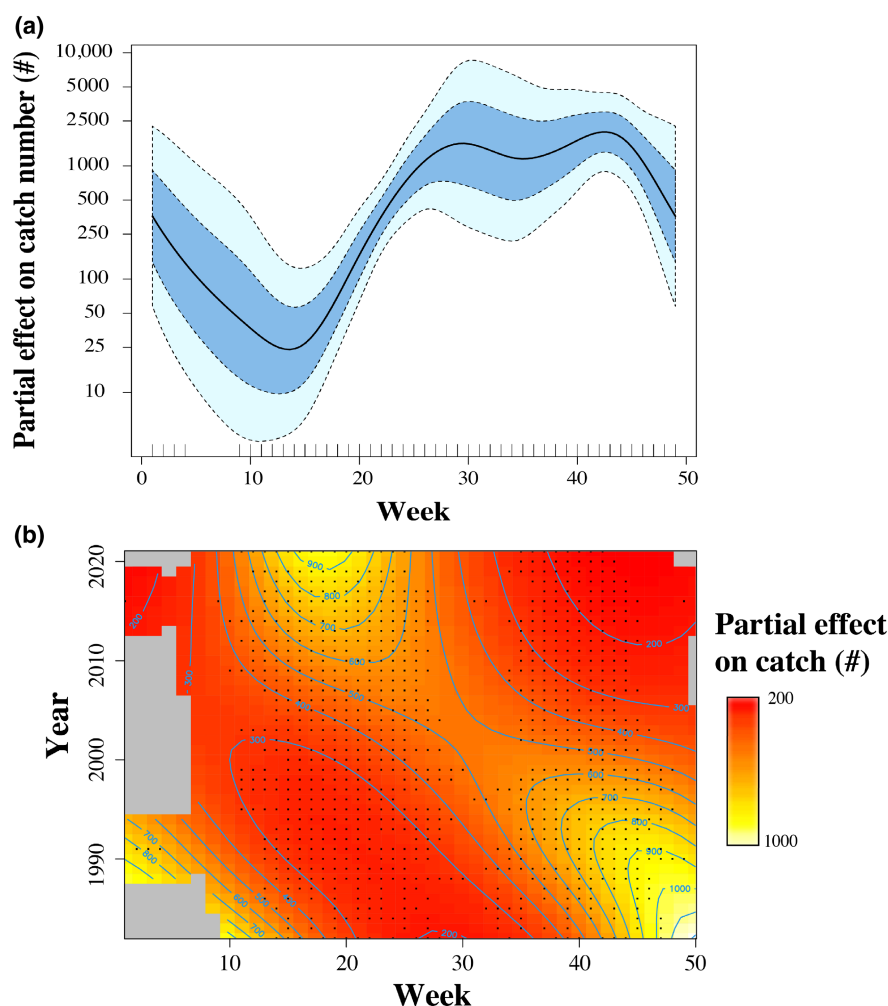
TABLE 2 Approximate significance of covariate smoother terms in the additive model ($R^2 = 43.5\%$, Deviance$= 45\%$).

Smooth	Edf.	Knots	F	p-value
S(Year)	5.755	9	5.072	<.001
S(NS temp)	4.864	9	0.719	<.001
S(WS temp)	4.887	9	0.000	.511
S(Tidal range)	1.546	9	0.859	.004
S(Lunar)	2.223	9	1.592	<.001
S(Week)	5.931	8	11.918	<.001
ti(Week, Year)	5.662	12	3.929	<.001

Note: Significance of a covariate smoother indicates that the null hypothesis is rejected, which means that the partial additive effect of a covariate upon weekly standardized catches cannot be modelled using a flat line. The ecological significance of the effect must be interpreted based on the effect size.

(a)

(b)

FIGURE 3 (a) Partial effect of week number on weekly standardized herring catches, shown on a logarithmic *y*-axis scaling. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the point-wise 95% CI. (b) Partial interaction effect of week and year on standardized herring catches. Over time, there has been a relative increase in catches early in the year (weeks 15–25) and a relative decrease in catches late in the year (weeks 35–45). The contour lines in the plot and the color bar outside the plot show the magnitude of the effect. The sampling effort is divided into two catch seasons per year (spring and fall) represented with black dots. Consistency of the effect with respect to sampling season is shown in Figures S5 and S6. Consistency of the effect with respect to spline choice is shown in Figures S7 and S8.
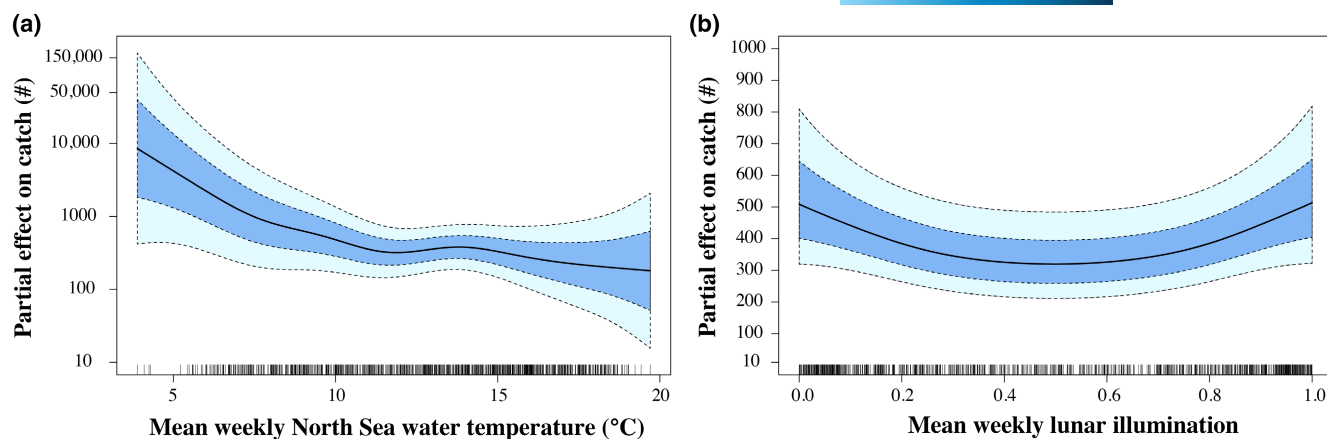
FIGURE 4 (a) Partial effect of mean weekly North Sea water temperature on herring catches, with values shown using a logarithmic y-axis scaling. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the point-wise 95% CI. (b) Partial effect of mean weekly lunar illumination on herring catches. Shaded dark blue area represents the point-wise standard errors, and the shaded light blue area the point-wise 95% CI.

TABLE 3 Comparison of model performance and approximate covariate effect sizes under different sampling frequencies.

Fishing effort	Daily sampling	Once per week	Biweekly	Monthly
Model summary				
R^2	43.5%	31.5%	36.5%	24.6%
Deviance	45%	32.8%	34.9%	27.9%
Partial effect size (Mean ± SD)				
S(Year)	443 ± 198***	28.29 ± 9.14***	34.12 ± 11.51***	32.21 ± 8.63**
S(NS temp)	1095 ± 1705***	40.22 ± 40.05**	30.89 ± 2.49	$30.83 ± 8.5 × 10^{-4}$
S(WS temp)	403 ± 0.002	30.44 ± 1.73	30.83 ± 3.56	29.56 ± 2.15
S(Lunar)	383 ± 59***	28.53 ± 5.37***	$30.83 ± 1.3·10^{-6}$	30.59 ± 1.28
S(Week)	757 ± 669***	52.09 ± 35.96***	53.61 ± 34.72***	45.71 ± 29.77***
ti(Week, Year)	446 ± 206***	34.50 ± 17.40***	34.79 ± 17.92***	31.31 ± 5.08

Note: Approximate effect sizes were calculated by extracting the fitted partial effect sizes for each individual covariate from the model and taking the mean and the standard deviation. A mean with a high standard deviation indicates a nonconstant and likely significant effect size of the covariate, while a mean with a low standard deviation indicates the fitted effect can be represented by a flat line and the covariate is therefore likely unsignificant.

***$0 < p < .001$. **$.001 < p < .01$. *$.01 < p < .05$.

seasonal trends differed considerably between (bi)weekly, and monthly sampling frequencies (Figure S15) and, in the monthly sampling case, the effect was nonsignificant (Table 3, see associated footnote for significance levels).

3.3 | Changes in body size

The relative contribution of size classes remained similar over time but differed markedly between seasons (Figure 5). In both the spring (March–June) and autumn (September–November) seasons, catches were dominated by juveniles between 5 and 15 cm in TL. Although larger adult herring (20–30 cm TL) were also abundant in samples collected in spring and summer, they were very rare in autumn and winter samples. Furthermore, compared to the 1980s, smaller fish have become more abundant with smaller minimum size classes observed

in the most recent decade. The size class distributions provided evidence that small juvenile herring drive the observed changes in the kom-fyke time series as opposed to changes in catches of adult individuals (Figure 5).

4 | DISCUSSION

Our analysis of the longest, highest resolution time series of marine fish species composition and abundance in Northern Europe detects phenological shifts in North Sea herring. Phenological shifts are challenging to detect in ecosystems but can indicate important climate-driven changes in the suitability and use of different habitats (Cohen et al., 2018; Socolar et al., 2017). Changes in the spatial coverage and timing of survey effort between years and geographic heterogeneity between survey locations can
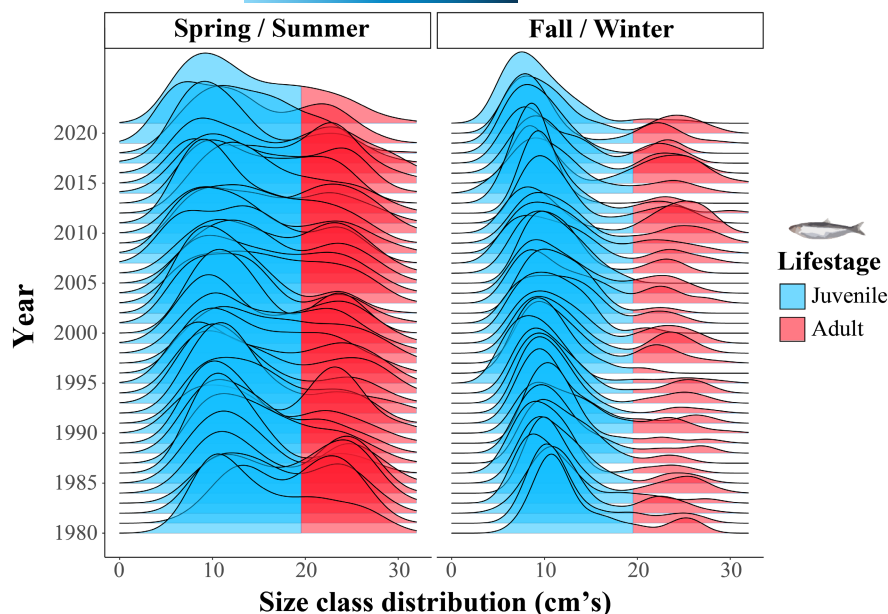
FIGURE 5 Annual and seasonal distributions of the number of individuals caught over the entire size range in standardized herring catches from NIOZ Wadden Sea kom-fyke, using a kernel density estimate function. Colors distinguish below and above the L_m50 maturation size of dissected individuals ($L_m50 = 19.5$ cm, Figure S2), although there will be small year-to-year differences in maturation size.

all confound the detection and interpretation of phenological changes (de Keyzer et al., 2017; Jordaan et al., 2013; Staudinger et al., 2019). In marine fish populations, the detection of phenological shifts is further complicated by tradeoffs in the spatial versus temporal sampling resolution of survey designs and the specificity of sampling gear (Staudinger et al., 2019). The longest and spatially largest marine fish surveys, such as bottom trawl surveys in the northeast and northwest Atlantic that target benthic species, are performed either annually or quarterly and follow a random stratified sampling design (Despres-Patanjo et al., 1988). These surveys, designed to monitor the abundance and biomass of commercially important marine fish, have proven to be powerful in detecting broad horizontal (longitudinal or latitudinal) or depth shifts of fish in response to climate-driven warming (Dulvy et al., 2008; Nye et al., 2009). However, these survey designs possess several factors that confound phenological analyses, namely their low temporal resolution, interannual variation in sampling locations, changing spatial coverage, and bias in species catchability.

As opposed to long-term quarterly or annual broad-scale surveys, long-term "local" monitoring surveys with high temporal resolution have been very important in detecting climate-driven changes in the phenology and coastal habitat use of fish communities, for example, in Narragansett Bay, RI (USA) (Langan et al., 2021). It remains challenging, however, to document phenological changes in marine fish at the species level (Sims, 2004). Using the power of large numbers, community-wide advances in the phenology of fish larvae have been predicted based on quarterly surveys conducted over multiple decades (Asch, 2015), but no species-level predictions could be made. In this type of approach, quarterly sampling data have to be aggregated across many species and statistically interpolated to monthly averages before subjecting these interpolated values to a (linear) regression to arrive at an (extrapolated) prediction of phenological change of the community at a daily resolution. This complicated procedure

highlights a mismatch between the level of observation and the desired level of inference.

In species with highly variable abundances, such as herring swimming in large schools, statistically interpolated data used to "fill" missing temporal resolution will likely deviate considerably from catch values obtained from surveys with higher temporal sampling frequency. Our species-specific outcomes show how the interpretation of phenological shifts is complicated when moving from high-resolution daily sampling to weekly, biweekly, or monthly sampling frequencies. In our analysis, predicted catches of herring declined over tenfold with decreasing sampling frequency. This seems to be because the chance of sampling peak migration days was greatly reduced with reduced sampling frequency. Furthermore, the detection of phenological shifts became more difficult with decreasing sampling frequency, and was no longer statistically significant at the lowest sampling frequency (monthly). Our results, therefore, stress the importance of long-term local monitoring surveys that can maintain high temporal resolution in improving our broader understanding of how different marine fish species respond to climate-driven changes by shifting their phenology of habitat use.

Changes in sea water temperature are known to be a major determinant of the distribution of small pelagic fish species such as clupeids (Peck et al., 2021; Schickele et al., 2021). We found a clear signal of regional North Sea water temperatures on herring catches in the coastal Wadden Sea system. The North Sea is among the fastest warming large marine systems on the globe (Belkin, 2009). Furthermore, the Marsdiep tidal basin, in which the kom-fyke is situated, has experienced an approximately 1.5°C increase in temperature over the past 25 years (Philippart et al., 2017). The large positive effect of relatively cold North Sea water temperatures on weekly catches in herring aligns with our finding of a relative increase in herring catches earlier in the year with time. We argue, therefore, that warming and increased water temperature could

provide a credible explanation for the forward phenological shift observed in herring in our study. From this perspective, changes in these local dynamics reflect larger scale response patterns in fish populations observed in other regions of the world (Asch, 2015; Langan et al., 2021). Additionally, lunar illumination played a weak role in describing changes in the abundance of herring in our passive sampling gear. Lunar illumination can be important in the timing of migration movement as well as for prey availability and foraging success (Grau et al., 1981; Hernández-León, 2008). There might also be an interaction effect with the tidal strength, as this is at its strongest around periods of full and new moon. However, certain important gaps in knowledge remain that limit the extent to which we can infer the importance of different (a)biotic environmental variables in driving observed changes in herring catches. For example, as seawater temperatures increase and decrease across the season, so does the planktonic food availability, and likely other important environmental factors. As these factors all change similarly within the year, their effects can be difficult to disentangle in statistical models, and establishing cause and effect is problematic. This is, in general, a limitation of any study relying on systematically collected field data, and highlights the importance of using not only long-term monitoring surveys but also complementary laboratory experiments and modeling examinations to advance process knowledge as was recently highlighted in a review of efforts to understand the population dynamics of an Atlantic herring stock in the southwestern Baltic Sea (Moyano et al., 2023).

Life stage-specific habitat utilization, such as juveniles using shallow coastal waters as nursery areas, is important for the life cycle closure and maintenance of large population sizes for many groups of marine species (Beck et al., 2001; Gillanders et al., 2003; Roughgarden et al., 1988), including commercially important fish such as flatfish and clupeids (Le Pape & Cognez, 2016; Ray, 2005). Here, we found life stage-specific changes in the coastal habitat use by North Sea herring. Changing suitability and use of such habitats due to climate-driven seawater warming potentially has broader, ecosystem-level consequences (Pörtner & Peck, Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding, 2010). Warming sea waters greatly reduced the nursery function of the Wadden Sea for flatfish such as plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), and flounder (*Platichthys flesus*), whereas conditions have improved for the more warm-tolerant sole (*Solea solea*) (Tulp et al., 2017; van der Veer et al., 2011, 2022). For pelagic fish species such as Atlantic herring, the long-term nursery function of the Wadden Sea was understudied. Our result, that catches were dominated by small (5–10 cm) juvenile herring, indicates that the Wadden Sea serves a nursery role for this species. This corroborates the recent results of Maathuis et al. (2023) who used echosounder measurements to identify large numbers of small clupeids passing through an inlet to the Wadden Sea (the Marsdiep). The long-term decrease in herring abundance that we reported here indicates that the nursery function of the Wadden Sea might be in decline (Tulp et al., 2017). Furthermore and in contrast to flatfish species (van der Veer et al., 2022), herring spawning stock biomass in the North Sea has decreased in recent decades (Arneberg et al., 2023). These observations suggest that it is unlikely that decreases in the nursery function of Wadden Sea for herring are being directly compensated by increased use of other coastal nursery areas in the North Sea.

An important question that remains is how changes in phenology observed in this study might impact the growth, development, and physiological status of sensitive life stages in marine fish. This is important because the rate of growth and development of juvenile fish is tightly linked to both ecological (competition, food availability), and physiological (thermal tolerance) processes that can have major impacts on population and community dynamics (Gårdmark et al., 2015; Pinsky et al., 2019). For example, increasing temperatures in the Wadden Sea coincided with decreases in the in situ abundance and, at the same temperatures, decreased individual growth in the laboratory in eelpout (*Zoarces viviparus*) (Pörtner & Knust, Climate change affects marine fishes through the oxygen limitation of thermal tolerance, 2007). Moreover, fish populations in temperate waters have been reported to be more sensitive to extirpation if juveniles are unable to build up enough reserves during times of abundant resources to survive the resource-limited overwinter period (Van de Wolfshaar et al., 2008). The timing of resource availability might shift under climate-driven warming and this has been suspected to lead to potential mismatches between the phenology of marine fish and the phenology of their prey resources (Cushing, 1990) (but see Kharouba, 2023; Samplonius et al., 2020). This widely studied but difficult to (dis)prove phenomenon is known as "phenological mismatch" (Kharouba, 2023; Renner, 2018), and the consequences of phenological mismatches have been studied most extensively in (migratory) birds (Zhemchuzhnikov et al., 2021). The general consensus is that organisms at lower trophic levels are more likely to advance their phenology than organisms at higher trophic levels (Thackeray et al., 2010, 2016), and that advancing phenology in resource availability has negative consequences for the growth and survival of offspring of species at higher trophic levels (Lameris et al., 2022). However, despite the negative impact on offspring at the individual level, no negative effect has been found on demographic measures at the population level (Reed et al., 2013). The lack of a population-level effect is thought to be due to density-dependent compensatory mechanisms, but this hypothesis remains untested. These studies from different systems show how understanding the general impacts of phenological shifts on fish populations requires wider research focus, where population-level measures are linked to both fine-scale data on individual development as well as to resource availability. Making these types of links for marine fish will require improved integration of existing surveys and modelling methodologies in future studies. Combining local surveys with high temporal resolution of different trophic levels will play a key role in this process by placing changes in marine fish phenology within a wider ecosystem context. This would enable studies to, for example, make fine-scale inferences on whether changing phenology of small juvenile fish follows changes in phytoplankton productivity; or whether changing phenology and body condition of small juvenile

fish affect the prey selection and reproductive success of predators that are less likely to change their phenology, such as seabirds and marine mammals. In this way, local long-term high-resolution time series of fish catches can be valuable in defining general thresholds of climate-driven warming and aid in defining ecological indicators of system-level change (Moyano et al., 2020).

CONFLICT OF INTEREST STATEMENT

There are no potential sources of conflict of interest of the authors with respect to the presented study.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are made openly available in Dryad at: https://datadryad.org/stash/dataset/doi:10.5061/dryad.1c59zw43g.

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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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