Early arrival of spring-spawning Atlantic herring *Clupea harengus* at their spawning ground in the Kiel Fjord, western Baltic, relates to increasing winter seawater temperature

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Abstract

The disturbance of marine organism phenology due to climate change and the subsequent effects on recruitment success are still poorly understood, especially in migratory fish species, such as the Atlantic herring (*Clupea harengus*; Clupeidae). Here we used the commercial catch data from a local fisher over a 50-year period (1971–2020) to estimate western Baltic spring-spawning (WBSS) herring mean arrival time Q_{50} (i.e., the week when 50% of the total fish catches had been made) at their spawning ground within the Kiel Fjord, southwest Baltic Sea, and the duration of the spawning season for each year. The relationship between the seawater temperature in the Kiel Bight and other environmental parameters (such as water salinity, North Atlantic and Atlantic multidecadal oscillations) and Q_{50} was evaluated using a general linear model to test the hypothesis that fish arrived earlier after warm than cold winters. We also estimated the accumulated thermal time to Q_{50} during gonadal development to estimate the effects of seawater temperature on the variations of Q_{50}. The results of this study revealed a dramatic decrease in herring catches within the Kiel Fjord since the mid-1990s, as documented for the whole southwestern Baltic Sea. Warmer winter seawater temperature was the only factor related to an earlier arrival (1 week for one January seawater temperature degree increase) of herring at their spawning ground. The relationship was found for the first time on week 52 of the year prior to spawning and was the strongest (50% of the variability explained) from the fourth week of January (8 weeks before the mean Q_{50} among the studied years). A thermal constant to Q_{50} (∼316°C day) was found when temperatures were integrated from the 49th week of the year prior to spawning. These results indicate that seawater temperature enhanced the speed of gonadal maturation during the latest phases of gametogenesis, leading to an early fish arrival under warm conditions. The duration of the spawning season was elongated during warmer years, therefore potentially

mitigating the effects of trophic mismatch when fish spawn early. The results of this study highlight the altering effects of climate change on the spawning activity of a migratory fish species in the Baltic Sea where fast global changes presage that in other coastal areas worldwide.

KEYWORDS
arrival at spawning area, Atlantic herring *Clupea harengus*, climate change, phenology changes, seawater warming, thermal time to arrivalwestern Baltic Sea

1 | INTRODUCTION

One of the most dramatic ecological consequences of global warming is the disturbance of the phenology (i.e., the timing of periodic life-cycle events related to environmental conditions) of organisms, which results in early animal migration, breeding and spawning (Dunn & Møller, 2014), or plant flowering (Cleland et al., 2007). Such effects have been well documented on land (Walther et al., 2002) but are less understood in marine organisms (but see Poloczanska et al., 2013), especially in fish species that migrate seasonally over large distances to spawn. Many seasonal spawning fish species worldwide are of great commercial importance (FAO, 2018), and the alteration in their phenology under climate change may yet be another stressor that jeopardizes the reproductive success and the recovery of some of the most overexploited species.

Early spawning migration following a warm winter is being increasingly reported over the past decades. For example, in the Gulf of Alaska, water temperature led the walleye pollock (*Gadus chalcogrammus*) to spawn up to 3 weeks earlier and for a longer period than normal (Rogers & Dougherty, 2018). A 40-years' time series in the North Sea and the Irish Sea also revealed that increased sea surface temperatures during winter induced early spawning in various sole (*Solea solea*) stocks (Fincham et al., 2013). Early spawning might result in a trophic asynchrony between the fish larvae and their food (the match–mismatch hypothesis; reviewed by Durant et al., 2007), thereby reducing the chances of survival of the fragile first-feeding larvae that have exhausted the energetic reserves of their yolk sac and need to feed consistently to grow fast (Anderson, 1988; Houde, 2008). Such trophic asynchrony may also potentially occur if the spawning season is shortened as the probability for the larvae to hatch during optimal conditions decreases.

The western Baltic fisheries are currently mostly targeting spring-spawning Atlantic herring *Clupea harengus* (thereafter referred as "herring"), of which stocks and recruitment have also been decreasing steadily for the past three decades to such an extent that the International Council for the Exploration of the Sea (ICES) has been recommending a complete ban of the exploitation since 2019 (ICES, 2018; ICES, 2020; ICES, 2021). Herring recruitment has continuously decreased since the end of the last century to reach its lowest levels in 2016 and 2017 (ICES, 2018). Although the decline of the western Baltic spring-spawning (WBSS) herring stocks is certainly mainly due to overfishing (Froese et al., 2022), ocean warming may also lead

some part to a decrease in juvenile herring recruitment (Polte et al., 2021).

Early studies have suggested a positive relationship between increasing seawater temperature and early herring spawning (Berenbeim & Sigaev, 1977; Hay, 1985; Lambert, 1987), but the strength of such association is still unclear. In addition, the plasticity of the timing of herring spawning may be controlled by local conditions (Haegele & Schweigert, 1985), which should be particularly true within the Baltic Sea where environmental gradients (e.g., seawater temperature and salinity) are pronounced (Stockmayer & Lehmann, 2023). Indeed, recent studies have described that *C. harengus* spawned up to 6 weeks earlier after warm than cold winter in the brackish water of the Gulf of Riga in the eastern Baltic (Arula et al., 2019), whereas the offset was of 2.5 weeks earlier in the more saline waters of the Greifswald Bay in the southwest Baltic (Polte et al., 2021). Also, herring may adjust the duration of their spawning season in response to interannual water temperature changes (Geffen, 2009).

In most temperate teleosts, photoperiod plays an important role in the timing of gametogenesis by triggering the start of certain reproductive developmental phases (dos Santos Schmidt et al., 2022; McPherson & Kjesbu, 2012). For example, the change in natural lighting around the autumn equinox begins the vitellogenesis of spring-spawning fishes (Klinkhardt, 1996; Ma et al., 1998). However, the yearly photoperiod fluctuation is constant over the years and is thus unlikely to be responsible for the interannual variability in the fish spawning timing. Seawater temperature appears to play an important role in regulating the pace at which gametes maturate in teleosts, mostly during the final stages of the gametogenesis (Alix et al., 2020; Kjesbu et al., 2010; Tveiten et al., 2001).

The influence of temperature on fish gonadal development can be related to a thermal constant time required by an organism to reach a certain developmental stage (Neuheimer & Taggart, 2007). The thermal time to spawning is estimated as the integrated temperature (the number of degree-days [DD] to spawning) above a temperature threshold experienced by the fish from the onset of temperature-dependent gonadal maturation to spawning. The threshold temperature defines the lower limit of the thermal performance curve above which physiological responses of the fish are near-linear (Trudgill et al., 2005). The measure of the thermal time to spawning is useful to disentangle the effects of temperature from other factors on the timing of spawning in ectotherm fish across time and space (Neuheimer & Taggart, 2007; Trudgill et al., 2005).

Environmental factors other than water temperature may also influence herring spawning timing, but the contribution of each factor to such response is still poorly understood. The salinity of the western Baltic Sea changes substantially within and between years under the effects of the wind and saline water inflows from the Kattegat (Lehmann et al., 2022), thereby potentially influencing the timing of herring migration toward their spawning ground (Miethe et al., 2013). Moreover, the variability in the large-scale atmospheric circulation (e.g., the North Atlantic oscillation [NAO] winter index; Lehmann et al., 2011) or the Atlantic multidecadal oscillation (AMO; Börgel et al., 2018) has been related to changes in the abundance of fishes and their planktonic prey in coastal waters (Alheit et al., 2014; Ottersen et al., 2001).

The aim of this study was to examine the relationship between water temperature and other environmental parameters (water salinity, NAO, and AMO) on the arrival time of herring at their spawning ground within the Kiel Fjord. More specifically, we used observed and reconstructed weekly catch weight data of herring captured in the Kiel Fjord throughout the entire spawning season of 50 consecutive years (1971–2020) to test the hypotheses that herring come to spawn earlier and for a longer duration during warm than cold years. Moreover, we tested the assumption that fish mean arrival time relates to a constant thermal time metric (DD to spawning). We also determined the maturation stages of some of the herring captured in 2018, 2020, and 2021 to verify that the majority of the fish were ready to spawn or already spawning upon their arrival within the Kiel Fjord.

2 | MATERIALS AND METHODS

2.1 | Western Baltic spring-spawning herring spawning

In autumn, WBSS herring migrate south from their summer feeding ground in the Skagerrak and the Kattegat (Figure 1a) to overwinter in the Øresund (Nielsen et al., 2001), a narrow strait between the Danish Zeeland Island and the south of Sweden (Figure 1b). The fish then migrate from their overwintering area to different spawning grounds along the shallow waters of the western Baltic Sea (ICES subdivisions 22 and 24), such as the Kiel Fjord and the Kiel Canal (Figure 1c), the Schlei and Trave estuaries, or Bodden area (Paulsen et al., 2013). The timing of herring migration into the Kiel Fjord is, however, unknown. Herring are synchronous and total spawners; they spawn only once a year, releasing all their gametes at once (Blaxter & Hunter, 1982); they leave the area after spawning within a few days (Axelsen et al., 2000; Biester et al., 1978).

2.2 | Spring-spawning herring catch weight

We used the catch data of a professional fisher who operated within the Kiel Fjord from 1971 to 2020 to determine the catch weight of spring-spawning herring captured for the duration of each spawning season and the date of the start and the end of the fishing season for all the years. The weekly catch weight throughout the whole fishing season was available for the years 2008–2020, whereas, from 1971 to 2007, only the data of the total catch weight of the entire fishing season and the start and end of the fishing season were available. The general type of distribution of the catch weight for each year of the period 1971–2007 has been identified and adopted from the annual catch weight distributions for the years 2008–2020. Given this as a theoretical template, the empirical annual catch weight distributions were then estimated using the yearly total catch and the start and the end of the fishing season for each year of the period 1971–2020 (the description of the calculation method used is described later).

2.3 | Fish collection

For the entire period of his professional activity, the fisher followed the same routine: Each fishing day, the net was deployed for about 10 h, between ∼ 6 p.m. and ∼ 5 a.m. the next morning. From 1971 to 2018, a 500-m-long net (28-mm mesh aperture) was deployed at the same location, near the entrance of the Kiel Canal, within the Kiel Fjord (Figure 1c). In 2018, the fisher moved his fishing area ∼1.5 km away inside the Kiel Canal (Figure 1c). The average catch per unit effort did not vary substantially between those two fishing areas (∼14 fish/h in 2008–2017 and ∼13 fish/h in 2018–2020), and most of the fish that were captured near the entrance of the canal were probably on their way to enter the canal. Inside the canal, the fisher deployed a net half as long (250 m long, 28-mm mesh aperture) as the one previously used outside of the canal; the catch effort for the years 2018–2020 was multiplied by 2 to be comparable with that of the period 1971–2017. Since 2000, a fishing quota was imposed to the fisher but was never filled.

Each year, the decision of the fisher to start fishing was motivated by the absence of sea ice cover at the surface of the Kiel Fjord, which, to his knowledge, prevents the fish from coming to spawn. The fisher was also in constant contact with recreational and other professional fishers in the Kiel Fjord to be informed about herring arriving in the area. Throughout a fishing season, the fisher fished every 2 days on average, and the time between two consecutive fishing days rarely exceeded 4 days.

2.4 | Herring maturation stage measurements

In 2018, 2020, and 2021 (2019 was not sampled due to logistical problems), a subsample of 1374 fish (250, 973, and 151 fish for each respective year) was collected every 2 to 7 days (Data S1) within the Kiel Fjord from the daily catch of the fisher to analyse the proportion of herring maturation stage over the course of the spawning season. On average, 55 ± 33 (mean ± SD) fish were collected on a single day, with a minimum and maximum of 12 and 102 fish, respectively. The fish were collected <1 h after they were landed and placed into a
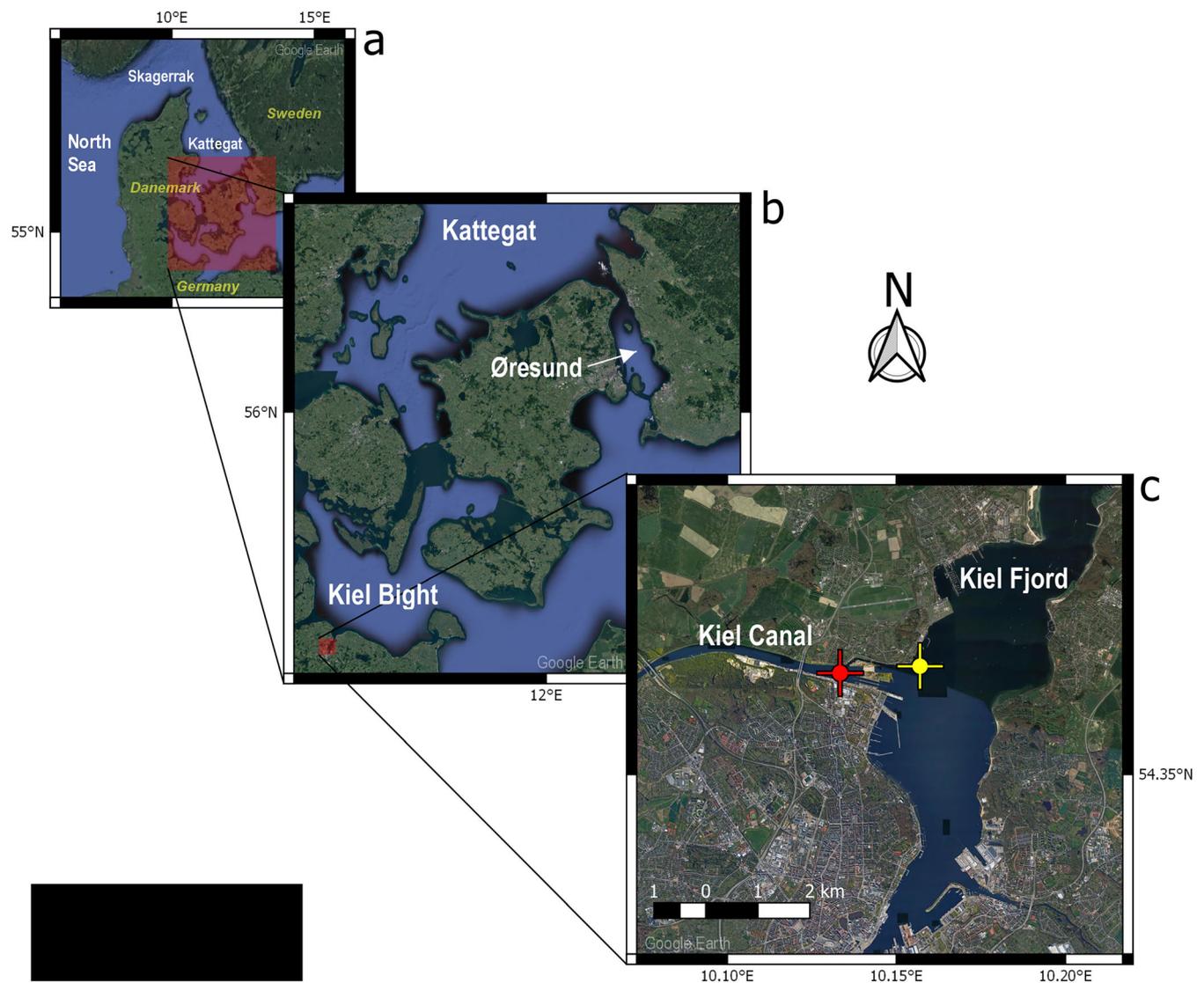
FIGURE 1 Location map of the (a) Skagerrak and Kattegat seas, summer feeding grounds of the western Baltic spring-spawning (WBSS) herring, (b) the Øresund strait, overwintering area of the WBSS herring, the Kiel Bight, where fish aggregate before entering their spawning ground within the Kiel Fjord and the Kiel Canal, and (c) the location where herring were fished near the entrance of (yellow cross) and inside (red cross) the Kiel Canal within the Kiel Fjord.

plastic cooler to be transported to the laboratory where they were analysed within the next hour, when possible, or otherwise frozen at −27°C for further analysis.

Frozen fish were left to thaw for 24 h before being analysed. All fish were weighed to the nearest 0.5 g and their standard length measured to the nearest 0.5 cm. They were then cut open from the anus to the gills, sexed, and their gonads were gently removed and weighed to the nearest 0.1 g. The maturity stage of all the fish was determined from the visual analysis of the gonads as detailed in Bucholtz et al. (2008). We distinguished eight maturity stages, which were then grouped into four maturity phases as follows: maturation (stages 2–4), spawning (stages 5–6; fish are ready to spawn within few days [stage 5] or are currently spawning [stage 6]; Tomkiewicz J, personal communication), spent-regeneration (stage 7; gonads with no more reproductive material and starting a new maturation cycle), and abnormal

(stage 8; malfunctional gonads). No juveniles (stage 1) were captured because the net mesh-size used was >25 mm and, therefore, were not included in this analysis. Maturity stages >4 can be identified when gonads are frozen at −18°C or colder (Bleil & Oberst, 1993).

2.5 | Environmental factor selection and data collection

The daily water temperature and water salinity at the Kiel Bight were obtained from a hydrodynamic coupled sea ice-ocean model of the entire Baltic Sea, including Kattegat and Skagerrak (BSIOM, Lehmann et al., 2014). The performance and applicability of BSIOM have been demonstrated in a number of publications (e.g., Hinrichsen et al., 2016; Lennartz et al., 2014; Stockmayer & Lehmann, 2023). The

Kiel Bight was used because fish aggregate for some time in this area before they enter their spawning ground within the Kiel Fjord when ready to spawn (Polte et al., 2021). The hydrodynamic model has a horizontal resolution of 2.5 km with 60 vertical levels of 3 m thickness down to 100 m depth. To the maximum model depth (250 m), the thickness of vertical levels increases to 6 m. Water temperature and salinity at a depth of 8 m were used in this analysis because it is the depth at which *C. harengus* had been found predominantly during previous acoustic surveys (ICES, 2019; Nielsen et al., 2001).

The model domain includes the entire Kiel Bight. The hydrodynamic model is realistically forced using the ERA5 global reanalysis in the preliminary extension version back to 1950 (Lehmann et al., 2014), with a three-hourly temporal and approximately 50-km spatial resolution, respectively. The forcing data were interpolated on the model grid; they include surface air pressure, precipitation, cloudiness, and air- and dew point temperatures at 2 m height from the sea surface. Wind speed and wind direction at 10 m height from sea surface were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, solar radiation, and heat fluxes, were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell & Andersson, 2012). The monthly values of the NAO index for the period 1970–2020 were obtained from the website https://crudata.uea.ac.uk/cru/data/nao/ (updated from Jones et al., 1997).

2.6 | Degree-days to arrival

The value of DD to the time of mean fish arrival time (Q_{50}; see below) at their spawning ground (DD_{50}) was calculated by summing the mean daily seawater temperature in the Kiel Bight, between a specific starting date (representing the onset of gonadal maturation), and Q_{50} for each year covered in this study (1971–2020). DD_{50} for year y ($DD_{50 \cdot y}$) was estimated as

$$DD_{50 \cdot y} = \sum_{i=\text{start}}^{Q_{50}} \max(T_i - T_{\text{Th}}, 0),$$

where T_i is the daily temperature (°C) at day i, T_{Th} is the estimated threshold temperature (T_{Th},°C) above which the influence of temperature on development rate can be considered near-linear (Neuheimer & Taggart, 2007), *start* is the start date (day of year) for the temperature-dependent gonadal maturation, and Δt is the time-step (1 day). T_{Th} is unknown for WBSS herring; therefore, we chose a T_{Th} of 0°C as it was shown to be relevant for other fish species (e.g., Atlantic cod, *Gadus morhua*, Neuheimer & Taggart, 2007; Pacific herring, *Clupea pallasii*, Ferreira & Neuheimer, in press). We calculated several DD_{50} values using different starting dates of gonadal maturation onset (*start*) from the autumn equinox (264th day of the year) and weekly until the fourth day of the year (i.e., before the first fish arrived in the Kiel Fjord). We examined the

linear relationship between DD_{50} across the studied years for each starting date using simple regressions analyses to test the null hypothesis that DD_{50} was constant over the studied years (1970–2020).

2.7 | Statistical analysis

2.7.1 | Estimated fish arrival time

For a 13-year period, between 2008 and 2020, the weekly *C. harengus* catch weight was available throughout the entire fishing season. For the years 1971 to 2007, only the 2 weeks when the fisher started and finished fishing were available, and the total catch weight for the entire fishing season. The distributions of the weekly catch weight for the 2008–2020 period were found to be normally distributed (Data S3). We therefore assumed that the distribution of the weekly catch weight of each of the years of the 1971–2007 period also followed a normal distribution $N(\mu, \sigma^2)$, as also observed in previous years in the western Baltic Sea (see fig. 8 in Nielsen et al., 2001). Based on the concept of a (weighted) normal distribution, the full week range, W_r, results as the number of weeks a fishing season lasted (i.e., the difference between the last [W_l] and the first [W_f] week of fishing), and thus defines the basis or tails (x axis) of a (weighted) $N(\mu, \sigma^2)$.

Consequently, the half-week range, W_h, of a fishing season is $W_h = \frac{W_r}{2}$. The weighted mean of the normal distribution (μ) was then approximated by $\mu = \frac{W_r}{2} + W_s$, with W_s being the week when fishing started. As almost all probability (99.7% of the area underneath a normal curve) is laying within a range of three SD (σ), the SD was approximated as $\sigma = \text{abs}\left(\frac{W_h}{3}\right)$. The empirical distribution of the weekly catch weight throughout a fishing season was then reconstructed for each year by multiplying the probability density function (PDF) of $N(\mu, \sigma^2)$ with μ and σ as being derived above by the yearly total catch weight.

We used a conservative 5% quantile (Q_{05}) of the reconstructed PDF of the fish catch over a fishing season to define the time of first arrival of the fish (Data S3) to account for the years when the fisher caught isolated fish or when he started to fish when the fish had already arrived. We used the 50% quantile (Q_{50}) and the 95% quantile (Q_{95}) of the PDFs to define the mean of fish arrival and the end of a fishing season, respectively (Data S3). The time period in weeks between Q_{05} and Q_{95} was used to define the duration of herring spawning.

2.7.2 | Herring spawning timing and environmental parameters

The relationship between the independent variables, the environmental factors (water temperature, water salinity, NAO averaged over December to February [NAO_{DJF}], and annual AMO), and the response variable (Q_{50}) was evaluated using a general linear model (GLM). The model was fitted using a stepwise regression procedure, which iteratively adds or removes to the initial null model potential significant

independent variables to be used in the final model (Littell et al., 1996). The normality of the residuals of the GLM was confirmed with a Q–Q plot and a cumulative function distribution (Data S4). All the GLM analyses were run using the programme SAS version 9.4 (TS1M4).

The strength of the relationship between Q_{50} and the weekly mean water temperature for all the years of the studied period (1971–2020) was preliminarily analysed for the autumn/winter months (October, November, and December) and the first six weeks (January and February) of the following year using simple linear regressions (Figure 2). The relationship was not tested at later dates to not overlap with the earliest Q_{50} (week 7 in 2020). The relationship between Q_{50} and the weekly mean seawater temperature was significant from the last week of the year onward (week 52; $R^2 = 0.13$, $df = 1$, $p = 0.005$; Figure 2). The strength of the relationship was the highest ($R^2 = 0.5$, $df = 1$, $p < 0.001$; Figure 2) from the fourth week of the year. The mean value of water temperature and water salinity at the fourth week of the year was therefore used as the independent variable against Q_{50} in the GLM model. Preliminary results revealed that NAO was strongly correlated with water temperature in the GLM model (Data S4) and was, therefore, excluded from the initial model to avoid multicollinearity (Zar, 2010).

The null hypothesis that the duration of the spawning season (response variable) did not vary in function of the time of herring's first arrival (Q_{50}; explanatory variable) at the level of error $\alpha = 0.05$ was tested using a simple linear regression in the base version of R version 4.0.3 (R Core Team, 2022).

2.7.3 | Fish maturity stages

A χ^2 test of independence was used to test the null hypothesis that the overall proportion of herring at different maturity phases did not differ among each other at the level of error $\alpha = 0.05$. The data from the year 2021 were not used in the statistical analysis because of the low sample size due to logistical problems but were still presented here as they indicate the maturity status of the fish at least for the beginning of the spawning season. The standardized residuals were calculated for each cell to identify the factors that contributed the most to the significance of the results. The χ^2 statistic was assumed to follow a χ^2 distribution because no more than 20% of the categories had expected frequencies <5 (Agresti, 2007). This analysis was performed using R base version 4.0.3 (R Core Team, 2022).

3 | RESULTS

The herring total catch weight over a whole fishing season ranged from 1139 kg (year 2019) to 61,041 kg (year 1995), with an average of 28,137 ± SD 15,651 kg among all the years (1971–2020; Figure 3). The herring catch weight was overall relatively stable over the years between 1971 and the mid-90s, after when it constantly decreased to reach its lowest levels in the last years of our sampling. A similar trend has been described for spring-spawning herring in the Skagerrak, Kattegat, and western Baltic (ICES, 2021; Parmanne et al., 1994), which confirms the validity of the data used in this study, and that the Kiel Fjord spring-spawning herring stock is representative of that from the whole western Baltic Sea.

The PDFs of the fish catch distribution over the different years of this study revealed that the fish first arrival (5% of the total fishing catches; Q_{05}) varied from the 3rd week (observed in 2020) to the 14th week (observed in 1972, 1987, and 1996) of the year (Data S5). On average, fish first arrival occurred on the ninth week of the year (March) ± SD 3 weeks. The fish mean arrival time (i.e., 50% of the yearly total fishing catches; Q_{50}) varied from the 7th week (observed in February 2020) to the 16th week (observed in April 1972, 1987, and 1996) of the year (Figure 4a and Data S5). The mean Q_{50} over all the years is on the 12th week of the year (March) ± SD 2.1 weeks. A simple regression analysis revealed that Q_{50} declined over the years ($R^2 = 0.11$, $df = 1$, $p = 0.02$; Figure 4b).

The last fish arrival time (95% of the yearly total fishing catches; Q_{95}) varied from the 12th week of the year (observed in March 1990,

FIGURE 2 Coefficients of determination (R^2) of the relationship between herring mean arrival week (Q_{50}) in the Kiel Fjord and the seawater temperature (Kiel Bight) at different weeks preceding the arrival of the fish. The week of the year when the value of R^2 was ≥0.5 for the first time was used to calculate the mean value of the independent variables used in the general linear model (GLM) model. The bold values above the bars indicate significant p-values of the linear regression at the alpha-level of error of 5%.
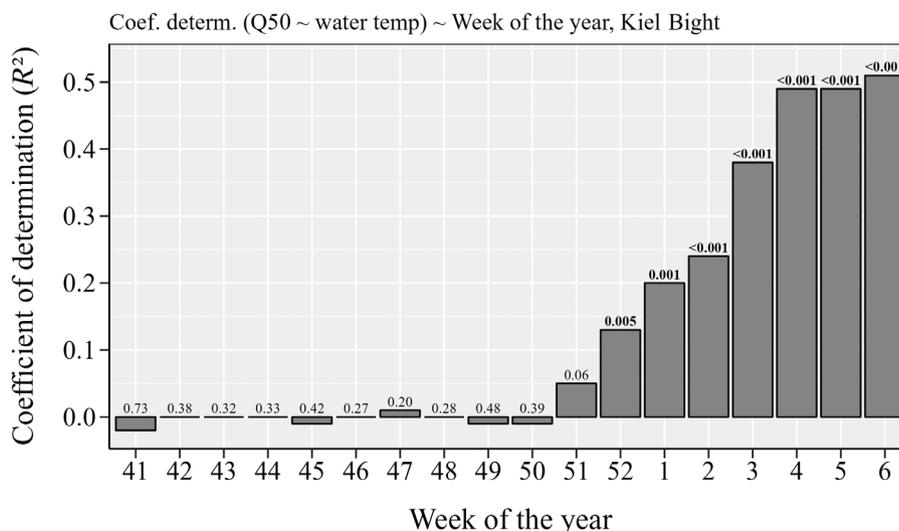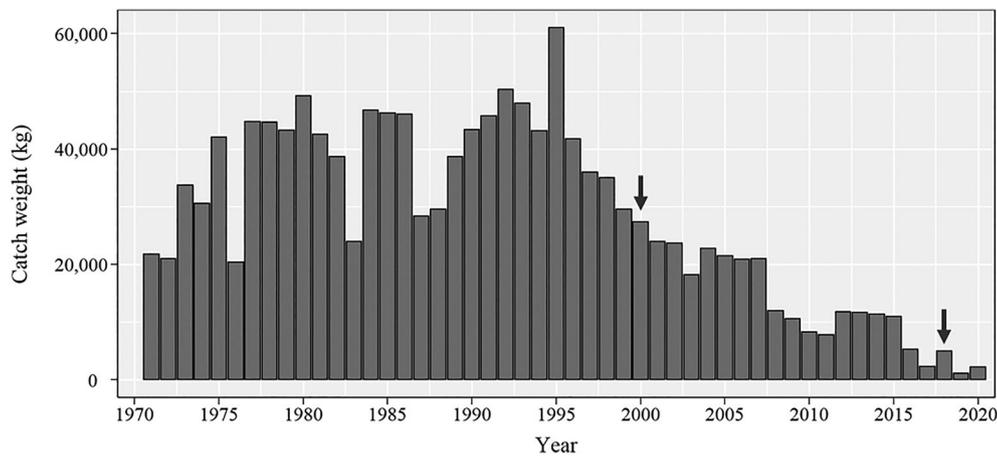
FIGURE 3 Yearly (1971–2020) total catch weight (in kilograms) of spring-spawning *Clupea harengus* within the Kiel Fjord. The vertical arrows indicate the year 2000, when fishing quotas were imposed to the fisher, and the year 2018, when the fisher moved its fishing area from the entrance to inside the Kiel Canal.
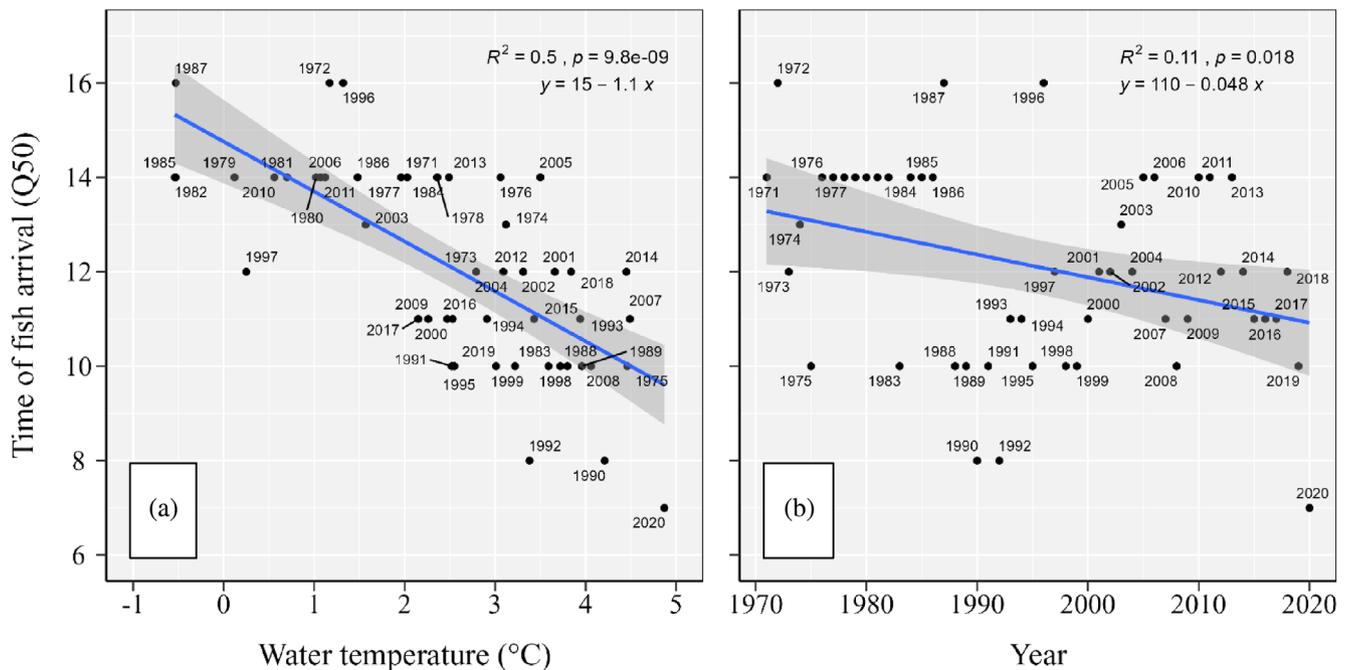
FIGURE 4 Relationship between the mean arrival time of herring (week of the year; 50% of the total yearly herring catch; Q_{50}) and (a) the mean water temperature in the Kiel Bight at the fourth week of the year for all the years (dots) studied (1971–2020) and (b) the years studied. The equation of the regression line (blue line; the gray shaded area represents the 95% CI), the coefficient of determination (R^2), and the *p*-value of the regression are indicated in the text in the upper-right corner of the plot.

1992, 2019, and 2020), at the earliest, to the 19th week of the year (observed in May 1972), at the latest (Data S5). The latest fish arrived on average on the 15th week of the year ± SD 1.7 weeks. The duration between Q_5 and Q_{95} varied from 3 weeks (observed in 1978) to 11 weeks (observed in 1991), with an average duration of 6 ± SD 2 weeks.

The GLM model revealed that, out of the variables used in the model, only water temperature at the fourth week of the year had an effect on the mean time of arrival Q_{50} of the fish ($R^2 = 0.5$, $F = 47.71$, $df = 1$, $p < 0.0001$; Data S5); it explained 50% of the variability of Q_{50}. Herring spawning duration (difference between Q_{95} and Q_{05}) varied from 3 to 11 weeks, with a median duration of 6 ± interquartile range (IQR) 3 weeks. A simple linear regression analysis revealed that

in the years when the first fish arrived earlier, the spawning duration was longer ($R^2 = 0.6$, $df = 1$, $p < 0.001$; Figure 5) than in the years when fish arrived later.

The trend of the thermal time to Q_{50} over the years (1971–2020) followed a linear increase when gonadal maturation onset was prior to the 341st day of the year (week 49, mid-December; Figure 6). On that date, for the first time, the mean thermal time to Q_{50} was constant (~316 DD; $R^2 = 0.04$, $df = 1$, $p = 0.09$; Figure 6), meaning that the variation in Q_{50} was temperature-dependent. The trend remained non-linear for later gonadal maturation onset starting dates.

Out of the 1374 adult *C. harengus* collected in the three sampling years (2018, 2020, and 2021), 738 (54%) were females and 636 (46%) were males. For the years 2018 and 2020, the proportion of the fish

FIGURE 5 Relationship between herring spawning duration, estimated as the number of weeks between Q_{05} (week of the year when 5% of the total fish had arrived) and Q_{95} (week of the year when 95% of the fish had arrived), and the time of mean arrival (Q_{50}) for all the years (dots) between 1971 and 2020. The equation of the regression line (blue line; the gray shaded area represents the 95% CI), the coefficient of determination (R^2), and the p-value are indicated in the text in the upper-right corner.
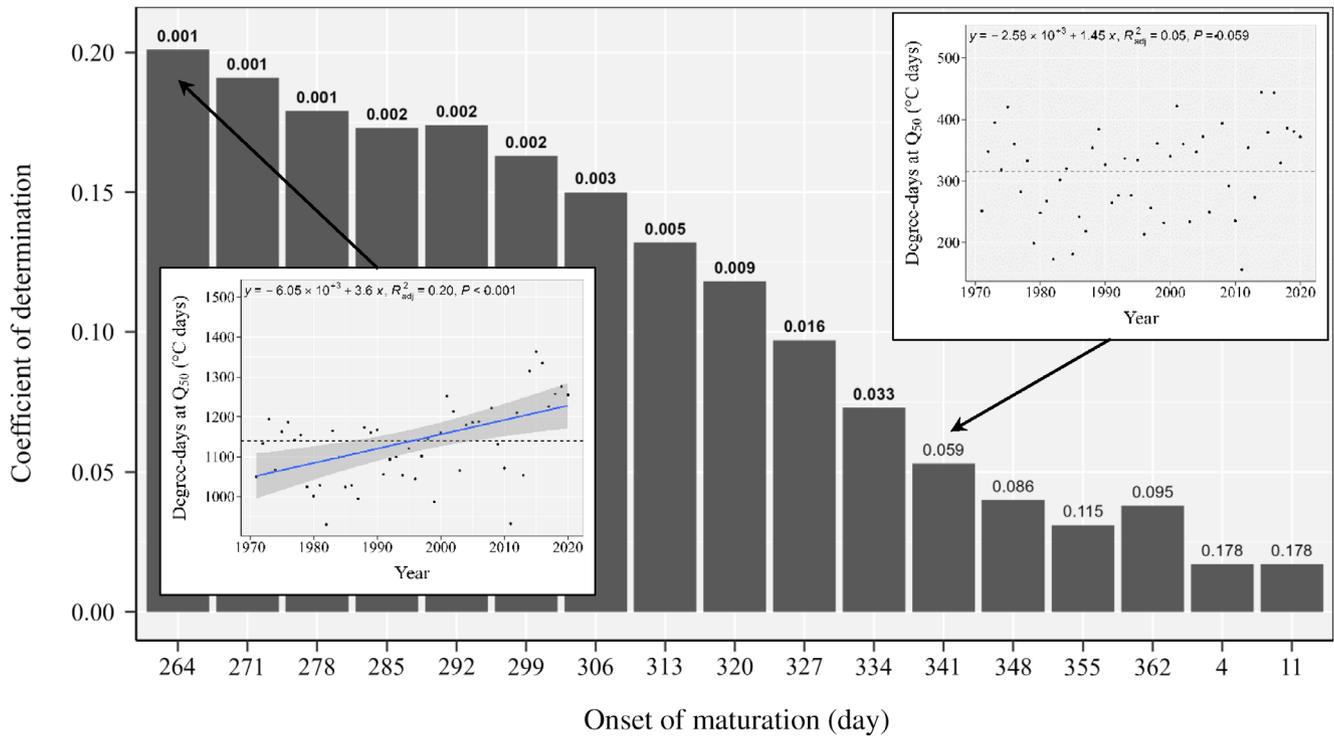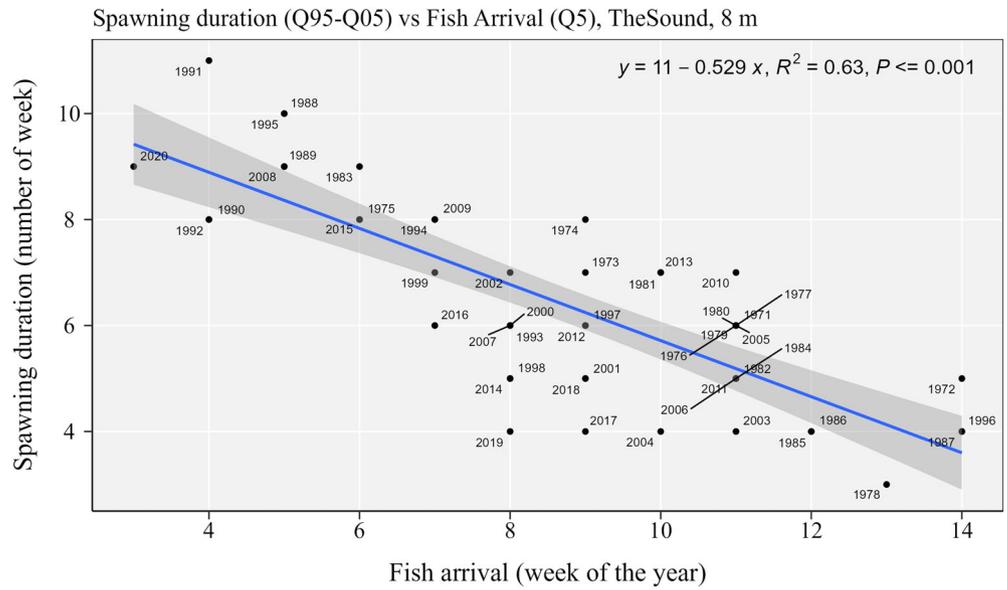
FIGURE 6 Coefficient of determination of the relationship between the degree-days (°C · day) to the mean fish arrival Q_{50} (DD_{50}) and the years studied (1971–2020) for different day of the year of gonadal maturation onset. The bold values above the bars indicate significant p-values of the linear regression at the alpha-level of error of 5%. The inserts show the trend of DD_{50} over the years for an onset of gonadal maturation at the autumn equinox (day 264; bottom left) and at the first time when the relationship was non-linear (day 341; top right). The equation of the significant regression line (blue line; the gray shaded area represents the 95% CI), the coefficient of determination (R^2), and the p-value of the regression analyses are indicated in the text at the top of each insert plot. The horizontal dashed lines represent the mean value of the DD_{50} for all the years (1971–2020).

differed among the different maturation phases ($\chi^2 = 1827$, $df = 3$, $p < 0.001$), mostly because of the high proportion of fish in spawning phase (77% of the total; Figure 7 and Data S6). About 15% of all the fish had already spawned, and only a small proportion was in maturation phase (6%) or had abnormal gonads (2%) that would have

prevented them from spawning. The trend of the data at the beginning of the spawning season in 2021 (not included in the statistical analysis due to a low sample size) was similar as the previous years, with a majority of fish in a spawning phase (83%) or already spent (8%).
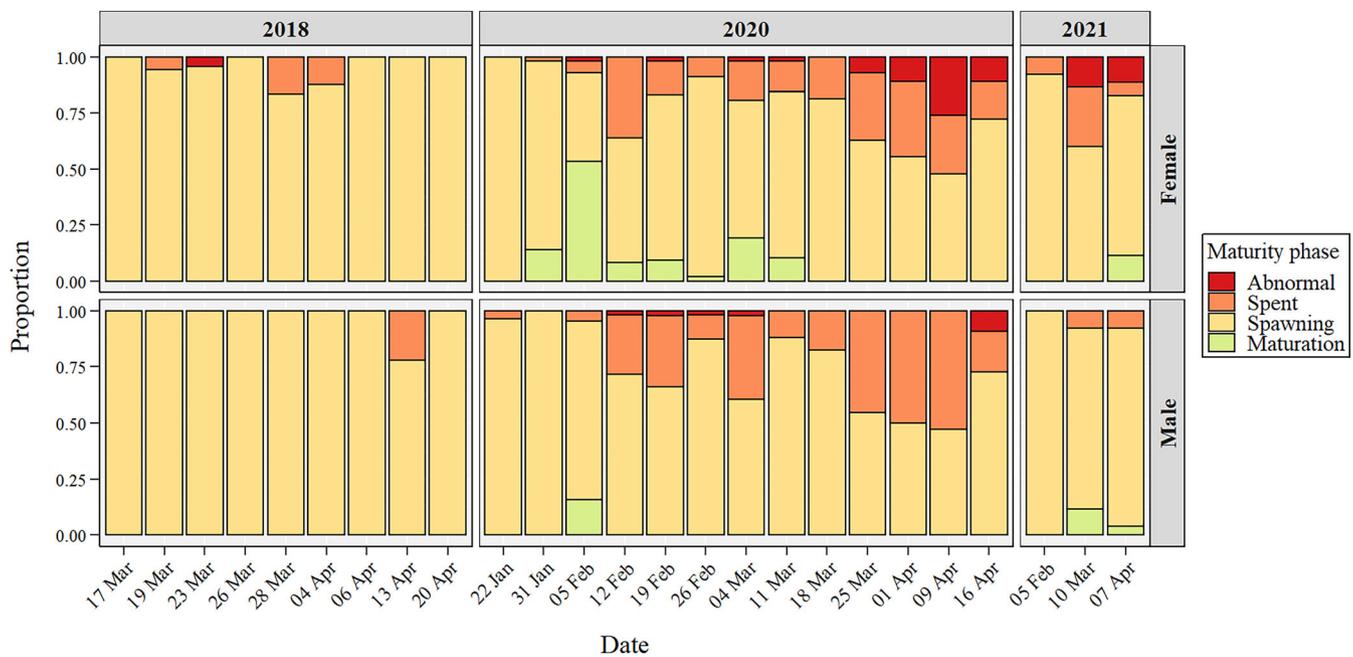
FIGURE 7 Proportion of the different maturity phases (maturation, spawning, spent, and abnormal) of male and female adult *Clupea harengus* captured within the Kiel Fjord at different dates during the spawning season in 2018, 2020, and 2021.

4 | DISCUSSION

The results of the GLM models revealed that seawater temperature was the main environmental parameter examined that was related to the time of herring mean arrival time (50% of the yearly total fishing catches; Q_{50}) in the Kiel Fjord. The strength of the relationship was relatively high as it explained about 50% of the variability in the response variable. Lambert ([1987](#)) also found that seawater temperature explained ∼60% of the variability in the arrival time of *C. harengus* to spawn in the Gulf of St. Lawrence. The parameters of our regression analysis predicted that the fish arrived at their spawning ground about 1 week earlier for one degree the January seawater temperature at low depth (8 m) increased (Figure [4](#)). An early arrival of Baltic spring-spawners (BSS) herring at their spawning ground in relation to warmer seawater temperature has also been documented in other areas of the Baltic Sea. For example, in the Gulf of Riga, herring started to spawn up to 6 weeks earlier after warm than cold winters (Arula et al., [2019](#)). In the western Baltic Sea, *C. harengus* larvae hatching peak was ∼2.5 weeks earlier during the recent decade of 2007–2017 compared to the overall colder period of 1992–1996 (Polte et al., [2021](#)). Such results indicate that the seawater temperature is a good predictor of *C. harengus* spawning time.

We found here that the relationship between seawater temperature and herring mean arrival time (Q_{50}) in the Kiel Fjord was first significant at the end of December (52nd week of the year) and was among the highest in the 4th week of the year, that is, 8 weeks before the mean Q_{50} over all the years (Figure [2](#)). Another study on spring-spawning herring from the North Atlantic found that the timing of *C. harengus* spawning was influenced by the sea temperature up to 5 months before spawning started (Winters & Wheeler, [1996](#)). Such

an early signal of seawater temperature on the timing of herring spawning suggests that water temperature influences the maturation of the fish, which extends over several months in *C. harengus* (Bucholtz et al., [2013](#); Klinkhardt, [1996](#)). Indeed, field observations estimated that the final maturation process and timing of spawning northeast Atlantic *C. harengus* spring-spawners were related to January seawater temperatures prior to spawning (Winters & Wheeler, [1996](#)). The relationship between early spawning and high temperature conditions during the fish maturation phase has also been documented in Norwegian spring-spawning herring (Husebø et al., [2009](#)). Ware and Tanasichuk ([1989](#)) also related faster gonadal development rate and earlier date of full maturity in the closely related Pacific herring, *Clupea pallasi*, to the mean sea surface temperature.

Here we found that the trend of the thermal time to Q_{50} with the years was constant (∼316 DD) when the onset of temperature-dependent gonadal maturation was on the 341st day of the year (week 49; mid-December) or later. This result indicates that ∼316 DD can be thought of as a thermal constant for fish arrival time, meaning that although the day of arrival varies from year to year, the thermal time to arrival is constant. The time of the year over the temperature integration corresponds to the vitellogenesis stage of female spring-spawning herring gonadal maturation (Bucholtz et al., [2013](#); Ma et al., [1998](#)), when the mean oocytes size (∼650 μm) has already grown about three-fourths of its size at spawning (Klinkhardt, [1996](#)). This result highlights the effects of seawater temperature on the growth of the gametes during the latest phases of gametogenesis, as also found in other fish species (Alix et al., [2020](#); Kjesbu et al., [2010](#); Tveiten et al., [2001](#); Zucchetta et al., [2012](#)). Additionally, the time of the year when the thermal time to Q_{50} was constant (week 49) was

consistent with the time of the year when we found that water temperature and Q_{50} were first positively correlated (week 52; see above). The aggregated thermal metric is therefore a valuable tool to predict the mean time of arrival of the fish at their spawning ground (see also Neuheimer & MacKenzie, 2014; Neuheimer & Taggart, 2007).

It is unclear whether herring spend most of their maturation phase within their overwintering area in the Øresund and migrate directly into the spawning ground in the Kiel Fjord and the Kiel Canal, or migrate from their overwintering area still in an early maturity stage and then gather in the coastal waters outside of the Kiel Fjord to wait to be fully mature before entering the spawning area. Fishing data from the Greifswald Bay, one of the most important spawning areas for the WBSS herring (Nielsen et al., 2001), indicate that herring aggregate outside of the bay for some weeks before entering the bay to spawn (Polte et al., 2021), which suggests that the fish wait to be fully mature before entering their spawning ground. Local fishermen also confirmed that immature herring aggregate in the Kiel Bight, outside of the Kiel Fjord, for at least 2 weeks before entering their spawning grounds within the Kiel Fjord and the Kiel Canal (A. Kardel and B. Fischer, personal communication). Surprisingly, little is known about the WBSS herring migration from their overwintering area to their spawning ground despite the importance of that species for the local economy. Monitoring campaigns using fish tagging are needed to clarify herring spawning migration patterns and the mechanisms underlying the effects of water warming on the migration.

One of the potential consequence of herring coming early to spawn during warm years is that fish larvae may hatch when their food is not yet available in the system (e.g., match–mismatch hypothesis; reviewed by Durant et al., 2007). Larvae are fragile and need to feed readily to grow fast and survive, especially the first-feeders that had just exhausted their yolk sac. The results of this study revealed that herring came to spawn earlier as the water temperature in their spawning area was warmer, thus potentially leading to a feeding asynchrony for their offspring. Furthermore, the spawning period duration extended as water temperature increased, thus potentially mitigating the risks of food asynchrony by increasing the chances that at least part of the larvae hatch when their food is available later in the season. The WBSS herring has evolved so that the individuals of a same stock come to spawn at a different time over several months to ensure that at least some of the larvae hatch when environmental conditions are favorable (Lambert, 1990). The occurrence and the intensity of a potential food mismatch during warm years when herring come to spawn early need to be investigated to better anticipate the consequences of such changes on the WBSS herring recruitment success.

Larval survival is not only dependent on food availability but also maternal provisioning of the eggs (Bang et al., 2006; Koenigbauer & Höök, 2023). It is unknown whether the fish that come to spawn early during warm years have lower physical condition or fecundity than later spawners, which may negatively affect larvae survival. Preliminary observations in this study found that the body condition and the

gonadal somatic index (GSI) of mature non-running females with relatively similar sizes did not vary over a spawning season (Data S7). Although we acknowledge that oocyte size is required to estimate fecundity (dos Santos Schmidt et al., 2017), relatively stable GSI throughout a spawning season implies, nevertheless, that the overall fecundity of the early and late spawners does not differ substantially. Another study found that a higher fecundity of the closely related Pacific herring (*C. pallasi*) was best related to warmer mean sea temperature (Tanasichuk & Ware, 1987), suggesting that the potential negative effects of an early arrival may be reduced by increased fecundity of early spawners. On the contrary, Arula et al. (2016) found a lower herring larval survival during warm years due to the low condition of the fish. The comparison of factors influencing the reproductive success (e.g., age, physical condition, and fecundity) of early and late spawning fish warrants to be tested between years with contrasted water temperature.

A recent study conducted in the Greifswald Bay (western Baltic Sea) suggested that herring spawning is onset by a specific water temperature threshold that ranges between 3.5 and 4.5°C (Polte et al., 2021). The sea temperature upon herring mean arrival time (Q_{50}) in the Kiel Fjord varied from 1.6 to 5.5°C over the 50 years of this study, and for more than half of these years, the lower limit of the temperature threshold (3.5°C) was not reached before the fish had arrived in the fjord (Data S8). The 3-year analysis of the maturity stages of herring captured in this study also revealed that the fish had already spawned, were currently spawning, or would have started to spawn within few days, meaning that the fish spawned readily upon entering their spawning ground. Another study in 2000 also found that 78% of the fish captured at the same location within the Kiel Fjord and by the same fisher, as in this study, were spawning upon arrival (Haslob, 2000), thereby providing further evidences that fish enter their spawning ground only when ready to spawn. Our results do not support the assumption that the start of herring spawning is conditioned by a narrow temperature threshold, but rather by temperature that positively influences the speed of gonadal maturation during the latest phases of gametogenesis that leads to an early time of arrival of the fish under warm conditions.

5 | CONCLUSION AND OUTLOOK

Here we used the prior knowledge of spring-spawning herring arrival time at their spawning ground each year between 1971 and 2020 to examine the relationship between the arrival time and weekly mean seawater temperature from October to February before the arrival. The results of this study revealed that the time of fish arrival (and spawning) of spring-spawning herring in the Kiel Fjord was related to the winter water temperature during the latest phase of gamete maturation. Such a delay suggested that water temperature influenced herring gonadal maturation, which lasts for several months in *C. harengus* and many other fish species, and is probably accelerated under warm conditions. The fish enter the spawning ground when they have reached the thermal constant that signifies that they are mature and

ready to spawn, independent of the water temperature at the time of arrival.

This study also highlights the various gaps in the knowledge of the western Baltic Sea herring ecology, as also pointed out by Moyano et al. (2023). For example, little is known about the migration pathways and timing of such an ecologically and commercially important fish species as *C. harengus* in the western Baltic Sea, of which stocks have been overexploited for many decades and are at historically low levels. Monitoring the fish using telemetry tagging methods should be valuable to better understand the fish spawning migration patterns and their changes due to seawater temperature warming.

Further similar collaborative studies with local fisher as used in this study would be useful to conduct at the feeding, overwintering, and spawning areas of the fish to follow the changes in fish maturation stages throughout spawning seasons over the years. Also, the effects of water warming on the factors influencing the reproductive success of the fish (e.g., age structure, fecundity, and body condition) should be examined to better predict fish recruitment. Genetic changes in the fish throughout the spawning seasons are also needed to determine the selective forces in response to water warming, especially in the Baltic Sea where fast global changes are suspected to presage that of other coastal ocean changes (Reusch et al., 2018).

AUTHOR CONTRIBUTION

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CONFLICT OF INTEREST STATEMENT

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SUPPORTING INFORMATION

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