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Sudden change in long-term ocean climate fluctuations corresponds with ecosystem alterations and reduced recruitment in Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae)

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Abstract

Fish stocks vary in abundance. The causes behind the fluctuations may be difficult to determine, especially ones caused by natural fluctuations, but long-term data series may provide indications of the mechanisms. Assessments show that the recruitment to the Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) has remained low since 2004, a year which produced the last really rich year-class. Long time-series of estimated recruitment and mean winter temperature in the ocean showed a significant positive correlation for the period 1921–2004. Here, we show that this positive correlation did not continue from 2005 onwards as the winter temperature increased to high levels while herring recruitment decreased and has remained low. The density of zooplankton in the drift route of the herring larvae dropped significantly after 2004, and their centre of gravity shifted northwards. There may currently be heavy predation on the larvae by Atlanic mackerel (*Scomber scombrus*, Scombridae), and top-down regulation is suggested to hamper successful recruitment. Our analysis indicates that the presence of food and overlap with high food concentrations are likely important regulators of survival in herring larvae. The findings may be important for future management and planning of fisheries of this stock because recruitment failure may continue if temperature remains high and food abundance remains low.

KEYWORDS
herring and climate, herring biomass fluctuations, pelagic fish recruitment and climate fluctuations

1 | INTRODUCTION

The Norwegian spring-spawning (NSS) herring (*Clupea harengus*, Clupeidae) is one of the world's largest herring stocks (Hay et al., 2001). It is widely distributed and one of few small pelagic fish stocks having oceanic distribution (Hay et al., 2001) (Figure 1). The peak spawning stock biomass was estimated to be more than 16 million metric tonnes (ICES, 2015; Toresen & Østvedt, 2000). Based on long-term data for the stock, including catch statistics, the abundance at age and spawning stock biomass (SSB) from 1907 to 1997 was reconstructed (Toresen & Østvedt, 2000). The SSB displayed large long-term fluctuations, positively correlated with ocean temperature
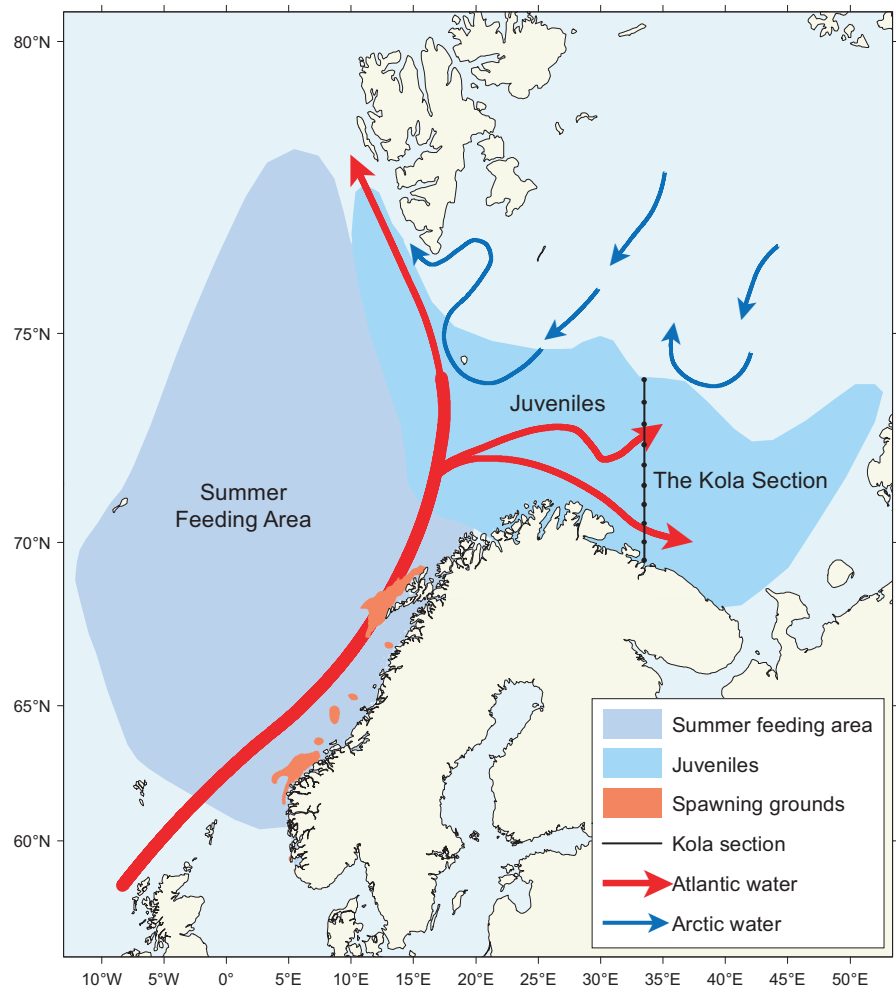
represented by the long-term annual mean temperature at the Kola section (Figure 1, Boitsov, Karsakov, & Trofimov, 2012). The positive correlation suggested that the long-term fluctuations of this stock were influenced by factors related to ocean temperature fluctuations, either directly or indirectly (Toresen & Østvedt, 2000).

The NSS herring spawns along the west coast of Norway in spring (Figure 1). The larvae feed on zooplankton, mainly copepods (Bjørke, Fossum, & Sætre, 1986), and they are dependent on finding sufficient quantities of the right composition and size of plankton to initiate growth (Bjørke et al., 1986; Dalpadado, Ellertsen, Melle, & Dommasnes, 2000; Fossum, 1988, 1996; Sætre, Toresen & Anker-Nilsen, 2002). The larvae drift northwards along the coast and metamorphose in June–July off the northwest coast of Norway (Bjørke et al., 1986; Sætre et al., 2002). The level of recruitment is to a large degree determined when the larvae reach the stage of metamorphosis, which occurs after they have drifted northwards from their spawning grounds and past the Lofoten Islands in Northern Norway (Barros, 1995; Dragesund, 1970; Sætre et al., 2002; Toresen & Østvedt, 2000). However, recruitment to the spawning stock is further adjusted due to predation of their early stages when the larvae enter the Barents Sea (Barros, 1995).

In general, important drivers for fish stock dynamics are recruitment and the fishery. The collapse of the NSS herring stock which

FIGURE 1 Distribution area of Norwegian spring-spawning herring in the Northeast Atlantic region [Colour figure can be viewed at wileyonlinelibrary.com]

started in the late 1960s was driven by the heavy fishery at the time, both on immature herring and on adults. This fishery reduced the incoming year-classes significantly and led to a collapse of the stock in the 1970s. The goal of the management at the time was to re-build the spawning stock as soon as possible to a level above the Minimum Biological Acceptable Level (MBAL) of 2.5 million tonnes. The fishery was therefore strictly regulated with a minimum landing size of 25 cm (from 1977 on) and the lowest possible catch of adult herring through the years 1976–1980 (Toresen & Jakobsson, 2001). The spawning stock increased further, and fishing mortality on ages 5–11 years varied between 0.03 (1990) and 0.25 (2000). The aver-age fishing mortality for the age groups 5–11 years for the period 1988–2015 was 0.14. For younger herring, the fishing mortality has been nearly negligible because of the minimum landing size regula-tion of 25 cm (ICES, 2016; Toresen & Jakobsson, 2001).

The other important driver for the dynamics of this herring stock, recruitment, as represented by the abundance of the 0-group (fish younger than 1 year), was found to correlate positively and signifi-cantly to the mean winter temperature (January–April) at the Kola section for the period 1921–1997 (Toresen & Østvedt, 2000). This is the winter temperature in the same year as the larvae are born, in March–April. It indicates that either the temperature has a direct effect on the survival of the larvae or the temperature has an indirect effect on other parameters which influence the survival of the larvae.

Despite an above average status of the spawning stock biomass, the recruitment to the NSS herring has remained low since 2004, the year which produced a very good year-class (ICES, 2016). The reason for poor recruitment to this herring stock has been addressed (Holst & Røttingen, 1994; Husebø et al., 2009; Skagseth, Slotte, Stenevik, & Nash, 2015; Skaret, Bachiller, Langøy, & Stenevik, 2013; Vikebø, Korosov, Stenevik, Husebø, & Slotte, 2012), but it has been challeng-ing to find clear answers on the mechanisms for recruitment vari-ability and why there are long periods with poor recruitment even if the spawning stock biomass is found to be well above average levels. For most fish stocks, and especially for herring, there is a huge lar-val mortality each year (Bailey & Houde, 1989; Barros, 1995). Rich year-classes occur when this mortality for some reason is reduced. It is important to note that mortality is expressed by an exponentially decaying function of number of survivors, where small changes in the exponential mortality coefficient are translated into large varia-tion in the small fraction of surviving recruits (Houde, 2008; Skjoldal & Melle, 1989). In all years, most larvae suffer predation mortality, and there is a strong interaction between low growth rate and high cumulative mortality (Beverton & Holt, 1957; Ottersen & Loeng, 2000; Skjoldal & Melle, 1989). The crucial point is to find the factors which cause the larvae to have a higher chance of survival, thus pro-ducing years with good recruitment. Early larval growth is believed to be one of those reasons (Bjørke et al., 1986; Fossum, 1988, 1996).

In this paper, we examine the data to shed light on possible rea-sons for the lack of rich year-classes of the NSS herring since 2005.

- We extend the time series of the stock size of NSS herring by Toresen and Østvedt (2000).

- We present the time series of recruitment per unit of spawning stock biomass (SSB) to show the development of relative recruit-ment success.
- We examine the time series of temperature to determine whether there is still a positive relation with the NSS herring SSB and the recruitment.
- We present the composition and abundance of zooplankton in the core areas of NSS herring larvae drift routes as well as the latitudi-nal larvae distributions.

We also ask the following questions:

- Have the abundance, geographical distribution, or size/species composition of zooplankton in the areas where newly hatched herring larvae drift changed?
- Are there indications of changes in the ecosystem in terms of the onset of the spring bloom which could affect the survival of her-ring larvae?
- Are there indications that the geographical distribution of herring larvae has changed and has influenced recruitment success?

2 | MATERIAL AND METHODS

2.1 | Long-term virtual population analysis

Toresen and Østvedt (2000) made a long-term (1907–1998) virtual population analysis (VPA) for the Norwegian spring-spawning her-ring. They described the long-term fluctuations of the stock with an estimated peak of abundance of some 16 million tonnes spawning stock biomass in 1945. The stock collapsed in late 1960s and 1970s due to a very high exploitation, both on young herring and on adult herring (Toresen & Jakobsson, 2001; Toresen & Østvedt, 2000). Since late 1970 and in the following decades, the stock recovered and the fishery have been strictly regulated with an international agreed harvest control rule and minimum landing size regulations. It was found that the long-term fluctuations of the stock were not driven by the fishery because it was only in the period 1965–1975s that the fishing mortality reached high values ($F > 0.5$).

The present population analysis is an update of what was done by Toresen and Østvedt (2000) and is a back-calculation of the size of the herring stock, cohort by cohort. The input data are the num-ber of fish by age in the catch each year (1907–2016). These are the number of fish of each cohort which we estimate to have been in the sea.

2.1.1 | Calculation of stock size

The starting point for the part of the VPA covering the period 1907–1950 was the stock numbers by age in 1950 as estimated by ICES (1999). The number of fish at age 10 (which is chosen as a reference age) was calculated based on the catch in numbers at this age per year applying the following equation:

$$N_t = \frac{C_t}{(1 - e^{-Z_t})} \left(\frac{F_t + M}{F_t} \right)$$

where C_t is the catch during the year t and F and M are estimated or assumed values of fishing mortality and natural mortality.

The age group 10 was chosen as a reference age because this is the age at which the relative strength of the cohort is representative. The herring is fully recruited to the spawning stock by the age of 10 years (ICES, 2016). The F at the reference age for the years 1907–1928 was derived from Lea (1930). He estimated an overall average survival rate of 0.81 for adult NSSH. However, in his paper, the survival rate is given as a mean proportion surviving each year. Recalculating to instantaneous rates, the total mortality is 0.21, and assuming a natural mortality equal to the level in recent years of 0.15, the average fishing mortality of adult herring is estimated to 0.06 for the period 1907–1928. A fishing mortality of 0.0375 for reference age (10-year-olds) in the years 1929–1949 is taken from the estimated fishing mortality at this age for the years 1950 and 1951 (ICES, 1999). In these years, the spawning stock biomass was estimated by ICES (1999) at more than 12 million tonnes, and it is assumed that this level of fishing mortality applies to this age group for the period in which the stock probably was at its highest abundance.

From this starting point, the stock size (number of fish at age) was derived by applying Pope's approximation for calculating N_t (Hillborn & Walters, 1992; Pope, 1972):

$$N_t = N_{t+1} e^M + C_t e^{\frac{M}{2}}$$

where N_t is number in the year t, M is natural mortality, and C_t is catch in the year t.

Fishing mortality was calculated as

$$F = -\ln\left(\frac{N_t}{N_0}\right) - M$$

Pope's approximation assumes that all the catch takes place in the middle of the year. But this is not the case as fishing occurs during various periods and often more or less continuously throughout the year. However, it is shown that if total mortality (Z) is small, the approximation is good (Hillborn & Walters, 1992), and even if Z is large, the discrepancy between the method based on the assumption of continuous fishing and the approximation is <10%.

The number of fish in the cohort as 9-year-olds was calculated based on the catch and adjusting positively for the natural mortality. The number of fish as 11-year-olds was, on the other hand, calculated from the number of 10-year-olds by withdrawing the catch as 10-year-olds and adjusting negatively for natural mortality.

For the period 1950–2016, the input data in the VPA are the most recent estimate of stock size (2016), the time series of the estimated numbers in the oldest age group (13) in the ICES assessments (ICES, 1999, 2016), and catch by numbers at age. The calculations of numbers at age are otherwise done in the same way as for the earlier period.

2.1.2 | Calculation of spawning stock biomass

The SSB was calculated as the product of the number at age, the proportion mature at that age and the weight at age. The resulting biomass for each age group is then summed over the entire range of ages.

The proportion mature at age is a function of the growth rate of the cohort. Because observations on maturation at age are sparse for the years prior to 1950, the average proportion of maturation for each age group for the years 1950–1965 was used for the period 1907–1949. For the period 1950–2016, the input data are the same as used in the ICES assessments (ICES, 1999, 2016).

The weight at age for the period prior to 1950 was calculated in the same way as the proportion mature for each age group. For some years (1935–1941 and 1948), data were available on weight at age in the spawning stock, and these observed weights were used for the years in which they were observed.

A part of the long-term population analysis is the estimation of recruits and SSB. In this context, it is important to make a special note on the development of the recruitment success of this stock, represented by number of recruits as 2-year-olds per unit of SSB. The average recruitment success, r/SSB, is the back-calculated number of 2-year-olds divided by tonnes of spawning stock biomass each year. Data for the year-classes 2011–2013 are taken from ICES (2016).

2.2 | Stock size in relation to ocean climate

The water temperature in the Kola section is an indication of the temperature regime in the water masses where the herring larvae live their first months. The annual average for 0–200 m from 1900 to 2016 (Bochov, 1982; Boitsov et al., 2012) was used. The average is calculated as average of temperatures at standard depths between 0 and 200 m. Station number 3–7 at the Kola section represents the standard series being used. Data have been provided by PINRO, Murmansk, Russia. The average values for the months January–April for the years 1921–2015 were provided by the Institute of Marine Research, Bergen, Norway.

The annual values were smoothed using the moving average.

$$Sm(x_t) = \frac{1}{2q + 1} \sum_{r=-q}^{+q} x_{t+r}$$

Two smoothed series of the temperatures in the Kola section were made. One series smoothed over 19 years ($q = 9$), and the other of the average temperature in winter (January–April) smoothed over 5 years ($q = 2$). The first series was related to the long-term fluctuations in the SSB. The annual long-term average temperature reflects the general oceanographic climate variability the herring stock experiences, while the winter temperature series, which is related to recruitment as 0-group fish, reflects the oceanographic conditions the herring larvae encounter drifting to nursery areas in the Barents Sea.

2.3 | Plankton and herring larvae

The Institute of Marine Research (IMR) carries out research vessel surveys along the drift route of the newly hatched herring larvae each year in April (Stenevik, Nash, Vikebø, Fossum, & Bakkeplass, 2012). The aim of these surveys is to map the distribution of the herring larvae and estimate their abundance. During the surveys, plankton is also sampled regularly. Herring larvae were sampled by a T-80 net during nighttime and a Gulf-III during daytime. Since 1992, two sampling gears have been used in each annual survey. An encased Gulf III (nose – cone diameter 20 cm, mesh size of 375 μm, towed at five knots) has been used during daytime in a double oblique haul between 75 m and the surface. A ring net (T-80, 80 cm diameter with 375 μm net) has been used during nighttime towed vertically from 150 m to surface (Stenevik et al., 2012).

The zooplankton data used in this analysis were sampled annually during the IMR herring larvae surveys. A standard sampling procedure with the same sampling gear has been used from 1993 to 2015. In this study, for the investigation of changes in zooplankton biomass and shift in geographical distribution of the zooplankton we have used all samples from stations shallower than 200 m depth, that is, limited to the Norwegian shelf. This limitation was chosen because there was a shift in the depth of the sampling of plankton in 2005, as 200 m was chosen as maximum depth for sampling after this year. We only apply stations shallower than 200 m to be able to compare data over the full period. The zooplankton material was analysed applying standard procedures for species and copepodite stage determination (Conway, 2012; Newell & Newell, 1963; Sars, 1903). The number of stations per year varied between 20 and 40. A few years had stations <20 (2007, 2011, 2015). In 2003, no stations were taken because of bad weather. In 1996, 42 stations were sampled.

Zooplankton is sampled by vertical hauls with a 180 μm WP2 net (opening 0.25 m², speed 0.5 m/s). The sample is divided in the laboratory on board using a modified Folsom-splitter; one part is preserved with formalin for later taxonomic analysis and the other part is used for determination of dry weight biomass in three size fractions (see Melle, Ellertsen, & Skjoldal, 2004, Skjoldal et al., 2013).

Since in situ measurements of zooplankton are not fixed between years, and some years have few or none in the northern parts of the domain considered, we quantified annual average zooplankton biomass and centre of gravity in the following steps. First, we divided all observations into three subdomains: 61°–64°, 64°–67° and 67°–70°N. Those years that did not have observations in all three subdomains were not included in the analysis as they would cause biases when quantifying the centre of gravity. We quantified mean zooplankton biomass and biomass-weighted centre of gravity within subdomains and thereafter the corresponding annual means and centre of gravity by averaging across the mean for each subdomain.

The centre of gravity of zooplankton, in terms of latitude, was calculated by multiplying the density of zooplankton for three fractions (1—<1,000 μm, 2—between 1000 and 2000 μm and 3—total)

with the latitude of each station. The densities were multiplied by latitude, to obtain the biomass-weighted mean latitude each year.

For the investigation of changes in species and size composition of zooplankton stations where herring larvae were used and the following sampling procedure was done: In each of ten randomly chosen years (5 years before and 5 years after 2005), ten samples were chosen. The subsampling was done because of limited capacity at the IMR laboratory to analyse samples.

The centre of gravity (in terms of latitude) of herring larvae was estimated in a similar manner, by weighting the latitude of each station with herring larvae abundance (number of herring larvae per m²). The sums of the weighted stations were divided by the total sum of larvae per square meter each year. The result is a latitude value each year indicating the centre of gravity in the north–south dimension of the herring larvae. This value is correlated with the strength of each year class as 2-year-olds estimated by the ICES assessment working group for Norwegian spring-spawning herring (ICES, 2016).

2.4 | Onset of spring bloom

The onset of spring bloom may affect or trigger the copepod egg production or the shift of copepod stages, and the onset of spring bloom may then affect the match between available food and the hatching and development/survival of the herring larvae. Remotely sensed SeaWIFS and MODIS Chl-a were used to estimate the onset of spring phytoplankton bloom along the larval drift routes, as described in Vikebø et al. (2012) (only SeaWIFS) and Vikebø et al. (unpublished data) (both SeaWIFS and MODIS). Eight-day composites of 9 × 9 km horizontally resolved remotely sensed Chl-a data were collected in 1.5 degree latitudinal bins (61.5°–64.5°N) distinguishing between shelf waters shallower than 300 m and deeper waters between 300 and 500 m depth. Whenever the average bin value rises above 0.85 mg Chl-a m^{-3} (the median of Chl-a values in the area and shallower than 300 m for the combined SeaWIFS and MODIS across 1998–2017) for two subsequent composites, the spring bloom is considered as having started.

3 | RESULTS

3.1 | Long-term relationship between herring and ocean temperature

The long-term time series of spawning stock biomass and ocean temperature presented by Toresen and Østvedt (2000) were updated to cover the period 1907–2015 (Figure 2). The spawning stock biomass after 2000 varied between 5 and 8 million tonnes. Even though the fisheries have been managed well, with a limited fishing mortality keeping *F* well below 0.2, a rich year-class has not been produced since 2004 (ICES, 2016). The positive correlation between ocean temperature and spawning stock biomass that prevailed until around 2000 failed, and in recent years, the relationship has become negative.
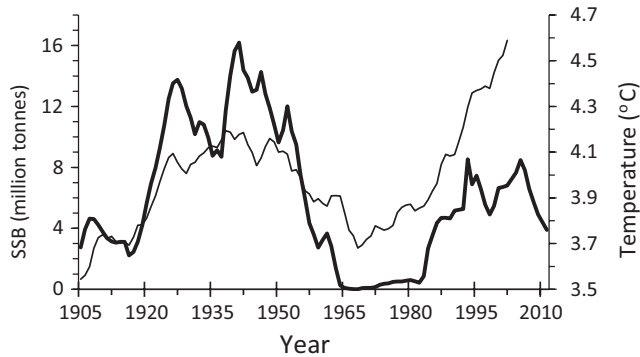
FIGURE 2 Fluctuations of spawning stock biomass (SSB) of Norwegian spring-spawning herring (thick line) and mean annual temperature (thin line) (moving average over 19 years, the time series for the Kola section is shorter because it is moving average values) at the Kola section (Bochov, 1982; Boitsov et al., 2012), 1907–2013

Toresen and Østvedt (2000) found a positive relationship between mean winter temperature (January–April) and herring recruitment. The updated time series showed that the positive relationship continued until 2004 (Figure 3). Since then, the temperature has increased to levels higher than previously observed, while recruitment dropped to low levels and has remained low, except for the 2013 year-class which seems to be somewhat stronger but still below average (ICES, 2016).

Recruitment as 2-year-olds per unit of SSB for the period 1984–2013 is presented in Figure 4. The 1983 year-class was very strong compared to the size of the spawning stock biomass at that time. In the following period, from 1984 to 2005, the recruitment per unit of SSB varied between 0.7 and 14.9 thousand per tonne. After 2005, the number was <2.0 for all years, except for the 2013 year-class which was 3.8 thousand per tonne. This indicates reduced recruitment success after 2005.
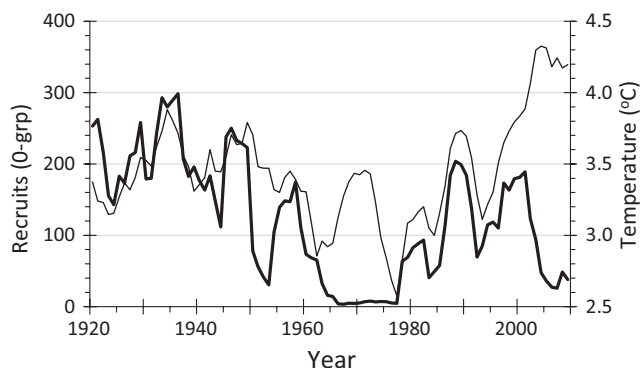

FIGURE 3 Time series of number of recruits (0-group) (thick line) and winter temperature (January–April) (thin line) (both series, moving average over 5 years) (°C) at the Kola section (Bochkov (1982). Test statistics: Recruits–Kola winter (1978–2004) R^2 = 0.60, Recruits–Kola winter (1978–2002) (smoothed, 5 years) R^2 = 0.95

3.2 | Biomass and composition of zooplankton in the drift route of the herring larvae

In the period 1993–2015, the biomass of zooplankton (g dry weight m^{-2}) changed. For all three size fractions (<1, 1–2, >2 mm; screen size), the average biomass dropped to a lower level after 2003. The average biomass for the small zooplankton fraction was 2.4 g/m^2 before 2003, while it dropped to 1.2 g/m^2 for the later period (Figure 5). The average total biomass decreased from 4.1 g/m^2 before 2003 to 2.1 g/m^2 after.

Calanus finmarchicus and *copepod nauplii* were the most abundant taxa followed by *Oithona* and *Oikopleura* (Table 1). Other abundant species were *Euphausiacea*, *Fritillaria borealis* and *Microcalanus pusillus*. The average density of the various species or groups dropped for all taxa after 2005, and the change was significant (the average of the first is outside the confidence limits of the number in the second period) for six species or groups (Table 1).

Nauplii and young copepodites of *Calanus finmarchicus* are the dominant prey in the diet of herring larvae. These forms are mainly collected in the smallest biomass size fraction, while older copepodites of *C. finmarchicus* are mainly found in the medium size fraction (Skjoldal, unpublished results). The copepodite stage composition of *C. finmarchicus* was fairly similar in the two periods, although the abundance of the youngest copepodites was higher (by a factor of about 2) in the first period prior to 2005 (Figure 6). Copepod eggs and nauplii (presumably most being of *Calanus finmarchicus* from abundance and size considerations) were also more abundant in the first compared to the last of the two periods (Figure 7).

3.3 | Shifts in horizontal distribution of zooplankton and herring larvae

The centre of gravity for the small zooplankton fraction showed a northward latitudinal shift between the two periods (8 years before and 9 years after 2003) (Figure 8). The shift in distribution of zooplankton is significant. In 2003, there were no data on zooplankton from this survey because of bad weather conditions.

The time series of the centre of gravity (COG) of the north–south component for herring larvae, and the time series of the estimated strength of recruits to the herring stock is presented in Figure 9. From the figure, there seems to be a positive correlation between the time series after 2000. This means that after 2000, year-class strength is positively associated with the latitude where the spawning takes place along the Norwegian coast.

3.4 | Onset of the spring bloom

The averaged onset of spring bloom as derived from remotely sensed data for the intervals 61.5°–63.0°N and 63.0°–64.5°N indicate no significant trends across the years 1998–2016 but there is considerable variability between years, ranging from early March until mid-April. The lack of trends in the onset of the spring bloom is
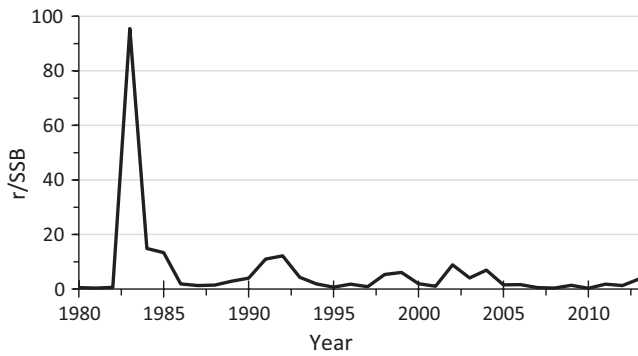
FIGURE 4 Recruitment (2-year-olds) per unit of spawning stock biomass (tonnes) of Norwegian spring-spawning herring, 1980–2013
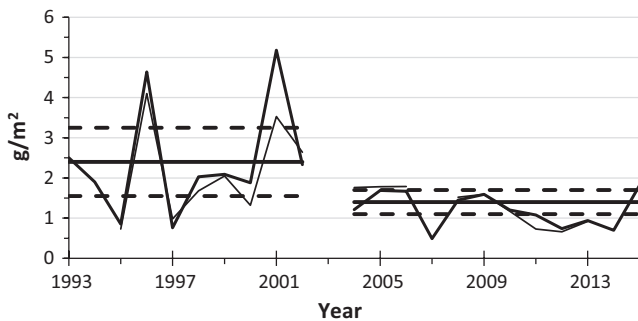

FIGURE 5 Biomass (g/m^2) of zooplankton, 1993–2015. Fraction, <1,000 μm. Average values (thick lines) and confidence limits (±1.96 × *SE*, *SE* = standard error). No data were collected in 2003. Thin lines are values adjusted for unequal area coverage in the surveys

consistent with similar stage composition of *C. finmarchicus* before and after 2005 (Figure 6).

4 | DISCUSSION

4.1 | Spawning stock, recruitment and oceanographic conditions

The Norwegian Sea and Barents Sea ecosystems are affected by climate variability and change (Drinkwater, 2011; Loeng & Drinwater, 2007), and substantial changes in both these ecosystems were observed in the early 2000s (Eriksen, Skjoldal, Gjøsæter, & Primicerio, 2017; Fossheim et al., 2015). The updates of the long time-series for Norwegian spring-spawning herring demonstrate a radical shift in the relationship between temperature and development of the herring stock in response to warming as part of the on-going climate fluctuations and possible changes.

Toresen and Østvedt (2000) documented a positive correlation between the time series of the spawning stock biomass of Norwegian spring-spawning herring and the mean annual temperature in the Kola section for the period 1907–2000. We demonstrate here that the positive relationship ceased sometime in the period

2000–2005. From 2005, the temperature increases to higher values than previously seen, for example during the warm 1930s (Toresen & Østvedt, 2000), while the spawning stock biomass levels off and subsequently decreases (Figure 2). A major reason for this shift is the lack of good herring recruitment after the relatively rich 2004 year-class, which recruited to the adult stock in the years 2008–2010 and caused the recent maximum in stock level in 2012 (ICES, 2016). Because of limited recruitment, the stock has levelled off and decreased in abundance thereafter.

The limited recruitment after 2004 is shown as a marked change also in the relationship between winter temperature in the Kola section and estimated recruitment as 0-group herring (Figure 3), and further by the drop in recruitment success (Figure 4) after 2005. There was a significant positive correlation between temperature and 0-group herring from 1921 to 1997 (Toresen & Østvedt, 2000), except for the collapse period in the 1970s when the stock did not produce recruits. The exact reason for the change of this relationship is not clear. Can the survival of herring larvae be due to a direct effect of temperature, or is temperature a proxy for other environmental factors affecting the survival success of the herring larvae? Somarakis and Nikolioudakis (2007) showed that temperature had a direct effect on the mortality of anchovy larvae, and according to Somarakis, Tsoukali, Giannoulaki, Schismenou, and Nikolioudakis (2018), temperature can affect all processes that determine growth rates. For example, the weight specific growth rate for larval Atlantic herring varies approximately 10-fold over 6–17°C (Houde, 1989). In a recent review by Peck, Reglero, Takahashi, and Catalán (2013), it was revealed that thermal niches (optimal and suboptimal ranges in temperatures) were species- and stage-specific for anchovies and sardines in non-upwelling systems and they argued that gaining a cause and effect understanding of climate-driven changes in small pelagic fish would require detailed information on the ecophysiology of the different species.

4.2 | Zooplankton and herring recruitment

The zooplankton biomass and abundance of zooplankton species and size groups were significantly reduced after 2005 compared to the 10-year period before 2005. The change in the density of zooplankton cannot be explained by a change in the onset of the spring bloom as data indicate that the spring bloom did not change significantly. The reduction in the density of plankton is observed for all species and stages of the plankton organisms. There was also a change in terms of centre of gravity for the plankton, as it has shifted northwards after 2005.

The copepod *Calanus finmarchicus* was the dominant species of zooplankton and contributed probably most of the recorded copepod nauplii larvae (Table 1, Figure 7). The abundance and stage composition of copepodites (dominated by early stages, but with relatively high numbers of adult females and males (around 2,000 and 1,000/m^2, respectively); see Figure 6) suggest that the breeding period was still on-going. There was no clear difference in timing of *Calanus* reproduction, as indicated by relative stage composition,

TABLE 1 Average number (n/m²) of the most important zooplankton species in 10 years, five before and five after 2005

Group of species	AV 1993–2001	AV 2006–2013	AV 2006–2013 + (1.96 × SE)
Acartia	2,505	1,502	2,081
Bryozoa cyphonautes	6,144	2,432	2,432
Calanus finmarchicus/ helgolandicus	100,991	50,456	69,948
Cirripedia	4,576	2,228	3,195
Copepoda	76,035	48,314	117,389
Echinodermata	6,272	3,405	6,483
Euphausiacea	15,776	11,676	21,565
Fritillaria borealis	15,646	4,548	8,512
Gastropoda		1,240	1,349
Metridia lucens		760	1,101
Metridia sp.	4,140	1,237	1,237
Microcalanus pusillus	14,944	13,296	20,193
Obelia		363	363
Oikopleura	35,688	506	506
Oithona	36,083	22,646	34,057
Polychaeta	2,224	1,600	1,600
Pseudocalanus	7,784	4,533	5,912

Note. AV: average; *SE*: standard error

between the two periods (prior to and after 2004). However, the lower abundance in the latter period is consistent with a marked decrease after 2003 in *Calanus finmarchicus* in the southern Norwegian Sea, both north of the Faroe Islands and at the Svinøy section close to our study area (Dupont, Bagøien, & Melle, 2017; Kristiansen, Gaard, Hátún, Jónasdóttir, & Ferreira, 2016). *Calanus finmarchicus* has also shown a pronounced decrease in the North Sea, starting earlier from the 1980s onwards (Beaugrand, Edwards, Brander, Luczak, & Ibanez, 2008; Greene et al., 2003; Papworth, Marini, & Conversi, 2016).

The northward shift in zooplankton production may be related to the warming of the ocean. There were also annual shifts in the latitudinal distribution of herring larvae. The shift in the distribution of zooplankton may have reduced the density of food particles for the

herring larvae if the shift in distribution of the herring and plankton did not match. This may have affected the herring larvae negatively, through an effect on the growth rate of the larvae. Slower growth may contribute to making the larvae more prone to increased (cumulative) predation. However, we observe that in recent years, there seems to be a positive relationship between the northward shift of herring larvae and recruitment, which means that the herring larvae from northern spawning grounds have probably had a higher chance of survival.

4.3 | Recruitment and main predators

Skaret et al. (2013) showed that Atlantic mackerel (*Scomber scombrus*, Scombridae) may be an important predator on herring larvae. In recent years, Atlantic mackerel have increased substantially
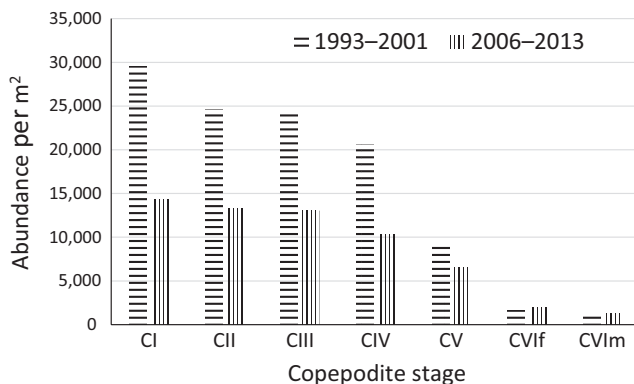

FIGURE 6 Mean copepodite stage composition of *Calanus finmarchicus* for sampling stations before (1993–2001) and after 2005 (2006–2013) shown as absolute (number of individuals per m²)
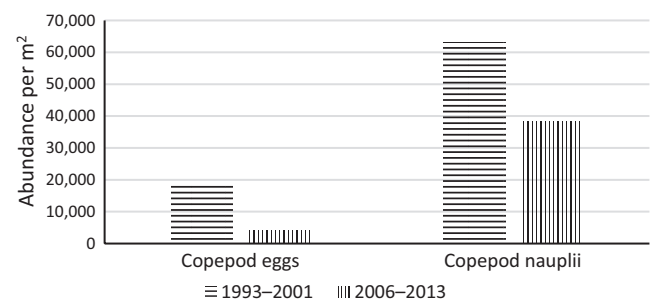

FIGURE 7 Mean abundance (numbers per m²) of copepod eggs and nauplii for the two periods, prior to (1993–2001) and after 2005 (2006–2013)
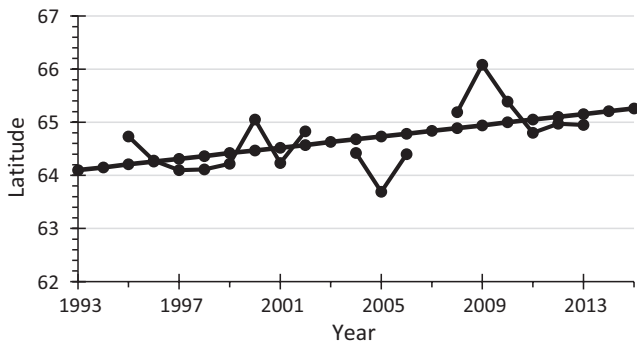
FIGURE 8 Centre of gravity of zooplankton, 1993–2015. The change of centre of gravity through the period is significant with an *R* = 0.54, and *p* < 0.05

in abundance (ICES, 2016), and the geographical distribution of mackerel has increased and overlap with the distribution of herring larvae during May and June. From diet studies (in 2013), Skaret et al. (2013) found that mackerel has a potential to feed heavily on herring larvae. They showed that mackerel preferred large larvae over smaller ones. However, it is assumed that in general, larval growth is an advantage for survival and that they avoid predators easier if they are in good condition (Ottersen & Loeng, 2000). It is important to keep in mind that as larvae grow, they pass through different predator fields and the duration in the different predator fields influences their mortality rate. The growth rate is therefore highly important for larval survival, with faster growth leading to lower overall mortality and better survival (Beverton & Holt, 1957; Somarakis et al., 2018).

The Norwegian spring-spawning herring is the only herring stock in the world with wide oceanic distribution (Hay et al., 2001). In the Northeast Atlantic, there are several smaller herring stocks distributed closer to shore, in fjords, or in shallower, sheltered and smaller oceanic areas like the North Sea. In the North Sea, the herring stocks are autumn-spawners and the larvae metamorphose in spring, the year after they are born. The factors determining the level of recruitment vary a lot and the different stocks are exposed to different oceanographic features and predators in their early phase of life.
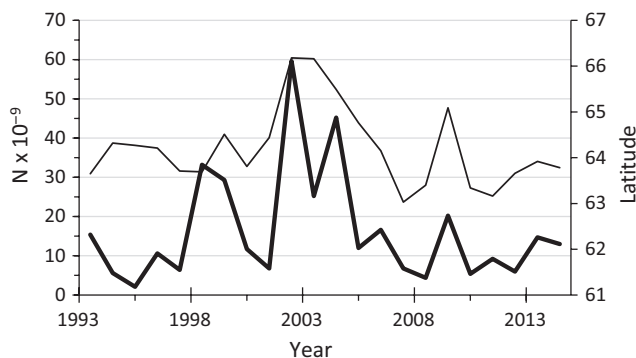

FIGURE 9 Recruitment as number of 2-year-olds and centre of gravity of herring larvae (latitude component)

5 | CONCLUSIONS

In this paper, we have compared different time series of data on the Norwegian spring-spawning stock of herring and climate expressed by temperature at the Kola section in the Barents Sea. Since 1921, there was a significant positive correlation between temperature and herring recruitment. From 2004, the herring stock has had relatively poor recruitment, and the positive correlation with temperature no longer held. There has been a clear reduction in the biomass and density of zooplankton, and a clear tendency to a more northern distribution of zooplankton, in the areas where the herring larvae drift in the early period following hatching. We have shown a positive correlation between latitudinal variation in concentrations of herring larvae and the recruitment to the Norwegian spring-spawning herring. It is probably significant for the low recruitment that there has been a substantial increase in abundance of mackerel, which could be an important predator on herring larvae. The herring larvae are prey for many organisms, and good year-classes occur when larger proportions of larvae avoid predation. Rapid larval growth is advantageous for the larvae as they grow more quickly through segments of their lives when they are exposed to given predator fields. Availability of food is therefore likely to be important for the survival of larvae. The findings in this paper support earlier results that food is important and that there needs to be a match in the overlap between food and larvae.

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