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Spatial separation of larval sprat (*Sprattus sprattus*) and sardine (*Sardina pilchardus*) related to hydrographical characteristics in the North Sea

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Abstract

Clupeid fish species are widely distributed and of highly variable stock sizes. In the North Sea, the common clupeid species are herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), but during recent decades, the generally more southerly distributed sardine (*Sardina pilchardus*) have been more frequently observed. Comparative studies of early life stages of small pelagic clupeids are scarce, and their abilities to co-exist and relations to environmental characteristics are vastly understudied. We here investigated and compared distributional patterns of co-occurring larval sprat and sardine in the North Sea, hypothesizing that they are separated into spatial niches linked to specific hydrographical characteristics. Sampling was carried out by a large ring-net during standard fish surveys (IBTS Q3) in August 2018, 2019, and 2020. Sprat larvae were found widespread across the area of investigation, with the highest concentration in the central North Sea off the eastern and northern flanks of Dogger Bank, where abundances could reach 20 larvae/m². Sardine larvae, on the other hand, showed their highest abundances in the Southern and German Bights. Distributions of the two species appeared complementary, and statistical correlations were indicative of separate hydrographical niches, where sardine larvae resided in relatively warmer and fresher water. The relative abundances of sardine versus sprat varied between years. Sardine larvae were especially abundant in 2020, twice as abundant as sprat, and observations indicate increasing importance of sardines in the North Sea.

KEYWORDS

biological dynamics, fish, larva, North Sea, oceanography, sardine, sprat

1 | INTRODUCTION

Small pelagic clupeid fishes are widespread in all oceans and contribute about 25% to the annual world fisheries (Alheit et al., 2009). In a given ecosystem, these fish often constitute relatively few species,

but make up some of the largest fish biomasses. They function as energy conveyers from the primary producers to higher trophic levels, grazing extensively on zooplankton while suffering high predation mortality (Cury et al., 2000; van Deurs et al., 2013). These fishes are often relatively short-lived and highly sensitive to environmental

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changes, leading to highly variable stock sizes and changes in distribution, and when co-occurring, different species of the small pelagic clupeid fishes may show asynchronous population dynamics (Barange et al., 2009; Lindegren et al., 2016; Tiedemann et al., 2022). However, much has yet to be unraveled regarding the mechanisms driving these asynchronous population dynamics and the life stages at which regulation takes place.

Most of what we know about co-existence of small clupeids comes from studies of systems involving sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) (Alheit et al., 2009), whereas other multi-species systems, such as those involving herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), or sprat and sardine are much less studied (e.g., Huwer, 2004; Keyl, 2017; Möllmann et al., 2004; Voss et al., 2009). Furthermore, the majority of such comparative and multi-species system studies have focused on feeding ecology and dynamic patterns in the adult stage, whereas environmental preferences during the early life phases have received much less attention (Peck et al., 2021).

In the North Sea, herring and sprat dominate, but also specimen of the generally more southerly distributed clupeids, sardine and anchovy, are frequently observed (e.g., Alheit, 1989; Alheit et al., 2012; Beare et al., 2004). The North Sea herring, which is spawning off the coasts of the United Kingdom in autumn and in the English Channel during winter, is the overall most abundant of the species, and historically, this species has been the most important to the fishery, primarily exploited for human consumption. North Sea sprat, on the other hand, is not targeted for human consumption, but mostly used for fish meal production (ICES, 2022). From a low in the 1980s, the sprat stock has increased, and in the last decade, the spawning stock has been fluctuating around 200,000 tons, with lower values of about 100,000 tons in 2021 and 2022 (ICES, 2022). Contrary to the demersal spawning of herring, sprat is a pelagic spawner and sprat eggs and larvae have been observed in a number of surveys carried out in the German and Southern Bights, as well as off the Dogger Bank (van Damme et al., 2011). Spawning takes place in an extended period from January to July, however predominantly during April–June.

While detailed information on North Sea herring larvae is available from the sampling programs of newly hatched larvae (IHLS surveys, ICES 2022) and half year-old recruiting larvae (MIK-survey in Q1, ICES 2022), only limited information is to be found on the distribution of the early life stages of North Sea sprat. Some sprat juveniles are caught during the Q1 MIK-surveys (predominantly before 1986); however, the numbers are quite low and do not allow for a description of early stage distributions across the North Sea. More localized studies on early stages of sprat have been carried out (e.g., Bartsch & Knust, 1994; Bils et al., 2012; Kanstinger & Peck, 2009), but for biophysical investigations, there is a need for information on early life stage distributions across the entire North Sea.

European sardine and anchovy have their main distribution and spawning areas south of the North Sea. Key areas for both species are the Bay of Biscay, the Portuguese coast, and the Mediterranean, and peak spawning takes place in the months May–June (Bellier

et al., 2007; Fernández-Corredor et al., 2021). In the North Sea, abundances of sardines and anchovy are generally sparse and variable. A period of enhanced abundances started around 1995 for anchovy and 2003 for sardine, peaking for both species during 2005–2009 (Alheit et al., 2012). This reappearance was observed both by catch of adult specimens during fisheries and scientific trawl surveys and from observations during eggs and larvae surveys; the latter was however limited to surveys covering the southernmost parts of the North Sea (Greve et al., 2005; Kanstinger & Peck, 2009). Specific oceanographic conditions may have played a role in these changes in the population dynamics of these warm water species in the North Sea (e.g., Beare et al. 2004), changes that might be linked to the major North Atlantic oscillations (NAO and AMO) (Alheit et al., 2012).

We here describe a comparative investigation of the population dynamics of the two taxonomically and functionally closely related species, sprat, and sardine. We investigate and compare distributional patterns of their larva in the North Sea during a sequence of years, focusing on the role of hydrographical gradients and dissimilar larval preferences in determining spatial distributions, and of potential importance to co-existence of the species. We hypothesize that the distributions of the two species are, at least partially, spatially segregated and that the segregation is linked to specific hydrographical characteristics important for their spawning and larval life. Observations for the study were obtained during IBTS, 3rd quarter surveys during the 3 years 2018, 2019, and 2020. During these surveys, significant parts of the central and southern North Sea were covered by MIK ring-net hauls, targeting larvae of fish species spawning during early summer.

2 | MATERIALS AND METHODS

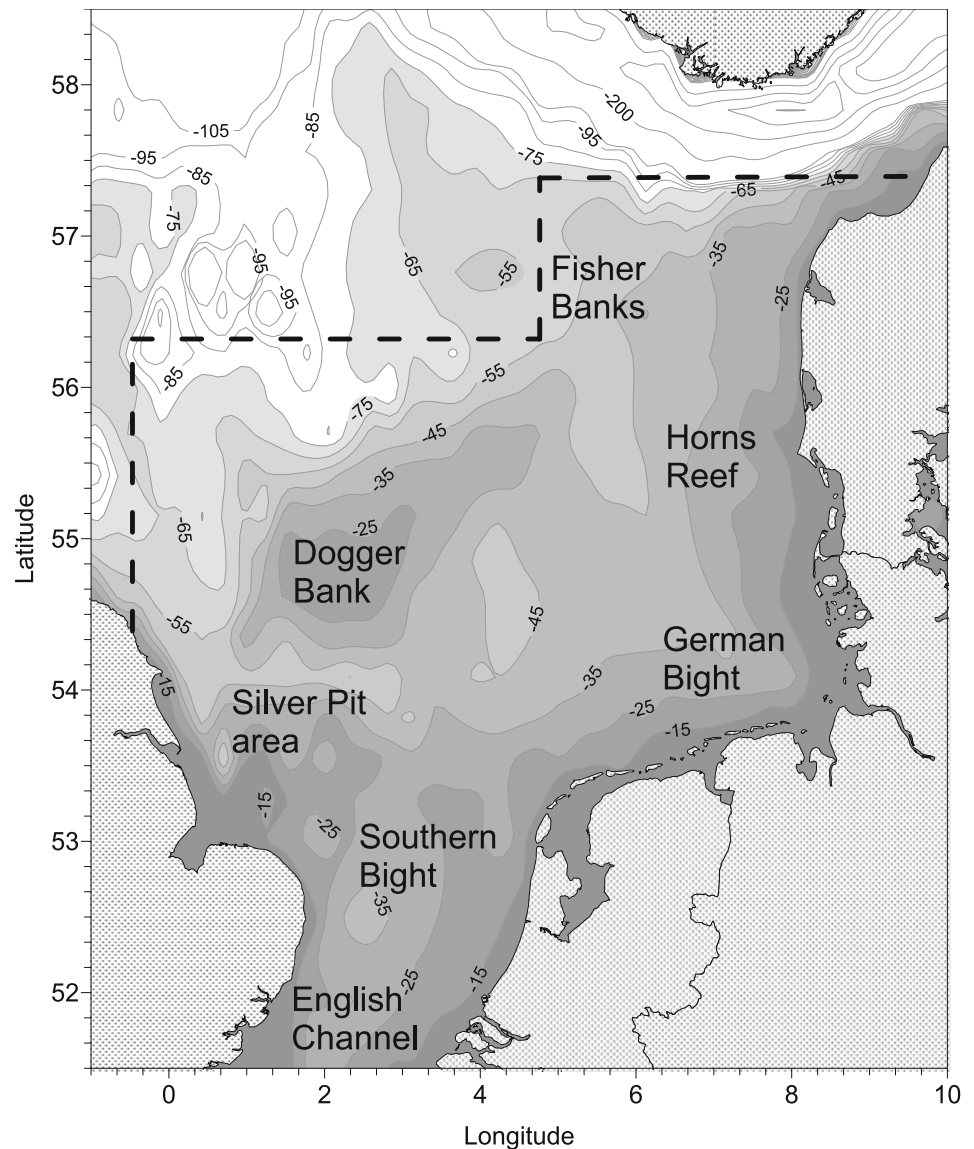
2.1 | Salinity and temperature measurements

Hydrographic information was obtained from specific CTD down casts vertically profiling from surface to 2 m above the bottom. These CTD casts have been carried out by a number of research vessels working in the North Sea and the information is available in a common database at ICES (<https://ocean.ices.dk/HydChem>). For the present study, we used all available casts carried out between July 1 to August 31 in 2018, 2019, and 2020 for the area north of 51°40'N and south of 58°50'N (Figure 1). In 2019, a Seabird SBE 25plus CTD was mounted on the ring-net, providing additional temperature and salinity information for this particular year. In total 711, 386 and 433 casts were available for 2018, 2019, and 2020, respectively.

2.2 | Gear and sampling

The area of sampling covered a large part of the central and southern North Sea, a relatively shallow area (depths <40 m) where a number of banks are identified (Figure 1). This area was surveyed between 30/7–16/8 in 2018, 30/7–14/8 in 2019, and 22/7–13/8 in 2020.

FIGURE 1 Bottom topography of the North Sea. Present survey area covers area north of $51^{\circ}40'N$ and south of hatched line.



The start- and end-positions of a given sequence of nighttime sampling were given by the last daytime trawling position visited during the preceding day and the first daytime trawl position the following day. Thus, during the period available for larvae sampling (22:00–5:00), four to five sampling stations were distributed between those positions. The larval sampling followed a standard procedure (ICES, 2017) using a so-called MIK net, a large ring net with an opening diameter of 2 m and a 13 m long net bag with a mesh size of 1.6 mm (the last 1 m before the cod end has however a smaller mesh size of 500 μm to avoid loss of larvae). The gear was towed in a v-path from surface to 5 m above bottom and subsequently back to the surface. If the haul duration had been below 10 min, the gear was again lowered when reaching the surface and the v-path was repeated. A mounted depth-sensor tracked the depth location of the ring-net at any time, and a flowmeter in the center of the net opening registered flow of water into the net. Vessel speed was three knots through water, and the wire was paid out at 25 m min^{-1} and retrieved at 15 m min^{-1} .

After the haul, the hindmost part of the net was washed into the cod-end bucket. The sample was subsequently sorted for fish larvae in the laboratory onboard the ship, and all clupeid larvae were separated from other larvae. For a limited number of samples in 2020 (28%), sorting was carried out after the cruise. Sorted samples were preserved in 96% ethanol.

2.3 | Processing of larvae

Clupeid larvae were length-measured (SL = standard length to the mm below, on ethanol preserved larvae) and identified to species in laboratories after each cruise. Due to the morphological resemblance of sprat and sardine larvae, particular care was taken during the species identification, which followed guidelines in the MIK manual (ICES, 2017). Specimens with developed pelvic fins (which appear at a size of approximately 18 to 20 mm) were identified to species by the position of the pelvic fins in relation to the pylorus (the pelvic fin is

located four to five myomeres posterior to the pylorus in sprat, while it is located directly at the pylorus in sardine). Specimens without developed pelvic fins were identified by systematic counting of the number of pre-anal myomeres in the trunk, using a stereo microscope. For samples with 50 larvae or less, all larvae were worked up. For samples with more than 50 larvae, a randomly chosen sub-sample of 50 larvae was analyzed (i.e., identified to species and length measured), and the proportion of sprat versus sardine among these 50 randomly chosen larvae was used to estimate the total number of each species in the whole sample.

The myomere counts for the species differed systematically with a slight overlap among species. The average count for both species declined at the same rate during ontogeny (Figure S1).

Larval abundance was estimated as numbers in m^{-2} , that is, numbers in catch divided by volume filtered (in m^{-3}) multiplied by water depth (m).

2.4 | Data treatment

In order to test the hypothesis that the number of larvae of a given species is related to hydrographic characteristics, we used the following linear mixed effect model (using the glmm. TMB package in R): $Y = X_1 + X_2 + X_3 + X_4 + X_5 + r(Z1) + r(Z2) + r(Z3)$, where Y is larval abundance (numbers m^{-2}), X_1 – X_5 are the explanatory variables bottom sigma-t (water density near the bottom at surface pressure with 1000 kg m^{-3} subtracted), surface temperature, bottom temperature, surface salinity, and bottom salinity. $r(Z1)$ – $r(Z3)$ are the random effects of depth, year (treated as a factor), and ICES rectangle (1 degree longitude \times 0.5 degree latitude). The latter to account for spatial autocorrelation. A negative binomial distribution structure and a log link function were used in the model to account for skewness and many zeros in the response variable. Sprat and sardine data were analyzed in

separate models. Based on recommendations in Morrissey and Ruxton (2018), all explanatory variables were kept in the models, irrespective of whether the estimated coefficients were significant (i.e., $p < 0.05$) and collinearity. It was also investigated if non-linear models (general additive models [GAM] with random effects, mgcv package in R) could reveal any significant and biological meaningful curvature. However, the GAMs produced either linear relationships similar to those produced by the models described above or wiggly curves (e.g., as the k parameter was increased), which were deemed biologically unrealistic.

All illustrated contouring of data were carried out using the “inverse distance” procedure in the program Surfer[®], for 50×50 grid cells and four search areas.

3 | RESULTS

3.1 | Hydrography

The water column across most of the studied area showed marked vertical stratification. During all years of investigation, the observed vertical stratification and the positioning of hydrographic fronts showed a range of general patterns. These are illustrated for a single offshore transect of CTD measurements in 2018, for stations within a range of ± 10 min along $56^\circ 10'N$ (Figure 2). The isotherms illustrate a thermocline in offshore areas at about 30 m depth, raising to about 12 m depth closer to the coast (Figure 2a). Salinity is relatively homogeneous in the water column in offshore areas, but outward-flowing fresher water from the coast leads to a halocline between 18 and 25 m in coastal areas (Figure 2b). The sigma-t contouring (Figure 2c) illustrates the combined effect of temperature and salinity differences, leading to both a bottom and a surface front.

We here use hydrographic measures at the bottom to characterize general horizontal variability. Both bottom temperatures and

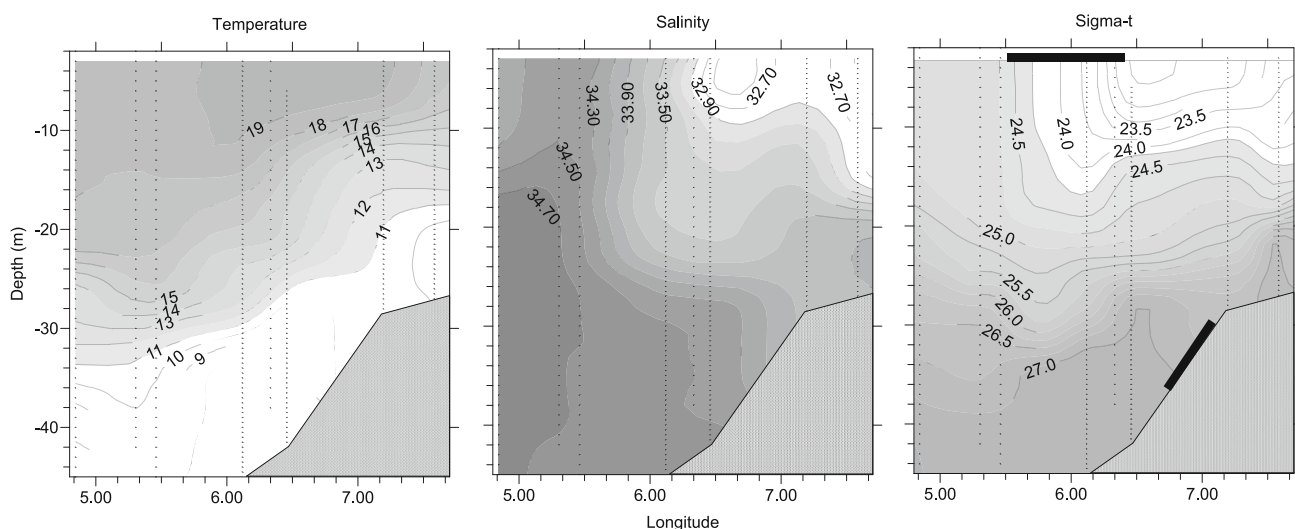
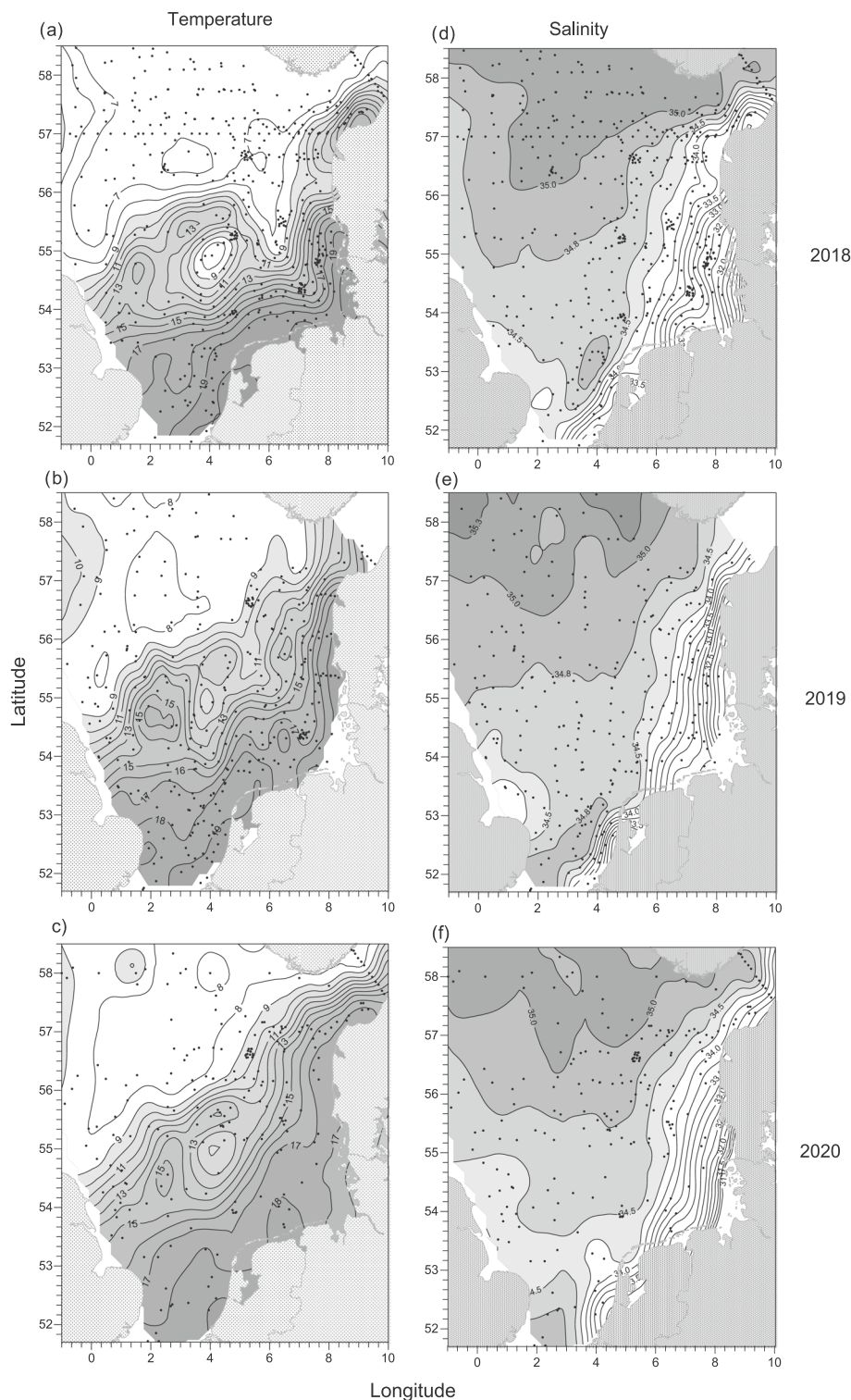


FIGURE 2 Vertical sections of hydrography off the Danish coast in 2018, along latitude $56^\circ N$. sections of (a) temperature in $^\circ C$, (b) salinity in ppm, and (c) sigma-t in kg m^{-3} . Heavy bars in (c) indicate position of surface and bottom fronts, respectively. Dots indicate vertical measurements.

FIGURE 3 Hydrographic conditions in the North Sea during August 2018, 2019, and 2020. (a–c) Bottom temperature, contours in °C. (d–f) Salinity, contours in ppm. Dots indicate positions of measurement.



salinities showed significant horizontal stratification, the strongest demarcating bottom fronts (Figure 3a–f). The observed patterns of stratification and frontal formation were quite consistent between the years. A hydrographic front predominantly based on thermal stratification is indicated west and north of Dogger Bank (Figure 3a–c), while salinity also showed strong horizontal gradients and front formation

off the coast (Figure 3d–f). Salinity patterns are strongly influenced by the freshwater outflow from rivers, predominantly the Rhine and Thames in the southwest and the Elbe in southeast. The differences in water density due to temperature and salinity variability lead to density fronts which basically follow the bathymetry contours (Figure 2c, Figure 4a–c, see also Figure 1).

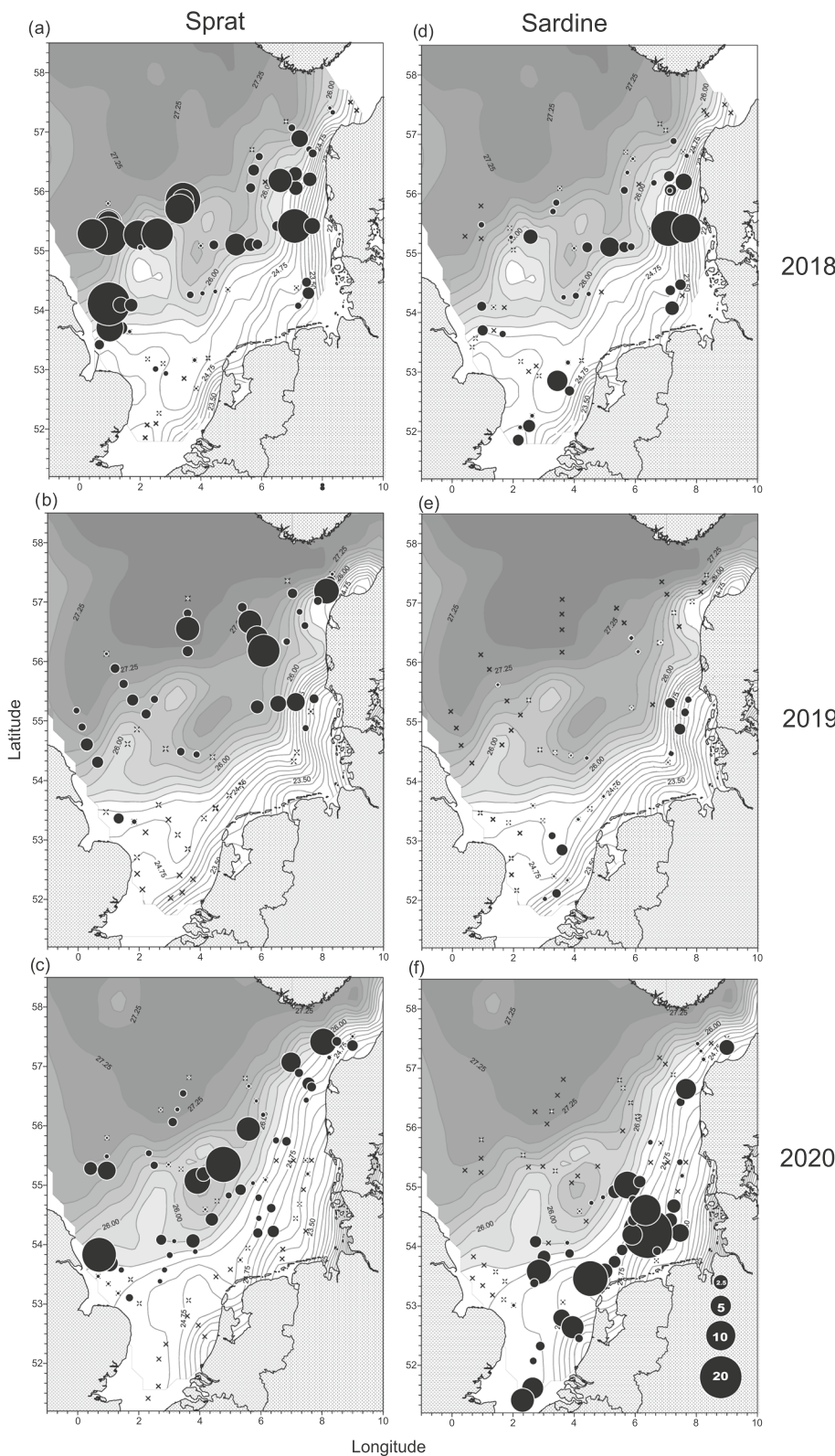


FIGURE 4 Distribution of sprat and sardine larvae during surveys in August 2018, 2019, and 2020. (a–c) Abundances of sprat larvae. (d–f) Abundances of sardine larvae. Abundance (no m^{-2}) illustrated by bubble areas as indicated for all in the legend at bottom of panel f). Crosses indicate zero catch. Imposed on map of bottom water density (as $\sigma\text{-t}$, kg m^{-3}).

3.2 | Sprat and sardine larvae

Sprat larvae were caught in large numbers, their abundance estimates at stations reaching 20 m^{-2} (Figure 4a–c). Overall distributions differed between years, but larvae showed generally higher abundances

in the northern/central parts of the investigation area, especially off Dogger Bank. In 2018 and 2019, significant concentrations were seen at the northern and western slopes of the Bank in vicinity of the apparent fronts in this area, while in 2020, the high abundances were seen at the eastern slopes. During all 3 years, sprat also showed

enhanced abundances at Horns Reef, Fisher Banks and into the Skagerrak (Figure 4a–c). Abundances declined northwards at all northern transects of sampling, indicating that these transects were close to the northern limits of larval distribution.

Sardine larvae showed their highest abundances in southern and eastern parts of the investigation area, with some differences between years of observations (Figure 4d–f). In 2018–2019, sardine larvae were mostly observed around Horns Reef and in the Southern Bight, while in 2020, additional high concentrations were sampled in the German Bight area.

Due to the mentioned constraints for carrying out sampling during surveys, the sampling intensity varied between areas and years. With these limitations, we estimate the observed average abundance of each species in given years by first averaging their abundances within ICES-rectangles and subsequently calculating an overall average abundance of these (rectangle values of zero, which are found outside distribution area, are not included). These tentative calculations indicate that sprat average abundances (given in numbers m^{-2}) during our sampling period declined from 2.7 in 2018 to 1.0 in both 2019 and 2020, while abundances of sardine larvae declined from 1.0 to 0.3 between 2018 and 2019 and increased to an average of 2.2 in 2020. Consequently, the relative proportions of species during

surveys varied between years, sardine average abundances being 36%, 26%, and 210% of sprat abundances for 2018, 2019, and 2020, respectively.

3.3 | Differences among species and relation to hydrography

Distributions of sardine and sprat larvae showed generally limited overlap. Only in the Horns Reef areas, some samples showed equal amounts of the two species; most other samples showed a distinct dominance of either sprat or sardine (Figure 5). As described above, the sprat larvae were predominantly in northwestern and offshore parts of the investigation area, while sardine dominated in the shallower southeastern part of the area. This characteristic appears linked to hydrographical features. Basically, sardine larvae were found in the fresher, warmer water off the Dutch, German, and Danish coasts. The water masses in these areas are strongly influenced by the river outflows and is bordered by the ROFI front (Souza & Simpson, 1996), approximately following the path of the 26 kg m^{-3} bottom sigma-t contour (Figure 4). Greater abundances of sprat larvae appeared linked to the offshore side of freshwater based front (mainly off the

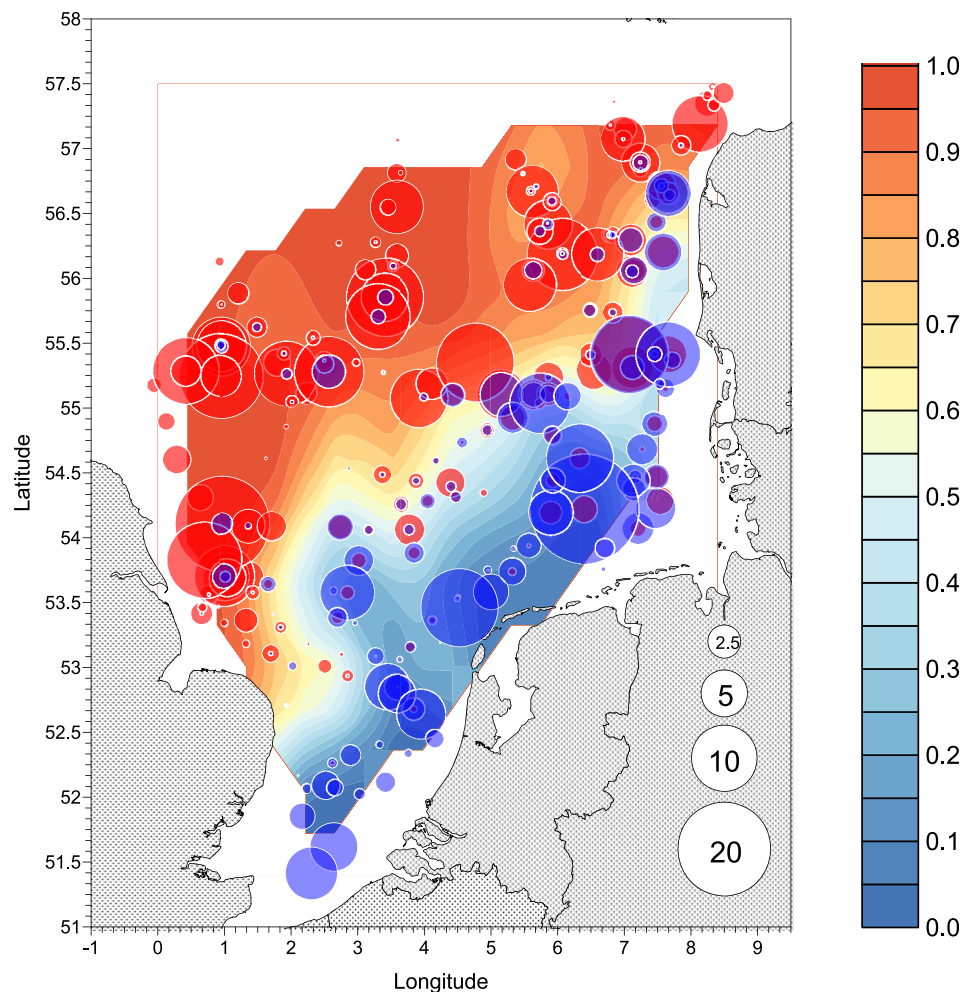


FIGURE 5 All observations from 2018 to 20. Red bubbles indicate sprat abundances, blue bubbles indicate sardine abundances (as in inserted legend, m^{-2}). Contouring illustrate proportion of sprat relative to sum of both species (as in legend bar, e.g., 0.5 = equal abundance).

Danish coast) and the tidal mixing front at the northern and eastern flanks of Dogger Bank (Figure 4).

In the analysis of the relationships between larval abundance and hydrography, the effects on sprat larvae abundance of bottom sigma-t, bottom salinity, and bottom temperature were highly significant ($p < 0.001$). Sprat larvae were abundant when bottom sigma-t and bottom temperature were high and bottom salinity low (Table 1). However, because of the high level of collinearity between bottom sigma-t and bottom salinity and between bottom sigma-t and bottom temperature (0.70 and 0.93, respectively), resulting from the fact that bottom sigma-t is derived from salinity and temperature at the bottom, interpretation of the relative relevance of the individual explanatory variable should be made with caution. Sardine larvae abundance was mainly affected by surface temperature (highly

significant) and the relationship was positive. The effects of bottom sigma-t, bottom salinity, and bottom temperature were also significant, but all with p -values in the range between 0.020 and 0.032 (Table 1). For illustration purposes, we also plotted larvae abundance against bottom sigma-t (strong driver of sprat) and surface temperature (strongest driver for sardine) together with predicted relationships from reduced models containing only these explanatory variables (Figure 6).

3.4 | Larval lengths

Across the sampling area, we observed patterns in larval mean lengths (Figure 7). The patterns showed some resemblance among the species, but they differed to some extent between years. During all years of investigation, the central-eastern North Sea (i.e., areas of Horns Reef, Jutland Reef, and Little Fisher Bank) showed clear minima in mean lengths. Although less consistent, relatively small larvae were also found near Dogger Bank, and in 2019, small larvae of both species were found in the southernmost part of the Southern Bight. (Figure 7). Generally, the stations with the smallest specimen were also stations of relatively high larval abundances. For both species, the average lengths of sampled larvae were about 16–17 mm in 2018–2019, while in 2020, they were somewhat shorter (average about 14 mm) probably due to the somewhat earlier survey period in this year (Figure S2).

TABLE 1 Summary results from the two linear mixed effect models.

Explanatory variable	Coefficient	SE	p -value
Sprat model			
Bottom sigma-t	16.4	2.85	<0.001***
Surface temperature	0.03	0.15	0.81
Bottom temperature	3.03	0.56	<0.001***
Surface salinity	0.37	0.26	0.16
Bottom salinity	-13.26	2.25	<0.001***
Sardine model			
Bottom sigma-t	7.3	3.42	0.032
Surface temperature	0.78	0.17	< 0.001***
Bottom temperature	1.59	0.7	0.024*
Surface salinity	0.3	0.4	0.45
Bottom salinity	-6.18	2.65	0.02*

Note: Slope coefficients, standard error, and p -value for the environmental drivers are shown.

4 | DISCUSSION

The relative abundance of early life stages of the different clupeid species inhabiting the North Sea has been subject to discussion for decades (see Alheit et al., 2012, and references therein). However, observational studies of clupeid larvae and juveniles in the North Sea are rare and

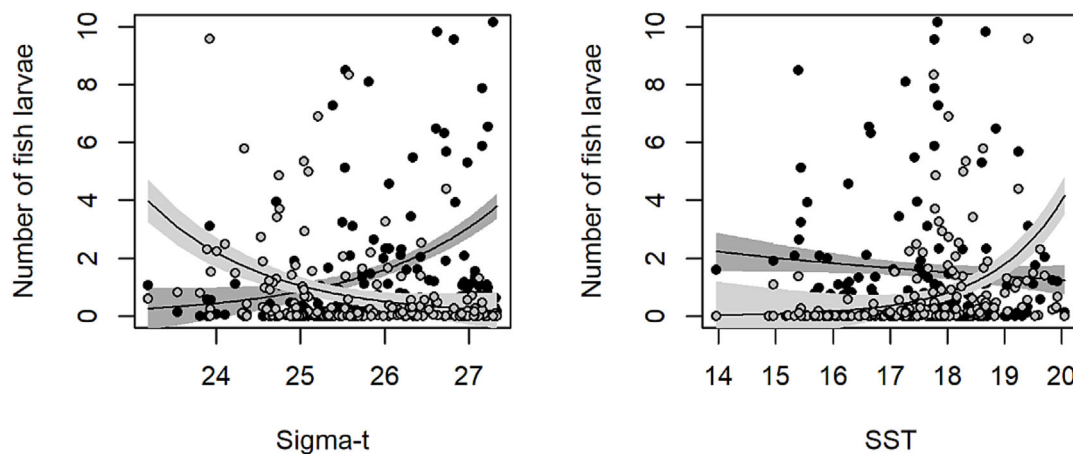
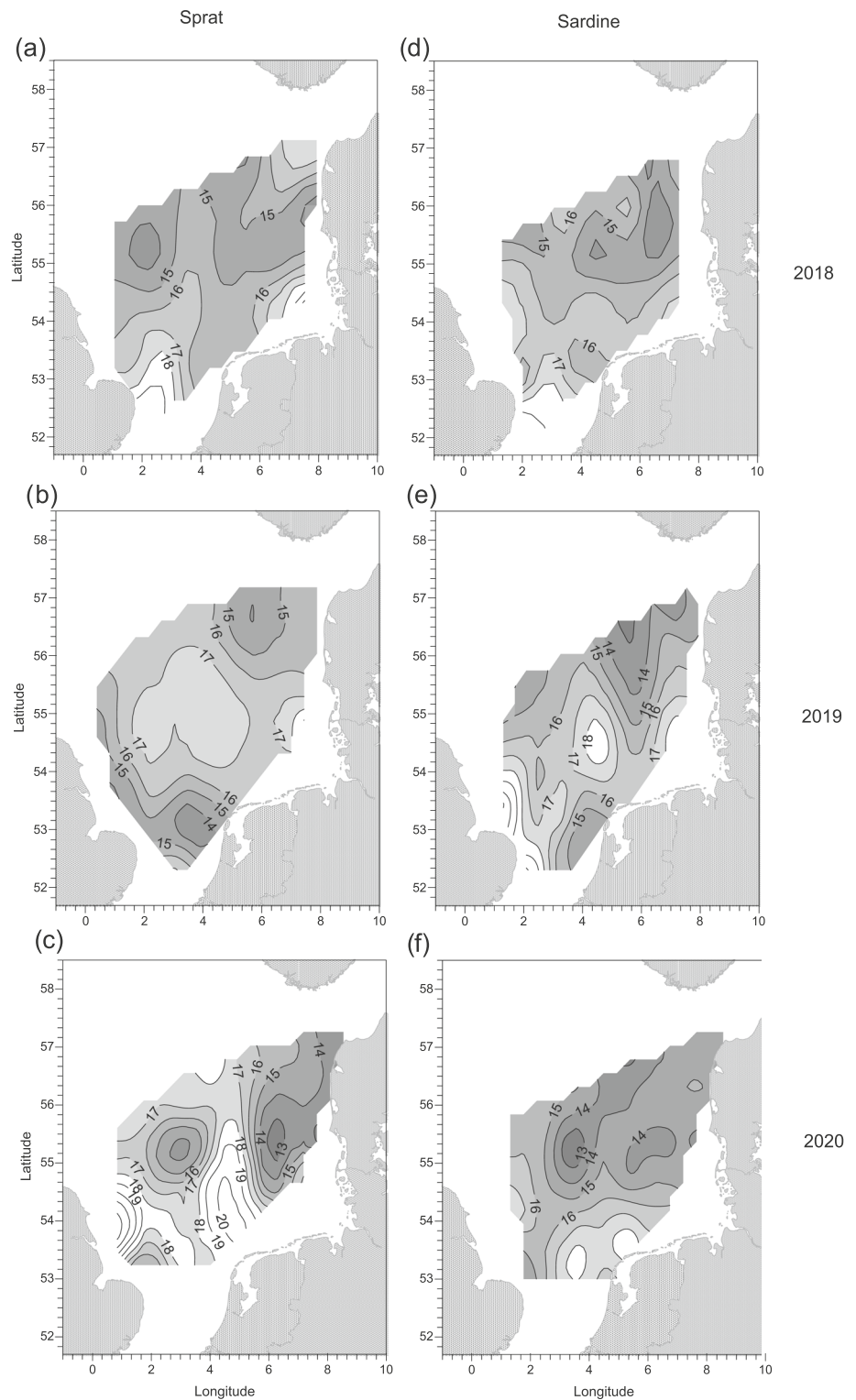


FIGURE 6 Larvae abundance (numbers m^{-2}) of sprat (black) and sardine (grey) larvae as function of sigma-t ($kg\ m^{-3}$) (left) at the bottom and surface temperature ($^{\circ}C$) (right). The illustrate main patterns, trend lines were produced from simple linear models (with just one explanatory variable) and with a negative binomial distribution structure and a log link function to account for skewness and many zeros in the response variable. The shadings around the trend lines represent two standard errors (dark grey shading represent sprat and light grey shading represent sardine).

FIGURE 7 Contouring of larval mean lengths as observed at each station. (a–c) Sprat and (d–f) sardine in 2018, 2019, and 2020. Areas of shortest mean lengths are of darkest shading, contour lines for each mm.



confined to smaller areas, which has prevented general consensus on overall patterns. In this respect, the present study provides a unique geographical coverage of sprat and sardine larvae from 3 years of dedicated sampling, explicitly revealing that sardine larvae presently are widespread and can be even more abundant than sprat (i.e., 2020). Sardine larvae showed a more southeasterly distribution than sprat.

The present study points to strong contrasting relationships between the local larval abundances of the two species and certain hydrographical conditions, where sardine tended to be found mainly associated with high water temperature (in particularly at the surface) and less saline bottom water (i.e., the areas in the southern North Sea influenced by river outflow) while sprat mainly occurred in colder and

denser water further from land near the transition to the deeper northern North Sea where the river influenced water body meets water from the North Atlantic. This pattern essentially follows the notion that the sardine is the “warm water species” of the two clupeids, and this is in accordance with the southerly and coastal distributions previously reported for sardine (Alheit et al., 2012). Furthermore, the bare indications from the present study and former studies (Alheit et al., 2012) that sardine may be increasingly reproducing in the North Sea, and not only enters in the adult stage through the prevailing inflow from the Channel, is in synchrony with other “southern” taxa, which have recently been able to reproduce in the North Sea, for example, cephalopods (e.g., Oesterwind et al., 2020).

While the abundance of adult sardines has been increasing in recent years according to the IBTS trawl survey, there is still a marked difference in the abundance of adult sprat and sardine (ICES DATRAS, 2021). An inspection of the IBTS trawl catches during the same years as the present study (2018–2020) indicates that abundance of adult sardine (year-1 and older) only mounts to a few percent of the sprat abundance (ICES DATRAS, 2021), which is in stark contrast to our findings of larval abundances where numbers of sardine and sprat larvae were found in the same order of magnitude. The discrepancy might be due to an underestimation of sardine in the bottom trawl of the IBTS survey, other observations from pelagic trawls in the North Sea indicate presence of significant schools of sardine (B. Huwer, unpubl. results). However, also differences in mortality, migrations, and spawning phenology may play a role in these discrepancies.

The observations made here supplement earlier studies of clupeid larvae in more confined areas. For example, the German Bight area has in earlier studies been identified as a nursery area for both sprat, sardine and anchovy (Aurich, 1953; Huwer, 2004; Kanstinger & Peck, 2009). However, these studies were unable to show different distributions of sprat and sardine larvae, likely because of the limited geographical extents of the study areas. Likewise, other studies report on linkage between sprat larvae concentrations and hydrographical fronts north of German Bight, Horns Reef (Munk, 1993), and north of Dogger Bank (Munk & Nielsen, 1994), but sardine larvae were not caught during these surveys.

Hydrographical affiliation of adult clupeids has been studied in several frontal systems around the world resulting in mixed findings and conclusions. For example, clupeids in the strait between Sicily and Tunisia (in the Mediterranean), and in Peruvian, waters show distinct species-specific affiliation with the physical oceanography, facilitating niche segregation temporally and spatially (Ayón et al., 2011; Ben Abdallah et al., 2018), while the anchovy-sardine dynamics in the Benguela current appears to be more trophodynamically controlled (Van der Lingen et al., 2006). Similarly, in the Baltic Sea, population dynamics of herring and sprat also show contrasting cycles, which appears to be driven by changes in the zooplankton species composition and density-dependent competition (Möllmann et al., 2004).

Observations of high abundances of relatively small larvae are likely indicators of the locations of the main spawning hubs in the preceding period. However, even the smallest sprat larvae in the present study were relatively large, about 12 mm, indicating that some time

had passed from peak spawning time to our sampling time. We estimate the time interval between spawning and capture (i.e., duration of drift) to be at least 28 days. This crude estimation is based on an egg development time of about 5 days (at temperature of 15°C; Petereit et al., 2008) and an average growth rate of 0.4 mm day⁻¹ (Munk, 1993) that a 12-mm larva is c. 23 days old. With the prevalent current directions in the North Sea (Otto, 1983), our observations of relatively small sprat larvae of high abundances in areas North of central Dogger Bank and north of Horns Reef, likely originate from spawning areas located northwest of Dogger Bank and in the Southern Bight/German Bight areas. Especially the German Bight has earlier been identified as an important spawning area for sprat (Munk, 1993; Ré & Gonçalves, 1993), but newly hatched larvae have been found also in the Horns Reef area (Munk, 1993). An egg survey carried out in 2010–2011 pointed to a relatively wide area of sprat spawning, along the 30-m depth contour from the Southern Bight to the Fisher Banks (van Damme et al., 2011).

Our sampling represent only a single picture from the entire spawning season of the species. Being in August, in the latest phase of the expected spawning period of both species, we might, however, describe a significant part of the spawning that had taken place. The upper part of larval size distribution includes larvae well above 20 mm (Figure S2). These larger larvae might well represent populations from spawning events several weeks earlier. Doing the same exercise as above, we estimate a larvae of 24 mm, growing at a rate of 0.4 mm day⁻¹ (Munk, 1993), could be in the order of 2 months old. Thus, the larvae sampled might cover specimen from spawning in June, well into the expected peak spawning periods for sprat and sardine. Accordingly, we will expect these larvae in much lower numbers than the younger main group due to a longer period of mortality. Further, the gear showed a capability of catching small sprat juveniles of about 45 mm length during the cruise in 2019 (unpubl. data), indicating that if larger larvae had been present during the surveys they would have been covered by our sampling.

The observations that the smallest sardine larvae displayed partial overlap with the smallest sprat larvae (i.e., in the Horns Reef area and south of Dogger Bank), indicated that the sardine larvae were also spawned in the North Sea, in the central and southern areas. However, the relatively large concentrations of sardine larvae in the Southern and German Bights are likely from other spawning locations within the North Sea, signifying that several spawning events could potentially have occurred across the southern North Sea. Sardines are batch spawners with a protracted spawning period (Munk & Nielsen, 2005), hence, the observed pattern could stem from temporally displaced spawning events undertaken by the same sardine spawning population.

The observations made in the current study, pointing to a geographical separation of sprat and sardine larvae in the North Sea, strongly related to hydrographical characteristics, are shedding new light on the comparative ecology of clupeid species in the North Sea. Furthermore, the discrepancy in hydrographical affiliations points to a need for better monitoring of ichthyoplankton communities, and for further investigations of climate-induced changes in species composition (Monteiro et al., 2021). In this context, we find that the present

survey shows great potential for the evaluation of key aspects of fish dynamics and bio-physical linkages during the earlier life stages in a climate-change perspective. Prevalent climate change projections foresee increasing temperatures and declining salinity in the North Sea (Støttrup et al., 2017) and ecosystem responses are already apparent (McLean et al., 2019).

We see several specific questions arising from the study: If the sardine larvae occur in about the same amounts as sprat larvae and if most are spawned within the North Sea, as the present observations indicate, is this a sign of a “subtropicalization” of the North Sea (Montero-Serra et al., 2015)? And if there are equal amounts of larvae, why do we then see an order of magnitude fewer adult sardines than sprat in the IBTS trawl survey? Lastly, if North Sea hydrography has the proposed strong influence on abundances of the two species, how will climate related changes in this hydrography affect the respective population dynamics of sardine and sprat in the North Sea in the decades ahead? Further information related to these questions will not only advance our understanding of how climate-ocean conditions control forage fish populations in general, it will also be of major relevance to industrial climate adaptations and development of a sustainable North Sea industrial forage fish fishery (Dickey-Collas et al., 2014).

AUTHOR CONTRIBUTIONS

Peter Munk did the lead in preparing and writing of the article. Peter Munk, Mikael van Deurs, and Bastian Huwer contributed equally to the writing, and Mikael van Deurs prepared the data analysis. Peter Munk, Bastian Huwer, Matthias Kloppmann, and Anne Sell contributed to field investigations and data, while Matthias Kloppmann and Anne Sell supplemented and reviewed article text.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest concerning this work.

DATA AVAILABILITY STATEMENT

The database on larval sprat and sardine abundances during the three surveys are stored at a repository in DTU Aqua, available by contact to the authors.

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SUPPORTING INFORMATION

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