



Original Article

Effect of zooplankton on fish larval abundance and distribution: a long-term study on North Sea herring (*Clupea harengus*)

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During the last decade, North Sea autumn spawning herring (*Clupea harengus*) has gone through consecutive years of low recruitment despite high spawning-stock biomass. Although several mechanisms, such as reduced larval growth and high early larvae mortality, have been identified as co-occurring during these years, the causes behind them have not been identified. In this study, we analyse a long-term dataset of larval distribution, obtained during the International Bottom Trawl Survey, in relation to environmental conditions during winter and zooplankton abundances, obtained from the continuous plankton recorder. These analyses assessed the potential influence of these factors on the reduced survival of larval stages. Generalized additive mixed models on 30 years of data showed the abundance of *Pseudocalanus* sp. during winter to have a strong relationship with larval distribution and abundance, suggesting that predator–prey processes are behind the low recruitment in recent years. According to our models, the direct effect of temperature on larval abundances was less than the effect of zooplankton abundances.

Keywords: herring, larval survival, North Sea, temperature, zooplankton.

Introduction

Marine ecosystems in the northeastern Atlantic region have shown great variability on decadal and multidecadal scales (e.g. Hurrell and van Loon, 1997; Butler *et al.*, 2013), which on a smaller scale significantly alter the hydrographic features like currents (Siegismund and Schrum, 2001), salinity (Häkkinen *et al.*, 2011), or temperature (Meyer *et al.*, 2011). These hydrodynamic changes, at the bottom of the foodweb, cascade through all trophic layers leading to match–mismatch events, changes in growth, feeding, and predator–prey interactions resulting in shifts in species distribution and productivity. Therefore, ecosystem changes seem to respond to global scale processes by displaying similar multidecadal variability (Alheit *et al.*, 2014; Drinkwater *et al.*, 2014; Goberville *et al.*, 2014). This variability has been recorded across ecosystem components from phyto- and zooplankton (Edwards *et al.*, 2001; McQuatters-Gollop *et al.*, 2007; Beaugrand, 2009; Alvarez-Fernandez *et al.*, 2012), through

planktivorous species (Hátún *et al.*, 2009a; Óskarsson *et al.*, 2009; Payne *et al.*, 2009), all the way to top predators (Hátún *et al.*, 2009b; Kirby and Beaugrand, 2009). Fish populations showed synchronous changes in different areas such as the North Sea (Kirby *et al.*, 2009), the Baltic Sea (Mollmann *et al.*, 2008), and the northeastern Atlantic Ocean (Hátún *et al.*, 2009a). Often these changes go along with anthropogenic-induced factors, such as increased or shifted fishing effort eutrophication, etc. (Eero *et al.*, 2011; Engelhard *et al.*, 2014), altering whole population structures and distributions. Decreasing population size subsequently leads to decreasing numbers of recruits described by spawning-stock biomass—recruitment relationships (Beverton and Holt, 1957). However, when time-series are “cleaned” from these stock size and reproductive potential driven factors, still a significant amount of interannual and decadal variability remains. Although the exact processes behind such changes are not determined, the current paradigm embraces the idea that often a number of

interacting processes affecting early life stages control the productivity of fish populations via starvation, predation, or unfavourable advection (Peck and Hufnagl, 2012).

In the North Sea, Atlantic herring (*Clupea harengus*) plays a key ecological and economic role with ~0.3–0.4 million tons landed per year between 2007 and 2012 (ICES, 2013). Herring exhibits a unique plasticity in temperate marine fish with a temperature tolerance ranging from -0.75 to 23°C and larvae capable of surviving relatively long periods while displaying little or no somatic growth (Blaxter, 1960; Johannessen et al., 2000). Hence, Atlantic herring inhabits environments across the North Atlantic with different water temperature, prey availability, and hydrography (Geffen, 2009). Despite this plasticity, during the last decade herring in the North Sea, has produced successive weak-year classes (ICES, 2013; Payne et al., 2013) responding to detected changes in global hydroclimatic indices such as North Atlantic Oscillation and Atlantic Multidecadal Oscillation (Gröger et al., 2010).

North Sea herring consists of four spawning-stock components (Orkney, Buchan, Banks, and Downs; Figure 1), which can be differentiated by their spawning area and times. Spawning starts in the northern components in late August (autumn spawners) and continues southward to the Southern North Sea until January (winter spawners; Gröger et al., 2010). Although spawning-stock biomass has been high during the last decade, recruitment of North Sea herring has decreased since 2002 (Figure 2; ICES, 2013; Payne et al., 2013).

Despite the wealth of data available for all life stages of herring (Simmonds, 2009; Sinclair, 2009), the main mechanisms causing this low recruitment have not been definitely determined. There are indications that the early larval stage seems to be the critical point, with reduced survival and growth rates during the 2000s (Payne et al., 2009; Fässler et al., 2011). Larval survival is known to be affected by the quantity, suitability, and timing of planktonic prey (Durant et al., 2005; Payne et al., 2009). Therefore, the effect of atmospheric patterns on prey of herring larvae seems a logical mechanism affecting herring recruitment (Payne et al., 2009, 2013).

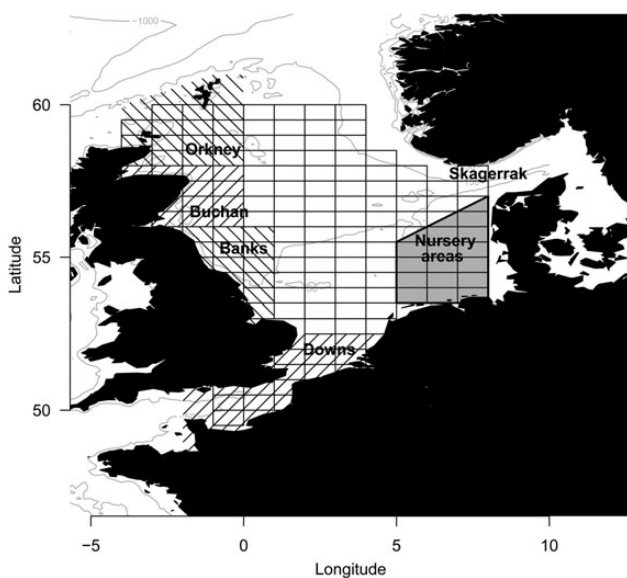


Figure 1. Study area showing spawning (striped) and nursery (shaded) areas. The grid represents ICES statistical rectangles.

Plankton community changes have already been connected to the dynamics of other fish species in the North Sea, e.g. cod (Beaugrand et al., 2003) and horse mackerel (Reid et al., 2001). For herring larvae, known zooplankton prey, such as *Temora* sp. and *Pseudocalanus* sp. (Blaxter, 1965; Arrhenius, 1996), have shown a sharp decline during the 2000s, halving the abundances recorded during previous decades (Alvarez-Fernandez et al., 2012). Most recent combined approaches that either link survey data with hydrodynamic features and larval physiology (Hufnagl et al., 2014) or indirect larval feeding indices with growth and hydrodynamic features (Lusseau et al., 2014) also point towards a bottom up control of herring recruitment strength.

In this study, the relationship between herring larvae and zooplankton prey has been assessed in space and time via generalized additive mixed modelling, considering the potential effect of different plankton regimes in the North Sea. With this analysis, we try to discern the effect of food availability on the survival of herring larval stages.

Material and methods

Datasets

Data on abundance of herring larvae were obtained from the MIK survey carried out during the International Bottom Trawl Survey (IBTS) in the first quarter of each year since 1977. Herring larvae are represented as the average number of larvae per length in each statistical rectangle (Figure 1). The number of larvae between 25 and 55 mm was considered as an index of pre-metamorphosis larvae (PML). These larvae come from autumn spawning herring, therefore excluding the Downs component which spawns during winter. Only data since 1981 were used, as earlier years had several unsampled statistical rectangles.

The spawning-component abundance index (SCAI) was used to address the different contribution of each spawning component through time (Payne, 2010). This index has been used in the herring stock assessment (ICES, 2013) since 2011 and replaced the formerly used larval abundance index. SCAI provides an index of the abundance of early larvae (<10–11 mm) on the spawning

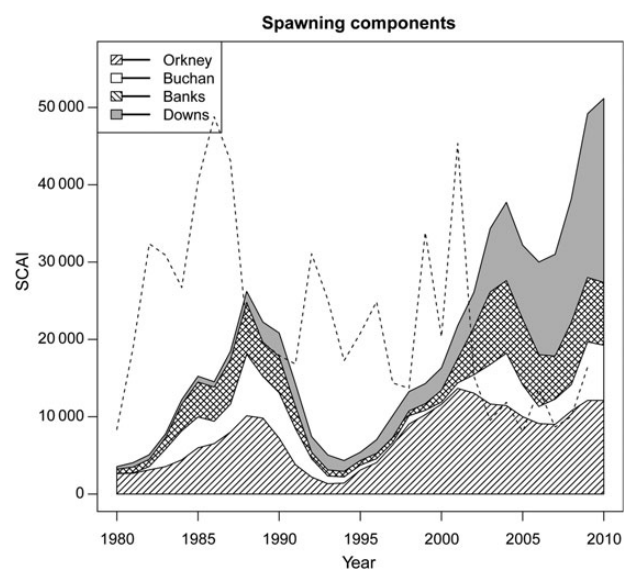


Figure 2. Contributions of each spawning component based on the SCAI during the study period. The dashed line represents herring recruitment (different y-scales). After Payne (2010).

grounds (ICES, 2013). Because of the later spawning of the Downs component, its dynamics are not represented by PML in February. Therefore, the SCAI of the Downs is not included in the analyses.

Data on zooplankton abundance were obtained from the continuous plankton recorder (CPR) data as provided by the Sir Allister Hardy Foundation for Ocean Science (SAHFOS). Four different species, considered prey of herring larvae, were included: *Temora longicornis*, *Oithona* sp., *Pseudocalanus elongates*, and *Acartia* spp. Plankton data were fitted on a grid of $1 \times 1^\circ$ (Figure 3). At each node, Inverse Distance Weighed averages (Isaaks and Srivastava, 1989) with a search distance of 1° were calculated for each year per month (October, November, and December). These data provide information on herring larvae prey abundances post-spawning.

Hydrographical backtracking

At each point, the gridded PML index was coupled with CPR prey-based prey index, as well as temperatures likely experienced by the larvae along their larval drift phase. This temperature was obtained from the HAMBURG Shelf Ocean Model (HAMSOM; Pohlmann, 1996a, b, 2006), and the drift path was obtained from an IBM-drift model (Hufnagl et al., 2014). In short, based on the herring larvae surveys, five spawning hot spots were identified, and in each area particles, over a period of 10 d 1000 particles (in total 50 000) were released following the main spawning periods in the respective area. For each statistical rectangle sampled in February, thus the average temperature experienced was determined along with the percentage of time spent in any other rectangle

at a given time before February. The latter allowed for an incorporation of prey abundance experienced by larvae sampled in one specific area in February. Thus, by the drift results, the datasets (Temperature, *T. longicornis*, *Oithona* sp., *P. elongates*, and *Acartia* spp.) were paired spatially in 72 nodes covering the whole study area during the period 1981–2005, representing PML abundance in February and prey and environmental conditions per month that these larvae would have found during their drift across the North Sea. The month of October was used as start of the analyses as, according to the duration of yolk phase (Blaxter and Hempel, 1963; McGurk, 1984; Fey, 2001; Bang et al., 2007) and after the results of Hufnagl et al. (2014), a size of between 15 and 20 mm was reached in October, allowing for the predation on our potential prey species (Hufnagl et al., 2014, and references therein).

For each datapoint, the absolute spawning contribution was calculated. The IBM-drift model provided the partial contribution of each spawning component to each spatial point in the study grid. An absolute spawning index was calculated as follows:

$$SAI_{x,j} = \sum_i SCAL_{i,j} \times SCAL_{f,x,i,j}$$

where $SAI_{x,j}$ represents the spawning abundance index in gridpoint x and year j , and $SCAL_f$ the partial contribution of spawning component i (obtained from the model) to gridpoint x in year j . Only the northern spawning components were considered for this spawning

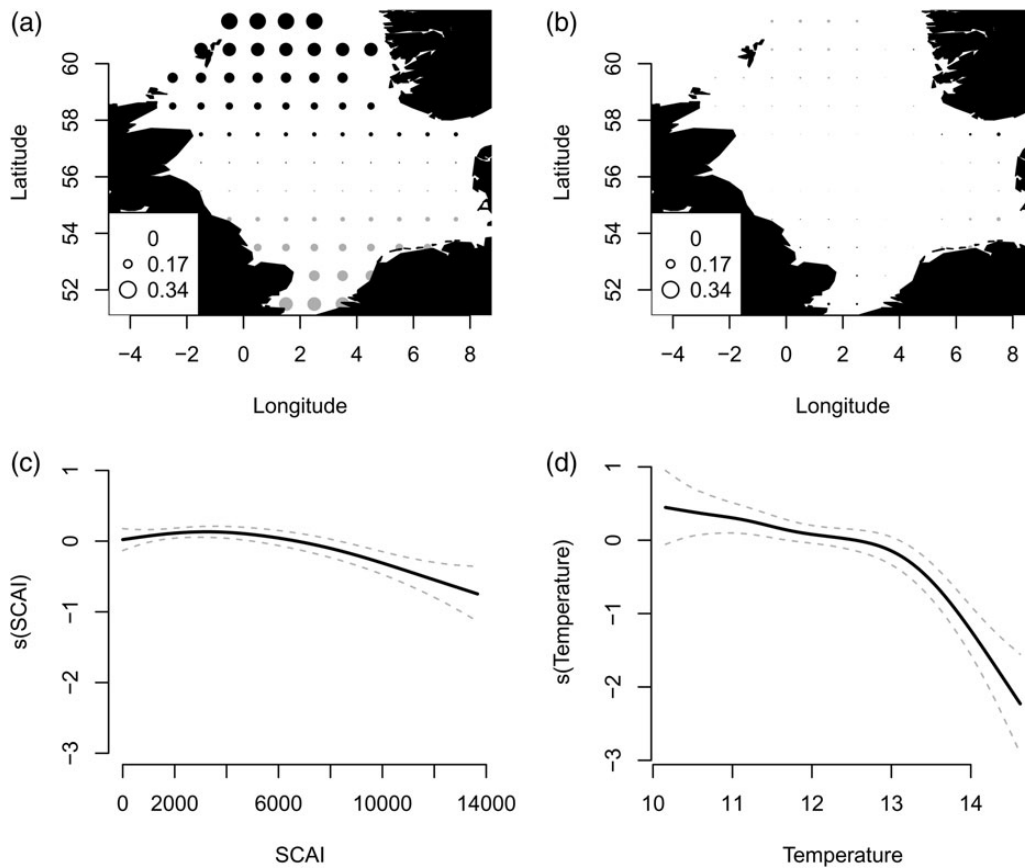


Figure 3. Contribution of each parameter to the predicted $\log(\text{PML abundance})$ of: (a) 10 ind l^{-1} increase in *Pseudocalanus* sp., (b) 10 ind l^{-1} increase in *Acartia* sp., (c) SCAI, and (d) temperature. Grey indicates a decrease, whereas black indicates an increase.

index, as the PML larvae in February do not represent the dynamics of the Downs component.

Analyses

Split-moving window

Split-moving window (SMW) boundary analyses (Beaugrand, 2003) were performed on each variable by creating a matrix of its geographical location in time (72 rows by 24 columns). For each matrix, the calculation of SMW is realized in four steps: (i) a window of even-numbered size is introduced at the beginning of the time-series matrix, (ii) this window is then divided into two half-windows, (iii) an association coefficient (Euclidean distance in this case) is used to evaluate the differences between those periods. A multiple response permutation procedure (Mielke et al., 1981) was applied to test the two periods based on the information provided by all latitudinal/longitudinal points. Finally, the window is then moved from year to year, repeating steps 2 and 3 until the end of the time-series is reached. This procedure provides a p -value for each year representing the statistical significance of a year being the limit between two different periods. By repeating this procedure for different window sizes, the sharpness of change was also assessed. Changes also detected at small window sizes are considered to be sharper (more sudden) than those detected only at big window sizes.

Generalized additive mixed models

Generalized additive mixed models (GAMMs) with Gamma distribution and a logarithmic link were used to analyse the relationship between herring larvae abundance, temperature, and its prey in space and time. Several models were fitted to assess all potential relationships between larvae and its prey. An overview of the models can be seen in Table 1. The full structure of the model was as follows:

$$\ln(\text{Larvae}_{(i,\theta)}) = f_0(\theta) + f_1(\text{SAI}_{(i,\theta)}) + f_2(T_{(i,\theta)}) + f_3(\text{Prey1}_{(i,\theta)}) + \dots + f_n(\text{Prey} - n_{(i,\theta)}) + \varepsilon_{(i,\theta)},$$

where i represents each year, θ the spatial location (longitude and latitude), SAI the spawning abundance index, T the temperature, Prey each different prey item, and ε is a residual term which is normally distributed with 0 mean and σ standard deviation related to noise in the data and not included in parameters. The relationship of explanatory variables with larvae abundance (f_{0-n}) varies between models, being either equal for the whole spatial range, or being allowed to change in space (Table 1). All models were fitted with a spatial Gaussian autocorrelation structure to account for spatial autocorrelation of the data (Wood, 2006).

A backwards model selection process was carried out for each model type, starting with the most complex model including all explanatory variables. Smooth terms with p -values > 0.05 threshold were removed one by one until all terms were statistically significant. Smooth terms with estimated degrees of freedom close to one were replaced by their parametric counterparts. Models in which all smooth and parametric terms were significant were compared by the Akaike Information Criterion (AIC). AIC takes into account both the goodness of fit of the model and model complexity with lower values indicating better models. The model with the lowest AIC was considered the best suited to represent herring larvae distribution (Wood, 2006).

Table 1. Different relationship between explanatory variables and herring larvae abundance.

Function type	Explanatory variables
f	Relationships modelled with a location-independent and period-independent smooth function.
f_p	Relationships modelled with a location-independent and period-dependent smooth function.
f_θ	Relationships modelled with a location-dependent tensor product, i.e. interaction between longitude, latitude tensor product (two-dimensional smooth), and explanatory variables.
$f_{(\theta,p)}$	Relationships modelled with a location-dependent tensor product. The interaction was allowed to be different in the different periods.

Results

Split-moving window boundary analysis

Several variables showed statistically significant shifts in their geographical distribution and abundances, i.e. temperature, *Pseudocalanus*, and *Oithona*. The three variables showed a shift between 1996 and 1998, p -value < 0.05 ; *Oithona* sp. (1996–1997), window size 20–24; temperature (1997–1999), window size 14–24; *Pseudocalanus* sp. (1997–1998), window size 20–24. The large window sizes indicate that the shift is not too sudden, it could even represent a relatively gradual change. Nonetheless, two different periods were detected; therefore, a “period” variable was created to allow some of the modelled relationships to change before and after 1997 (Table 1).

Model selection

According to the AIC, the best five models included zooplankton abundances in October as predictors (Table 2). The November abundance of *Temora* was significant in only one of the models (Table 2, M3). The best five models according to AIC also always included spatial interactions of zooplankton abundance effects (Table 2). Spawning abundance index and temperature were also significant explanatory variables.

The best model, according to AIC scores, included non-linear predictors for SAI and temperature in October, and linear predictors for *Pseudocalanus* sp. and *Acartia* sp. also in October, which vary in space (Table 2 and Figure 3). According to the AIC scores, the spatially defined smoothers are consistently a better fit than the period-defined smoothers, as none of the period-defined predictors was selected in the top 10 models. This indicates that the spatial variation in the responses of PML abundance is of greater importance than their change in different periods.

Pseudocalanus sp. showed a positive relationship with PML in the northern part of the North Sea, and a negative relationship in the southern part (Figure 3a). *Acartia* sp. on the contrary only showed considerable negative relationship with PML in the southern nursery area and the Orkneys, and positive relationship in the English Channel and the Skagerrak mouth (Figure 3b). These relationships were always weaker than those of *Pseudocalanus*.

The spawning abundance index showed a non-linear relationship with PML abundance in the study area (Figure 3c). This relationship was positive for the lower values of SAI and became negative for high values of SAI. There was also a negative relationship between temperature during October and PML abundance independently of location (Figure 3d). This relationship was non-linear, becoming more negative as temperature increases.

Table 2. Best models as selected by the AIC index.

Model		d.f.	AIC	R ² -adjusted (%)
M1	$f(\text{SAI}) + f(\text{Temperature}_{\text{Oct}}) + f_{\theta}(\text{Acartia}_{\text{Oct}}) + f_{\theta}(\text{Pseudocalanus}_{\text{Oct}})$	18	3362.108	21
M2	$f(\text{Temperature}_{\text{Oct}}) + f_{\theta}(\text{Acartia}_{\text{Oct}}) + f_{\theta}(\text{Pseudocalanus}_{\text{Oct}})$	16	3378.465	19.8
M3	$f(\text{SAI}) + f(\text{Temperature}_{\text{Oct}}) + f_{\theta}(\text{Acartia}_{\text{Oct}}) + f_{\theta}(\text{Pseudocalanus}_{\text{Oct}}) + \text{Temora}_{\text{Nov}}$	19	3385.252	21.2
M4	$f(\text{SAI}) + f(\text{Temperature}_{\text{Oct}}) + f_{\theta}(\text{Pseudocalanus}_{\text{Oct}})$	15	3395.912	20.3
M5	$f(\text{SAI}) + f(\text{Temperature}_{\text{Oct}}) + f_{\theta}(\text{Acartia}_{\text{Oct}})$	17	3404.479	19.9

Smaller AIC values mean better models; d.f. represents the degrees of freedom of the model. The different functions representing relationship between explanatory variables and PML abundance are defined in Table 1. The subscript indicates the month at which larvae encounters the prey.

Discussion

The results presented here suggest that zooplankton abundances in October are an important predictor of post-winter PML abundance in the North Sea. Models with zooplankton as explanatory variables always performed better than their counterparts without zooplankton variables (Table 2). The different regimes detected in explanatory variables did not affect the relationship between larvae and zooplankton, as both zooplankton and temperature effect showed no difference before and after 1997, the year of sudden change in several explanatory variables. Although temporal differentiation did not improve model performance, spatial differentiation of *Acartia* and *Pseudocalanus* effects was shown to improve it.

Pre-metamorphosis larvae

Despite the abundant spawning in recent years (Figure 2), PML abundance decreased in the second period, particularly in the eastern North Sea between 54 and 57° latitude (Figure 4a and b). This decrease is captured here as shown by the model errors (Figure 4c and d), although there was some overestimation of PML by the model for the years after 1998 in this area (eastern North Sea). The decrease of PML while spawning values are high points in the direction of increased mortality or slower growth in early larval stages in recent years (Fässler *et al.*, 2011; Payne *et al.*, 2013) also reflected in a decrease in herring larvae size (Hufnagl *et al.*, 2014).

The predictive value of this model is not very high, nor was it the intention of these analyses, but it serves the purpose of determining good explanatory variables for PML abundance and distribution and infers what processes may affect herring larvae dynamics. When interpreting the spatial effects of parameters on PML, it has to be taken into account that these data represent a snapshot in time. The larvae collected between February and March each year were coupled with the average zooplankton and temperature conditions they would encounter in the months after hatching, from October to December, along their larval drift. In the best model, abundances of *Acartia* and *Pseudocalanus* in October were the best explanatory variables. This represents the conditions post-spawning which have been suggested to be of importance in the survival of larvae to juveniles by Fässler *et al.* (2011) and is also in line with recent findings by Lusseau *et al.* (2014).

Temperature

Temperature post-spawning showed a negative relationship with abundance of PML. This relationship was consistent in space, and became more intense as temperature increased (Figure 3d).

Average temperature in October has increased during the last decade (Figure 5a), showing a warmer period during the 2000s. Although temperature in different periods has been suggested to play an important role in larval survival (Payne *et al.*, 2009; Fässler

et al., 2011), it has been suggested that its direct role might be less important than previously thought (Payne *et al.*, 2013). This would be in agreement with our results, which show temperature in October to have a weaker effect on PML than zooplankton abundances (Figure 3c) until high temperatures are reached (>13°C). Blaxter (1960) showed autumn spawning larval herring to withstand a wide range of temperatures (−1.8–23°C). However, at $T > 14^{\circ}\text{C}$, growth rates do not seem to increase further (Oeberst *et al.*, 2009), indicating that an optimum is reached which is in line with laboratory investigations on survival (Marta Moyano, pers. com.). Temperatures in the North Sea are in an appropriate range for larval survival, but the effect of temperature affecting metabolic rates and growth energetics is still in place within this range.

Spawning abundance

The spawning abundance index (SAI) used here takes into account the proportional contribution of each autumn spawning component and represents the potential spawning abundance contributing to each gridpoint (in space and time) in our analyses. This index showed a negative effect on the abundance of PML during the sampling period at high values, while showing a positive effect at low values (Figure 3c). The positive phase of this effect can be interpreted as increased post-winter larvae due to increased spawning output. The negative phase might represent increased cannibalistic pressure of adult herring on recently spawned larvae, particularly at very high values of SAI, decreasing the early larval survival. The possibility of higher abundance of adult herring in the spawning areas during the post-hatching period should be further investigated to assess the validity of this interpretation. Another reason for this non-linear-shaped relation between SAI and PML could be habitat limitation factors, which would be supported by the importance of zooplankton concentration on PML. Thus, especially in years with low dispersion and high larval concentrations, a general decrease in survival can be expected.

Zooplankton

Zooplankton abundance and distribution in October have been shown here to have a relationship with the abundance and distribution of autumn spawning herring PML in February (Figure 3a and b). *Pseudocalanus elongates* showed the strongest connection with PML abundance, and a latitudinal gradient was detected on this effect (Figure 3a). The relationship is positive in the northern North Sea, and negative in the southern North Sea. *Pseudocalanus* sp. is known to be a primary prey of recently hatched larvae (Blaxter, 1965; Arrhenius, 1996). In a compilation of previous studies, Blaxter (1965) showed that *Pseudocalanus* sp. was an important prey of herring larvae for smaller sizes (<20 mm), which could be expected to be abundant during the winter period. In the last decade, there has been a decrease in *Pseudocalanus* abundance across the North Sea

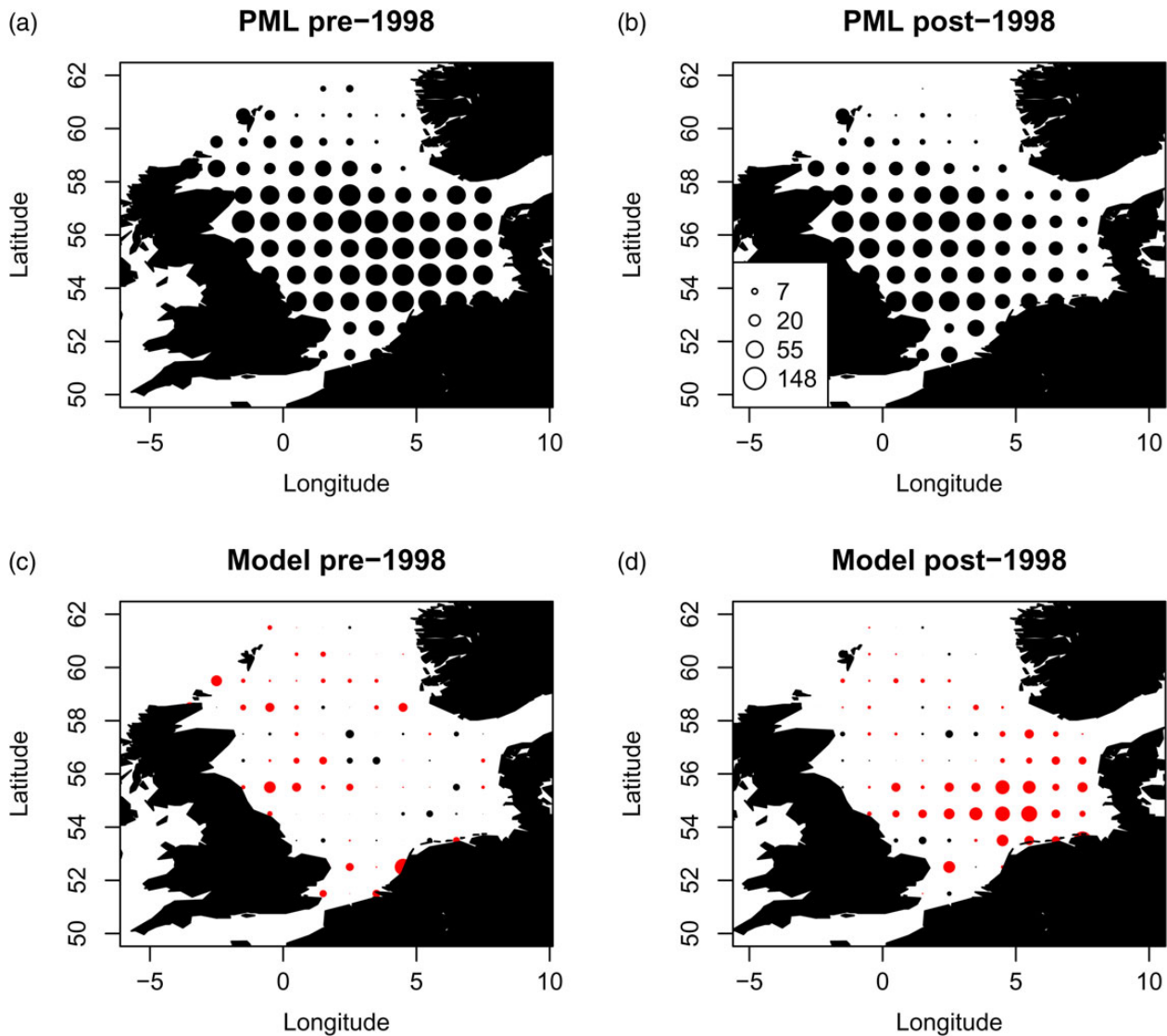


Figure 4. Average abundance per period of herring PML (top) in the study area and residuals of the best model (bottom). Red indicates negative values. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

(Figure 5b); this change was particularly pronounced in the northern North Sea and becomes less going south along the east coast of the United Kingdom. This spatio-temporal trend can explain the latitudinal gradient on PML response. On the northern North Sea, where *Pseudocalanus* abundances were clearly reduced post-1998, there was a positive relationship between *Pseudocalanus* and PML. The weaker relationship in the southern North Sea (Figure 3a) was caused by the relatively constant abundances of *Pseudocalanus* in the Banks and Buchan spawning areas (Figure 5). These results would suggest that the latitudinal shift on herring PML, already detected by Röckmann *et al.* (2011), can be explained by changes in abundance and distribution of *Pseudocalanus* in October and is in line with Hufnagl *et al.* (2014), who suggested prey quality and abundance to play an important role in larval survival and larval length in February.

Acartia sp. was also shown to influence PML abundance, although to a much lesser extent than *Pseudocalanus* (Figure 3b). Here, a negative relationship between *Acartia* sp. and PML in the nursery area (German bight) and the northwest of the study area

was determined. Closer to the English Channel and the Skagerrak opening, a positive relation was found. *Acartia* also displayed a decreasing abundance in the 2000s along the longitudinal margins of the North Sea, and an increase closer to the English Channel.

Results of the models including *Temora* sp. in November (M3 in Table 2, not presented here) showed a positive linear relationship of *Temora* sp. in November with herring PML. This relationship was consistent in space. Although the inclusion of *Temora* sp. improved the explanatory performance of the model, it also increased its complexity, and it was therefore not chosen as a best model based on the AIC coefficient. Despite this, the fact that *Temora* was chosen as a good explanatory variable in November, whereas *Acartia* and *Pseudocalanus* are the best explanatory variables in October, suggests that our model is capturing the influence of these species as prey of herring larvae. *Pseudocalanus* and *Acartia* spp. were already reported by Blaxter (1965) as prey for smaller herring larvae, whereas *Temora* is suitable prey for herring larvae of larger size. The influence of *Temora* abundances was less than that of

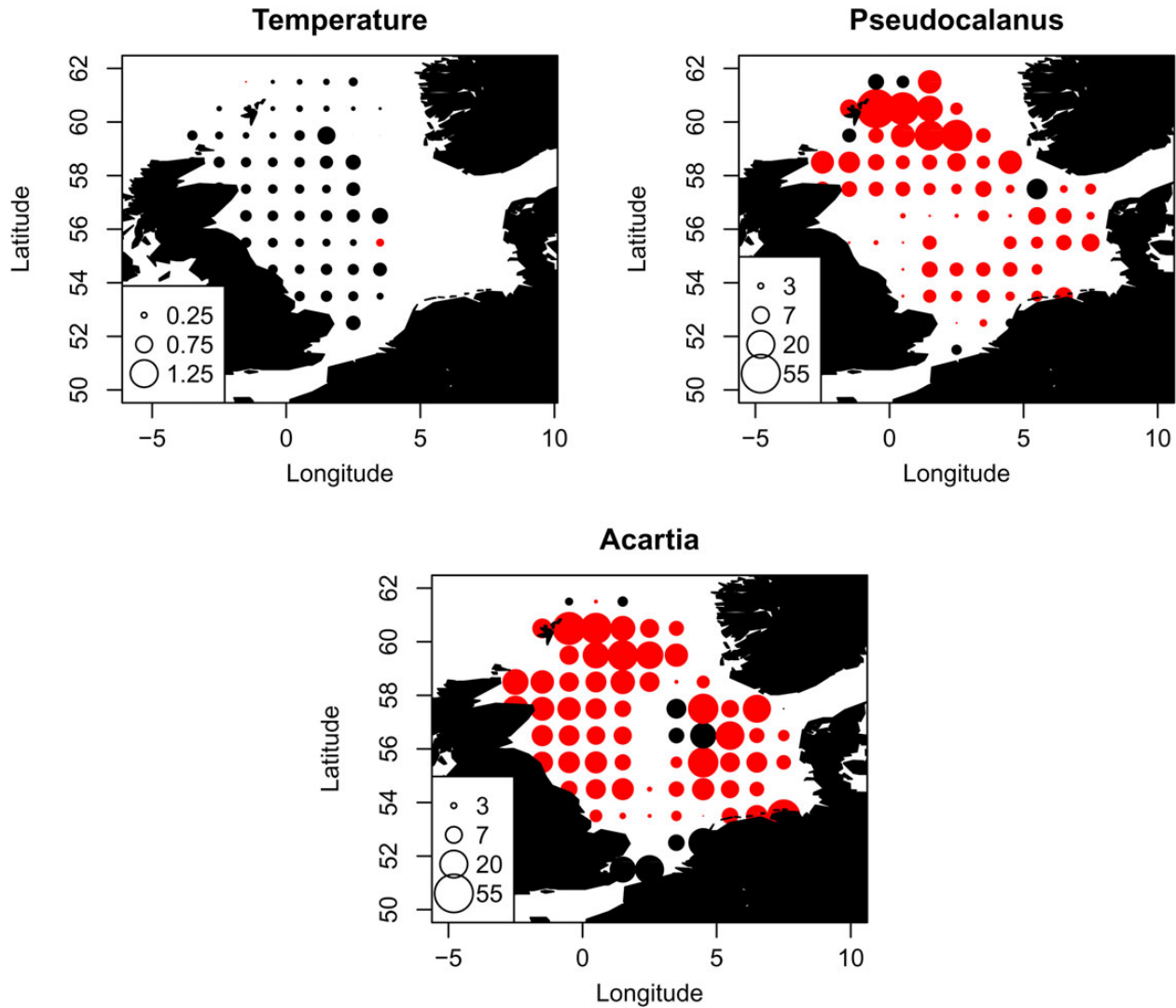


Figure 5. Differences between the average values post-1998 and pre-1998 of the different explanatory variables. Red (black) points indicate a decrease (increase) post-1998.

Acartia and *Pseudocalanus*, and the increase in explanatory value of the model was low. This indicates that the first month of feeding is most important determining the winter survival of herring larvae, which would indicate a “critical period” following Hjorts hypothesis (Hjort, 1914).

Taken together, these results indicate the importance of the abundance of small copepod species, such as *Acartia* spp. and *Pseudocalanus* sp., on the winter survival of recently spawned herring larvae. The dynamics of other zooplankton species, such as *T. longicornis*, also affect the winter survival, but the results indicate the main bottle-neck before this prey becomes important. It has been shown that timing, abundance, and distribution of prey affect the recruitment of the predator species (Durant *et al.*, 2005), extending the classical view of the match–mismatch hypothesis (Cushing, 1990) from a synchronicity problem to a timing and abundance interaction. Alvarez-Fernandez *et al.* (2012) showed that in the 2000s, seasonal patterns of copepod assemblages in the North Sea have changed, whereby abundances of small copepod species decreased, particularly after summer. These changes in plankton

abundance are shown here not to be homogeneous in space (Figure 5), therefore affecting differently the different spawning components of North Sea herring. This mismatch between herring larvae and potential prey should be further investigated at a finer spatial resolution in the spawning areas. Different conditions of other parameters not included in these models could be responsible for the differential northern/southern responses. In particular, the potential availability of other types of prey in the shallower southern North Sea or differential feeding in northern and southern drifting routes should be carefully investigated.

It should be noted that all results related to plankton in these analyses are based on CPR data; therefore, some assumptions are implicitly made. The CPR dataset provides a long-term view of the mesoplankton state ($>270\ \mu\text{m}$) in the North Sea and northeastern Atlantic area, but only in terms of catch rates and species composition, and only in surface waters, without any information on the size spectra of the plankton community. We assumed here that the plankton trends detected in the CPR dataset also represent the dynamics of slightly smaller individuals of the same species.

Conclusion

The results presented here give a new indication of the importance of zooplankton abundance, distribution, and composition in explaining the low herring recruitment during the last decade. As expected, our investigations indicated the importance of spawning abundance of autumn spawning components to be an important factor affecting post-winter PML abundances. However, even more important was the availability and distribution of prey organisms. Especially zooplankton abundance in October and the spatial distribution of suitable prey for early larval stages of herring (i.e. *P. elongates* and *Acartia* spp.) were the major factors affecting the abundance of PML. The spatial differentiation of the response of herring larvae to zooplankton abundances was shown to be important in the North Sea, and this should be taken into account in future investigations of herring larvae dynamics. The analyses were constrained by the spatial and temporal resolution of the data. Furthermore, size-structured data of the plankton community were not available for the analyses, and recent studies have highlighted the importance of microzooplankton for larval herring feeding ecology (de Figueiredo *et al.*, 2007; Peck *et al.*, 2012).

Further coordinated zooplankton and larvae sampling, in addition to modelling efforts, are needed to describe the zooplankton dynamics (micro- and mesoplankton) in spawning areas. Even more, the inclusion of size-structured plankton composition in these data collection efforts would greatly improve our understanding of the potential trophic relationships broadly represented in our model.

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