ORIGINAL ARTICLE

Winter zooplankton dynamics in the English Channel and southern North Sea: trends and drivers from 1991 to 2013

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Winter has long been regarded as a period of minor importance in marine zooplankton ecology with static, low concentrations and growth rates of organisms. Yet, there is growing evidence that winter conditions influence spring bloom strength. With rising water temperatures, growing importance of fish larvae survival during winter and the lack of data to parameterize ecosystem models for this period, research focus shifted on winter zooplankton ecology. To enable looking into past changes in winter zooplankton ecology, we established a new winter zooplankton time series based on samples collected in the eastern English Channel and southern North Sea by the International Herring Larvae Survey since 1988. Four areas of the study region were identified containing different congregations of zooplankton. Overall, zooplankton size decreased while total zooplankton abundance increased, reaching its maximum in 2011. Zooplankton abundance dynamics were mainly related to temperature, chlorophyll *a* concentration and North Atlantic Oscillation index. Depth and Atlantic water inflow strongly influenced zooplankton size. Increased chlorophyll *a* concentration and high abundances of small copepods indicated bottom-up controlled secondary production since 2010 and a possible winter bloom in 2011. Based on the analysed parameters, no relation between herring larvae abundance and zooplankton or environmental drivers was determined.

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INTRODUCTION

European marine ecosystems have experienced several changes and shifts in the past decades (Alheit *et al.,* 2005; Weijerman *et al.,* 2005; Conversi *et al.,* 2010). Owing to high fishing efforts and increasing water temperatures, the North Sea has seen an increase in environmental pressures from both ends of the food chain (Baudron *et al.,* 2014). This led to further research investigating the reasons and impacts of the changes in North Sea ecology indicating that zooplankton composition and abundance were main bottom-up drivers of ecosystem dynamics (Beaugrand, 2003; Beaugrand and Ibanez, 2004). In the North Sea, trends in zooplankton dynamics could mainly be attributed to increased Atlantic water inflow, temperature change (Beaugrand *et al.,* 2000; Edwards *et al.,* 2002; Heath *et al.,* 1991; Reid *et al.,* 2003) and changing primary production (Bedford *et al.,* 2020; Capuzzo *et al.,* 2018; Schmidt *et al.,* 2020). In their recent study, Bedford *et al.* (2020) found decreasing trends in holoplankton abundance, in particular small copepods, which could in part be attributed to rising water temperatures. Yet, despite the inclusion of multiple time series data sets, the study could not produce coherent results for the important transition zones between Atlantic and North Sea water. One of the two gateways for Atlantic water into the North Sea is the English Channel (Becker and Pauly, 1996). Especially during winter, when the temperature difference between the cold North Sea and warmer Atlantic water is largest, the influence of the water exchange may have a strong ecological impact on this transition area (Mathis *et al.,* 2015). Beaugrand *et al.* (2000) and previously Fromentin and Planque (1996) indicated that winter North Atlantic Oscillation (NAO) and air temperature can negatively affect the phyto- and zooplankton abundance in the North Sea and English Channel, although this relationship ceased since 1996 for the cold-water-related copepod assemblage in the North Sea (Planque and Reid, 1998). Despite a veritable need for studies on winter plankton assemblages in the North Sea, concrete research regarding this crucial time period is still lacking.

The zooplankton community in this area consists of generalists, warm water-adapted species from the Bay of Biscay, where the English Channel forms the Northern distribution margin, and cold water-adapted species from the North Sea, where this region forms the southern distribution margin (Le Fevre-Lehoerff *et al.,* 1995; Beaugrand, 2002; Eloire *et al.,* 2010). As a transitional zone between the North Atlantic and the North Sea with its hourglass shape and strong tidal mixing, the hydrographic conditions in this area are very dynamic (Pingree, 1980). Using continuous plankton recorder (CPR) data, Alvarez-Fernandez *et al.* (2012) threw some light into this dynamic region and showed the occurrence of

ecological shifts in the 1980s and 1990s. The obtained results were consistent with the only two other time series in this region, Plymouth (L4; UK; John *et al.,* 2001) and Gravelines (France; Le Fevre-Lehoerff *et al.,* 1995). Similar changes in zooplankton dynamics can also be found in the time series of Stonehaven (UK; Valdés *et al.,* 2005), Dove (UK; Clark *et al.,* 2001c) and Helgoland (Germany; Boersma *et al.,* 2015) in the North Sea. Yet, these time series serve either the purpose of local monitoring (fixed station) or spatial coverage (CPR). Bedford *et al.* (2020) combined both and was able to detect not only larger scale trends but also local differences and contradicting results between some monitoring stations. These monitoring stations and the CPR data sets are, however, the only available data sets on zooplankton dynamics during winter conditions. That is why the data are often used to tune and evaluate ecosystem models with a zooplankton component (Broekhuizen *et al.,* 1995; Lewis *et al.,* 2006). Model runs are usually started in winter as they focus on spring bloom dynamics and therefore need winter data as start conditions. While the existing data from CPR and the Plymouth station provide insights into zooplankton composition, abundance and seasonal trends, the use of such fixed-point data or fixed-depth data for ecosystem modelling must be treated with caution due to the amplification of sampling bias effects when modelled over larger scales than covered by the data (as discussed in de Mora *et al.,* 2013). Only permanent larger scale surveys can overcome this problem. Unfortunately, these exist only for a short time span—due to a lack of permanent funding—and are therefore embedded in different projects (e.g. GLOBEC, Kühn *et al.,* 2008) with different foci. It is hence desirable to make the best use of existing surveys or to reanalyse existing data and to use stored samples from long established surveys to get a better and holistic picture of zooplankton dynamics.

Most ecosystem models use existing data sets of zooplankton to validate and tune their parameters and functions (e.g. ECOHAM, Pätsch and Kühn, 2008; ERSEM, Baretta *et al.,* 1995). The starting bulk of zooplankton is estimated so that the model predictions fit with the field data, which are usually collected in spring or summer or at a single station (e.g. Helgoland Roads time series, Boersma *et al.,* 2015). Maar *et al.* (2018) recently highlighted the need for zooplankton calibration data for ecosystem models in the North Atlantic. In these models, trophic cascades were influenced by a priori model assumptions and parameterization of zooplankton groups. Due to the lack of winter zooplankton data, modelled zooplankton is mostly validated using single-station time series. In the case of the North Sea ecosystem models like ECOHAM, the eastern English Channel is a boundary region where parameterization is difficult and

deviance is high (Girardin *et al.*, 2018). Like the rest of the North Sea, temperature has risen in this area over the past decade (Emeis *et al.*, 2015). Experimental and field studies suggested that temperature affects growth and size of zooplankton (Leandro *et al.*, 2006), but ecosystem models—with few exceptions (Baird and Suthers, 2007; Stock *et al.*, 2008)—only estimate total zooplankton biomass while size of zooplankton has rarely been implemented. This is not only a shortcoming of the models but mainly based on the fact that field surveys mostly neglect zooplankton size. Hence, individual zooplankton sizes from surveys have rarely been investigated in relation to environmental pressures so far. With the wider use of optical sensors like ZooScan (Gorsky *et al.*, 2010), Underwater Vision Profiler (Picheral *et al.*, 2010) or Laser Optical Plankton Counter (Herman *et al.*, 2004), recording and reporting of plankton size has nevertheless become more common.

In this study, we supply a spatially resolved time series of winter zooplankton abundance and size in the eastern English Channel spanning the years 1991–2013. The aim of our analysis was to investigate whether zooplankton abundance and size have changed over time and whether changes have a spatial component. We further wanted to identify if environmental factors caused these changes. We analysed trends in zooplankton size and abundance in relation to temperature, salinity, phytoplankton density, depth, Atlantic water inflow and NAO and herring larvae abundance index using stored, but so far unanalysed samples and the ZooScan optical device. We identified four areas, and in all of them, size and biodiversity showed decreasing trends while abundance of zooplankton—especially of small copepods—increased. A maximum in zooplankton abundance and a minimum in zooplankton size were determined for winter 2010/2011, when a winter plankton bloom occurred. Our statistical models found large-scale and small-scale environmental drivers to be affecting zooplankton dynamics. Herring larvae abundance seemed to be unrelated to any variables used in this analysis. The analysis will help parameterize starting conditions for North Sea ecosystem models and help accounting for winter bloom conditions if certain thresholds are surpassed.

METHOD

International herring larvae survey

The international herring larvae survey (IHLS) started under the administration of the International Council for the Exploration of the Seas (ICES) in 1967 (Gröger and Schnack, 1999). It has covered the four spawning areas of North Sea autumn spawning herring, Orkney-Shetlands, Buchan, Banks and Downs, and collected zooplankton
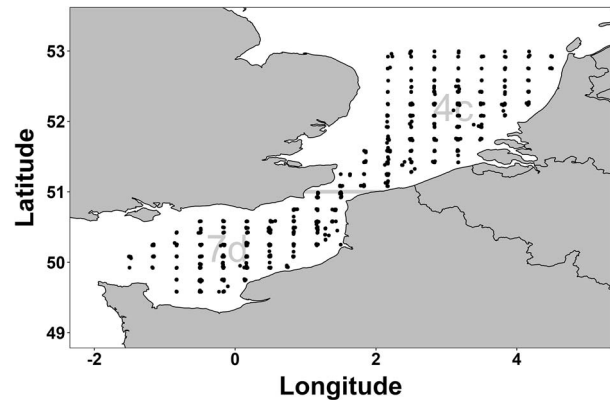

Fig. 1. Map of the English Channel showing the location of all 968 stations used for the time series analysis. Numbers refer to ICES management Areas 4c (southern North Sea) and 7d (English Channel).

and ichthyoplankton on a regular grid between September and January. Only the German samples collected each January from 1991 onwards in the Downs part of the region (ICES Areas 4c and 7d between latitudes 49.5°N and 53.5°N and longitudes 2°W and 5°E) have been stored and were thus used in this study. As displayed in Fig. 1, zooplankton was sampled on stations roughly 10 nautical miles apart using a modified Gulf III sampler ("Nackthai") with 280–335 μm mesh size (Bridger, 1958). The device was towed in an oblique fashion at 5 knots for ∼3–10 minutes depending on water depth. Samples were preserved in 4% formaldehyde–freshwater solution. The number of stations covered by the surveys varied from 20 to over 100 depending on weather conditions. Sampling took place throughout the day roughly every hour. The oblique hauls filtered the entire water column to about 5 m above the seabed. We randomly selected 50 stations each year for our analysis, except for 2009 (only 20 stations available). Unfortunately, samples for the years 1993, 1996 and 2008 were missing altogether, making it a 20-year time series between 1991 and 2013 with 968 stations.

Sample processing and ZooScan analysis

Samples were filtered with a 330-μm gaze. Formaldehyde was flushed off with freshwater and the sample content split into analysable fractions using the Motoda method (Motoda, 1959). To reach a number of particles suitable for scanning (Gorsky *et al.*, 2010), usually less than five splits were necessary (1/32). We used a ZooScan device (Gorsky *et al.*, 2010; version 2) with a 2400 dpi resolution to take images of the whole subsample. Scanning and automatic plankton identification was done by ImageJ software (version 1.41o) with ZooProcess (version 7.19) and Plankton Identifier software (Gasparini and Antajan, 2013; version 1.3.4). Yet, automatic classification

of plankton had its limits. As summarized by Vandromme *et al.* (2012), automatic classification may be biased due to contamination, e.g. copepod-shaped debris classified as a copepod. Because of the turbulent waters in the English Channel during winter, removing debris and contamination was one focus of our method development. Prior to deciding which stations to analyse, we excluded all stations with a debris fraction higher than 20% as these may have clogged the net and influenced its catchability. Further, we followed three steps to reduce the occurrence of contamination: (i) particles on the scanning tray were separated by hand, (ii) digital separation was carried out with the B/W mask function of the ZooProcess software to divide all touching objects and (iii) after classification, all particles were rechecked by eye for correct classification as the large diversity of debris shapes caused a poor performance of automatic classification (77.7% mean success rate).

Environmental data

We decided to use reanalysed and modelled data from the OPerational ECology (OPEC) database for two reasons. Firstly and despite the "Nackthai" having an integrated CTD, a full range of CTD data were not available for 240 stations, leaving considerable gaps in the environmental data time series. Secondly, zooplankton displacement is often driven by hydrodynamic conditions and less by active movement. Therefore, we also included data from the months before the survey, as earlier conditions could have affected the dynamics and distribution more significantly than the instantaneously measured hydrographic conditions. In the OPEC database, a POLCOMS-ERSEM system was used to backward model and extract sea surface temperature, salinity and chlorophyll *a* data (Allen *et al.,* 2001; Holt and James, 2001). The high correlation of the field temperature data and the modelled data ($r = 0.83$) justified the use of the OPEC database as input for the abiotic variables. Further, we used Atlantic water inflow into the North Sea from the Hamburg Shelf Ocean Model (Backhaus, 1985) as annual indicator for water exchange and the NAO Index for December as an indicator for large-scale processes.

General time series analyses

Due to the hourglass shape of the Channel region and complex hydrography, we divided the study area into different compartments depending on a similarity index of the samples. Every station was assigned to a grid cell using a 28 by 14 raster defined with the R package "raster" by Hijmans and van Etten (2013). Using all environmental and biological variables, a cluster analysis

based on Euclidean distances was applied to cluster the stations into areas. Each grid cell was assigned to the four main areas depending on the largest proportion of samples in the cell belonging to that one area. An analysis of variance with Bonferroni adjustment was carried out to test for differences between areas. For the following analyses, we used data within each compartment separately in case that trends and signals in the data were masked due to local processes and dynamics. To prepare for the visualization of trends, we rescaled the data by subtracting the variable means from the annual means and divided them by the standard deviation. This standardization procedure was used so that all variables could be used for equal scaling of anomalies in a traffic light plot. In an effort to have a higher taxonomic resolution, we further used a subset of 638 stations for the calculation of taxon-specific data. These samples were separated into 14 taxa: unidentified copepods and copepodites, *Temora sp.*, *Candacia armata*, calanoid copepods, Chaetognatha, Malacostraca, *Zoea* larvae, Cumacea, Amphipoda, euphausiids/mysids, Cladocera, Appendicularia, echinodermata and Polychaeta. All copepods and other crustaceans were only identified as copepods or malacostraca in the remaining samples. Size diversity and taxonomic diversity were calculated using the Shannon–Wiener Index (Shannon and Weaver, 1949, in Pielou, 1969). We calculated size diversity based on the Normalised Biomass Size Spectrum method of Checkley *et al.* (2008). Herring larvae abundance data were directly derived from the IHLS samples.

Generalized additive mixed models

Before applying generalized additive models, we checked for correlations between ecological variables. Temperature, salinity and chlorophyll *a* concentration were extracted for the months November, December and January from the OPEC database, and average values for those months were calculated. Due to the dynamic hydrography, we considered the previous two months as possibly affecting the zooplankton prior to sampling. Pearson correlation index was then used to determine if a certain monthly value or the overall mean was more related to the biotic variables. By applying this procedure, we avoided inflating the models explanatory power while keeping only the variables of the most relevant time period for modelling. The biotic response variables were zooplankton abundance and size. Atlantic water inflow and NAO Index from December of the previous year (NAO) were used as annual variables.

We applied generalized additive mixed models (GAMM) to investigate the significance of effects of environmental variables on zooplankton abundance and size.

To compensate for unknown annual disturbances of unaccounted natural variation, we added "year" as a random mixed effect to the model. Using the gam function provided by the "mgcv" package in R (Wood, 2006), we selected the best model by selecting only the significant variables of the model in a stepwise method. The smoothing functions were restricted to five basis dimensions to avoid overfitting and get more mechanistic relations that could be used for numerical modelling. All GAMMs were based on a Gaussian error distribution.

RESULTS

Spatial clustering

A spatial representation of the regional environmental drivers, herring larvae and zooplankton abundance as well as zooplankton size is given in Fig. 2. It verifies the different local conditions present in the study area and the distribution of herring larvae and zooplankton. Based on the composition of the clusters in a particular spatial grid cell, we identified four spatial compartments. Figure 3 shows the resulting spatial segregation. It comprises an area resembling the British North Sea coast (Area 1), an area around the Belgian–Dutch coast (Area 2), a centre region from the French coast spreading northeast into the North Sea (Area 3) and an area of Atlantic waters at the western boundary (Area 4). Analyses of variances revealed significant differences between the areas concerning average temperature, chlorophyll a concentration and zooplankton size (Table I). Areas 2 and 4 were also different from the other areas regarding zooplankton abundance. The low herring larvae abundance found in Area 2 was significantly different from the higher abundances in Areas 4 ($P < 0.001$) and 3 ($P < 0.05$), while the herring larvae abundance in Area 4 was significantly higher than those found in Areas 1 ($P < 0.001$) and 2 ($P < 0.001$).

Area 2 (close to the Rhine-Oosterschelde estuary) was the coldest and most chlorophyll rich, while Area 4 (the most western one) was the warmest and least chlorophyll rich. These areas were also the least and most saline, respectively, but the difference was only significant between these two areas and not significant regarding Areas 1 and 3. The data were split according to these areas and analysed separately to account for spatial differences in zooplankton dynamics.

General trends in zooplankton dynamics

In general, we found a significant difference between zooplankton abundance and size between the four regions.

These differences proved to be quite stable over the course of the time series as seen in Figs 4 and 5. Nevertheless, the multiannual trends in zooplankton abundance and size are similar across all regions. We found a generally decreasing size trend as seen in Fig. 4. The reduction in overall size was mainly driven by a decrease in copepod size and an increase in their abundance. Copepods made up over 90% of the zooplankton taxa found. The years 2010–2013 showed exceptionally low mean zooplankton sizes (839.2 ± 64.85 μm ESD) compared to the overall mean size (978.9 ± 103.62 μm). This decreasing size trend was correlated with the increased abundance of smaller copepods and copepodites ($P < 0.05$). Most non-copepod taxa also decreased in mean size, which implies that it was not only a composition effect. The higher standard deviations in size for Areas 1 and 4 indicate higher zooplankton diversity, which rendered the negative size trend in Area 4 insignificant. Yet, the mean size decreased visibly in both areas. In conjunction with the reduced size, zooplankton abundance was elevated from 2010 to 2013 (Fig. 5). Before 2010, comparatively lower annual mean abundances were observed.

In Area 2, zooplankton abundance was the highest while size was the lowest (Table I). Area 4 on the other hand showed the lowest abundance and largest size of zooplankton. Abundance and size in the northern and central part of the study area, Areas 1 and 3, respectively, were of intermediate level, but showing the same temporal trends as the other areas. These findings support the view that the English Channel is a very dynamic area with spatial differences in zooplankton abundance and size. Hence, the English Channel and southern North Sea should not be treated as one region for studying zooplankton.

Most taxonomic groups showed a negative size versus abundance relation with fewer, but larger individuals at the beginning of the 1990s, followed by a period of variable sizes and abundances in the 2000s and very abundant, but small zooplankton since 2011 (Fig. 6). Most of the size-related and environmental data declined in this area (top part of Fig. 6). Abundance indicators, however, have increased over time. Considerable variability was evident for all variables. For example, temperature generally increased, but very cold winters like 1996/1997 deemed the trend insignificant over the considered period. Chlorophyll a concentration was elevated since 2010. Mean salinity varied only slightly and remained on a comparatively high level between 1994 and 2010.

Drivers of change

Despite unusually high chlorophyll a concentrations in the entire study area since 2011 and a slow warming of
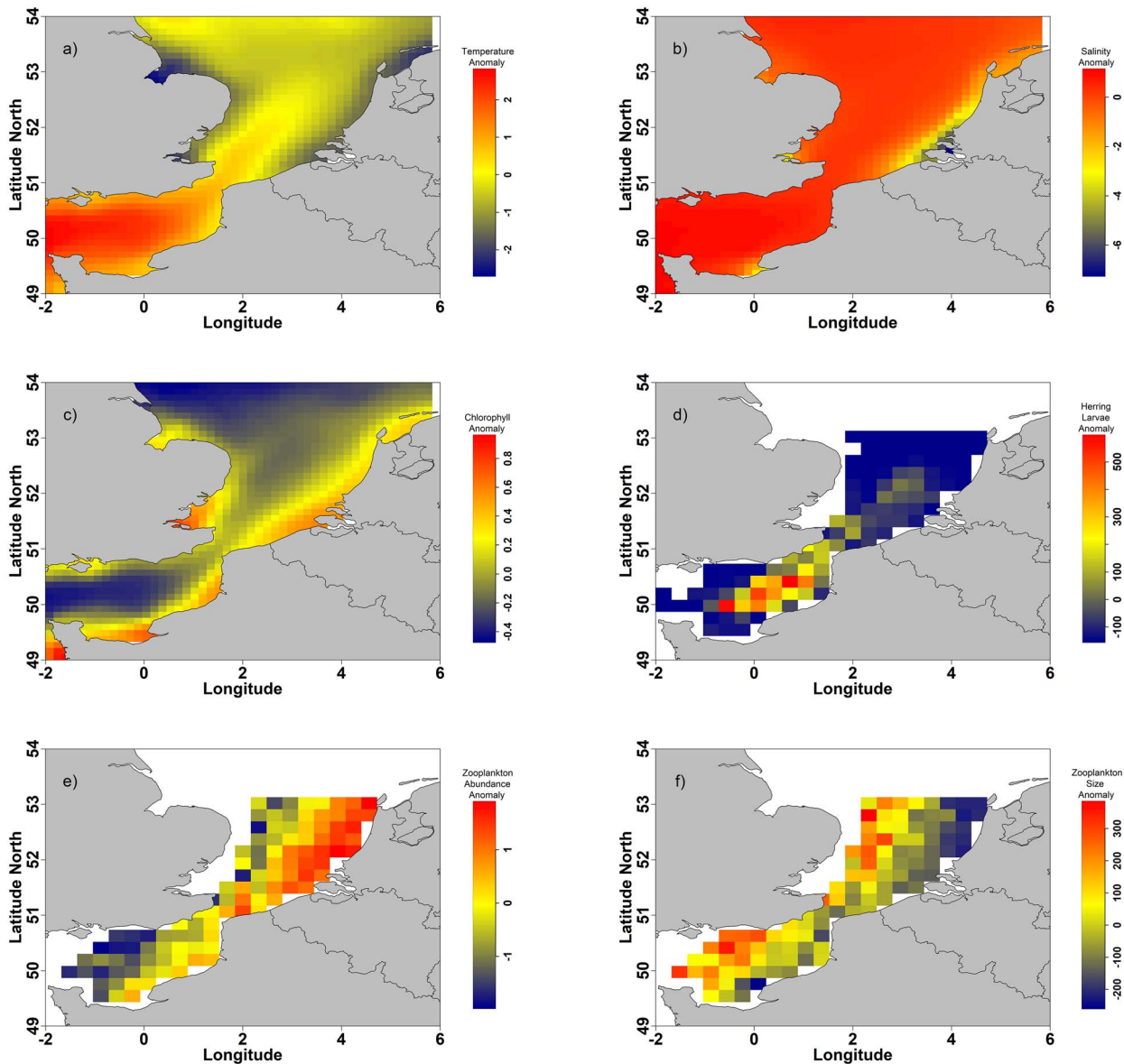
Fig. 2. (a–f) Spatial representation of temperature (a, °C), salinity (b, psu) and chlorophyll *a* (c, mg C m^{-3}) from the POLCOMS-ERSEM Model used for this analysis as the mean cellwise anomaly from the global mean of the study area. Spatial distribution of herring larvae abundance (d, N m^{-3}), zooplankton abundance (e, log N m^{-3}) and zooplankton size (f, μm ESD) as anomaly from the global mean of the study area.

the water, there was no significant linear trend in winter chlorophyll *a* concentration, temperature and salinity over the 20-year period. Correlation analysis revealed that the mean value between November, December and January had a higher explanatory power than any specific month. Therefore, the 3-month means were used for the GAMM analysis. A very cold winter of 1997 and high interannual variance asked for non-linear methods such as GAMMs to be used for the identification of potential environmental drivers. The addition of year as a random effect factor improved the overall performance and the

residual structure of the generalized additive models. All models resulted in including large-scale and small-scale influences as well as depth as a spatial indicator (Tables II and III). NAO was included as a significant variable of abundance models in all four areas and in Areas 2 and 3 of the size models. It indicates the influence of large-scale mechanisms in this region. For zooplankton size, the large-scale influence seemed to be better represented by Atlantic water inflow as it appeared in every model except for Area 3. Temperature and chlorophyll *a* concentration resembled the most important environmental drivers for

Table I: Regional ecosystem characteristics

		Area 1	Area 2	Area 3	Area 4
Temperature	Mean	6.88	6.40	7.85	8.96
°C	SD	0.94	0.98	0.82	0.72
	Trend	0.03	0.02	0.03	0.01
	ANOVA	***	***	***	***
Salinity	Mean	33.97	32.86	34.15	34.60
psu	SD	0.41	0.77	0.33	0.20
	Trend	−0.01	−0.01	0.01	0.00
	ANOVA		***	***	***
Chlorophyll *a*	Mean	0.43	0.81	0.61	0.32
mg C m⁻³	SD	0.14	0.28	0.19	0.11
	Trend	0.01	0.01	0.01	0.01
	ANOVA	***	***	***	***
Zooplankton	Mean	165.02	676.57	181.78	43.17
N m⁻³	SD	176.51	637.09	137.16	29.89
	Trend	16.28**	48.54*	9.16*	1.81
	ANOVA		***		***
Zooplankton Size	Mean	1012.32	829.01	956.91	1150.09
µm ESD	SD	155.82	82.65	100.73	131.92
	Trend	−16.70***	−7.65**	−9.16**	−8.17
	ANOVA	***	***	***	***
Herring Larvae	Mean	48.35	41.42	249.36	391.33
N m⁻²	SD	122.19	62.72	342.43	694.36
	Trend	8.63*	3.44	30.60**	63.57**
	ANOVA	*, not with Area 2	*, not with Area 1	*, not with Area 4	*, not with Area 3

ANOVA, analysis of variance; SD, standard deviation; *, level of confidence; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
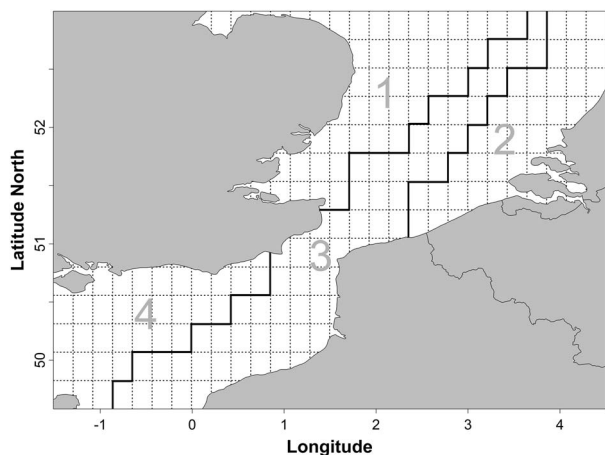

Fig. 3. Map of spatially segregated compartments as revealed by cluster analysis. Underlying raster grid and area identification number shown in grey.
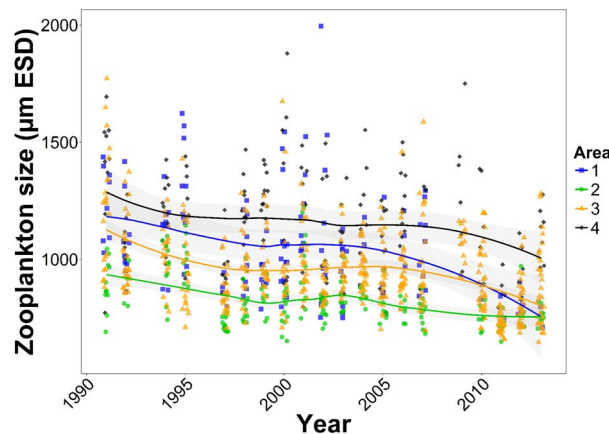

Fig. 4. Mean size of zooplankton per station and year as equivalent spherical diameter (µm ESD). Solid lines are based on Loess smoothing function per cluster area with the shaded area representing the standard error.

zooplankton abundance. For the regions influenced by North Sea waters, Areas 1 and 2, chlorophyll *a* concentration explained most of the deviance in the data. In contrast to our expectations, size was not related to temperature. Variations in chlorophyll *a* concentration significantly explained zooplankton size in the Atlantic water-influenced waters, Areas 3 and 4, whereas size was mainly explained by depth and inflow or NAO in Areas 1 and 2. Salinity was only a significant predictor variable in Area 1.

All in all, zooplankton abundance was influenced by local as well as large-scale mechanisms. Local drivers like temperature and chlorophyll *a* defined the annual differences in zooplankton abundance and size between the regions. Large-scale drivers like NAO were responsible for the multiannual trends across all regions. These mechanisms explained between 0.414 and 0.615 of the deviance. GAMMs for zooplankton size reached an explained deviance between 0.24 and 0.54. Temperature showed a positive effect up to 8.9°C. Beyond 9°C, the

Table II: Drivers of zooplankton abundance

Area	Best model	Random	Expl. dev.
1	Chlorophyll, salinity, depth, NAO_{Dec}, inflow		0.615
2	Chlorophyll, temperature, depth, NAO_{Dec}	Year	0.527
3	Temperature, depth, NAO_{Dec}	Year	0.542
4	Temperature, depth, NAO_{Dec}		0.414

Components of best GAMM model and random year component as well as the explained deviance of the model.

Table III: Drivers of zooplankton size

Area	Best model	Random	Expl. dev.
1	Depth, salinity, inflow	Year	0.444
2	Depth, NAO_{Dec}, inflow	Year	0.536
3	Chlorophyll, depth, NAO_{Dec}	Year	0.389
4	Chlorophyll, depth, inflow		0.237

Best GAMM model components and random year component. Explained deviance of the best model is also shown.
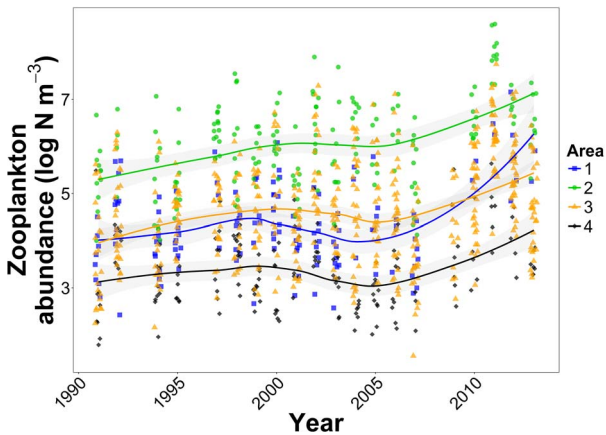

Fig. 5. Zooplankton abundance as mean number per cubic metre per station and year (natural logarithmic scale). Solid lines are based on Loess smoothing function per cluster area. Shaded area represents standard error.

relationship was negative. Overall, higher temperature resulted in a more negative effect on zooplankton size. Each area exhibited similarly shaped smoothing functions for the environmental drivers as shown in Fig. 7 a–d. Chlorophyll *a* concentration showed an increasing positive effect on zooplankton abundance after a certain threshold. This was 0.8 mg C m⁻³ in Area 2 and 0.45 mg C m⁻³ in Area 1. We also found this threshold-like influence of chlorophyll *a* concentration in Area 4 (0.3 mg C m⁻³) and Area 3 (0.45 mg C m⁻³), but the small number of data points at the positive end of the curve deemed these insignificant. Above-threshold concentrations of chlorophyll *a* coincided with the elevated abundances of small copepods in Area 2. It therefore suggests a bottom-up relationship resulting in a winter plankton bloom in 2011 in this region. Increasing depth was generally

negatively associated with zooplankton abundance and positively with zooplankton size. A neutral NAO index affected zooplankton abundance positively between −0.4 and 0.5. Once reaching beyond these, from −0.4 to −1 and from 0.5 to 2, the NAO negatively affected zooplankton abundance. Extreme anomalies beyond these NAO index values had a very positive effect. This was mainly due to the fact that the NAO index between 2010 and 2012 was extreme (−1.88; −1.80 and 2.25, respectively), which correlated well with the highest abundances and smallest zooplankton sizes during these years. It confirms the potentially combining effects of large-scale and small-scale influences on local zooplankton dynamics.

DISCUSSION

In our analysis, we could show that there is interannual variability in zooplankton dynamics also during winter. Zooplankton abundance was, of course, generally low compared to annual averages reported elsewhere (3064.31 N m⁻³ at L4 station, Eloire *et al., 2010*; 3308.33 N m⁻³ at Gravelines, ICES, 2013; Antajan *et al., 2017*). Zooplankton size decreased over time, while zooplankton abundance increased during the study period. These trends were evident in all of the four identified areas, which enabled us to reject the hypothesis that local differences of trends exist. Indicators of these large-scale effects were NAO and Atlantic water inflow. They showed a strong influence on zooplankton size. Years with a high NAO and strong inflow, such as in the year 2000, coincided with the higher abundance of larger zooplankton, whereas in 2011, higher abundances of small zooplankton coincided with low NAO and reduced
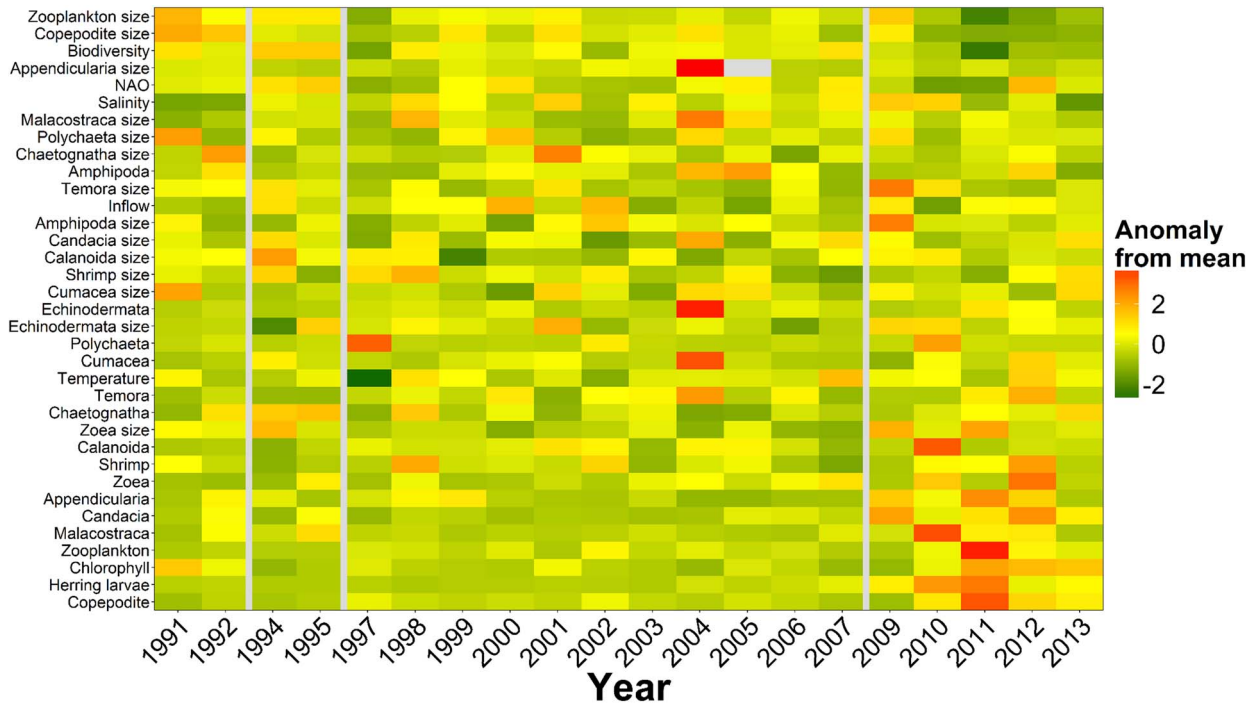
Fig. 6. Traffic light plot with all environmental and biological variables considered in the analysis. Colours display annual deviation from the overall mean per variable. Missing years 1993, 1996 and 2008 are marked as grey vertical lines. Especially, the period 2010–2013 stands out of the overall variability. Grey tiles represent missing data.

inflow. This is most likely due to the shift in zooplankton composition that showed a gradient from west to east (Pitois and Fox, 2006) and varied during recent decades (Alvarez-Fernandez *et al.*, 2012). High NAO and a strong inflow from the Atlantic into the North Sea will drive more of the larger western individuals into the English Channel and southern North Sea, raising the average size of zooplankton. This is reflected in our study of zooplankton size in the different spatial clusters. Area 2 off the Dutch and Belgian coasts contained most of the small- to medium-sized copepods, while Area 4, the most western part of the study region, contained comparatively more quantities of larger calanoid copepods as well as individuals of the large copepod *C. armata*. The difference in copepod composition was also reflected by the size diversity and taxonomic diversity, which were highest in Area 4 and lowest in Area 2. Nevertheless, the generally decreasing size trend of individual organisms could be attributed to rising water temperatures. Halsband and Hirche (2001) found a negative correlation between temperature and size of individuals of *Temora longicornis* in the North Sea. These cold water-adapted species made up a majority of the copepods in the samples, and our results support the findings that a rise in temperature negatively affects copepod size, although these signals

may be masked by composition changes. Overall, our results indicate a change in community size composed of a decrease in individual body size and decrease due to a higher proportion of small species and development stages, which supports the ecological hypotheses on the effects of global warming discussed by Daufresne *et al.* (2009).

In contrast to zooplankton size, the increasing trend in zooplankton abundance was mainly a response to slightly rising water temperatures and higher concentrations of chlorophyll *a*. These findings largely contradict the results of Bedford *et al.* (2020), who found a large-scale decrease of holoplankton on the northeast Atlantic shelf and North Sea. Due to the lack of data, no conclusive results could be found for the eastern English Channel region in Bedford's study. In our study, we may thus show a local phenomenon or a temporal phenomenon since most of the changes in zooplankton were attributed to summer abundances in Bedford *et al.* (2020). Schmidt *et al.* (2020) also argued that most changes in phytoplankton composition and abundance occurred in summer. Our results support several hypotheses that rising water temperatures may alter the zooplankton taxonomic and size composition (Daufresne *et al.*, 2009; Bedford *et al.*, 2020), has a combined effect with large-scale and small-scale
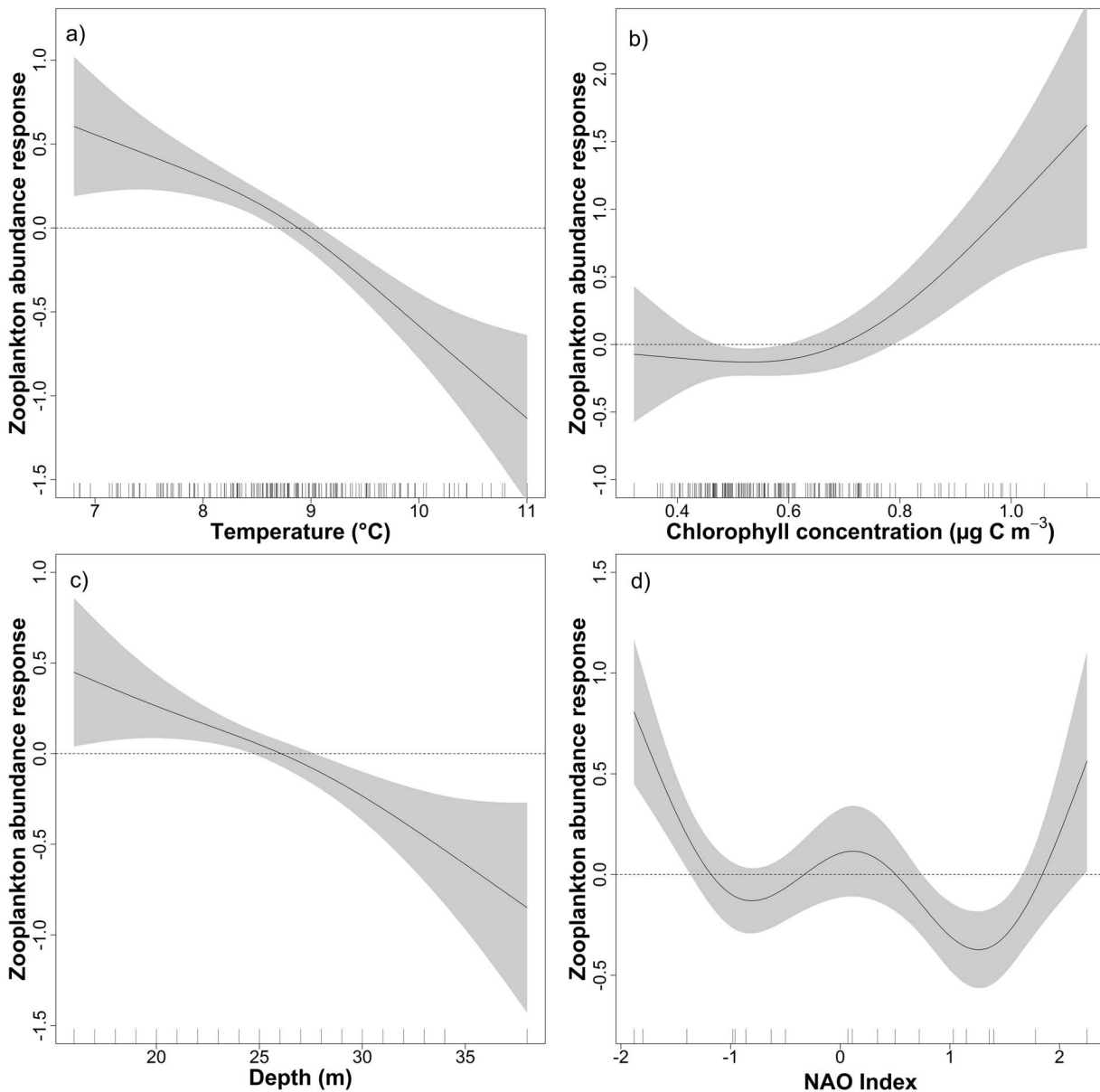
Fig. 7. (a–d) Smoothing functions of temperature (a), chlorophyll *a* concentration (b), depth (c) and NAO index (d) as explanatory variable for zooplankton abundance in Area 2.

factors such as NAO and riverine input and that rising water temperatures change the timing of primary production (Capuzzo *et al.*, 2018). In this respect, more studies are needed to investigate the trophic dynamics between winter, spring and summer with regard to potential winter primary production and its effect on spring and summer production. Food limitation is a common reason for the delay of secondary production in many zooplankters (Durbin *et al.*, 2003). An increase in temperature with a simultaneous increase in food supply may thus trigger the

hatch and survival of copepod nauplii and copepodites, starting an early food chain in winter and leading to higher abundances of zooplankton. While this causality holds true for much of the time series, chlorophyll *a* levels and zooplankton abundance were high in 2011 despite low water temperatures. Durbin *et al.* (2003) already documented a similar scenario in the Gulf of Maine, where a winter plankton bloom occurred in 1999 that led to an increase of zooplankton. Durbin et al. argued that the cold, less saline shelf waters helped stratify the water

column, enabling phytoplankton to stay above critical depth. The elevated chlorophyll *a* concentration and very high abundance of small copepods in Area 2 of our study region indicate that a similar winter bloom occurred in early 2011. Phytoplankton and zooplankton data at Gravelines station in the English Channel support our findings (ICES, 2013). The occurrence of the plankton bloom mainly in Area 2 near the Rhine-Oosterschelde estuary, with about 2200 m³ s⁻¹ of discharge the greatest riverine freshwater source of the North Sea (Berendsen, 2005), suggests a similar source for stratification and improved conditions for primary producers. McQuatters-Gollop *et al.* (2007) also indicated that North Sea primary production is limited by light and low temperatures during winter. Our results further support the hypotheses by Capuzzo *et al.* (2018) that van Leeuwen *et al.*'s (2015) permanently mixed areas are less productive than freshwater-influenced areas, which corresponds to Area 2 in our study. Yet, there is no documentation that the strong mixing in the eastern English Channel has been overcome by freshwater input to form a stratified water column and better light conditions for phytoplankton. In essence, the combination of increased food supply and low energy demand due to low temperatures could have been the cause for enhanced zooplankton growth in Area 2 (Gillooly *et al.*, 2001).

The numbers of herring larvae caught on the survey were independent of both environmental and biological variables. Our study suggests that the missing relationship may be rooted in the spatially separated congregations of herring larvae and zooplankton. Highest abundances of zooplankton were recorded in Area 2, while herring larvae were largely located in Area 4 and the western part of Area 3. The majority of herring larvae caught was less than 16 mm in size and mostly fed on plankton smaller than 500 μm ESD (Hufnagl and Peck, 2011), which is the effective minimum size of the modified Gulf III net catches. Hence, it can be excluded that herring larvae had a direct predatory effect on the analysed zooplankton in Areas 3 and 4. What the effect of the grown herring larvae will be when they have been transported by the currents to Area 2, where large quantities of small prey are located, cannot be examined here and will require more studies on samples taken later in the season. The identified chlorophyll *a*–zooplankton relation suggested potential secondary production if certain thresholds are overcome as shown by the generalized additive models (Fig. 7b). When the growing herring larvae reach Area 2, and the zooplankton standing stock found there, the predator–prey connection could provide more details on herring larvae survival. In this case, it would be necessary to sample zooplankton and herring larvae after the IBTS0 survey (International Bottom Trawl Survey for 0-ringer

herring) in February. It needs confirmation whether the local hotspot of winter primary and secondary production near the Rhine-Oosterschelde delta persists. If so, it could explain the enhanced survival of Downs herring larvae in recent years (Fässler *et al.*, 2011).

CONCLUSIONS

There are large-scale effects like NAO index and the Atlantic water inflow that alter the composition of zooplankton in the east English Channel. While we identified four separate regions in this area with differences in zooplankton abundance and size, a decrease in both response variables was observed for the entire study region and could be linked to a general increase in temperature and phytoplankton biomass. This led to a winter bloom situation in 2011. Why the cold year of 2011 supported enhanced phytoplankton and zooplankton growth remains unclear. It could not be linked to physical conditions nor herring larvae abundance and needs further investigations with spatially resolved environmental data.

DATA ARCHIVING

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