A century of change in North Sea plankton communities explored through integrating historical datasets

Jacob Bedford[a], David Johns[b] and Abigail McQuatters-Gollop[a]

[a]Centre for Marine Conservation and Policy Research, Plymouth University, Drake Circus, Plymouth, UK, PL4 8AA

[b]The Marine Biological Association, The Laboratory, Citadel Hill, Plymouth, UK, PL1 2PB

Corresponding author: Jacob Bedford, jacob.bedford@plymouth.ac.uk

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Abstract

Plankton communities make useful ecosystem indicators, and taking a historical perspective on plankton community composition provides insights into large-scale environmental change. Much of our understanding of long-temporal scale change in plankton communities in the North Sea has been provided by the Continuous Plankton Recorder (CPR) survey, operating since 1931, with consistent time-series data available since 1958. This paper further increases the temporal scale of our understanding of community change in the North Sea by combining the CPR dataset with a digitised collection of plankton surveys undertaken by ICES from 1902 to 1912. After steps taken to integrate the two disparate datasets, differences in overall community composition between time-periods suggest that the multidecadal changes observed through the CPR survey time-period may have occurred from a non-stable baseline that was already on a trajectory of change. Therefore, a stable historical time period in which plankton communities are assessed against for any impact of human pressures may be hard to define for the North Sea and instead underlying variation needs to be encompassed within any baseline chosen. Further evidence for the influence of large scale changes in SST driving change in plankton community composition was found using the extended dataset.

1 Introduction

Climate change is causing widespread changes in marine ecosystems, superimposed on a background of climate variability that acts at different temporal scales (Hoegh-Guldberg and Bruno, 2010). Plankton communities are sensitive to changes in the physical marine environment, and have been shown to be responsive to interannual and multi-decadal climate variability as well as anthropogenic climate change (Hays et al., 2005). As the base of the pelagic food web, phytoplankton are primary producers (Boyce and Worm, 2015), transferring energy through zooplankton to higher trophic levels (Richardson, 2008). This sensitivity to environmental conditions and their role in the pelagic foodweb makes tracking plankton community change useful as an indicator of change in the wider ecosystem. Much of our understanding of multi-decadal change in plankton communities in the North Sea comes from the Continuous Plankton Recorder (CPR) survey (McQuatters-Gollop et al., 2015). Consistent monitoring data available from 1958 through the present has documented widespread shifts in both phytoplankton and zooplankton communities, specifically the occurrence of basin-scale regime shifts in the North Atlantic (Beaugrand et al., 2014; Reid et al., 2015).

The value of plankton time series as evidence for policy and management increases with time. Through using long temporal scale data, the influence of multi-decadal changes in environmental conditions on plankton communities can be investigated, and the most important environmental influences structuring plankton communities on this scale can be identified (Edwards et al., 2010; Giron-Nava et al., 2017). For example, the Atlantic Multidecadal Oscillation is a term for the natural low-frequency SST variability in the North Atlantic that oscillates between warm and cool phases on a ~60yr time scale (Edwards et al., 2013). It has been identified as the second largest macroecological signal in North Atlantic plankton communities, but requires long temporal-scale time-series in order to detect the influence of transitions between oscillatory phases on community change (Edwards et al., 2013). Furthermore, the long temporal scale of the CPR survey can help separate these wider oceanographic and climatic influences on plankton communities, such as the influence of SST, from direct anthropogenic pressures such as eutrophication, which is particularly useful during formal policy assessments (McQuatters-Gollop et al., 2015).

’Rescuing’ historical ecological datasets, that otherwise may be lost or deemed redundant, has been identified as a useful way of increasing temporal scale in ecological studies, and can be used to address contemporary marine policy challenges, including understanding effects of long-term climate change (Hawkins et al., 2013). Specifically, the use of rescued historical datasets in avoiding 'shifting baselines syndrome' in biodiversity state has received much attention (Pauly, 1995). This is the phenomenon where neglecting historical changes obscures the magnitude of change or variability in ecosystem components. Therefore, rescued historical plankton data can be a tool for avoiding shifting baseline syndrome in our understanding of the multi-decadal dynamics of plankton communities (Ward et al. 2008). The ICES historical plankton dataset used in this study is a dataset of plankton samples collected in the North Atlantic between 1902 and 1912, digitised from historical log books. Hällfors et al. (2013) compared phytoplankton records from this 'rescued' ICES historical dataset in the Baltic Sea with contemporary phytoplankton samples, and documented compositional differences between the two time periods, potentially driven by both climate change and eutrophication. By comparing the ICES historical dataset with North Sea data from the CPR survey, we can better understand changes occurring in North Sea plankton communities pre-1950s, facilitating further exploration of the effects of large scale temperature change to the Continuous Plankton Recorder temporal coverage.

Disparities in sampling and analysis methodologies between the ICES historical data and the CPR survey, however, present challenges in their direct comparison, which need to be addressed before using the datasets together. Handling disparate data-types is a key challenge facing regional scale monitoring and assessment where data from multiple different sampling programmes often needs to incorporated (Olli et al., 2013; Zingone et al., 2015). For example, the OSPAR IA2017 regional-scale assessment of plankton communities incorporated multiple time-series from across Europe, where taxa were sampled using different methods, and analysed to differing taxonomic resolutions (OSPAR, 2017). In this study, by integrating and combining the CPR historical time series with the rescued ICES historical dataset, we aim to provide additional contextual information to the changes in North Sea plankton communities between 1958 and 2015 detected by the CPR survey, specifically to address the following questions:

- **Is there a difference in plankton community structure (both phytoplankton and zooplankton) between the early 20th century and the beginning of the consistently-sampled CPR time period (1960s)?**
- **Which plankton communities and individual taxa are most responsive to SST when examining the two datasets combined (1902-12, 1958-2015)?**

2 Data and Methods

2.1 Data sources

2.1.1 Plankton samples

Data from the period 1902-1912 have become available through the ICES historic plankton digitisation project where 13,379 plankton samples have been digitised from seven historical ICES volumes (McQuatters-Gollop et al. 2011). The data are collated from different sampling programmes, across the North-East Atlantic, North Sea, Irish Sea, Baltic Sea and Arctic Sea. After digitisation, data tables from the historical volumes were quality checked. The samples are all spatially referenced and consist of records of taxa at the presence/ absence level or with semi-quantitative abundance information. In this study, we used all data at the presence/absence level, as to be able to compare with the Continuous Plankton Recorder survey data. We extracted data from the months February, May, August and November, as these had the greater numbers of samples. This historical plankton dataset is now freely available via the ICES data portal (ecosystemdata.ices.dk/HistoricalPlankton/Download.aspx).

The Continuous Plankton Recorder survey has been collecting samples in the North Sea on a routine, consistent basis since 1958 (Kirby and Beaugrand, 2009). CPRs consist of a filtering mechanism housed in an external body that is towed behind ships of opportunity at a depth of approximately 6-7m. The speed at which the silk is drawn from a storage spool is controlled by a propeller, with 10.16 cm of silk corresponding to 18.5 km of tow through the sea (Batten et al., 2003). CPR data for the months February, May, August and November were obtained for the North Sea area for phytoplankton (DOI 10.7487/2016.236.1.999) and zooplankton (DOI 10.7487/2016.236.1.998). Although abundance information is collected for each taxon identified on each sample, for this study data were converted to presence/absence to make comparable to the ICES historical database.

As well as differences in quantitative resolution between the datasets, there are major structural differences between the historical ICES surveys and the CPR survey (McQuatters-Gollop et al. 2010). Firstly, the CPR is a continuous plankton sampling method, using a 270 micron mesh size silk (Richardson et al., 2006).The ICES database, in contrast, consists of net samples, , collected at fixed point locations by a multitude of disparate sampling cruises by northern European nations. Therefore, whereas the analysis methodology has remained consistent throughout the CPR series, the composite nature of the ICES dataset means that the sampling and analysis methodologies are not reliably consistent throughout the database. However, both sampling methodologies incorporated sub-sampling, where only a proportion of the sample is analysed, reducing any differences as a result of volume of water filtered (e.g. Hällfors et al. 2012).

The mesh sizes of the net samples in the ICES historical database are missing from the sample metadata, and are likely to be varied. The mesh size of the Continuous Plankton Recorder, 270 microns, is larger than the majority of standard plankton nets, which tend to range between 5µm - 80 µm for phytoplankton and 125 µm – 200 µm for zooplankton (John et al., 2001; Castellani and Edwards, 2017) . Importantly therefore, any biases in sampling as a result of mesh size differences between the ICES historical plankton dataset and the CPR data are likely to come from the side of the CPR survey, evidenced by a lower number of species recorded overall than the ICES historical dataset. For example, CPR methodology likely undersamples smaller phytoplankton taxa, although they often are retained on the silk strands of the mesh (taxa as small as 5-10 µm are regularly recorded), which constitutes 30-40% of the mesh area (Batten et al., 2003)Similarly, the CPR survey likely undersamples small zooplankton taxa. A previous study however, comparing CPR data to net samples taken at the L4 sampling station in the Western English channel, that used a mesh size of 200 microns, concluded that although the abundance of zooplankton taxa were generally lower, all dominant zooplankton species recorded at L4 were also common to CPR data (John et al., 2001). In this study, occurrence frequencies of select plankton taxa, based on presence/absence resolution data, were compared between datasets.

Samples from both datasets located in the North Sea region were divided into a ‘Northern’ North Sea region and a ‘Central/Southern’ North Sea region based on the border between ICES regions 4b and 4c (Figure 1). The two spatial areas represent a balance between the need for spatial specificity in comparing plankton communities with known differences occurring across latitudes, and the retention of a reliable sample size within each area. To ensure the depth of the ICES samples were comparable to the CPR dataset all ICES historical samples collected below 15m, or vertical hauls that started below 15m were removed from the resulting sample list, along with samples for which no depth information was given. To compare plankton communities from the same area, CPR samples within half a degree of the ICES historical sample locations were then selected.

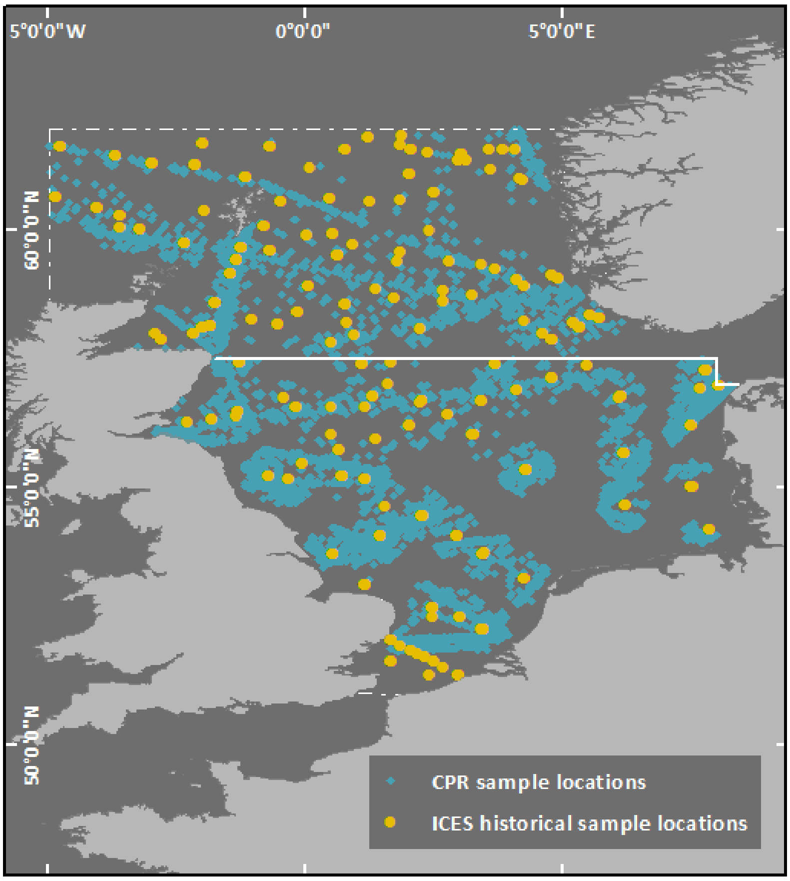

Figure 1. *Location of historical samples (large yellow) and centre points of CPR samples (small blue), included in the study. North Sea area (dashed white line) divided into 'Northern' and 'Central/Southern' areas based on the boundary between ICES subregions 4b and 4c (solid white line).*

2.1.2 Sea surface temperature (SST) data

Monthly SST data were downloaded for the North Sea region from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) at a 2 degree resolution. Data points were extracted from the Northern and Central/Southern North Sea area, and averaged for each year between 1902 and 2015.

2.2 Data preparation

Taxa lists of both phytoplankton and zooplankton were extracted from the historical ICES and CPR databases and both the ICES taxa lists and the CPR taxa lists were run through the Taxon Match Tool available on the WoRMS

(World Register of Marine Species) website (http://www.marinespecies.org) to update all names to the most up-to-date accepted nomenclature. Due to the ICES database being a composite of multiple sampling programmes, sporadically occurring taxa were removed, as these may not have been recorded or identified inconsistently between the different sampling programmes. For both datasets, a threshold of 1% frequency of occurrence was selected as a cut-off point for taxa to include in analyses of taxonomic composition. This represented a balance between the need to remove sporadic taxa, as highlighted by Hällfors et al. (2013), but still include rare species in analyses. Because of the decade time-span of the ICES historical dataset, this list for the CPR data was constructed based on a 1% occurrence frequency threshold *in any decade* , to ensure consistency.

The taxa lists differed in the taxonomic resolutions of recorded taxa. As the CPR time-period is the longer of the two, and the taxa are generally more coarsely taxonomically resolved, the taxa within the ICES list were aggregated to their equivalent resolution within the CPR taxa list. For example, the CPR taxon name 'Radiozoa' is a phylum, whereas in the ICES taxa list there were four taxon names within the phylum Radiozoa. These taxa were therefore aggregated to the coarser CPR resolution. In some cases, new groups were constructed to aggregate multiple taxa. 'Gelatinous zooplankton' was created as Cnidarians and Ctenophores were sometimes recorded as 'Coelenterata' within the ICES dataset. This nomenclature is outdated, and is not a monophyletic group, and so it would be impossible to determine whether these records related to '*Cnidaria*' taxa or '*Ctenophora*' taxa. Some taxa had resolutions too low for aggregation, for example records of '*Crustacea*' with associated life stages 'larvae' or 'nauplius'. Samples containing these records were removed before analysis, so the low taxonomic resolution did not skew results. Lastly, taxa that are not consistently recorded throughout the CPR time series, as a result of analysis changes, were removed. Similarly, any taxa within the ICES taxa list that would not be reliably sampled by the CPR due to their small size or delicate nature were removed, thus reducing biases from differing mesh sizes.

After integrating the taxonomic nomenclature and resolution of the two taxa lists, of taxa that occurred in over 1% of samples, 39 phytoplankton taxa and 27 zooplankton taxa were unique to the ICES list, whilst 10 phytoplankton taxa and 13 zooplankton taxa were unique to the CPR list. These differences could represent large changes in occurrence frequency over the time period, but could also still be a result of sampling biases between the two datasets, for example though different mesh sizes. We therefore only used taxa that occurred in over 1% of samples in both datasets. These lists of common phytoplankton and zooplankton taxa shared between the two datasets represented taxa that were assumed to be consistently sampled by both surveys (Hällfors et al., 2013), further minimising biases from differing mesh sizes , and consisted of 44 phytoplankton taxa and 30 zooplankton taxa respectively (Table 1). Records of these shared common taxa were then extracted from the CPR and ICES samples, before determining the occurrence frequency of each taxon for each sampling month. Months with fewer than 5 samples were removed before analysis.

Table 1. *'Matching' taxa lists, at aggregated taxonomic resolution, used in analysis*

Phytoplankton Matching List

Diatoms

Asterionellopsis glacialis	*Navicula spp.*
Bacillaria paxillifera	*Odontella aurita*
Bacteriastrum spp.	*Odontella sinensis*
Bellerochea horoglacialis	*Paralia sulcata*
Ceratoneis closterium	*Proboscia alata*
Chaetoceros spp.	*Pseudo-nitzschia delicatissima*
Corethron spp.	*Pseudo-nitzschia seriata*
Coscinodiscus spp.	*Rhaphoneis amphiceros*
Coscinodiscus concinnus	*Rhizosolenia hebetata f.semispina*
Ditylum brightwellii	*Rhizosolenia setigera*
Eucampia zodiacus	*Rhizosolenia styliformis*
Fragilaria	*Skeletonema costatum*
Guinardia delicatula	*Thalassionema spp.*
Guinardia striata	*Thalassiosira spp.*
Halosphaera spp.	*Thalassiothrix longissima*
Lauderia danicus	

Dinoflagellates, silicoflagellates and haptophytes

Ceratium fusus	*Tripos furca*
Ceratium horridum	*Tripos lineatus*
Ceratium tripos	*Tripos longipes*
Dictyochophyceae	*Tripos macroceros*
Dinophysis spp.	
Gonyaulax	
Phaeocystis	
Prorocentrum spp.	
Protoperidinium spp.	

Zooplankton Matching List

Holoplankton

Acartia spp.	*Oithona spp.*
Anomalocera patersoni	*Para-Pseudocalanus spp.*
Appendicularia spp.	*Paraeuchaeta norvegica*
Calanus spp.	*Podon spp.*
Centropages spp.	*Temora longicornis*
Centropages hamatus	*Thecosomata*
Centropages typicus	*Tintinnidae*
Chaetognatha spp.	
Copepoda spp.	
Corycaeus spp.	
Euphausiacea spp. and Mysida spp.	
Evadne spp.	
Foraminifera spp.	
Isias clavipes	
Labidocera wollastoni	
Metridia lucens lucens	

Meroplankton

Bivalvia spp.
Bryozoa spp.
Cirripedia spp.
Decapoda spp.
Echinodermata spp.
Pisces spp.
Polychaeta spp.

2.3 Multivariate analysis

To investigate whether significant change occurred in the plankton community between the ICES historical time-period and the beginning of the time-period covered by the CPR survey, we tested for an effect of time period (historical dataset, 1902-1912, to the 1960s decade of the CPR time period) on plankton community composition using multivariate generalised linear models with the '*mvabund*' package in R (Wang et al., 2012). This method fits a generalised linear model to each taxon separately, and then gives a summed likelihood ratio for the given predictors for each model, which can be used as a test statistic ('Sum-of-LR') for the effect of predictors on the community as a whole. Resampling is then done at the whole-sample level (here the sampling month) to test for significance while accounting for correlations between taxa (Wang et al., 2012). The method accounts for a mean-variance relationship in the data (Warton et al., 2012). The generalised linear models were fitted for the occurrence frequency of each taxa in each sampling month, with a complementary log-log link to accommodate the proportional, binomial data (Wang et al., 2012). For each model, the log of the sampling month occurrence frequency total was used as an offset as an approximate method of analysing relative compositional change, and weights were included so that sampling months with higher sample sizes were given stronger weighting. We extracted the univariate statistics for each taxon in the model, to examine the contribution of each taxon to any overall effect.

Furthermore, we visualised change in the plankton community over the extended time period using non-metric Multidimensional Scaling (nMDS) ordination plots. Plots were constructed for each area and plankton type using the vegan package in R (Oksanen et al., 2007). These were constructed based on the relative occurrence frequency of each of the matching list taxa in each sampling month. .

After testing for the effect of time period on community composition, we tested whether SST difference between the two periods could explain any observed differences in community composition using multivariate generalised linear models. Here, models including SST were compared to models including SST and time-period, as a significant effect of time-period over and above SST suggests there is variation between the time-periods not explained by changes in SST alone. Lastly, we tested for any overall effect of SST on plankton community composition, over the whole extended time period, when examining the two datasets combined. Models with SST and season as predictors were compared against models with just season as a predictor to look for the influence over and above seasonality.

3 Results

3.1 Changes in plankton community composition over time

Significant differences in overall community composition were found for both phytoplankton and zooplankton in both the Northern and Central/Southern North Sea areas, suggesting a change in the North Sea plankton community between the beginning of the 20^{th} century and the 1960s. The zooplankton communities showed a stronger overall difference, with larger overall summed likelihood ratios for an effect of time period, despite a lower number of taxa within the list of shared common taxa (Northern North Sea: Sum-of-LR= 1891.3, p= 0.004; Central/Southern North Sea: Sum-of-LR= 2355.5, P=0.003). In contrast, the overall effect of time period, although significant, was lower for phytoplankton communities, suggesting a smaller community change (Northern North Sea: Sum-of-LR= 299.44, p=<0.001; Central/Southern North Sea: Sum-of-LR= 825.65, p<0.001).

However, when extracting the individual contributions of each taxon to the overall community response, a low number of taxa in all communities showed significant contributions to overall community responses. Furthermore, the overall community responses were largely dominated by a low number of taxa. For example, in each community over 20% of the variation was driven by one individual taxon, which showed changes in relative occurrence frequency in all months. These were Protoperidinium (a heterotrophic group) and *Tintinnidae* in the Northern North Sea area for phytoplankton and zooplankton communities respectively, which showed declines. In the Central/Southern North Sea area *Guinardia striata* showed adecline, whilst '*Euphausiacea* and *Mysida'* showed an increase. Out of these taxa, only the decline in *Tintinnidae* in the Northern North Sea was a statistically significant contribution to community change. Other taxa showing large contributions to overall effect were *Dinophysis* within the Northern North Sea phytoplankton community, and *Anomalocera patersoni* within the Northern North Sea zooplankton community, both of which showed a decline ,although the decline in *Dinophysis* was not a statistically significant contribution to community change. Aside from these particular taxa, the overall community change between the beginning of the 20^{th} century and the 1960s was distributed relatively evenly between the taxa, suggesting a holistic community change between the two time periods.

As sampling biases between the datasets, such as varying mesh sizes, may have influenced the taxa that had disproportionate contributions to overall community change, we removed taxa contributing over 20% of variation between time periods before visualising community composition over the extended time period using nMDS plots (Figure 2). ’May 1912’ was removed due to being highly anomalous. Here, the stronger effect of time-period on zooplankton composition can be seen with a clearer distinction between the historical (1902-1912) decade and the 1960s . Furthermore, there is a clearer distinction between the 1960s and the 2000s within the zooplankton plots, especially for the Central/Southern North Sea, suggesting phytoplankton to be more stable in terms of change in community composition over multi-decadal scales.

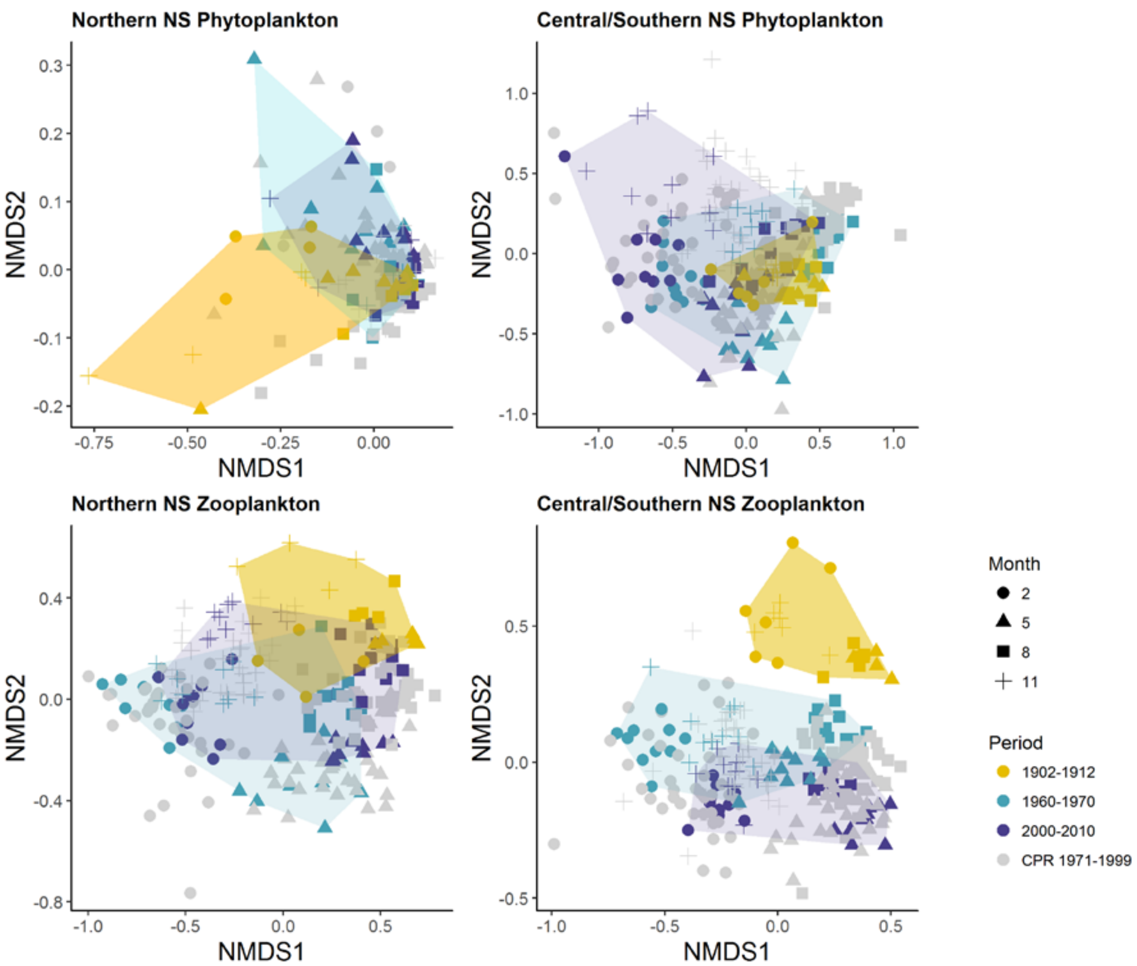

***Figure 2**. nMDS plots using Bray Curtis dissimilarity, based on monthly occurrence frequency of the matching list taxa in each North Sea region. Data points from the ICES historical dataset (1902-1912) are shown in orange and are bound by orange polygon (convex hull). K=3 for all except Northern NS zooplankton, where k=4 to lower stress. Data points from 1971-1999 from the CPR survey are shown in grey, with data from the 1960s shown in blue and bounded by blue polygon. Data from the 2000s decade are in purple and bounded by purple polygon, for additional context.*

3.2 Influence of SST change on plankton communities

Taxa contributing over 20% of between-dataset variation then remained removed when analysing the effect of SST on plankton community composition, to ensure any effects of SST found were not being driven by a small proportion of the taxa. SST has increased in both the Northern and Central/Southern North Sea areasand particularly sharp increases occurred during the late 1920s and 1980s (Figure 3). The average annual SST for the ICES historical time period (1902-1912) was 9.00 °C for the Northern North Sea area, rising to 9.53 °C in the 1960s. In the Central/Southern North Sea area, the average SST for the ICES historical time period was 9.59 °C, rising to 9.86 °C in the 1960s.

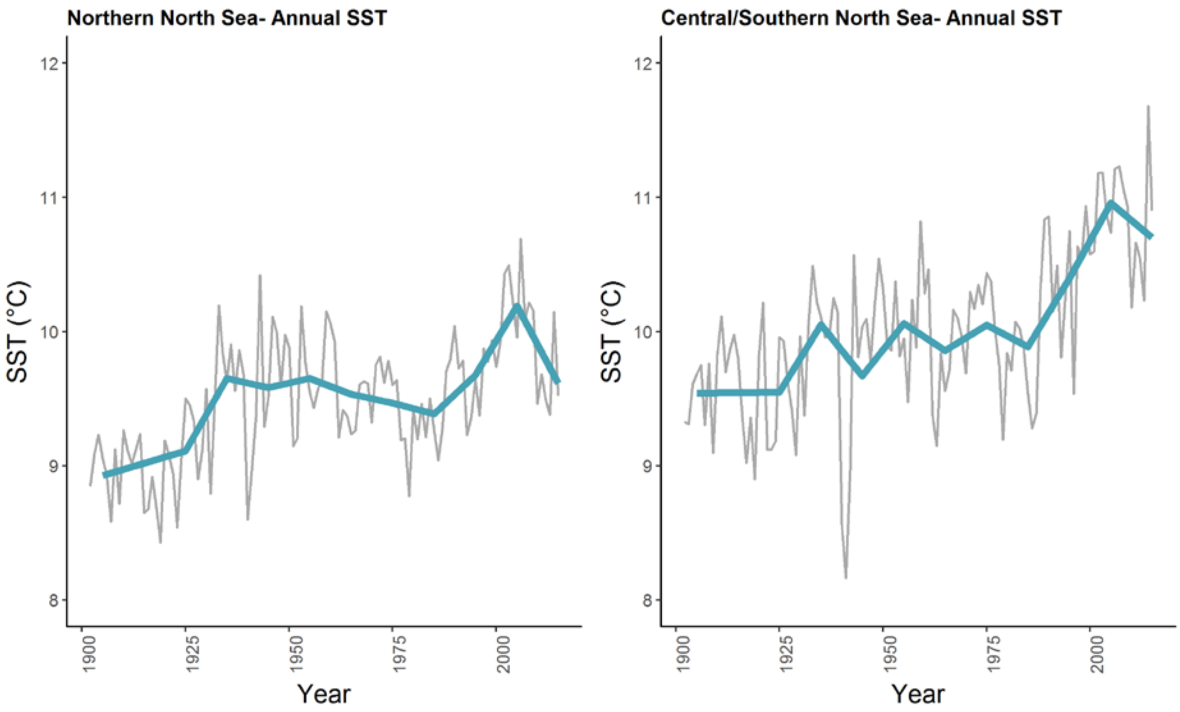

Figure 3. *North Sea SST variation between 1902 and 2015. Annual data are in grey and the 5 year mean is in blue.*

Differences in SST between the time periods suggest that changes observed in overall plankton community composition between 1902-1912 and the 1960s coincided with changes in environmental conditions within the North Sea. We tested this further using multivariate generalised linear models; a significant effect of time-period over and above SST suggests there is variation between the time-periods not explained by changes in SST alone. A significant effect of time period over and above SST was found only in the Central/Southern North Sea phytoplankton community (p=0.023), suggesting variation between time-periods could not be explained by SST change only in this community. In the Northern North Sea zooplankton and phytoplankton communities, as well as the Central/Southern zooplankton community there was no significant effect, suggesting variation could be linked to large-scale SST change.

When then using both the ICES historical dataset and the full CPR dataset together, giving an extended temporal coverage, we found significant effects of SST on phytoplankton and zooplankton communities in both the Northern and Central/Southern North Sea areas (Table 2). SST had a greater influence in the Central/Southern North Sea than the Northern North Sea area on both phytoplankton and zooplankton composition, and a larger influence on zooplankton than phytoplankton overall. No phytoplankton taxa showed individual significant contribution to overall community response. In contrast, there were multiple individual significant contributions to the overall response within zooplankton communities, with the most number of significant individual contributions shown in the Central/Southern North Sea. These included both meroplankton and holoplankton taxa, with the largest contributions to overall community response from *Centropages typicus* and the multi-species group *Bivalvia*. *Centropages typicus* showed an increase in relative occurrence frequency over time, whilst *Bivalvia* showed a decrease in relative occurrence frequency over time, coinciding with increasing annual SST (Figure 4).

***Table 2**. Plankton community responses to SST when examining both datasets combined (1902-1912, 1958-2015). Sum-of-LR= Summed likelihood ratio.*

Plankton community	**Overall community response**		**Taxa with significant contributions to community response to SST over the extended time period**
	Sum-of-LR	**p**	
Northern NS phytoplankton	195.7	0.044	*N/A*
Central/Southern NS phytoplankton	542.86	<0.001	*N/A*
Northern NS zooplankton	669.94	<0.001	*Anomalocera patersoni*
			Decapoda spp.
			Echinodermata spp.
Central/Southern NS zooplankton	1999.7	<0.001	*Bivalvia*
			Calanus spp.
			Centropages typicus
			Corycaeus spp.
			Decapoda spp.
			Oithona spp.
			Para-Pseudocalanus spp.
			Polychaeta spp.

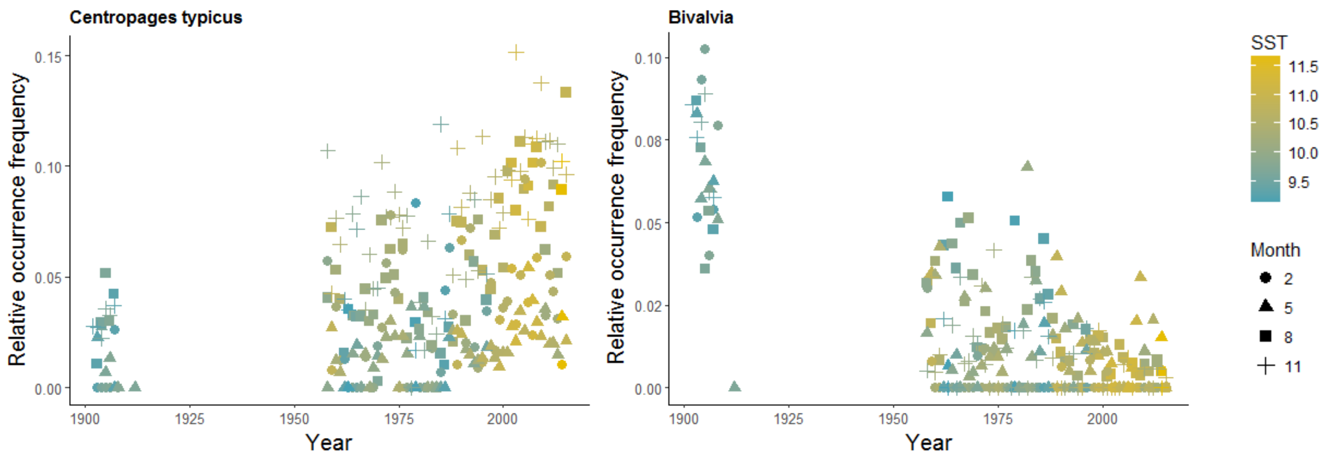

Figure 4. **A)** *Occurrence frequency of* Centropages typicus *by month from wider time-period.* ***B)*** *Occurrence frequency of* Bivalvia *by months from wider time-period.*

Although overall community composition change between 1902-1912 and the 1960s may be linked to changes in SST, taxa that had the largest univariate contributions to community change did not necessarily have large responses to SST across the wider time period (1902-1912, 1958-2015). This suggests that although a change in temperature conditions may have contributed to the overall community response, it does not necessarily explain individual taxon changes between the two time periods. Furthermore, any potential influences of specific environmental drivers on community composition differences between the two time-periods may be at least partially obscured by the differences in sampling and analysis methodologies between the two datasets used, and the low quantitative resolution available.

4 Discussion

Here, we have demonstrated the value of 'rescued' historical plankton data in increasing the temporal scale of understanding of community change. By harmonising the taxonomic lists from the two datasets in order to ensure comparability and then further selecting a subset of shared, common taxa based on a 1% occurrence frequency threshold, and using presence/absence semi-quantitative resolution, we have reduced the influence of disparate sampling and analysis methodologies. Results suggest that the 1960s had a significantly different plankton community composition compared to the early 1900s, indicated by variation in the relative occurrence frequency of shared common taxa. Differences in community composition between time periods were largely driven by a small number of taxa. The remaining effect was shared relatively evenly between the remaining taxa, suggesting the overall significant changes in community composition are a result of subtle change across the taxa list, with individual taxa having mainly non-significant contributions to overall community response.

Zooplankton communities showed a greater difference between the ICES historical time period and the 1960s decade of the CPR time period than phytoplankton communities. The nMDS plots also revealed clearer visual distinctions between the 1960s decade and the 2000s decade within the zooplankton communities than within the phytoplankton communities. This suggests that although differences between the time periods were found within phytoplankton communities, over the whole time period the phytoplankton community showed less directional change in community composition at the multi-decadal scale than zooplankton communities. A similar result was found during the OSPAR (Oslo-Paris Convention for the Protection of the North-East Atlantic) Intermediate Assessment 2017, where larger changes in indicators of zooplankton community structure were found compared to phytoplankton communities (OSPAR, 2017). This assessment result could therefore be representative of multi-decadal patterns of variation occurring at the century-scale.

Furthermore, we found that the plankton community change identified between 1902-1912 and the 1960s could be explained through changes in SST in Central/Southern North Sea zooplankton and Northern North Sea phytoplankton and zooplankton. These community changes in response to SST could therefore be attributed to a regime shift that has been shown to have occurred in the North Atlantic during the 1920s and 1930s, which is argued to be the largest and most significant climate-induced regime shift of the 20th century (Drinkwater, 2006), associated with increases in SST. Furthermore, change in the Central/Southern North Sea phytoplankton community could not be explained by SST change. It is likely, therefore, that finer scale changes, in variables other than SST, drove the change in the Central/Southern North Sea phytoplankton community. Hällfors et al. (2013) similarly described an unknown 'period effect' between the ICES historical time period and contemporary phytoplankton samples in the Baltic Sea, where variation could not be explained by environmental change alone, and instead they hypothesise a potential signal of eutrophication in the change observed. At the regional scale in the North Sea however, previous research has suggested that eutrophication occurs mainly in coastal regions, rather than open sea (McQuatters-Gollop et al., 2009). Furthermore, although we are confident that differences in taxonomic nomenclature and resolution are not driving any patterns observed, we cannot rule out an influence of the low quantitative resolution resulting from sampling and analysis biases, especially for the taxa showing disproportionate contributions to the overall community response.

By integrating the CPR survey with the ICES historical data, we facilitated exploration of the influence of warming SSTs on multidecadal plankton community change at the century-scale, although focusing on occurrence frequency, rather than abundance values. Over the extended time period (1902-1912, 1958-2015), SST had a stronger influence on zooplankton communities than phytoplankton, in both the Northern and Central/Southern North Sea areas. In particular, it is known that temperature is an important structural variable for zooplankton communities and is a key determinant of the limits to distributions (Richardson, 2008). In contrast, although SST was a significant driver of community composition in phytoplankton in both the Northern and Central/Southern North Sea, no single taxa showed significant contributions to the overall community effect. Previous studies have suggested the importance of physical variables other than SST directly influencing phytoplankton community composition including salinity and wind stress (Hinder et al., 2012).

Multiple zooplankton taxa in the Central/Southern North Sea area showed significant univariate responses to SST change, with *Centropages typicus* and the multi-species group *Bivalvia* showing the largest responses. A positive association between the abundance of *Centropages typicus* and SST has previously been identified in the North Sea (Lindley and Reid, 2002), and this pattern is also shown here when examining the CPR time-series at a presence/absence resolution. The lack of a large difference in relative occurrence frequency between the beginning of the 20th century and the 1960s found here however suggests that the response of *Centropages typicus* to SST occurred since the 1960s. In contrast, the larger difference in the occurrence frequency of *Bivalvia* found here between the beginning of the 20th century and the 1960s suggests the decline in the abundance of bivalve larvae previously identified in the North Sea (Kirby et al., 2008) occurred over a longer time scale. Kirby et al. hypothesise that the long-term decline in bivalve larvae found through the CPR survey is a result of predation from increasing abundance of decapod larvae, also observed through the CPR survey, and the increase in decapod larvae is associated with increasing SST (Lindley et al., 2010). In this study, decapod larvae in the Central/Southern North Sea had a significant response to SST, and increased in relative occurrence between 1902-1912 and the 1960s, suggesting that trophic amplification of a climate signal could explain the decrease in bivalve larvae also at the century scale. The differences in whether the taxa with strong overall responses to SST also showed large differences in occurrence frequency between time periods suggests that the temporal scale of responses to SST change, and temporal scale of baseline shifts, is variable between individual taxa.

4.1 Conclusions and policy implications

Through integrating and directly comparing the CPR dataset to the ICES historical database, important considerations have been identified for using disparate plankton datasets together, with applications for large scale assessment and integrated monitoring programmes, such as regional scale assessments undertaken at the OSPAR level (OSPAR 2017). Particularly, zooplankton taxa varied greatly in the taxonomic resolution in which they were recorded between surveys, and much attention needs to be drawn to this when designing integrated monitoring programmes constructed from different surveys. However, we have shown that a subset list of shared common taxa can inform on community change when combining data from disparate sources. Furthermore, occurrence frequency seems to be a relevant proxy for abundance, when abundance data is non-comparable, for example occurrence frequency resolution still revealed strong seasonality signals. As sampling and analysis biases cannot ever be fully reconciled in contemporary comparisons of rescued historical datasets, such as varying mesh sizes, often resulting in low quantitative resolution, we suggest that 'rescued' historical datasets can be useful as an additional contextual tool for understanding climate change effects on plankton communities, but caution should be employed when using disparate historical datasets as robust evidence bases on their own.

A stable historical baseline, from which plankton communities are assessed for impacts of direct anthropogenic pressures, may be hard to define in the North Sea, as the plankton communities vary on inter-annual, multi-decadal and, suggested here, century-wide scales in response to environmental change. Phytoplankton community composition may show less directional change in community composition, in terms of the relative occurrence frequency of common taxa, over multi decadal time scales than zooplankton communities. Although statistically significant changes were observed in particular individual taxa between time periods, and across the wider time-series in response to SST, this does not necessarily inform on the ecological significance of changes. When formally assessing change in North Sea plankton communities under policy drivers, it is important to consider the functional consequences of community change, as well as the century-scale shifts in community composition baselines.

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