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Sensitivity of plankton assemblages to hydroclimate variability in the Barents Sea

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Abstract. Warming, loss of sea icea and changes in ocean currents in the Arctic has led to biochemical changes in pelagic systems that propagate into, and disrupt the Arctic food web. The responses of plankton to environmental variability is critical in understanding how climate change may shape the structure of pelagic ecosystems in the Arctic. To further this understanding, we used a partial canonical correspondence analysis on remotely sensed and modelled hydroclimate together with plankton abundance data from the Continuous Plankton Recorder Survey from the Barents Sea in the European Arctic – one of the fastest warming regions globally – to assess the spatial and interannual variability of plankton community assemblages. The hydroclimate explained ~50 % of interannual variability in species assemblage of plankton communities. *Calanus* spp. copepod abundances were particularly sensitive to changes in the hydroclimate, which were strongly associated with the mixed layer depth and nutrient concentrations. In warmer years, where SST exceeded those predicted under various future climate scenarios, we saw evidence of thermal stratification of the water column that supported populations of appendicularians, and the potentially toxin-producing diatom *Pseudo-nitzschia*. Spatial variability of the assemblage was strongly associated SST and salinity gradients that reflect different water masses. Such changes to plankton assemblages in response to hydroclimatic variability are likely to impact trophic interactions with associated organisms, many with ecological and economic significance in Barents Sea food webs.

1 Introduction

Plankton at the base of the food web play a vital role in pelagic ecosystems, providing energy for higher trophic levels, as well as supporting fish stocks, seabird and marine mammal populations. Phytoplankton form the primary basal resource in planktonic food webs, providing the majority of carbon for herbivorous zooplankton; and > 58 % of phytoplankton derived carbon is transferred to higher tropic levels via predation (McMeans et al., 2013). Planktonic food webs play a crucial role in arctic ecosystems as highly abundant herbivorous calanoid copepods take advantage of intense seasonal phytoplankton blooms, converting dietary fatty acids to energy dense wax esters for storage inside their bodies (Renaud et al., 2018; Søreide et al., 2010). The high energy lipid stores of calanoid copepods are propagated through the food chain, sustaining large populations of fish (Olsen et al., 2010), seabirds (Jakubas et al., 2017), seals (Falk-Petersen et al., 2009; Øigård et al., 2013) and whales (Blanchet et al., 2019; Skern-Mauritzen et al., 2011). Therefore, changes to the structure and abundance of planktonic assemblages are likely to have repercussions of both ecological (Moore and Huntington, 2008; Stige et al., 2019) and economical (Alvarez et al., 2020) significance, particularly in highly productive regions of the Arctic such as the Barents Sea.

The structure and abundance of planktonic communities is inextricably linked to the physical and chemical environment, and varies in both space and time (Dalpadado et al., 2020; Litchman and Klausmeier, 2008). Plankton species distributions are partly dictated by ocean currents, (Hunt et al., 2016), so the physiological state of plankton is usually reflective of the water masses in which they reside (Clarke and Peck, 1991). Phytoplankton and zooplankton species have specific physiological tolerances to abiotic conditions and an optimal abiotic niche where they can survive, grow and reproduce. Therefore, plankton communities are shaped from contrasting responses of individual species to environmental factors (Huertas et al., 2011; Litchman et al., 2013; Litchman and Klausmeier, 2008).

Long term shifts in plankton communities have been observed in the Arctic and attributed to increasing ocean warming (Leu et al., 2011). Over the last 30 years, the volume of cool, fresh Arctic water in the Barents Sea has been reduced by half, whilst the volume of warmer, more saline Atlantic Water has increased from 33 $\times 10^3$ km^3 to 84 $\times$ 10^3 km^3 (Oziel et al., 2016) a process termed 'Atlantification' (Årthun et al., 2012). Atlantification has led to warmer and more saline sea surfaces conditions and the restructuring of plankton locally in the Barents Sea, as well as northwards shifts of sub-arctic and temperate phytoplankton and zooplankton species (Aarflot et al., 2018; Møller and Nielsen, 2019; Oziel et al., 2020). For example, north Atlantic diatom and dinoflagellate species distributions are progressing poleward at a rate of 0.1° per decade (Barton et al., 2016). Similarly, in the Barents Sea, the copepod *Calanus finmarchicus* is also shifting its range poleward at a rate of 0.1° of latitude per decade (Helaouët and Beaugrand, 2009). The introduction of sub-Arctic phytoplankton and zooplankton species will result in changes to Arctic plankton community structure, changing predator-prey interactions, and modifying food webs.

Atlantification is contributing to earlier ice break-up and the retreat of the seasonal ice zone (Årthun et al., 2019; Onarheim and Årthun, 2017), and it enhances mixing that increases the supply of nutrients to surface waters, leading to increased net primary production and altering the timing and intensity of phytoplankton blooms in the Barents Sea (Lewis et al., 2020). These changes to plankton phenology create a trophic mismatch between the base of the food web and primary consumers (Søreide et al., 2010). This trophic mismatch desynchronises herbivorous arctic zooplankton feeding and reproduction events, which are precisely timed with both the ice algal and phytoplankton blooms required for successful development and survival of their offspring (Feng et al., 2016; Søreide et al., 2010).

These ecological changes are projected to extend further northward and eastward into the Barents Sea throughout this century (Long and Perrie, 2017; Oziel et al., 2017). To date, most research into pelagic systems has described decadal (Beaugrand and Reid, 2003; Mutshinda et al., 2017) and seasonal (Arashkevich et al., 2002; Rat'kova and Wassmann, 2002) trends of plankton communities. Interannual variability over shorter time-periods (<10 years) and the underlying drivers of this variability are not well documented, and is vital for understanding longer-term (decadal) shifts in planktonic ecosystem functioning (Wilkinson et al., 2020). Variation of hydroclimatic variables over interannual time scales, such as SST, salinity, mixed layer depth and net primary production, can reach levels similar to their projected values for 2050 (Årthun et al., 2019; Lewis et al., 2020). Such levels of interannual varaibilty can offer a glimpse into the potential responses of plankton communities to environmental states that may not be observed for several decades. Therefore, incorporating knowledge of interannual time scales into our understanding of ecological responses to the environment is paramount for effective prediction and mitigation of potential climate change-induced ecosystem collapse.

The Continuous Plankton Recorder (CPR) Survey has been operating since 1932 and is the longest and most spatially extensive plankton survey that collects and records over 500 plankton taxonomic entities on an automated mechanical device (Reid et al., 2003; Richardson et al., 2006). It offers an unqiue dataset for studying interannual variability in plankton communities and its relationship with the hydroclimate. In this study, we focus on the Arctic transect of the CPR, in the Barents Sea between Svalbard and Tromsø (hereafter known as the ST route). Previous time-series studies assessing short-term plankton interannual variability in the arctic have only focussed on total biomass of phytoplankton (Juul-Pedersen et al., 2015), zooplankton biomass (Prokopchuk and Trofimov, 2019) or on a more specific group of taxa (Møller and Nielsen, 2019; Stige et al., 2019). In this interannual time series study we cover a period of six years (2010 – 2016) and focus on the abundance of phytoplankton and zooplankton taxa to the genus or species level. Our time-series analyses were coupled with satellite-derived hydroclimate variables, within three hydrologically distinct regions of the Barents Sea Opening (BSO). We used this unique time-series from the CPR survey to address three questions: 1) How variable is the plankton community assemblage over interannual time-scales, and how does this temporal variability compare with the spatial variability across the ST route? 2) Which species of plankton are the most sensitive to interannual and spatial environmental variation? 3) What are the most important hydroclimate drivers mediating these changes? We address these questions using a broad taxonomic structure that allows us to indiscriminately assess which species are the most sensitive to the hydroclimate, and to highlight broad scale patterns in interannual variability in plankton communities and their environmental controls.

2 Methods

2.1 Study region and time-series

To understand the effects of inter-annual hydroclimate variability on phytoplankton communities in the Arctic, we used a time-series Continuous Plankton Recorder dataset from the northernmost route than traverses the Barents Sea Opening (BSO) between Tromsø (70 °N, 20 °E) and Svalbard (78 °N, 12 °E) (hereafter ST route; Fig. 1). The ST route covers an arctic gateway in the south-western Barents Sea where warm (T > 3°C) and saline (S > 35 PSU) North Atlantic water masses are advected north of and into the central Barents Sea shelf, and cold/fresh waters (T < 0°C / S < 34.7 PSU) masses are advected south around the northern edge of Bear Island (Barton et al., 2018). The two waters masses meet creating a frontal zone at 74 °N along the transect (Supplementary Fig. S1 & S2). The water column depth of the main ST route is between 100 and 400 m, with some samples from 2011 being collected on the western shelf slope at a maximum depth of 1150 m.

We used 89 samples from the month of June for interannual comparisons of the phytoplankton community between the years 2010 and 2016 (excluding 2012 as no sampling was conducted). June was selected as the month of study because this sampling period coincides with the summer phytoplankton bloom (Dalpadado et al., 2020) and with the timing of high zooplankton grazing (Hassel, 1986; Verity et al., 2002), offering a better overall representation of species occurrence and prey availability to primary consumers. Sampling effort in June was also the most consistent on a spatial and annual scale across the time series.

As the ST transect covers such a hydrologically diverse region in terms of bathymetry and water masses (Fig. 1; Supplementary Fig. S1 & S2), it is likely that spatial trends will obscure interannual trends in plankton communities. To counter this, we used the average SST and salinity values between 2010 and 2016 to separate the transect into three regions representing different water mass characteristics: a) ST1: the southern coastal region between 70 and 72 °N, which is influenced by the freshwater Norwegian Coastal Current (NCC); b) ST2: 72 and 74 °N region, which is away from the coastal influence, and where warm saline waters enter from the north Atlantic; c) ST3: 74 and 76 °N region that is situated parallel to the polar front, shaped by the bathymetry and hydrology surrounding Bear Island. Only one sample was collected in 2015 in ST2, and so that data was removed from all subsequent analyses.

2.2 Continuous plankton recorder sampling

Phytoplankton and microzooplankton abundance data were provided by the Continuous Plankton Recorder (CPR) Survey. The CPR survey collects plankton samples using a continuous plankton recorder that is towed behind ships of opportunity at a depth of 10 m. Plankton are collected on a moving band of silk (mesh size of 270 µm) and instantly preserved in a 4 % formalin solution. The silks are cut into segments that represents 10 nautical miles of the ocean surface along the transect. Phyto-, micro-, and meso- zooplankton were all identified to the lowest possible taxonomic level using a light microscope and their abundances recorded in a semi-quantitaive manner (Richardson et al., 2006).

2.3 Environmental datasets

We selected a suite of environmental variables that have previously been known to influence arctic plankton community assemblages. These were obtained from remotely sensed and modelled data described in Supplementary Information S1. We used average monthly values at each sampling location for Sea Surface Temperature (SST), salinity, density, mixed layer depth, chlorophyll-a concentration, phosphate (PO_4), nitrate (NO_3), silicate (Si), oxygen concentration and pH. In addition, we included the average seasonal SST for the spring and summer prior to sampling to capture any lagged effects of SST changes on plankton communities. Seasons here are defined meteorologically, with spring SST representing the March to May average, and summer representing the June to August average.

2.4 Statistical analysis

All statistics were carried out in R Studio (Version 1.3.1073; R Development Core Team, 2020). In order to delineate the interannual and spatial variability of plankton communities and identify the environmental drivers underpinning these patterns, we used a partial canonical correspondence analysis (pCCA). For a full description of this analysis see ter Braak and Verdonschot (1995), and a visualisation of the statistical framework can be seen in Fig. 2. In brief, pCCA is a cluster analysis that describes variability in the plankton assemblage by producing an artificial 'axis' that represents a certain plankton community. To identify hydroclimate associations of each community, the analysis clusters the hydroclimate variables along another axis and uses multiple linear regressions to identify which combination of environmental variables most strongly correlates with the species axis. The resulting pair of axes describes the plankton community and its hydroclimate associations. For the interannual pCCA, we provided a conditioning matrix containing the latitude, longitude and water column depth of each sample to spatially constrain the analysis. For the spatial analysis, the conditionion matrix contained the year of sampling (treated as a factor) to interannually constrain the analysis (Fig. 2).

Using the 'vegan' package in R, a total of four pCCAs were performed on plankton abundance and hyroclimatic data from June CPR samples for all years (2010 – 2016). To determine interannual patterns, one pCCA was run for each of the three regions. For the spatial analysis, one pCCA was run for the whole transect that included all years (Fig. 2). Any taxa that contributed less than 5 % of the total count zooplankton and phytoplankton counts were removed prior to the pCCA analysis. Species counts in both phytoplankton and zooplankton datasets differed by several orders of magnitude and tended towards zero inflation. To mitigate against these effects, species counts were standardized from 0 and 1. For each axis produced, each species, each hydroclimate variable and each sample was scored to describe how each component relates to that axis. A

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species and hydroclimate variable with a similar score for an axis were positively correlated, and a sample with a similar axis score for the corresponding species and hydroclimate axes indicated that species was in higher abundance in that sample.

Analysis of Variance (ANOVA) and Tukey's HSD post-hoc tests were used to identify significant differences between years in the environmental and species axes scores. The proportion of variation in the species assemblage explained by each axis was an output of the pCCA. The sum of the proportion of variation for each axis that showed significant interannual variation was used to estimate the total proportion of the plankton assemblage that was interannually variable in each region.

The paired environmental and species axes produced in the pCCA were tested for correlation using a linear model. F-statistics, Adjusted R^2 and p values were reported to assess the strength of correlations between plankton and the hydroclimate drivers. In addition, to estimate the proportion of the species assemblage that can be predicted by a specific hydroclimate driver, the Adj. R^2 values were evaluated for the linear regressions between the species axis and the corresponding hydroclimate axis.

The species axis scores were used to identify which taxa were the most variable over interannual and spatial scales. As the scores are both negative and positive values, we took the absolute values of each as a greater distance from zero describes a more variable taxa. For each taxon, we averaged their scores from each axes across all regions. This was repeated for the hydroclimate axis to identify which hydroclimate driver was the most important in influecing the species assemblage.

To then identify which taxa were correlated with specific hydroclimate variables, we used a biplot to visualize the outputs from the pCCA. Species labels that are close to each other are more positively correlated, hydroclimate labels that are in proximity to species labels have a more positive correlation with that species' abundance. Bayesian standard ellipses were calculated and overlain to represent the standard error in the biplot space of the species axes scores for each year in each region (Jackson et al., 2011).

To determine the impact of phenology on the results of the pCCA, we estimated seasonal abundances by comparing the monthly mean abundance of those taxa. To account for the heavily skewed, zero-inflated distribution of the data, as is common for spatially heterogenous plankton communities, we conducted a zero-inflated negative binomial regression using the 'pscl' package in R. The percentage of zeros in the count data was > 50 % for all species, and so zero inflated models were chosen. Model selection was carried out using the Vuong test and a likelihood ratio test to assess over-/under-dispersion of the count variable in the model (Yang et al., 2017).

3 Results

3.1 Interannual plankton assemblage variability and drivers

Our partial canonical correspondence analysis successfully identified strong evidence for interannual differences in the plankton community assemblage and hydroclimate drivers in all three regions across the transect (Fig. 3a-f). *Calanus finmarchicus* had the highest level of interannual variability in its abundance across the whole transect (Fig. 4a). This variation was mostly attributed to the higher abundance in 2014 relative to all other years, evident by the consistently negative values for axis 1 across all regions for *C. finmarchicus* and the low 2014 sample scores (Table 1; Fig. 3a, c and e). High levels of interannual variation were also observed in coccolithophores, *Calanus* stages I-IV, appendicularians, *Ceratium* spp. and *Pseudo-nitzschia* spp. (Fig. 4a). The abundance of appendicularians, *Ceratium* spp., and *Pseudo-nitzschia* spp., were highly variable in both the ST2 and ST3 regions, with particularly high abundance in 2013. All had similar axis scores for axis 2 in ST2 (Table 1; Fig. 3d), and axis 1 in ST3 (Table 1; Fig. 3e). Echinoderm larvae, *Cortheron hystrix* and *Rhizosolenia* spp. all had the lowest levels of interannual variability of all taxa observed across the transect (Fig. 4a).

In ST1, axis 1 and 3 described a plankton assemblage that was interannual variable, whereas it was axis 1 and 2 in ST2 and ST3. Interannual variation of the plankton assemblage was greatest in ST1, and least in ST3, with axis 1 and 3 accounting for 57 % of the variation in the plankton assemblage in ST1, but axes 1 and 2 accounting only for 49 % and 38 % in ST2 and ST3, respectively. Of the axes that described plankton assemblages that varied interannually, all were significantly correlated with their corresponding hydroclimate axis (Table 2). The hydroclimate exerted the greatest influence over the interannual variability in the plankton community assemblage in ST1 and ST2 (Adj. R^2 range: 0.64 to 0.9; Table 2), and the least influence in ST3 (Adj. R^2 range: 0.58 to 0.36; Table 2).

The greatest hydroclimatic influence on the interannual variability of plankton communities across the whole transect were from the SST values of the previous summer and autumn (Fig. 4c). This was followed by nutrient concentrations, current years SST (June) and the mixed layer depth (Fig. 4c; Table 3). The variable with the least impact on interannual variation of the plankton community assemblage was chlorophyll-a concentration (Fig. 4c; Table 3).

Hydroclimate values can be found in Supplementary Table S1. The extremes of the variables that were influencing the plankton community variability were consistently recorded in 2014 and 2013 (Fig. 5a-c). In ST1 and ST2, 2013 had the greatest June SST values, with the shallowest mixed layers and lowest nutrient concentrations (Fig. 5a-c). Contrastingly, the greatest nutrient concentrations and deepest mixed layers were evident in 2014 in ST2, and above the average in ST3 (Fig. 5b & c).

The elevated abundance of *C. finmarchicus* in 2014 compared to other years was positively correlated with a deeper mixed layer, and with higher SST in the previous summer and spring, across all regions (Fig. 6a-c), and with the higher nutrient concentrations in ST2 and ST3 (Fig. 6b-c). Unfortunately there was no nutrient data for ST1. The higher abundances of appendicularians, *Ceratium* spp., and *Pseudo-nitzschia* spp. in 2013 in ST2 and ST3 were correlated with shallower mixed layers, lower concentrations of NO_3, PO_4 and Si, and higher SST in June (Fig. 6b-c).

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3.2 Spatial plankton assemblage variability and drivers

There was strong evidence for differences in the species assemblages between the three regions, as revealed by the first three pCCA axes (Fig. 7a-c). All three axes were significantly correlated with their corresponding hydroclimate axes (Table 5). High spatial variation in adundance was observed in cirripede larvae, followed by tintinnids, copepod eggs and echinoderm larvae (Fig. 4b). *C. finmarchicus*, *Calanus* stages I-IV and *Chaetoceros* spp. dominated the assemblages and so had little spatial variation (Fig. 4b).

A higher abundance of *Corethron hystrix*, and lower abundance of cirrepede larvae were observed in ST2 compared to the other regions (Table 4; Fig. 7a). ST1 had higher abundances of tintinnids and *Oithona* spp. relative to the other regions as these two taxa had positive axis 2 scores (Table 4: Fig. 7b). ST3 had higher abundances of *Pseudo-nitzschia* spp. compared to the other regions evident by their negative axis 3 scores (Table 4; Fig. 7c).

SST in June was the most influential driver of spatial variability in the species assemblage assemblage across the ST transect (Fig 4d). Density, latitude, depth, longitude and salinity had similar contributions to the spatial variation in the species assemblage (Fig. 4d; Table 6). These variables contributed to the differences between the three regions, with fresher waters from the NCC influencing ST1, warm saline waters in ST2, and colder but saline waters in ST3 (Supplementary Fig. S1 & S2). The variables that contributed the least to the spatial variation in the species assemblage were chlorophyll-a concentration and the mixed layer depth (Fig. 4d; Table 6).

3.3 Phenology of sensitive species

We assessed whether the high interannual variability in some species was a result of phenological shifts in their seasonal appearance by comparing their monthly-averaged abundances for all years. *Ceratium* spp.abundance peaked August for all regions (Fig. 8a – c). *Psuedo-nitzschia* spp. abundances peaked twice, in early spring (March) and in mid-summer (July), and were highest in July for both ST1 (Fig. 8d) and ST2 (Fig. 8e), but in June for ST3 (Fig. 8f).

The abundance of appendicularians was highest in June for ST2 and ST3, however these were driven by a few samples with very high counts, reflected in the high standard deviations in (Fig. 9k & l). In ST1, appendicularians had a main peak in April and a smaller peak August (Fig. 9j). *Calanus finmarchicus* abundance peaked in June for all latitude groups (Fig. 9g – i), and *Calanus* I-IV stages peaked in both late spring (May) and mid-summer (July) for all regions (Fig. 9d – f).

4 Discussion

We present new information on the spatial and temporal variability of both the zooplankton and phytoplankton assemblage across a unique time series in the Barents Sea Opening. We have demonstrated the high interannual variability of the hydroclimate environment, and the different responses of plankton to this variability that was, in some cases, ubiquitous along the transect, and in others regionally specific. Our study highlights the importance of incorporating interannual variability into our understanding of plankton communities and their relationship with the environment.

4.1 Food web implications of assemblage variability

The standout finding was that of high interannual variation of *C. finmarchicus* abundance across the entire transect, with particularly high abundances in 2014, both of which were linked to elevated SST in the previous seasons, deeper mixed layer and increased surface nutrients, which is discussed later in Sect. 4.2. Deeper mixed layers are indicative of increased intrusion of Atlantic waters into this system, which advects more of the Atlantic-associated *C. finmarchicus* into the BSO. With the future Atlantification of the Barents Sea predicted to deepen mixed layers in northern and eastern areas of the Barents Sea where *Calanus glacialis* dominates (Lind et al., 2018), *C. finmarchicus* will likely replace its congener. This would constrain the energy budget of secondary and tertiary consumers as *C. glacialis* is has a higher energy denisty with larger lipid stores than *C. finmarchicus* (Falk-Petersen et al., 2007).

Variability of appendicularians, *Ceratium* spp. and *Pseudo-nitzschia* spp. was also notable, with high abundances observed in 2013 in ST2 and ST3 linked to warm and stratified surface waters. Differences in SST values observed between 2013 and all other years in June exceeded the predicted increase of 0.5 – 1°C from the 2010-2019 average to the 2060 – 2069 average in the Barents Sea under a moderate future emissions scenario (RCP4.5; (Skogen et al., 2018)). Such sea surface warming and earlier or more intense thermal stratification of the water column may have detrimental effects on the pelagic food web. An increased occurrence of *Pseudo-nitzschia* spp. can be harmful to grazers such as copepods, upon ingestion since both arctic species potentially produce the toxin domoic acid (Haroardóttir et al., 2015). Increases in appendicularian abundance have implications for nutrient retention in surface waters. This is because the rate of appendicularia 'house' renewal (a feeding efficiency indicator) increases in fresher and warmer environments (Sato et al., 2001), and the shedding and sinking of old houses can contribute significantly to the vertical carbon flux (Vargas et al., 2002), supplying energy to the benthos at the expense of the surface. Furthermore, appendiularians have a boom and bust life cycle (López-urrutia et al., 2004) meaning there is a smaller window of opportunity for their consumption by predators, which must time their seasonal feeding strategies to coincide with prey occurrence, which in turn could lead to a predator-prey mismatch.

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4.2 Hydroclimate drivers

The average SST in the summer of the previous year from 2014 was 7.8°C in ST3, which is within the optimal thermal range of 4.5 to 8.5°C for *C. finmarchicus* (Reygondeau and Beaugrand, 2011a). This provided *C. finmarchicus* with favourable conditions in the summer of 2013, which may have benefitted their growth and reproduction, and therefore increased their chance of survival into the following year of 2014, as we observed in their increased abundance. However, this explanation seems unlikely as SST in the previous summer in ST1 and ST2 was 10.3°C and 8.98°C, respectively, which is above the optimal thermal range of *C. finmarchicus*. Therefore, despite our analysis correlating adult *C. finmarchicus* and *Calanus* I-IV stages with previous summer SST, we see this as an unlikely driver of *C. finmarchicus* abundance. *C. finmarchicus* and younger copepodite stages have been found to decrease with increasing stratification (Reygondeau and Beaugrand, 2011b), so their correlation with mixed layer depth and nutrient concentrations is more likely an indirect cause of their increased abundance through its effects on food supply or predation.

Warmer temperatures in June, and lower nutrient concentrations and shallower mixed layers were the factors predicting higher abundances of appendicularians, *Ceratium* spp. and *Pseudo-nitzschia* spp. in 2013. In June 2013, surface waters were warmer and fresher with a shallow mixed layer compared to other years. We conclude that these anomalously higher temperatures were not due to intrusion of Atlantic waters, as this would have caused an increase rather than decrease in salinity. Instead, we conclude that the increased SST is a result of atmospheric heating of the surface layer, resulting in a thermally stratified water column. The influence of stratification on the phytoplankton community has been previously reported in the Canadian arctic (Ardyna et al., 2011). As stratification decreases, plankton communities shift from autotrophic flagellate dominated protist communities to diatom dominated communities (Ardyna et al. 2011). However, the direction of the stratification-modereated phytoplankton community shifts have been found to be regionally specific depending on proximity to coastlines, sea ice shelves and upwelling regions (Blais et al., 2017). Regional specificity of our observations in interannual phytoplankton community variation was also evident as greater abundances of *Ceratium* spp. and *Pseudo-nitzschia* spp., in 2013 were only observed in ST2 and ST3.

The prevalence of *Pseudo-nitzschia* spp. and *Ceratium* spp. were found in thermally stratified waters. This finding agrees with previous studies that have reported a positive relationship between *Pseudo-nitzschia* spp. and high temperature, low salinity environments, (Joli et al., 2018; Sugie et al., 2020). *Pseudo-nitzschia* are known to be positively influenced by nutrient concentrations (Lafond et al., 2019), and silicate and phosphate imitation increases the production of the toxic domoic acid (Pan et al., 1998; Tatters et al., 2012). In this study in a contrasting correlation was found between *Psuedo-nitzschia* spp. and nutrients; resulting in a positive correlation in ST2 and a negative correlation in ST3. This contrasting correlation in our analysis suggests that the nutrient concentrations used in this study had little causation on the abundance of *Pseudo-nitzschia* spp., and that SST and low salinity are the strongest predictors of *Pseudo-nitzschia* spp. abundance. Future measurements that include trace metal ions such as iron, which influences diatom growth and domoic acid production could reveal significant influences on the growth and toxicity of this diatom.

Thermal stratification of surface waters is a feature of summertime hydrology in the Barents Sea Opening as air temperatures increase and wind mixing decreases (Oziel et al., 2017; Signorini and McClain, 2009). Therefore, the plankton community changes in 2013 that were linked with stratification may be a result of earlier onset of summer-time stratification relative to other years. This would cause the earlier appearance of phytoplankton taxa that usually occur later in the summer, and may explain the increased abundance of *Ceratium* spp. in June 2013, which would reflect a shift in phenology, as our analysis suggests that the peak abundance of *Ceratium* spp. usually occurs in August.

A higher abundance of appendicularians (probably *Fritillaria* spp. (Basedow et al., 2014)), in association with warm stratified waters, were present in only a few 2013 samples, particularly in June. Such hydroclimates benefit appendicularia populations as they are opportunistic and reproduce rapidly when environmental conditions become favourable (López-urrutia et al., 2004). Previous studies have found positive correlations between the abundance of appendicularians, and small copepods (e.g. *Oithona* spp.), with higher temperatures across steep environmental gradients in the Barents Sea, such as in frontal zones (Basedow et al., 2014). In contrast to appendicularians, *C. finmarchicus* and other calanoid copepods are slower growing, less opportunistic and thrive in well mixed environments with a high nutrient supply (Reygondeau and Beaugrand, 2011b). This, and the fact that copepods have been found to predate on the appendicularia *Oikopleura dioica* (López-urrutia et al., 2004), and could explain why we consistently found contrasting correlations to the pCCA axes between appendicularians and *Calanus finmarchicus.*

4.3 Top-down vs bottom-up impacts

Variability in biomass and composition of phytoplankton (Rat'kova and Wassmann, 2002) and zooplankton (Dalpadado et al., 2014; Prokopchuk and Trofimov, 2019; Stige et al., 2009) assemblages in the Barents Sea is found to be influenced by both bottom-up and top-down processes, and the interplay between the two processes being both spatially and temporally variable. Our findings corroborate this, where a strong correlation between the plankton community assemblage and the hydroclimate in ST1 and ST2 suggests a greater role for bottom-up control of the community assemblage compared to ST3 - where a potentially greater influence of top-down pressures from planktivorous organisms such as capelin and herring is present (Olsen et al., 2010; Stige et al., 2009).

Capelin (*Mallotus villosus*) abundance has been found to explain large proportions of the variability in Barents Sea zooplankton biomass (Dalpadado et al., 2014, 2020; Prokopchuk and Trofimov, 2019), and are known to feed extensively on calanoid copepods in the Barents Sea (Dalpadado and Mowbray, 2013), resulting in an inverse relationship between zooplankton and capelin abundance (Gjøsæter et al., 2009). Capelin stocks in the Barents Sea were relatively stable between 2010 and 2013 at ~3.5 million tonnes, however there was a dramatic reduction to ~1.5 million tonnes in 2014 (ICES, 2015). This would have substantially reduced predation pressure on *C. finmarchicus,* and could help explain why we observed such high temporal variation in their abundance. In addition to planktivorous fish, plankton assemblage variability can be impacted by predation from seals (Falk-Petersen et al., 2009) and whales (Skern-Mauritzen et al., 2011), as well as parasitism and viral infection, both of which can increase plankton mortality rates (Daase et al., 2014).

4.4 Caveats

While our analysis was limited to detecting bottom-up drivers of plankton assemblages, interannual variability in some species may have remained undetected by our analysis. This is because, firstly, smaller phytoplankton species may be under sampled due to the large mesh size of the silks on the CPR recorder (270 µm). Secondly, due to the resolution of identification for some taxa not surpassing the genus level. For example, there are 55 species of *Chaetoceros* diatoms in the Artic (Gogorev and Samsonov, 2016), and this was one of the dominant phytoplankton species in all years and regions of this study (Supplementary Fig. S3; Supplementary Information S2), and whilst we observed little variation in the abundance of its genus, there may have been variation in the abundance of specific species. However, we could not detect this as the lowest taxonomic resolution of *Chaetoceros* in our study was to the subgenus' *Hyalochaete* and *Phaeoceros*.

In addition, the counting methodology used in the CPR survey is semi-quantitative, in that plankton are assigned to abundance 'categories' rather than absolute abundance. This has minimal impacts on the goals of this study, as we were focused on broad trends in the plankton dataset rather than small inter-specific differences. Despite these caveats, there is widespread agreement that the CPR is spatially and temporally consistent in recording a reliable estimate of plankton abundances, and so is an appropriate tool for assessing interannual and spatial variability in the plankton community (Richardson et al., 2006). Finally, our study did not specifically address seasonal variation within the plankton community but rather multiannual variation centered around June. We recognise that whilst we tried to address seasonality through analysing the phenology of certain species, higher seasonal resolution of plankton abundances, particularly in spring, is needed to fully understand the phenological ? changes occurring within the system.

5 Conclusions

Phytoplankton and zooplankton community characteristics in June in the south-western Barents Sea showed strong interannual variation, around half of such variation being attributable to yearly fluctuations in the hydroclimate. We hypothesise that the remaining variation could be explained by top-down pressures such as predation by fish species and other organisms at higher trophic levels and posit this as a need for further research on the CPR dataset in conjunction with fisheries or predator data. The hydroclimate variables that we identified as having the strongest influence on interannual variation in plankton communities were those that affect the growth conditions of phytoplankton such as nutrient supply and mixed layer depth. Spatial variation was strongly associated with temperature and salinity that act on the physiological tolerances of zooplankton and phytoplankton assemblages. *Calanus* spp. copepods were particularly sensitive to changes in the hydroclimate, mostly to mixed layer depth and nutrient concentrations. In warmer years, such as those in 2013 where sea surface temperatures exceeded those predicted under various future climate scenarios, we saw evidence of thermal stratification of the water column that supported populations of the zooplankton taxa appendicularia, and the toxic forming diatom *Pseudo-nitzschia*. This has implications for consumer-resource interactions in Barents Sea food webs that depend on energy rich, and nutritionally viable plankton species to transfer energy to higher trophic levels, and to sustain the functionality and productivity of the ecosystem in coming decades.

Data Availability

Continous Plankton Recorder data is available on request from https://www.cprsurvey.org/. The dataset used in the current study can be found at: DOI:10.7487/2017.325.1.1090

Author Contribution

Conceptualization: RJ, CM, RS, CC & EP. Data Curation: CPR. Formal analysis: EP. Funding Acquisition: CM, RJ, RS & CC. Investigation: EP. Methodology: EP. Project administration and supervision: EP, RJ, CM, RS & CC. Resources: CPR. Visualizations: EP. Writing – original draft preparation: EP. Writing – reviewing and editing: EP, RJ, CM, RS & CC.

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References

Aarflot, J. M., Skjoldal, H. R., Dalpadado, P. and Skern-Mauritzen, M.: Contribution of Calanus species to the mesozooplankton biomass in the Barents Sea, ICES J. Mar. Sci., 75(7), 2342–2354, doi:10.1093/icesjms/fsx221, 2018.

Alvarez, J., Yumashev, D. and Whiteman, G.: A framework for assessing the economic impacts of Arctic change, Ambio, 49(2), 407–418, doi:10.1007/s13280-019-01211-z, 2020.

Arashkevich, E., Wassmann, P., Pasternak, A. and Wexels Riser, C.: Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea, J. Mar. Syst., 38(1–2), 125–145, doi:10.1016/S0924-7963(02)00173-2, 2002.

Ardyna, M., Gosselin, M., Michel, C., Poulin, M. and Tremblay, J. É.: Environmental forcing of phytoplankton community structure and function in the Canadian High arctic: Contrasting oligotrophic and eutrophic regions, Mar. Ecol. Prog. Ser., 442, 37–57, doi:10.3354/meps09378, 2011.

Årthun, M., Eldevik, T., Smedsrud, L. H., Skagseth and Ingvaldsen, R. B.: Quantifying the influence of atlantic heat on barents sea ice variability and retreat, J. Clim., 25(13), 4736–4743, doi:10.1175/JCLI-D-11-00466.1, 2012.

Årthun, M., Eldevik, T. and Smedsrud, L. H.: The role of Atlantic heat transport in future Arctic winter sea ice loss, J. Clim., 32(11), 3327–3341, doi:10.1175/JCLI-D-18-0750.1, 2019.

Barton, A. D., Irwin, A. J., Finkel, Z. V. and Stock, C. A.: Anthropogenic climate change drives shift and shuffle in North Atlantic phytoplankton communities, Proc. Natl. Acad. Sci. U. S. A., 113(11), 2964–2969, doi:10.1073/pnas.1519080113, 2016.

Barton, B. I., Lenn, Y.-D. and Lique, C.: Observed Atlantification of the Barents Sea Causes the Polar Front to Limit the Expansion of Winter Sea Ice, J. Phys. Oceanogr., 48(8), 1849–1866, doi:10.1175/JPO-D-18-0003.1, 2018.

Basedow, S. L., Zhou, M. and Tande, K. S.: Secondary production at the Polar Front, Barents Sea, August 2007, J. Mar. Syst., 130(August 2007), 147–159, doi:10.1016/j.jmarsys.2013.07.015, 2014.

Beaugrand, G. and Reid, P. C.: Long-term changes in phytoplankton, zooplankton and salmon related to climate, Glob. Chang. Biol., 9(6), 801–817, doi:10.1046/j.1365-2486.2003.00632.x, 2003.

Blais, M., Ardyna, M., Gosselin, M., Dumont, D., Bélanger, S., Tremblay, J. É., Gratton, Y., Marchese, C. and Poulin, M.: Contrasting interannual changes in phytoplankton productivity and community structure in the coastal Canadian Arctic Ocean, Limnol. Oceanogr., 62(6), 2480–2497, doi:10.1002/lno.10581, 2017.

Blanchet, M. A., Primicerio, R., Frainer, A., Kortsch, S., Skern-Mauritzen, M., Dolgov, A. V. and Aschan, M.: The role of marine mammals in the Barents Sea foodweb, ICES J. Mar. Sci., 76, I37–I53, doi:10.1093/icesjms/fsz136, 2019.

ter Braak, C. J. F. and Verdonschot, P. F. M.: Canonical correspondence analysis and related multivariate methods in aquatic ecology, Aquat. Sci., 57(3), 255–289, doi:10.1007/BF00877430, 1995.

Clarke, A. and Peck, L. S.: The physiology of polar marine zooplankton, Polar Res., 10(2), 355–370, doi:10.3402/polar.v10i2.6752, 1991.

Daase, M., Varpe, O. and Falk-Petersen, S.: Non-consumptive mortality in copepods: Occurrence of Calanus spp. Carcasses in the Arctic Ocean during winter, J. Plankton Res., 36(1), 129–144, doi:10.1093/plankt/fbt079, 2014.

Dalpadado, P. and Mowbray, F.: Comparative analysis of feeding ecology of capelin from two shelf ecosystems, off Newfoundland and in the Barents Sea, Prog. Oceanogr., 114, 97–105, doi:10.1016/j.pocean.2013.05.007, 2013.

Dalpadado, P., Arrigo, K. R., Hjøllo, S. S., Rey, F., Ingvaldsen, R. B., Sperfeld, E., Van Dijken, G. L., Stige, L. C., Olsen, A. and Ottersen, G.: Productivity in the Barents Sea - Response to recent climate variability, PLoS One, 9(5), doi:10.1371/journal.pone.0095273, 2014.

Dalpadado, P., Arrigo, K. R., van Dijken, G. L., Skjoldal, H. R., Bagøien, E., Dolgov, A. V., Prokopchuk, I. P. and Sperfeld, E.: Climate effects on temporal and spatial dynamics of phytoplankton and zooplankton in the Barents Sea, Prog. Oceanogr., 185(April), 102320, doi:10.1016/j.pocean.2020.102320, 2020.

Falk-Petersen, S., Pavlov, V., Timofeev, S. and Sargent, J.: Climate variability and possible effects on arctic food chains: The role of Calanus., in Arctic Alpine Ecosystems and People in a Changing Environment., edited by J. Ørbæk, R. Kallenborn, I. Tombre, E. Hegseth, S. Falk-Petersen, and A. Hoel, pp. 147–166, Springer Berlin Heidelberg, Berlin, Heidelberg., 2007.

Falk-Petersen, S., Haug, T., Hop, H., Nilssen, K. T. and Wold, A.: Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland, Deep. Res. Part II Top. Stud. Oceanogr., 56(21–22), 2080–2086, doi:10.1016/j.dsr2.2008.11.020, 2009.

Feng, Z., Ji, R., Campbell, R. G., Ashjian, C. J. and Zhang, J.: Early ice retreat and ocean warming may induce copepod biogeographic boundary shifts in the Arctic Ocean, J. Geophys. Res. Ocean., 121(5), 3010–3028, doi:10.1002/2015JC011516, 2016.

Gjøsæter, H., Bogstad, B. and Tjelmeland, S.: Ecosystem effects of the three capelin stock collapses in the Barents Sea, Mar. Biol. Res., 5(1), 40–53, doi:10.1080/17451000802454866, 2009.

Gogorev, R. M. and Samsonov, N. I.: The genus chaetoceros (bacillariophyta) in Arctic and Antarctic, Nov. Sist. Nizshikh

Rastenii, 50, 56–111, doi:10.31111/nsnr/2016.50.56, 2016.

Haroardóttir, S., Pančić, M., Tammilehto, A., Krock, B., Møller, E. F., Nielsen, T. G. and Lundholm, N.: Dangerous relations in the arctic marine food web: Interactions between toxin producing Pseudo-nitzschia diatoms and Calanus copepodites, Mar. Drugs, 13(6), 3809–3835, doi:10.3390/md13063809, 2015.

Hassel, A.: Seasonal changes in zooplankton composition in the Barents Sea, with special attention to Calanus spp. (Copepoda), J. Plankton Res., 8(2), 329–339, doi:10.1093/plankt/8.2.329, 1986.

Helaouët, P. and Beaugrand, G.: Physiology, ecological niches and species distribution, Ecosystems, 12(8), 1235–1245, doi:10.1007/s10021-009-9261-5, 2009.

Huertas, E. I., Rouco, M., López-Rodas, V. and Costas, E.: Warming will affect phytoplankton differently: Evidence through a mechanistic approach, Proc. R. Soc. B Biol. Sci., 278(1724), 3534–3543, doi:10.1098/rspb.2011.0160, 2011.

Hunt, G. L., Drinkwater, K. F., Arrigo, K., Berge, J., Daly, K. L., Danielson, S., Daase, M., Hop, H., Isla, E., Karnovsky, N., Laidre, K., Mueter, F. J., Murphy, E. J., Renaud, P. E., Smith, W. O., Trathan, P., Turner, J. and Wolf-Gladrow, D.: Advection in polar and sub-polar environments: Impacts on high latitude marine ecosystems, Prog. Oceanogr., 149, 40–81, doi:10.1016/j.pocean.2016.10.004, 2016.

ICES: Report of the Arctic Fisheries Working Group (AFWG), 23-29 April 2015, Hamburg, Germany., 2015.

Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S.: Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R, J. Anim. Ecol., 80, 595–602, doi:10.1111/j.1365-2656.2011.01806.x, 2011.

Jakubas, D., Wojczulanis-Jakubas, K., Iliszko, L. M., Strøm, H. and Stempniewicz, L.: Habitat foraging niche of a High Arctic zooplanktivorous seabird in a changing environment, Sci. Rep., 7(1), 1–14, doi:10.1038/s41598-017-16589-7, 2017.

Joli, N., Gosselin, M., Ardyna, M., Babin, M., Onda, D. F., Tremblay, J. É. and Lovejoy, C.: Need for focus on microbial species following ice melt and changing freshwater regimes in a Janus Arctic Gateway, Sci. Rep., 8(1), 1–11, doi:10.1038/s41598-018-27705-6, 2018.

Juul-Pedersen, T., Arendt, K. E., Mortensen, J., Blicher, M. E., Søgaard, D. H. and Rysgaard, S.: Seasonal and interannual phytoplankton production in a sub-Arctic tidewater outlet glacier fjord, SW Greenland, Mar. Ecol. Prog. Ser., 524, 27–38, doi:10.3354/meps11174, 2015.

Lafond, A., Leblanc, K., Quéguiner, B., Moriceau, B., Leynaert, A., Cornet, V., Legras, J., Ras, J., Parenteau, M., Garcia, N., Babin, M. and Tremblay, J. É.: Late spring bloom development of pelagic diatoms in Baffin Bay, Elementa, 7(1), doi:10.1525/elementa.382, 2019.

Leu, E., Søreide, J. E., Hessen, D. O., Falk-petersen, S. and Berge, J.: Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality, Prog. Oceanogr., 90(1–4), 18–32, doi:10.1016/j.pocean.2011.02.004, 2011.

Lewis, K. M., van Dijken, G. L. and Arrigo, K. R.: Changes in phytoplankton concentration now drive increased Arctic Ocean primary production, Science, 369(6500), 198–202, doi:10.1126/science.aay8380, 2020.

Lind, S., Ingvaldsen, R. B. and Furevik, T.: Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import, Nat. Clim. Chang., 8(7), 634–639, doi:10.1038/s41558-018-0205-y, 2018.

Litchman, E. and Klausmeier, C. A.: Trait-Based Community Ecology of Phytoplankton, Annu. Rev. Ecol. Evol. Syst., 39(1), 615–639, doi:10.1146/annurev.ecolsys.39.110707.173549, 2008.

Litchman, E., Ohman, M. D. and Kiørboe, T.: Trait-based approaches to zooplankton communities, J. Plankton Res., 35(3), 473–484, doi:10.1093/plankt/fbt019, 2013.

Long, Z. and Perrie, W.: Changes in ocean temperature in the Barents Sea in the twenty-first century, J. Clim., 30(15), 5901–5921, doi:10.1175/JCLI-D-16-0415.1, 2017.

López-urrutia, A. Á., Harris, R. P. and Smith, T.: Predation by calanoid copepods on the appendicularian Oikopleura dioica, Limnol. Oceanogr., 49(1), 303–307, doi:https://doi.org/10.4319/lo.2004.49.1.0303, 2004.

McMeans, B. C., Rooney, N., Arts, M. T. and Fisk, A. T.: Food web structure of a coastal Arctic marine ecosystem and implications for stability, Mar. Ecol. Prog. Ser., 482(MacArthur 1955), 17–28, doi:10.3354/meps10278, 2013.

Møller, E. F. and Nielsen, T. G.: Borealization of Arctic zooplankton—smaller and less fat zooplankton species in Disko Bay, Western Greenland, Limnol. Oceanogr., 1–14, doi:10.1002/lno.11380, 2019.

Moore, S. E. and Huntington, H. P.: Arctic marine mammals and climate change: Impacts and resilience, Ecol. Appl., 18(SUPPL.2), 157–165, doi:10.1890/06-0571.1, 2008.

Mutshinda, C. M., Finkel, Z. V., Widdicombe, C. E. and Irwin, A. J.: Phytoplankton traits from long-term oceanographic time-series, Mar. Ecol. Prog. Ser., 576(August), 11–25, doi:10.3354/meps12220, 2017.

Øigård, T. A., Lindstrøm, U., Haug, T., Nilssen, K. T. and Smout, S.: Functional relationship between harp seal body condition and available prey in the Barents Sea, Mar. Ecol. Prog. Ser., 484, 287–301, doi:10.3354/meps10272, 2013.

Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A. and Gjøsæter, H.: Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: A review of the biological value of the area, ICES J. Mar. Sci., 67(1), 87–101, doi:10.1093/icesjms/fsp229, 2010.

Onarheim, I. H. and Årthun, M.: Toward an ice-free Barents Sea, Geophys. Res. Lett., 44, 8387–8395, doi:10.1002/2017GL074304, 2017.

Oziel, L., Sirven, J. and Gascard, J. C.: The Barents Sea frontal zones and water masses variability (1980-2011), Ocean Sci., 12(1), 169–184, doi:10.5194/os-12-169-2016, 2016.

Oziel, L., Neukermans, G., Ardyna, M., Lancelot, C., Tison, J.-L., Wassmann, P., Sirven, J., Ruiz-Pino, D. and Gascard, J.-C.: Role for Atlantic inflows and sea ice loss on shifting phytoplankton blooms in the Barents Sea, J. Geophys. Res. Ocean., (122), 5121–5139, doi:10.1002/2016JC012582.Received, 2017.

Oziel, L., Baudena, A., Ardyna, M., Massicotte, P., Randelhoff, A., Sallée, J. B., Ingvaldsen, R. B., Devred, E. and Babin, M.: Faster Atlantic currents drive poleward expansion of temperate phytoplankton in the Arctic Ocean, Nat. Commun., 11(1), 1–8, doi:10.1038/s41467-020-15485-5, 2020.

Pan, Y., Canada, C., Bates, S. S., Canada, O. and Cembella, A.: Environmental stress and domoic acid production by Pseudo-nitzschia: A physiological perspective, Nat. Toxins, 6(1), 127–135, doi:10.1002/(SICI)1522-7189(199805/08)6, 1998.

Prokopchuk, I. P. and Trofimov, A. G.: Interannual dynamics of zooplankton in the Kola Section of the Barents Sea during the recent warming period, ICES J. Mar. Sci., 76, doi:10.1093/icesjms/fsz206, 2019.

R Development Core Team: R: A Language and Environment for Statistical Computing., [online] Available from: https://www.rproject.org, 2020.

Rat'kova, T. N. and Wassmann, P.: Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea, J. Mar. Syst., 38(1–2), 47–75, doi:10.1016/S0924-7963(02)00169-0, 2002.

Reid, P. C., Colebrook, J. M., Matthews, J. B. L., Aiken, J., Barnard, R., Batten, S. D., Beaugrand, G., Buckland, C., Edwards, M., Finlayson, J., Gregory, L., Halliday, N., John, A. W. G., Johns, D., Johnson, A. D., Jonas, T., Lindley, J. A., Nyman, J., Pritchard, P., Richardson, A. J., Saxby, R. E., Sidey, J., Smith, M. A., Stevens, D. P., Tranter, P., Walne, A., Wootton, M., Wotton, C. O. M. and Wright, J. C.: The Continuous Plankton Recorder: Concepts and history, from Plankton Indicator to undulating recorders, Prog. Oceanogr., 57(2–4), 117–173, doi:10.1016/j.pocean.2003.08.002, 2003.

Renaud, P. E., Daase, M., Banas, N. S., Gabrielsen, T. M., Søreide, J. E., Varpe, Ø., Cottier, F., Falk-Petersen, S., Halsband, C., Vogedes, D., Heggland, K. and Berge, J.: Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience, ICES J. Mar. Sci., 75(6), 1871–1881, doi:10.1093/icesjms/fsy063, 2018.

Reygondeau, G. and Beaugrand, G.: Future climate-driven shifts in distribution of Calanus finmarchicus, Glob. Chang. Biol., 17(2), 756–766, doi:10.1111/j.1365-2486.2010.02310.x, 2011a.

Reygondeau, G. and Beaugrand, G.: Water column stability and Calanus finmarchicus, J. Plankton Res., 33(1), 119–136, doi:10.1093/plankt/fbq091, 2011b.

Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D. and Witt, M.: Using continuous plankton recorder data, Prog. Oceanogr., 68(1), 27–74, doi:10.1016/j.pocean.2005.09.011, 2006.

Sato, R., Tanaka, Y. and Ishimaru, T.: House production by Oikopleura dioica (Tunicata, Appendicularia) under laboratory conditions, J. Plankton Res., 23(4), 415–423, doi:10.1093/plankt/23.4.415, 2001.

Signorini, S. R. and McClain, C. R.: Environmental factors controlling the Barents Sea spring-summer phytoplankton blooms, Geophys. Res. Lett., 36(10), 1–5, doi:10.1029/2009GL037695, 2009.

Skern-Mauritzen, M., Johannesen, E., Bjørge, A. and Øien, N.: Baleen whale distributions and prey associations in the Barents Sea, Mar. Ecol. Prog. Ser., 426, 289–301, doi:10.3354/meps09027, 2011.

Skogen, M. D., Hjøllo, S. S., Sandø, A. B. and Tjiputra, J.: Future ecosystem changes in the Northeast Atlantic: a comparison between a global and a regional model system, ICES J. Mar. Sci., 75(7), 2355–2369, doi:10.1093/icesjms/fsy088, 2018.

Søreide, J. E., Leu, E. V. A., Berge, J., Graeve, M. and Falk-Petersen, S.: Timing of blooms, algal food quality and Calanus glacialis reproduction and growth in a changing Arctic, Glob. Chang. Biol., 16(11), 3154–3163, doi:10.1111/j.1365-2486.2010.02175.x, 2010.

Stige, L. C., Lajus, D. L., Chan, K.-S., Dalpadado, P., Basedow, S. L., Berchenko, I. and Stenseth, N. C.: Climatic forcing of zooplankton dynamics is stronger during low densities of planktivorous fish, Limnol. Oceanogr., 54(4), 1025–1036, doi:10.4319/lo.2009.54.4.1025, 2009.

Stige, L. C., Eriksen, E., Dalpadado, P. and Ono, K.: Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea, ICES J. Mar. Sci., 76, 24–36, doi:10.1093/icesjms/fsz063, 2019.

Sugie, K., Fujiwara, A., Nishino, S., Kameyama, S. and Harada, N.: Impacts of Temperature, CO2, and Salinity on Phytoplankton Community Composition in the Western Arctic Ocean, Front. Mar. Sci., 6(January), doi:10.3389/fmars.2019.00821, 2020.

Tatters, A. O., Fu, F. X. and Hutchins, D. A.: High CO 2 and silicate limitation synergistically increase the toxicity of pseudo-nitzschia fraudulenta, PLoS One, 7(2), doi:10.1371/JOURNAL.PONE.0032116, 2012.

Vargas, C. A., Tönnesson, K., Sell, A., Maar, M., Møller, E. F., Zervoudaki, T., Giannakourou, A., Christou, E., Satapoomin, S., Petersen, J. K., Nielsen, T. G. and Tiselius, P.: Importance of copepods versus appendicularians in vertical carbon fluxes in a Swedish fjord, Mar. Ecol. Prog. Ser., 241, 125–138, doi:10.3354/meps241125, 2002.

Verity, P. G., Wassmann, P., Frischer, M. E., Howard-Jones, M. H. and Allen, A. E.: Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer, J. Mar. Syst., 38(1–2), 109–123, doi:10.1016/S0924-7963(02)00172-0, 2002.

Wilkinson, G. M., Walter, J., Fleck, R. and Pace, M. L.: Beyond the trends: The need to understand multiannual dynamics in aquatic ecosystems, Limnol. Oceanogr. Lett., 5(4), 281–286, doi:10.1002/lol2.10153, 2020.

Yang, S., Puggioni, G., Harlow, L. L. and Redding, C. A.: A comparison of different methods of zero - inflated data analysis and an application in health surveys, J. Mod. Appl. Stat. Methods, 16(1), 518–543, doi:10.22237/jmasm/1493598600, 2017.

Table 1: Contribution of each plankton taxa to interannually variable axes of the three interannual pCCA's.

	ST1		ST2		ST3	
Species	Axis 1	Axis 3	Axis 1	Axis 2	Axis 1	Axis 2
Appendicularia	0.00	0.00	0.76	-1.21	0.88	-0.50
Calanus finmarchicus	-2.05	0.28	-2.04	-0.38	-2.05	-0.60
Calanus I-IV	-1.22	0.05	-0.74	0.19	-0.85	0.41
Ceratium	0.46	-0.19	0.50	-1.43	0.50	-0.25
Chaetoceros	0.46	1.14	0.32	0.26	0.27	-0.17
Cirripede larvae	0.00	0.00	0.00	0.00	-0.17	1.59
Coccolithaceae	0.37	-0.64	0.29	0.86	0.67	-0.83
Copepod eggs	0.48	1.06	0.00	0.00	0.00	0.00
Copepod nauplii	0.42	-0.17	0.24	0.20	0.34	-0.12
Corethron hystrix	0.00	0.00	-0.06	-0.46	0.00	0.00
Echinoderm larvae	0.34	-0.03	0.00	0.00	0.00	0.00
Foraminifera	0.28	-0.24	0.07	0.80	0.00	0.00
Oithona	0.67	-0.50	0.50	0.19	0.00	0.00
Para-pseudocalanus	0.61	-0.51	0.55	0.36	0.17	-0.57
Pseudo-nitzschia	0.00	0.00	0.72	-1.39	0.68	-0.46
Rhizosolenia	0.22	0.00	0.00	0.00	0.32	0.23
Silicoflagellates	0.00	0.00	0.39	1.09	0.00	0.00
Thalassiosira	0.23	0.37	0.28	-0.17	0.07	1.18
Tintinnida	0.69	0.89	0.00	0.00	-0.08	0.58

Table 2: Correlations between the pCCA species community axis and its corresponding hydroclimate axis that showed significant interannual variation as identified in the pCCA for all three regions.

Region	pCCA axis	Adj. R^2	F-statistic	p value
ST1	Axis 1	0.79	97.22	< 0.0001
	Axis 3	0.9	235.7	< 0.0001
ST2	Axis 1	0.64	58.32	< 0.0001
	Axis 2	0.88	242.7	< 0.0001
ST3	Axis 1	0.58	39.63	< 0.0001
	Axis 2	0.36	16.75	0.0003

Table 3: Contribution of each hydroclimate variable to the interannually variable axes of the three interannual pCCA's.

	ST1		ST2		ST3	
Hydroclimate variable	Axis 1	Axis 3	Axis 1	Axis 2	Axis 1	Axis 2
Chlorophyll-a	-0.02	-0.11	0.02	0.31	0.00	-0.27
Density	-0.03	-0.19	-0.14	0.63	0.31	0.06
Winter SST	0.05	0.17	0.20	-0.16	0.04	-0.70
June SST	0.07	0.50	0.13	-0.70	-0.16	-0.10
MLD	-0.11	0.15	-0.36	0.15	-0.65	0.12
NO3	NA	NA	-0.33	-0.31	-0.32	0.30
PO4	NA	NA	-0.32	-0.33	-0.31	0.26
Prev Autumn SST	-0.29	0.71	-0.20	-0.25	0.04	-0.58
Prev Summer SST	-0.84	0.40	-0.61	-0.03	-0.47	-0.45
Salinity	0.02	0.15	-0.15	0.28	0.33	-0.10
Sil	NA	NA	-0.33	-0.21	-0.31	0.28
Spring SST	-0.13	0.21	-0.18	0.11	-0.36	0.18

Table 4: Contribution of each plankton taxa to first three axes of the spatial pCCA

Species	Axis 1	Axis 2	Axis 3
Appendicularia	-0.03	-0.52	-0.34
Calanus finmarchicus	0.17	0.03	-0.11
Calanus I-IV	-0.14	-0.17	-0.15
Ceratium	-0.31	0.28	0.71
Chaetoceros	-0.40	-0.06	-0.17
Cirrepede larvae	2.02	-1.46	0.48
Coccolithaceae	-0.53	-0.36	0.37
Copepod eggs	0.57	1.09	0.90
Copepod nauplii	-0.58	-0.16	0.08
Corethron hystrix	-1.27	-0.08	0.20
Echinoderm larvae	0.93	0.95	0.22
Foraminifera	-0.46	-0.36	0.38
Oithona	-0.61	1.12	-0.11
Para-pseudocalanus	-0.39	-0.07	-0.50
Pseudo-nitzschia	0.27	-0.41	-1.20
Rhizosolenia	0.92	-0.02	-0.09
Silicoflagellates	-0.45	-1.00	-0.15
Thalassiosira	0.54	-0.53	0.24
Tintinnida	-0.11	1.95	-0.80

Table 5: Correlations between the first three pCCA species community axis and its corresponding hydroclimate axis in the spatial variability analysis.

pCCA axis	Adj. R^2	F-statistic	p value
Axis 1	0.45	71.27	< 0.0001
Axis 2	0.48	82.73	< 0.0001
Axis 3	0.40	59.57	< 0.0001

Table 6: Contribution of each hydroclimate variable to the first three axes of the spatial pCCA

Hydroclimate variable	Axis 1	Axis 2	Axis 3
Chlorophyll-a	0.02	0.19	-0.33
Density	0.21	-0.59	-0.50
Depth	-0.47	-0.39	-0.28
Latitude	0.11	-0.66	-0.48
Longitude	-0.01	0.56	0.57
MLD	-0.27	0.10	-0.13
Salinity	-0.20	-0.63	-0.29
SST June	-0.36	0.63	0.56

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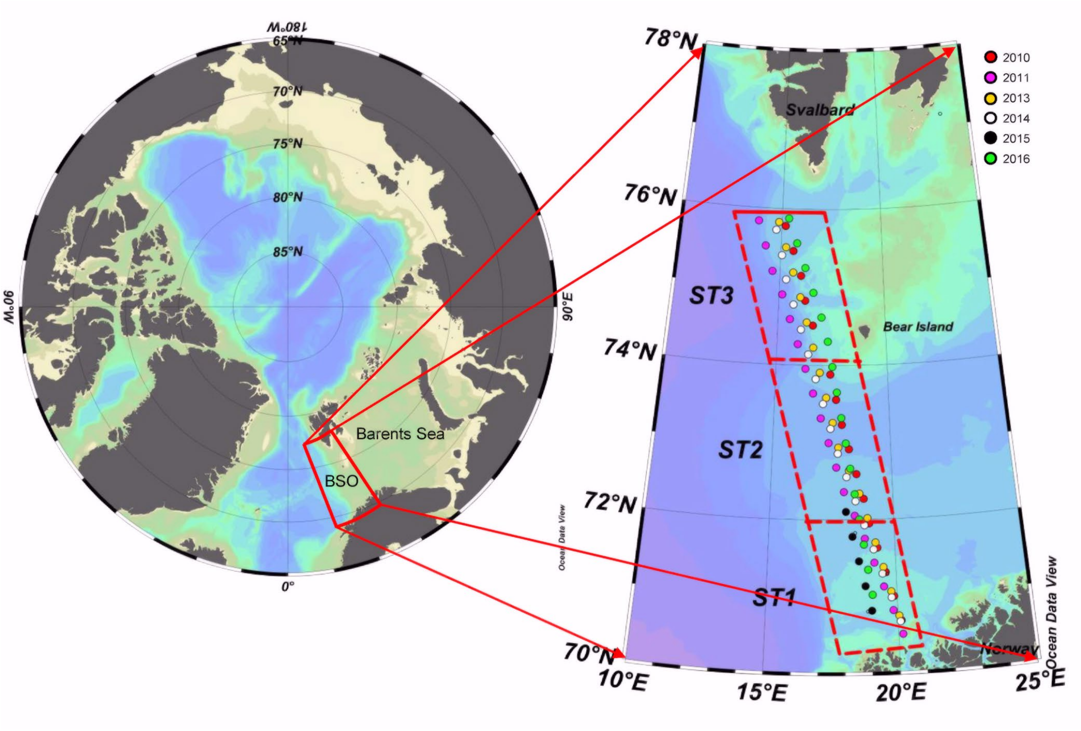

Figure 1: Location of Continuous Plankton Recorder sampling (coloured dots) route (ST route) in June in the southwestern Barents Sea between 2010 and 2016. The dotted red lines show the segregation if the transect into the three regions. The colour of the dots are indicative of certain years.

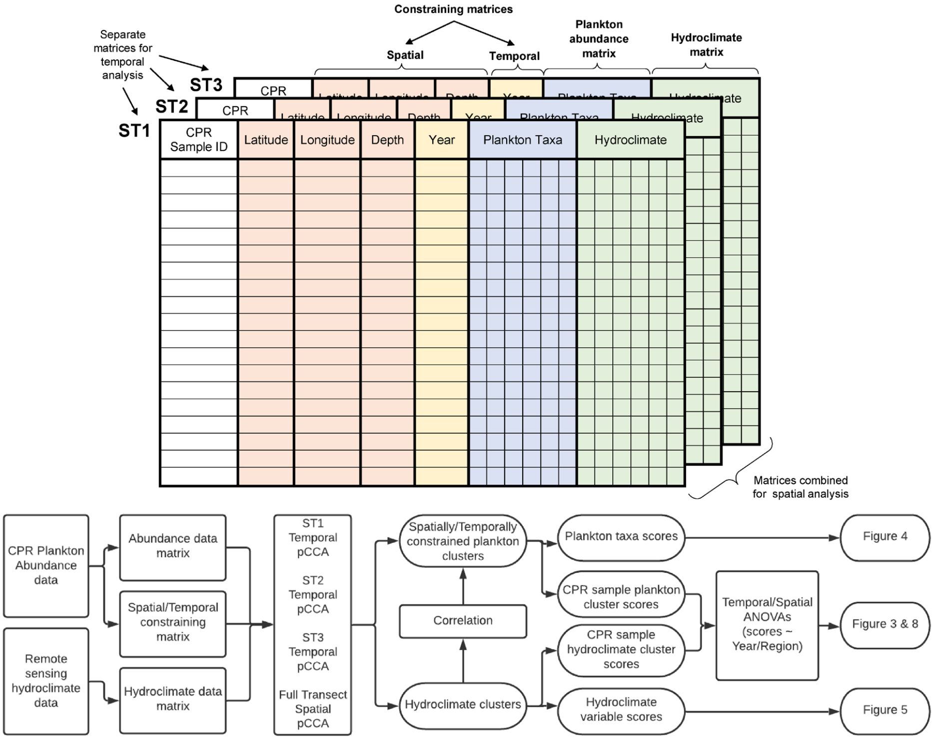

Figure 2: Visualisation of the statistical multivariate framework used to identify interannual and spatial variability of the plankton assemblage, and to associate the variation with hydroclimate drivers.

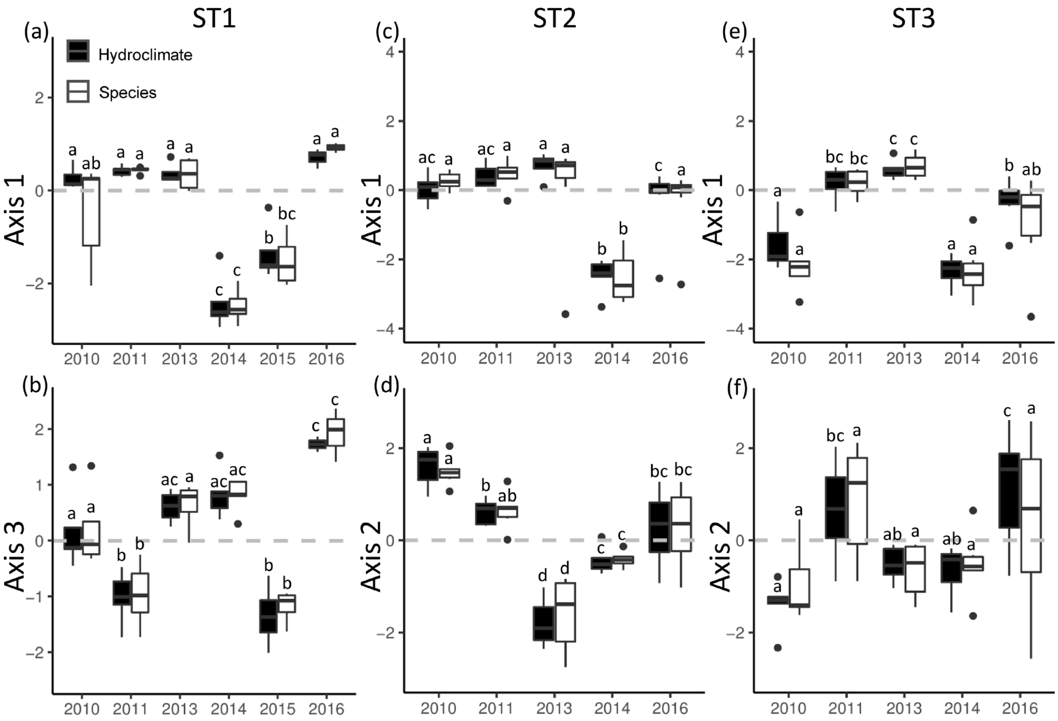

Figure 3: Interannual variability of the species assemblage and hydroclimate in ST1 (a & b), ST2 (c & d) and ST3 (e & f). Boxplots represent the average hydroclimate (black boxes) and species (white boxes) axis scores for each year in the three regions. The axis explaining the highest proportion of the variation in data (i.e. axis 1) are in panels a-c, and the axis explaining the next highest proportion of the variation in data whilst being significantly interannually variable are in panels b-d. Differing letters denote significant differences between years for the black boxes and for the white boxes. Black dots represent outliers.

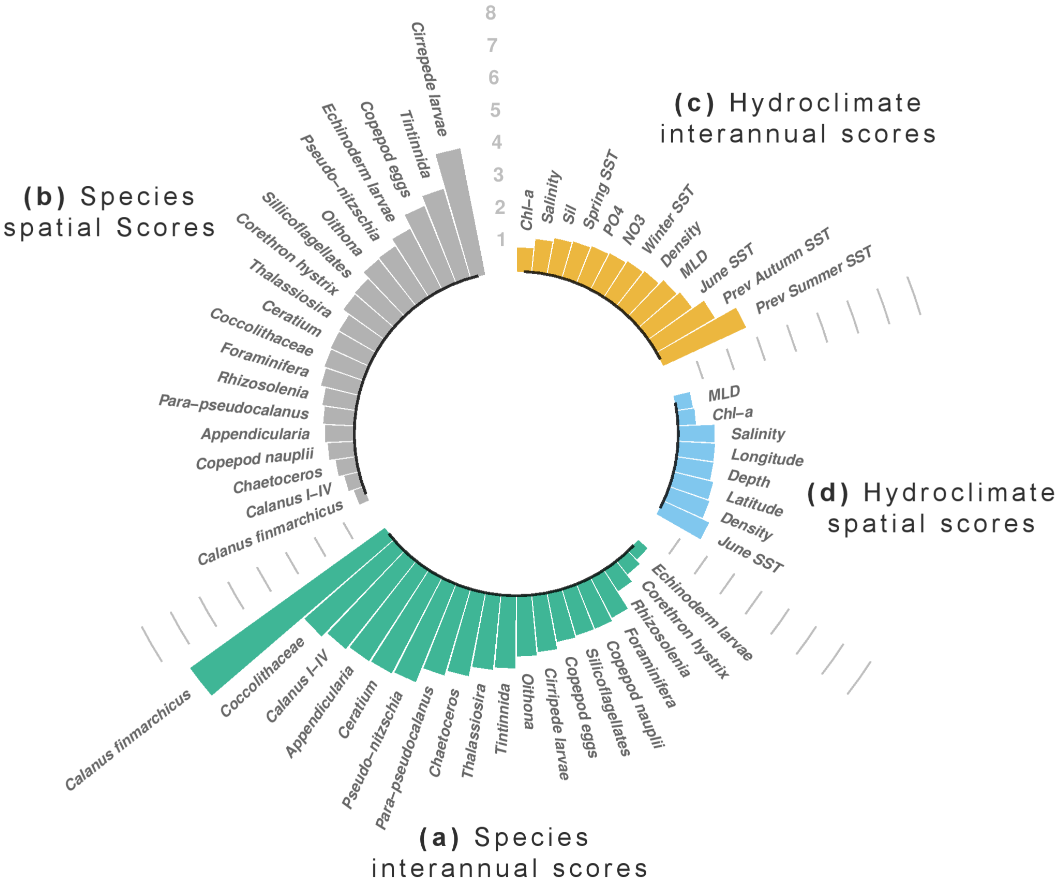

Figure 4: Level of interannual (a & c) and spatial (b & d) variability for each each species (a & b) and hydroclimate variable (c & d), measured as their total axis scores from the pCCA's. Higher bars represent greater variation.

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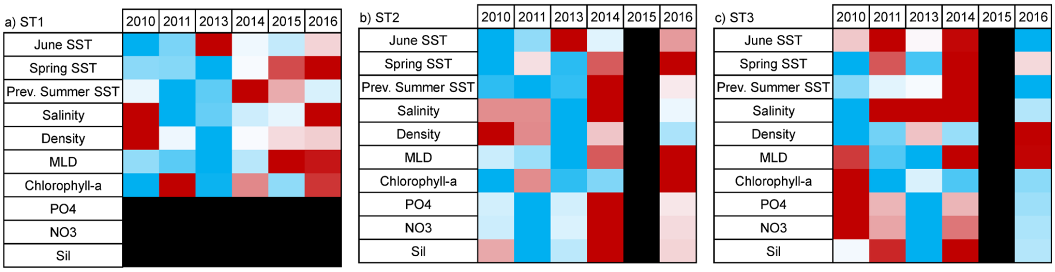

Figure 5: Estimates of yearly anomalies of environmental variables matched to the CPR sampling locations in June (unless stated otherwise in the variable name) in the three Barents Sea regions. White squares represent the 2010-2016 average. Red squares represent above average measurements and blue squares represent below average measurements. Black squares indicate missing data.

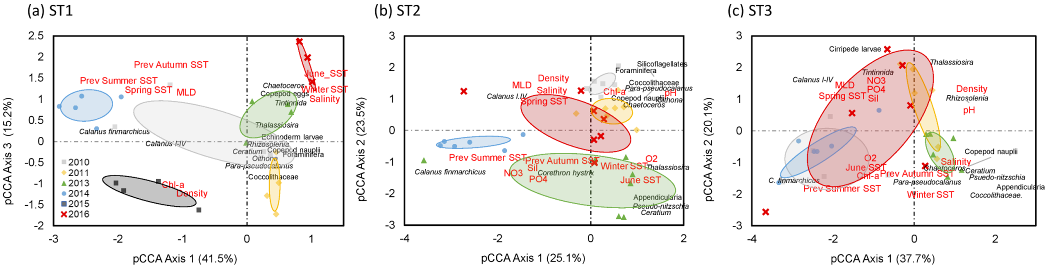

Figure 6: Biplots of two partial canonical correspondence axes for plankton in the (a) ST1, (b) ST2 and (c) ST3 region. Proportions in parentheses in the x and y axis titles represent the amount of variation explained in the plankton community by that axis. Note that the y axis for panel (a) represents pCCA axis 3, whilst panels (b) and (c) represent pCCA axis 2. The relationship of the hydroclimate variables (red lettering), species (black lettering) and year scores (coloured points) with Bayesian standard ellipses - that represent the standard error for multivariate data - for each year. Non-overlapping ellipses represent significant differences between years for the species axis scores

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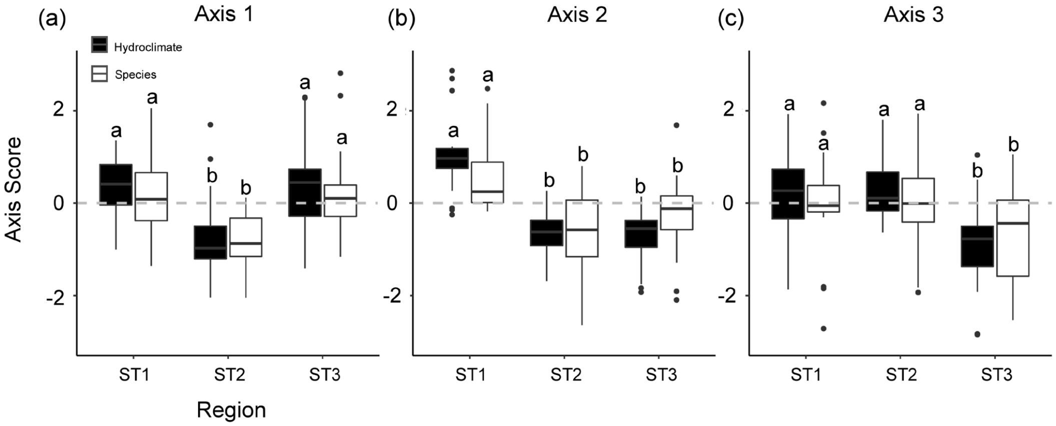

Figure. 7: Spatial pCCA results. Boxplots represent the hydroclimate (black boxes) and species (white boxes) axis scores for each CPR sample in the three regions. Letters denote significant differences between regions for the first three pCCA axes.

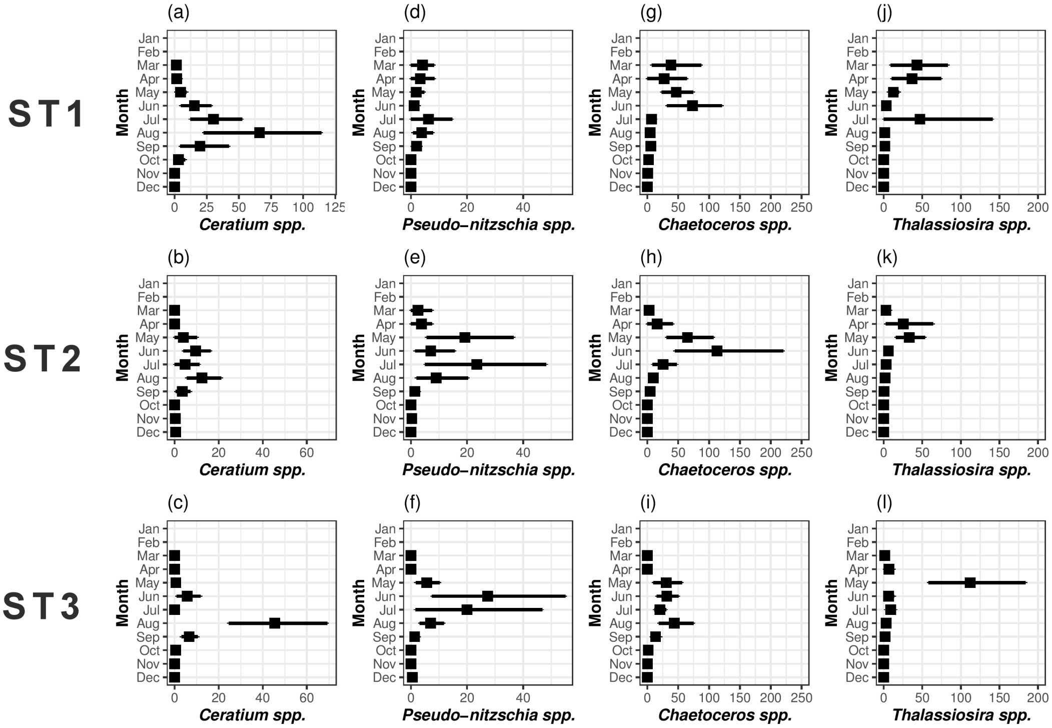

Figure 8: Seasonal phenology of four of the most interannually variable phytoplankton taxa as identified by the pCCA analysis in ST1 (panels a, d, g, j), ST2 (b, e, h, k) and ST3 (c, f, I, l). Note differing x axis scales between species, and between panel (a), (b) and (c) for *Ceratium* spp..

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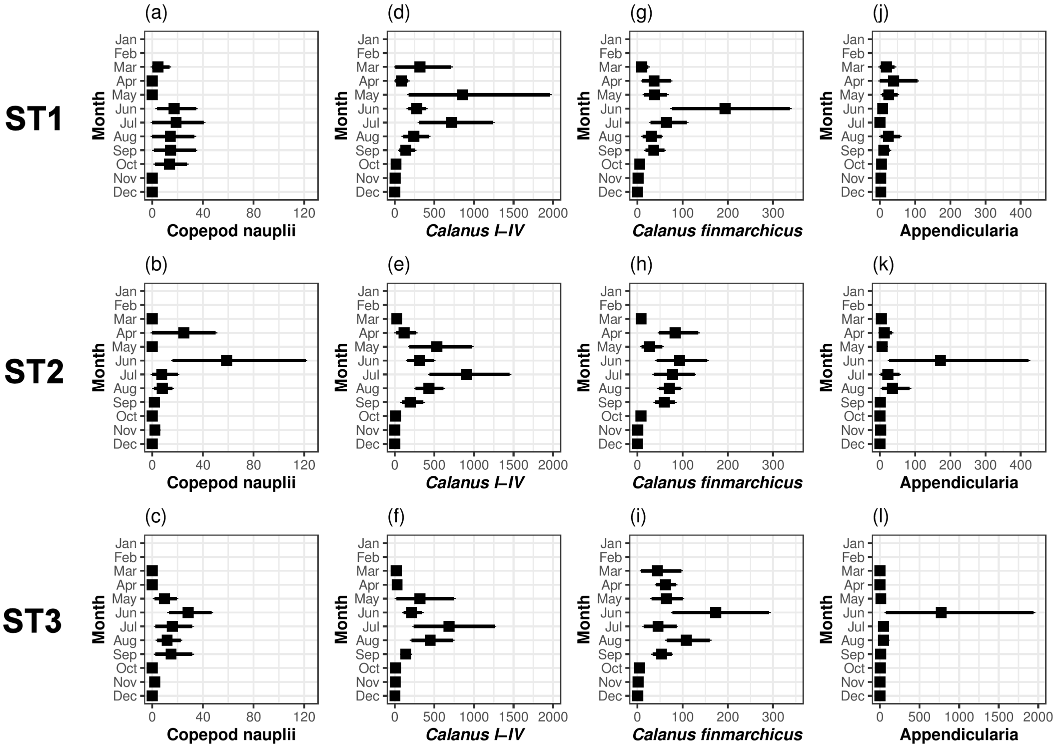

Figure 9: Seasonal phenology of four of the most interannually variable zooplankton taxa as identified by the pCCA analysis in ST1 (panels a, d, g, j), ST2 (b, e, h, k) and ST3 (c, f, I, l). Note differing x axis scales between species, and between panel (j), (k) and (l) for Appendicularians.