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Science of the Total Environment

Warming increases the compositional and functional variability of a temperate protist community

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HIGHLIGHTS

- The species' thermal traits primarily drive community reorganisation under warming
- Many North Sea protists tolerate and coexist at temperatures of + 12 °C
- Biomass accumulation in- and oxygen production decreases with warming
- Temperature increases the compositional and functional variability
- *Phaeocystis globosa* drives functional dissimilarity regarding the C:P but not the C:N ratio

GRAPHICAL ABSTRACT
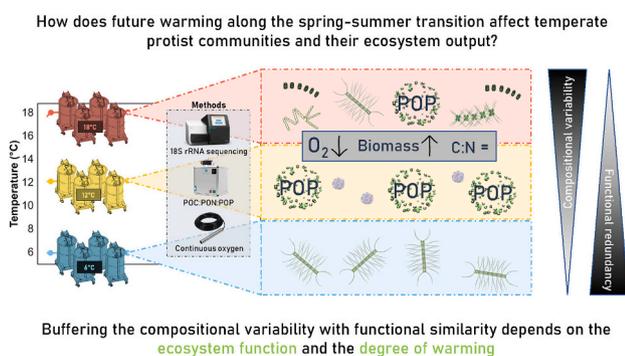
ARTICLE INFO

ABSTRACT

Phototrophic protists are a fundamental component of the world's oceans by serving as the primary source of energy, oxygen, and organic nutrients for the entire ecosystem. Due to the high thermal seasonality of their habitat, temperate protists could harbour many well-adapted species that tolerate ocean warming. However, these species may not sustain ecosystem functions equally well. To address these uncertainties, we conducted a 30-day mesocosm experiment to investigate how moderate (12 °C) and substantial (18 °C) warming compared to ambient conditions (6 °C) affect the composition (18S rRNA metabarcoding) and ecosystem functions (biomass, gross oxygen productivity, nutritional quality – C:N and C:P ratio) of a North Sea spring bloom community. Our results revealed warming-driven shifts in dominant protist groups, with haptophytes thriving at 12 °C and diatoms at 18 °C. Species responses primarily depended on the species' thermal traits, with indirect temperature effects on grazing being less relevant and phosphorus acting as a critical modulator. The species *Phaeocystis globosa* showed highest biomass on low phosphate concentrations and relatively increased in some replicates of

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both warming treatments. In line with this, the C:P ratio varied more with the presence of *P. globosa* than with temperature. Examining further ecosystem responses under warming, our study revealed lowered gross oxygen productivity but increased biomass accumulation whereas the C:N ratio remained unaltered. Although North Sea species exhibited resilience to elevated temperatures, a diminished functional similarity and heightened compositional variability indicate potential ecosystem repercussions for higher trophic levels. In conclusion, our research stresses the multifaceted nature of temperature effects on protist communities, emphasising the need for a holistic understanding that encompasses trait-based responses, indirect effects, and functional dynamics in the face of exacerbating temperature changes.

1. Introduction

Phototrophic protists play a central role in the ecosystem by providing energy, oxygen and organic nutrients for organisms higher up the food chain (Naselli-Flores and Padisák, 2023). Especially in coastal temperate areas, their habitat is characterised by a high seasonality in temperature. For instance, a typical North Sea spring bloom spans from early March to late April, during which the temperature gradually increases from around 6 °C to approximately 12 °C (Käse et al., 2020). A few months later in August, temperature peaks near 18 °C (Wiltshire and Manly, 2004). Many species are adapted to this wide temperature range and therefore often reside below their optimum temperature for growth (Boyd et al., 2013; Giesler et al., 2023). Despite this variability, most experiments investigating warming effects on temperate plankton employ treatments of +3 °C to +6 °C (Happe et al., 2024), which fall well within the range of what they naturally experience (Wiltshire and Manly, 2004). These temperatures may represent the average increases projected for the North Sea (IPCC, 2021); however, they do not encompass heatwaves, which are anticipated to become more frequent, intense, and long-lasting in the upcoming decades (Oliver et al., 2019; Sánchez-Benítez et al., 2022). Many studies also tend to overlook the seasonal dynamics in the field (Gerhard et al., 2023) and, instead, capture a snapshot of a specific point in the year (but see Staehr and Sand-Jensen, 2006). Consequently, the outcomes of these experiments heavily depend on the selection of the starting point, possibly failing to fully represent the actual temperature variations that temperate protist communities will encounter in the future.

Temperature can affect protist community structure via different ways. One of them is through its direct effect on the physiology of single organisms by increasing all metabolic rates until they reach an optimum temperature and then drop (Raven and Geider, 1988). This relationship is described by thermal performance curves (TPCs) and mostly expressed in terms of growth rate (Thomas et al., 2012). Although it can be expected that many temperate phototrophic species tolerate a wide range of temperatures in single strain incubations (Boyd et al., 2013), interspecific competition may alter the response on the community level (Huertas et al., 2011; Denny, 2017). The reason for this lies in species-specific TPC characteristics such as the temperature optimum, the thermal breadth and the maximum growth rate at a given temperature, leading to different growth increments under warming and ultimately entailing species sorting (Bestion et al., 2018; Anderson et al., 2021; Wieczynski et al., 2021). Furthermore, warming can have indirect effects such as stronger grazing (Gibert, 2019) or the acceleration of nutrient incorporation causing earlier limitation (Berges et al., 2002), which in turn affects the TPC of organisms by lowering their thermal optimum or limits (Thomas et al., 2017). Variations in all relevant traits can translate into temperature-induced community shifts, reflected in the compositional transition from spring to summer and between years with different mean temperatures (Alvarez-Fernandez et al., 2012; Bruhn et al., 2021).

Shifts in the community composition of phototrophic protists may mediate a changed output for the ecosystem (Di Pane et al., 2022). But even when the composition remains the same, temperature can alter attributes relevant for higher trophic levels such as the provision of oxygen, energy and organic nutrients (Naselli-Flores and Padisák,

2023). These ecosystem functions stem from a variety of cellular processes and could therefore respond differently to changes in temperature. Functions that are mainly driven by biophysical mechanisms, such as oxygen production, may be affected less strongly compared to functions that rather depend on biochemical reactions, like biomass accumulation (Falkowski and Raven, 2007; Rehder et al., 2023). Another trait tightly linked to temperature is the stoichiometry, specifically the cellular carbon to nutrient ratios (i.e. C:N and C:P), which are used as proxies for the nutritional quality for heterotrophic organisms (van de Waal et al., 2010). While warming favours the investment in nitrogen-rich proteins over phosphorus-rich ribosomes and thus may raise the cellular C:P ratio more than the C:N ratio (Woods et al., 2003; Armin and Inomura, 2021), both ratios could generally increase due to indirect temperature effects such as faster nutrient drawdown (De Senerpont Domis et al., 2014; Matsumoto et al., 2020). Ultimately, all of these processes depend on the environmental context, leading to great variations between the warming responses observed for ecosystem functions (Lewandowska et al., 2014; Striebel et al., 2016).

Differences in functional traits in combination with warming can increase the variability of a system. For example, small variations in the abundance of a species with a high nutrient uptake affinity can quickly build up to large differences when temperatures rise and then affect the surrounding conditions, e.g. induce earlier nutrient limitation (Serra-Pompei et al., 2019). In a setting where this species was slightly less abundant, another species with different traits could outcompete it and nutrient limitation might be induced later. The lag between these scenarios creates a phase with varying competition conditions and could shift the system to fundamentally different compositional states. Consequently, the existing stochasticity within planktonic systems can create several different trajectories and thereby lead to a higher unpredictability (Huisman and Weissing, 2001; Pálffy et al., 2021; Rogers et al., 2022). However, an increased compositional variability does not necessarily result in a higher variability of the respective ecosystem functions as it might be buffered by functional similarity between different species (Eisenhauer et al., 2023). While this has been shown to increase ecosystem stability to abiotic stressors (Biggs et al., 2020), temperature may context-dependently compromise this capacity (Garcia et al., 2018; Zhong et al., 2020).

Despite the urgent need to understand warming responses for projecting future ecosystem properties, current studies on temperate communities do not cover the full potential natural temperature range (Gerhard et al., 2023). To fill this gap, we mechanistically investigated the effect of warming on temperate protist communities in an indoor-mesocosm setting, covering three temperatures from the start of the spring bloom up to the summer peak. The aim was to experimentally determine the compositional output including its variability and to assess potential consequences for ecosystem functions provided to the North Sea by the spring bloom community. We hypothesized that warming leads to a relative increase in species with the respective thermal niche; a higher oxygen production and biomass accumulation but lower nutritional quality; and finally, an increasing compositional and functional variability that depends on the temperature increment, resulting in functional similarity of the communities under moderate but not under substantial warming.

2. Material & methods

2.1. Seawater collection and experimental set-up

The experiment was carried out in the mesocosm facility of the Institute for Chemistry and Biology of the Marine Environment (ICBM) in Wilhelmshaven in March/April 2022. Experimental units were the Planktotrons – twelve stainless steel indoor-mesocosms (Gall et al., 2017). A total of 8000 L of surface seawater was collected from the open North Sea, 60 km off the German coast at the long-term ecological research station Helgoland Roads (DEIMS ID: https://deims.org/1e96 ef9b-0915-4661-849f-b3a72f5aa9b1) during a cruise with the German *RV Heincke* on March 6th, 2022. The water was pumped with a diaphragm pump through a 200 μm mesh (reducing the abundance of larger grazers) into eight acid-cleaned 1000 L polyethylene Intermediate Bulk Containers (IBC, AUER Packaging GmbH, Amerang, Germany). On March 7th, we filled the mesocosms by evenly spreading 75 L from each IBC tank into each mesocosm via gravity, resulting in a total of 600 L per mesocosm.

The experiment was conducted using three different temperature treatments, with a replication of four. Upon incubation, the water temperature of all twelve tanks was set to 6 °C, which is representative of the water temperature for the North Sea in March over the last 12 years (based on Helgoland Roads LTER time series) and close to the field temperature during water collection (5.4 °C). As we wanted to cover a wide temperature range, we aimed our highest temperature treatment to be around the optimum temperature for growth (e.g. the highest possible temperature before community growth deteriorates). Therefore, we determined the temperature reaction norm of the phototrophic community at the start of the incubation with a thermal performance curve (TPC) assay. This was started one day after filling the mesocosms (March 8th) by taking a pooled water sample from all mesocosms that was filled into 40 mL cell culture flasks (SARSTEDT, Nümbrecht, Germany) and randomly spread across ten temperatures (3 °C to 30 °C in 3 °C steps) in triplicates. The incubation of the units was achieved by placing them on heating/cooling mats (Inkbird, Shenzhen, China) in different temperature rooms under the same light conditions as the mesocosms. Fluorescence (395/680 nm excitation/emission) was measured daily for eight days to determine growth using a SYNERGY H1 microplate reader (BioTek, Winooski, Vermont, USA) and the thermal performance curve was fitted according to the model by Thomas et al. (2017) using the "rTPC" package (Padfield and O'Sullivan, 2022). We chose the treatment temperatures to span the minimum (6 °C) and optimum temperature (18 °C) for growth, as well as an intermediate temperature (12 °C; Fig. S1). We performed a gradual temperature increase by 1 °C per day starting 24 h after the mesocosms have been filled (incubation days 0–12; Fig. S2). During this phase, temperatures and replicates behaved similarly in terms of community composition as well as ecosystem functions (Figs. S10–14). Therefore, and for comparability, we focus on the period from day 13 onwards.

All parameters that required water to be taken out (DNA, particulate nutrients, dissolved nutrients) were sampled every 3rd day using a self-built tube of the same height as the mesocosms to equally obtain water from all depths. This water was poured into a sample-rinsed bucket, from which subsamples were taken for each parameter after gentle hand-stirring. The starting conditions were assessed on the 8th of March by combining ~4 L of water from each mesocosm and taking technical triplicates from this pool for each parameter. From then onwards, each mesocosm was sampled individually.

2.2. Abiotic conditions

Non-invasive parameters (temperature, pH, salinity) were sampled daily at 10 am. To promote water convection, an integrated, mechanically driven mixing paddle with silicone lips homogenised the water column every two hours at a slow speed to prevent disturbing fragile organisms. Water temperatures were measured constantly with built-in PT100 sensors (Temperature Control, Donaueschingen, Germany) to confirm and adjust the target temperatures in each tank (Fig. S2). Two LED units (IT2040, Evergrow, Shenzhen, China) above each mesocosm were set to a 12:12 h day-night cycle (07:00–19:00 UTC light) with an intensity of 180 μmol photons m^{-2} s^{-1} (spherical PAR-sensor (US-SQS/ L, Walz, Effeltrich, Germany) connected to a LI-250 A (Li-Cor, Lincoln, NE, USA)). These settings were selected based on the natural conditions at Helgoland Roads during this time of the year (Wiltshire, 2008, 2010). Although the light intensity changed in all mesocosms over time (potentially due to biomass acuumulation), we observed no differences between the treatments, excluding light as a confounding factor (Fig. S3). Translucent float glass plates (Pilkington Optiwhite, Tokyo, Japan) were placed on top of the mesocosms to prevent evaporation, outgassing, and contamination. Daily salinity measurements (WTW IDS TetraCon, Xylem Analytics, Rye Brook, NY, USA) indicated no differences between temperatures (Fig. S4).

The experiment was conducted under ambient nutrient conditions. To monitor the concentrations of dissolved nitrate and phosphate, a subsample was filtered through a 0.2 μm polyethersulfon syringe filter (Sartorius, Göttingen, Germany) every third day and stored at −20 °C until the colorimetric measurement on a continuous flow analyser (Euro EA 3000, HEKAtech GmbH, Wegberg, Germany). Samples for dissolved silicate were taken every other day and quantified by molybdate reaction according to Wetzel and Likens (2003).

The pH was measured daily (WTW Multi 3630 IDS, Xylem Analytics, Rye Brook, NY, USA). Samples for total alkalinity were taken at the beginning, middle (day 15), and end (day 27) of the incubation by filtering a 100 mL subsample through a 0.2 μm polyethersulfon syringe filter (Sartorius, Göttingen, Germany) into a borosilicate bottle. The sample was kept at 4 °C until it was measured by duplicate potentiometric titration using a TitroLine alphaplus autosampler (Schott Instruments, Mainz, Germany) and subsequent correction with certified reference materials from A. Dickson (Scripps Institution of Oceanography, San Diego, CA, USA). The concentration of dissolved inorganic carbon (DIC) was calculated for incubation day 0, 15, and 27 using the software CO2sys (Pierrot et al., 2011) with dissociation constants of carbonic acid by Mehrbach et al. (1973), refitted by Dickson and Millero (1987).

2.3. Grazing assessment

Despite the initial filtering procedure, mesozooplankton appeared in all mesocosms, possibly due to early developmental stages (<200 μm) passing the mesh during water collection. Therefore, ~ 8 L water from each mesocosm were filtered through a 200 μm mesh and any mesozooplankton were transferred into 250 mL brown glass bottles before being fixed with Lugol's iodine solution at the end of the experiment (incubation day 27). Mesozooplankton was enumerated and identified to the lowest possible taxonomic level based on scientific literature (Conway, 2012) using a stereo-microscope (S8 AP0O, Leica, Wetzlar, Germany).

Additionally, protist herbivorous-induced mortality (m) rates were measured with the dilution method (Landry and Hassett, 1982) in a two-point modification (Chen, 2015a; Landry et al., 2022) using undiluted (100 %) and diluted (30 %) seawater. Samples from each mesocosm were pooled together for each temperature treatment. From the original water, we prepared 500 mL undiluted (100 %) and diluted (30 %) samples (two technical replicates per temperature treatment at 0 h (t0) and one for 24 h (tf)). Following Landry and Hassett (1982) and Chen (2015a) net phototrophic growth rate (k) was calculated as:

$$k = ln\left(\mathrm{Chla_{tf}}/\mathrm{Chla_{t0}}\right)/t$$

where $\mathrm{Chla_{tf}}$ and $\mathrm{Chla_{t0}}$ are the Chl*a* concentration measured at the end (tf) and at the beginning (t0) of the incubation period, respectively, and t

represents the duration of the incubation period (24 h). From both rates (that is, k_{30} and k_{100}), we calculated grazing of protist herbivores as:

$$m = (k_{30} - k_{100})/(1 - \times)$$

with $\times$ being the dilution factor used.

2.4. Community composition and diversity

Protist community composition was assessed via 18S rRNA gene amplicon sequencing of the V4 region as described by Ahme et al. (2023) and the results were validated qualitatively using light microscopy (fixed with 1 % Lugol's solution). Briefly, a subsample of 500 mL was gently vacuum-filtered (< -200 mbar) onto 0.8 μm polycarbonate filters (Nucleopore, Whatman, Maidstone, UK), which were stored in extraction buffer at -80 °C. DNA extraction was performed according to the manufacturer's protocol (NucleoSpin Soil extraction kit, Macherey-Nagel GmbH, Düren, Germany). All samples were normalised to 5 ng μL^{-1} before generating amplicons of the variable region 4 (V4) of the 18S rRNA gene following the standard protocol (16S Metagenomic Sequencing Library Preparation, Part #15044223 Rev. B. Illumina, San Diego, CA, USA). To best target the phototrophic community, we chose the forward and reverese primers of Bradley et al. (2016). Using the Nextera XT Index Kit v2 Set A primers (Illumina, San Diego, CA, USA), single samples were indexed and the barcoded amplicons were pooled equimolarly into one library. The library was sequenced with a 2×300 bp paired-end setup on a MiSeq sequencer (Illumina, San Diego, CA, USA) and generated amplicon reads which were demultiplexed by the Generate FASTQ workflow of the MiSeq software.

Primers were removed with v2.8 cutadapt (Martin, 2011) and the data was further processed with v1.18 DADA2 (Callahan et al., 2016). Forward reads were quality-trimmed after 240 and reverse reads after 210 base pairs. Sequences were denoised and paired-end reads merged with a minimum overlap of 20 base pairs. Subsequently, chimeras were predicted and removed (Table S1). The resulting amplicon sequence variants (ASVs) were taxonomically annotated using the protist reference databases v4.12.0 PR2 (Guillou et al., 2013). Samples with a sequencing depth outside of the 90 % quantile range were removed, sufficient depth was confirmed using rarefaction curves (Fig. S5) and all samples were scaled to the lowest depth (Beule and Karlovsky, 2020). ASVs with a count of fewer than ten reads in replicate sample means were excluded, as well as metazoans, fungi, plastids and nuclei. All larger hetero- and mixotrophic taxa were separately analysed and grouped based on their primary feeding strategy (de Vargas et al., 2015; Ramond et al., 2018; Adl et al., 2019). For an assessment of diversity of each sample, we calculated species richness as number of species in each sample, species evenness (Pielou, 1966) and the Shannon index (Ortiz-Burgos, 2016). Processing of the data was performed using R v4.21 (RCoreTeam, 2022) with RStudio v2022.07.2 (RStudioTeam, 2022) and the packages v0.2.3 SRS (Heidrich et al., 2021), v1.40.0 phyloseq (McMurdie and Holmes, 2013), v0.0.22 microbial (Guo and Gao, 2022), and v4.2.6 propr (Quinn et al., 2017).

The replicates diverged in terms of their community composition and therefore no analyses were performed to compare mean compositions between temperature treatments. To get a measure for compositional dissimilarity between replicates, the pairwise Aitchinson distances were calculated between all replicates for each temperature and day. Then, the distances of the replicates to their centroids in multivariate space of a principal coordinate ordination were calculated with the betadisper function (vegan v2.6–2) as described by Anderson et al. (2006) and Pálffy et al. (2021). The compositional variability at a constant temperature of 6 °C represents the "baseline"-variability within our experimental incubation. An increase in variability under warming (to 12 °C or 18 °C) compared to 6 °C indicates a temperature-driven effect rather than experimental duration/bottle effects. Therefore, we consider compositional variability to be driven by temperature if the beta-dispersion at a given warming treatment is significantly higher than at 6 °C.

2.5. Ecosystem functions

To assess the effect of temperature on different ecosystem functions, we chose several proxies: the concentration of particulate organic carbon (POC) for community biomass (Andersson and Rudehäll, 1993), the molar ratios between POC and particulate organic nitrogen (PON)/phosphorus (POP) for nutritional quality (Thomas et al., 2022), as well as the rate of change of dissolved oxygen per POC for gross oxygen productivity (GOP; Sanz-Martín et al., 2019). Furthermore, samples for chlorophyll *a* (Chl*a*) were taken as a proxy to track the development of the phototrophic biomass throughout the experiment.

For Chl*a*, POC/PON and POP, subsamples were filtered onto precombusted glass-fibre filters (GF/F Whatman, Maidstone, UK), and kept frozen until processing. Filters for Chl*a* were extracted according to the method of Thrane et al. (2015) and measured using a microplate reader (614 nm/680 nm; SYNERGY H1, BioTek, Winooski, Vermont, USA). For POC/PON, filters were dried and measured with an elemental analyser (Flash EA 1112, Thermo Scientific, Waltham, MA, USA). The POP filters were quantified by molybdate reaction after digestion with a potassium peroxydisulfate solution (Wetzel and Likens, 2003). Particulate nutrient ratios were calculated by dividing the molar masses of the respective nutrients.

Dissolved oxygen concentration in mmol m^{-3} was measured continuously by the built-in OXYBase WR-RS485-L5 sensors (PreSens, Regensburg, Germany), calibrated by PreSens. Daily community production and respiration were calculated via the slope of the linear regression of oxygen concentration over the light period (09:00–19:00) and dark period (19:00–09:00), respectively. Daily GOP was then obtained by summing community production and respiration for each day, as described by Sanz-Martín et al. (2019). To account for differences in biomass, we normalised the daily GOP to POC.

2.6. Statistics

A two-way repeated measures ANOVA (rmANOVA) was conducted to assess the effect of temperature, time and their interaction on the Shannon diversity, Chl*a*, ecosystem functions and the compositional variability. Normality was confirmed visually using quantile-quantile-plots. Sphericity was tested using Mauchly's test, and whenever it was violated, a Greenhouse-Geisser correction was applied. In analysing the beta-dispersion and Shannon diversity, day 24 had to be excluded because of too few data points. If a main effect of either temperature or time and no interaction was observed, pairwise *t*-tests were performed and the *p*-values were adjusted using the Bonferroni correction. For both, a main effect and a significant interaction, a one-way ANOVA of the main effect variable was performed before pairwise t-testing. All data are shown as arithmetic mean with one standard deviation in parentheses and analyses were conducted with a significance level of 0.05, using the v0.7.0 R package rstatix (Kassambara, 2021).

3. Results

3.1. Bloom development and abiotic conditions

Chl*a* was significantly higher at 18 °C than both at 6 °C ($p < .001$) and 12 °C ($p < .001$) without any effect of time (Table 1, Fig. 1). Both phosphate and nitrate concentrations showed no temperature effect but decreased over time, while silicate concentrations showed both main effects of temperature and time and an interaction (Table 1, Fig. 1). Silicate concentrations showed significant effects of temperature and time as well as an interaction (Table 1, Fig. 1). They decreased slightly at 6 °C and strongest at 18 °C (all $p < .001$), whereas the concentrations at 12 °C remained constant over time. Between replicates, phosphate and

Table 1

Results of the two-way rmANOVA for temperature, time, and their interactive effects on chlorophyll *a*, dissolved nutrients, diversity parameter and ecosystem functions. Dfn is the degree of freedom for the numerator of the F ratio, and DFd is for the denominator. Significant effects are highlighted in bold.

Parameter	Effect	DFn	DFd	F	p
Chlorophyll *a*	Temperature	2.00	9.00	30.5	**<0.001**
	Time	1.99	17.89	2.3	0.134
	Temperature:Time	3.98	17.89	1.3	0.293
Nitrate	Temperature	2.00	9.00	1.5	0.275
	Time	1.88	16.91	8.3	**0.003**
	Temperature:Time	3.76	16.91	1.9	0.158
Phosphate	Temperature	2.00	9.00	2.0	0.197
	Time	4.00	36.00	6.0	**<0.001**
	Temperature:Time	8.00	36.00	0.2	0.995
Silicate	Temperature	2.00	9.00	15.8	**0.001**
	Time	2.07	18.61	55.4	**<0.001**
	Temperature:Time	4.13	18.61	10.2	**<0.001**
Micrograzing rate	Temperature	2.00	3.00	2.1	0.268
	Time	1.00	3.00	1.3	0.343
	Temperature:Time	2.00	3.00	384.7	**<0.001**
Shannon index	Temperature	2.00	8.00	0.097	0.909
	Time	3.00	24.00	9.497	**<0.001**
	Temperature:Time	6.00	24.00	7.572	**<0.001**
Richness	Temperature	2.00	8.00	1.118	0.373
	Time	3.00	24.00	7.576	**<0.001**
	Temperature:Time	6.00	24.00	0.616	0.715
Evenness	Temperature	2.00	8.00	0.056	0.946
	Time	3.00	24.00	5.635	**0.005**
	Temperature:Time	6.00	24.00	9.818	**<0.001**
Biomass	Temperature	2.00	9.00	4.9	**0.037**
	Time	4.00	36.00	14	**<0.001**
	Temperature:Time	8.00	36.00	2.1	0.059
GOP	Temperature	2.00	8.00	7.3	**0.015**
	Time	4.00	32.00	6.2	**0.005**
	Temperature:Time	8.00	32.00	1.4	0.220
C:N	Temperature	2.00	9.00	3.6	0.070
	Time	4.00	36.00	11.8	**<0.001**
	Temperature:Time	8.00	36.00	3.4	**0.006**
C:P	Temperature	2.00	9.00	0.2	0.791
	Time	4.00	36.00	33.5	**<0.001**
	Temperature:Time	8.00	36.00	3.9	**0.002**

silicate concentrations remained similar but they diverged in terms of nitrate, with replicates C and D at 12 °C and C at 18 °C decreasing more (Fig. S6). The pH increased from 8.09 (sd 0.01) to 8.36 (sd 0.05) in all mesocosms during the whole incubation period, but again replicates C and D at 12 °C and replicate C at 18 °C stood out by increasing the pH to 8.55–8.63 (Fig. S7). The same replicates additionally had the strongest decrease of DIC down to a minimum of 1920.17–1823.79 mmol kg SW^{-1} (Fig. S7). The DIC concentration in all other mesocosms decreased to a lesser extent, i.e. 2032.87 (sd 31.75) mmol kg SW^{-1}.

3.2. Grazing impact

In terms of mesozooplankton, we found no significant differences between the temperature treatments regarding their abundances (Kruskal-Wallis test, $\chi 2$ (2) = 1.08, p = .5836) or composition (Fig. S8). The micro-grazing rates showed a significant interaction between temperature and time (Table 1, Fig. S9). Pairwise t-tests revealed a significant decrease over time at 6 °C (p = .008) but an increase at 12 °C (p = .053) and 18 °C (p = .061). Thus, the micro-grazing rates at 6 °C were initially higher compared to 12 and 18 °C ($p_{6-12} = 0.021$, $p_{6-18} = 0.012$) but lower at the end ($p_{6-12} = 0.039$, $p_{6-18} = 0.012$). Between the two warming treatments, we found no significant differences at any time ($p_{15} = 0.669$, $p_{27} = 0.198$). The community composition was consistent between replicates at 6 °C, but became more variable under warming (Fig. S10).

3.3. Community composition and diversity

On phylum level, the main response pattern showed diatoms to be dominant at 6 °C and 18 °C, whereas they relatively decreased at 12 °C and instead haptophytes and dictyochophytes increased their relative abundance (Fig. S11). At 18 °C, either green algae or haptophytes comprised the rest of the community. Dinoflagellates showed similarly low relative abundances between all temperatures except for larger shares in the warming treatments, especially replicate C and D at 18 °C (*Prorocentrum* sp.; Fig. S12).

On lower taxonomic levels, the responses were more complex (Fig. 2). At 6 °C, the species *Chaetoceros debilis* relatively increased during the incubation while *Minidiscus variabilis*, *Skeletonema marinoi*, and *Thalassiosira punctigera* relatively decreased (Fig. S12). Additionally, the haptophyte *Phaeocystis globosa* had a low but stable relative contribution (Fig. S12). At 12 °C, *Dictyocha speculum* relatively increased in replicates A and B while the haptophytes were either dominated by *Gephyrocapsa oceanica* (replicate B), by *P. globosa* (replicates C & D) or switched from *P. globosa* to *G. oceanica* over time (replicate A; Fig. 2 & S12). At 18 °C, diatoms comprised more different species compared to 6 °C (several *Chaetoceros* species, *Dytilum brightwellii*, *T. punctigera* etc.; Fig. S12). In replicate A, *G. oceanica* was the main residual species whereas in replicate C it was *P. globosa*. In replicates B and D, *Pyramimonas* sp. made up a major part (Fig. 2, S12).

The Shannon diversity showed a significant effect of time and an interaction between time and temperature (Table 1, Fig. 3a). It stayed stable under warming and decreased over time at 6 °C ($p_{15-27} = 0.002$, $p_{18-27} = 0.003$), leading to 6 °C having an initially higher but at the end lower Shannon diversity compared to the warming treatments. This was mainly driven by differences in species evenness (Fig. 3c) as opposed to species richness (Fig. 3b), which only showed significant decreases over time at all temperatures (Table 1). The mean beta-dispersion was significantly higher at 18 °C but not at 12 °C compared to 6 °C (Table S2). Ellipsoids in multivariate space were more circular at 6 °C compared to 12, indicating that the differences between replicates at 6 °C were equal while at 12 °C two replicates each were more similar to each other but more dissimilar to the other pair (Fig. S13).

3.4. Ecosystem functions

Biomass (as POC) and gross oxygen productivity (GOP) were the only two ecosystem functions that significantly differed between temperatures (Table 1, Fig. 4a & b). Pairwise comparisons between the temperatures revealed biomass to be significantly higher at 18 °C than both at 6 °C (p < .001) and 12 °C (p = .018), but similar between 6 and 12 °C (p = .340). GOP was significantly higher at 6 °C compared to 12 °C (p < .001) and 18 °C (p = .002).

All four ecosystem functions showed a significant effect of time (Table 1). Pairwise *t*-tests for biomass across the timepoints showed an increase at all temperatures from the first two sampling days (day 15 and 18) towards the last two sampling days (day 24 and 27; $p_{15-24} = 0.032$, $p_{15-27} = 0.013$, $p_{18-24} = 0.024$, $p_{18-27} = 0.005$). GOP decreased over time but only from sampling day 21 to sampling day 27 (p = .035). Both particulate nutrient ratios additionally exhibited a significant interaction between time and temperature (Table 1). The C:N ratio only significantly decreased over time at 12 °C (Fig. 4c; p = .003), while the C:P significantly increased over time at all temperatures (Fig. 4d; 6 °C: $p_{C:P}$ = .003, all other p < .001).

Inspecting differences within the temperatures, the mesocosms in which *P. globosa* made up a large proportion (12 °C C & D, 18 °C C) had higher values of biomass, the C:P ratio and pH and lower concentrations of nitrate compared to the other replicates at the same temperature (Fig. S14). Towards the end, replicate A at 18 °C also increased its biomass more compared to other replicates of the same temperature.
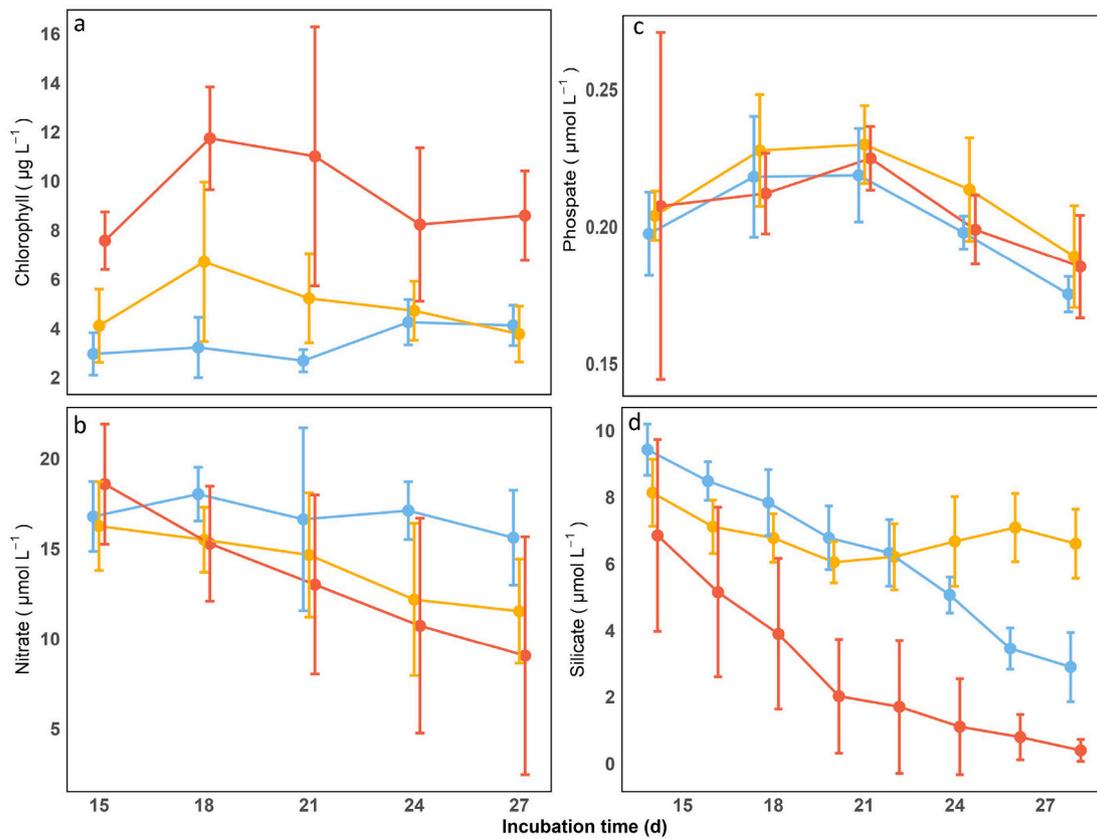
Fig. 1. Chlorophyll a (a), nitrate (b), phosphate (c), and silicate (d) of each temperature over time. Dots represent the arithmetic mean of the temperatures (6 °C: blue, 12 °C: yellow, 18 °C: red) and error bars the standard deviation.
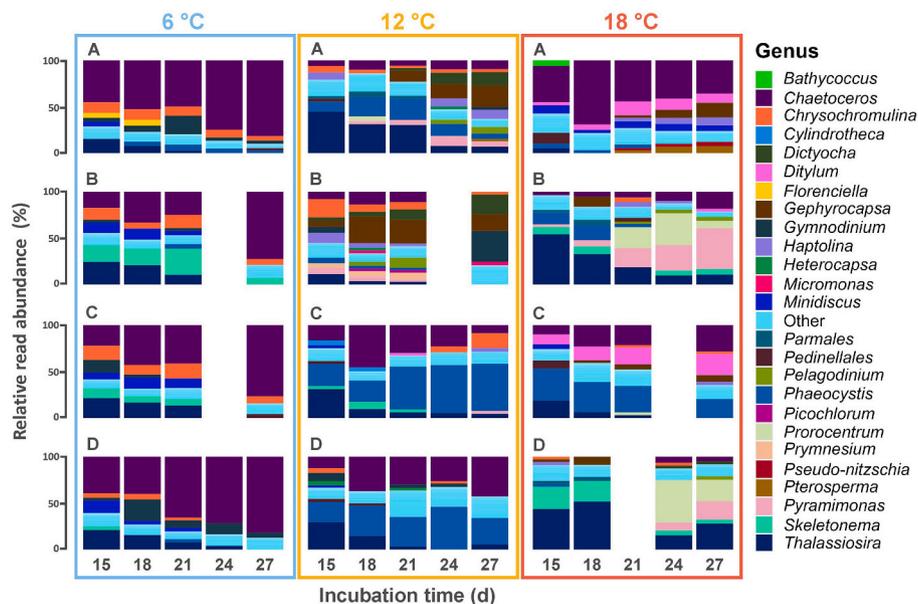

Fig. 2. Metabarcoding-based phototrophic community composition on genus level over time for all replicates (A-D; vertical alignment) and temperatures (6–18 °C; horizontal alignment). For readability, ASVs with an abundance of fewer than 150 reads among temperatures were categorized as "other".

4. Discussion

The aim of this study was to mechanistically investigate warming effects on the composition and resulting ecosystem functions of a temperate protist community. Our results indicate that thermal traits are the most important factor for community reorganisation but can be amended by nutrients (here phosphorus) as modulators. Overall, we observed a high capacity of many North Sea species to tolerate and coexist at increased temperatures. Resulting ecosystem functions showed both warming-driven as well as species-specific responses and, due to reduced functional similarity, consequences for the ecosystem may be severe.
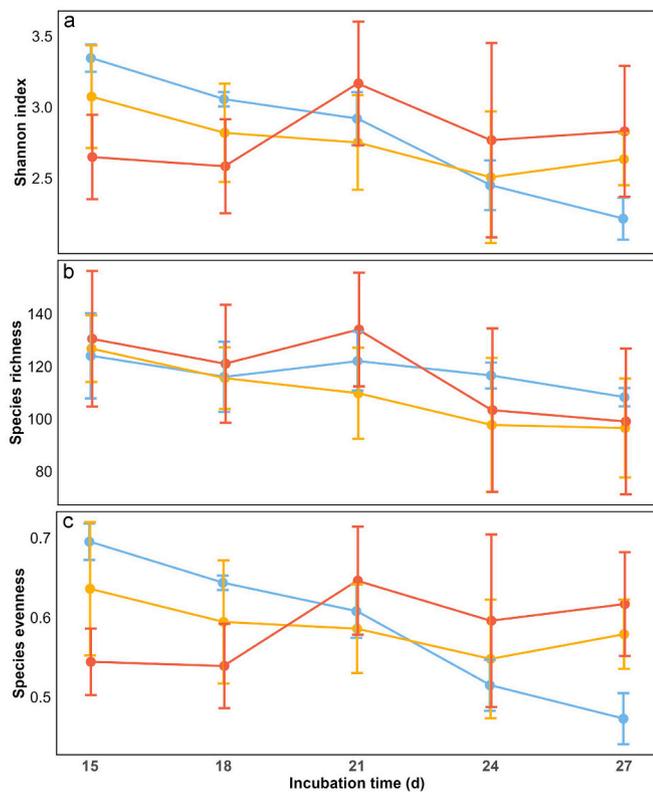
Fig. 3. Shannon index (a), species richness (b), and species evenness (c) of each temperature over time. Dots represent the arithmetic mean of the temperatures (6 °C: blue, 12 °C: yellow, 18 °C: red) and error bars the standard deviation.

Thermal traits are the main driver of community reorganisation under warming

At 6 °C, the species evenness was lower than under warming towards the end of the incubation. This indicates that 6 °C low temperatures to pose a higher selective pressure for species-sorting and dominance. A study by Anderson and Rynearson (2020) on temperate diatoms supports this argument by showing that community dynamics were driven more by thermal limits than thermal optima. Furthermore, we could not confirm previous projections on declining diversity with warming (Benedetti et al., 2021; Henson et al., 2021; Ahme et al., 2023). A potential explanation is that most of these studies depict Arctic communities with narrower thermal breadths, while temperate species usually reside far below their optimum temperature (Thomas et al., 2012). This likely enables many species to prevail under warming, as long as their (comparably high) thermal limits are not reached.

We observed a clear separation of the community composition at the phylum level. Diatoms dominated the communities at 6 °C and 18 °C while at 12 °C, it was largely haptophytes (either *P. globosa* or *Gephyrocapsa oceanica*). *Phaeocystis* spp. are known to decrease grazing pressure via large mucus-embedded colonies or potential toxicants (Stelfox-Widdicombe et al., 2004; Nejstgaard et al., 2007; Liang et al., 2020) and some studies pose that warming disproportionally favours heterotrophs, increasing top-down control (Chen et al., 2012; Boscolo-Galazzo et al., 2018). However, there were no significant differences in micro-grazing or mesozooplankton abundances and neither a clear pattern of certain grazer groups between 12 and 18 °C. In our experiment, grazing pressure can thus be excluded to drive the community composition under warming, consistent with the idea that the temperature-grazing relationship depends on other factors like nutrient levels (Chen et al., 2012).

The ability of diatoms to dominate communities both at low and high temperatures might be indicative of the high thermal niche diversity and a wider thermal breadth compared to haptophytes (Chen, 2015b;
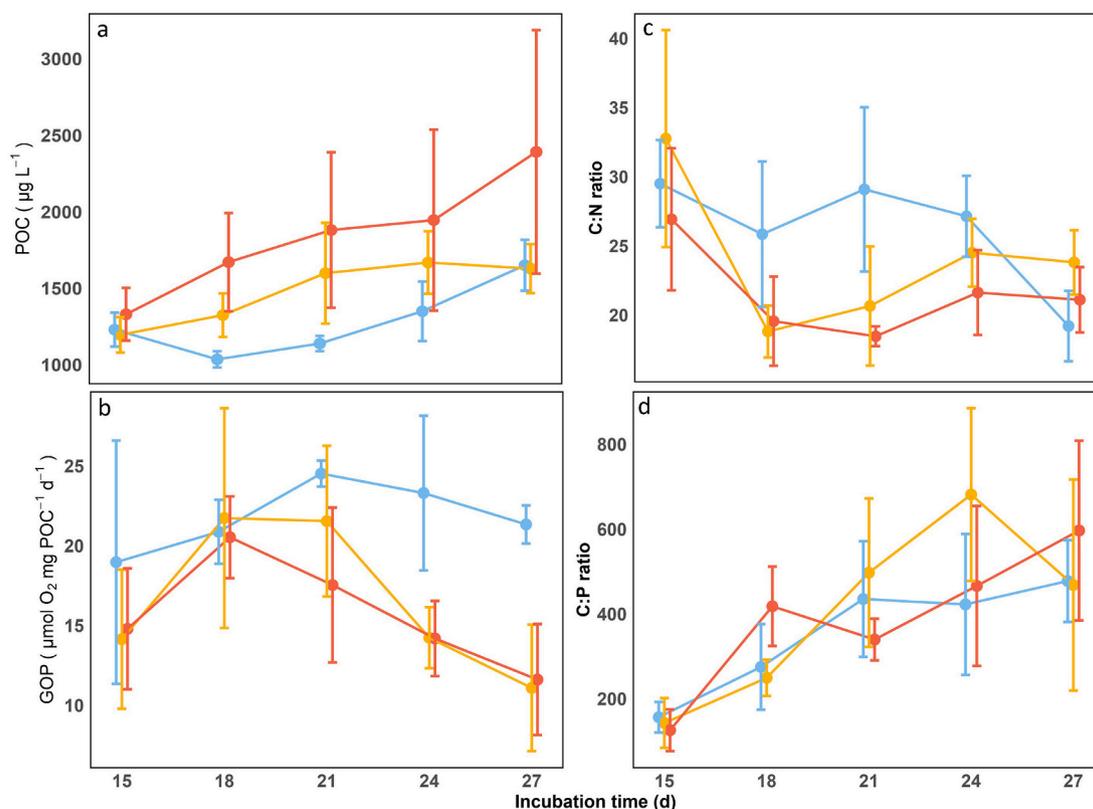

Fig. 4. Ecosystem function values of each temperature over time for (**a**) biomass, (**b**) GOP, (**c**) the C:N ratio, and (**d**) the C:P ratio. Dots represent the arithmetic mean of the temperatures (6 °C: blue, 12 °C: yellow, 18 °C: red) and error bars the standard deviation.

Anderson et al., 2021). For haptophytes, warming may have alleviated potential temperature limitation at 6 °C explaining their dominance at 12 °C (Wang et al., 2010; Wang et al., 2024). However, they could not outcompete diatoms anymore at 18 °C, despite having their optima at temperatures >15 °C (Wang et al., 2010; Müller et al., 2021). Indeed, diatoms are known to deal better with temperatures that exceed the multiyear upper temperature limit of the community at a given point of year (Kling et al., 2020), which could be reflected in the high number of different diatom species at 18 °C. Furthermore, the highest competitive abilities for nutrients are shown to be at colder temperatures compared to growth rate optima (Sunday et al., 2023). Considering the low phosphate concentrations in our experiment, this could have contributed to the dominance of haptophytes at 12 °C. Coccolithophores and *Phaeocystis* are known for thriving under low inorganic phosphorus concentrations (McKew et al., 2015; Moreno et al., 2022) and several studies indicate *Phaeocystis* to outcompete diatoms under inorganic phosphorus depletion under intermediate temperatures (Mori et al., 2021; Breton et al., 2022; Chai et al., 2023). At 18 °C, the competitive ability of haptophytes for low nutrient concentrations may have diminished and the higher growth rates of diatoms became more prevalent (Kremer et al., 2017; Sunday et al., 2023). Therefore, we found the main compositional patterns to arise from thermal traits, while nutrients acted as modulators.

Further support for the importance of thermal traits arises from the species level composition. At 6 °C, the diatom *C. debilis* increasingly dominated over time, reflecting its thermal niche as it is mainly found in colder waters (Ahyong et al., 2022). On the other hand, the decreasing *T. punctigera* is rather common in warmer waters (Ahyong et al., 2022). This is in line with *T. punctigera* being the dominant species in one replicate at 18 °C (C) while in two other replicates (B & D) *Pyramimonas* sp. and *Prorocentrum* sp. made up a large share, consistent with their thermal optima near 18 °C (Thomas et al., 2012; Edullantes et al., 2023). Furthermore, *D. speculum* is known to grow between 11 °C and 15 °C (Henriksen et al., 1993) and had a large contribution in two replicates (A & B) at 12 °C. Overall, our results show that literature-derived thermal traits can be considered a good predictor for community reorganisation under warming.

Temperature-dependence of ecosystem functions is mediated by the presence of Phaeocystis

The higher biomass accumulation under warming is consistent with other studies (De Senerpont Domis et al., 2014; Lewandowska et al., 2014) and reflects the seasonal dynamics in the field (González-Gil et al., 2022). Taken together with the higher species evenness, it may indicate a higher niche complementarity (Zhang et al., 2012). Another explanation could be temperature-stimulated higher carbon fixation rates of all community members taken together as shown by De Senerpont Domis et al. (2014) who also observed increased biomass despite changes in community composition.

The response of gross oxygen productivity (GOP) deviated from expectations. Instead of increasing with temperature, it was significantly lower at 12 °C and 18 °C compared to 6 °C towards the end of the incubation. One potential reason is an enhanced respiration rate of heterotrophs (Yvon-Durocher et al., 2012), exceeding the oxygen production by phototrophs. Indeed, the higher grazing rates observed at 12 °C and 18 °C can be a proxy for higher heterotrophic biomass (Freibott et al., 2016; Cabrerizo and al., in prep.) and therefore might underpin this theory. But even in phototrophs, the ratio of respiration to photosynthesis can increase with temperature (Bozzato et al., 2019; Bestion et al., 2020). Interestingly, there was no further decrease in GOP with temperature. As there were no differences in grazing rates or heterotrophic community composition between 12 °C and 18 °C, this can only be explained by differences in phototrophic community composition based on species- and size-specific variations in metabolic rates (López-Sandoval et al., 2014; Chen and Laws, 2017).

The C:N ratio was observed to be unresponsive to warming, confirming other studies (Yvon-Durocher et al., 2017; Verbeek et al., 2018). This may be based on the tight coupling between nitrate uptake and carbon assimilation as well as a limited ability to store surplus nitrogen in many species (Frost et al., 2023). On the other hand, the C:P ratio showed no mean differences among temperatures but consistently increased over time, implying an enhanced resource use efficiency over the incubation period (Breton et al., 2022) that could be based on species sorting (Verbeek et al., 2018). However, considering the higher C:P ratio of *Phaeocystis*-containing mesocosms which increased under warming, consequences regarding the nutritional quality for higher trophic levels cannot be ruled out (Bukovinszky et al., 2012).

Generally, the mesocosms with major proportions of *P. globosa* behaved differently compared to the other replicates. With higher relative amounts of *P. globosa*, more biomass was built up via more DIC uptake from the water, which resulted in a higher pH. The C:N ratio remained similar to the other replicates via a higher nitrate uptake. However, the C:P ratio was much higher, indicating that *P. globoa* could build up more organic carbon and nitrogen on the same amount of phosphorus compared to other species. This is consistent with other studies (Smith and Trimborn, 2024) and stresses *P. globosa*s high capability of growing on low inorganic phosphorus levels, potentially because it better exploits the advantages of alkaline phosphatases (van Boekel and Veldhuis, 1990; Veldhuis et al., 1991). While the biomass of the *Phaeocystis*-dominated replicate at 18 °C was much higher than at 12 °C, the C:P ratio was similar between them, indicating a potential upper threshold of phosphorus resource use efficiency.

Temperature increases compositional variability and decreases functional similarity

The compositional variability increased with warming, which confirms the expectation that the enhanced growth rates until the community T_{opt} increase the potential for small differences in abundances to amplify. This is supported by the results of Pálffy et al. (2021), as they observed higher compositional variability of pioneer communities with warming. We also found an increased functional variability, which was mainly induced by *P. globosa*. But also the non-*Phaeocystis* containing replicate A at 18 °C experienced a stronger biomass increase than the other replicates towards the end (Fig. S14). This indicates that substantial warming (i.e. +12 °C) lowered the functional similarity even more than a moderate temperature increase (i.e. +6 °C). Consistently, modelling studies have observed increased functional uncertainty with warming (Laufkötter et al., 2015; Dutkiewicz et al., 2013; Sarker et al., 2020). Considering the high patchiness of plankton communities in the ocean (Robinson et al., 2021), this stresses the importance of experimentally covering a broad range of potential starting communities that may yield different functional outputs.

Overall, we observed that some functional responses appear universal between different organisms, while others exhibit species-dependence. Especially the C:N ratio can be considered robust across different community compositions. The communities additionally appeared to be functionally similar in terms of GOP under warming, which is in line with the findings of López-Sandoval et al. (2014). However, biomass and the C:P ratio depended on the exact community composition, consistent with the idea that functional and taxonomic diversity can covary (Ramond et al., 2019). A balanced nutrient supply to higher trophic levels under warming can therefore only be assumed for nitrogen, but not for phosphorus. Accordingly, functional similarity can buffer compositional differences only for specific functions (Biggs et al., 2020). However, it has to be kept in mind that the nutrient regime may modulate responses (Fetzer et al., 2015), yielding different results when nutrients are replete (Hoppe et al., 2018). We thus support the notion that functional similarity depends on the ecological context and can differ between ecosystem functions (Meyer et al., 2018; Eisenhauer et al., 2023).

5. Ecological implications and conclusion

From our study, we can derive several implications for resulting ecosystem processes. Firstly, higher temperatures may induce nutrient limitation of either nitrogen or phosphorus, depending on the community composition and the nutrient availability. Considering that phosphorus limitation is increasingly common for the North Sea (Grizzetti et al., 2012; Breton et al., 2022; Rönn et al., 2023), we expect the C:P ratio to increase, potentially limiting the growth of organisms higher up the food chain. Secondly, gross oxygen production could decrease, although this is likely no major problem in most areas of the shallow and well-mixed North Sea. Lastly, we discovered that the presence of *P. globosa* has the potential to shift the ecosystem to an alternative state with implications for the entire food web and biogeochemical cycles. It has to be noted that our incubation only lasted for a month so that we could not capture the aspect of evolution. As this can change the outcome of warming responses (Barton et al., 2020), longer-term incubations and field monitoring are needed to complement our results and infer consequences for the future North Sea more realistically.

In conclusion, our study demonstrates that thermal traits well explain community restructuring, modulated by nutrient-related traits. Considering the strong selective pressure posed by the lowest temperature, the temperature drop at the end of potential heatwaves requires more scientific attention. Furthermore, the degree of warming also determined the development of haptophyte vs. diatom-dominated communities and thereby may affect higher trophic levels and biogeochemical cycles, but the mechanisms for this are still poorly understood and need further investigation. While warming partly affected the mean differences between temperatures, the most striking result of this study was the increased compositional and partly functional variability at higher temperatures. Overall, we can conclude that stronger warming likely results in a less predictable ecosystem and an increased probability of fundamental shifts.

CRediT authorship contribution statement

Antonia Ahme: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anika Happe:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Maren Striebel:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Marco J. Cabrerizo:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation. **Markus Olsson:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation. **Jakob Giesler:** Writing – review & editing, Validation, Formal analysis, Data curation. **Ruben Schulte-Hillen:** Writing – review & editing, Methodology, Investigation. **Alexander Sentimenti:** Writing – review & editing, Methodology, Investigation. **Nancy Kühne:** Writing – review & editing, Methodology, Investigation. **Uwe John:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

Anika Happe, Marco J. Cabrerizo, Markus Olsson reports financial support was provided by European Commission. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The DNA data are available from the European Nucleotide Archive at EMBL-EBI under the accession ID PRJEB72441 (https://www.ebi.ac.uk/ena/browser/view/PRJEB72441) and was submitted via GFBio (Diepenbroek et al., 2014). The TPC data can be obtained from Ahme et al. (2023a) and all other data from Ahme et al. (2023b). Abiotic conditions at Helgoland Roads are available in the Data Publisher for Earth & Environmental Science PANGAEA, at https://doi.pangaea.de/10.1594/PANGAEA.960375, or will be shared on reasonable request to LTER.HRSR@awi.de. Code to produce the graphs and results of the manuscript can be found online on GitHub: https://github.com/AntoniaAhme/TopTronsMesocosmIncubation (accessed on 06.11.2023).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171971.

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