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RESEARCH ARTICLE

Plankton communities today and tomorrow—potential impacts of multiple global change drivers and marine heatwaves

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Abstract

In the context of global change, marine organisms are subjected not only to gradual changes in abiotic parameters, but also to an increasing number of extreme events, such as heatwaves. However, we still know little about the influence of heatwaves on the structure of marine communities, and experimental studies are needed to test the impact of heatwaves alone and in combination with other environmental drivers. Here, we conducted a mesocosm experiment to assess the potential impact of heatwaves on plankton communities, which we did under ambient and future environmental conditions. To simulate future environmental conditions, we simultaneously manipulated temperature and pH based on IPCC predictions for 2100, and dissolved N : P ratios based on the conditions expected in European coastal zones. While we did not observe any effects of simulated heatwaves on phytoplankton abundances, we identified that future environmental conditions may favor smaller phytoplankton species and that additional heatwaves may especially favor small phytoflagellates and coccolithophores. We also observed that future environmental conditions may reduce the abundances and modify the species composition of bacterioplankton, microzooplankton, and mesozooplankton, and that heatwaves may exacerbate these effects. Using a unique approach to examine the potential impacts of heatwaves under current and future environmental conditions on a natural multi-trophic marine plankton community, we show that the combination of multiple global change drivers has the potential to perturb the entire basis of marine food webs.

Greenhouse gas emissions resulting from human activities are causing concurrent changes in multiple marine abiotic parameters. The Intergovernmental Panel on Climate Change (IPCC) developed a suite of different scenarios projecting that, by 2100, temperatures will increase by 0.6–4.0°C and pH will decrease by 0.1–0.4 units in the oceans' upper hundred meters (Pörtner et al. 2022), depending on humanity's ability to curb greenhouse gas emissions. However, global warming is not uniform, and long-term data series analyses have shown that marine coastal areas are warming at a faster rate than the global average

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(De Amorim et al. 2023). Coastal zones are among the most productive systems in the world, but numerous studies indicate that warming and acidification may have profound implications for coastal marine ecosystems (Wernberg et al. 2012). Moreover, these ecosystems are subjected to changes in dissolved nutrient concentrations which may also alter the performance and survival of many organisms (Doney 2010). For instance, the nitrogen-to-phosphorus (N : P) ratio has steadily increased in European coastal waters over the past decades, and coastal systems are becoming increasingly P-limited while receiving N in excess (Balkoni et al. 2023; Van Beusekom et al. 2019). Marine organisms are consequently exposed to the concurrent effects of multiple anthropogenic drivers, which put marine systems under pressure, potentially affecting community structure and functioning, and altering the associated ecosystem services.

In the context of global change, marine organisms are subjected not only to gradual changes in abiotic parameters, but also to an increasing number of extreme weather events (Pörtner et al. 2022). The most recent IPCC report outlines a rise in the number and intensity of marine heatwaves across the global ocean (Lee et al. 2023). Heatwaves have led to mass mortalities of marine organisms, reductions in biodiversity in several coastal systems around the world, and have been suggested to increase infections by pathogens such as *Vibrio* sp. (Brehm et al. 2021). Heatwaves are not uniform on a regional to local scale, and it is important to consider that the seasonality of heatwaves is an essential aspect determining their impact. This may be especially true in temperate systems which have high variability in weather conditions, and for short-lived organisms with a limited seasonal window of occurrence, such as plankton. However, we still know little about the influence of heatwaves on the structure of marine communities, and experimental studies are needed to test the effect of abrupt temperature increases alone and in combination with other environmental drivers. Altogether, the combination of short- and long-term changes in physico-chemical conditions exerts pressure on coastal marine organisms such as plankton.

Studies have shown that temperature changes in temperate regions alter the phenology of phytoplankton blooms and of zooplankton development, which can create a mismatch between prey availability and food demands of higher trophic levels (Boersma et al. 2015; Edwards and Richardson 2004). Indeed, changes in interactions between trophic levels are not constrained to the basis of the food web, and warming, for instance, is known to increase zooplankton nutritional demands and, consequently, grazing pressure on prey communities (Caron and Hutchins 2013; Garrido et al. 2013). While studies testing the influence of single drivers are undeniably important for our understanding of mechanisms driving plankton dynamics, they offer limited realism and large-scale ecological relevance. Indeed, global change is characterized by simultaneous alterations in multiple environmental drivers that interact and affect the physiology and ecology of organisms with potential consequences for entire food webs. The rare studies investigating the combined effects of different global change drivers on community scales observed high synergy between drivers with, for example, adverse effects on copepod abundance or shifts in phytoplankton organismal size (Garzke et al. 2015; Gazeau et al. 2021; Moreno et al. 2022; Sommer et al. 2015; Troedsson et al. 2013). Furthermore, thus far, only a handful of studies have assessed the impacts of heatwaves in the context of global change by considering the combined effects of both long-term average environmental change and extreme events. The impact of heatwaves on planktonic organisms may be exacerbated under future environmental conditions if warming, increasing pCO_2, or changes in nutrient availability already push planktonic organisms toward the edge of their tolerance windows. Given that global change impacts plankton biodiversity (Bellard et al. 2012) and community composition and biomass (Greve et al. 2004; Telesh et al. 1999) may, in turn, alter energy transfer to higher trophic levels and nutrient recycling, there is an urgent need for studies addressing the combined effects of short- and long-term environmental changes on planktonic food webs.

Here, we conducted a mesocosm experiment and applied an integrated multiple driver design to assess the potential impact of heatwaves under ambient and future environmental conditions on natural coastal plankton communities. In similar studies, Moreno et al. (2022) and Di Pane et al. (2024) observed that simultaneous warming, acidification, and increased dissolved N : P ratio altered coastal plankton assemblages by favoring smaller phytoplankton and zooplankton species, and favored heterotrophic over autotrophic processes. Hence, here, we expect to obtain similar results and hypothesize that these changes are exacerbated by heatwaves. To represent future environmental conditions, temperature and pH were manipulated based on the Representative Concentration Pathway 8.5 proposed by the IPCC for 2100, and dissolved N : P ratios were increased to simulate the conditions expected in European coastal zones. Throughout the experiment, we assessed the influence of the different scenarios on the abundance and taxonomic composition of multiple trophic levels, including bacterioplankton, phytoplankton, microzooplankton, and mesozooplankton. Among the different methods that can be used to study community responses to multiple global change drivers, mesocosm experiments offer the highest level of ecological relevance while still enabling experimental manipulations and rigorous replication (Boyd et al. 2018; Stewart et al. 2013). Hence, by incorporating natural assemblages and by manipulating environmental conditions according to realistic scenarios, our mesocosm experiment goes beyond tightly controlled microcosm experiments that suffer from limited realism and provides unique insights on the potential influence of marine heatwaves today and tomorrow on the structure of coastal planktonic food webs.

Material and methods

Experimental design

To assess the potential impact of heatwaves under ambient and future environmental conditions on natural coastal plankton communities, we carried out an integrated multiple-driver mesocosm experiment. We investigated the response of planktonic communities to four scenarios: An "Ambient" scenario displaying the climatic conditions of today (ambient temperature, pH, pCO_2) and a scenario based on the RCP 8.5 scenario developed by the IPCC for the year 2100 (+3.0°C, −0.3 pH, $pCO_2 = 1000$ ppm) (IPCC 2021). As dissolved nutrient concentrations are expected to change toward considerably higher nitrogen to phosphorus ratios (N : P) in coastal seas (Grizzetti et al. 2012), we extended the RCP scenario (ERCP) to simulate changing nutrient concentrations, with an N : P ratio (molar) of 25, whereas the N : P ratio was adjusted to 16 (Redfield ratio) for the "Ambient" scenario. Each of these two scenarios was either subjected to a heatwave ("Ambient HW," "ERCP 8.5 HW") or not ("Ambient," "ERCP 8.5"). These four scenarios were carried out in four replicates each.

Setup

The experiment was conducted on the island of Sylt, Germany, at the mesocosm facility of the Wattenmeerstation, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (Dummermuth et al. 2023). The general design of the experiment followed the one described by Moreno et al. (2022). After filling the mesocosms (520 L final volume) with seawater collected at Sylt Roads (55°1′48″N, 8°27′36″E) on the 1st of September 2021 (Supporting Information Methods), we directly measured dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) concentrations according to the method described in Grasshoff et al. (1999), and we subsequently adjusted the dissolved N : P ratios to 16 (Ambient and Ambient HW) and 25 (ERCP 8.5 and ERCP 8.5 HW). We also manipulated seawater pH in the ERCP scenario by adding 1.8 L of CO_2 saturated seawater to the mesocosm bags to reduce the initial pH values by 0.3 units. On the first day of the experiment, seawater temperature of the Ambient and Ambient HW scenarios was set to the temperature measured at Sylt Roads station when the seawater was collected, and was progressively increased by 3.0°C for the ERCP scenarios. The temperature of each experimental day was calculated based on data provided by the ecological long-time series of Sylt Roads (Rick et al. 2023). The average daily temperature during the years of 1986–2016 was calculated at the exact same time span as that of the experiment (September 3rd to 30th), and we adjusted the temperature daily during the experiment accordingly (Supporting Information Fig. S1). On Day 10 of the experiment, four tanks of each the Ambient and the ERCP 8.5 scenario were subjected to a 5-d heatwave in which the water temperature was increased by 2°C. The intensity of this heatwave was based on calculation of the average marine heatwave in the North Sea (Supporting Information, Materials and Methods). To minimize the mortality risk from heat-shock and to adjust the temperature realistically, the water temperature was increased gradually by 1°C on Day 9, and by another 1°C on Day 10 of the experiment. Similarly, temperature was decreased gradually by 1°C on Day 16, and by another 1°C on Day 17 to end the heatwave (Supporting Information Fig. S1). The position of the replicates in the different mesocosm tanks was randomized.

Sampling and measurements

Abiotic parameters, namely temperature, pH, total alkalinity, and dissolved nutrient concentrations were regularly measured (Supporting Information, Materials and Methods). To quantify the bacterioplankton abundance, 10 mL of sampled mesocosm water was fixed with 0.2-μm-filtered formaldehyde (1% final concentration, 1 h at room temperature). Using a standard bottle top set-up (polysulfon), fixed cells were subsequently filtered (≤ 200 mbar) onto 0.2-μm polycarbonate filters (47 mm diameter; Sigma Aldrich, Taufkirchen, Germany), which were placed on 0.45-μm cellulose nitrate support filters (Sigma Aldrich). Total cell counts (TCC) were determined using the DNA stain 4′,6-diamidino-2-phenylindole (DAPI) and automated microscopy as described previously by Brüwer et al. (2023). Since this group may benefit from environmental change and severely impact other organisms as well as human health, we quantified the bacterial abundance of the genus *Vibrio* via qPCR. Samples were extracted using DNeasy®PowerWater®Kit. For DNA quantification prior to qPCR, a fluorometric quantification method was applied using the Quant-iTTMPicoGreen®dsDNAassayKit in black bottom 96-well plates with TECAN® infinit200 microplate reader. In order to quantify the amount of DNA in a single *Vibrio alginolyticus* cell, the isolate DSM2171 was utilized as a control value. For the qPCR approach, the LightCycler® 480 SYBR Green I Master kit (Roche) was applied using the oligonucleotide primers Vib-567F and Vib2-r (Supporting Information Table S1) targeting the 16S rRNA gene covering the whole *Vibrio* genus (Thompson et al. 2004b). The PCR conditions were chosen according to LightCycler® 480 SYBR Green I Master and the specific primer conditions (Thompson et al. 2004b). The concentration, that is, the number of template molecules in the original sample, was calculated using a standard curve (Bustin et al. 2009; Fraga et al. 2014). *Vibrio alginolyticus* (DSM 2171) was used as an external standard to perform an absolute quantification. Seven standard concentrations in a 10-fold serial dilution were analyzed in duplicate to calculate a standard curve (Supporting Information Table S2). Further taxonomic analyses of the bacterioplankton community were also conducted but go beyond the scope of the current paper and will be published at a later stage.

To determine phytoplankton and microzooplankton abundance and species composition, 100 mL of mesocosm water were poured into brown-glass bottles and fixed with 2 mL of Lugol's acid iodine solution. These samples were stored cool and dark and were analyzed following the method described

in Utermöhl (1958) using an inverted microscope Olympus CKX41 (Olympus Scientific Solutions, Tokyo, Japan). Planktonic organisms were identified to species level when possible, or pooled into size-shape dependent groups. Biovolume of each phytoplankton and microzooplankton taxon was calculated from the measurement of cell dimensions using geometric formulae according to information provided by Hillebrand et al. (1999). Cell volume was converted into carbon following the equations of Menden-Deuer and Lessard (2000) for diatoms (pg C $cell^{-1} = 0.288 \times V^{0.811}$), dinoflagellates (pg C $cell^{-1} = 0.760 \times V^{0.819}$) and other protist plankton with the exception of ciliates (pg C $cell^{-1} = 0.216 \times V^{0.939}$), where V is the cell volume in μm^3. Ciliate carbon content was calculated as pg C $cell^{-1} = 0.19 \times V$ according to Putt and Stoecker (1989). Since toxin-producing planktonic species which may cause harmful algal blooms may benefit from environmental changes (Coyne et al. 2021; Gu et al. 2022), we also collected samples at the beginning and at the end of the experiment to conduct quantitative and qualitative toxin analyses (*see* Supporting Information). In addition, protist community composition and diversity were assessed using 18S rRNA metabarcoding, results are presented in Ahme et al. (2025).

Samples for mesozooplankton were obtained by sieving 4 L of mesocosm water over a 150 μM mesh. The material captured by the mesh was flushed back into a 200 mL Kautex container (Kautex Textron GmbH & Co. KG, Bonn, Germany) with sterile filtered seawater (0.2 μM) and fixed with 20 mL 37% borax-buffered formol. The mesozooplankton community was determined by counting the whole sample or splitting it up into sub-samples with a Folsom-Splitter (Mcewen et al. 1954; Sell and Evans 1982). The counting took place in a Bogorov chamber under a stereomicroscope (Leica M205; Leica Microsystems GmbH, Wetzlar, Germany) and identification was conducted up to the highest taxonomic level possible, as in Boersma et al. (2015).

Functional groups of the plankton were determined as bacterioplankton, phytoplankton, microzooplankton, and mesozooplankton. The phytoplankton group included diatoms, phytoflagellates, and autotrophic dinoflagellates, according to the descriptions of trophic mode for each taxonomic group provided in Kraberg et al. (2010), which were grouped by size in nanophytoplankton (< 20 μm) and microphytoplankton (> 20 μm). The microzooplankton group comprised heterotrophic and mixotrophic dinoflagellates and ciliates, according to the descriptions of trophic mode for each taxonomic group provided in Löder et al. (2011a), including nanociliates (< 20 μm). Mesozooplankton species were all the heterotrophic organisms larger than 200 μm. Although *Noctiluca scintillans* is a single-celled species, we classified it as mesozooplankton because the cells are larger than 200 μm. It is important to note that carbon computation for this species is not trivial as the carbon content of *N. scintillans* can vary significantly among cells (e.g., Tada et al. 2000); hence, we also report cell abundances in the following text.

Statistical analyses

For all statistical analyses, we used R 4.1.2 with the interface RStudio and the packages "vegan," "dplyr" and "pairwise.adonis2" (Martinez Arbizu 2020; Oksanen et al. 2007; R Core Team 2021; Wickham et al. 2018). All statistical tests were conducted at a significance threshold of $\alpha = 0.05$. Until the heatwaves were initiated on Day 9, the eight Ambient mesocosms and the eight ERCP 8.5 mesocosms were replicates. For a clearer depiction of our results, we averaged the data of the eight Ambient and the eight ERCP 8.5 mesocosms for the first 9 d in Figs. 1–7. For all statistical analyses, we considered four individual replicates per scenario during the entire experiment, each representing one tank of the mesocosm system. To assess the impacts of the different scenarios on planktonic abundances (bacterioplankton, phytoplankton, microzooplankton, mesozooplankton), we fitted general linear models (GLMs). Therefore, a first model of total cumulative abundances depending on scenarios was fitted, allowing us to check for a general scenario effect on planktonic abundances, followed by a second model including scenario and time. By comparing these two models with a likelihood ratio test (LRT), we tested if abundances changed differently in the four scenarios over time. Effects of the ERCP scenarios on the phyto- and microzooplankton species composition and affinity of species to the scenarios were analyzed through the principal response curve (PRC) using the "vegan" R package. This test shows the degree of difference in the community composition over time in the ERCP scenarios in comparison to the Ambient condition, which is set as a control (effect "0"). Species weights are analyzed as means of their regression coefficient against the control. When the curve of difference of the ERCP scenario has a positive slope, positive values for species weights represent the affinity of this species to the scenario, whereas negative values would represent the negative effect of the scenario on such species, and vice versa. Differences in mesozooplankton abundance were analyzed through ANOVA followed by a post hoc test (Tukey test). If data were not normally distributed, they were either log-, square-root, or exponentially transformed, depending on skewness.

Results

Physical–chemical conditions

At the onset of the experiment, the seawater had a pH of 8.00. The initial addition of CO_2-saturated water to the ERCP 8.5 and ERCP 8.5 HW mesocosms, and the subsequent control of atmospheric pCO_2 in these scenarios, lowered the pH by 0.10 to 0.15 compared to the Ambient scenarios (Supporting Information Table S3). While this difference was maintained throughout the entire experiment, the absolute pH values increased from Day 1 to Day 6, and subsequently decreased until reaching initial values on Day 20, where they remained stable until the end of the experiment. Following their initial adjustment, concentrations of dissolved N, P, and Si rapidly decreased until being depleted on Day 4–6, and these

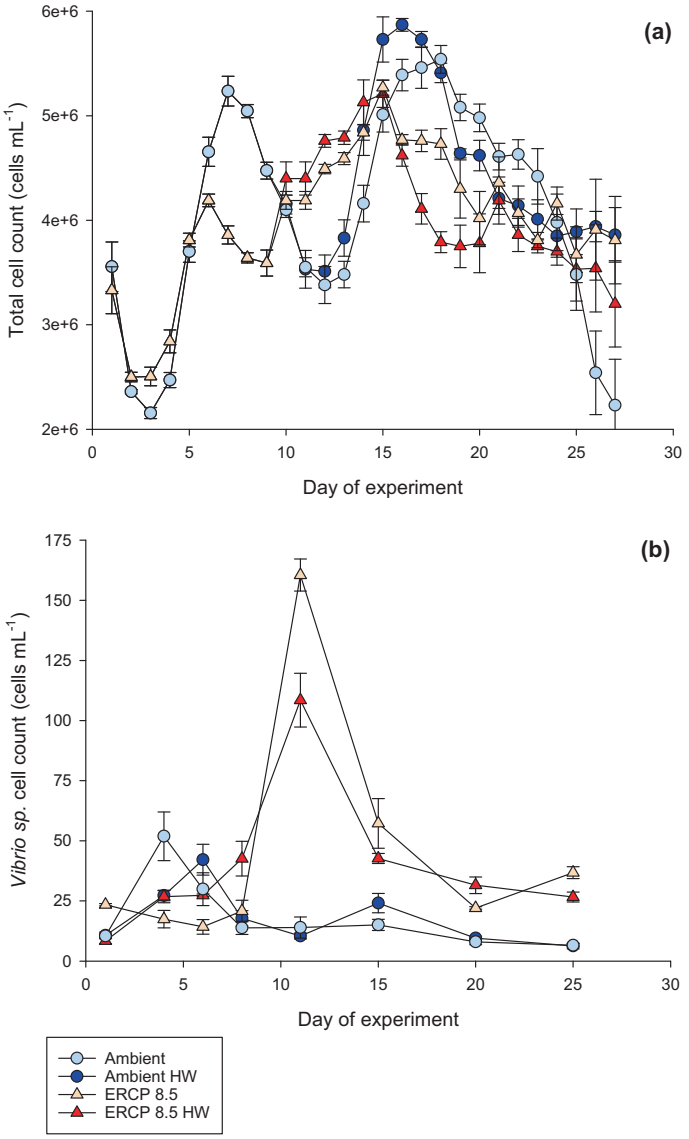

Fig. 1. Bacterioplankton abundances in the mesocosms throughout the experiment. Total Cell Counts (TCC) based on DAPI counts (**a**), and *Vibrio* sp. cell counts based on qPCR analysis (**b**). Different colors and symbols represent the Ambient scenario (circle) and Extended Representative Concentration Pathway (ERCP) scenario (triangle) with and without heatwave (light blue = Ambient, dark blue = Ambient HW, orange = ERCP 8.5, red = ERCP 8.5 HW). Symbols represent means and standard errors of four replicates per scenario.

concentrations remained close to zero until the end of the experiment (Supporting Information Table S4). Seston stoichiometry was not significantly different between scenarios (Supporting Information Fig. S3). Seston C : N ratios fluctuated between ca. 7 and 11 during the experiment, albeit without any clear temporal trend. Seston C : P and N : P ratios had relatively low initial values, around 70 and 8, respectively; they increased over the first few days of the experiment and fluctuated around 100 and 11 throughout the rest of the experiment.

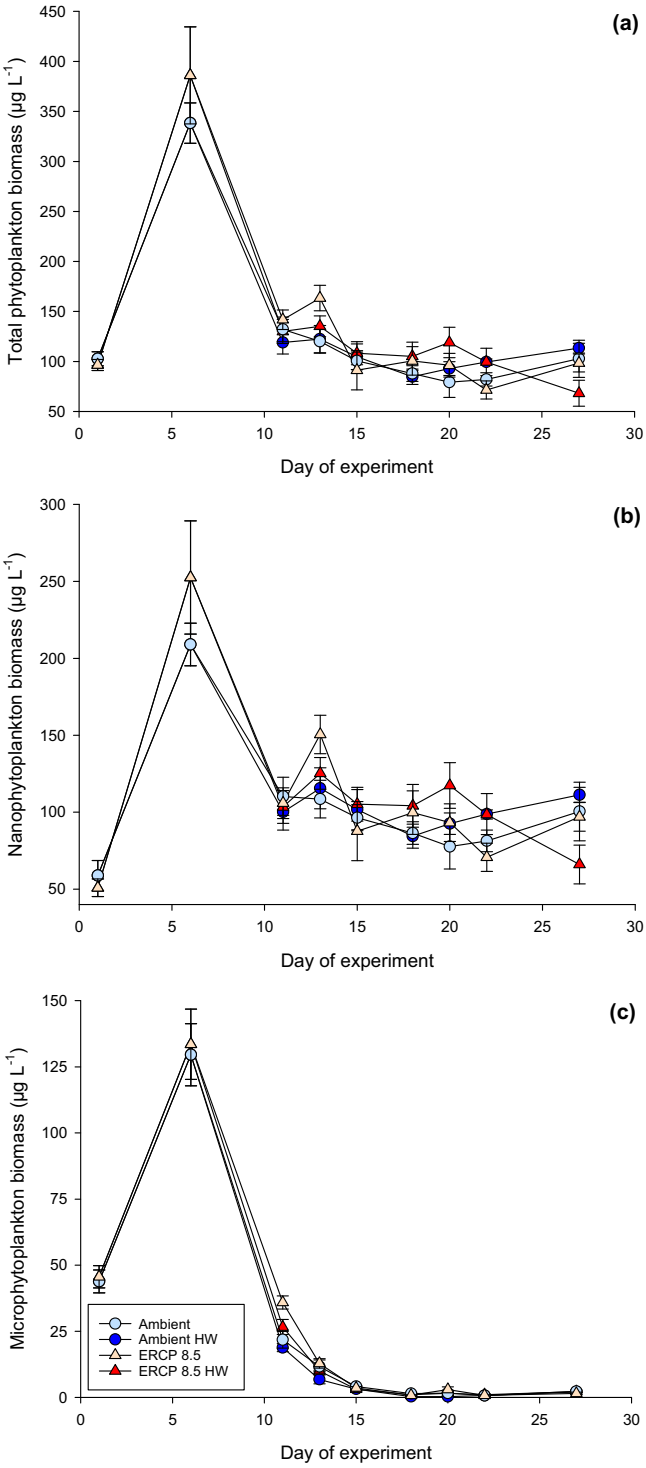

Fig. 2. Phytoplankton carbon biomass in the mesocosms throughout the experiment of total phytoplankton (**a**), and different size classes: nanophytoplankton (**b**) and microphytoplankton (**c**). Different colors and symbols represent the Ambient scenario (circle) and Extended Representative Concentration Pathway (ERCP) scenario (triangle) with and without heatwave (light blue = Ambient, dark blue = Ambient HW, orange = ERCP 8.5, red = ERCP 8.5 HW). Symbols represent means and standard errors of four replicates per scenario.

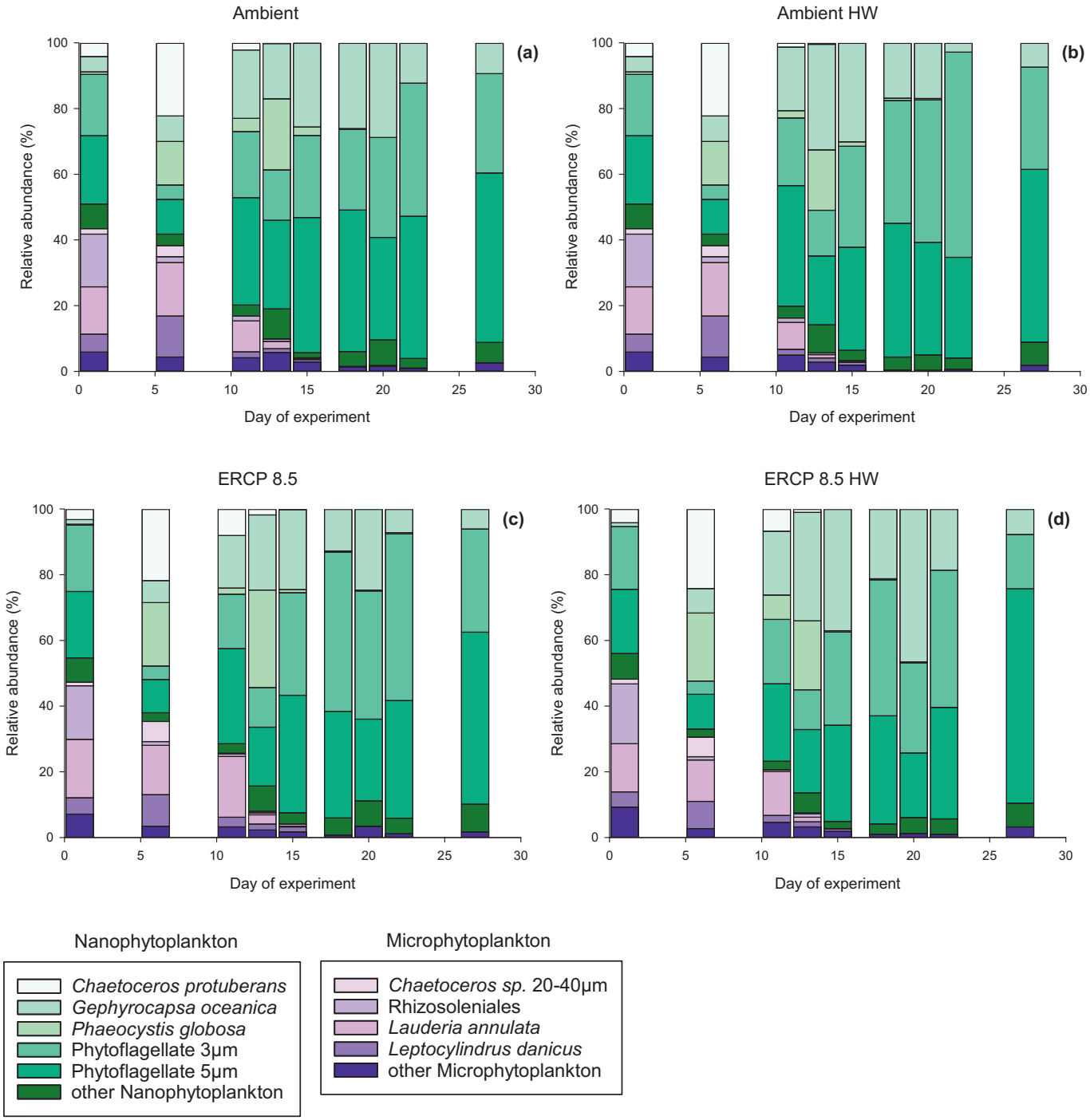

Fig. 3. Phytoplankton community composition in the mesocosms throughout the experiment. Different colors represent different phytoplankton size classes (green shades = nanophytoplankton, purple shades = microphytoplankton). The figures represent the four scenarios: Ambient (**a**), Ambient HW (**b**), ERCP 8.5 (**c**), ERCP 8.5 HW (**d**).

Bacterioplankton

We observed a statistically significant effect of the scenarios on bacterioplankton (TCC, Fig. 1) abundances (GLM, Ambient HW $p < 0.05$, ERCP 8.5 $p < 0.05$, ERCP 8.5 HW $p < 0.05$), which fluctuated over time (GLM, $p < 0.05$), with an interactive effect of scenario and time (GLM and Likelihood Ratio Test, $p < 0.05$). Bacterioplankton abundances rapidly declined at the onset of the experiment and started increasing again from Day 3 to 6 (Fig. 1), reaching substantially higher levels in the Ambient (ca. 5.2×10^6 cells mL^{-1}) than in the

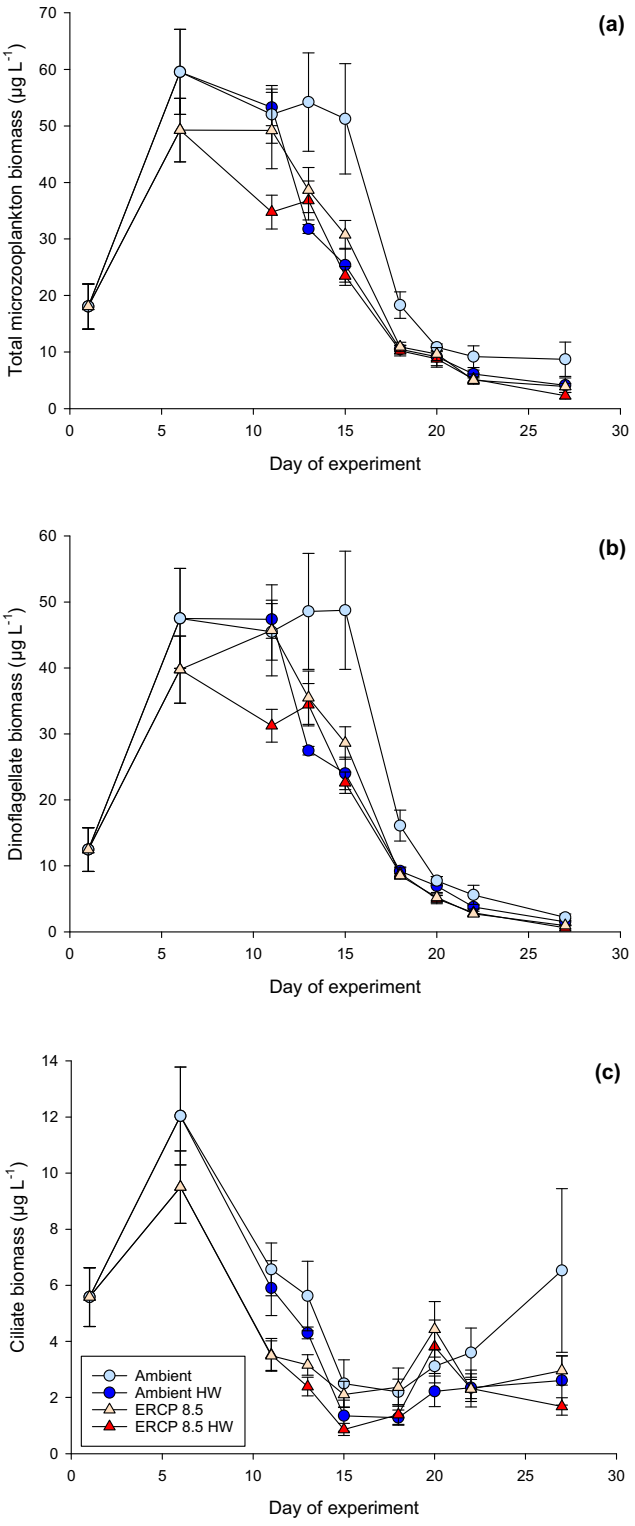

Fig. 4. Microzooplankton carbon biomass in the mesocosms throughout the experiment of total microzooplankton (**a**), and different groups: dinoflagellates (**b**) and ciliates (**c**). Different colors and symbols represent the Ambient scenario (circle) and Extended Representative Concentration Pathway (ERCP) scenario (triangle) with and without heatwave (light blue = Ambient, dark blue = Ambient HW, orange = ERCP 8.5, red = ERCP 8.5 HW). Symbols represent means and standard errors of four replicates per scenario.

ERCP 8.5 scenario (ca. 4×10^6 cells mL^{-1}). From Day 6 to 14, bacterioplankton abundances declined in the Ambient scenario before increasing again to peak at 5.5×10^6 cells mL^{-1} on Day 18. This biomass peak occurred faster in the Ambient HW scenario with a peak on Day 16, and, while it collapsed to reach initial abundances of about 2×10^6 cells mL^{-1} in the Ambient scenario, bacterioplankton abundances stabilized around 4×10^6 cells mL^{-1} on Day 22 in the Ambient HW scenario. During the simulated heatwave, bacterial abundances increased faster in the ERCP 8.5 HW than in the ERCP 8.5 scenario, but also decreased faster after the heatwave. The biomass reached during this second growth period was weaker in the ERCP 8.5 and ERCP 8.5 HW scenarios than in the Ambient and Ambient HW scenarios. Bacterial abundances in the ERCP 8.5 and ERCP 8.5 HW stabilized at the same level as in the Ambient HW scenario from Day 22. We also observed that the abundances of *Vibrio* sp. fluctuated over time, and that cell concentrations were significantly higher in the ERCP 8.5 and ERCP 8.5 HW scenarios than in the other two scenarios (Fig. 1b).

Phytoplankton

In all scenarios, total phytoplankton carbon biomass rapidly increased from 100 μg C L^{-1} at the beginning of the experiment to reach a maximum of about 350 μg C L^{-1} on Day 6, followed by an overall decrease to almost initial concentrations on Day 15, where it stayed relatively stable until the end of the experiment (Fig. 2a). Nanophytoplankton and microphytoplankton carbon biomasses followed the same pattern as total phytoplankton carbon biomass throughout the experiment, but from Day 10 on, nanophytoplankton carbon biomass remained relatively stable at concentrations twice as high as the initial concentrations, around 100 μg C L^{-1} (Fig. 2b), whereas microphytoplankton carbon biomass continued decreasing until being negligible from Day 15 on (Fig. 2c). Overall, we did not observe any statistically significant effect of the scenarios on the total phytoplankton carbon biomass (GLM, Ambient HW $p = 0.40$, ERCP 8.5 $p = 0.16$, ERCP 8.5 HW $p = 0.47$), nanophytoplankton carbon biomass (GLM, Ambient HW $p = 0.52$, ERCP 8.5 $p = 0.24$, ERCP 8.5 HW $p = 0.35$), and microphytoplankton carbon biomass (GLM, Ambient HW $p = 0.62$, ERCP 8.5 $p = 0.57$, ERCP 8.5 HW $p = 0.48$). While total phytoplankton, nanophytoplankton, and microphytoplankton biomasses were affected by time (GLM, $p < 0.001$), there was no interactive effect of scenario over time (GLM and Likelihood Ratio Test, $p = 0.553$).

Nanophytoplankton composed 50%–60% of the phytoplankton community at the onset of the experiment, with the 3 and 5 μm phytoflagellates being the most abundant taxa (Fig. 3). Species of the order *Rhizosoleniales* and the diatom *Lauderia annulata* dominated the microphytoplankton assemblage. In all scenarios, the phytoplankton bloom was characterized by an increase in the dominance of *Phaeocystis globosa* and *Chaetoceros protuberans* in the nanophytoplankton assemblage at the expense of phytoflagellates, and by a decrease of *Rhizosoleniales* and an increase of

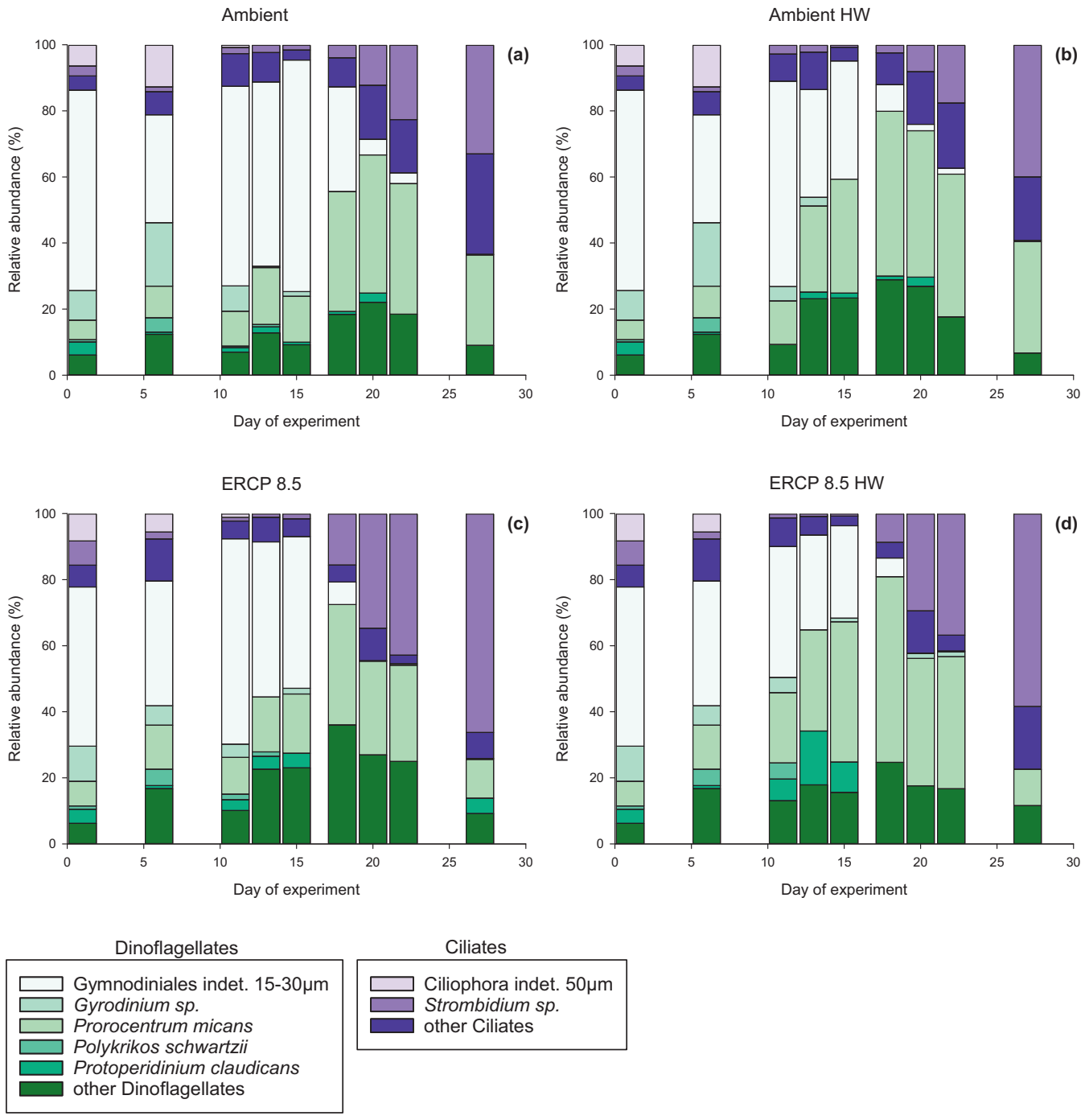

Fig. 5. Microzooplankton community composition in the mesocosms throughout the experiment. Different colors represent different groups (green shades = dinoflagellates, purple shades = ciliates). The figures represent the four scenarios, Ambient (**a**), Ambient HW (**b**), ERCP 8.5 (**c**), ERCP 8.5 HW (**d**).

Leptocylindricus danicus in the microphytoplankton assemblage (PRC test). Further, nanophytoplankton built up 70% of the total phytoplankton carbon biomass at the peak of the bloom in the ERCP 8.5 and ERCP 8.5 HW scenarios, compared to only 60% in the Ambient and Ambient HW scenarios (Fig. 3). The second half of the experiment was characterized by a dominance of phytoflagellates in all scenarios, whereby the smaller ones (3 μm) were particularly abundant in the Ambient HW and ERCP 8.5 scenarios. We observed a remarkable increase of the coccolithophore *Gephyrocapsa oceanica* after the phytoplankton bloom, particularly in the ERCP 8.5 HW scenario in which this species made up 50% of the total phytoplankton carbon biomass

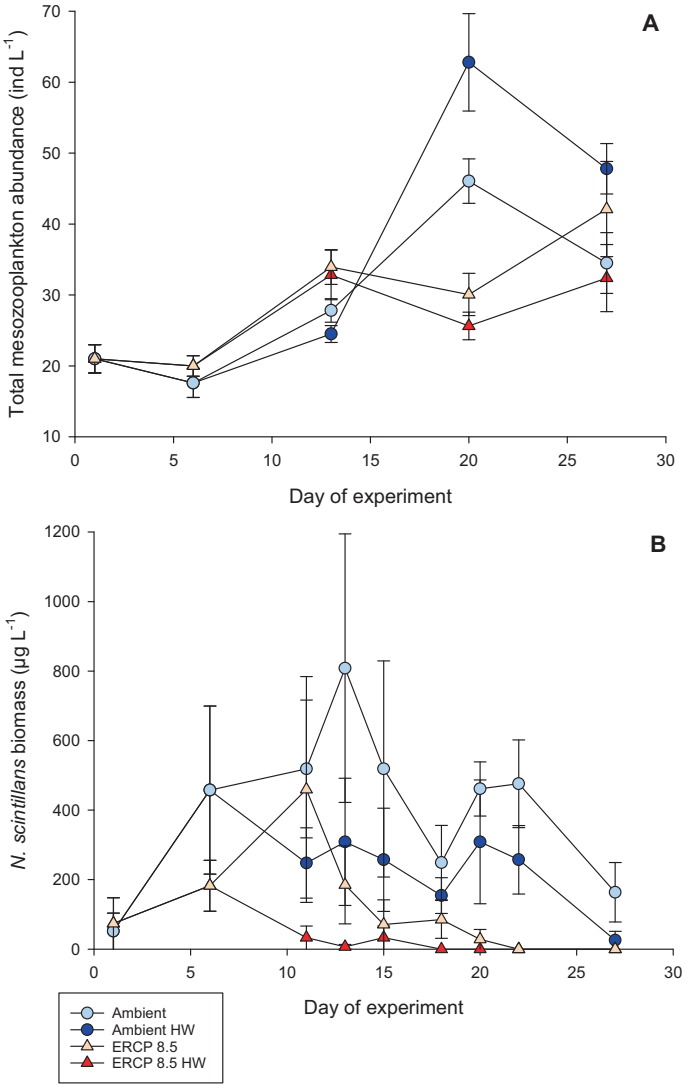

Fig. 6. Mesozooplankton abundances in the mesocosms throughout the experiment: total mesozooplankton excluding *Noctiluca scintillans* (**a**), carbon biomass of *N. scintillans* (**b**). Different colors and symbols represent the Ambient scenario (circle) and Extended Representative Concentration Pathway (ERCP) scenario (triangle) with and without heatwave (light blue = Ambient, dark blue = Ambient HW, orange = ERCP 8.5, red = ERCP 8.5 HW). Symbols represent means and standard errors of four replicates per scenario.

on Day 20, compared to only ca. 25% in the other scenarios (Fig. 3, PRC test).

In the net tow sample taken on the initial day for qualitative analysis of phycotoxins, a total of 3.2 ng of domoic acid was detected. While no domoic acid was found in the fraction > 200 μm, 55% and 45% of the amount detected were in the 50–200 μm and in the 20–50 μm size fractions, respectively. No domoic acid or other phycotoxins were found (*see* Supporting Information), neither in the 800 L of filtered seawater taken on the initial day, nor in the mesocosm water at the end of the experiment.

Microzooplankton

In all scenarios, total microzooplankton carbon biomass rapidly increased at the onset of the experiment and reached higher levels in the Ambient and Ambient HW scenarios than in the ERCP 8.5 and ERCP 8.5 HW scenarios (Fig. 4a, GLM, $p < 0.05$). In the Ambient scenario, total microzooplankton carbon biomass remained relatively constant around 55 μg C L^{-1} until Day 15, after which it quickly declined. This decline occurred 4 d earlier in the other scenarios and was particularly pronounced in the ERCP 8.5 HW scenario (GLM, $p < 0.05$). Hence, total microzooplankton carbon biomass fluctuated over time; it was affected by the scenarios, and an interactive effect of scenario over time was observed (GLM and Likelihood Ratio Test, $p < 0.05$). Heterotrophic dinoflagellates largely dominated the microzooplankton community (Fig. 4b), and their carbon biomass was significantly influenced by the scenarios, time, and their interaction (GLM, Ambient HW $p < 0.05$, ERCP 8.5 $p < 0.05$, ERCP 8.5 HW $p < 0.05$; GLM and Likelihood-Ratio Test, $p < 0.05$). The carbon biomass of ciliates increased concomitantly to that of dinoflagellates until Day 5, after which it declined and remained relatively low from Day 15 on (Fig. 4c, GLM $p < 0.05$). Ciliate carbon biomass was higher in the Ambient and Ambient HW scenarios than in the ERCP 8.5 and ERCP 8.5 HW scenarios from Day 5 to 15 (GLM, Ambient HW $p = 0.23$, ERCP 8.5 $p < 0.05$, ERCP 8.5 HW $p < 0.05$).

The microzooplankton community was largely dominated by dinoflagellates, which represented 80%–90% of the total microzooplankton carbon biomass in all scenarios until Day 20 (Fig. 5). During this period, species of the order Gymnodiniales between 15 and 30 μm dominated the microzooplankton community in all scenarios. Further, *Prorocentrum micans* was more abundant in the Ambient HW and ERCP 8.5 HW scenarios than in the other two scenarios, especially on Days 11 to 17, and *Gyrodinium* sp. was more abundant in the Ambient and Ambient HW scenarios than in the ERCP 8.5 and ERCP 8.5 HW scenarios on Day 6 (PRC test). From Day 20 on, the proportion of ciliates increased, in particular due to an increase of *Strombidium* sp., which was particularly pronounced in the ERCP 8.5 and ERCP 8.5 HW scenarios (Fig. 5, PRC test).

Mesozooplankton

Mesozooplankton abundances significantly varied over time (GLM, $p < 0.05$), and increased from 20 to 32 individuals L^{-1} in the ERCP 8.5 HW and from 20 to 41 individuals L^{-1} in the ERCP 8.5 scenarios throughout the experiment (Fig. 6a). Mesozooplankton reached significantly higher abundances in the Ambient and Ambient HW scenario, with maxima of 47 and 62 individuals L^{-1} on Day 20, respectively (Fig. 6a; GLM, Ambient HW $p < 0.05$, ERCP 8.5 $p < 0.05$, ERCP 8.5 HW $p < 0.05$). The mesozooplankton community was dominated by *Acartia* sp. copepods in all scenarios (Fig. 7). In terms of taxonomic composition, the mesozooplankton community only differed between scenarios on Day 13, on which *Acartia* sp. and

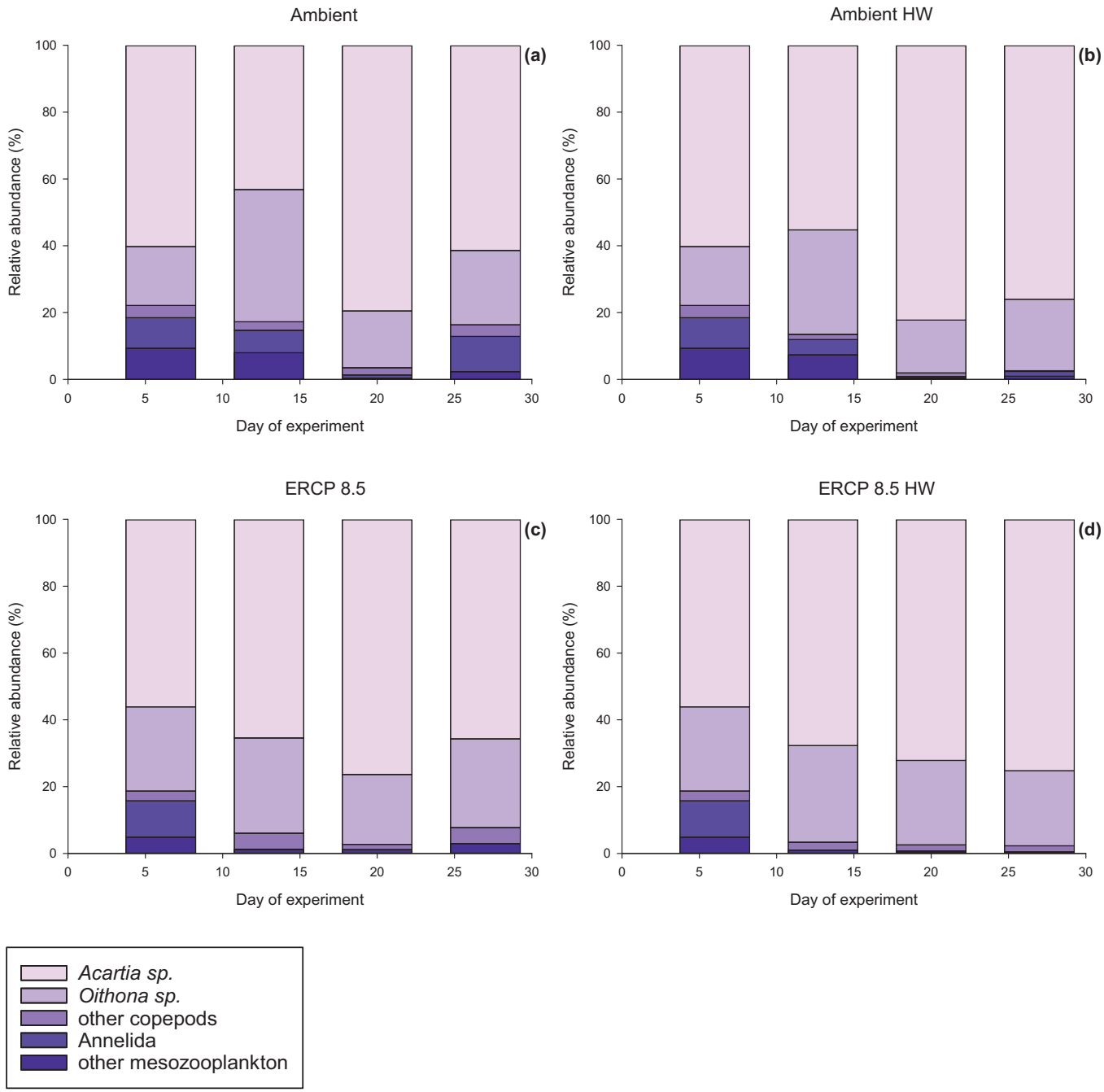

Fig. 7. Mesozooplankton community composition in the mesocosms throughout the experiment, excluding *Noctiluca scintillans*. Different shades of purple represent different mesozooplankton groups. The figures represent the four scenarios: Ambient (**a**), Ambient HW (**b**), ERCP 8.5 (**c**), ERCP 8.5 HW (**d**).

Oithona sp. were equiproportional in the Ambient scenario, whereas *Acartia* sp. was more abundant in the other three scenarios.

The abundance of *N. scintillans* was low at the onset of the experiment; it increased to reach ca. 800 μg C L^{-1} on Day 13 (ca. 400 cells L^{-1}) in the Ambient scenario and subsequently decreased until the end of the experiment (Fig. 6b). In the Ambient HW scenario, *N. scintillans* reached significantly lower abundances that never exceeded 400 μg C L^{-1}, ca. 150 cells L^{-1} (Fig. 6b; GLM, $p < 0.05$). In the ERCP 8.5 scenario, the abundance of *N. scintillans* increased to reach about 400 μg C L^{-1} on Day 11 (ca. 300 cells L^{-1}), but rapidly collapsed afterward, and this species was not found anymore after Day 22 (Fig. 6b; GLM, $p < 0.05$). The ERCP 8.5 HW was the least suitable for

N. scintillans, which did not significantly grow in this scenario and was not found anymore after the end of the heatwave.

Discussion

Here, we conducted a mesocosm experiment to study how coastal plankton communities may be influenced by heatwaves under current ambient and future conditions characterized by elevated temperature, pCO_2, and dissolved N : P ratios. Our results indicate that these environmental changes influence the abundance and species composition at several trophic levels and modify the overall planktonic food web structure (Fig. 8).

We observed altered dynamics of bacterioplankton in the ERCP 8.5 scenario compared to the Ambient scenario. These results are in line with the findings of Di Pane et al. (2024) who reported altered bacterial carbon recycling under the ERCP 8.5 scenario. Certain bacterioplankton populations may be more sensitive to environmental changes than others, altering the overall dynamics and successions within the bacterioplankton community (e.g., Von Scheibner et al. 2014), which may explain the different dynamics we observed between scenarios. For instance, we observed higher abundances of the potentially harmful genus *Vibrio* in the ERCP 8.5 and ERCP 8.5 HW scenarios than in the other two scenarios. This genus is known to thrive in warmer waters (Oliver 2015), and climate warming has been suggested to positively influence its geographic distribution and incidence (Martinez-Urtaza et al. 2010; Oliver 2015), which may explain the higher abundances we observed in the future environmental conditions. These results are significant since some *Vibrio* species are animal pathogens, but also human pathogens that cause wound infections associated with recreational bathing, as well as septicemia or diarrhea after ingestion of contaminated foods (Thompson et al. 2004a). Moreover, we observed that a marine heatwave may exacerbate the effects observed on bacterioplankton, with faster dynamics in the Ambient HW and ERCP 8.5 HW scenarios than in the respective scenarios without heatwave, and we observed lower biomass in the ERCP 8.5 HW than in the ERCP 8.5 scenario. These results are supported by the study of Joint and Smale (2017) in which heterotrophic productivity was quantified across temperature gradients in the western English Channel. This work showed that episodically high temperatures can change nutrient and energy flow patterns through the microbial loop. Altogether, the influence of long-term environmental change and short-term temperature variability on bacterioplankton dynamics and assemblage structure may have important implications for ecosystem functions, including alterations of biogeochemical processes (Traving et al. 2021).

We did not observe any effect of the scenarios on phytoplankton biomass (Fig. 8), which stands in contrast to many studies that have shown an influence of heatwaves (Arteaga and Rousseaux 2023; Soulié et al. 2022; Zhan et al. 2023), warming (Behrenfeld et al. 2016; Lewandowska et al. 2014), higher pCO_2 (Bach et al. 2017; Kroeker et al. 2013; Sommer et al. 2015), or dissolved nutrient ratios (Burson et al. 2016; Klausmeier et al. 2004) on phytoplankton biomass. In our

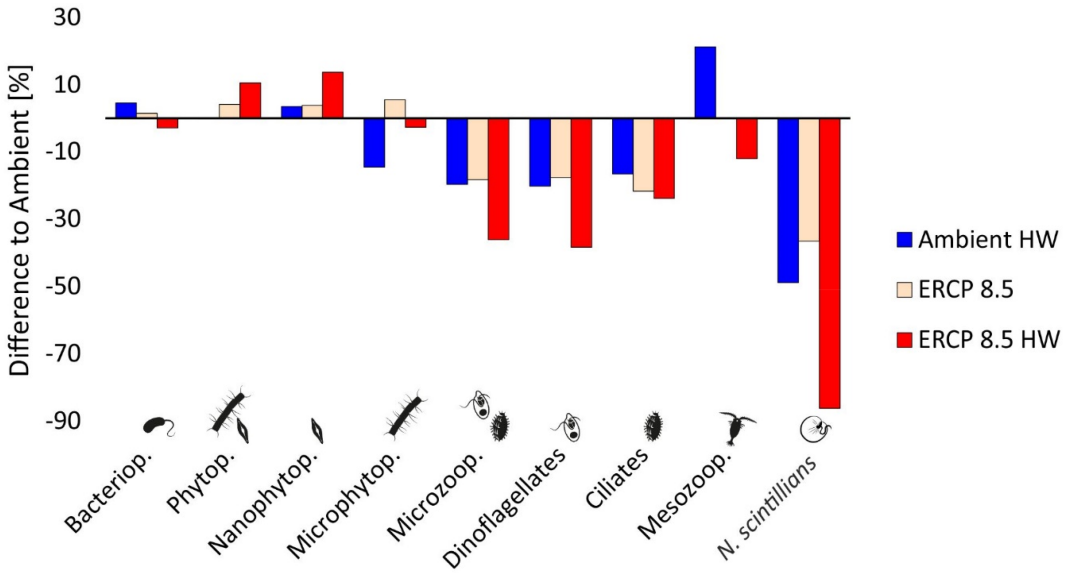

Fig. 8. Synthesis of the influence of the different scenarios on the abundance of individual planktonic groups. The bars represent the percentage change in biomass between the Ambient scenario and the other three scenarios, represented by different colors (dark blue = Ambient HW, orange = ERCP 8.5, red = ERCP 8.5 HW) for the following groups: bacterioplankton (Bacteriop.), phytoplankton total (Phytop.), nanophytoplankton (Nanophytop.), microphytoplankton (Microphytop.), microzooplankton total (Microzoo.), dinoflagellates, ciliates, mesozooplankton (Mesozoop.), and *Noctiluca scintillans*. The data were obtained by first summing the abundance of each group at all sampling days over the experiment for each of the four replicates per scenario, then computing the average of these four summed abundances for each scenario and computing the percentage difference between the average summed abundance of the Ambient scenario and the average summed abundance of the other three scenarios.

experiment, the simulated marine heatwave occurred at the end of a phytoplankton bloom, which may explain why it did not influence the overall phytoplankton biomass. However, the simulated marine heatwave, as well as the potential future environmental conditions, altered the taxonomic composition of the phytoplankton community, which is in line with recent studies (Moreno et al. 2022; Zhan et al. 2023). We observed a higher relative abundance of nanophytoplankton species in the ERCP 8.5 than in the Ambient scenario (Fig. 8), which goes hand in hand with observations that average phytoplankton community cell size decreases under future environmental conditions (Moreno et al. 2022; Sommer et al. 2015). We quantified low amounts of domoic acid, a toxin produced by diatoms of the genus *Pseudo-nitzschia*, in the seawater used to fill the mesocosm. *Pseudo-nitzschia* abundances remained low during the entire experiment, which explains that we did not find any domoic acid at the end of the experiment, and suggests that a harmful bloom of this genus may not be triggered by the scenarios tested in our experiment. However, we observed that the simulated marine heatwaves in the Ambient HW and ERCP 8.5 HW scenarios favored small phytoflagellates and the coccolithophore *G. oceanica*. This is supported by the results of a recent mesocosm study which also found that coccolithophores may benefit from higher temperature, pCO_2 levels, and N : P ratios (Moreno et al. 2022). Changes in blooming patterns of coccolithophores could have considerable impacts on the biological carbon pump and biogeochemical processes of coastal zones (Rost and Riebesell 2004). Furthermore, alterations of phytoplankton community structure, and an overall increase in the abundance of small phytoplankton species may have consequences for primary consumers.

Microzooplankton carbon biomass significantly differed between scenarios, with lower biomasses in the ERCP 8.5 than in the Ambient scenario (Fig. 8). Further, *Gyrodinium* sp., a taxon which may be more sensitive to temperature changes than other microzooplankton taxa (Calbet et al. 2022; Calbet and Saiz 2022), was less abundant in the ERCP 8.5 than in the ambient scenario. This is in contrast with the results of Moreno et al. (2022) who also studied a late-summer plankton community and observed a significant increase in microzooplankton biomass with warming, acidification, and higher N : P ratios. It is important to note that, in their study, the positive response of microzooplankton was triggered by a higher prey availability, which was not the case in our experiment. This suggests an interaction between food availability and nutritional requirements under future environmental conditions. Although we observed an increase in the relative proportion of nanophytoplankton, whose size generally better suits the feeding preference of microzooplankton than microphytoplankton does (Calbet 2008; Naustvoll 2000), the overall phytoplankton biomass was not affected by the scenarios (Fig. 8). Further, as seston C : N : P stoichiometry was similar among scenarios (Supporting Information Fig. S3), bottom-up effects were likely dominated by prey availability rather than by elemental stoichiometric quality. Interestingly, the negative effect of future environmental conditions on microzooplankton biomass was exacerbated by simulated marine heatwaves. Only *P. micans*, a species known to cope well with high temperatures (El Abd Fatah et al. 2022; Zhang et al. 2023), increased in relative abundance in response to the heatwave. Microzooplankton is one of the major functional groups in planktonic food webs, as it facilitates the rapid recycling of nutrients back to primary producers (Calbet and Saiz 2005; Suzuki et al. 1996). As they contribute substantially to mesozooplankton diets, microzooplankton also link the smaller planktonic unicellular organisms with higher metazoan trophic levels (Löder et al. 2011b; Sherr and Sherr 2007). Hence, decreases in microzooplankton biomass may upset the functioning of planktonic food webs and, for instance, negatively influence secondary consumers.

We observed substantially lower mesozooplankton abundances in the ERCP 8.5 and ERCP 8.5 HW scenarios than in the Ambient and Ambient HW scenarios, respectively (Fig. 8). As for microzooplankton, the combination of higher metabolic requirements under altered environmental conditions and low prey availability may have reduced mesozooplankton abundances. While *Acartia* sp. and *Oithona* sp., the dominant mesozooplankton taxa in our experiment, have been shown to have higher fitness when feeding on larger-sized prey items (Berggreen et al. 1988; Castellani et al. 2005; Støttrup and Jensen 1990), nanophytoplankton dominated the phytoplankton community. Further, microzooplankton, which make up a significant share of copepods' diet (Calbet and Saiz 2005; Castellani et al. 2005), were more abundant in the Ambient and Ambient HW scenarios than in the other two scenarios (Fig. 8). Our results are supported by a mesocosm study in which mesozooplankton from the Baltic Sea were exposed to a temperature gradient (Garzke et al. 2015). The authors observed significant temperature effects on copepod and copepodite abundances, with lower zooplankton peak abundance in the warmer treatments (Garzke et al. 2015). The simulated marine heatwave had a positive influence on mesozooplankton abundances in the Ambient scenario, but a negative effect in the ERCP 8.5 scenario. Similar findings were obtained by Siegle et al. (2018), who observed that, in natural environments, copepods suffered from higher mortality after multiple exposures to warm events. We also observed a negative effect of warming, acidification, and higher N : P ratios on the abundance of *N. scintillans*, which was substantially exacerbated by a simulated marine heatwave that entirely suppressed the growth of this species in the ERCP 8.5 HW scenario (Fig. 8). This result contrasts with recent findings from Kordubel et al. (2024) indicating that the incidence of *N. scintillans* increased over the past decades in the North Sea, but our observations are supported by a mesocosm study that also predicts that this species may be impaired by global change in the next decades (Moreno et al. 2022). Overall, both biotic, i.e., the availability of suitable prey, and abiotic conditions may have influenced

the mesozooplankton community (Troedsson et al. 2013). However, our experimental setup does not enable us to specifically disentangle these effects, which future studies could focus on. Since there was no top-down control on mesozooplankton during the experiment, it is important to note that the negative effects seen here could differ, and potentially be enhanced, in communities in which their predators are present. Conversely, we suggest that reduced mesozooplankton abundances under future environmental conditions may create suboptimal feeding conditions for higher trophic levels.

Conclusion

Our experiment indicates that heatwaves under current and future environmental conditions have the potential to influence the biomass and taxonomic composition of multiple trophic levels, and to alter the overall structure of planktonic communities. We observed that the future environmental conditions we tested alter bacterioplankton dynamics and reduce their abundances, and that these effects may be exacerbated further by a heatwave. While we did not observe any effect on total phytoplankton carbon biomass, we observed reduced microzooplankton carbon biomass under future environmental conditions, and that this negative effect may be exacerbated by a heatwave. Our results indicate that future environmental conditions may favor smaller phytoplankton species, and that heatwaves may especially favor small phytoflagellates and coccolithophores. These results are supported by Ahme et al. (2025) who identified through metabarcoding that future environmental conditions may reduce protist diversity, in particular that of phototrophic organisms, and that the coccolithophore *G. oceanica* may thrive. While Ahme et al. (2025) observed that microzooplankton were largely unaffected by heatwaves, here, we observed alterations in the composition of microzooplankton assemblages with *Gyrodinium* sp. being less abundant under future environmental conditions, and *P. micans* being more abundant in the heatwave scenarios. We identified that mesozooplankton abundances were lower under future conditions, and that a simulated heatwave intensified this negative effect on the biomass of *N. scintillans*. Using a unique experimental approach to examine the possible impacts of heatwaves under current and future environmental conditions on a natural multi-trophic marine plankton community, we show that the combination of multiple global change drivers has the potential to perturb the entire basis of marine food-webs.

Author Contributions

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Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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