Hot and hungry: A mechanistic approach to the direct and indirect effects of marine heatwaves on plankton communities

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Abstract

Marine heatwaves, increasingly frequent, impact marine ecosystems and services. Still, understanding how temperature affects observed responses remains limited due to complex interactions among temperature, abiotic and biotic factors, and community dynamics. Here we try to fill this gap by exposing simulated plankton communities to seasonal heatwaves of 4°C with a trait- and size-structured model that accounts for protists and the life cycle of copepods. Despite the short lifespans and fast growth rates of plankton, results show that heatwaves affect communities differently and for an extended period up to six years after their appearance. Temperature affects species physiology and ecosystem dynamics, directly and indirectly, shaping structure and biomass. Species traits, interactions, and functional diversity under changing temperatures emerge as pivotal. Our study advances mechanistic insights into marine heatwave impacts, highlighting the complex connections between temperature, species traits, and ecological interactions.

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Authors contributions

M.G and A.P. designed the study. C.S.P. provided the code of the NUM model (Serra-Pompei et al., 2020), insights on the model behavior, and feedback on the model development. A.K. provided the Sea Surface Temperature data metanalysis, provided feedback, and developed the code for Figures. M.G. developed the model, provided the data metanalysis for the mixed layer depth, ran the simulations, and analyzed the model output. A.P. provided feedback on model development and model output. M.G. wrote the manuscript with the support of all authors.

Data and code availability statement

The code for the model and the figures and the model output are publicly available and can be found online on https://zenodo.org/doi/10.5281/zenodo.10822886 (Grigoratou, Serra-Pompei, Kemberling, and Pershing, 2024).

Abstract

Marine heatwaves, increasingly frequent, impact marine ecosystems and services. Still, understanding how temperature affects observed responses remains limited due to complex interactions among temperature, abiotic and biotic factors, and community dynamics. Here we try to fill this gap by exposing simulated plankton communities to seasonal heatwaves of 4°C with a trait- and size-structured model that accounts for protists and the life cycle of copepods. Despite the short lifespans and fast growth rates of plankton, results show that heatwaves affect communities differently and for an extended period up to six years after their appearance. Temperature affects species physiology and ecosystem dynamics, directly and indirectly, shaping structure and biomass. Species traits, interactions, and functional diversity under changing temperatures emerge as pivotal. Our study advances mechanistic insights into marine heatwave impacts, highlighting the complex connections between temperature, species traits, and ecological interactions.

Introduction

Marine heatwaves, periods characterized by temperatures well above the mean ranges for at least five days , are increasing in presence and duration with various impacts on marine communities and ecosystem services across spatial and temporal scales . Even if temperature has been identified as the major environmental driver, our mechanistic understanding of how temperature affects marine populations is still incomplete, which limits our ability to forecast changes in marine ecosystems.

Filling this knowledge gap is challenging, as temperature is strongly linked with multiple biogeochemical processes, and each one of them is a potential driver for changes at the individual level that can lead to alterations in population, community, and ecosystem dynamics . For example, temperature has a direct effect on an individual's enzymatic kinetics resulting in changes in physiological rates, e.g., metabolism, cell division, growth, ingestion, and respiration that can alter oxygen and resource needs and impact species traits like size, mobility, and reproduction . Temperature also affects organisms indirectly by altering the environmental status of their habitat (e.g., stratification, oxygen concentration, abundance, distribution, resources, and predators). Thus, the fitness of an individual in its environment during a heatwave is determined by the combination of temperature effects on an organismal and environmental scale filtered through the organism's morphological, behavioral, and life-history traits . Therefore, understanding and identifying ecosystem drivers requires a perspective that encompasses both individual-level traits and community dynamics.

Plankton regulates marine life and has been recognized as an Essential Ocean and Climate Variable linked with various ecosystem services such as climate stabilization, fisheries, water quality, or tourism . Hence, it is crucial to understand how climate variability and human activities affect plankton organisms and communities. Observations have shown that the duration of community change depends on the nature of the heatwave (e.g., seasonal appearance, temperature anomaly, duration), the environmental and community properties; some ecosystems respond and return to the pre-heatwave condition faster than others . For planktonic metazoans, the main observed *in-situ* pattern during and after a heatwave is the alteration in community structure and composition, either via indigenous or the appearance of invasive species that enter the ecosystems through new warm water masses in an area . The*in-situ* observations reflect a mixed Eulerian perspective of advection and ecosystem processes, which complicates pinpointing the drivers of observed ecosystem changes before and after the heatwave. Are the alterations of the observed ecosystem dynamics driven by the impact of temperature on physiological processes (direct effects), the resulting environmental changes (indirect effects), or both?

Laboratory and modeling studies, even if they may lack realism, can scale down complexity and isolate drivers. Studies have revealed that temperature triggers different responses in physiological processes and rates of individuals . If these responses will be reflected on a population or community level depends on how individuals react to their entire environment, rather than just one environmental factor . Therefore, it is important to design studies that focus on causation and not only on the correlation between individual responses and environmental drivers.

The present study investigates the direct and indirect effects of temperature on plankton communities during seasonal heatwaves within a mechanistic framework. Our study aims to answer three key questions:

What impact do seasonal heatwaves have on functional diversity, biomass, and community structure during and after the heatwave?

What is the recovery time for a plankton community to regain its pre-heatwave composition and characteristics, such as biomass size distribution and functional diversity?

Which plankton community changes result from temperature itself versus indirect effects from food web dynamics?

We examine those questions using the Nutrients-Unicellular-Multicellular (NUM) model . NUM is a mechanistic size and trait-based model that simulates community structures and predator-prey interactions for protists (autotrophs, mixotrophs and heterotrophs) and the life cycle of active and passive feeding copepods. We focus on the direct temperature effects on individual rates and predator-prey interactions, without considering species adaptation and any temperature effect on other environmental factors like changes in the mixed layer depth and nutrient concentration. For our experiment, we assume a Lagrangian view and track a community as it experiences warming caused by a surface heat flux anomaly. Using this model, we analyze how seasonal heatwaves impact community biomass, diversity, and structure.

Methods

Nutrients-Unicellular-Multicellular (NUM) model

Here we provide a short presentation of the NUM model and of the modifications we made related to the temperature norm (see below and the Supplementary Materials for more details). A detailed description of the model and its governing equations can be found in Serra-Pompei et al. (2020). NUM is a semi-chemostat size and trait-based plankton functional type model that accounts for protists and copepod life cycles. The model includes four abiotic factors: light, ambient temperature, mixed layer depth, and nutrient concentration (nitrogen). The plankton populations are homogeneously distributed in the upper mixed layer. Nitrogen enters the system via the mixing rate between the upper and the deep layer and leaves the system via sinking or particulate organic matter, but no vertical migration (daily or seasonal) or other biological activity is resolved in the deep layer. Nitrogen is channeled in the food web via diffusive uptake by protists and predator-prey interactions. Finally, the particulate matter generated by organisms is recycled, returning nutrients to its dissolved form in the surface layer.

Each plankton group in the model represents a population of various individuals with shared traits like size and foraging behavior. The population growth rate depends on the uptake, encounter, ingestion, assimilation, respiration, growth, and reproduction rates. Protists are assumed to be spherical cells, distinguished by their size and temperature norm (below and SM). As potential mixotrophs, protists constantly move within the trait spectrum of autotrophy, mixotrophy, and heterotrophy, depending on the available resources. Their uptake rates follow a Holling type II response, and their biomass concentration is the balance between energy gain and losses from predation and background mortality (losses not caused by predation).

The life cycle of copepods is represented by 8 discrete life stages, 7 juveniles, and one adult. The juvenile stages invest all their energy gain in somatic growth and the adult stage only in reproduction. Like protists, the ingestion rate of copepods follows a Holling type II functional response. All copepods are omnivorous and can prey on protists or other copepods within their grazing kernel. Copepods are distinguished by two traits: the maximum adult body length and foraging mode – active or passive. Active feeders have higher ingestion and growth rates but face increased respiration costs and predation mortality. In contrast, passive feeders have lower rates and predation risks. Copepod losses arise from predation and background mortality, with larger individuals facing additional predation from unspecified larger predators (e.g., fish).

Temperature norm

In the model, ambient temperature affects both protist and copepod uptake, respiration, clearance, and ingestion rates. Serra-Pompei et al. (2020) represent the temperature dependency as a Q_{10}. In the present study, we follow the approach and use an environmental trait in the form of a temperature norm (Figure 1, and Supplementary Materials). Groups can only grow within the temperature range of their norms (Figure 1).

Model set up

Environmental forcing

For the environmental forcing, we used the Sea Surface Temperature and Mixed Layer Depth (ECCO Consortium et al., 2021) daily mean of 10 years (2000- 2010) of an offshore region of the Mid-Atlantic Bight, a representative North Atlantic temperate ecosystem (Figures 1, SM1, and Supplementary Materials).

We ran the model for 50 years to allow the community to reach a steady-state condition (hereafter pre-heatwave conditions). Our focus is solely on examining the temperature effects on plankton communities of a specific water mass. Thus, we didn't change the mixed layer depth (MLD) and nutrient input, acknowledging that this simplification reduces the complexity typically found in natural ecosystems. For the marine heatwave scenarios, we exposed the steady-state community to a 4 @C temperature anomaly lasting for one season (three months) for either winter (December- February), spring (March- May), summer (June- August), or autumn (September- November). Observed heatwaves range in duration from days to months, with no universally applicable average duration due to variations influenced by factors like event intensity, geographic location, and specific oceanographic conditions . For example, the oceanic waters of the Northeastern United States Continental Shelf have experienced long seasonal heatwaves up to 3 @C since 2012 . In this context, we have opted to investigate the impact of an extended and intense heatwave on plankton communities, portraying it as an extreme scenario that may become increasingly common within ecosystems due to ongoing climate change. After the heatwave event, we ran the model for another 19 years with the pre-heatwave SST to examine the period needed for the community to readjust to the pre-heatwave condition. To isolate the processes responsible for the observed changes, we ran two additional simulations. In the first, heatwaves solely affect protists' rates, while in the second, only copepods are sensitive to the elevated temperature. These experiments enabled us to examine whether changes in communities are driven by direct temperature effects, indirect temperature effects, or a combination of both.

Initial conditions and plankton groups

We used the same initial conditions as in Serra-Pompei et al. (2020; i.e., 1 µg N L^{-1} for the nitrogen and 5 µgC L^{-1} for each plankton size class (protists and copepods). We included 14 size classes of protists ranging from 10^{-7} µg C to 10^{-1} µg C mass per cell. The size of adult copepods ranged from 0.2 µg C to 1000 µg C and 0.2 µg C to 5 µg C for active and passive copepod feeders, respectively. The model had 8 temperature norms from 0 @C to 28 @C with a 4 @C interval. Each temperature norm included 25 populations (14 protists, eight active, and three passive copepod feeders). In total, the model included 200 populations: 112 protists, 64 active and 24 passive copepods. We also categorized the plankton biomass in size bins based on protists and copepods' cell/body volume (six for protists and active copepods, four for passive copepod feeders, Table SM1). We used the Shannon Diversity Index to estimate the functional diversity of the modelled plankton community (Supplementary Materials).

Results

We used a trait- and size-structure model to examine (1) if and how a temperature anomaly of a seasonal heatwave can affect plankton communities, (2) how long it takes for the plankton communities to return to their pre-heatwave state in terms of seasonal patterns of the biomass size-bin concertation, diversity and dominant functional groups, and (3) if and how the individual responses of different trophic levels (protists and metazoans) can mitigate potential disturbances of temperature in ecosystem dynamics.

Modeled pre-heatwave conditions

In the pre-heatwave conditions the Sea Surface Temperature (SST) ranges from 13.5 @C (March 1) to 26.2 @C (August 4, Figure 1) with winter exhibiting the lowest mean SST, followed by spring, autumn, and summer (Fig 1). The Mixed Layer Depth (MLD) varies from 28 m (September 14) to 93 m (February 23, Figure 1). Winter and spring have the deepest MLD, followed by similar depths in autumn and summer (Figure 1).

The overall daily modeled biomass concentration of protists and copepods declines from early winter (December) until the end of April (Figure 2). Copepod biomass gradually increases from May to its peak in autumn (September/October). The biomass concentration of protists has a strong variation in summer and autumn. Still, overall, it shows an increasing trend from summer to mid-autumn with three biomass peaks in summer (August), early autumn (September) and early winter (December). Autumn holds the highest mean biomass concentration for protists and copepods, followed by summer, winter, and spring (Figure 2).

Protists constitute the most diverse community, followed by active and passive copepod feeders. Depending on the season, ten functional groups contribute 70 % to 86 % of the total protist biomass, while five functional groups represent 82 % to 100% of the total copepod biomass. Protists' highest diversity is not only due to their big pool of initial groups in the model set-up (112 groups) but mostly due to their short life cycle (asexual, one life stage), their opportunistic ability to grow with different resources (nitrogen, prey, mixotrophy) at any time, and the dynamic losses (grazing, background mortality). In contrast, copepods have longer life cycles (sexual, eight life stages), and their growth relies only on one energy source (prey availability). These trait disparities account for variations in population coexistence, biomass distribution among groups, and temperature norms (Figures 2, 3). Overall, the plankton community is dominated by groups with temperature optima of 20 @C and 24 @C (Figure 3). Both optima cover temperatures from 10 to 30 @C and are within the daily (14 – 30 @C) and annual (20 @C) temperature range. The temperature norms of dominant groups track the annual mean temperature, not the Sea Surface Temperature seasonality (Figure 3), as life cycles, growth rates, and population dynamics introduce delays between abiotic and biotic seasonalities, allowing populations to persist even when some environmental conditions fall outside their optimal growth range .

Biomass, functional diversity and community composition during seasonal heatwaves

In our modelling study, we observed that heatwaves induce changes in community biomass, diversity, and dominant functional groups of plankton (Figures. 3-6, SM4- SM6). Summer and autumn heatwaves (Figure 4, SM4) cause the highest anomalies in terms of biomass concentration and recovery times followed by spring and winter (Figures SM5-SM6). The strongest copepod biomass decline occurs during summer heatwaves, persisting for two years and eventually recovering to pre-heatwave concentrations after six years (Figure 4). Protists also experience strong biomass declines during and after the summer heatwaves with a stronger periodic signal than in copepods. The biomass anomalies for the autumn heatwave (September- November) are similar to the summer heatwave (Figure SM4). The only exception is that the biomass of active feeders increases when the autumn heatwave occurs. The winter heatwave (Dec-Feb) positively impacts plankton biomass, particularly for active and passive feeders, while total protist biomass declines for the remainder of the year (Figure SM5). The biomass anomalies are less profound a year after the winter heatwave and the biomass returns to pre-heatwave conditions after three years. The spring heatwave (Mar-May) exhibits similar biomass anomaly patterns to the winter heatwave (Figure SM6). The total biomass of both active and passive copepod feeders increases, while the total protist biomass stays the same despite the fluctuations in the size bins.

Looking at the Shannon Diversity Index (Figure 5, Supplementary Material section: "Shannon Index"), heatwaves also affect plankton functional diversity with the anomaly signal being extended into subsequent seasons. For both protists and copepods, functional diversity stays the same or increases during winter, spring, and summer heatwaves, while it decreases during the autumn heatwave. The autumn heatwave causes the strongest anomaly, followed by summer, winter, and spring. After the heatwave, the time-traveling anomaly signals show that heatwaves affect plankton functional groups differently.

Examining community composition, heatwaves alter the order of dominant groups based on their relative contribution to the total biomass at the time (Figure 3). These changes persist for up to six years before returning to pre-heatwave conditions. Like biomass and diversity, the alterations in dominant groups are more profound for the summer and autumn heatwaves (Figure 5). All four heatwave scenarios cause more changes in protists than in copepods. We speculate that this is due to protists shorter live-cycles, higher community diversity, and stronger ecosystem dynamics (resource competition, predation). Still, two temperature norms (20 @C and 24 @C) dominate the community before, during, and after all heatwaves. Our findings indicate that despite temperature impacts on individuals' physiology, populations and communities remain resilient during seasonal heatwaves. Smaller-size groups may benefit, but larger groups also show increased biomass, suggesting the influence of resource competition and predator-prey dynamics alongside temperature.

Direct versus indirect effects of temperature on community properties

Complex ecosystem dynamics pose challenges in determining whether the primary driver of plankton community changes is the temperature on organismal physiology (direct effects), predator-prey dynamics (indirect effects), or both. We conducted two sets of simulations to separate the direct and indirect effects of temperature; one where we exposed solely protists on the heatwave and one only on copepods. Looking at the biomass size bins, both copepods and protists show a variety of biomass anomalies depending on the temperature simulations (Figure 6). For copepods, functional diversity exhibits similar anomaly patterns between the initial heatwave simulations (which consider heatwave impacts on both protists and copepods' physiology) and simulations where the heatwave solely affects copepods' physiological rates while protists show more diverse anomaly patterns (Figure 3). The model outputs suggest that pinpointing a clear environmental driver becomes challenging as we move from individuals to populations, functional groups, and communities.

Discussion

Marine heatwaves are an increasing phenomenon with effects on plankton organisms, food webs, biogeochemistry, and ecosystem services . Thus, the development of reliable forecasting tools on heatwaves properties (e.g., duration, intensity, depth) and ecosystem responses is crucial for successful mitigation and adaptation actions for ocean sustainability . Still, we lack a mechanistic understanding of how temperature relates to the observed ecological alterations during and after the heatwaves. This is mostly due to the strong connection of temperature with various abiotic and biotic factors and the complex temporal and spatial dynamics of marine communities.

In this study, we examine how the temperature anomaly of surface seasonal heatwaves is affecting ecosystem dynamics in plankton communities. We use a trait- and size-structured model that accounts for protists and the life cycle of active and passive feeding copepods. We highlight and discuss three key findings: Firstly, seasonal heatwaves trigger contrasting, lasting effects on plankton communities (biomass, size distribution, functional diversity), extending up to six years post-heatwave onset. Secondly, it is difficult to separate temperature as the key driver of the ecosystem changes we observe when we move from individual processes to community dynamics. Lastly, temperature anomalies can trigger functional groups differentially, with direct and indirect effects varying across groups.

The model results show that the duration of community anomalies depends on when the heatwave occurs. The system takes up to three years for the winter and spring heatwaves and up to six years for the summer and autumn heatwaves to reach the pre-heatwave state. The different mixed layer depth of the seasons (shallow in summer/autumn, deeper in winter/spring) could be a potential driver for this outcome, as it is strongly related to the density of nutrients and plankton in the model and the ocean . Though, since we kept the mixed layer depth fixed in our experiments, we speculate that this outcome is driven by the temperature differences among seasons caused by the heatwaves. The mean seasonal temperature before the heatwaves varies between 15 @C and 16 @C for winter and spring and 22 @C to 24 @C for autumn and summer, leading to a temperature difference of up to 9 @C between seasons. The seasonal heatwaves of 4 @C do not alter the mean annual temperature (20 @C). Still, while winter and spring heatwaves maintain temperature fluctuations within pre-heatwave seasonal ranges, summer and autumn heatwaves lead to fluctuations exceeding the pre-heatwave ranges by 2 @C (autumn) and 4 @C (summer). Thus, the model indicates that the ecological disruption and recovery time are related to the temperature anomaly compared to seasonal temperature fluctuation.

Our results show changes in biomass size bins, dominant groups, and functional diversity index during and after heatwaves, differing across protist and copepod functional groups. Starting with the temperature environmental trait, the model includes functional groups of eight temperature norms. For both protists and copepods, heatwaves lead to changes in the relative biomass and order of the dominant groups during and after the heatwave. Still, functional groups with temperature norms of 20 @C and 24 @C dominate the plankton community before, during, and after the heatwaves and between seasons.

The community size structure also reflects periodic variations caused by marine heatwaves. However, no consistent pattern emerges across biomass size bins for all heatwave scenarios, revealing the intricate synergy of direct and indirect temperature effects. For years after the heatwaves, the model shows changes in the order of dominant size groups, highlighting that the effect of a seasonal heatwave on the community properties can persist for a long period. However, the reposition of some dominant size groups does not affect the core community size structure. Our model output is supported by previous studies that show that environmental factors beyond temperature likely contribute to size structure variations we observe in nature . *In-situ* observations have shown that surface heatwaves alter the properties of plankton communities like diversity and size distribution, strongly connected with other environmental conditions such as the passive entrance of species via water masses, stratification, and changes in nutrient concentrations . Field observations show a shorter recovery period than our model projects ranging from a few months to three years depending on the duration of the heatwave . *In-vitro* and mesocosm experiments also indicate that warming can trigger alterations and different recovery times on physiological rates, species density, and community structure in the same direction as our model.

Our results are in a parallel direction with *in-situ* and*in-vitro* observations but are not directly comparative as model-observation disparities stem from differences in design, environment representation, and ecological realism. *In-situ*observations are snapshots of an ecosystem shaped by many physical, chemical, and biological processes, most of them recorded with a limited temporal and spatial resolution. In comparison to the Eulerian view of*in-situ* observations, this study assumes a Lagrangian view and allows us to focus on the theoretical community as moving through time. Mesocosm and laboratory experiments also follow a Lagrangian approach, but they run for shorter periods compared to our model experiments (days to weeks). We also note that descriptive language in most published studies (e.g., small vs big, warm vs cold species) lacks quantitative data (e.g., body size, species temperature optima, and physiological rates) necessary for direct model-observation comparisons. Given plankton's adaptive plasticity and morphological variations species can manifest as "cold" or "warm" depending on regional context, contributing uncertainty to model-observations comparisons.

We propose two more drivers of this model-observational mismatch other than the differences between our model design and*in-situ/in-vitro* marine heatwaves on the Lagrangian vs Eulerian approach and heatwave properties (e.g., temperature anomaly and heatwave duration): (1) the lack of a 3-dimensional dynamic environment in our model and (2) the need for enhanced ecological and plankton diversity representation. In marine ecosystems, surface heatwaves do not occur in isolation, as in our modelling set-up. They are strongly connected with other abiotic drivers of ecosystem dynamics (e.g., mixed layer depth, nutrient cycling, salinity) that can alter nutrient resources, prey concentrations, and community dynamics during the heatwave . These environmental drivers can also mitigate or aggravate the signal of temperature effect through time. Additionally, even if our model design has complex ecosystem dynamics and higher functional diversity than most ecosystem models (Petrick et al., 2022), it does not consider phenotypic plasticity, evolution, or behavioral decisions like vertical migration and changes in foraging and predation avoidance that can maximize fitness on an individual level and resilience on a community level . These physiological and behavioral responses might allow species persistence that could dampen the impact of the heatwave and accelerate recovery periods.

Our study highlights the essential role of functional diversity in population dynamics. In the model, protists are the most diverse community with plasticity on energy uptake and short life cycles. They show dynamic responses to environmental conditions and experience more changes in community composition compared to copepods. Passive copepod feeders are more vulnerable than active feeders and have the longest recovery time in terms of biomass concentration. This is probably due to their trade-off disadvantage on resource competition combined with predation losses from active feeders. Traditionally, research has focused on prey density and properties, but studies have shown that the modes of energy uptake and foraging also have a strong impact on ecosystem dynamics, biogeography patterns, and biogeochemistry . For example, studies have shown that mixotrophy evolved as a survival strategy against prolonged periods of darkness and that some copepod species can actively switch between passive and active feeding depending on the environmental conditions (Kiørboe et al., 2018a). Closer attention to the feeding mode and organismal behavioral decisions that lead to trait optimization and fitness can help us to better understand the community status in different environmental conditions and extreme events. A gradual increase of functional diversity in the model could provide us with a new level of mechanistic understanding of ecosystem dynamics but probably increase the difficulty of distinguishing drivers. It could also highlight suggestions on data needs for advancing the state-of-the-art of forecasting tools and our confidence in trustworthy projections crucial for policy advice and actions. Our model is a useful tool for mechanistically exploring the effect of abiotic parameters in ecosystems from individuals to community levels. We wish to see future studies using and adjusting the model design to explore the resilience of plankton communities under different environmental conditions.

Conclusions

As extreme events caused by climate change are increasing in frequency and duration, it is important to develop a mechanistic understanding of how ecosystems respond to temperature changes. Here we use a trait- and size-structured model to study the effect of seasonal heatwaves on plankton organisms. In the model, the plankton functional diversity is represented by the traits of cell/body size, energy uptake (auto-, mixo- and heterotrophy) for protists, and the life cycle of copepods with two feeding modes (active, passive). The model showed that heatwave effects on biomass, diversity, and community composition are present not only during the heatwave but for up to six years after the temperature perturbation. Autumn and summer heatwaves have the most profound anomalies and longest-lasting effects, followed by winter and spring heatwaves. Our results indicate that temperature can alter the dominance of size groups, but temperature alone cannot lead to fundamental changes in the community size structure and more environmental factors need to be taken into consideration. In our study, we found a variety of population and community alterations during the heatwave and different recovery times to the pre-heatwave state. Two factors drive those results: the heatwave temperature anomaly compared to the mean seasonal temperature fluctuation and plankton functional diversity. Communities have longer recovery times when experiencing seasonal heatwaves with temperature anomalies outside the pre-heatwave seasonal temperature fluctuation. Including functional diversity is crucial for exploring ecosystem changes as protists, active, and passive copepod feeders have dissimilar responses to the heatwaves, as well as recovery periods. Our model provides a mechanistic framework with ecological realism, flexible enough to scale up and down in complexity and test hypotheses for future studies.

Acknowledgements

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References

Figure Legends FIGURE 1: A graphic summary of the model design, with the environmental forcing (mixed layer depth and sea surface temperature) and a graphic illustration of the temperature norm environmental trait.

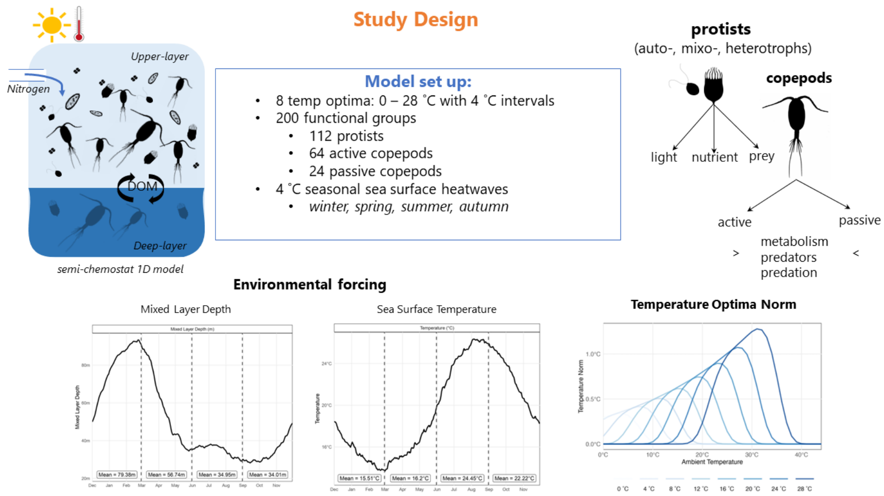
FIGURE 2 : Absolute biomass concentrations (mg C m-3) expressed in size bins for the pre-heatwave conditions for active and passive copepod feeders and for protists: (a) daily biomass size bins (b) seasonal total and mean biomass of the size bins. Dashed lines in indicate the end of each season (winter, spring, summer, autumn).

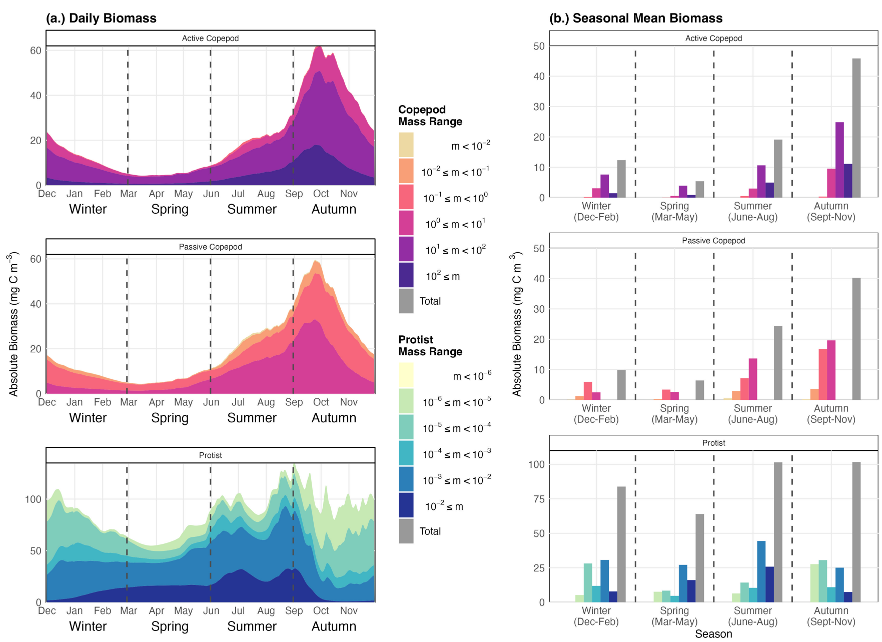
FIGURE 3: Absolute seasonal biomass concentration of the five dominant functional groups (in terms of their relative contribution to total biomass) of (a.) active and (b.) passive copepod feeders and (c.) protists for the winter (December- February), spring (March-May), summer (June- August) and autumn (September-November) heatwave scenarios. Year 1: Heatwave. Years 2-7: years after the heatwaves.

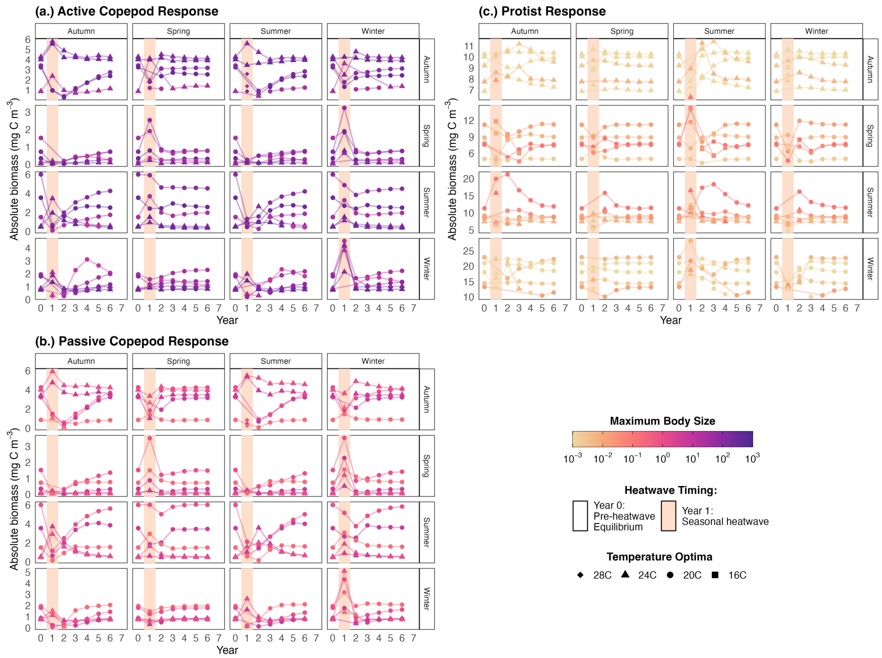
FIGURE 4: Absolute Biomass concentration (mg C m-3) anomalies during and after the summer seasonal heatwave (June-August) for the biomass size bins of (a.) active and (b.) passive copepod feeders and (c.) protists. Year 1 shows the seasonal biomass anomaly during the heatwave (heatwave- pre heatwave biomass concentration). Years 2- 9 show the seasonal biomass anomaly for 8 years after the seasonal heatwave (after heatwave – pre heatwave biomass concentration). HW on all plankton groups: the heatwave directly affects the physiological rates of all plankton groups. HW on copepods only: the heatwave directly affects the physiological rates of copepods only. HW on protists only: the heatwave directly affects the physiological rates of protists only.

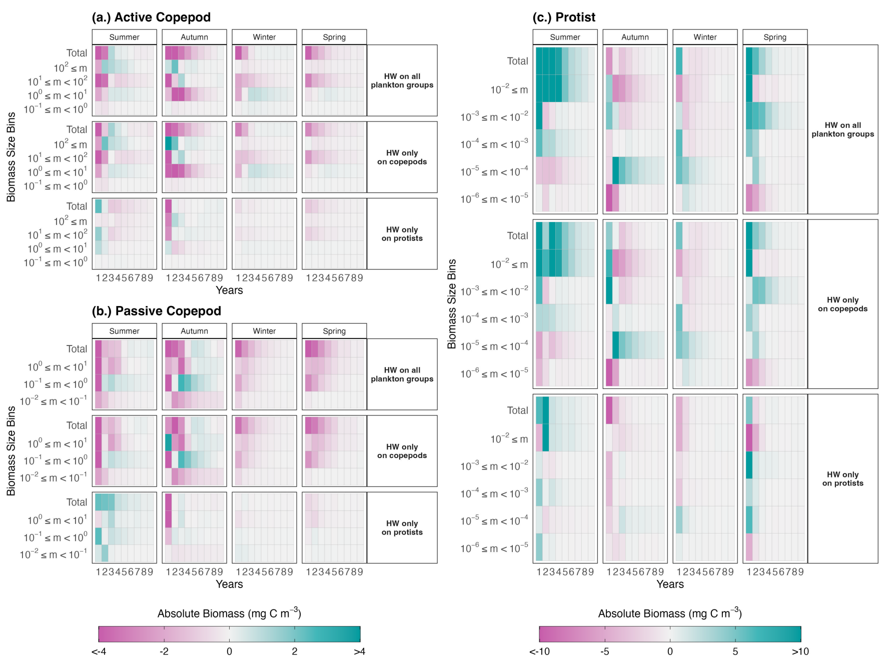
FIGURE 5 : Seasonal Shannon Diversity Index for (a.) active and (b.) passive copepod feeders and (c.) protists for the winter (December- February), spring (March- May), summer (June- August) and autumn (September- November) heatwave scenarios. X-axis: years. Year 0: pre-heatwave, Year 1: heatwave (in red) Years 2-5: after-heatwave. More details about the Shannon Diversity Index can be found in the SM.

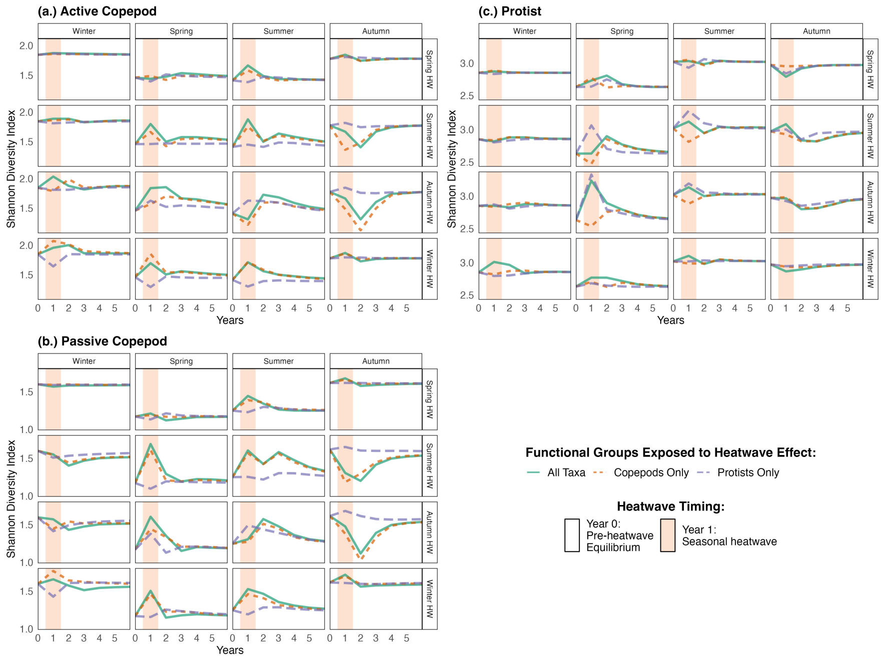
FIGURE 6 : Biomass anomalies (heatwaves (HW) on protists or copepods only – heatwaves (HW) on both protists and copepods) during all seasonal heatwaves and the seven seasons afterwards for (a.) active and (b.) passive copepod feeders, and (c.) protists.


Study Design
Upper-layer
Nitrogen
DOM
Deep-layer
semi-chemostat 1D model
Model set up:
8 temp optima: 0 – 28 ˚C with 4 ˚C intervals
200 functional groups
112 protists
64 active copepods
24 passive copepods
4 ˚C seasonal sea surface heatwaves
winter, spring, summer, autumn
protists
(auto-, mixo-, heterotrophs)
light
nutrient
prey
copepods
active
passive
metabolism
predators
predation
>
<
Environmental forcing
Mixed Layer Depth
Sea Surface Temperature
Temperature Optima Norm
Ambient Temperature
0 ˚C
4 ˚C
8 ˚C
12 ˚C
16 ˚C
20 ˚C
24 ˚C
28 ˚C

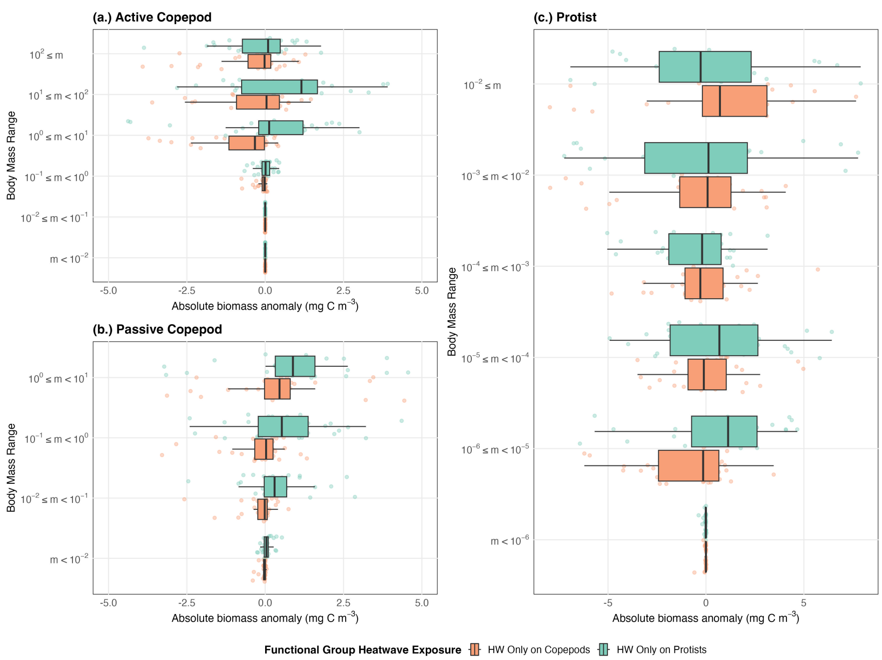

(a.) Daily Biomass
(b.) Seasonal Mean Biomass
Active Copepod
Passive Copepod
Protist
Absolute Biomass (mg C m^{-3})
Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov
Winter Spring Summer Autumn
Winter (Dec-Feb)
Spring (Mar-May)
Summer (June-Aug)
Autumn (Sept-Nov)
Season
Copepod Mass Range
$m < 10^{-2}$
$10^{-2} \le m < 10^{-1}$
$10^{-1} \le m < 10^{0}$
$10^{0} \le m < 10^{1}$
$10^{1} \le m < 10^{2}$
$10^{2} \le m$
Total
Protist Mass Range
$m < 10^{-6}$
$10^{-6} \le m < 10^{-5}$
$10^{-5} \le m < 10^{-4}$
$10^{-4} \le m < 10^{-3}$
$10^{-3} \le m < 10^{-2}$
$10^{-2} \le m$
Total


(a.) Active Copepod Response
(b.) Passive Copepod Response
(c.) Protist Response
Autumn
Spring
Summer
Winter
Absolute biomass (mg C m-3)
Year
Maximum Body Size
Heatwave Timing:
Year 0: Pre-heatwave Equilibrium
Year 1: Seasonal heatwave
Temperature Optima
28C
24C
20C
16C


(a.) Active Copepod
(b.) Passive Copepod
(c.) Protist
Summer
Autumn
Winter
Spring
Total
Biomass Size Bins
HW on all plankton groups
HW only on copepods
HW only on protists
Years
Absolute Biomass (mg C m-3)
<-4
-2
0
2
>4
<-10
-5
0
5
>10



(a.) Active Copepod
(b.) Passive Copepod
(c.) Protist
Winter
Spring
Summer
Autumn
Spring HW
Summer HW
Autumn HW
Winter HW
Shannon Diversity Index
Years
Functional Groups Exposed to Heatwave Effect:
All Taxa
Copepods Only
Protists Only
Heatwave Timing:
Year 0: Pre-heatwave Equilibrium
Year 1: Seasonal heatwave



(a.) Active Copepod
(b.) Passive Copepod
(c.) Protist
Body Mass Range
$10^2 \le m$
$10^1 \le m < 10^2$
$10^0 \le m < 10^1$
$10^{-1} \le m < 10^0$
$10^{-2} \le m < 10^{-1}$
$m < 10^{-2}$
$10^{-2} \le m$
$10^{-3} \le m < 10^{-2}$
$10^{-4} \le m < 10^{-3}$
$10^{-5} \le m < 10^{-4}$
$10^{-6} \le m < 10^{-5}$
$m < 10^{-6}$
Absolute biomass anomaly (mg C m^{-3})
Functional Group Heatwave Exposure
HW Only on Copepods
HW Only on Protists