RESEARCH ARTICLE

Responses of the mesozooplankton community to marine heatwaves: Challenges and solutions based on a long-term time series

Margot M. Deschamps[1] | Maarten Boersma[1,2] | Luis Giménez[1,3]

[1]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany

[2]University of Bremen, Bremen, Germany

[3]School of Ocean Sciences, Bangor University, Menai Bridge, UK

Correspondence
Margot M. Deschamps
Email: margot.deschamps@awi.de

Abstract

1. Marine heatwaves (MHWs) are extreme weather events that have major impacts on the structure and functioning of marine ecosystems worldwide. Due to anthropogenic climate change, the occurrence of MHWs is predicted to increase in future. There is already evidence linking MHWs with reductions in biodiversity and incidence of mass mortality events in coastal ecosystems. However, because MHWs are unpredictable, the quantification of their effects on communities is challenging.

2. Here, we use the Helgoland Roads long-term time series (German Bight, North Sea), one of the richest marine time series in the world, and implement a modified before-after control-impact (BACI) design to evaluate MHW effect on mesozooplankton communities. Mesozooplankton play an essential role in connecting primary producers to higher trophic levels, and any changes in their community structure could have far-reaching impacts on the entire ecosystem.

3. The responses of mesozooplankton community to MHWs in terms of community structure and densities occurred mainly in spring and autumn. Abundances of seven taxa, including some of the most abundant groups (e.g. copepods), were affected either positively or negatively in response to MHWs. In contrast, we observed no clear evidence of an impact of summer and winter MHWs; instead, the density of the most common taxa remained unchanged.

4. Our results highlight the seasonally dependent impacts of MHWs on mesozooplankton communities and the challenges in evaluating those impacts. Long-term monitoring is an important contributor to the quantification of effects of MHWs on natural populations.

KEYWORDS
BACI design, community structure, Helgoland Roads, marine ecosystems, marine heatwaves, North Sea, zooplankton

1 | INTRODUCTION

As consequence of anthropogenic climate change, the frequency and magnitude of extreme weather events such as droughts, storms and floods are expected to increase in the coming decades (IPCC et al., 2022). This predicted increasing frequency of extreme events, including marine heatwaves (MHWs), is currently causing ecological and socio-economic concern (Holbrook et al., 2020; Oliver et al., 2021). Mass mortalities, habitat loss, shift in species distributions and reduction in biodiversity in all living compartments (Smith et al., 2023), including plankton (Arteaga & Rousseaux, 2023; Brodeur et al., 2019; Nielsen et al., 2021), macroalgae (Weitzman et al., 2021) and sea birds (Jones et al., 2018), have been attributed to intense and long MHWs. These effects of MHWs on biological systems may have profound socio-economic implications on a global scale, as MHWs compromise essential ecosystem services, including provisioning (i.e. fisheries), cultural (i.e. loss of iconic species) and regulating (i.e. carbon sequestration; Smith et al., 2021).

A critical point in the quantification of MHW effect on marine ecosystems is their lack of predictability, although some forecasting methods have been developed recently (Jacox et al., 2022). Therefore, most studies in this area have been opportunistic, concentrating on a single large-scale event (Supporting Information Appendix 1). Indeed, most studies are based on individual MHW events, examining the differences in processes or the density of species of interest before, during and after events. Some studies also compare conditions during the MHW to those in the same season but in a year without recorded heatwaves. In both cases, the control condition is restricted to a single period, which is used as a reference to quantify the MHW impact. Given the unpredictability of marine heatwaves, such designs have been one of the most effective options and have provided the first warnings about the effects of marine heatwaves on organisms. As longer time series become available, there is the opportunity of applying stronger designs, based on several controls and impacted years, which essentially means that one obtains a higher level of replication.

Another important point is that most studies on MHWs are limited to specific regions that have experienced one single intense event (Supporting Information Appendix 1). For instance, approximately 75% of the studies we identified (Supporting Information Appendix 1) exploring MHW impacts on communities using time series data, were carried out either in the North Pacific Ocean, during the 2014–2016 MHW ('the Blob') or in the Indian Ocean during the 2010–2011 MHW (see also Joyce et al., 2023). Other regions, such as the North Sea, have been overlooked. Despite experiencing numerous heatwaves ranging from normal to severe over the past decades (Giménez et al., 2024), a comprehensive understanding of community changes in response to MHW in the North Sea is still missing.

Here, we quantify the effect of MHWs on a coastal mesozooplankton community, using a modified BACI design, based on a high sampling frequency long-term time series (Helgoland Roads, North Sea). The Helgoland Roads (HR) time series (Amorim et al., 2023; Boersma et al., 2017; Wiltshire et al., 2010) is a unique data set and one of the richest marine time series in the world. Located near the island of Helgoland in the German Bight (54°11′18″ N 7°54′ E), HR started in 1962 with daily measurements of sea surface temperature, nutrients and phytoplankton. In 1975, the data set was expanded to include zooplankton samples taken three times a week. At HR, multiple MHW events were recorded from 1962 to 2018 (Giménez et al., 2024). Here, MHWs are defined as periods of time ≥5 days during which seawater temperature exceeds the 90th quantile (i.e. Q90th percentile) of a baseline temperature time series (Hobday et al., 2016). We used the long MHW events (i.e. all MHW of a duration ≥14 days to meet the conditions required for our design) occurring at specific seasons as replicate units. We then compared mesozooplankton densities, diversity and community structure during periods of MHWs with those observed in the same times and seasons of 'control' years where MHWs did not occur. This comparison aimed to understand the specific effect of MHWs on the mesozooplankton community structure, diversity and density depending on the season in which the event occurred. This design enabled us to (i) achieve replication at the level of MHW events, (ii) compare responses in terms of community structure against replicate controls of season response and (iii) quantify season-specific effects of MHWs on key taxa in terms of density and diversity.

The quantification of MHWs effects on mesozooplankton (i.e. zooplankton from 0.2 to 20 mm) is central to understand their impact on the entire marine food web and associated ecosystem services. Mesozooplankton play a central role in the trophodynamics of pelagic ecosystems, as well as in nutrient recycling and export of nutrients and carbon to depths (Helaouët & Beaugrand, 2007; Steinberg & Landry, 2017). In addition, because of their short generation time, mesozooplankton, including copepods, respond rapidly to temperature increase (Richardson, 2008) and are therefore likely to respond to MHWs.

During MHWs, zooplankton are subjected to rapid and extreme temperature increases over short periods. This sudden thermal stress can exceed their thermal tolerance limits, leading to significant changes in physiological and life history traits, such as altered metabolic rates, accelerated development and potentially mortality if temperatures surpass survival thresholds (Smith et al., 2023). Species with narrow thermal tolerance ranges are particularly vulnerable to MHWs compared to those with broader tolerances (Smith et al., 2023). Furthermore, invasive species, smaller species and warm-adapted species may thrive during intense MHWs at the expense of native, larger and cold-adapted species (Evans et al., 2020; Gubanova et al., 2022). The timing of MHWs is also critical; if they coincide with key biological events such as reproduction, they can shift species phenology, potentially causing mismatches situation with predators (Cushing, 1990), which could then have strong repercussions on higher trophic levels. While MHWs can have similar effects to long-term warming, the latter involves a gradual increase in average temperatures over decades, allowing more time for mesozooplankton to adapt or shift their distribution. In contrast, the rapid onset of MHWs leaves insufficient time for

adaptation or migration, leading to abrupt and sometimes irreversible changes in community composition and ecosystem dynamics. For instance, in the Tasman Sea, a shift in the zooplankton community was recorded in response to the 2015–2016 MHW (Evans et al., 2020): Smaller warm-water copepods dominated the community and gelatinous zooplankton increased in density, replacing large temperate or cold-water zooplankton, including copepods, Cladocera and Appendicularia. Likewise, the 2014–2016 Pacific MHW resulted in an increase in warm-water copepod density in autumn, which persisted through the winter months (McKinstry et al., 2022). In the Gulf of Alaska, the 2014–2016 MHW resulted in increased zooplankton densities, particularly copepods (Batten et al., 2022). The studies mentioned above focus on single long-term events with durations of months to years. However, because zooplankton organisms have short life cycles, we expect responses to MHWs occurring at shorter timescales. Indeed, seasonal variations play a crucial role in shaping many communities in the world, including zooplankton, due to the annual cycle of environmental conditions such as temperature, light and nutrient (Mackas et al., 2012). These factors influence primary production, which in turn affects food availability for zooplankton. For example, in spring, increased sunlight and warmer temperatures typically lead to phytoplankton blooms (Wiltshire et al., 2008). In response to this increase in food availability, zooplankton also increase in density. Conversely, during autumn and winter, reduced light and lower temperatures can decrease phytoplankton levels, leading to a decline in zooplankton. These seasonal fluctuations not only impact the density and composition of the community but also affect the broader marine ecosystem. Changes in mesozooplankton populations can influence the distribution and density of higher trophic levels, including fish (Beaugrand et al., 2003). Therefore, we hypothesize that the mesozooplankton response to MHWs should vary among seasons. For instance, planktonic responses to winter MHWs may be less severe than those in other seasons as biological activity is lower during this time (van Beusekom & Diel-Christiansen, 2009). Moreover, temperature alone is not the sole driver of mesozooplankton changes. Other factors, such as light availability, turbidity and phytoplankton, play equally significant roles alongside temperature. We hypothesize that spring and autumn MHWs could influence community structure and densities of mesozooplankton taxa, especially those undergoing growth or decline phase. In the North Sea, spring and autumn MHWs are unlikely to exceed the thermal tolerance of mesozooplankton taxa. For instance, *T. longicornis*, a cold-temperate species, has an upper thermal limit of around 22.5°C (Halsband-Lenk et al., 2002). Given that spring and autumn temperatures are usually around 6°C and 13°C, respectively (Amorim et al., 2023), it is improbable for temperatures to reach such high levels during these seasons even in case of MHW events. Consequently, heatwave events could promote an earlier and faster growth period for taxa peaking in spring. Similarly, for taxa that peak in late summer or early autumn, MHWs could lead to an extended and slower decline phase, up to a point where temperatures fall below the lower thermal limits.

In contrast, summer MHWs are more intense than those in other seasons, often far exceeding the intensity threshold, with most of the top 10 events (intensity larger than three times the difference between the threshold and the climatology) identified in summer (Giménez et al., 2024). Therefore, we anticipate a shift in the community structure of mesozooplankton, favouring warm-water assemblage over cooler-water ones.

2 | MATERIALS AND METHODS

2.1 | The Helgoland Road time series

Mesozooplankton counts (density: ind.m^3) from the HR data set (Boersma et al., 2017; Dummermuth et al., 2023; Wiltshire et al., 2010) were used in this study. From 1975 onwards, monitoring of mesozooplankton has been conducted near the island of Helgoland in the German Bight (54°11′18″ N 7°54′ E). Mesozooplankton are sampled three times a week using a Nansen net (aperture 17 cm, net length 100 cm) fitted with a 150 μm mesh net coupled with a flowmeter. The complete monitoring method was described by Greve et al. (2004). The current analysis of the mesozooplankton response to MHWs was carried out for the period 1975–2018. Mesozooplankton taxa identified over the complete time period and with a mean relative density higher than 3% were extracted from the HR data set (PANGAEA doi: 10.1594/PANGAEA.872023) (Table 1). This threshold was applied to exclude very rare (zero-inflated) taxa while still preserving a significant portion of the overall mesozooplankton community. This approach ensures that the analysis maintain sensitivity and minimize the potential influence of rare taxa, thereby enhancing the reliability and interpretability of the results.

To assess the impacts of MHWs on the mesozooplankton community, the timing and duration of MHWs detected at HR between 1975 and 2018 were used and obtained from Giménez et al. (2024, see their supplemental information, table S1). Sea surface temperature data (°C) used for MHW detection are measured on a work daily basis directly from the research vessel using a thermometer at the same sampling site of the mesozooplankton. Due to strong tidal currents and shallow depth, the water column at the sampling site is well-mixed ensuring that depth does not affect temperature. At HR, MHWs show a positive correlation with atmospheric heatwaves across the German Bight (Giménez et al., 2024). Additionally, sea surface temperature anomalies are positively correlated with those at Sylt Roads in the Wadden Sea and the wider North Sea (Amorim et al., 2023). This suggests that MHWs recorded at HR occur on a wider spatial scale, encompassing the German Bight. Therefore, the observed correlations with broader regional data underscore the relevance of using MHWs recorded at HR to understand the general MHW pattern in the German Bight.

All analyses are based on the detection of MHW events using a fixed 30-year baseline period set between 1 January 1962 and 31 December 1991 (Giménez et al., 2024) to calculate the climatology

TABLE 1 Mesozooplankton identified at HR and used in the study.

	Order	Taxa
Copepods	**Calanoida**	*Calanus* spp., ***Acartia* spp.**, *Centropages* spp. ***Pseudo***/***Paracalanus* spp.**, ***Temora longicornis***
	Cyclopoida	*Oithona* spp., *Corycaeus anglicus*, other non-identified
	Harpacticoida	*Euterpina acutifrons*, other non-identified
		Copepoda nauplii
Non-Copepods	Amphipoda, **Cladocera**, Cumacea, Decapoda, Isopoda, Mysida, Pantopoda	
		Annelida larvae, **Appendicularia**, **Chaetognatha**, **Cirripedia larvae**, **Echimodermata larvae**

Note: Most abundant (i.e. relative density <3%) are represented in bold. For copepods, other taxa were only used to calculate density at order level and diversity indices. For non-copepods, other orders were only used to calculates diversity indices.

and identify deviations from this baseline (Hobday et al., 2016; Oliver et al., 2021). For each specific day, all temperature values within a specific window, over all the baseline, are pooled together and organized into a frequency distribution. From this distribution, the 90th quantile (Q90) is calculated, identifying the temperature below which 90% of the observations fall (see Giménez et al., 2024 for more information). An event of unusually warm sea temperature will be then identified as a MHW if the temperature exceed this Q90 for more than 5 days (Hobday et al., 2016). From this MHW data set, only the longest events (i.e. ≥14 days) were selected to meet the conditions required for our design.

Giménez et al. (2024) provided both a fixed and a 30-year shifting baselines and comparing the response to MHW using both baselines will be insightful. However, here, we will focus solely on the fixed baseline for two reasons. First, the comparison between both baselines is valid only for the second part of the time series as it assumes that organisms experienced the MHW according to the previous 30 years of temperature. As a result, the shifting baseline produced a shorter time series with fewer number of MHW and, consequently, fewer replicate units, directly reducing the power of the test. Second, it would be more informative to create species-specific shifting baselines calibrated with the timescale of mesozooplankton adaptive responses to temperature, rather than using a fixed 30-year duration. However, we lack information about the timescale of adaptation of mesozooplankton in the German Bight. Interestingly, MHW effects observed in this study (see Section 3)

might not be detected using a shifting baseline, as some replicates units currently classified under the MHW treatment would be reassigned to the control years. This could potentially mask the effects of thermal fluctuations on organisms.

2.2 | BACI design

One approach which helps to understand the effect of natural or anthropogenic disturbance on a community is the use of a Before-After-Control-Impact (BACI) design (Underwood, 1991). BACI allows the comparison of the state of a community if a disturbance occurs, defined as impact treatment (**I**) with a control treatment (**C**) in which no disturbance was recorded (Underwood, 1991). Both, the impact and the control treatment are sampled before (**B**) and after (**A**) the disturbance. The BACI design typically defines control and impacted conditions as spatial units, with both control and impacted sites sampled simultaneously (Conner et al., 2016). Because our variation was temporal rather than spatial, we modified the design (Figure 1) by defining replicate units in time, with each unit representing a different year. Thus, in our study, the before and after periods refers to the week preceding and following the MHW, respectively. The control refers to a period of a year (defined by week of year) without MHW, while impact refers to a period of a different year (same week in the year as the control, ±3 days), when MHW occurred. To mitigate any potential lagged temporal responses of zooplankton to heatwaves, control treatments were carefully assigned to minimize the likelihood of residual effects from MHW. Specifically, control periods were chosen to be as distant as possible from any MHWs included in this study. As a result, the average duration between a MHW and the following control period for another MHW was approximately 172 days.

An important aspect of the spatial BACI is that both control and impacted sites should be defined in similar habitats to avoid sampling different communities. We applied the same logic for our modified BACI design considering that both the pelagic habitat (e.g. temperature) and the mesozooplankton community sampled at HR has changed over the past 50 years (Amorim et al., 2023; Di Pane et al., 2023). Hence, to consider comparable years, we used a paired design (identification: **ID**) where the control was assigned within 5 years preceding or following the impacted year. In cases where several controls were eligible for a given impact, the one closest to the impact was chosen.

For each impacted or control unit, we defined two other periods per treatment, within the MHW, that is start (**S**) defined by the first week of MHW and end (**E**) defined as the last week of MHW. By including these periods, we aimed to capture the immediate impact of MHWs but also observe the trajectory of the response over time. This allows for a better understanding of how a community adapts or recovers after the MHWs and gives more credibility to the statistical output. Each period was composed of three replicates, which is equivalent to 1 week of data per period (Figure 1). Analysis focussed exclusively on extended MHWs (i.e. ≥14 days, Table 2), and
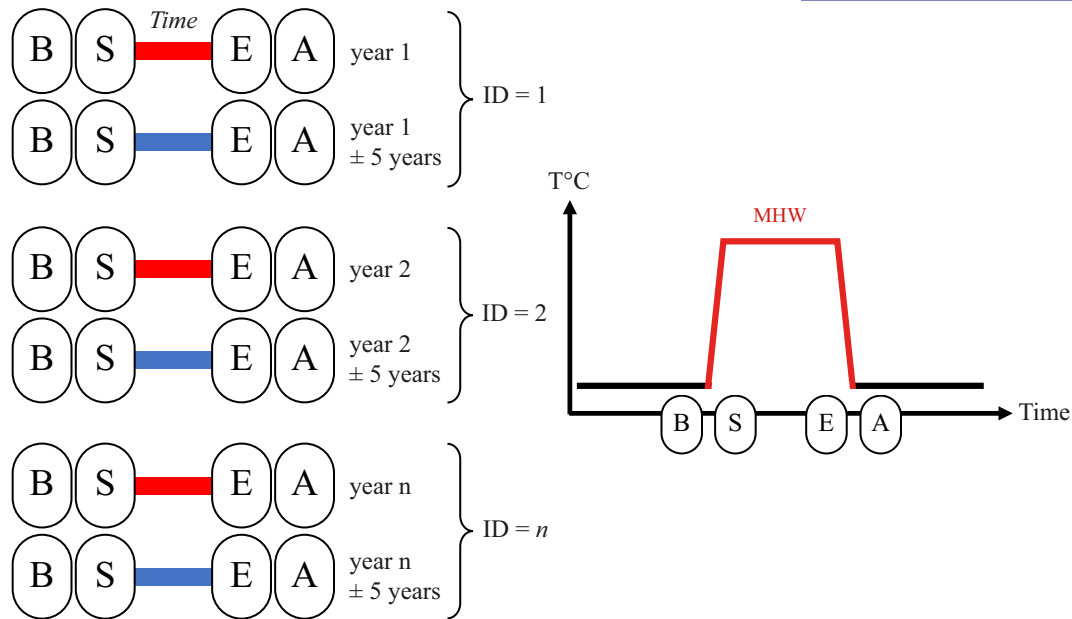
FIGURE 1 Modified BACI design. Red line represents the impact treatment (i.e. MHW). Blue line represents the control treatment (i.e. no MHW). The control is assigned in the 5-years window around the impact year. The oval shape indicates the sampling period with two periods outside the MHW (B: Before treatment; defined as one week preceding the MHW. A: After treatment; defined as the week following the MHW) and two periods inside the MHW (S: Start of treatment; defined as the first week of the MHW and E: End of treatment; defined as the last week on the MHW). A period of one week ensures that at least three samplings took place in each period. An ID number is assigned to each pair of treatments. The design is repeated for each season where a MHW occurred.

TABLE 2 MHW events used in this study and associated traits.

Season of occurrence	Number of MHW	Temperature intensity	Maximum temperature intensity	Duration	Range	ΔT°C control versus impact
Spring	11	0.48±0.02	1.27±0.24	50±11	[16-149]	2.48±0.14
Summer	7	0.76±0.04	1.78±0.21	34±11	[17-103]	1.85±0.09
Autumn	8	0.61±0.03	1.40±0.30	44±9	[14-90]	1.75±0.13
Winter	7	0.37±0.02	0.92±0.15	34±9	[14-83]	2.20±0.17

Note: Temperature intensity (difference between the Q90 and the temperature observed), maximum temperature intensity and Δ Temperature between Control versus Impact are given in°C; Duration is given in days. Range is given in days and corresponds to the minimal and maximal number of MHW days in a season. Values shown are the mean ± standard error. Notes that duration and range do not correspond to the average length of individual MHW, but rather to the average length of events, which can include several MHW.

shorter MHWs were discarded due to insufficient data to include the start and end treatments. In the same way, MHWs separated by <14 days were considered as one MHW event as there would be an overlap between the period following the first MHW and the period preceding the second one. We categorized each MHW based on the season during which it occurred. When a MHW extended across two seasons, we attributed it to the season that included the majority of its duration as well as the peak of intensity (i.e. day of maximum temperature intensity recorded during the MHW). MHWs extended across more than two seasons were discarded from the analysis. Overall, our design contained 33 MHW events (Table 2) including four of the 10 most severe MHWs identified since 1975 (Giménez et al., 2024). The remaining six severe MHWs could not be incorporated due to the lack of comparable control periods or their spanning of multiple seasons (e.g. the 2006–2007 event comprised two consecutive MHWs affecting all seasons, Giménez et al., 2024).

2.3 | Data analysis

All analyses were conducted under R environment (R Core Team, 2023) with a threshold of significance set at 5%.

To assess the response of mesozooplankton community structure to MHWs, a permutational-based ANOVA (PERMANOVA) was performed. The first step was to quantify dissimilarities between taxa by using a Bray–Curtis dissimilarity index, previously standardized with the Hellinger method. Through PERMANOVA (999 permutations), we tested the interaction between treatments (**CI**, two levels: Control C; Impact I) and periods (**P**, two levels: Before B; After A) for each season to evaluate mesozooplankton community response to MHWs. Multivariate homogeneity of groups dispersions was tested, followed by a permutation test with 999 permutations. Start and End periods showed significant heterogeneity of group dispersion in spring, summer and winter and were therefore

excluded from the analysis to ensure the validity of the assumptions. When a significant interaction was observed, multilevel pairwise-comparisons were carried out posteriori. To integrate the dependencies in the data, the control/impact pairs (**ID**) were considered as a random factor in the models.

A Canonical Analysis of Principal Coordinates (CAP, 999 permutations) was used to visualize the community structure in response to MHWs. CAP is a flexible constrained ordination method that allows any dissimilarity measures to be used (Anderson & Willis, 2003). It is particularly useful when there is a prior hypothesis regarding the possible dissimilarities between the groups being analysed. By identifying the axis that best separates the groups, CAP enabled the detection of differences that might not be apparent through other ordination methods such as Principal Coordinates Analysis (PCoA) or Non-Metric Multidimensional Scaling (NMDS). To identify taxa responsible for the differences among groups, correlation coefficients (r^2) and associated p-value between taxa and canonical axes were calculated. A significance threshold was then applied to select taxa significantly correlated with canonical axes. Additionally, the distance between each control/impact pair for both before and after treatment was quantified to provide a clear quantitative measure of community dynamics in response to MHWs. This involved calculating the difference for each axis by comparing the coordinates of the impacted year against those of its corresponding control. Data points centred around zero indicate no divergence between the impact and control, that is, stability in community structure. Conversely, a deviation from zero indicates a shift in the community structure.

Our second objective was to examine densities of single taxa as well as two alpha diversity indices (i.e. Shannon diversity and Pielou's evenness). The indices were calculated for the whole mesozooplankton community and, at a finer scale, for the copepod community. This separation ensures a consistent measure of diversity, as these two communities are identified at different taxonomic resolutions (Table 1). Additionally, maintaining taxonomic resolution allows for a better understanding of the specific contributions of copepods and other mesozooplankton to overall biodiversity. Gamma Generalized Linear Mixed Effect models (GLMMs: Zuur et al., 2009) with a log link function were then performed seasonally by using the *lme4* R package (Bates et al., 2015). The fixed factor period (**P**, four levels: Before B; Start S, End E, After A) was included in the model, in interaction with treatment (**CI**, two levels: Impact I, Control C). The ID was used as a random factor. Here, all model assumptions were verified by checking residuals and overdispersion using the *DHARMa* package (Hartig & Lohse, 2022). The family function was replaced by a negative binomial (*glmmTMB* package) in case of violation of model assumptions. To assess model fit, model selection procedures (Zuur et al., 2009) were used based on the corrected Akaike Information Criterion (AICc). Specifically, the best-fitting model was determined by identifying the one with the lowest AICc value, with an exception made when the ΔAICc (i.e. difference between a candidate model and the model with the lowest AICc) was ≤2. Accordingly, we considered these models to represent a similar fit (Burnham et al., 2011; Zuur et al., 2009).

We used monotonic nonlinear link functions, and hence, we must pay attention to the type of interaction being detected. An important point is to recognize that some types of interaction among factors (here, BA:CI effect) are defined according to the scale where the variable is analysed and visualized (Spake et al., 2023). There is a subset of interactions, called 'non-interpretable' or 'quantitative' (Loftus, 1978; Spake et al., 2023), thereafter called 'quantitative', where the scale determines whether they are removed (i.e. not detected in plots, considered significant) or retained through model selection procedures by a monotonic non-linear transformation. For example, interactions among two factors measured in a response variable (e.g. density) in the raw scale will result in additive contributions in the log-scale if the underlying process is multiplicative and if all treatments differ in density. However, there is an important subset of interactions, here referred to as 'qualitative', where the statistical detection and visualization is robust to a monotonic nonlinear transformation. In the context of the BACI design used here, the latter group include two subgroups: G1, characterized a lack of a 'before effect' (i.e. density does not differ between control and impact before the MHW but it does, during or after the MHW); G2, characterized by a 'before effect' and where the temporal trend in density differ between the control and impact before the MHW. Therefore, G1 is the one providing the evidence of MHWs effects as the change in density between control and impact is restricted to the period when the MHW is experienced or immediately after it. We will point to the type of interaction in the results section.

3 | RESULTS

3.1 | Changes in mesozooplankton community structure

PERMANOVA analysis revealed a significant CI×P interaction for spring and autumn seasons (Table 3). Multilevel pairwise comparison tests between treatments highlighted no significant differences in the community structure between control and impact before the treatment. Significant differences in community structure were observed for the after periods (Supporting Information Appendix 2). Mesozooplankton community data dispersion did not differ significantly across P and CI for spring (*betadisper*, $F_{(3,126)} = 2.14$; $p = 0.10$) and autumn (*betadisper*, $F_{(3,90)} = 2.15$; $p = 0.12$) indicating homogeneous dispersion of the data. The CAP conducted on the spring and autumn seasons for the CI×P interaction showed strong evidence of separation among factor groups (Figure 2a–c). Specifically, while there was no significant difference in the community structure between the before control and the before impact, significant multivariate dispersion was observed between the after periods. This suggests that the combined effect CI and P resulted in distinct changes in community composition during these seasons. Temporal dissimilarities between before and after were represented along the first axis while dissimilarities between the control and impact

TABLE 3 PERMANOVA results for spring, summer, autumn and winter.

	Spring					Summer					Autumn					Winter				
	Df	SS	R²	F-value	p-value	Df	SS	R²	F-value	p-value	Df	SS	R²	F-value	p-value	Df	SS	R²	F-value	p-value
P	1	0.49	0.09	12.52	<0.001	1	0.39	0.1	8.97	<0.001	1	0.40	0.09	9.26	<0.01	1	0.28	0.09	8.03	<0.001
CI	1	0.09	0.02	2.42	<0.01	1	0.08	0.02	1.88	<0.05	1	0.06	0.01	1.49	0.10	1	0.08	0.03	2.38	<0.05
P×CI	1	0.14	0.02	3.47	**<0.001**	1	0.06	0.01	1.36	0.14	1	0.07	0.01	1.57	**<0.05**	1	0.01	0.003	0.26	0.91
Res	126	4.94	0.87			80	3.52	0.87			90	3.94	0.88			79	2.75	0.88		
Total	129	5.66	1.0			83	4.06	1.0			93	4.48	1.0			82	3.12	1.0		

Note: PERMANOVA were performed on a Bray–Curtis dissimilarity matrix with 999 permutations. ID was used as a random factor. Significant interactions are indicated in bold.

Abbreviations: CI, control/impact treatment; Df, degree of freedom; P, period; Res, residuals; SS, sum of squares.

treatments were represented along the second axis. Further analysis of the coordinate distances between paired control/impact treatments reinforces these findings; the coordinate distances before treatment clustered around zero, indicating minimal initial disparity. In contrast, after treatment revealed a deviation from zero, suggesting a significant shift. For example, in spring, *T. longicornis* and Echinodermata larvae dominated the community structure after the control treatment while *Acartia* spp. and Appendicularia were dominant after the MHW (Figure 2a). In autumn, Cyclopoida dominated the community structure of the after-control treatment while Harpacticoida were dominant after the MHW (Figure 2c).

PERMANOVA test showed no significant interaction between CI and P in the mesozooplankton communities for summer ($F_{(1,80)}=1.36$; $p=0.14$, Table 3) and winter ($F_{(1,79)}=0.26$; $p=0.91$, Table 3) and no clear separation can be observed on the CAP ordination plot (Figure 2b–d). Both the coordinate distances before and after treatments clustered around zero, indicating minimal disparity.

3.2 | Diversity and density responses to MHWs

We did not find any evidence of diversity and evenness response to MHWs. The interaction term (P×CI) for the Shannon diversity and Pielou's evenness was not retained in the model for copepods and for the complete mesozooplankton community, irrespective of season (Supporting Information Appendices 3 and 4).

We found evidence of mesozooplankton response to spring MHWs for 8 out of 13 taxa, with all the interactive patterns being consistent with a qualitative interaction and most of them not showing evidence of differences in density between control and impact before the MHW. For copepods, the best model did not include the interaction for Harpacticoida and Cyclopoida. The best model included the interaction for Calanoida (Supporting Information Appendix 5): Both treatments showed a significant increase in density throughout the periods (Figure 3e), and higher density was observed at the end of MHW compare to the control (7.51 vs. 6.70; $p<0.001$). The interaction was also retained in the model for 3 Calanoida taxa (*Acartia* spp., *Pseudo/Paracalanus* spp. and *T. longicornis*: Supporting Information Appendix 6). *Acartia* spp. density increased for both treatments throughout the periods (Figure 3a), and higher density was observed at the beginning (4.25 vs. 4.97; $p<0.05$) and end (4.91 vs. 6.09; $p<0.001$) of the MHW compare to the control. Copepoda nauplii followed the exact same trend (Figure 3d). *Pseudo/Paracalanus* spp. density increased during the impacted treatment (Figure 4b) with higher densities at the end (5.40 vs. 6.66; $p<0.001$) and after (6.04 vs. 6.58; $p<0.05$) the MHW compare to the control. Density remained constant during the control treatment. These two taxa responded positively to spring MHW, in contrast to *T. longicornis*. While *T. longicornis* density increased for both treatments (Figure 3c), smaller density was observed after the MHW (6.06 vs. 5.82; $p<0.01$) compare to the control.

For mesozooplankton taxa, the interaction effect was not included in the model for Chaetognatha, Cirripedia larvae and
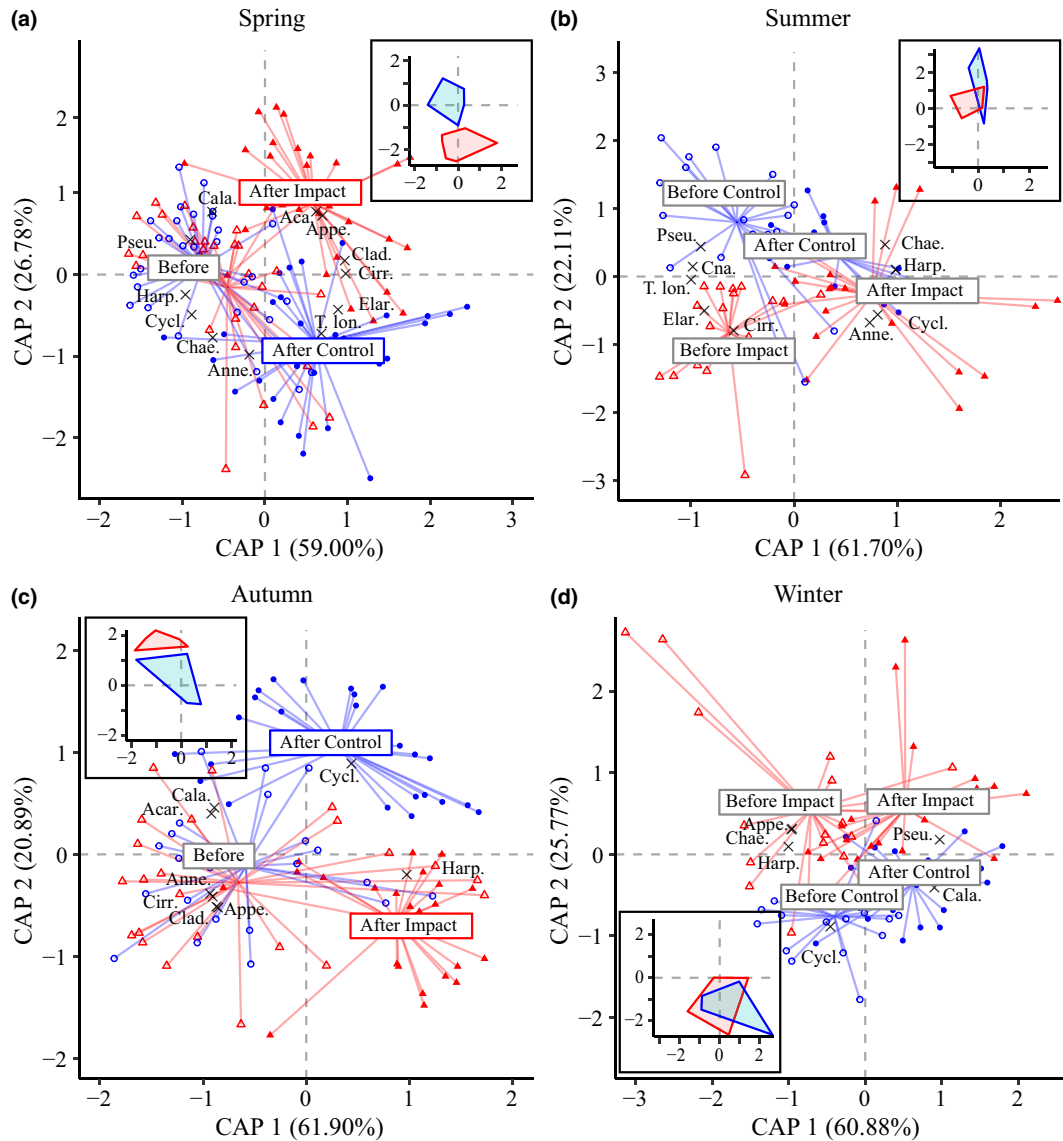
FIGURE 2 CAP on Bray–Curtis dissimilarity matrix of Hellinger transformed densities. Results of the CAP in (a) spring, (b) summer, (c) autumn and (d) winter showing canonical axes that best discriminate the structure from treatment-period interaction term with: Control-before (○) control-after (●) impact-before (△), impact-after (▲). The grey label indicates no significant difference between treatments while red and blue indicated significant differences. Taxa significantly correlated with the canonical axes are represented by the vectors (Scaling type I). Acar: Acartia spp., Anne: Annelida larvae, Appe: Appendicularia, Cala: Calanus spp., Chae: Chaetognatha, Cirr: Cirripedia larvae, Clad: Cladocera, Cna: Copepoda nauplii, Cycl: Cyclopoida, E.lar: Echinodermata larvae, Harp: Harpacticoida, Pseu: Pseudo/Paracalanus spp., T.lon; T. longicornis. Distances between the control/impact pairs before (blue) and after (red) are displayed in the inset for each panel. *X* and *Y* axes correspond to the ΔCAP2 and ΔCAP1 coordinates, respectively (Impact−Control).

Cladocera. Only Appendicularia, Annelida larvae and Echinodermata larvae showed significant interactions (Supporting Information Appendix 6; Figure 3h−i). A before effect was detected for Echinodermata larvae ($p < 0.001$) and Appendicularia ($p < 0.01$), indicating that the observed changes are not the result of a response to MHW. Therefore, only the changes observed for Annelida larvae could be associated with MHW; density increased throughout the control treatment but remained unchanged for the impacted treatment (Figure 3i). The interaction showed higher density at the start of the MHW compared to the control treatment (3.46 vs. 4.56;

$p < 0.01$). The trend reversed during the MHW with lower density at the end (5.17 vs. 4.85; $p < 0.05$) and after (5.84 vs. 5.08; $p < 0.01$) the event compared to the control.

In summer, most of the mesozooplankton taxa did not show any evidence of a response to MHWs and the interaction effect was included in the model for only two taxa, namely Cladocera and Echinodermata larvae (Figure 4l,m; Supporting Information Appendix 6). Interaction was qualitative and significant variations were observed between control and impact for both taxa at the end of the MHW. Specifically, Cladocera experienced an increase
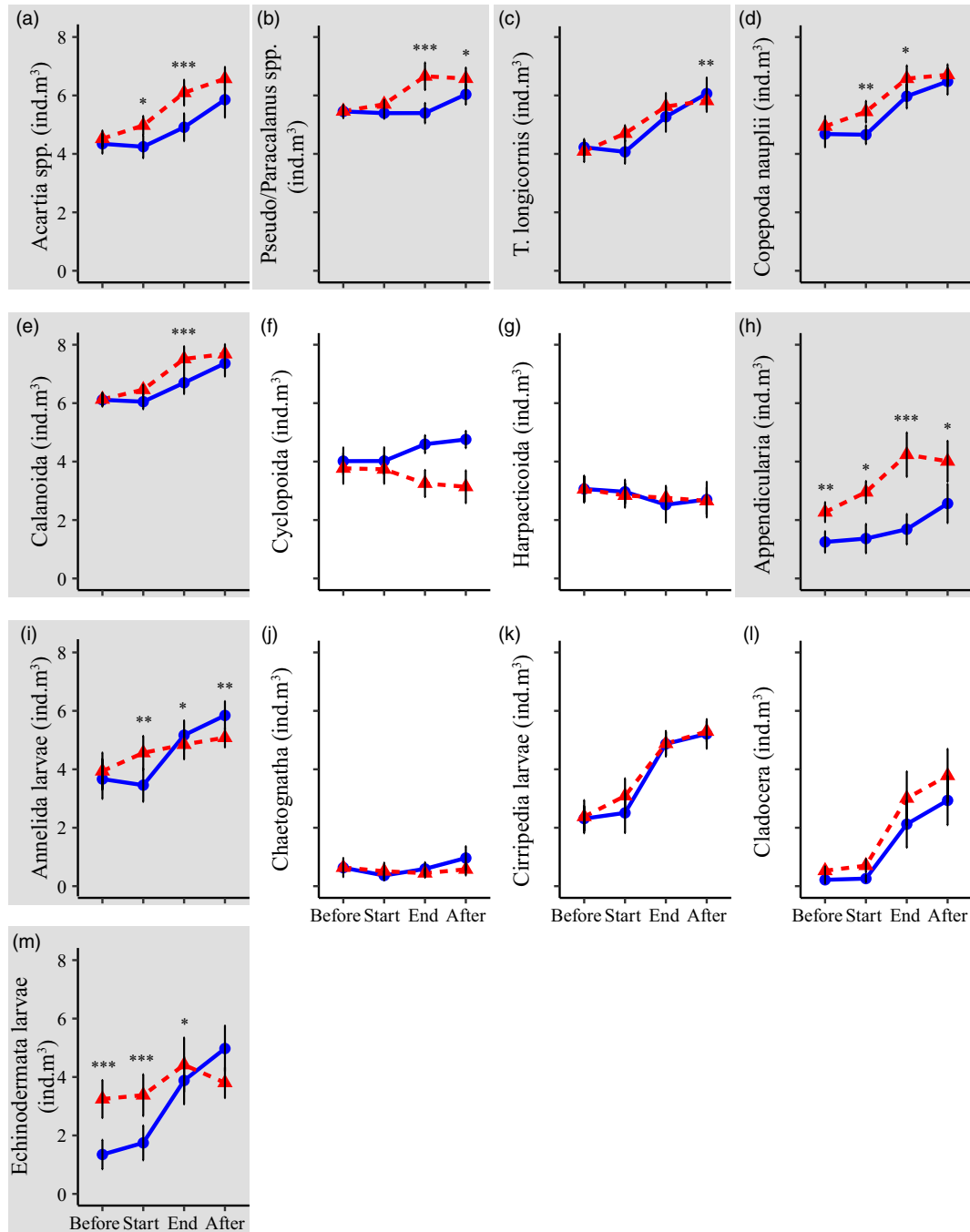
FIGURE 3 Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: Impact) or absence (●: Control) of spring MHWs. (a) *Acartia* spp., (b) *Pseudo/Paracalanus* spp., (c) *T. longicornis*, (d) Copepoda nauplii, (e) Calanoida, (f) Cyclopoida, (g) Harpacticoida, (h) Appendicularia, (i) Annelida larvae, (j) Chaetognatha, (k) Cirripedia larvae, (l) Cladocera, and (m) Echinodermata larvae densities. Values shown are the means (log-transformed) ± standard error for each period per ID. Grey shape indicate significant interactions. Asterisks represent significant difference between control and impact for each period: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

in density until the end of the MHW, after which their numbers decreased (Figure 4l). The density at the end of the MHW was higher compared to the control (6.03 vs. 4.33; $p < 0.001$). In contrast, Echinodermata larvae showed a decrease in density in both treatments (Figure 4m), with smaller density at the end of the MHW compared to the control (3.76 vs. 4.93; $p < 0.001$).

For the copepod community in autumn, the interaction term was retained in the model for Calanoida Harpacticoida and *Pseudo/Paracalanus* spp., and these interactions were all of a qualitative type (Figure 5). However, a before effect was detected for Calanoida ($p < 0.05$) and *Pseudo/Paracalanus* spp. ($p < 0.01$), indicating that the observed changes are not a result of a response to MHW (Figure 5b–e).
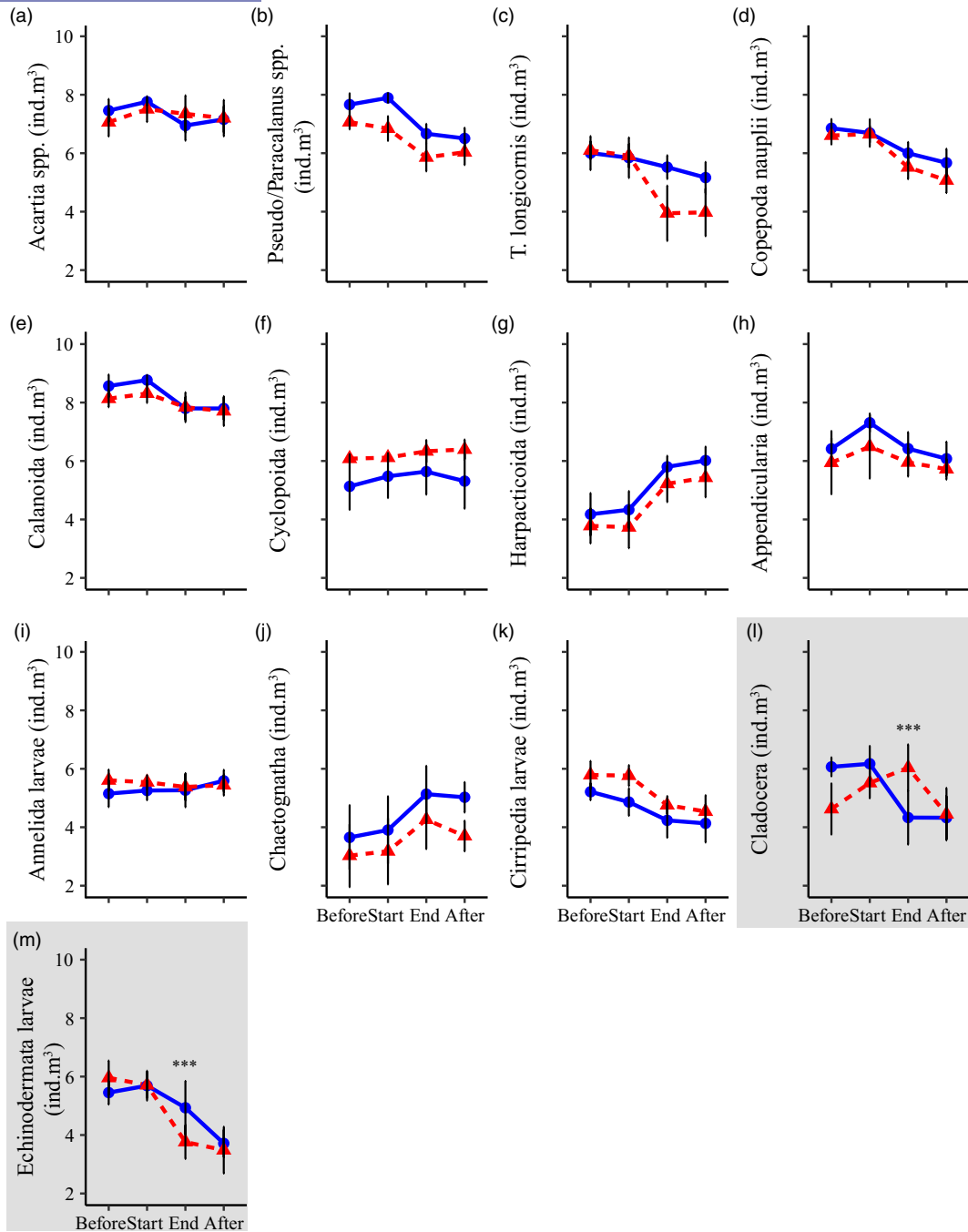
FIGURE 4 Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: Impact) or absence (●: Control) of summer MHWs. (a) *Acartia* spp., (b) *Pseudo/Paracalanus* spp., (c) *T. longicornis*, (d) Copepoda nauplii, (e) Calanoida, (f) Cyclopoida, (g) Harpacticoida, (h) Appendicularia, (i) Annelida larvae, (j) Chaetognatha, (k) Cirripedia larvae, (l) Cladocera, and (m) Echinodermata larvae densities. Values shown are the means (log transformed)±standard error for each period per ID. Grey shape indicate significant interaction. Asterisks represent significant difference between control and impact for each period: $p<0.05^{*}$, $p<0.01^{**}$, $p<0.001^{***}$. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

Therefore, Harpacticoida was the only copepod taxa to respond to autumn MHW; density increased during the impact treatment while it stayed constant during the control (Figure 6g). Pairwise comparisons showed higher density at the start (4.74 vs. 5.64; $p<0.01$), end (4.81 vs. 6.19; $p<0.001$), and after (4.98 vs. 6.25; $p<0.001$) the MHW compared to the control.

For mesozooplankton taxa, Annelida larvae, Cirripedia larvae and Cladocera showed significant evidence of response to autumn MHW. Annelida larvae density decreased for both treatments and was higher at the end of the MHW compared to the control (2.81 vs. 3.51; $p<0.001$) (Figure 5i). Cirripedia larvae density decreased for both treatments and pairwise comparisons showed higher density after the MHW (1.33 vs.
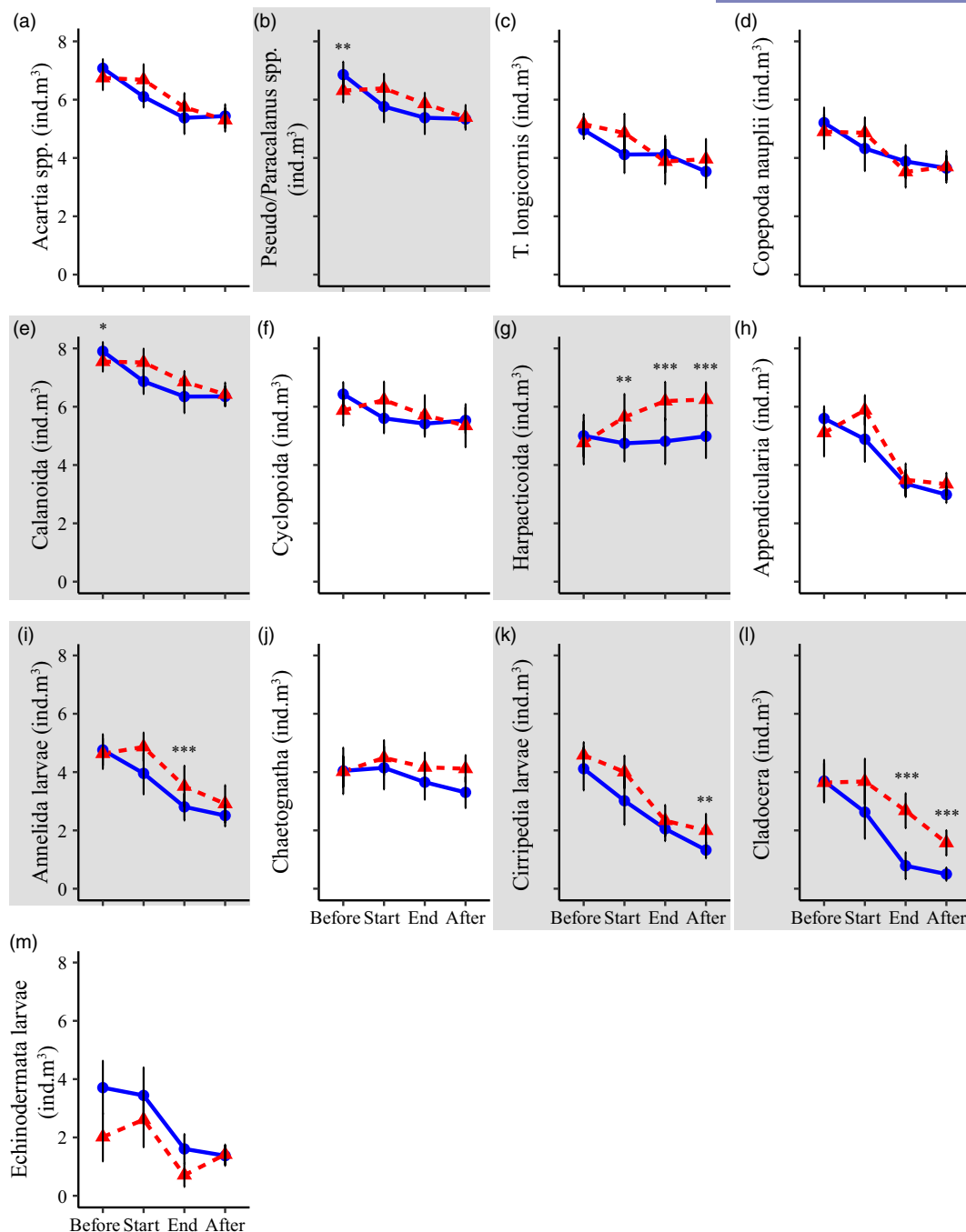
FIGURE 5 Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: Impact) or absence (●: Control) of autumn MHWs. (a) *Acartia* spp., (b) *Pseudo/Paracalanus* spp., (c) *T. longicornis*, (d) Copepoda nauplii, (e) Calanoida, (f) Cyclopoida, (g) Harpacticoida, (h) Appendicularia, (i) Annelida larvae, (j) Chaetognatha, (k) Cirripedia larvae, (l) Cladocera, and (m) Echinodermata larvae densities. Values shown are the means (log transformed) ± standard error for each period per ID. Grey shape indicate significant interaction. Asterisks represent significant difference between control and impact for each period: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

2.00; $p < 0.01$) compared to the control (Figure 5k). Cladocera density decreased for both treatments but to a much greater extent for the control (Figure 5l). Pairwise comparisons showed higher density at the end (0.78 vs. 2.68; $p < 0.001$) and after (0.50 vs. 1.57; $p < 0.001$) the MHW compared to the control.

In winter, most of the mesozooplankton taxa did not show evidence of a response to MHWs (11 out of 13 groups), and the interaction effect was included in the model for only two taxa, namely the copepod Cyclopoida and Harpacticoida. Cyclopoida density stayed constant during the control treatment but decreased during the MHW with lower densities after the MHW (3.41 vs. 4.60; $p < 0.05$; Figure 6f). A before effect was detected for Harpacticoida ($p < 0.01$) indicating that the observed changes are not a result of a response to MHW (Figure 6g).
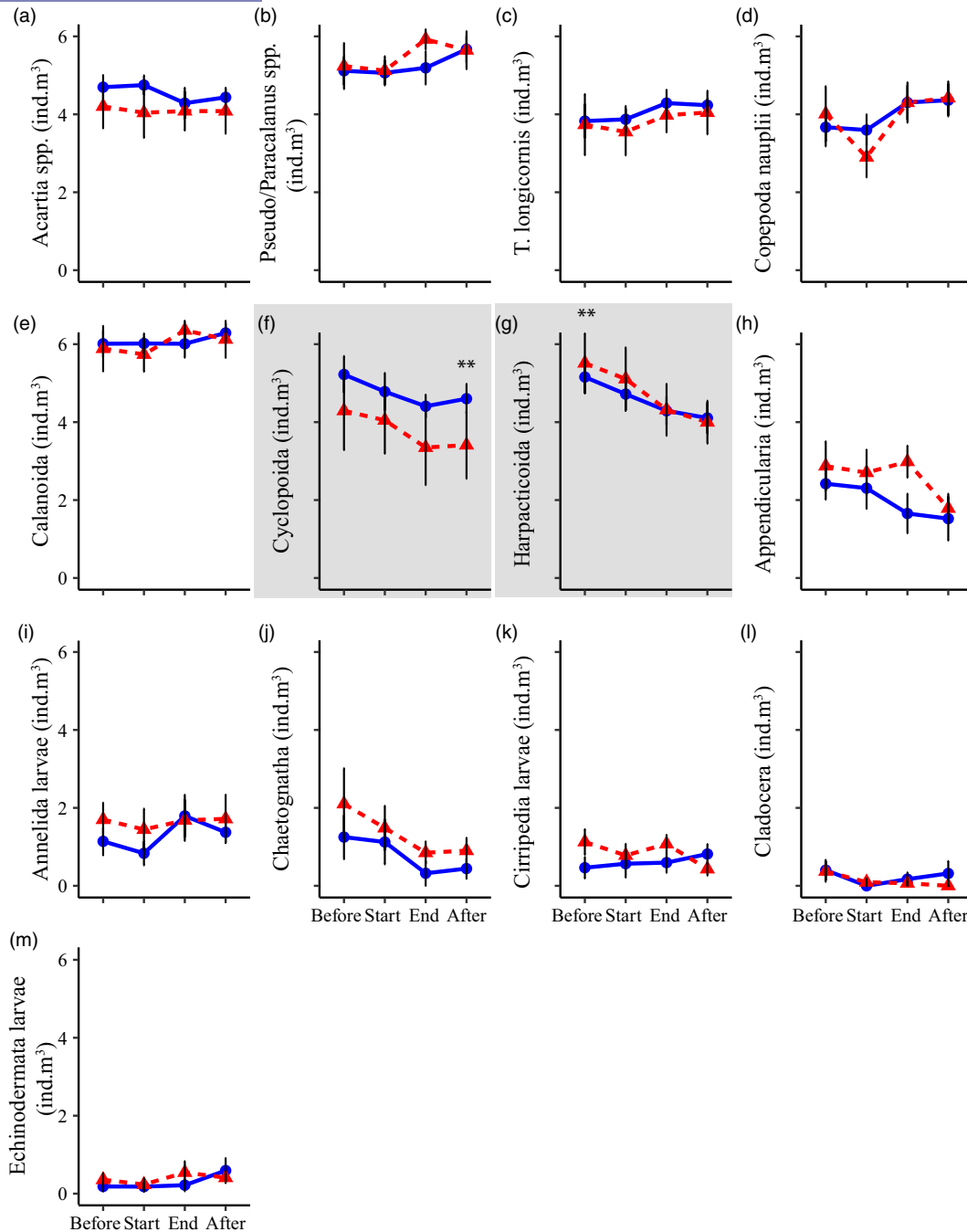
FIGURE 6 Results of the modified BACI design on the most abundant mesozooplankton taxa in presence (▲: Impact) or absence (●: Control) of winter MHWs. (a) *Acartia* spp., (b) *Pseudo/Paracalanus* spp., (c) *T. longicornis*, (d) Copepoda nauplii, (e) Calanoida, (f) Cyclopoida, (g) Harpacticoida, (h) Appendicularia, (i) Annelida larvae, (j) Chaetognatha, (k) Cirripedia larvae, (l) Cladocera, and (m) Echinodermata larvae densities. Values shown are the means (log transformed) ± standard error for each period per ID. Grey shape indicate significant interaction. Asterisks represent significant difference between control and impact for each period: $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. Models for each taxa were run using Gamma GLMMs with a log link or negative binomial function. The ID was included as a random factor.

4 | DISCUSSION

We examined the mesozooplankton community of the HR time series, during the most extensive seasonal MHWs recorded between 1975 and 2018. We found evidence of response to MHWs in both the structure of the community and the density of single taxa, particularly in the seasons of strongest temperature change, spring and autumn. In support of the community level response in spring, 8 of the 13 taxa showed variations in density during the MHW, yet only 6 were directly linked to it. Indeed, two taxa displayed changes before the MHW, which could not be directly associated with the event. Five taxa exhibited no response to the spring MHW. Likewise, the community-level response in autumn was supported by similar responses in 4 out of 13. Seven of the remaining taxa showed no

evidence of response to MHWs. Additionally, in two taxa, temporal changes were independent of the MHWs, as they occurred during the period before the MHW. There was no indication of a change in community structure related to MHW during summer and winter and few individual taxa were influenced. Because our study was based on intensive sampling of mesozooplankton organisms, which are characterized by short generation times (weeks to months), we were able to observe season-dependent responses to heatwave events.

4.1 | Seasonal response to MHWs

For spring, we observed a divergence in the community composition between the post-MHW and post-control periods. Following a period without MHW, the community was primarily dominated by *T. longicornis* and Echinodermata larvae and shifted after the MHW to a community dominated by *Acartia* spp. and Appendicularia with less Cyclopoida, Chaetognatha and Annelida larvae. Those results were supported by the positive response in density of the most important groups: Copepoda nauplii, Calanoida, *Acartia* spp., *Pseudo/Paracalanus spp* and Appendicularia. The dominance of Appendicularia is consistent with the reported quick response to short-term increases in temperature (Winder et al., 2017) and the positive effect of warming on gelatinous zooplankton (Winder et al., 2017). As MHW are expected to become more frequent in the coming decades (Hobday et al., 2016; Oliver, 2019) it is likely that Appendicularia will become more dominant in the German Bight. Unlike copepods, Appendicularia are able to feed on small particles, within the size range of the microbial loop (Acuña & Anadón, 1992). A shift to a dominance of Appendicularia could therefore significantly impact the microbial loop and subsequent energy transfer to higher trophic levels (Gorsky & Fenaux, 1998).

We hypothesised that spring MHWs would influence densities of mesozooplankton taxa, that are undergoing growth phase. We found that copepods (including *Acartia* spp., a cold-temperate taxa; Alvarez-Fernandez et al., 2012) responded positively to MHWs. This response is logical given that spring MHWs may not reach the thermal tolerance limits but instead result in faster growth rate or forward shifts in phenology. Copepod nauplii reach their maximum density in May in the North Sea (Atkinson et al., 2015), while Calanoida species exhibit strong seasonality with a growth phase in spring, followed by a peak in June–July (Atkinson et al., 2015; Greve et al., 2004; O'Brien et al., 2013). The effects on phenology would explain why density of Calanoida, *Acartia* spp., and Copepoda nauplii were higher during but not after the MHW (similarly, *T. longicornis* decrease in density after the MHW). Thus, it appears that these taxa reached their respective density maxima earlier in the impact than would be expected in a normal season. Seasonal shifts may also explain why Annelida larvae decrease in density at the end of the MHW events. In our samples, Annelida larvae are mostly spionids (Deschamps pers. Obs.), which appear to respond to warming with a delayed timing of occurrence (Mackas et al., 2012).

Similarly, we hypothesised that autumn MHW could lead to an extension and slower decline phase for species peaking in late summer or early autumn. As spring MHWs, the observed responses in autumn are also consistent with a phenological effect, with taxa exhibiting an extension of their seasonal peaks at the time when density typically decreases, except for Harpacticoida. For Harpacticoida, while the density remained stable throughout the control treatment, a sharp increase was observed during the MHW. In the North Sea, Harpacticoida reach their peak in late summer/autumn (Deschamps et al., 2023; Mortelmans et al., 2021). *Euterpina acutifrons* and *Microsetella* spp., two commonly found taxa in the HR times series, exhibit a seasonal peak in August (O'Brien et al., 2013). An autumn MHW may have therefore facilitated Harpacticoid copepods in the environment for a longer period than expected during a normal season. These responses are important as late summer and autumn MHWs characterized the seasonal pattern at HR, especially since the 1990s (Giménez et al., 2024).

It is important to highlight that some mesozooplankton taxa did not exhibit changes in density during spring or autumn MHW. In spring, Cyclopoida and Harpacticoida are notable examples. The lack of response could be linked to their phenological cycle. Indeed, At HR, Cyclopoida is predominantly composed of *Corycaeus anglicus* and *Oithona* spp. (mainly *O. similis* and *O. nana*). These species are known to reach their density peak towards the late summer or early autumn, similar to Harpacticoida (Deschamps et al., 2023; Mortelmans et al., 2021; O'Brien et al., 2013). The same reason might account for the absence of a response to autumn MHW for Copepoda nauplii, *Acartia* spp., and *T. longicornis*, as these taxa typically peak in summer (Deschamps et al., 2023). These observations suggest that the timing of copepod reproduction does not coincide with autumn MHW events, potentially minimizing the impact on their populations.

We did not find clear evidence of mesozooplankton community responses to winter and summer MHWs; interactive effects were observed in only a small number of groups. The lack of responses in most groups is logical in winter because of very low biological activity (van Beusekom & Diel-Christiansen, 2009) and the low phytoplankton productivity (Townsend et al., 1994) limiting mesozooplankton density in the North Sea (van Beusekom & Diel-Christiansen, 2009). In summer, we expected a shift in the copepod community with smaller taxa and warm water species becoming more abundant at the expense of large cold-water ones, driven by differences in thermal tolerance thresholds. However, the summer temperature recorded at HR exceeded 20°C only in August 1995, 2002 and 2006, which is still within the tolerance range known for most mesozooplankton species in the North Sea (e.g. *T. longicornis*: threshold temperature of 22.5°C; Halsband-Lenk et al., 2002). Therefore, we believe that the summer MHWs recorded from 1975 to 2018 may not have been sufficiently intense to adversely affect cold water taxa or promote warm water taxa. Given the projection that MHWs are expected to increase in intensity (Hobday et al., 2016; Oliver, 2019), our observations regarding the impact of summer MHW on mesozooplankton communities could change in the upcoming decades.

4.2 | Mechanisms driving mesozooplankton changes in response to MHWs

Different mechanisms may have driven the observed changes in density associated with MHWs. We cannot establish causal mechanisms but instead hypothesize about the potential drivers of the responses. For instance, temperature may have direct physiological impacts on metabolic, developmental and growth rates (e.g. copepod reproduction; Richardson, 2008), but also indirect effects. Copepod density is positively correlated with temperature especially in spring when the effect of temperature is much larger (Mortelmans et al., 2021). In the North Sea, copepod density peak occurs 11 to 52 days earlier for each 1°C increase (Beaugrand, 2004) and *Acartia clausii* (present in the HR time series) experienced a shift in the phenology of 16 days ahead for every 1°C increase (Atkinson et al., 2015). *A. clausii* always appears earlier in warm years in the English Channel (Plymouth L4 sampling site: Mackas et al., 2012) and both Copepoda nauplii and *A. clausii* experienced a forward shift in phenology in response to the 2016 MHW in Alaska (McKinstry et al., 2022). These studies strongly support the 'earlier when warmer' trend in copepods, which may also occur in response to short and acute temperature increase such as MHW. Likewise, favourable temperature may explain the reduced rate of decline observed in autumn, as expected from the positive effects of temperature on the duration of the seasonal plankton peaks (Mackas et al., 2012; McKinstry et al., 2022). The case of Cladocera taxa provides a clear illustration (i.e. density remained stable throughout the entire MHW period, but declined in the control years). Indeed, our results are consistent with the known occurrence of the tropical/subtropical Cladocera *Penilia avirostris* in the North Sea, which increases during warm autumn (Johns et al., 2005). In September 1999, when a prolonged MHW was detected in HR (i.e. 42 days: Giménez et al., 2024, see Table 1), sea surface temperature was 2–4°C higher than normal, leading to the rapid spatial expansion of *P. avirostris* (Johns et al., 2005).

In addition, mesozooplankton response to MHWs may be mediated by changes in other trophic levels. In the North Sea, characterized by wind and well-mixed conditions in the water column, warming drives phytoplankton metabolic rates and densities, which subsequently enhance mesozooplankton (Richardson, 2008; Richardson & Schoeman, 2004). In high latitudes, MHWs can lead to elevated chlorophyll concentrations (Noh et al., 2022) and can trigger intense phytoplankton blooms in nutrient-rich areas (Hayashida et al., 2020). Moreover, during the 'Blob', the MHW detected in the Pacific Ocean between 2013 and 2016, the phytoplankton community in the Gulf of Alaska transitioned from a dominance of diatoms to dinoflagellates (Arteaga & Rousseaux, 2023). In the North Sea, dinoflagellates are an important nutritional resource for copepods (Gentsch et al., 2009; Ianora et al., 2004). We could therefore hypothesize that MHWs would favour copepods through changes in the composition of planktonic prey. This shift in prey composition may have broader implications for the food web. Species that rely on planktonic prey less favoured by heatwaves may experience reduced food availability, potentially leading to shifts in their population dynamics. Conversely, species consuming copepods, such as fish larvae, might benefit from an increase in copepod abundance. Currently, it appears that MHWs primarily increase growth rates and shift the peak of abundance over small temporal scale. However, with the projected increase in the intensity, duration and frequency of MHWs in the coming decades (Oliver et al., 2018), we can hypothesize that copepod abundance peak could shift earlier in the season. This could lead to mismatches between the larvae of spring-spawning fish species and the peak abundance of their prey (Cushing, 1990), potentially impacting fish recruitment. For example, the temperature increases since the mid-1980s in the North Sea has altered the copepod community (e.g. abundance and timing) in ways that have reduced the survival of early life stages of cod (Beaugrand et al., 2003). Although these changes have been linked to long-term warming, prolonged heatwaves could have similar impacts. Therefore, understanding these changes is crucial for predicting the overall impact of marine heatwaves on marine biodiversity and food web structures.

4.3 | Challenges and future research

One of the great challenges in studying responses to MHWs in plankton is the limited capacity to perform field experiments, which would require sustained spatial sampling over long periods. Additionally, the occurrence of large heatwaves over wide spatial scales demands important efforts to conduct such replicated experiments. The length of our time series, in combination with the high frequency sampling of HR (Amorim et al., 2023), has enabled us to use a modified BACI design and overcome several challenges. First, we defined replicated control and heatwave-impacted years to test MHWs effects. Second, we defined controls within 5-year distance from the impacted treatments, crucial for accounting for potential decadal changes in plankton communities (Reid et al., 2016). We were also able to compare the density of key organisms at similar times of the year and explore season-dependent response. Finally, we noted that the type of interaction needed to establish clear evidence of a heatwave effect was robust to a change in measurement scale (Spake et al., 2023).

There are, however, some limitations and potential confounding factors that are relevant for the analysis. First, we did not include heatwaves running for more than two seasons because appropriate replicates within each season could not be established (e.g. 2006–2007 with two MHWs covering all seasons: Giménez et al., 2024). While such MHWs were rare, they may constitute the primary source of data elsewhere: In such cases, one would have to find control years lacking MHWs over long time periods. This might be difficult if the pool of potential control years contains some with several short MHWs. A possible solution to increase the number of control years could be to compare the planktonic responses in years with short MHWs against years without any event. Moreover, in a few cases, taxa showed significant differences in density between

control and impact years during the 'before' period, and we refrained from making conclusions about them. One may therefore restrict the application of BACI to periods of the year when the 'before' produces non-significant effects. In seasonal habitats, spring is perhaps the best period, because the "before" could be set at the end of winter when density is consistently low.

In summary, we found that planktonic communities can respond to MHWs of the scale of several weeks of duration, with average durations ranging from 30 to 50 days depending on the season. This was found through a BACI design applied over a time series of several decades. We also highlight the challenge of ascertaining whether the event is the sole cause of the observed changes. The HR time series helped us to implement a design to control the response to MHW and to replicate it over several events. In synthesis, applying such design to other time series, will help to quantify the effects of MHWs in other regions. This method could be challenging for organisms with long generation times, as their responses might take months rather than days or weeks. At these timescales, extensive replication is needed (due to additional environmental variables), and finding enough control replicates over several months without MHW events can be difficult. Nonetheless, our method can be applied for time series involving organisms with short generation times or life phases (i.e. larvae).

AUTHOR CONTRIBUTIONS

Margot Marie Deschamps was involved in conceptualization, formal analysis, investigation, methodology and writing. Maarten Boersma was involved in data curation, writing, validation and supervision. Luis Giménez was involved in conceptualization, data curation, methodology, writing, validation and supervision.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST STATEMENT

The authors 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 STATEMENT

The data underlying this article are available in the Data Publisher for Earth & Environmental Science PANGAEA, at https://doi.org/10.1594/PANGAEA.873032 for mesozooplankton counts and in Giménez et al. (2024) (table S1) for marine heatwaves timing and duration.

ORCID

Margot M. Deschamps https://orcid.org/0000-0002-0039-819X
Maarten Boersma https://orcid.org/0000-0003-1010-026X
Luis Giménez https://orcid.org/0000-0002-1472-2915

REFERENCES

Acuña, J. L., & Anadón, R. (1992). Appendicularian assemblages in a shelf area and their relationship with temperature. *Journal of Plankton Research*, *14*(9), 1233–1250. https://doi.org/10.1093/plankt/14.9.1233

Alvarez-Fernandez, S., Lindeboom, H., & Meesters, E. (2012). Temporal changes in plankton of the North Sea: Community shifts and environmental drivers. *Marine Ecology Progress Series*, *462*, 21–38. https://doi.org/10.3354/meps09817

Amorim, F. d. L. L. d., Wiltshire, K. H., Lemke, P., Carstens, K., Peters, S., Rick, J., Gimenez, L., & Scharfe, M. (2023). Investigation of marine temperature changes across temporal and spatial gradients: Providing a fundament for studies on the effects of warming on marine ecosystem function and biodiversity. *Progress in Oceanography*, *216*, 103080. https://doi.org/10.1016/j.pocean.2023.103080

Anderson, M., & Willis, T. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology*, *84*, 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2

Arteaga, L., & Rousseaux, C. (2023). Impact of Pacific Ocean heatwaves on phytoplankton community composition. *Communications Biology*, *6*, 263. https://doi.org/10.1038/s42003-023-04645-0

Atkinson, A., Harmer, R. A., Widdicombe, C. E., McEvoy, A. J., Smyth, T. J., Cummings, D. G., Somerfield, P. J., Maud, J. L., & McConville, K. (2015). Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Progress in Oceanography*, *137*, 498–512. https://doi.org/10.1016/j.pocean.2015.04.023

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Batten, S. D., Ostle, C., Hélaouët, P., & Walne, A. W. (2022). Responses of Gulf of Alaska plankton communities to a marine heat wave. *Deep Sea Research Part II: Topical Studies in Oceanography*, *195*, 105002. https://doi.org/10.1016/j.dsr2.2021.105002

Beaugrand, G. (2004). Monitoring marine plankton ecosystems. I: Description of an ecosystem approach based on plankton indicators. *Marine Ecology Progress Series*, *269*, 69–81. https://doi.org/10.3354/meps269069

Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, *426*(6967), 661–664. https://doi.org/10.1038/nature02164

Boersma, M., Greve, W., & Renz, J. (2017). Mesozooplankton abundances at time series station Helgoland Roads since 1974 [Dataset]. Alfred Wegener Institute—Biological Institute Helgoland. PANGAEA. https://doi.org/10.1594/PANGAEA.873032

Brodeur, R. D., Auth, T. D., & Phillips, A. J. (2019). Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Frontiers in Marine Science*, *6*, 212. https://www.frontiersin.org/article/10.3389/fmars.2019.00212

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Conner, M. M., Saunders, W. C., Bouwes, N., & Jordan, C. (2016). Evaluating impacts using a BACI design, ratios, and a Bayesian

approach with a focus on restoration. *Environmental Monitoring and Assessment*, *188*(10), 555. https://doi.org/10.1007/s10661-016-5526-6

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, *26*, 249–293. https://doi.org/10.1016/S0065-2881(08)60202-3

Deschamps, M. M., Boersma, M., Meunier, C. L., Kirstein, I. V., Wiltshire, K. H., & Di Pane, J. (2023). Major shift in the copepod functional community of the southern North Sea and potential environmental drivers. *ICES Journal of Marine Science*, *81*, 540–552. https://doi.org/10.1093/icesjms/fsad160

Di Pane, J., Boersma, M., Marques, R., Deschamps, M., Ecker, U., & Meunier, C. L. (2023). Identification of tipping years and shifts in mesozooplankton community structure using multivariate analyses: A long-term study in southern North Sea. *ICES Journal of Marine Science*, *81*, 553–563. https://doi.org/10.1093/icesjms/fsad071

Dummermuth, A., Wiltshire, K. H., Kirstein, I., Brodte, E.-M., Wichels, A., Shama, L., Bergmann, A., Hofmann, C., Fischer, P., Mölter, K., & Strasser, M. (2023). Marine Stations Helgoland and Sylt operated by the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research. *Journal of Large-Scale Research Facilities*, *8*(1), Article 1. https://doi.org/10.17815/jlsrf-8-184

Evans, R., Lea, M.-A., Hindell, M. A., & Swadling, K. M. (2020). Significant shifts in coastal zooplankton populations through the 2015/16 Tasman Sea marine heatwave. *Estuarine, Coastal and Shelf Science*, *235*, 106538. https://doi.org/10.1016/j.ecss.2019.106538

Gentsch, E., Kreibich, T., Hagen, W., & Niehoff, B. (2009). Dietary shifts in the copepod Temora longicornis during spring: Evidence from stable isotope signatures, fatty acid biomarkers and feeding experiments. *Journal of Plankton Research*, *31*(1), 45–60. https://doi.org/10.1093/plankt/fbn097

Giménez, L., Boersma, M., & Wiltshire, K. H. (2024). A multiple baseline approach for marine heatwaves. *Limnology and Oceanography*, *69*(3), 638–651. https://doi.org/10.1002/lno.12521

Gorsky, G., & Fenaux, R. (1998). The role of Appendicularia in marine food webs. In *The Biology of Pelagic Tunicates* (pp. 161–169). Oxford University Press.

Greve, W., Reiners, F., Nast, J., & Hoffmann, S. (2004). Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: Lessons from 30 years of single spot, high frequency sampling at the only off-shore Island of the North Sea. *Helgoland Marine Research*, *58*(4), 274–288. https://doi.org/10.1007/s10152-004-0191-5

Gubanova, A., Goubanova, K., Krivenko, O., Stefanova, K., Garbazey, O., Belokopytov, V., Liashko, T., & Stefanova, E. (2022). Response of the Black Sea zooplankton to the marine heat wave 2010: Case of the Sevastopol Bay. *Journal of Marine Science and Engineering*, *10*(12), Article 12. https://doi.org/10.3390/jmse10121933

Halsband-Lenk, C., Hirche, H.-J., & Carlotti, F. (2002). Temperature impact on reproduction and development of congener copepod populations. *Journal of Experimental Marine Biology and Ecology*, *271*(2), 121–153. https://doi.org/10.1016/S0022-0981(02)00025-4

Hartig, F., & Lohse, L. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (0.4.5) [Computer software]. https://CRAN.R-project.org/package=DHARMa

Hayashida, H., Matear, R., & Strutton, P. (2020). Background nutrient concentration determines phytoplankton bloom response to marine heatwaves. *Global Change Biology*, *26*, 4800–4811. https://doi.org/10.1111/gcb.15255

Helaouët, P., & Beaugrand, G. (2007). Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series*, *345*, 147–165. https://doi.org/10.3354/meps06775

Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuysen, J. A., Burrows, M. T., Donat, M. G., Feng, M., Holbrook, N. J., Moore, P. J., Scannell, H. A., Sen Gupta, A., & Wernberg, T. (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, *141*, 227–238. https://doi.org/10.1016/j.pocean.2015.12.014

Holbrook, N. J., Sen Gupta, A., Oliver, E. C. J., Hobday, A. J., Benthuysen, J. A., Scannell, H. A., Smale, D. A., & Wernberg, T. (2020). Keeping pace with marine heatwaves. *Nature Reviews Earth and Environment*, *1*(9), 482–493. https://doi.org/10.1038/s43017-020-0068-4

Ianora, A., Miralto, A., Poulet, S. A., Carotenuto, Y., Buttino, I., Romano, G., Casotti, R., Pohnert, G., Wichard, T., & Colucci-D'Amato, L. (2004). Aldehyde suppression of copepod recruitment in blooms of a ubiquitous planktonic diatom. *Nature*, *429*(6990), 403–407. https://doi.org/10.1038/nature02526

IPCC. (2022). *Climate change 2022: Impacts, adaptation and vulnerability Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Pörtner, H.-O., Roberts, D., Tignor, M., Poloczanska, E. S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B., & Ayanlade, S. (Eds.)). Cambridge University Press. https://doi.org/10.1017/9781009325844

Jacox, M. G., Alexander, M. A., Amaya, D., Becker, E., Bograd, S. J., Brodie, S., Hazen, E. L., Pozo Buil, M., & Tommasi, D. (2022). Global seasonal forecasts of marine heatwaves. *Nature*, *604*(7906), 486–490. https://doi.org/10.1038/s41586-022-04573-9

Johns, D. G., Edwards, M., Greve, W., & SJohn, A. W. G. (2005). Increasing prevalence of the marine cladoceran Penilia avirostris (Dana, 1852) in the North Sea. *Helgoland Marine Research*, *59*(3), 214–218. https://doi.org/10.1007/s10152-005-0221-y

Jones, T., Parrish, J. K., Peterson, W. T., Bjorkstedt, E. P., Bond, N. A., Ballance, L. T., Bowes, V., Hipfner, J. M., Burgess, H. K., Dolliver, J. E., Lindquist, K., Lindsey, J., Nevins, H. M., Robertson, R. R., Roletto, J., Wilson, L., Joyce, T., & Harvey, J. (2018). Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophysical Research Letters*, *45*(7), 3193–3202. https://doi.org/10.1002/2017GL076164

Joyce, P. W. S., Tong, C. B., Yip, Y. L., & Falkenberg, L. J. (2023). Marine heatwaves as drivers of biological and ecological change: Implications of current research patterns and future opportunities. *Marine Biology*, *171*(1), 20. https://doi.org/10.1007/s00227-023-04340-y

Loftus, G. R. (1978). On interpretation of interactions. *Memory & Cognition*, *6*(3), 312–319. https://doi.org/10.3758/BF03197461

Mackas, D. L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M. G., Batten, S., Richardson, A. J., Johnson, C., Head, E., Conversi, A., & Peluso, T. (2012). Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Progress in Oceanography*, *97–100*, 31–62. https://doi.org/10.1016/j.pocean.2011.11.005

McKinstry, C. A. E., Campbell, R. W., & Holderied, K. (2022). Influence of the 2014–2016 marine heatwave on seasonal zooplankton community structure and abundance in the lower Cook Inlet, Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, *195*, 105012. https://doi.org/10.1016/j.dsr2.2021.105012

Mortelmans, J., Aubert, A., Reubens, J., Otero, V., Deneudt, K., & Mees, J. (2021). Copepods (Crustacea: Copepoda) in the Belgian part of the North Sea: Trends, dynamics and anomalies. *Journal of Marine Systems*, *220*, 103558. https://doi.org/10.1016/j.jmarsys.2021.103558

Nielsen, J. M., Rogers, L. A., Brodeur, R. D., Thompson, A. R., Auth, T. D., Deary, A. L., Duffy-Anderson, J. T., Galbraith, M., Koslow, J. A., & Perry, R. I. (2021). Responses of ichthyoplankton assemblages to the recent marine heatwave and previous climate fluctuations in several Northeast Pacific marine ecosystems. *Global Change Biology*, *27*(3), 506–520. https://doi.org/10.1111/gcb.15415

Noh, K., Lim, H.-G., & Kug, J.-S. (2022). Global chlorophyll responses to marine heatwaves in satellite ocean color. *Environmental Research Letters*, *17*(6), 064034. https://doi.org/10.1088/1748-9326/ac70ec

O'Brien, T. D., Wiebe, P. H., & Falkenhaug, T. (2013). *ICES zooplankton status report 2010/2011* [report]. ICES Cooperative Research Reports (CRR). https://doi.org/10.17895/ices.pub.5487

Oliver, E. C. J. (2019). Mean warming not variability drives marine heatwave trends. *Climate Dynamics*, *53*(3), 1653–1659. https://doi.org/10.1007/s00382-019-04707-2

Oliver, E. C. J., Benthuysen, J. A., Darmaraki, S., Donat, M. G., Hobday, A. J., Holbrook, N. J., Schlegel, R. W., & Sen Gupta, A. (2021). Marine heatwaves. *Annual Review of Marine Science*, *13*(1), 313–342. https://doi.org/10.1146/annurev-marine-032720-095144

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*(1), 1324. https://doi.org/10.1038/s41467-018-03732-9

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reid, P. C., Hari, R. E., Beaugrand, G., Livingstone, D. M., Marty, C., Straile, D., Barichivich, J., Goberville, E., Adrian, R., Aono, Y., Brown, R., Foster, J., Groisman, P., Hélaouët, P., Hsu, H.-H., Kirby, R., Knight, J., Kraberg, A., Li, J., … Zhu, Z. (2016). Global impacts of the 1980s regime shift. *Global Change Biology*, *22*(2), 682–703. https://doi.org/10.1111/gcb.13106

Richardson, A. J. (2008). In hot water: Zooplankton and climate change. *ICES Journal of Marine Science*, *65*(3), 279–295. https://doi.org/10.1093/icesjms/fsn028

Richardson, A. J., & Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, *305*(5690), 1609–1612. https://doi.org/10.1126/science.1100958

Smith, K. E., Burrows, M. T., Hobday, A. J., King, N. G., Moore, P. J., Sen Gupta, A., Thomsen, M. S., Wernberg, T., & Smale, D. A. (2023). Biological impacts of marine heatwaves. *Annual Review of Marine Science*, *15*(1), 119–145. https://doi.org/10.1146/annurev-marine-032122-121437

Smith, K. E., Burrows, M. T., Hobday, A. J., Sen Gupta, A., Moore, P. J., Thomsen, M., Wernberg, T., & Smale, D. A. (2021). Socioeconomic impacts of marine heatwaves: Global issues and opportunities. *Science*, *374*(6566), eabj3593. https://doi.org/10.1126/science.abj3593

Spake, R., Bowler, D. E., Callaghan, C. T., Blowes, S. A., Doncaster, C. P., Antão, L. H., Nakagawa, S., McElreath, R., & Chase, J. M. (2023). Understanding 'it depends' in ecology: A guide to hypothesising, visualising and interpreting statistical interactions. *Biological Reviews*, *98*(4), 983–1002. https://doi.org/10.1111/brv.12939

Steinberg, D. K., & Landry, M. R. (2017). Zooplankton and the ocean carbon cycle. *Annual Review of Marine Science*, *9*(1), 413–444. https://doi.org/10.1146/annurev-marine-010814-015924

Townsend, D. W., Cammen, L. M., Holligan, P. M., Campbell, D. E., & Pettigrew, N. R. (1994). Causes and consequences of variability in the timing of spring phytoplankton blooms. *Deep Sea Research Part I: Oceanographic Research Papers*, *41*(5–6), 747–765. https://doi.org/10.1016/0967-0637(94)90075-2

Underwood, A. (1991). Beyond BACI: Experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Marine and Freshwater Research*, *42*(5), 569. https://doi.org/10.1071/MF9910569

van Beusekom, J. E. E., & Diel-Christiansen, S. (2009). Global change and the biogeochemistry of the North Sea: The possible role of phytoplankton and phytoplankton grazing. *International Journal of Earth Sciences*, *98*(2), 269–280. https://doi.org/10.1007/s00531-007-0233-8

Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D., & Lindeberg, M. (2021). Changes in rocky intertidal community structure during a marine heatwave in the Northern Gulf of Alaska. *Frontiers in Marine Science*, *8*, 115. https://doi.org/10.3389/fmars.2021.556820

Wiltshire, K. H., Kraberg, A., Bartsch, I., Boersma, M., Franke, H. D., Freund, J., Gebühr, C., Gerdts, G., Stockmann, K., & Wichels, A. (2010). Helgoland roads, North Sea: 45 years of change. *Estuaries and Coasts*, *33*(2), 295–310. https://doi.org/10.1007/s12237-009-9228-y

Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B. F. J., & Boersma, M. (2008). Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland roads. *Limnology and Oceanography*, *53*(4), 1294–1302. https://doi.org/10.4319/lo.2008.53.4.1294

Winder, M., Bouquet, J.-M., Rafael Bermúdez, J., Berger, S. A., Hansen, T., Brandes, J., Sazhin, A. F., Nejstgaard, J. C., Båmstedt, U., Jakobsen, H. H., Dutz, J., Frischer, M. E., Troedsson, C., & Thompson, E. M. (2017). Increased appendicularian zooplankton alter carbon cycling under warmer more acidified ocean conditions. *Limnology and Oceanography*, *62*(4), 1541–1551. https://doi.org/10.1002/lno.10516

Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 1–574). https://doi.org/10.1007/978-0-387-87458-6_1

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix 1. Studies of MHW effect on marine communities involving time series (>2 years).

Appendix 2. Multilevel pairwise comparison results table for spring and autumn.

Appendix 3. Model selection results (AICc values) for zooplankton and copepod Shannon diversity index in response to treatment (CI), period (P) and pair identity (ID).

Appendix 4. Model selection results (AICc values) for zooplankton and copepod Pielou's evenness in response to treatment (CI), period (P) and pair identity (ID).

Appendix 5. Model selection results (AICc values) for Cyclopoida, Harpacticoida and Calanoida abundances in response to treatment (CI), period (P) and pair identity (ID).

Appendix 6. Model selection results (AICc values) for taxa abundances in response to treatment (CI), period (P) and pair identity (ID).