LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–15

doi: 10.1002/lno.70012

RESEARCH ARTICLE

Heatwave intensity drives eco-physiological responses in infaunal bivalves: A mesocosm experiment

Maren A. Staniek[1,2] **Christian Pansch**[3] **Lisa N. S. Shama**[4] **Knut Mehler**[4] **Anna Steinmann**[4] **Jack J. Middelburg**[5] **Lukas Meysick**[2,6*]

[1]Utrecht University, Utrecht, The Netherlands; [2]Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany; [3]Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi University, Turku, Finland; [4]Coastal Ecology Section, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Wadden Sea Station Sylt, List, Germany; [5]Department of Earth Sciences, Utrecht University, Utrecht, The Netherlands; [6]Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB), Oldenburg, Germany

Abstract

Marine heatwaves are increasing globally in intensity and duration. To investigate the potential consequences for coastal ecosystems, the effects of short-term heat stress must be better understood. This study examined eco-physiological responses in two common intertidal bivalves, *Cerastoderma edule* and *Macoma balthica*, to different heatwave intensities in a mesocosm experiment under near-natural environmental conditions. Single-species assemblages were exposed to a 15-d heatwave of either +2.8°C (mild heatwave) or +4.4°C (strong heatwave) above ambient temperatures. Survival and condition were monitored, and filtration rates were measured before and during heatwave exposure to investigate feeding behavior. Bivalve respiration rates were measured before, during, and after heatwave exposure as a proxy for metabolic responses. For *C. edule*, we found significantly elevated filtration rates during the mild but not the strong heatwave. For *M. balthica*, survival was similar across treatments, but marine heatwaves had a significant effect on the condition index (tissue/shell mass ratio). During heatwave exposure, respiration rates were similar across treatments for both species. However, following the heatwaves, bivalves previously exposed to a strong heatwave showed lower respiration rates compared to those exposed to an ambient or a mild heatwave. This study revealed that short-term heatwaves can have persisting negative effects on bivalve metabolism and that the two species responded differently to the heatwave intensities. Further research is needed on the potential long-term effects of marine heatwaves on intertidal fauna and their capacity to continue providing crucial ecosystem services.

Marine heatwaves are increasing in frequency, intensity, and duration globally because of anthropogenic climate change and the associated increase in sea surface temperature (SST; Frölicher et al. 2018; Oliver et al. 2021). In the North Sea and adjacent systems such as the Wadden Sea, SST increases have been significant, with +0.3°C to +0.7°C per decade on average, and the frequency of extremely hot days has increased more strongly than in other Eastern Atlantic coasts (Lima and Wethey 2012). The Wadden Sea, a UNESCO World Heritage Site, has one of the largest coherent intertidal areas globally and exceptionally high biodiversity (Reise et al. 2010). The increase in heatwaves and their potential implications for Wadden Sea ecosystems and key species has recently received considerable attention within the scientific community (Engel et al. 2020; Smale et al. 2019; Wethey and Woodin 2022), as well as within

---

*Correspondence: lukas.meysick@hifmb.de

Associate editor: Maren Striebel

Data Availability Statement: All data is available in Supporting Information; Tables S1–S4 will be linked to PANGEA (https://www.pangaea.de/) citations following their final acceptance.

Special Issue: Mesocosms: Bridging the Gap Between In-Situ and Laboratory Studies. *Edited by: Christopher Cornwall, Christian Pansch-Hattich, Maren Striebel, Jens Nejstgaard and Deputy Editors Julia C. Mullarney, Steeve Comeau, and Elisa Schaum.*

advisory and summary papers for policymakers (Heron et al. 2020; Philippart et al. 2017; Smith et al. 2023). Although organisms living in intertidal areas are naturally exposed to highly fluctuating temperature patterns, sudden increases in temperature, such as during a heatwave, can constitute a severe additional stressor that decreases organism fitness or even leads to mass mortalities (Domínguez et al. 2021; Macho et al. 2016). This is especially true for sessile benthic species with limited avoidance capacities (Pansch et al. 2018; Zhou et al. 2022), for species constrained to the surface sediment layer, and for those living in the upper intertidal zone where the substratum falls dry for several hours a day and for which temperature fluctuations can generally be more extreme compared to subtidal habitats (Hesketh and Harley 2022; Somero 2002).

In the Wadden Sea, with its extensive intertidal areas, suspension feeders play a major role in energy and nutrient flows linking pelagic and benthic food webs. The common cockle (*Cerastoderma edule*) and the Baltic clam (*Macoma balthica*) are infaunal bivalves that are prominent members of intertidal communities. *Cerastoderma edule* is a filter feeder that lives just below the sediment surface and contributes substantially to bioturbation (Flach 1996), nutrient circulation, and water filtration (Carss et al. 2020). The metabolic activity of *C. edule* is assumed to increase with increasing temperatures in the context of seasonal acclimatization (Boyden 1972; Newell and Bayne 1973; Smaal et al. 1997). Recently, Zhou et al. (2022) reported increased respiration and mortality for *C. edule* under heat stress. However, potential physiological responses to short-term heat stress, such as during a marine heatwave, are still not fully understood.

In contrast to *C. edule*, *M. balthica* burrows deeper (down to 10 cm) in the sediment and has both a filter-feeding and a deposit-feeding mode. Among other functions, *M. balthica* plays an important role in bioturbation and nutrient cycling (Michaud et al. 2006). Compared to other bivalve species, *M. balthica* is considered to be relatively vulnerable to high temperatures, with a lower heat tolerance limit than *C. edule* (upper boundary of tolerance range at 16.9°C for *M. balthica* and 32.9°C for *C. edule* according to van der Veer et al. (2006)). *Macoma balthica* has been observed to reproduce less, lose weight, and show higher mortality following above-average seasonal temperatures (Beukema et al. 2009). Further, Pansch et al. (2018) found that the cumulative heat stress of consecutive heatwaves causes significant biomass loss and mortality in *M. balthica*. While metabolic responses of *M. balthica* to different temperatures were previously studied in the context of seasonality (Jansen et al., 2007a; Kennedy and Mihursky 1972), much less is known about the potential responses to short-term thermal stress. However, there are indications that sudden warming can lead to overly elevated physiological activity in *M. balthica*, ultimately leading to starvation (Hummel et al. 2000; Jansen et al., 2007a).

In the present study, we conducted a mesocosm experiment to investigate the potential effects of heatwaves on survival, condition, feeding activity (filtration rates) and metabolic activity (respiration rates) of *C. edule* and *M. balthica*. Using a near-natural mesocosm system (unfiltered flow-through seawater, tidal simulations, and a natural day–night light cycle) enabled more accurate predictions of organism and ecosystem responses to environmental changes than would be possible in constant, controlled laboratory conditions. Bivalves were exposed to one of three SST scenarios computed using a local climatological time series: an ambient treatment reflecting natural seasonal temperature variation without a heatwave and two heatwave treatments containing a single 15-d heatwave event each, one reaching +2.8°C above ambient (mild heatwave) and the other +4.4°C above ambient (strong heatwave). The aims of this study were threefold: (i) to quantify and implement representative heatwave events for the area based on a local temperature time series, (ii) to monitor the survival and condition (biomass, size, condition index [CI]) of both bivalve species, and (iii) to measure filtration rates of single-species assemblages as well as respiration rates in response to heatwave exposure.

For both species, we hypothesized that eco-physiological response patterns to heatwave stress would differ from those documented for seasonal temperature changes or mean (climatological) warming in the scientific literature due to the sudden temperature onset of heatwaves. Whereas a mild heatwave was expected to induce elevated filtration and respiration activity, stress in response to the strong heatwave was anticipated to negatively impact biomass, CI, and even survival.

Methods

Study area

The experiment was conducted on the island of Sylt, which stretches along the North Sea shore of Germany and Denmark. The research site is characterized by a semidiurnal tide with a range of 1.8–2.0 m (Blossier et al. 2017) and by a salinity ranging from 24 (winter) to 32 (summer) (van Beusekom et al. 2008). Seasonal mean SST ranges from approximately 3°C (winter) to 17.5°C (summer); the annual mean SST is 10°C (period: 1991–2019) and has increased by 0.31°C per decade since 1962 (de Amorim et al. 2023). In our experiment, we collected sediment and organisms from the study area and aimed to mimic its environmental conditions using the methodologies outlined below.

Climatological mean and historical heatwaves

To design the experimental temperature treatments, a climatological baseline of daily average water temperatures was calculated based on a 20-yr time series (February 2001–June 2020) of SSTs from around Sylt. The time series is based on surface water temperatures monitored daily by two buoys off the island coast (List1: 55°3′15.6″N, 8°23′25.2″E for the years 2001–2011 and BunkersHill: 54°4′30″N, 8°16′18″E for 2011–2020) using a 3-d interpolation. Marine heatwave events were extracted from the time series using the heatwaveR package (Schlegel and Albertus 2018) following the definitions of Hobday et al. (2016) and Hobday et al. (2018). By these definitions, a temperature abnormality is identified as a heatwave event if water temperatures exceed a high percentile threshold (here: 90%) of the climatological baseline for a minimum of five consecutive days. Recorded heatwaves in the study area are shown in Fig. 1, including their length and intensity for each year of the time series, as well as the deviation of each year's annual mean temperature from the climatological annual mean (i.e., mean across the 20-yr time series). For a full list of the recorded historical heatwaves and their individual characteristics, *see* Supporting Information Table S1 and Supporting Information Fig. S1 for annual temperature time series by individual years.

Experimental heatwave design

Following the time series and historical heatwave analyses, three experimental temperature treatments considered representative of the study area were computed: (i) an ambient temperature treatment reflecting natural temperature variability, (ii) a mild heatwave treatment, and (iii) a strong heatwave treatment. The three temperature treatments were randomly assigned to a total of 12 mesocosm tanks (*see* experimental set-up below) in four replicate blocks. The experiment started on June 1st and was terminated on August 24th, 2022.

Water temperatures in the mesocosms were set to reflect field temperatures (ambient), as measured twice a week in the Sylt-Rømø Bight throughout the experiment (Rick et al. 2023). However, only field temperatures falling between the climatological baseline and its upper 90th percentile were adopted for the experiment to avoid unwanted heatwave exposure and cold conditions (Supporting Information Fig. S2).

Both heatwave treatments followed ambient temperatures over the course of the experiment and included a deliberately induced 15-d heatwave event occurring between July 24th and August 8th, 2022. This duration corresponds to the upper quantile of summer heatwave duration recorded for the area (14.8 d for May–August) with a 9-d peak temperature plateau plus 3 d onset and offset. On- and offset are defined as the temperature increase and decrease phases above the upper 90th percentile threshold (Hobday et al. 2016), which was at approximately 21°C on July 24th and August 8th. In the mild heatwave treatment, peak water temperatures reached 2.8°C above ambient (22.3°C with on- and offset rate at 0.4°C per day; ambient was at 19.5°C), resulting in a cumulative heatwave intensity that corresponds to the historical median. For the strong heatwave, the upper quantile of historical cumulative intensity was selected, resulting in peak water temperatures of 4.4°C above ambient

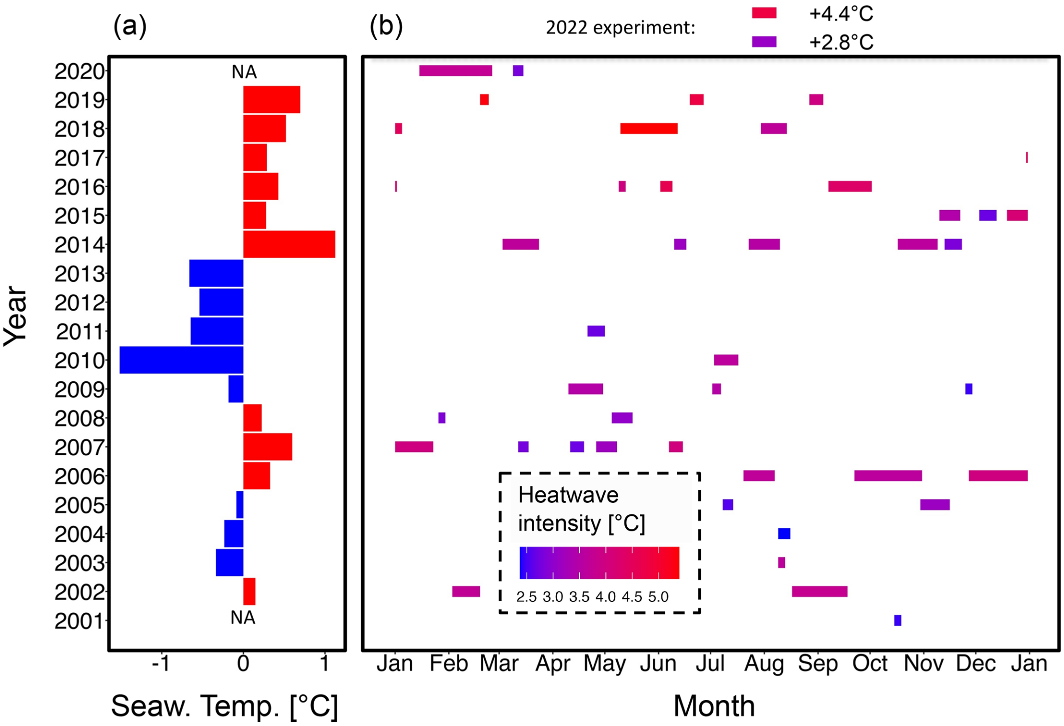

Fig. 1. Deviations of annual mean seawater temperature (Seaw. Temp.) from a 20-yr (2001–2020) mean (**a**), and heatwave durations and intensities in different months over the 20-yr record (**b**). The years 2001 and 2020 are excluded from (**a**) as the data did not cover the entire year. The heatwave intensities in (**b**) represent the maximum amplitude above the climatological value. The mild (+2.8°C above ambient) and strong (+4.4°C above ambient) heatwave treatments during the experiment (timing and intensity) are illustrated above the panels.

(23.9°C, with on- and offset rate at 1°C per day, *see* also: Supporting Information Methods S1).

Experimental set-up

The study was conducted using 12 mesocosm tanks located at the Wadden Sea Station Sylt (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar-und Meeresforschung 2023; Supporting Information Fig. S3a,b). Each tank is an independently operating unit connected to a custom software system for tidal simulation and temperature control. The mesocosms with a water volume of 1800 L were designed as a flow-through system sourcing unfiltered local seawater. The water exchange rate was set to 1250 L d^{-1}, implying a residence time of 1.4 d for this experiment. All tanks feature a moving platform for tidal simulation, translucent top lids, and built-in Multi-Parameter Measurement Systems that inter alia measure temperature every 30 min (Hydrolab DS5X Probe, OTT Messtechnik GmbH, Kempten Germany). Temperature is regulated through the software (Labview based, 4H-Jena engineering, Jena, Germany) and via external coolers (Titan 2000 or Titan 4000 Aqua Medic, Bissendorf, Germany) and internal heaters (Titanium heater 500 W, Aqua Medic, Bissendorf, Germany, *see* Pansch et al. 2016, for a full technical description of the mesocosms).

Taking a nested experimental design approach, each of the 12 tanks contained single-species assemblages of *C. edule* and *M. balthica* as well as a bare sediment control. To house these assemblages, clear plastic containers of 10 L volume ($h = 22.5$ cm) were modified with garden fleece-covered holes drilled into the lower half of both short sides to enable water exchange between sediment and tank water during the tidal cycle (Supporting Information Fig. S3c). Containers were filled (11 cm sediment column) with sieved (< 1000 μm), freshwater-rinsed, and homogenized sediment (fine sand with mud content, $D_{50} \approx 200\ \mu$m) collected from the upper intertidal (55°1′32.8″N, 8°26′6.0″E) in April 2022. For this experiment, all tanks simulated semidiurnal tides (12 h 14 min period) where the sediment surface of the containers fell dry during low tide. To record temperature exposure of the organisms throughout the experiment, two HOBO® loggers were installed in each tank: one buried in the upper sediment (within the top 5 cm, corresponding roughly to the burrowing depth of the bivalves), and another installed on top of the sediment. The loggers recorded temperature at 5-min intervals for the full duration of the experiment.

Organisms were collected from the same area as the sediment in May 2022 and stored in sediment-filled containers within the mesocosms set to ambient temperature until further handling. Organisms were then wet weighed and introduced into their destination containers for the experiment within 48 h. To that end, initial organism abundances and total wet weights were kept constant across replicates, with *C. edule* assemblages each consisting of eight individuals of 53.5 ± 0.7 g (mean ± SD) wet weight per container, and *M. balthica* assemblages consisting of 24 individuals of 28.8 ± 0.1 g wet weight per container. Wet weights of both *C. edule* and *M. balthica* corresponded to an ash-free dry weight of 35.7 g m^{-2}, and abundances corresponded to a density of 119 individuals m^{-2} (*C. edule*) and 357 m^{-2} (*M. balthica*), mimicking natural densities found in the study area. Additional individuals of *C. edule* and *M. balthica* were stored within subtidal containers in the same mesocosm tanks for respiration measurements (*see* respiration methods below).

Response traits

As indicators for potential changes in bivalve ecophysiology, we recorded various response traits either of the single-species assemblages or at the individual level over the course of the experiment. For both species, we monitored total abundance and total biomass per assemblage at initialization and termination of the experiment, as well as shell length (hereafter: size) and CI at termination. Additionally, we measured assemblage filtration rates and individual respiration rates at different time points (Fig. 2): (i) "pre-treatment" prior to any heatwave exposure, functioning as a baseline (sampling conducted on June 25th for respiration and July 19th for filtration), (ii) "mid-treatment" during heatwave exposure (sampling conducted between July 31st and August 2nd for respiration and between August 2nd and 3rd for filtration), and (iii) "post-treatment" encompassing the recovery phase and potential persisting effects of heatwave exposure (sampling conducted on August 22nd and August 23rd for respiration only).

Survival and condition

After the experiment was terminated, sediment was sieved through a 1000 μm mesh and bivalves were collected to obtain their post-experiment abundances and wet weights (tissue plus shell) per container (Supporting Information Table S2). Survival rates (%) and total biomass changes were calculated for *C. edule* and *M. balthica* assemblages based on differences between abundances and wet weights at initialization and termination. Bivalves were then frozen (−20°C) for subsequent analyses. Specifically, size as well as tissue and shell dry weight (after drying at 60°C for 48 h) were determined for each bivalve (Supporting Information Table S3). Condition index, a commonly used indicator of the physiological state of bivalves (e.g., Nilin et al. 2012; Norkko and Thrush 2006), was calculated using the formula of Lucas and Beninger (1985):

$$\mathrm{CI} = \frac{\text{dry tissue weight}}{\text{dry shell weight}} \times 100 \qquad (1)$$

Filtration rates

In this study, filtration rates are defined as the removal of chlorophyll *a* (Chl *a*) from incubation water per unit time and presented as μg Chl *a* $L^{-1}\ h^{-1}$. Filtration rates were measured in situ per single-species assemblage for both species, using their host containers as incubation chambers within the mesocosm tanks to minimize disturbance. To this end, three

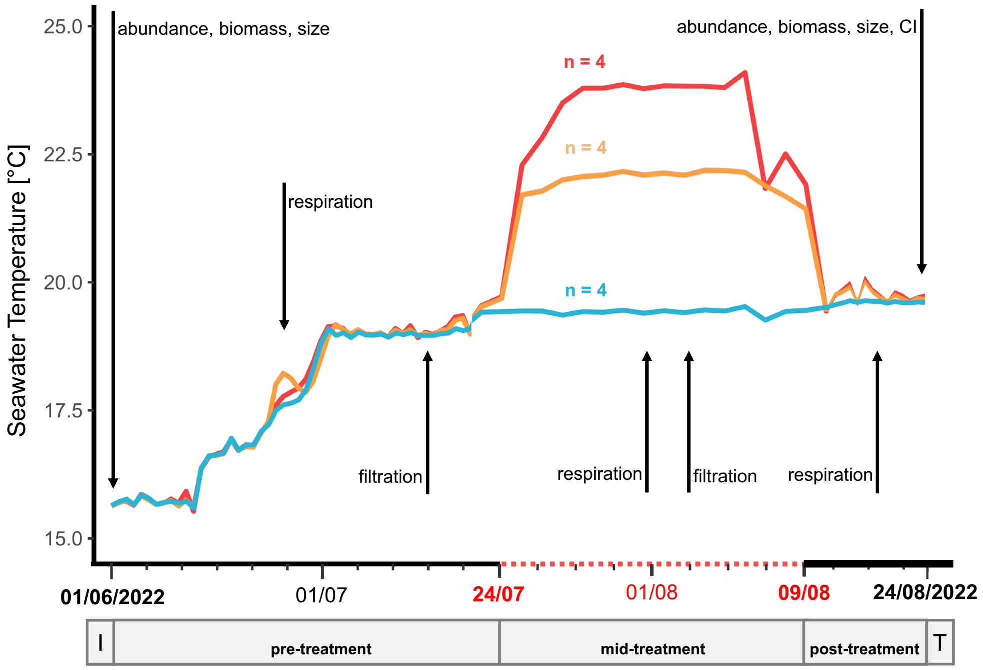

Fig. 2. Seawater temperature profiles monitored by the MPMS during the mesocosm experiment, including measurement times indicated with arrows. Temperature treatments are visualized by the colored lines, as ambient (blue), a mild (+2.8°C above ambient, orange) and a strong (+4.4°C above ambient, red) heatwave. "CI" = condition index, "I" = initialization of the experiment, "T" = termination. Note that the time scale for the mid-treatment stage is visually enlarged (red dotted line). MPMS, Multi-Parameter Measurement Systems.

replicate mesocosms per treatment were randomly selected for measurements, and tidal platforms were positioned so that the container walls reached 2–3 cm out of the tank water, creating incubation water columns of constant volume (Supporting Information Fig. S3b). Air-stones were installed on the inner wall of each measured container (single-species assemblages and sand controls) to ensure constant mixing and distribution of the algae during measurements. A spike of lab-cultivated *Rhodomonas salina* algae monoculture (Supporting Information Methods S2) was added by replacing 400 mL of the incubated water, resulting in an average initial Chl *a* concentration of 15.2 μg L^{-1} ± 3.7 (SD), relative to a background Chl *a* concentration of 0.95 ± 0.37 μg L-1 (mean ± SD, measured mid-treatment). Following the spike addition, two types of water samples were taken regularly to monitor Chl *a* concentration over time: (1) At the beginning, after 20, and after 60 min, 100 mL samples were taken to determine Chl *a* concentrations via spectrophotometric analysis (750, 663, 645, and 630 nm wavelengths, UVIKON© XS UV/Vis) and following the method of Jeffrey and Humphrey (1975) (Supporting Information Methods S3). (2) Additional 50 mL samples were taken in 10-min intervals for 1 h to monitor the relative change in Chl *a* concentration, analyzing the unprocessed samples immediately using a bbe© AlgaeLabAnalyser (ALA, 370–610 nm, six discrete wavelengths) (Supporting Information Methods S3). As the ALA is calibrated to freshwater algae fingerprints, only the relative changes in concentration were used to interpolate Chl *a* concentrations for every 10 min from the traditionally obtained values (sample type 1) (Supporting Information Methods S3 and Table S4). Next, filtration rates F (μg Chl *a* L^{-1} h^{-1}) were calculated for each 10-min interval, assuming constant water volume during incubation due to the moderate backflow through the below-sediment pathways in our container walls. The resulting dilution effect was considered acceptable as it applied to all incubations equally.

Notice that our filtration rates are based on seston removal from incubated water and are presented as μg Chl *a* L^{-1} h^{-1}, and differ from clearance rates (expressed as volume cleared per unit time) based on a flow-through system approach with constant seston concentrations (Foster-Smith 1975; Riisgård 2001; Navarro and Widdows 1997). Results may reflect both individual- and assemblage-level changes in feeding activity, and abundance changes due to mortality cannot be excluded. Therefore, the presented filtration rates should not be interpreted as a sum of individual responses, but rather as the relative change in water clearance performed by bivalve assemblages in response to the temperature treatments. It should also be noted that *M. balthica* is a facultative suspension/deposit feeder, which results in the effectiveness of our methodology for measuring feeding in this species being uncertain, and in filtration rates not being proportional to consumption rates.

Respiration rates

Respiration rate measurements were conducted in water baths in the laboratory with a built-in temperature control system (± 0.3°C). Respiration rates were measured at the temperature of the mesocosm from which the bivalves were extracted. Pre-treatment respiration rates were measured at 17°C. For mid-treatment, temperatures were set to 19.5°C (ambient), 22.3°C (mild heatwave) and 23.9°C (strong heatwave). Finally, the temperature was set to 19.5°C for all water baths during the post-treatment measurements. Airtight glass bottles of 100 mL (pre-treatment), 50 or 500 mL (mid- and post-treatment for *C. edule* and *M. balthica*, respectively) volume were used as respiration chambers with glued-on oxygen sensors on the inside. Chambers were filled with filtered (0.45 μm) and temperature-adjusted seawater immediately before introducing the organisms. Individuals of *C. edule* and *M. balthica* were randomly sampled from the subtidal communities (one from each tank and species), transported within tank water, and introduced to individual chambers within 30 min. Chambers filled with only filtered seawater were used as controls for each run of measurements and temperature. Oxygen concentration was logged in real time at 15 s frequency using a PreSens OXY-4SMA meter (pre-treatment) and a PreSens OXY 4 mini meter (mid- and post-treatment) connected to the PreSens Measurement Studio 2/Oxy4v2_30 software and to the chambers via optical fibers (Supporting Information Fig. S4). Post incubation, bivalves were frozen at −20°C for later size measurements and tissue dry weights (Supporting Information Table S5). For each sampling time (pre-, mid-, post-treatment), respiration measurements were conducted on a new set of individuals.

Respiration rates R (mg O_2 g^{-1} dry tissue h^{-1}) were calculated for each bivalve based on the formula by Ong et al. (2017):

$$R = \frac{V(R_0 - R_1)}{g(t_1 - t_0)} \tag{2}$$

where V is the chamber volume (L), g is the dry tissue weight (g), and t_0 and t_1 (h) are the starting and end time points of the incubation. Oxygen concentrations at t_1 and t_0 are represented by R_0 and R_1 (mg O_2 L^{-1}) in the formula. Measurements were considered initialized once oxygen declined and bivalves were open ($t = t_0$). The incubation was terminated ($t = t_1$) when the oxygen saturation in the chamber had decreased to 70% (Jansen et al. 2007b; Stumpp et al. 2019) based on smoothed saturation values using a 5-min centered moving average, or otherwise after 150 min. Individual respiration rates for both species and all three experimental stages can be found in Supporting Information Table S5.

Statistical analyses

Differences in bivalve survival between heatwave treatments were tested for each species using generalized linear models with a binomial error distribution and a logit link function (logistic regression), while differences in wet weight change were tested using general linear models with Gaussian error distributions.

Differences in bivalve sizes and CI values between heatwave treatments were analyzed for each bivalve species using generalized linear mixed models with mesocosm identity as a random effect to account for multiple bivalves coming from each mesocosm. All models were run using a Gaussian error distribution. To meet the assumptions of homoscedasticity and normality of residuals, the models for CI were performed with a logarithmic link function. To account for the size dependence of CI (Bonsdorff and Wenne 1989), size was included as a covariate.

Filtration rates (*Ft*) were analyzed with generalized linear mixed models, with mesocosm identity as a random effect to account for repeated measures along concentration gradients. Filtration rates were square-root transformed to meet assumptions of normality and homoscedasticity of residuals. Differences between species were analyzed during the pre-treatment stage, with species assemblage (*C. edule*, *M. balthica*, and the bare sediment control) as a factor and water column Chl *a* concentration as a covariate. Differences between heatwave treatments were analyzed for each bivalve species during the mid-treatment stage, with heatwave treatment as a factor and water column Chl *a* concentration and total biomass as covariates.

The response of bivalve respiration rates to heatwave exposure was tested at each of the three experimental stages (pre-, mid-, and post-treatment) using linear models.

Model assumptions for all models were tested via visual assessment of residual plots (homoscedasticity) and quantile–quantile plots (normality of residuals). All statistical models were performed in the R environment version 4.2.1 (R Core Team 2022). Generalized linear mixed models were performed with the “lme4” package (Bates et al. 2015). The significance of fixed effects was tested using likelihood-ratio tests for generalized linear models (including linear models) and Wald tests for generalized linear mixed models with the “car” package (Fox and Weisberg 2019). When a significant treatment effect was determined, a Tukey Honest Significant Difference post hoc test was performed for pairwise comparisons among treatments using the “emmeans” package (Lenth et al. 2023).

Results

The established daily mean water temperatures during the mid-treatment phase were 19.5°C ± 0°C for the ambient treatment, 22.2°C ± 0.1°C for the +2.8°C treatment (mild heatwave), and 23.8°C ± 0.1°C for the +4.4°C treatment (strong heatwave; mean ± SD). On average, temperatures were higher at the sediment surface (by 0.9°C for ambient, 0.8°C for +2.8°C and 0.7°C for +4.4°C treatments) and within the sediment (by 0.5°C for ambient and +2.8°C and 0.4°C for +4.4°C treatments) compared to the water column.

Diurnal temperature variability (daily maximum minus minimum) was relatively low in the water column, with 0.4°C ± 0.1°C, 0.8°C ± 0.1°C, and 0.7°C ± 0.2°C for ambient, +2.8°C, and +4.4°C treatments, respectively. However, exposure to air during low tide caused much higher variability at the sediment surface (15.6°C ± 8.6°C, 15.5°C ± 6.9°C, and 10.3°C ± 4.1°C) and to a lesser extent within the sediment (4.7°C ± 3.1°C, 3.7°C ± 1.4°C, and 4.1°C ± 1.5°C).

Survival and condition

The heatwave treatments did neither affect survival (*C. edule*: $\chi^2 = 1.37$, $p = 0.51$; *M. balthica*: $\chi^2 = 1.35$, $p = 0.51$) nor total biomass (*C. edule*: $\chi^2 = 1.27$, $p = 0.53$; *M. balthica*: $\chi^2 = 0.62$, $p = 0.73$) of both bivalves over the course of the experiment (Fig. 3, Supporting Information Table S6a). Survival of *C. edule* (87.5% [95% confidence interval: 71.1–95.2%] in ambient and +2.8°C, 79% [60.7–89.2%] in +4.4°C; Fig. 3a) was on average lower than that of *M. balthica* (96.9% in ambient and +2.8°C [90.7–99.0%], and 99% [93.0–99.9%] in +4.4°C; Fig. 3b). Total biomass of *C. edule* slightly decreased over the course of the experiment across all treatments (−1.2% [−20.2% to 17.9%] in ambient, −3.9% [−22.9% to 15.2%] in +2.8°C, and −13.94% [−32.9% to 5.2%] in +4.4°C; Fig. 3c). In contrast, *M. balthica* showed a slight increase in total biomass (3.0% [−1.9% to 7.9%] in ambient, 4.8% [0–9.8%] in +2.8°C, and 5.3% [0.4–10.2%] in +4.4°C; Fig. 3d).

Bivalve size was not affected by the heatwave treatments, neither for *C. edule* ($\chi^2 = 0.32$, $p = 0.85$) nor for *M. balthica* ($\chi^2 = 2.5$, $p = 0.29$; Fig. 3e,f, Supporting Information Table S6b). The CI of both bivalves was size-dependent and decreased with increasing size (*C. edule*: $\chi^2 = 87.66$, $p < 0.001$; *M. balthica*: $\chi^2 = 190.53$, $p < 0.001$). There was a significant heatwave treatment effect on the CI of *M. balthica* ($\chi^2 = 6.22$, $p = 0.045$; Fig. 3h). Overall, the CI of both bivalve species was lowest after the +4.4°C heatwave (Fig. 3g,h). However, Tukey Honest Significant Difference revealed no significant pairwise differences between heatwave treatments (Supporting Information Table S6b).

Filtration rates

Pre-treatment measurements revealed that filtration rates were dependent on the underlying Chl *a* concentration in the water column, with higher rates at higher background concentrations ($\chi^2 = 102.51$, $p < 0.001$; Fig. 4a, Supporting Information Table S7a). Importantly, there was a significant interaction between species and Chl *a* concentration ($\chi^2 = 16.61$, $p < 0.001$). Chlorophyll *a* profiles for *M. balthica* did not differ from those in the bare sediment controls. In *C. edule*, however, filtration rates were more than four times higher compared to bare sediment at the high end of background Chl *a* concentration (20 μg L^{-1}), and nearly twice as high at 10 μg L^{-1} (Fig. 4a, Supporting Information Table S7a).

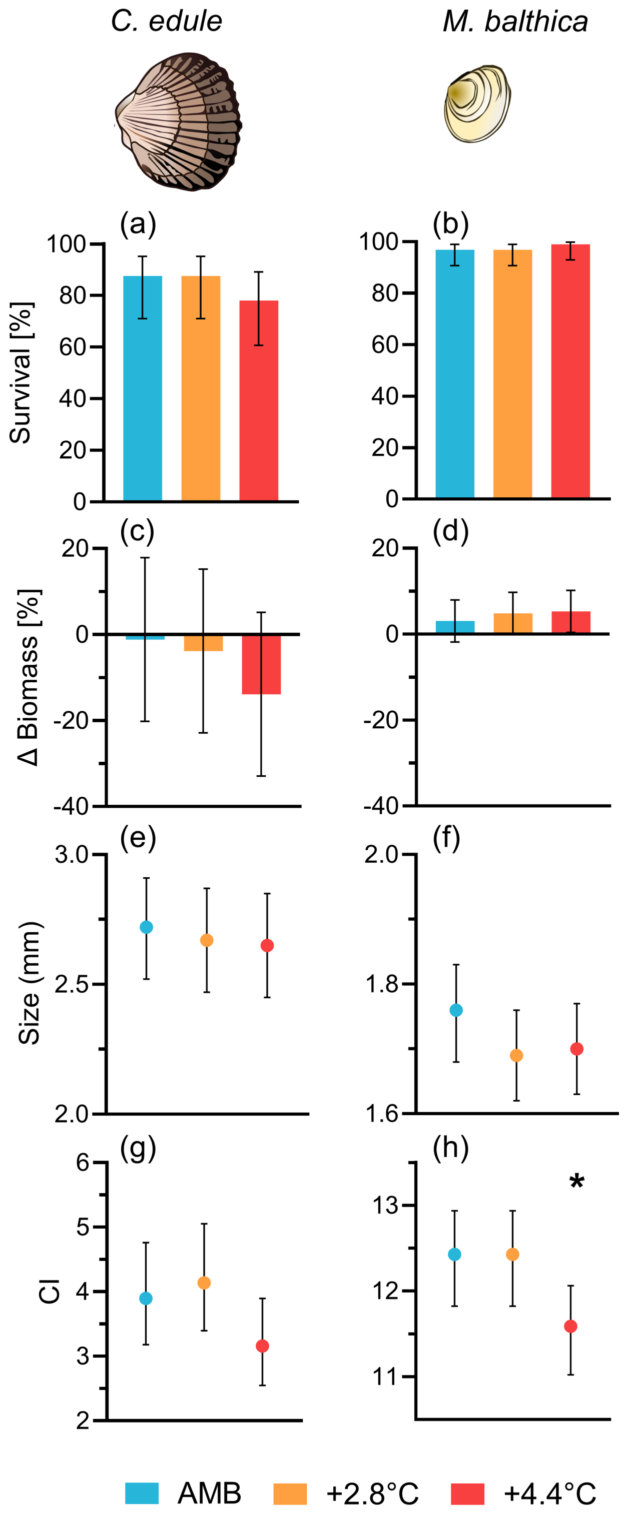

Fig. 3. Survival (**a**, **b**), change in total biomass (wet weight) over the course of the experiment (**c**, **d**), sizes (= shell length as measured at the widest point) (**e**, **f**), and condition index (CI) (**g**, **h**) for *Cerastoderma edule* (a, c, e, g) and *Macoma balthica* (b, d, f, h), under ambient conditions (AMB, blue) and in response to a mild (+2.8°C, orange) and a strong (+4.4°C, red) heatwave. Error bars reflect 95% confidence intervals. Asterisk indicates significant treatment effect by $p < 0.05$.

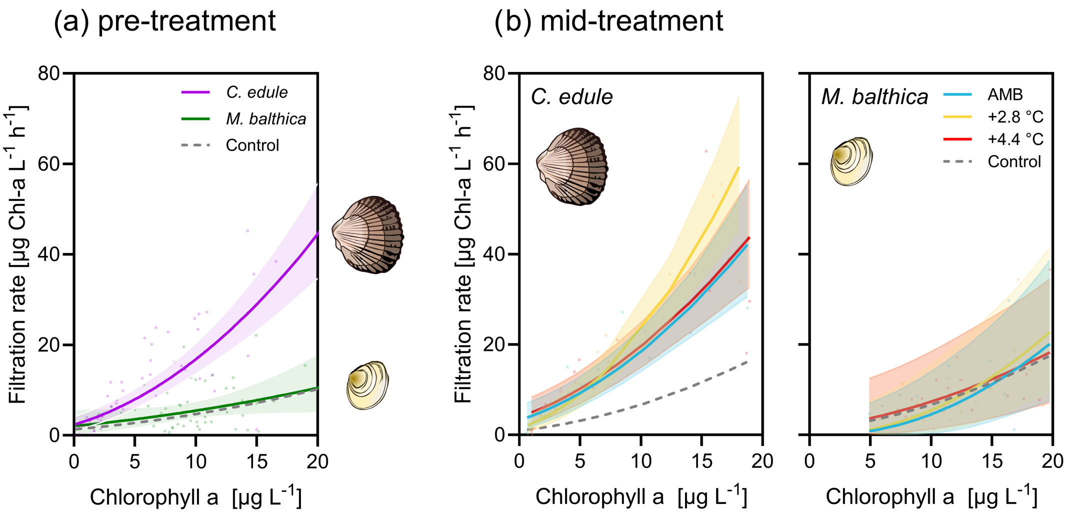

Fig. 4. Filtration rates (in μg Chl *a* per liter and hour) for *Cerastoderma edule* and *Macoma balthica*, as well as bare sediment controls, for (**a**) pre-treatment (before heatwave exposure) and (**b**) mid-treatment (during heatwave exposure) under ambient conditions (AMB, blue) in response to a mild (+2.8°C, orange) and a strong (+4.4°C, red) heatwave. Lines correspond to coefficients from GLMMs, and shaded areas correspond to 95% confidence intervals. GLMMs, generalized linear mixed models.

Mid-treatment filtration measurements revealed no direct effect of treatment on the filtration rates of both bivalves (*C. edule*: $\chi^2 = 3.11$, $p = 0.21$; *M. balthica*: $\chi^2 = 1.45$, $p = 0.48$), but there was a significant interaction between the treatment and water column Chl *a* concentration in *C. edule* ($\chi^2 = 6.59$, $p = 0.04$; Fig. 4b, Supporting Information Table S7b). At high Chl *a* concentrations, *C. edule* filtration rates were up to 40% higher in the +2.8°C treatment compared to ambient and the +4.4°C treatment. This difference, however, diminished with decreasing Chl *a* concentration in the water column.

Respiration rates

Under ambient conditions, respiration rates were generally higher at mid- and post-treatment compared to pre-treatment (Fig. 5). For both bivalves, linear models revealed no significant difference in respiration rates between treatments during the mid-treatment stage (*C. edule*: $\chi^2 = 0.001$, $p = 0.99$; *M. balthica*: $\chi^2 = 0.02$, $p = 0.99$; Fig. 5b). However, there were significant treatment effects during the post-treatment stage for both bivalves (*C. edule*: $\chi^2 = 8.51$, $p = 0.014$; *M. balthica*: $\chi^2 = 12.66$, $p = 0.002$; Fig. 5c, Supporting Information Table S8). For *C. edule*, Tukey Honest Significant Difference revealed no significant pairwise differences between treatments, although mean respiration was lowest following the strong heatwave. It should be noted that due to mortality, measurements for *C. edule* were conducted on 8 individuals instead of 12, with only two replicates for the +4.4°C treatment. For *M. balthica*, Tukey Honest Significant Difference revealed significantly lower respiration rates in the +4.4°C treatment compared to ambient (t-ratio $= -3.317$, $p = 0.022$) and nearly significantly lower rates compared to the +2.8°C treatment (t-ratio $= -2.774$, $p = 0.051$).

Discussion

This mesocosm study investigated the eco-physiological response of two infaunal bivalve species to summer heatwaves of different intensities under near-natural conditions (tidal simulation, unfiltered seawater flow-through and natural light conditions). For *M. balthica*, we observed a reduction in CI and respiration rates following exposure to a strong heatwave (+4.4°C), indicating potential negative long-term effects of marine heatwaves. *Cerastoderma edule* exhibited similar trends in mean CI and mean respiration, though these changes were not statistically significant. *C. edule*, however, showed increased filtration activity under the mild heatwave scenario (+2.8°C) when food availability was sufficient.

Although survival and total biomass tended to be lowest for *C. edule* following the strong heatwave, neither parameter was significantly affected by the heatwave treatments. The observed trend in total biomass loss can likely be attributed to mortality, as neither size nor CI in surviving organisms was negatively affected by the strong heatwave, although the latter still appears to have decreased slightly, indicating potential negative effects on an individual level. The daily mean temperatures in all treatments were within the thermal tolerance range of *C. edule* (5–33°C according to van der Veer et al. 2006), while hourly maxima occasionally exceeded 30°C even below the sediment surface (Supporting Information Fig. S5), potentially imposing additional heat stress on these bivalves. Short-term thermal stress was previously demonstrated to lead to mortality in *C. edule*, albeit for slightly higher acclimatization and exposure temperatures (Domínguez et al. 2021; Verdelhos et al. 2015). Older individuals are more at risk during heat stress (Beukema and Dekker 2020), a factor we cannot isolate from our measurements on differently sized individuals. Despite no

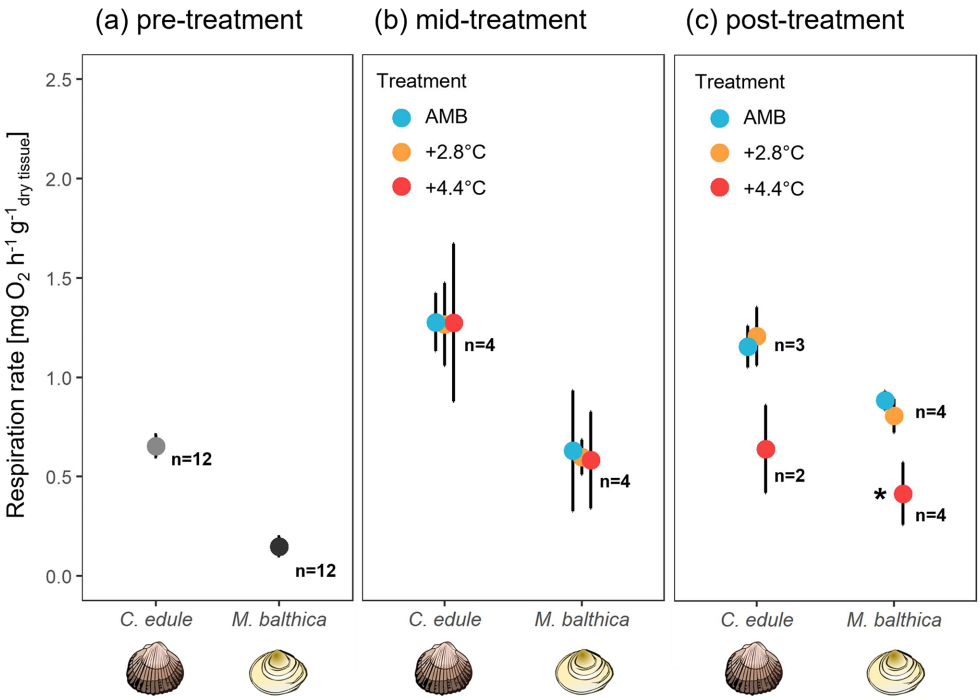

Fig. 5. Respiration rates (in mg O_2 per g dry tissue per hour, normalized to incubation volume) of *Cerastoderma edule* and *Macoma balthica*, for (**a**) pre-treatment (before heatwave exposure), (**b**) mid-treatment (during heatwave exposure), and (**c**) post-treatment (after heatwave exposure). Number of replicates (bivalves) are given for each mean value ± SE. An asterisk indicates a significant treatment effect by $p < 0.05$.

significant differences found among treatments in our experiment, the observed trends suggest that during prolonged or repeated heatwaves, *C. edule* could experience heat stress from a heatwave adding to the strong hourly temperature peaks naturally occurring in an intertidal environment.

In *M. balthica*, survival was generally higher (97–99%) than observed for *C. edule* (79–88%). In contrast to *C. edule*, total biomass slightly increased in all treatments over the course of the experiment (3–5% increase). Neither parameter was affected by the heatwave treatment. This result was somewhat unexpected as this species is considered to be especially vulnerable to high temperatures compared to other bivalves (Beukema et al. 2009; Jansen et al., 2007a), including *C. edule* (van der Veer et al. 2006). However, these studies either focused on the effects of seasonal temperature differences or on climatological warming. Yet, the results are in concordance with Pansch et al. (2018), who also did not find decreased abundances or wet weight loss in *M. balthica* in response to a single marine heatwave, potentially questioning the notion of strong heat sensitivity of this species. One potential explanation is that *M. balthica* has the ability to burrow deeper as an evasion strategy (Clements and Hunt 2017; McGreer 1979; Tallqvist 2001), thereby being less affected by hourly peak temperatures. This is supported by a lower temperature variance measured within the sediment than above the sediment in the present experiment (Supporting Information Fig. S5). Nonetheless, *M. balthica* mean size appeared lower in either heatwave than in the ambient treatments, and CI was lowest following the strong heatwave. This was also observed for the mean CI in *C. edule*. While these observations are not mirrored in survival and total biomass, they may still indicate potential lasting negative effects of short-term warming on this species when observed over a longer time frame, a supposition that is supported by this species' respiratory response discussed below.

Assemblages of *C. edule* displayed elevated filtration activity during the mild (+2.8°C) heatwave, while, in contrast, filtration rates during the strong heatwave (+4.4°C) were nearly identical to rates measured under ambient temperature conditions. Testing for filtration activity prior to heatwave exposure, Chl *a* decline in containers with *C. edule* significantly differed from bare sediment, indicating a successful methodology and actively filtering bivalves at the time of measurement. Moreover, filtration activity in *C. edule* increased with increasing Chl *a* concentrations both before and during heatwave exposure, which aligns with this species' feeding behavior but indicates that the maximum filtration activity was not reached (Navarro and Widdows 1997). Our mid-treatment results for *C. edule* could be interpreted as a bell-shaped feeding response to temperature, in line with previous findings for this species (Brock and Kofoed 1987; Verdelhos et al. 2015) and for *Mytilus edulis* (Schulte 1975) under similar acclimatization and experimental temperatures. This pattern, however, contrasts with studies suggesting that filtration rates increase consistently along our tested temperature range (for *C. edule*: Javanshir 2001; for *M. edulis*: Jørgensen et al. 1990). Note that comparability between these studies and ours could be impaired by differences in experimental set-ups and temperature increase rates (more abrupt in the referenced studies). Following the alternative hypothesis of consistently increasing filtration with rising temperature, our results might just reflect elevated mortality under the strong heatwave. While the surviving bivalves may have maintained or even increased filtration rates compared to other treatments, the overall filtration could be reduced due to the decline in population. Due to the nature of our mesocosm experiment, potential factors responsible for *C. edule* assemblage filtration cannot be isolated. Regardless, our results suggest that heatwave intensity influences the direction of the heatwave effects on ecosystem services (e.g., water clearance) provided by *C. edule*-dominated communities in the Wadden Sea, ranging from positive during a mild to neutral or even negative during a strong heatwave.

Filtration activity in *M. balthica* assemblages resembled the Chl *a* decline observed for the bare sediment controls. Most likely, the dominant feeding mode for this species was deposit-feeding at the time of both measurements (before and during heatwave exposure). There is ongoing debate as to what drivers cause *M. balthica* to switch between feeding modes. Deposit-feeding was demonstrated to occur more often in small individuals (Rossi et al. 2004) and in the (upper) intertidal zone (Beukema et al. 2014; Rossi and Middelburg 2011), both of which could be relevant for our study as differently sized adult individuals were kept in intertidal simulation. Additionally, limited food availability in the mesocosm tanks ($< 2\,\mu$g Chl *a* L^{-1}) could have triggered the deposit-feeding mode (Olafsson 1986; Riisgård and Kamermans 2001; Törnroos et al. 2015). Notably, filtration measured for *M. balthica* still interacted with Chl *a* concentration. We cannot entirely exclude a particle settling effect when assessing the feeding activity in the present study, as we aimed for the most natural settings for the single-species bivalve assemblages. Also, the presence of filter-feeding recruits, other organisms that settled in the mesocosms during the experiment, could have contributed to some part of the measured signal. The methodology applied in this experiment to test potential feeding responses to heatwave exposure may not have been appropriate in the case of *M. balthica*. To further improve our mechanistic understanding of the filter-feeding mode of this species, we suggest experimentally testing the feeding responses of *M. balthica* under the exclusion of sediment and with a larger span of food concentrations.

While respiration rates were not affected during heatwave exposure (mid-treatment), we found persisting negative effects following the strong heatwave for both species (post-treatment). For ectotherms such as the bivalve species tested herein, the respiration rate is directly linked to metabolic activity (Haider et al. 2020; Jansen et al. 2007b; Kennedy and Mihursky 1972). The observed respiration rates concur with values reported in the literature for *C. edule* (Boyden 1972; Brock and Kofoed 1987; but lower values in Ong et al. 2017; Zhou et al. 2022) and *M. balthica* (Hummel et al. 2000; Jansen et al. 2007b). Nonetheless, some level of error could have been introduced by the lack of mixing in our respiration measurements in addition to equipment changes mid-experiment, both of which could impair the comparability of our results to other studies.

Respiration rates of both *C. edule* and *M. balthica* increased between pre- and mid-treatment measurements (5 weeks apart), which is to be expected since metabolic activity in bivalves directly relates to temperature in both *C. edule* (Boyden 1972; Wilson 1983; Zhou et al. 2022) and *M. balthica* (Jansen et al. 2007b), and ambient temperatures increased by +2.5°C between measurement dates. However, it is important to note that the observed increases were not measured within individuals, but rather, a new set of individuals was used for each round of measurements (pre-, mid-, and post-treatment), and respiration rates can differ between individuals of the same flesh weight, inter alia due to age (Iglesias and Navarro 1991). Surprisingly, there was no heatwave effect on respiration in either of the bivalve species during heatwave exposure itself. For *M. balthica*, there are indications that metabolic response patterns are down-regulated in summer, which is assumed to occur as a protection mechanism against peak temperatures (Hummel et al. 2000; Jansen et al., 2007a). A similar response pattern could have occurred in *C. edule* in this experiment, as acclimation temperatures are also suspected to influence respiratory response patterns to short-term thermal stress in this species (Brock and Kofoed 1987). The results of this experiment suggest that for both species, respiration increases with seasonal warming but not in immediate response to a short-term warming event.

In contrast, respiration was significantly lower in post-treatment measurements for *M. balthica* if previously exposed to the strong +4.4°C heatwave, and indications (although not significant) were found that *C. edule* could display a similar metabolic response. However, post-treatment sample sizes in our experiment were small for *C. edule* ($n = 2$ for the strong heatwave, $n = 3$ for the other treatments) due to bivalve mortality over time. As a result, the statistical inference is less robust. One potential explanation for the observed response patterns could be that both species acclimated to elevated temperatures after 2 weeks of heatwave exposure and (further) downregulated their metabolic activity, leading to a "delayed" signal in respiration. Metabolic down-regulation is known to occur on a time scale of weeks to seasons for *M. balthica* (Hummel et al. 2000; Jansen et al., 2007a), and Ong et al. (2017) found an initial increase in respiration in *C. edule* but a following decrease in response to 3–6 weeks of heat exposure. Additionally, the lower respiration rates in individuals previously exposed to the strong heatwave could mirror a decline in condition, which is supported by the lower CI measured for respective individuals of *M. balthica*. However, no indication of such a relationship was found in the case of *C. edule*. Further post-stressor response measurements on a larger sample size and potentially with the investigation of heat-shock proteins (Feder and Hofmann 1999; Pante et al. 2012; Sokołowski and Brulińska 2018) could give additional insights into the observations made herein. Nonetheless, our results indicate potential persisting negative effects of intensified heatwaves in the Wadden Sea on the metabolic capacity of two key bivalve species. It should be noted that, due to technical constraints (specifically, weight limitations on the tidal platforms), respiration measurements for both bivalve species were conducted on individuals kept under subtidal conditions (i.e., in containers not exposed to diurnal tides). As a result, these findings may not fully represent bivalves from the upper intertidal zone, where daily temperature fluctuations are more pronounced. Instead, the results are more reflective of responses from bivalves acclimatized to deeper areas of the Wadden Sea.

Our study demonstrated that *C. edule* and *M. balthica* display different eco-physiological responses to varying summer heatwave intensities. By taking a near-natural experimental approach, it was possible to investigate response patterns both on the population and individual levels. While bivalves were apparently able to withstand a mild heatwave, there were some indications that a more intense heatwave could negatively affect bivalve survival, filtration, and metabolic capacities in *C. edule* in the short term, and condition as well as metabolic capacities in *M. balthica* (and potentially *C. edule*) in the long term. Here, this occurred even though daily mean temperatures (max. 4.4°C above ambient) did not exceed species-specific heat tolerance limits, indicating that short-term heatwaves pose considerable thermal stress to bivalves, adding to the effects of intertidal temperature fluctuations, seasonal temperature changes, and climatological warming.

With heatwaves increasing in intensity and frequency in the North Sea area and other coastal habitats worldwide (Frölicher et al. 2018; Oliver et al. 2021), our findings could have considerable implications for future changes to intertidal communities and the ecosystem services provided by them. Mortality and reduced metabolic capacities in bivalve populations could negatively affect water clearance (Beukema and Cadée 1996; Cranford 2019), nutrient cycling (Carss et al. 2020; Michaud et al. 2006), and intertidal food web composition and fluxes (Beukema and Cadée 1996; Christianen et al. 2017). To better estimate the potential long-term effects of marine heatwaves on intertidal communities, our results suggest further investigations of especially post-stress responses in bivalves and other species. Furthermore, eco-physiological response patterns in bivalves should be linked to abiotic and biotic parameters influenced by temperature in their natural habitats. Among others, hypoxia (Zhou et al. 2022), increased parasite infections (Larsen and Mouritsen 2014; Thieltges 2006), or hampered algal growth (Román et al. 2020; Schiel et al. 2004) often co-occur with heatwaves, making research on bivalve responses to (short-term) multi-stressor events essential for more precise future predictions of heatwave impacts on coastal ecosystems (Burdon et al. 2014; Javanshir 2001; Weijerman et al. 2005). Importantly, strategies for coastal management should prioritize monitoring the impacts of marine heatwaves to preserve ecosystem services provided by bivalves, such as filtration, nutrient cycling, and food web stability.

Author Contributions

Maren A. Staniek: conceptualization (equal), data curation (lead), formal analysis (equal), investigation (lead), methodology (equal), visualization (equal), writing – original draft preparation (lead). **Christian Pansch:** conceptualization (equal), funding acquisition (supporting), project administration (supporting), resources (supporting), supervision (supporting), validation (lead), visualization (equal), writing – original draft preparation (supporting), writing – review & editing (equal). **Lisa N. S. Shama:** Funding acquisition (supporting), investigation (supporting), project administration (supporting), resources (supporting), supervision (supporting), validation (supporting), writing – original draft preparation (supporting), writing – review & editing (equal). **Knut Mehler:** Investigation (supporting), resources (supporting), supervision (supporting), writing – review & editing (equal). **Anna Steinmann:** Investigation (supporting), methodology (equal), resources (supporting), writing – review & editing (equal). **Jack J. Middelburg:** Supervision (supporting), writing – review & editing (equal). **Lukas Meysick:** Conceptualization (equal), data curation (supporting), formal analysis (equal), funding acquisition (lead), investigation (supporting), methodology (equal), project administration (lead), resources (lead), supervision (lead), visualization (equal), writing – original draft preparation (supporting), writing – review & editing (equal).

Acknowledgments

We thank Helen Spence-Jones (Coastal Ecology Section, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Wadden Sea Station Sylt, List, Germany), Lucinda Kraufvelin (Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi University, Turku, Finland), and Monica Ionita-Scholz (Department of Paleoclimate Dynamics, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany) for their considerable contributions to the computation of our time series of water temperatures, the historical heatwave analysis, and the heatwave treatment design. Further, we thank Antje-Marie Mischke (Faculty of Biology and Chemistry, University of Bremen, Germany) for her extensive assistance both in the field and during measurements, and the research station's on-site staff for their continuous technical support prior to and throughout the experiment. This research was conducted at and in collaboration with the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Wadden Sea Station Sylt, List, Germany. Open Access funding enabled and organized by Projekt DEAL.

Conflicts of Interest

None declared.

References

Alfred-Wegener-Institut Helmholtz-Zentrum für Polar-und Meeresforschung. 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, no. A184: 1–15. https://doi.org/10.17815/jlsrf-8-184.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1–48. https://doi.org/10.18637/jss.v067.i01.

Beukema, J. J., and G. C. Cadée. 1996. "Consequences of the Sudden Removal of Nearly All Mussels and Cockles from the Dutch Wadden Sea." *Marine Ecology* 17, no. 1–3: 279–289. https://doi.org/10.1111/j.1439-0485.1996.tb00508.x.

Beukema, J. J., G. C. Cadée, R. Dekker, and C. Philippart. 2014. "Annual and Spatial Variability in Gains of Body Weight in *Macoma balthica* (L.): Relationships With Food Supply and Water Temperature." *Journal of Experimental Marine Biology and Ecology* 457: 105–112. https://doi.org/10.1016/j.jembe.2014.04.003.

Beukema, J. J., and R. Dekker. 2020. "Winters Not Too Cold, Summers Not Too Warm: Long-Term Effects of Climate Change on the Dynamics of a Dominant Species in the Wadden Sea: The Cockle *Cerastoderma edule* L." *Marine Biology* 167: 44. https://doi.org/10.1007/s00227-020-3659-1.

Beukema, J. J., R. Dekker, and J. M. Jansen. 2009. "Some Like It Cold: Populations of the Tellinid Bivalve *Macoma balthica* (L.) Suffer in Various Ways From a Warming Climate." *Marine Ecology Progress Series* 384: 135–145. https://doi.org/10.3354/meps07952.

Blossier, B., K. R. Bryan, C. J. Daly, and C. Winter. 2017. "Spatial and Temporal Scales of Shoreline Morphodynamics Derived From Video Camera Observations for the Island of Sylt, German Wadden Sea." *Geo-Marine Letters* 37, no. 2: 111–123. https://doi.org/10.1007/s00367-016-0461-7.

Bonsdorff, E., and R. Wenne. 1989. "A Comparison of Condition Indices of *Macoma balthica* (L.) From the Northern and Southern Baltic Sea." *Netherlands Journal of Sea Research* 23, no. 1: 45–55. https://doi.org/10.1016/0077-7579(89)90042-2.

Boyden, C. R. 1972. "Aerial Respiration of the Cockle *Cerastoderma edule* in Relation to Temperature." *Comparative Biochemistry and Physiology Part A: Physiology* 43, no. 3: 697–712. https://doi.org/10.1016/0300-9629(72)90256-3.

Brock, V., and L. H. Kofoed. 1987. "Species Specific Irrigatory Efficiency in *Cardium* (Cerastoderma) *edule* (L.) and *C. lamarcki* (Reeve) Responding to Different Environmental Temperatures." *Biological Oceanography* 4, no. 3: 211–226.

Burdon, D., R. Callaway, M. Elliott, T. Smith, and A. Wither. 2014. "Mass Mortalities in Bivalve Populations: A Review of the Edible Cockle *Cerastoderma edule* (L.)." *Estuarine, Coastal and Shelf Science* 150, no. B: 271–280. https://doi.org/10.1016/j.ecss.2014.04.011.

Carss, D. N., A. C. Brito, P. Chainho, et al. 2020. "Ecosystem Services Provided by a Non-Cultured Shellfish Species: The Common Cockle *Cerastoderma edule*." *Marine Environmental Research* 158: 104931. https://doi.org/10.1016/j.marenvres.2020.104931.

Christianen, M. J. A., J. J. Middelburg, S. J. Holthuijsen, et al. 2017. "Benthic Primary Producers Are Key to Sustain the Wadden Sea Food Web: Stable Carbon Isotope Analysis at Landscape Scale." *Ecology* 98, no. 6: 1498–1512. https://doi.org/10.1002/ecy.1837.

Clements, J. C., and H. L. Hunt. 2017. "Effects of CO_2-Driven Sediment Acidification on Infaunal Marine Bivalves: A Synthesis." *Marine Pollution Bulletin* 117, no. 1–2: 6–16. https://doi.org/10.1016/j.marpolbul.2017.01.053.

Cranford, P. J. 2019. "Magnitude and Extent of Water Clarification Services Provided by Bivalve Suspension Feeding." In Goods and Services of Marine Bivalves, edited by A. C. Smaal, J. G. Ferreira, J. Grant, J. K. Petersen, and Ø. Strand, 119–142. Cham, Switzerland: Springer Open. https://doi.org/10.1007/978-3-319-96776-9_8.

de Amorim, F. L. L., K. H. Wiltshire, P. Lemke, et al. 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.

Domínguez, R., C. Olabarria, S. A. Woodin, et al. 2021. "Contrasting Responsiveness of Four Ecologically and Economically Important Bivalves to Simulated Heat Waves." *Marine Environmental Research* 164: 105229. https://doi.org/10.1016/j.marenvres.2020.105229.

Engel, F. G., B. Matthiessen, and B. K. Eriksson. 2020. "A Heatwave Increases Turnover and Regional Dominance in Microbenthic Metacommunities." *Basic and Applied Ecology* 47: 1–11. https://doi.org/10.1016/j.baae.2020.03.003.

Feder, M. E., and G. E. Hofmann. 1999. "Heat-Shock Proteins, Molecular Chaperones, and the Stress Response: Evolutionary and Ecological Physiology." *Annual Review of Physiology* 61: 243–282. https://doi.org/10.1146/annurev.physiol.61.1.243.

Flach, E. C. 1996. "The Influence of the Cockle, *Cerastoderma edule* on the Macrozoobenthic Community of Tidal Flats in the Wadden Sea." *Marine Ecology* 17, no. 1–3: 87–98. https://doi.org/10.1111/j.1439-0485.1996.tb00492.x.

Foster-Smith, R. L. 1975. "The Effect of Concentration of Suspension on the Filtration Rates and Pseudofaecal

Production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu).” *Journal of Experimental Marine Biology and Ecology* 17, no. 1: 1–22. https://doi.org/10.1016/0022-0981(75)90075-1.

Fox, J., and S. Weisberg. 2019. An R Companion to Applied Regression. 3rd ed. Thousand Oaks (CA): Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Frölicher, T. L., E. M. Fischer, and N. Gruber. 2018. “Marine Heatwaves Under Global Warming.” *Nature* 560: 360–364. https://doi.org/10.1038/s41586-018-0383-9.

Haider, F., S. Timm, T. Bruhns, M. N. Noor, and I. M. Sokolova. 2020. “Effects of Prolonged Food Limitation on Energy Metabolism and Burrowing Activity of an Infaunal Marine Bivalve, *Mya arenaria*.” *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* 250: 110780. https://doi.org/10.1016/j.cbpa.2020.110780.

Heron, S. F., J. C. Day, R. Zijlstra, et al. 2020. Climate Risk Assessment for Wadden Sea World Heritage property: Application of the Climate Vulnerability Index—Outstanding Universal Value (OUV) Vulnerability (Workshop report). Wilhelmshaven, Germany: Common Wadden Sea Secretariat (CWSS).

Hesketh, A. V., and C. D. G. Harley. 2022. “Extreme Heatwave Drives Topography-Dependent Patterns of Mortality in a Bed-Forming Intertidal Barnacle, With Implications for Associated Community Structure.” *Global Change Biology* 29, no. 1: 165–178. https://doi.org/10.1111/gcb.16390.

Hobday, A. J., L. V. Alexander, S. E. Perkins, et al. 2016. “A Hierarchical Approach to Defining Marine Heatwaves.” *Progress in Oceanography* 141: 227–238. https://doi.org/10.1016/j.pocean.2015.12.014.

Hobday, A. J., E. C. J. Oliver, A. S. Gupta, et al. 2018. “Categorizing and Naming Marine Heatwaves.” *Oceanography* 31, no. 2: 162–173. https://www.jstor.org/stable/26542662.

Hummel, H., R. Bogaards, G. Bachelet, F. Caron, J. Sola, and C. Amiard-Triquet. 2000. “The Respiratory Performance and Survival of the Bivalve *Macoma balthica* (L.) at the Southern Limit of Its Distribution Area: A Translocation Experiment.” *Journal of Experimental Marine Biology and Ecology* 251, no. 1: 85–102. https://doi.org/10.1016/S0022-0981(00)00208-2.

Iglesias, J. I. P., and E. Navarro. 1991. “Energetics of Growth and Reproduction in Cockles (*Cerastoderma edule*): Seasonal and Age-Dependent Variations.” *Marine Biology* 111: 359–368. https://doi.org/10.1007/BF01319407.

Jansen, J. M., A. E. Pronker, S. W. Bonga, and H. Hummel. 2007. “*Macoma balthica* in Spain, a Few Decades Back in Climate History.” *Journal of Experimental Marine Biology and Ecology* 344, no. 2: 161–169. https://doi.org/10.1016/j.jembe.2006.12.014.

Jansen, J. M., A. E. Pronker, S. Kube, et al. 2007*b*. “Geographic and Seasonal Patterns and Limits on the Adaptive Response to Temperature of European *Mytilus* spp. and *Macoma balthica* Populations.” *Oecologia* 154, no. 1: 23–34. https://doi.org/10.1007/s00442-007-0808-x.

Javanshir, A. 2001. “Influence of *Labratrema minimus* (Trematoda: Digenea) on Filtration Rate Performance of Edible Cockle *Cerastoderma edule* the Extreme Temperature and Salinity Conditions (an In Vitro Experiment).” *Iranian Journal of Fisheries Sciences* 3, no. 2: 73–94. http://jifro.ir/article-1-3167-en.html.

Jeffrey, S. W., and G. F. Humphrey. 1975. “New Spectrophotometric Equations for Determining Chlorophylls a, b, c1 and c2 in Higher Plants, Algae and Natural Phytoplankton.” *Biochemie und Physiologie der Pflanzen* 167, no. 2: 191–194. https://doi.org/10.1016/S0015-3796(17)30778-3.

Jørgensen, C. B., P. S. Larsen, and H. U. Riisgård. 1990. “Effects of Temperature on the Mussel Pump.” *Marine Ecology Progress Series* 64, no. 1/2: 89–97. http://www.jstor.org/stable/24844593.

Kennedy, V. S., and J. A. Mihursky. 1972. “Effects of Temperature on the Respiratory Metabolism of Three Chesapeake Bay Bivalves.” *Chesapeake Science* 13, no. 1: 1–22. https://doi.org/10.2307/1350546.

Larsen, M. H., and K. N. Mouritsen. 2014. “Temperature–Parasitism Synergy Alters Intertidal Soft-Bottom Community Structure.” *Journal of Experimental Marine Biology and Ecology* 460: 109–119. https://doi.org/10.1016/j.jembe.2014.06.011.

Lenth, R. V., B. Bolker, P. Buerkner, et al. 2023. Estimated Marginal Means, aka Least-Square Means: Package ‘emmeans’. CRAN Repository. https://cran.r-project.org/web/packages/emmeans/emmeans.pdf.

Lima, F. P., and D. S. Wethey. 2012. “Three Decades of High-Resolution Coastal Sea Surface Temperatures Reveal More Than Warming.” *Nature Communications* 3: 704. https://doi.org/10.1038/ncomms1713.

Lucas, A., and P. G. Beninger. 1985. “The Use of Physiological Condition Indices in Marine Bivalve Aquaculture.” *Aquaculture* 44, no. 3: 187–200. https://doi.org/10.1016/0044-8486(85)90243-1.

Macho, G., S. A. Woodin, D. S. Wethey, and E. Vázquez. 2016. “Impacts of Sublethal and Lethal High Temperatures on Clams Exploited in European Fisheries.” *Journal of Shellfish Research* 35, no. 2: 405–419. https://doi.org/10.2983/035.035.0215.

McGreer, E. R. 1979. “Sublethal Effects of Heavy Metal Contaminated Sediments on the Bivalve *Macoma balthica* (L.).” *Marine Pollution Bulletin* 10, no. 9: 259–262. https://doi.org/10.1016/0025-326X(79)90482-X.

Michaud, E., G. Desrosiers, F. Mermillod-Blondin, B. Sundby, and G. Stora. 2006. “The Functional Group Approach to Bioturbation: II. The Effects of the *Macoma balthica* Community on Fluxes of Nutrients and Dissolved Organic Carbon Across the Sediment–Water Interface.” *Journal of Experimental Marine Biology and Ecology* 337, no. 2: 178–189. https://doi.org/10.1016/j.jembe.2006.06.025.

Navarro, J. M., and J. Widdows. 1997. “Feeding Physiology of *Cerastoderma edule* in Response to a Wide Range of Seston

Concentrations." *Marine Ecology Progress Series* 152: 175–186. https://doi.org/10.3354/meps152175.

Newell, R. C., and B. L. Bayne. 1973. "A Review on Temperature and Metabolic Acclimation in Intertidal Marine Invertebrates." *Netherlands Journal of Sea Research* 7: 421–433. https://doi.org/10.1016/0077-7579(73)90063-X.

Nilin, J., J. L. T. Pestana, N. G. Ferreira, S. Loureiro, L. V. Costa-Lotufo, and A. M. V. M. Soares. 2012. "Physiological Responses of the European Cockle *Cerastoderma edule* (Bivalvia: Cardidae) as Indicators of Coastal Lagoon Pollution." *Science of the Total Environment* 435-436: 44–52. https://doi.org/10.1016/j.scitotenv.2012.06.107.

Norkko, J., and S. F. Thrush. 2006. "Ecophysiology in Environmental Impact Assessment: Implications of Spatial Differences in Seasonal Variability of Bivalve Condition." *Marine Ecology Progress Series* 326: 175–186. https://doi.org/10.3354/meps326175.

Olafsson, E. B. 1986. "Density Dependence in Suspension-Feeding and Deposit-Feeding Populations of the Bivalve *Macoma balthica*: A Field Experiment." *Journal of Animal Ecology* 55, no. 2: 517–526. https://doi.org/10.2307/4735.

Oliver, E. C. J., J. A. Benthuysen, S. Darmaraki, et al. 2021. "Marine Heatwaves." *Annual Review of Marine Science* 13: 313–342. https://doi.org/10.1146/annurev-marine-032720-095144.

Ong, E. Z., M. Briffa, T. Moens, and C. Van Colen. 2017. "Physiological Responses to Ocean Acidification and Warming Synergistically Reduce Condition of the Common Cockle *Cerastoderma edule*." *Marine Environmental Research* 130: 38–47. https://doi.org/10.1016/j.marenvres.2017.07.001.

Pansch, A., V. Winde, R. Asmus, and H. Asmus. 2016. "Tidal Benthic Mesocosms Simulating Future Climate Change Scenarios in the Field of Marine Ecology." *Limnology and Oceanography: Methods* 14, no. 4: 257–267. https://doi.org/10.1002/lom3.10086.

Pansch, C., M. Scotti, F. R. Barboza, et al. 2018. "Heat Waves and Their Significance for a Temperate Benthic Community: A Near-Natural Experimental Approach." *Global Change Biology* 24, no. 9: 4357–4367. https://doi.org/10.1111/gcb.14282.

Pante, E., A. Rohfritsch, V. Becquet, K. Belkhir, N. Bierne, and P. Garcia. 2012. "SNP Detection From De Novo Transcriptome Sequencing in the Bivalve *Macoma balthica*: Marker Development for Evolutionary Studies." *PLoS One* 7, no. 12: e52302. https://doi.org/10.1371/journal.pone.0052302.

Philippart, C., L. Mekkes, C. Buschbaum, K. M. Wegner, and K. Laursen. 2017. Wadden Sea Quality Status Report: Climate ecosystems. Wilhelmshaven, Germany: Common Wadden Sea Secretariat.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Reise, K., M. Baptist, P. Burbridge, et al. 2010. The Wadden Sea—A Universally Outstanding Tidal Wetland (Wadden Sea Ecosystem No. 29), 7–24. Wilhelmshaven, Germany: Common Wadden Sea Secretariat (CWSS).

Rick, J. J., M. Scharfe, T. Romanova, et al. 2023. "An Evaluation of Long-Term Physical and Hydrochemical Measurements at the Sylt Roads Marine Observatory (1973–2019), Wadden Sea, North Sea." *Earth System Science Data* 15, no. 3: 1037–1057. https://doi.org/10.5194/essd-15-1037-2023.

Riisgård, H. U. 2001. "On Measurement of Filtration Rate in Bivalves—The Stony Road to Reliable Data: Review and Interpretation." *Marine Ecology Progress Series* 211: 275–291. https://doi.org/10.3354/meps211275.

Riisgård, H. U., and P. Kamermans. 2001. "Switching Between Deposit and Suspension Feeding in Coastal Zoobenthos." In Ecological Studies. Ecological Comparisons of Sedimentary Shores, edited by I. T. Baldwin, M. M. Caldwell, G. Heldmaier, O. L. Lange, H. A. Mooney, E.-D. Schulze, U. Sommer, and K. Reise, vol. 151, 73–101. Berlin Heidelberg: Springer. https://doi.org/10.1007/978-3-642-56557-1_5.

Román, M., S. Román, E. Vázquez, J. Troncoso, and C. Olabarria. 2020. "Heatwaves During Low Tide are Critical for the Physiological Performance of Intertidal Macroalgae Under Global Warming Scenarios." *Scientific Reports* 10, no. 1: 21408. https://doi.org/10.1038/s41598-020-78526-5.

Rossi, F., P. M. J. Herman, and J. J. Middelburg. 2004. "Interspecific and Intraspecific Variation of δC and δN in Deposit- and Suspension-Feeding Bivalves (*Macoma balthica* and *Cerastoderma edule*): Evidence of Ontogenetic Changes in Feeding Mode of *Macoma balthica*." *Limnology and Oceanography* 49, no. 2: 408–414. https://doi.org/10.4319/lo.2004.49.2.0408.

Rossi, F., and J. J. Middelburg. 2011. "Intraspecific Diet Shift of *Macoma balthica* During Community Reassembly in an Estuarine Intertidal Flat." *Estuarine, Coastal and Shelf Science* 92, no. 3: 496–501. https://doi.org/10.1016/j.ecss.2011.02.008.

Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2004. "Ten Years of Induced Ocean Warming Causes Comprehensive Changes in Marine Benthic Communities." *Ecology* 85, no. 7: 1833–1839. https://doi.org/10.1890/03-3107.

Schlegel, R. W., and A. J. Albertus. 2018. "heatwaveR: A Central Algorithm for the Detection of Heatwaves and Cold-Spells." *Journal of Open Source Software* 3, no. 27: 821. https://doi.org/10.21105/joss.00821.

Schulte, E. H. 1975. "Influence of Algal Concentration and Temperature on the Filtration Rate of *Mytilus edulis*." *Marine Biology* 30, no. 4: 331–341. https://doi.org/10.1007/BF00390638.

Smaal, A. C., A. Vonck, and M. Bakker. 1997. "Seasonal Variation in Physiological Energetics of *Mytilus edulis* and *Cerastoderma edule* of Different Size Classes." *Journal of the Marine Biological Association of the United Kingdom* 77, no. 3: 817–838. https://doi.org/10.1017/S0025315400036213.

Smale, D. A., T. Wernberg, E. C. J. Oliver, et al. 2019. "Marine Heatwaves Threaten Global Biodiversity and the Provision of Ecosystem Services." *Nature Climate Change* 9, no. 4: 306–312. https://doi.org/10.1038/s41558-019-0412-1.

Smith, K. E., M. T. Burrows, A. J. Hobday, et al. 2023. "Biological Impacts of Marine Heatwaves." *Annual Review of Marine Science* 15, no. 1: 119–145. https://doi.org/10.1146/annurev-marine-032122-121437.

Sokołowski, A., and D. Brulińska. 2018. "The Effects of Low Seawater pH on Energy Storage and Heat Shock Protein 70 Expression in a Bivalve *Limecola balthica*." *Marine Environmental Research* 140: 289–298. https://doi.org/10.1016/j.marenvres.2018.06.018.

Somero, G. N. 2002. "Thermal Physiology and Vertical Zonation of Intertidal Animals: Optima, Limits, and Costs of Living." *Integrative and Comparative Biology* 42, no. 4: 780–789. https://doi.org/10.1093/icb/42.4.780.

Stumpp, M., S. Dupont, and M. Y. Hu. 2019. "Measurement of Feeding Rates, Respiration, and pH Regulatory Processes in the Light of Ocean Acidification Research." *Methods in Cell Biology* 150: 391–409. https://doi.org/10.1016/bs.mcb.2018.11.017.

Tallqvist, M. 2001. "Burrowing Behaviour of the Baltic Clam *Macoma balthica*: Effects of Sediment Type, Hypoxia and Predator Presence." *Marine Ecology Progress Series* 212: 183–191. https://doi.org/10.3354/meps212183.

Thieltges, D. W. 2006. "Parasite Induced Summer Mortality in the Cockle *Cerastoderma edule* by the Trematode *Gymnophallus choledochus*." *Hydrobiologia* 559, no. 1: 455–461. https://doi.org/10.1007/s10750-005-1345-4.

Törnroos, A., M. C. Nordström, K. Aarnio, and E. Bonsdorff. 2015. "Environmental Context and Trophic Trait Plasticity in a Key Species, the TELLINID clam *Macoma balthica* L." *Journal of Experimental Marine Biology and Ecology* 472: 32–40. https://doi.org/10.1016/j.jembe.2015.06.015.

van Beusekom, J. E. E., S. Weigelt-Krenz, and P. Martens. 2008. "Long-Term Variability of Winter Nitrate Concentrations in the Northern Wadden Sea Driven by Freshwater Discharge, Decreasing Riverine Loads and Denitrification." *Helgoland Marine Research* 62, no. 1: 49–57. https://doi.org/10.1007/s10152-007-0092-5.

van der Veer, H. W., J. F. Cardoso, and J. van der Meer. 2006. "The Estimation of DEB Parameters for Various Northeast Atlantic Bivalve Species." *Journal of Sea Research* 56, no. 2: 107–124. https://doi.org/10.1016/j.seares.2006.03.005.

Verdelhos, T., J. C. Marques, and P. Anastácio. 2015. "Behavioral and Mortality Responses of the Bivalves *Scrobicularia plana* and *Cerastoderma edule* to Temperature, as Indicator of Climate Change's Potential Impacts." *Ecological Indicators* 58: 95–103. https://doi.org/10.1016/j.ecolind.2015.05.042.

Weijerman, M., H. Lindeboom, and A. F. Zuur. 2005. "Regime Shifts in Marine Ecosystems of the North Sea and Wadden Sea." *Marine Ecology Progress Series* 298: 21–39. https://doi.org/10.3354/meps298021.

Wethey, D. S., and S. A. Woodin. 2022. "Climate Change and *Arenicola marina*: Heat Waves and the Southern Limit of an Ecosystem Engineer." *Estuarine, Coastal and Shelf Science* 276: 108015. https://doi.org/10.1016/j.ecss.2022.108015.

Wilson, J. G. 1983. "The Uptake and Accumulation of Ni by *Cerastoderma edule* and Its Effect on Mortality, Body Condition and Respiration Rate." *Marine Environmental Research* 8, no. 3: 129–148. https://doi.org/10.1016/0141-1136(83)90047-8.

Zhou, Z., T. J. Bouma, G. S. Fivash, et al. 2022. "Thermal Stress Affects Bioturbators' Burrowing Behavior: A Mesocosm Experiment on Common Cockles (*Cerastoderma edule*)." *Science of the Total Environment* 824: 153621. https://doi.org/10.1016/j.scitotenv.2022.153621.

Supporting Information

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

Submitted 19 June 2024
Revised 11 November 2024
Accepted 05 February 2025