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Response of foundation macrophytes to near-natural simulated marine heatwaves

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Abstract

Marine heatwaves have been observed worldwide and are expected to increase in both frequency and intensity due to climate change. Such events may cause ecosystem reconfigurations arising from species range contraction or redistribution, with ecological, economic and social implications. Macrophytes such as the brown seaweed *Fucus vesiculosus* and the seagrass *Zostera marina* are foundation species in many coastal ecosystems of the temperate northern hemisphere. Hence, their response to extreme events can potentially determine the fate of associated ecosystems. Macrophyte functioning is intimately linked to the maintenance of photosynthesis, growth and reproduction, and resistance against pathogens, epibionts and grazers. We investigated morphological, physiological, pathological and chemical defence responses of western Baltic Sea *F. vesiculosus* and *Z. marina* populations to simulated near-natural marine heatwaves. Along with (a) the control, which constituted no heatwave but natural stochastic temperature variability (0HW), two treatments were applied: (b) two late-spring heatwaves (June, July) followed by a summer heatwave (August; 3HW) and (c) a summer heatwave only (1HW). The 3HW treatment was applied to test whether preconditioning events can modulate the potential sensitivity to the summer heatwave. Despite the variety of responses measured in both species, only *Z. marina* growth was impaired by the accumulative heat stress imposed by the 3HW treatment. Photosynthetic rate, however, remained high after the last heatwave indicating potential for recovery. Only epibacterial abundance was significantly affected in *F. vesiculosus*. Hence both macrophytes, and in particular *F. vesiculosus*, seem to be fairly tolerant to short-term marine heatwaves at least at the intensities applied in this experiment (up to 5°C above mean temperature over a period of 9 days). This may partly be due to the fact that *F. vesiculosus* grows in a highly variable environment, and may have a high phenotypic plasticity.

KEYWORDS
Baltic Sea, extreme events, foundation species, *Fucus*, heat stress, macrophytes, marine heatwaves, *Zostera*

1 | INTRODUCTION

Current climate models predict not only an increase in average global temperatures but also increased climate variability characterized by extreme events as heatwaves, floods and storms (IPCC, 2013). Over the past 90 years (1925–2016) both the northern and the southern hemispheres experienced marine heatwaves with increasing intensity (17%) and frequency (34%), resulting in an increase of annual marine heatwave days by 54% (Oliver et al., 2018). Such extreme events, of sustained hot temperatures, cause noteworthy impacts on humans and local economies and affect terrestrial and marine ecosystems (Easterling et al., 2000; Walther et al., 2002) in various ways, such as by causing species range contractions and extirpations of marginal populations (Smale & Wernberg, 2013; Wernberg et al., 2016). For example, a marine heatwave in early 2011 in Western Australia caused a range contraction of the habitat forming macrophyte *Scytothalia dorycarpa* by ~100 km, which is ~5% of its global distribution (Smale & Wernberg, 2013). In Central Europe, 3 weeks of extreme temperatures in summer 2003 (Schär & Jendritzky, 2004) led to sea surface temperatures (SST) of up to 28.8°C in the Mediterranean Sea, about 2.2°C above mean annual maximum temperature (Marbà & Duarte, 2010). Another heatwave hit the same region in 2006 resulting in temperatures of up to 28.5°C. Both heatwave events caused high mortality of the seagrass *Posidonia oceanica*, with long-lasting ecosystem-wide consequences (Marbà & Duarte, 2010).

Marine macrophytes, that is, seaweeds and seagrasses, represent the dominant flora in coastal ecosystems worldwide. They are ecosystem engineers (Miller et al., 2018; Teagle, Hawkins, Moore, & Smale, 2017) that provide a suite of ecologically valuable functions such as nutrient cycling, carbon sequestration and sediment stabilization (Krause-Jensen & Duarte, 2016; Smith, 1981). They provide habitat to a range of other dependent marine flora and fauna (Christie, Norderhaug, & Fredriksen, 2009; Sogard & Able, 1991; Thomaz & Cunha, 2010) and also act as nursery grounds to diverse juvenile fishes (Cheminée et al., 2013). Hence, macrophytes support one of the most productive and diverse coastal marine ecosystems (Kumar, Kuzhiumparambil, Pernice, Jiang, & Ralph, 2016; Thomson et al., 2015), which also provide a range of commercially important products such as nutraceuticals, pharmaceuticals, food for humans and animals, soil conditioner, biofuels and hydrocolloids (Holdt & Kraan, 2011). Seagrass meadows in particular are important as a nursery ground for a range of economically important fish (Heck, Hays, & Orth, 2003). The brown seaweed *Fucus vesiculosus* is a perennial species that inhabits cold and temperate regions on the Eastern and Western North Atlantic. The eelgrass *Zostera marina* is the most widely spread and often dominant marine angiosperm in the northern hemisphere (Den Hartog, 1970), providing many of the above-mentioned ecosystem services (Hughes & Stachowicz, 2009; Rönnbäck et al., 2007). Thus, their response to climate change, including an increase in the occurrence of extreme events such as marine heatwaves can potentially determine the fate of the related ecosystems and the provided ecosystem functions and economic services.

Temperature can affect various physiological traits of macrophytes, while the magnitude and extent of thermal stress determines the severity of effects. Photosynthesis, the source of carbon and energy in plants, is highly responsive to temperature, following a typical optimum curve (with increasing temperature, the photosynthetic rate increases gradually until reaching its highest rate at optimal temperature, followed by a rapid decrease of photosynthetic rate at temperatures above the optimum, due to damage to the photosystem; Bulthuis, 1987; Graiff, Bartsch, Ruth, Wahl, & Karsten, 2015). The photosynthetically gained energy is allocated into growth, reproduction and cell maintenance, and defence mechanisms against grazers, epiphytes and pathogens. Extremely high temperatures, in turn, can cause stress responses in macrophytes, which may include an overall lower energy input and a reallocation of energy normally used for growth into mechanisms preventing cell damage (e.g. production of heat shock proteins and superoxide dismutase; Bergmann et al., 2010; Harvell, 1998; Ireland et al., 2004; Jueterbock et al., 2014; Winters, Nelle, Fricke, Rauch, & Reusch, 2011). Furthermore, increased temperatures can promote the abundance and/or activity of grazers, pathogens and epiphytes (Harvell et al., 2002; Wahl et al., 2010), which would require higher defence activity by macrophytes against these organisms (Harvell, 1998). Depending on a macrophyte's resilience capacity and fitness (e.g. stress tolerance, abundance of energy reserves, etc.) defence activity may be increased (Saha & Wahl, 2013), remain unaltered with increasing threat (Saha et al., 2014) or be decreased in cases of resource limitation (Sudatti, Fujii, Rodrigues, Turra, & Pereira, 2011). Specific components of the defence mechanism may also be impaired due to temperature stress (Weinberger et al., 2011).

The brown algae *F. vesiculosus* is generally prone to fouling by micro- and macroepibionts (Saha et al., 2012; Saha, Rempt, Grosser, Pohnert, & Weinberger, 2011; Wahl et al., 2010) and to grazing, for example, by the isopod *Idotea balthica* in the Baltic Sea (up to 95% loss of biomass, Kangas et al., 1982). At the same time, *F. vesiculosus* is known to be chemically well-defended against foulers (e.g. Brock, Nylund, & Pavia, 2007; Saha et al., 2011; Wahl et al., 2010) and grazers (Rohde, Molis, & Wahl, 2004). However, relatively little is known about its regulation of chemical defence upon temperature stress (but see laboratory experiments of Wahl et al., 2010; Weinberger et al., 2011). In contrast to *F. vesiculosus*, the chemical defence of *Z. marina* is poorly understood, despite being frequently found infected by the slime-net mould *Labyrinthula zosterae* (hereafter *L. zosterae*) causing seagrass wasting disease. This disease can be epidemic and caused nearly a complete collapse of the Atlantic eelgrass population in the 1930s (Muehlstein, 1989; Sullivan, Sherman, Damare, Lilje, & Gleason, 2013). Whether the infection of *Z. marina* with *L. zosterae* is more likely to increase under extreme temperature stress imposed by marine heatwaves is unknown.

There is a general understanding on how the physiology of macrophytes may respond to temperature stress, but there is a lack of understanding on how foundation species may react to temporally imposed stress from marine heatwaves in situ. Most of our knowledge to date comes from experiments conducted on single species

under constant temperature stress, neglecting potentially important features of the natural habitat such as fluctuating environmental variables (Wahl et al., 2015) along with a variety of potentially interacting abiotic and biotic factors. Abiotic factors include, for example, natural sunlight, diurnal and day-to-day fluctuations of temperature and natural nutrient concentrations. Biotic factors comprise the diverse community associated with the macrophyte ecosystems, ranging from microbes to grazers present on the macrophyte surface and in the water column, which interact with the macrophytes and respond to temperature themselves (Werner, Graiff, & Matthiessen, 2016).

Recently, Pansch et al. (2018) described a mesocosm experiment in which benthic in- and epi-fauna associated to macrophyte communities were subjected to different short-term heatwave regimes. Such experiments, which aim to maintain and manipulate 'near natural' conditions, involve trade-offs between ecological realism and replication. As a result, they often lack statistical power (Kraufvelin, 1998, 1999). Despite low replication, the results of Pansch et al. (2018) concluded that different species-level responses can drive changes at the community level, that the frequency of heatwaves can be an important factor determining changes in community structure and that species that do not respond to heatwaves (50% of all tested species) are rather tolerant to short-term heatwaves. In the present study, we report the effect of short-term heatwaves (with near-natural fluctuations) on the structurally important macrophytes *F. vesiculosus* (adults and germlings) and *Z. marina* (adults). We tested whether single and sequential heatwaves lead to an increase or decrease in sensitivity to thermal stress (when treatments were compared to the control and among each other) on *F. vesiculosus* and *Z. marina* populations of the Baltic Sea. *F. vesiculosus* germlings were included in the experiment, in order to determine whether early life-history stages (which are critical to maintain seaweed or seagrass beds; Coelho, Rijstenbil, & Brown, 2000) are more sensitive to environmental changes, as often proposed (Andrews, Bennett, & Wernberg, 2014; Capdevila et al., 2019; Coelho et al., 2000; Wernberg et al., 2010). We investigated the impacts of single and repeated heatwaves on crucial responses of *F. vesiculosus* and *Z. marina*, which included (a) photosynthesis and respiration of *Z. marina*, (b) growth rates of *F. vesiculosus* and *Z. marina*, (c) abundance of the *Z. marina* pathogen (*L. zosterae*) and *Z. marina*'s ability for defence against this pathogen (anti-*L. zosterae* defence), (d) abundance of epibacteria on *F. vesiculosus* and the macroalga's ability to deter epibacterial colonization (antibacterial defence), (e) defence against grazers in *F. vesiculosus* (antigrazing defence) and (f) survival and growth of *F. vesiculosus* germlings.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up and temperature treatments

The experiment was conducted from 6 May to 20 August 2015, using the Kiel Outdoor Benthocosm (KOB) at GEOMAR Helmholtz Centre for Ocean Research. The KOB is situated on a floating dock in the Kiel Fjord, southwestern Baltic Sea (see Wahl et al., 2015 for a detailed description of the facility). The KOB is organized in 12 experimental units, each consisting of a 1,500 L thermally insulated tank that is open at the top to allow for natural sunlight conditions. During the experiment, a constant flow-through (1,800 L/day) of unfiltered surface seawater from Kiel Fjord was supplied to each unit, which guaranteed availability of natural concentrations of nutrients and organic matter and daily fluctuations of abiotic conditions such as temperature, salinity, pH and oxygen. A water pump and a wave-generator induced water movement within each tank. Temperature was manipulated by a GHL feedback system (GHL Advanced Technology), controlling connected heaters and chillers independently in each tank (Wahl et al., 2015).

Three different temperature regimes were applied, each replicated in four independent tanks: (a) a control regime with no simulated heatwave, but natural stochastic temperature variability (0HW); (b) a three heatwaves treatment that simulated the occurrence of two spring/early summer heatwaves in June and July followed by a more severe heatwave in August (3HW); and (c) a one heatwave treatment that simulated a single more severe heatwave event in August (1HW). A generalized additive mixed model (GAMM) fitted to a 15 year temperature time series recorded at 1.5 m depth in the Kiel Fjord (data provided by the Marine Meteorology research unit of GEOMAR by F Nevoigt, U Hecht and K Bumke) was used to identify long-term changes and within-year temperature variability. The temperature profile of the year 2009 was selected for the control tanks (0HW), since this year constituted the lowest deviation from the GAMM (at 95% confidence interval; for detailed description of the model and the treatment justification, see Pansch et al., 2018). The same GAMM was used to identify temperature anomalies (Pansch et al., 2018). A temperature increase of at least 0.7°C/day over a period of two or more days was defined as a common heatwave within the Kiel Fjord, while increases up to 1.2°C/day occurred as well. A maximum temperature anomaly of 5.2°C above the average occurred twice in the 15 year time series. Hence, the first (June) and second (July) heatwaves of the 3HW treatment followed a temperature increase of 1.2°C/day over 3 days, remained at the target temperature (3.6°C above the average temperature of the year 2009) for 4 days and dropped to the control conditions over a period of 2 days. The heatwave in August, in the 3HW and 1HW treatments, increased by 1.7°C/day over 3 days, remained at the target temperature (5.2°C above the average temperature of the year 2009) for 4 days and dropped to the control conditions within 2 days. Naturally occurring stochastic and diel temperature fluctuations were included in all tanks to simulate near-natural background conditions (Figure 1). Maximum temperatures obtained for the control regime (0HW) was 20.4°C, while it was 25.2°C for 1HW and 3HW treatments (Figure 1).

2.2 | Macrophyte collection and distribution to the experimental units

Sixty *F. vesiculosus* attached to small rocks were collected from 0.5 m depth in the Kiel Fjord, western Baltic Sea (Bülk: 54°27′8.13″N,

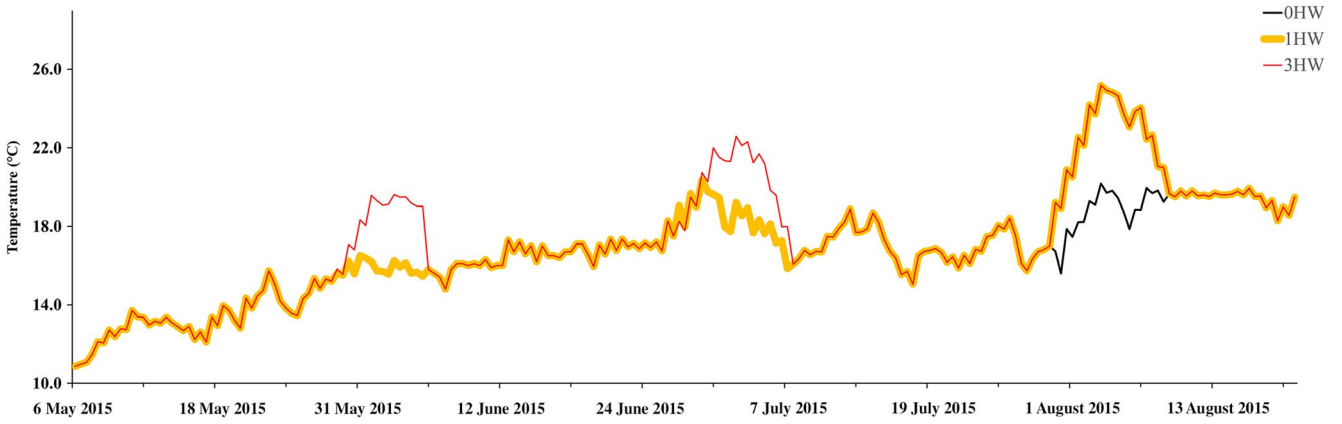

FIGURE 1 Implemented temperature regime within the experimental units over the experimental period (May–August 2015). Control (0HW), one summer heatwave (1HW) and two late spring/early summer heatwaves followed by a summer heatwave (3HW). Figure has been adapted from Pansch et al. (2018). The dates on *X*-axis are given as dd-mm-yyyy

10°11′58.42″E). The algae were transported in large coolers to the KOB facility within 2 hr after collection and five individuals were placed in each control and treatment tank, resulting in 20 individuals per temperature regime. Whole *Z. marina* plants were collected from an eelgrass meadow in the Kiel Fjord (Falkenstein: 54°24′24.69″N, 10°11′38.74″E) along a 100 m transect at 2–3 m depth. Plants were carefully dug out, placed in large coolers and transported to the KOB within 2 hr after collection. The plants were randomly distributed among the tanks after being planted into sediment-filled 5 L plastic boxes or 1 L plastic beakers (1:1 ratio of fine/mud-like and coarse/sand-like sediment). Every tank received 18 boxes with six plants in each box and 10 beakers with two plants each, resulting in a total of 134 plants per tank. In total, each temperature regime received 332 plants, resulting in 1,608 plants for the entire experiment. All response variables were analysed at the end of the experiment within 1 week after the third heatwave.

To recreate similar communities to those observed in the field, 14 common organisms found in *F. vesiculosus* beds and *Z. marina* meadows were added to the tanks (Pansch et al., 2018) in near-natural densities (Werner et al., 2016). Those included, amongst others, the bivalves *Cerastoderma edule* and *Mytilus edulis*, the amphipods *Gammarus salinus* and *Gammarus locusta*, the isopod *I. balthica*, the snail *Littorina littorea* and a number of sediment dwelling worms. The response of these organisms to the heatwaves has been published by Pansch et al. (2018).

Responses below of *Z. marina* and *F. vesiculosus* were measured on two individuals from each treatment tank and two individuals from each control tank. Thus, eight individuals were used for each treatment and eight individuals for control.

2.3 | *Z. marina* response variables

2.3.1 | Photosynthesis and respiration rates

In each tank, one beaker with two *Z. marina* plants was placed in a custom-built 6 L cylindrical incubation chamber equipped with a battery-run stirrer and an oxygen sensor spot (PreSens Precision Sensing GmbH) on the inside of the lid allowing optical oxygen measurements through the wall of the chamber. In addition, one beaker with sediment only was placed in a second incubation chamber and served as a control. Both incubation chambers (with and without *Z. marina*) were filled with water from the respective tank and remained inside the tank to guarantee incubation under similar conditions as experienced by the plants inside the experimental units. Photosynthesis and respiration were measured as changes in oxygen concentration over a 5 hr period. Photosynthesis was measured from 10:00 to 15:00, and respiration was measured after darkening the chambers from 15:00 to 20:00. Incubations for the 12 experimental units were performed on two consecutive days (six on each day). After the incubations, the surface area of the seagrass leaves was determined and used to normalize net photosynthesis and respiration rates (μg O_2 cm^{-2} hr^{-1}).

2.3.2 | Growth

Growth rate was measured on the same two plants (from each tank) used for the incubations described above. Growth marks, consisting of a small plastic ring open on one side, were carefully penetrated through each leaf 3 cm above the base (one ring per leaf) and growth was measured after 2 weeks. The same data were also used to calculate how long it takes to grow a new leaf (P_L). The hole in the seagrass leaves containing the plastic ring was similar in size to holes punched following general recommendations (Short & Coles, 2001). The ring assisted in finding the growth mark.

2.3.3 | Wasting disease and *L. zosterae* (pathogen) abundance

Two plants were randomly chosen from the boxes in each tank and were used to quantify wasting disease symptoms by counting the number of leaves with lesions. Subsequently, their leaves were frozen (−20°C) for quantifying *L. zosterae* abundance and defence capacity of *Z. marina* against *L. zosterae*. *L. zosterae* was quantified

using RTqPCR. For this, DNA was extracted using the Invisorb DNA plant kit (Stratek). The manufacturer's protocol was modified by adding 1 µl of untargeted salmon sperm DNA (Invitrogen, Life Technologies) at 500 ng/µl to saturate silica columns with DNA to increase the yield of target DNA (Bergmann et al., 2011). Cell numbers of *L. zosterae* were determined following a TaqMan-based RTqPCR assay (as described in Bockelmann, Tams, Ploog, Schubert, & Reusch, 2013), using a fluorescent labelled probe binding to the internal transcribed spacer region and standardized *L. zosterae* DNA solutions of known cell numbers.

2.3.4 | *Z. marina* defence capacity against *L. zosterae*

To quantify the defence capacity of *Z. marina* against *L. zosterae*, part of the frozen leaves mentioned above (Section 2.3.3) were freeze-dried, homogenized and extracted. Extraction was done at 1/16 of the natural concentration to facilitate good comparisons between treatments, since *Z. marina* extracts at natural concentrations strongly inhibit *L. zosterae* growth (Jakobsson-Thor, Toth, Brakel, Bockelmann, & Pavia, 2018). For this, 10 ml methanol/dichloromethane 1:1 was added to each sample for 1 hr, the resulting extract was filtered through a GF/F filter (pore size 0.45 µm) and the solvent was removed by evaporation (Speedvac, at 40°C). Each sample extract was redissolved in 0.5 ml serum seawater media (SSM) and 1% dimethyl sulphoxide. The SSM was prepared with 1 g glucose/L, 0.1 g pepton/L, 0.1 g yeast extract/L, 3 mg germanium dioxide/L, 10 ml horse serum/L, 25 ml streptomycin/penicillin (10 mg streptomycin/ml and 10,000 units penicillin) and dissolved in sterile-filtered sea water (35 psu). The inhibitory capacity of metabolites extracted from *Z. marina* on *L. zosterae* growth was investigated in a bioassay described by Martin, Boone, Caldwell, Major, and Boettcher (2009). Extracts were transferred to 6 well plates (Thermo Scientific), and an agar disc (Ø = 7 mm) containing *L. zosterae* was placed upside down in the centre of each well. The *L. zosterae* strain used in the assay was isolated from a seagrass meadow just outside the Kiel Fjord in 2015 (Bockelmann et al., 2013). SSM without *Z. marina* extract served as controls. The plates were sealed with parafilm and incubated in the dark at 25°C for 18 hr. Following incubation, the edge of each colony was outlined, photographed and ImageJ software was used to calculate the area of growth of *L. zosterae*.

2.4 | *F. vesiculosus* response variables

As for *Z. marina*, photosynthesis and respiration were determined for *F. vesiculosus*. However, sensor failure precluded reliable results.

2.4.1 | Growth in adults

In each tank, two of the five *F. vesiculosus* plants were chosen and two thallus tips per plant were marked by inserting a coloured thread 22 mm below the apical meristem 2 weeks prior to the end of the experiment. Growth rate was determined by comparing the distance between thread and thallus tip measured initially and at the end.

2.4.2 | Survival and growth of germlings

Additional *F. vesiculosus* were collected on 24 April 2015 to produce germlings in order to assess their sensitivity to heatwaves. Immediately after sampling, algae were transported to the laboratory in cooler boxes. Fertile receptacles were cut from the dioecious algae and the gender was determined under the microscope (Olympus BH-2), confirming 26 males and 54 females. Receptacles were rinsed in freshwater, blotted dry and stored in the dark at 10–12°C for 6 days (Al-Janabi, Kruse, Graiff, Karsten & Wahl, 2016). Twelve parental pairs were established by the combination of receptacles stemming from one male and one female alga. The receptacles of each parental pair were immersed in seawater (15–16 psu, mean salinity of Kiel Fjord) and exposed to aquarium light (110 µmol photons m^{-2} s^{-1}) to initiate the gamete release and fertilization (Al-Janabi et al., 2016). A volume of 40 ml of zygote solution was pipetted on the upper surface of a sandstone cube (2 × 2 × 2 cm) and zygotes were allowed to settle. Each sandstone cube received germlings of one parental pair and each tank received germlings of all parental pairs resulting in a total of 32 cubes (fixed to two plexiglass plates) and about 380 germlings per tank. The survival of *F. vesiculosus* germlings was determined as the percentage of surviving germlings between the beginning and the end of the experiment.

To determine the growth rate of germlings, digital images of 10–15 randomly chosen individuals per tank were taken at 40× magnification (Steen & Scrosati, 2004). Individual germlings were chosen randomly during the measurement, since germlings were too small for labelling. The side-view area of the germlings was measured with the image analysis software ImageJ. The mean area of germlings of each experimental population was calculated.

2.4.3 | Epibacterial abundance and *F. vesiculosus* defence capacity against fouling

From two individuals per tank, the biofilm was harvested by swabbing a sterile cotton tip over 1 cm^2 of algal surface (1 cm below the apical meristem). The cotton tip was vortexed for 30 s in an Eppendorf vial containing 1 ml of sterile-filtered seawater (16 psu) and 100 µl of the solution was transferred to a 96 well plate (Greiner). The relative abundance of diatoms (and any other possible photoautotroph) was determined by measuring the fluorescence of chlorophyll *a* at 477–491 nm (excitation) and 677 nm (emission), using a plate reader (Hidex Chameleon IV). Subsequently, the relative density of all microfoulers (including bacteria and diatoms) was determined by staining all particles in the same 100 µl subsample with the fluorescent DNA-binding dye Syto 9, 0.005 mM (Invitrogen GmbH). Following an incubation time of 10 min in darkness, fluorescence was measured (excitation 477–491 nm, emission 540 nm), using the same plate reader. The first measurement quantified the relative density of microalgae, while the second measurement quantified relative abundance of all epibiotic cells.

The same *F. vesiculosus* individuals used for abundance of microfoulers were used to test the defence capacity of *F. vesiculosus* against

fouling bacteria. Following the protocol of Saha et al. (2011), 12 algal thalli (<5 cm length) were dipped in a 1:1 solution of MeOH:Hexane for 4 s. The obtained extract was freeze-dried and redissolved in acetonitrile at fivefold concentration. The bottom and lower wall section of the wells in a 96 well plate (Greiner) were coated with the extract and the solvent was allowed to evaporate under a fume hood. Controls #1 for bacterial settlement rate were coated with equivalent amount of solvents only. Controls #2 for extract autofluorescence received the same extract loading. Then 100 µl of bacterial suspension was added to each well, except to control #2. The following strains were tested (with an optical density between 0.6–0.8): *Bacillus aquimaris* and *Cytophaga* sp., *Cobetia marina* (isolated from seawater), *Ulvibacter littoralis* (isolated from *Fucus serratus*), *Pseudoalteromonas* BSw 20057, *Alteromonadaceae bacterium* E1 (isolated from *Polysiphonia stricta*), *Vibrio* sp. and *Pseudoalteromonas* sp. (both isolated from stones). The defence capacity was quantified by the ratio of bacteria settled in the presence versus absence of extract.

2.4.4 | *F. vesiculosus* defence capacity against grazers

The defence capacity of *F. vesiculosus* against grazers was quantified following Rohde et al. (2004). For this, thalli of two individuals from each experimental unit were collected, freeze-dried for 48 hr, weighed and ground. Food pellets were made of each alga by mixing 0.5 g of powdered thallus with 2 ml of deionized water and adding it to a hot agar solution (0.18 g in 2.5 ml deionized water). The gelatinous mixture was quickly poured onto a piece of gauze (mesh size 1.5 mm) and squeezed between two sheets of paper. After cooling for 10 min, the hardened agar sheet with the gauze was cut into 1 × 1 cm food pellets. For the feeding experiment, Petri dishes were filled with seawater (16 psu) and one treatment pellet and one control pellet were added to each dish. *I. balthica* (isopods, common grazer of *F. vesiculosus*) was collected from the Kiel Fjord, and single individuals were placed into each Petri dish. Petri dishes were placed in a climate chamber (20°C) under dark conditions. The experiment was stopped for each Petri dish independently, when approximately 50% of one pellet in a dish was eaten. Using the mesh squares of the gauze as a reference, the amount of pellet eaten was quantified. Five subreplicates were used per treatment level to account for the possible variation in feeding rates. Preference ratios were calculated based on the amount of treated and control pellets consumed.

2.5 | Statistics

Each experimental unit (or tank) served as a true replicate (n = 4 for each treatment, n = 4 for control). Each replicate was the mean of two individuals measured per experimental unit. Generalized linear mixed models (GLMM) and permutation-based ANOVAs (PERMANOVA) were used to test the effect of treatments on each variable measured.

The GLMM (Bolker et al., 2009; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) were preformed using the lme4 package from the software R (Bates et al., 2017). The heatwave treatments were included as fixed effects, testing the hypotheses that 1HW is different from 0HW, 3HW is different from 0HW and 1HW is different from 3HW. Since the KOB experimental units (tanks) are arranged in pairs (6 × 2 pairs) along a floating platform and the treatments were equally spaced between units, the identity of these pairs was considered as a random intercept adjusting potential sources of variability related to the spatial arrangement of tanks. The gamma distribution and a logarithmic link function were used for all models. Differences between treatments were expressed as logarithmic response ratios calculated using the GLMM estimates (see a detailed description of the calculations in Data S1). Diagnostic plots of residuals were visually inspected for every model (see Figure S1).

For the PERMANOVA approach, the PERMANOVA+ add-in (Anderson, Gorley, & Clarke, 2008) for PRIMER v7 (Clarke & Gorley, 2015) was used. Although the use of permutations in PERMANOVA avoids an assumption of normality for each of the variables, there is still an assumption of homogeneity of dispersions among treatments. This was assessed using the PERMDISP routine and for the majority of variables there was no significant heteroscedasticity (p > .05). A log transformation was used to stabilize the variance of *Z. marina* photosynthesis measurements. PERMANOVA is known to be robust to small departures from homogeneity, so no transformation was used for *F. vesiculosis* germling survival (PERMDISP p = .050). The variance of counts of epibacteria on *F. vesiculosis* could not be stabilized, so an alternative nonparametric test (ANOSIM; Clarke & Green, 1988) was used to check the PERMANOVA results. For each variable a one-way PERMANOVA (999 unrestricted permutations of the raw data, Type III sum of squares) with subsequent pairwise tests was implemented.

3 | RESULTS

3.1 | *Zostera marina*

The results of the GLMM revealed that five out of the seven response variables measured for *Z. marina* did not change significantly with applied heatwave treatments (Figure 2, Table 1). Growth, however, was affected by the accumulative heat stress (3HW), which reduced the growth rate by 40% (0HW: 2.65 ± 0.63 cm/day; 1HW: 2.45 ± 0.75; 3HW: 1.59 ± 0.62 [mean ± *SD*]) and increased the time to produce a new leaf by 52% (P_L 0HW: 13 ± 3 days; 1HW: 12 ± 2; 3HW: 27 ± 18). In contrast, net photosynthesis rates were similar between treatment and control tanks (0HW: 0.55 ± 0.33 µg O_2 cm^{-2} hr^{-1}; 1HW: 0.61 ± 0.28; 3HW: 0.59 ± 0.38). Respiration rates changed among treatments; however, no significant differences were found due to the high variability between replicates (0HW: 0.27 ± 0.07 µg O_2 cm^{-2} hr^{-1}; 1HW: 0.58 ± 0.51; 3HW: 0.18 ± 0.24). The abundance of wasting disease, the abundance of *L. zosterae* and the defence against *L. zosterae* were not affected by the applied treatments. Signs of wasting disease were low with 19.5 ± 5.3% (0HW), 12.0 ± 9.5% (1HW) and 15.0 ± 8.1% (3HW) of leaves with lesions. The defence capacity against *L. zosterae* was not affected by the heatwave treatments, with growth inhibition of *L. zosterae* being 58 ± 9% in 0HW, 52 ± 17.9% in 1HW and 46 ± 16.9% in

3HW. In contrast to the GLMM, PERMANOVA revealed a significant difference between treatments only in *Z. marina* leaf production, while *Z. marina* growth was (marginally) insignificant ($p = .078$). Furthermore, pairwise tests revealed that the differences were found between the 1HW and 3HW treatments, and that neither of these differed significantly from the control (0HW) treatment.

3.2 | *Fucus vesiculosus*

GLMM indicated that none of the response variables for *F. vesiculosus* changed significantly between treatment and control tanks, except for the abundance of epibacteria (Figure 2, Table 1). Epibacterial abundance was significantly lower in 1HW ($1.5 \times 10^3 \pm 4{,}400$ cells/cm^2) compared to 0HW tanks ($3.0 \times 10^3 \pm 1{,}500$ cells/cm^2), while they were similar in the 3HW (3HW: $2.7 \times 10^3 \pm 8{,}050$ cells/cm^2) and 0HW tanks. Growth rates of adult algae were 0.67 ± 0.08 mm/day in 0HW, 0.45 ± 0.40 in 1HW, and 0.57 ± 0.36 in 3HW. Growth rates of *F. vesiculosus* germlings were 0.74 ± 0.66%/day in 0HW, 0.90 ± 0.44 in 1HW and in 0.75 ± 0.52 in 3HW. Survival of germlings was generally high with 92 ± 5.1% in the control and 87 ± 4.35% in 1HW and 85 ± 17% in the 3HW treatment. The defence capacity of *F. vesiculosus* against bacterial foulers and grazers was not significantly affected by the heatwave treatments. PERMANOVA (Table 2) followed the GLMM results, revealing a significant change due to applied treatments in epibacterial abundance only. As dispersions could not be stabilized, a nonparametric ANOSIM test was used to confirm the significance of this difference (ANOSIM $R = 0.523$, $p = .012$). Pairwise tests showed that the difference was only between the 0HW and 1HW treatment.

4 | DISCUSSION

Although there is a growing body of literature on the possible effects of temperature stress on macrophytes and their related ecosystems (Duarte et al., 2018), very few studies attempted to conduct experiments applying realistic heatwave regimes (but see Ehlers, Worm, & Reusch, 2008; Winters et al., 2011), and even fewer studies mimicked near-natural conditions i.e. including natural seasonality, stochastic and daily variability (but see Pansch et al., 2018). In order to overcome the lack of near-natural experiments, we used an outdoor mesocosm approach. Our experiment: (a) was conducted in relatively large mesocosms to overcome the limits of small-scale laboratory

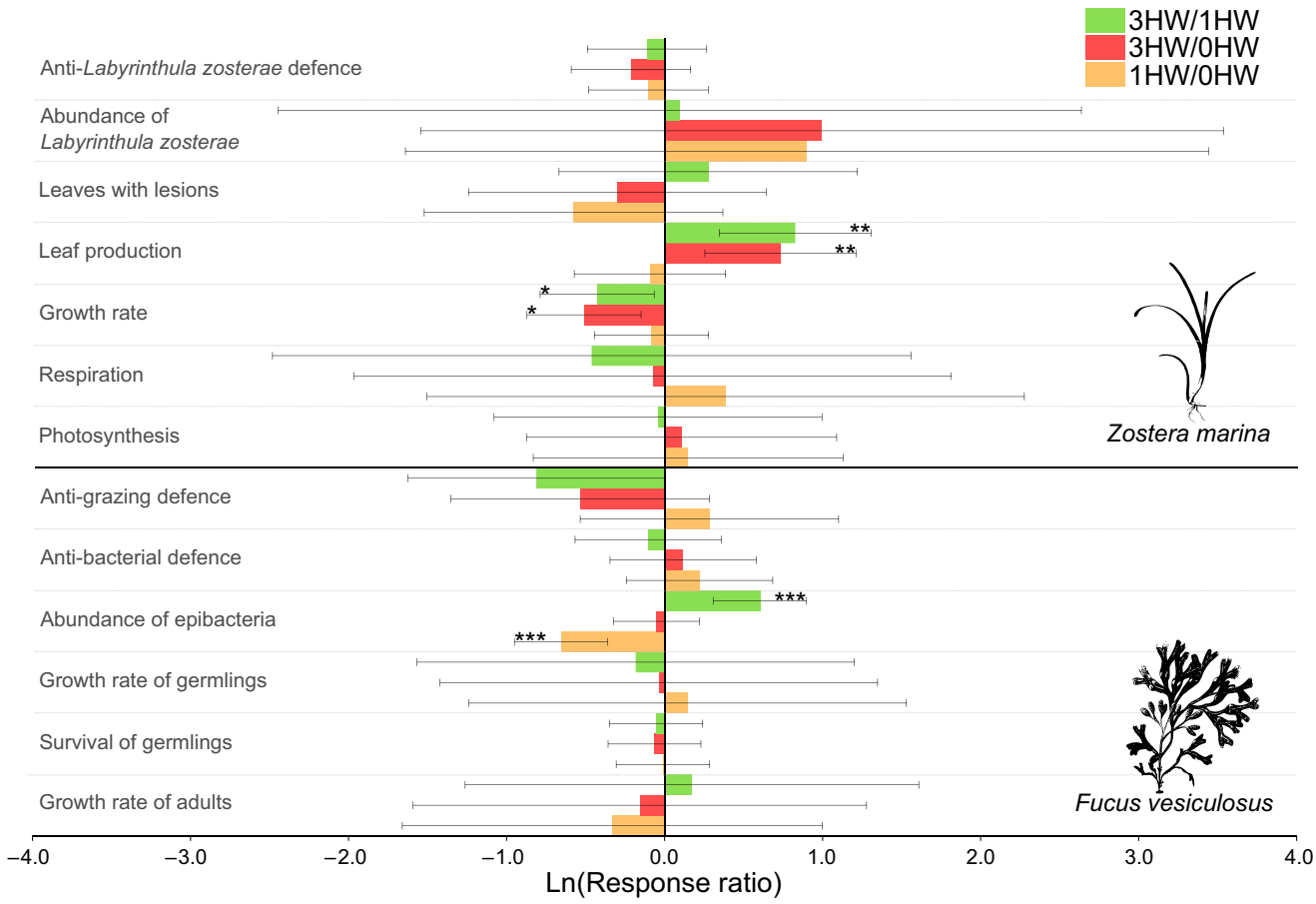

FIGURE 2 Mean logarithmic response ratios for 13 response variables measured in *Zostera marina* and *Fucus vesiculosus*, showing the proportional change in the means of one heatwave (orange, 1HW/0HW) and three heatwaves (red, 3HW/0HW) treatments in relation to the 0HW, and 3HW in relation to 1HW (green, 3HW/1HW). Response ratios and 95% confidence intervals were estimated using generalized linear mixed models. Asterisks show logarithmic response ratios significantly different from 0 (*$p \leq .05$, **$p < .01$ and ***$p < .001$), meaning that the ratio between numerator and denominator was different from 1 (0 in logarithmic scale)

TABLE 1 Generalized linear mixed model results for different response variables measured in *Zostera marina* and *Fucus vesiculosus*, in response to one heatwave (1HW) and three heatwaves (3HW) treatments in relation to 0HW, and 3HW in relation to 1HW (3HW/1HW)

Macrophyte	Response variable	Treatment	Mean	*z* value	*p* value
Z. marina	Photosynthesis	1HW/0HW	0.15	0.302	.951
		3HW/0HW	0.11	0.218	.974
		3HW/1HW	−0.04	−0.079	.997
	Respiration	1HW/0HW	0.39	0.401	.915
		3HW/0HW	−0.07	−0.077	.997
		3HW/1HW	−0.46	−0.447	.895
	Growth rate	1HW/0HW	−0.08	−0.452	.894
		3HW/0HW	−0.51	−2.769	.016
		3HW/1HW	−0.43	−2.317	.050
	Leaf production	1HW/0HW	−0.09	−0.381	.923
		3HW/0HW	0.73	3.002	.008
		3HW/1HW	0.83	3.384	.002
	Leaves with lesions	1HW/0HW	−0.58	−1.195	.456
		3HW/0HW	−0.30	−0.623	.808
		3HW/1HW	0.28	0.573	.834
	Abundance of *Labyrinthula zosterae*	1HW/0HW	0.90	0.695	.767
		3HW/0HW	1.00	0.769	.722
		3HW/1HW	0.10	0.074	.997
	Anti-*Labyrinthula zosterae* defence	1HW/0HW	−0.10	−0.528	.858
		3HW/0HW	−0.21	−1.104	.512
		3HW/1HW	−0.11	−0.576	.833
F. vesiculosus	Growth rate of adults	1HW/0HW	−0.33	−0.488	.877
		3HW/0HW	−0.16	−0.215	.975
		3HW/1HW	0.17	0.236	.970
	Survival of germlings	1HW/0HW	−0.01	−0.070	.997
		3HW/0HW	−0.06	−0.426	.905
		3HW/1HW	−0.05	−0.356	.933
	Growth rate of germlings	1HW/0HW	0.15	0.207	.977
		3HW/0HW	−0.04	−0.052	.999
		3HW/1HW	−0.18	−0.259	.964
	Abundance of epibacteria	1HW/0HW	−0.66	−4.366	<.001
		3HW/0HW	−0.05	−0.373	.926
		3HW/1HW	0.60	4.021	<.001
	Antibacterial defence	1HW/0HW	0.22	0.938	.616
		3HW/0HW	0.12	0.500	.871
		3HW/1HW	−0.10	−0.437	.900
	Antigrazing defence	1HW/0HW	0.28	0.659	.787
		3HW/0HW	−0.53	−1.300	.395
		3HW/1HW	−0.81	−1.959	.123

investigations and to reduce potential impacts from wall effects; (b) included the natural variability in temperature (in contrast to a steady-state temperature regime); (c) had a constant flow-through system utilizing unfiltered seawater directly from the Fjord (no storage tank) and thus a natural supply of plankton, microbes, nutrients at ecologically relevant concentrations; (d) allowed natural light conditions; and (e) included a number of macrophyte-associated organisms, which potentially entailed indirect heatwave effects on macrophytes.

Both habitat-forming macrophytes, *Z. marina* and *F. vesiculosus*, showed little or no response to the occurrence of a single 9 day summer heatwave or successive 9 day heatwaves from late spring to summer (9 days = 3 days of temperature increase, 4 days of sustained high temperature and 2 days of temperature decrease). At the end of the experiment, the only significant effect from the applied heatwave treatments was found in the growth of *Z. marina* (linear extension rates and time required for leaf production) after three

TABLE 2 Summary of PERMDISP and PERMANOVA tests for differences among treatments in response variables from *Zostera marina* and *Fucus vesiculosus*. Missing values: the number of missing replicates for that variable. Pairwise: pairwise PERMANOVA tests with $p < .05$ (all other pairwise tests with $p > .05$)

Macrophyte	Response variable	Missing values	PERMDISP		PERMANOVA		Pairwise
			F	*p*	*F*	*p*	
Z. marina	Log photosynthesis	2	2.070	.280	0.551	.580	
	Respiration	2	1.199	.640	0.078	.948	
	Growth rate	1	2.679	.142	3.723	.078	3HW, 1HW
	Leaves with lesions		0.544	.732	0.811	.477	
	Leaf production		4.499	.159	2.478	.049	3HW, 1HW
	Abundance of *Labyrinthula zosterae*		0.370	.275	0.236	.987	
	Anti-*Labyrinthula zosterae* defence		1.339	.352	0.542	.620	
F. vesiculosis	Growth rate of adults		1.932	.349	0.481	.675	
	Survival of germlings		3.974	.050	0.367	.842	
	Growth rate of germlings		0.448	.675	0.102	.911	
	Abundance of epibacteria	1	42.102	.002	6.460	.034	0HW, 1HW
	Antibacterial defence		2.387	.206	1.762	.215	
	Antigrazing defence	1	0.756	.553	0.727	.497	

successive heatwaves, and in the abundance of *F. vesiculosus* epibacteria after one heatwave. Although the growth of *Z. marina* was reduced by the sum of three consecutive short-term heatwaves, the maintained photosynthetic rate can likely restore *Z. marina*'s biomass after the heatwaves. Furthermore, potential indirect heatwave effects through changes in the abundance of the associated fauna could not be detected. Indeed, the fauna with potentially the strongest effect on macrophytes (the grazer community) did not change in abundance and biomass (Pansch et al., 2018). This fauna includes the snail *L. littorea* that grazes upon *F. vesiculosus* and *Z. marina* epiphytes, thereby sustaining high light availability for photosynthesis, and the grazer *I. balthica* feeding preferably on *F. vesiculosus*.

In contrast to the present study, Pansch et al. (2018) found mixed responses of the macrophyte-associated invertebrate community to the simulated heatwaves of the same experiment. About 50% of the benthic, free living and infaunal species showed either positive or negative responses in abundance and/or biomass demonstrating a large range of invertebrate susceptibilities to heatwaves leading to shifts in community structure (Pansch et al., 2018).

In contrast to the findings by Winters et al. (2011), showing that a continuous 3 week heatwave treatment impaired seagrass photosynthesis, our results showed that photosynthesis was not affected by a single or several 9 day heatwaves. This indicates that the length of heatwaves is likely critical with respect to the detrimental impact of increased temperatures on species and communities. Indeed, an optimum temperature range between 25 and 30°C was found during a short-term experiment with *Z. marina* of the temperate East coast of the USA (Marsh, Dennison, & Alberte, 1986), suggesting that the temperature initially increases the activity of photosynthesis-related enzymes. Elevated temperatures over longer time periods (weeks), however, damages the photosystems of *Z. marina* and leads to reduced photosynthetic rates (Bulthuis, 1987; Nejrup & Pedersen, 2008). Respiration rates likewise did not vary significantly in the current experiment between controls and treatments after the more severe summer heatwave, indicating that these extreme events had no lasting effects on the *Z. marina* metabolism.

We hypothesized that high temperatures would increase the abundance and activity of pathogens in *Z. marina*, resulting in a further increase in the energy invested into antimicrobial defence and repair of damage caused by pathogens. However, the assessment of microorganisms at the end of the experiment revealed that heatwaves did not affect the abundance of *L. zosterae* or wasting disease symptoms on *Z. marina* leaves. Contrary to our hypothesis, a study in the Mediterranean found a decrease in wasting disease lesions with increasing temperature, although on different seagrass species (*Cydomocea nodosa* and *P. oceanica*; Olsen & Duarte, 2015; Olsen, Potouroglou, Garcias-Bonet, & Duarte, 2015). This suggests that heatwaves in general do not seem to foster detrimental effects on *Z. marina* through wasting disease. Furthermore, there was no difference in anti-*L. zosterae* defence of *Z. marina* among the treatments. In contrast to studies on phenolic acids, considered as deterrents of *L. zosterae* and known to decrease with warming (Vergeer, Aarts, & De Groot, 1995), an abrupt increase of temperature for few days did not reduce the production of inhibitory compounds against *L. zosterae* in the present study. Altogether, little is known about how a changing environment affects secondary metabolites in seagrasses (Zidorn, 2016). Identification of the inhibitory compounds is required to gain a deeper understanding on the effects from extreme heat stress on chemical defences against *L. zosterae*.

Zostera marina growth (linear extension and time required for production of new leaves) was significantly reduced in the 3HW

treatment. Since growth is an integrative response (here measured over a period of ~2 weeks), changes in this variable indicate that metabolic rates were likely affected during the heatwaves (e.g. higher respiration rates and loss of carbon), leading to overall reduced growth. Similar findings were previously reported for *Z. marina* in the Baltic Sea at elevated temperatures over extended periods of time (25°C for 6 weeks; Nejrup & Pedersen, 2008) and elsewhere (reviewed in Lee, Park, & Kim, 2007). The fact that this effect has been only found in the 3HW treatment may indicate that abnormal temperatures led to an imbalance of the carbon budget (photosynthesis vs. respiration), not only in summer, but also in spring. Thus, spring heatwaves may have detrimental accumulative effects on the physiology of *Z. marina* rather than a 'hardening' effect towards the summer heatwave as postulated (Wahl, Saderne, & Sawall, 2016; Walter, Jentsch, Beierkuhnlein, & Kreyling, 2013).

Reduced growth and prolonged leaf production rates may entail a decrease in biomass, in particular, if seagrass consumption is high. In the Baltic Sea, however, there is no evidence for significant *Z. marina* consumption. In the neighbouring North Sea, *Z. marina* consumption was estimated to be <10% of the annual production, where the main consumers are birds and the isopod *Idotea chelipes* (Nienhuis & Groenendijk, 1986). In the Baltic Sea, the isopod *I. balthica* (inhabiting a similar ecological niche as *I. chelipes* in the North Sea; Leidenberger, Harding, & Jonsson, 2012) was included in the mesocosms, but was not found to feed on *Z. marina* (no evident grazing marks, Y. Sawall, personal observation). Therefore, we conclude that even though *Z. marina* growth is impaired by three heatwaves, overall, short-term heatwaves may not necessarily be detrimental. Also, the capacity of *Z. marina* to store large amounts of carbon (energy) in rhizomes (up to 90%; Olsen et al., 2016), may allow for buffering short-term stress events such as heatwaves (Carruthers & Walker, 1997).

In contrast to *Z. marina*, *F. vesiculosus* did not show growth inhibition at temperatures up to 25.2°C, indicating that *F. vesiculosus* in the western Baltic Sea is well acclimatized to temperature anomalies above 20°C. This might be explained by adaptations of *F. vesiculosus* to its habitat, being in shallow water where thalli often reach the surface and can even desiccate. On calm and sunny days in summer, temperatures can reach up to 30°C within the first few decimetres (Wahl et al., 2010). Although these temperature peaks are usually very short (few hours), dropping down to normal summer SST at night (~18–19°C; supporting information in Pansch et al., 2018), the generally strong temperature variability is likely to facilitate higher thermal tolerance in *F. vesiculosus* with respect to heatwaves. Seagrass, in contrast, grows slightly deeper and is less exposed to temperature fluctuations. A comparatively high thermal tolerance of western Baltic Sea *F. vesiculosus* is further supported by a laboratory study where *F. vesiculosus* was able to survive temperatures of 26–27°C for 3 weeks (Graiff et al., 2015).

In line with adult *F. vesiculosus* growth, growth and survival of their germlings were also unaffected by the heatwaves. Our results on germling survival are in contradiction to those observed for the brown algae *Cystoseira zosteroides* (order *Fucales*) growing in slightly deeper water, where a reduction in germling survivorship of 42% and 67% at 20 and 24°C were reported from the Mediterranean Sea (Capdevila et al., 2019). Contradictory results were also obtained by Andrews et al. (2014) for the brown seaweed *S. dorycarpa* (order *Fucales*), where temperatures greater than 20°C delayed germling settlement and increased mortality rates, with no germlings surviving at temperatures above 23°C. In an earlier study with *F. vesiculosus* populations from the Baltic Sea, it was found that warming of mean water temperatures (Δ5°C) over a period of 12 weeks in spring and early summer increased growth rates of *F. vesiculosus* germlings, while warming in late summer (Δ5°C, 12 weeks) decreased their survival (Al-Janabi et al., 2016). In an extensive review by Lüning (1984), the upper temperature limits for germling survival in temperate brown seaweeds were found to be in the range of 18°C (*Chorda tomentosa*) t.0o 28°C (*F. vesiculosus* and *F. spiralis*). Our results, together with previous findings, indicate that the offspring of some shallow water macrophytes (unlike subtidal species like *Cystoseira* and *Scytothalia*) display a rather high thermal tolerance, therefore, remaining unaffected by short-term marine heatwaves.

Antibacterial defence of *F. vesiculosus* was not affected by the heatwave treatments. In earlier studies, production of defence metabolites by *F. vesiculosus* were found to be unaffected by temperatures up to 25°C over a period of 4 weeks (Saha et al., 2014). Thus, the absence of an effect of heatwaves may not be surprising, at least with respect to net defence strength. The antibacterial net defence of *F. vesiculosus* is a product of several active metabolites, with some of them being up- or down-regulated when temperature changes (Saha et al., 2014). Despite maintained antibacterial defence, epibacterial abundance on the surface of adult algae was significantly reduced in 1HW. This may be explained by an increased abundance of the grazing isopod *Gammarus locusta* in the same treatment (Pansch et al., 2018). *G. locusta* feeds on *F. vesiculosus* macro-epibionts and may thereby remove parts of the epibacterial biofilm. Heatwaves also did not have a significant effect on *F. vesiculosus* palatability for *I. balthica* grazing. This may be explained by the fact that the abundance and biomass of *I. balthica* remained unaffected by the applied short-term heatwaves (Pansch et al., 2018).

Given that growth and leaf production rate of *Z. marina* was negatively impacted by the three subsequent heatwaves, we may speculate that an increase in heatwave frequency and intensity, as predicted, may eventually reduce the abundance of *Z. marina*. This may only be mitigated by selection of more stress-resistant and phenotypically plastic *Z. marina* genotypes after heatwave events as suggested previously for the Baltic Sea (Bergmann et al., 2010; Franssen et al., 2011; Jueterbock et al., 2016; Winters et al., 2011). In contrast to the overall low impact of simulated heatwaves on the macrophytes, the macrophyte-associated invertebrate community showed substantial community shifts, in particular after three consecutive heatwaves (Pansch et al., 2018). These community shifts did not show immediate effects on the macrophytes, but could eventully lead to a negative feedback on the macrophyte community.

Mesocosm approaches have the potential to provide a more realistic understanding of the impacts of natural temperature extremes on marine communities than small-scale laboratory experiments (Wahl et al., 2015). They come, however, at the cost of considerably increased investment, which limits replication (in the present study n = 4 tanks for each temperature regime), and thereby statistical power (Kraufvelin, 1998, 1999). At the same time, environmental variability is higher in outdoor mesocosms than in more controlled indoor conditions, which may be a reason for the relatively high response variability observed in our study. A further explanation for a high response variability may be a generally high genotypic diversity in a species-poor coastal ecosystem of the Baltic Sea (Reusch, Ehlers, Hammerli, & Worm, 2005). This, in turn, was previously hypothesized to enhance ecosystem resilience due to its ability to buffer against extreme climatic events (Reusch et al., 2005). Additionally, the Baltic Sea currently provides combinations of multiple stressors that mimic those expected for many coastal areas in the future (Reusch et al., 2018), training organisms to tolerate abiotic stressors like acidification (Thomsen, Casties, Pansch, Körtzinger, & Melzner, 2013).

Our study aimed to understand the response of two foundation macrophytes to realistic heatwave scenarios of the Western Baltic Sea under near-natural conditions (e.g. presence of common associated faunal species and fluctuating abiotic conditions). Simulated short-term heatwaves, either as a single summer heatwave or as a series of two spring and one summer heatwaves, showed an overall low impact on the morphology, physiology and the chemical defence of *Z. marina* and *F. vesiculosus*. A negative impact was only evident in reduced growth of *Z. marina* under reoccurring heatwaves. While we cannot rule out the possibility of longer term effects, maintained photosynthesis and respiration indicate that recovery from biomass loss is likely. The high variability of response variables may partly be explained by the low replication of this mesoscale experiment. However, it can also be well explained by the fact that in particular *F. vesiculosus* is adjusted to a highly variable environment. The consequent high physiological and metabolic plasticity of *F. vesiculosus* may, therefore, be an indicator of its tolerance capacity (Wahl et al., 2011). While we cannot conclude that the species is resilient based on the experimental results alone, additional lines of evidence such as its habitat preferences suggest that certain populations may be well adapted to short-term extreme temperature fluctuations as applied in our study.

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AUTHOR CONTRIBUTIONS

M.S. and Y.S. wrote the paper. M.S. organized the data collection and assembly for this paper. F.R.B. and P.J.S. ran the statistical analysis. M.S. performed the antibacterial defence experiment, measured epibacterial abundance and growth measurements on *F. vesiculosus*. B.A. and J.N.S. performed the experiments on *F. vesiculosus* germlings. M.B. performed the antigrazing experiments with *F. vesiculosus*. J.B. and F.W. performed the *Labyrinthula* abundance experiment and counted the leaf production rate. S.J.T. performed the anti-*Labyrinthula* experiments. Y.S. and M.I. performed the photosynthesis and respiration experiments on *Z. marina*. Y.S. conducted the growth measurements on *Z. marina*. All co-authors contributed to the design of the study, to the final draft of the manuscript and to different experimental aspects of the study.

DATA AVAILABILITY STATEMENT

All data are available at PANGAEA database: https://doi.pangaea.de/10.1594/PANGAEA.904644

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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