

Pulsed pressure: Fluctuating impacts of multifactorial environmental change on a temperate macroalgal community

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Abstract

Global change impacts marine organisms and communities mainly through ocean warming, acidification, deoxygenation, and changes in nutrient inputs and water circulation. To assess the ecological impacts of global change, the effects of multiple interacting environmental drivers, including their fluctuations, should be tested at different levels of biological organization. In an outdoor mesocosm study, we investigated the differential effects of three simulated upwelling events coupled with ocean warming (1–5°C above ambient) on a temperate benthic community in the Western Baltic Sea. Ocean warming, especially in summer when temperatures are close to or above the physiological optimum of many species, is likely to impose thermal stress with species-specific impacts. As the properties of deep water vary seasonally, so will the effects of upwelling. Upwelling of cooler deep water in midsummer may alleviate thermal stress, although this mitigation may be modulated by upwelling-associated shifts in other water-quality parameters such as salinity, nutrients, or late-summer hypoxia. This investigation showed that in the Western Baltic Ocean warming was rather beneficial in early and late summer but detrimental when ambient temperatures were highest in midsummer. The effects of upwelling in the absence of ocean warming were generally weakly beneficial, while this effect tended to vanish with intensifying imposed ocean warming. Hypoxia associated with the late summer upwelling impacted some of the grazer species but did not impact the macroalgae. We conclude that in coastal temperate benthic communities, ocean warming is the predominant stressor that may partially and seasonally be buffered by upwelling.

Intensifying global change is a major driver of ecological change, with already many documented alarming manifestations (Harley et al. 2006). Yet, empirical (experimental) understanding of the complex nature of these impacts is needed to

develop improved predictive models of future impacts. Experimental research on the ecological impacts of global change faces a threefold challenge (Boyd et al. 2018): (1) upscaling from single to multiple drivers, (2) incorporating their natural and often asynchronous fluctuations in space and time (Gunderson et al. 2016), and (3) upscaling from physiological to community responses (Bates et al. 2018). In marine ecosystems, ecological realism requires considering the combined effects of numerous baseline-shifting drivers. These can be of mechanical, physical, chemical or biological nature. Depending on their synchronous or sequential occurrence, these shifting drivers can have synergistic, additive, or antagonistic effects (Gunderson et al. 2016; Kroeker et al. 2016). While the need for multistressor experiments designed to evaluate effects across ecological scales is increasingly recognized, it represents a major conceptual and practical challenge for researchers, which requires the consideration of compromises

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

Author Contribution Statement: M.W., C.P., and B.B. developed concept and set-up of the investigation. S.D., T.G.H., G.R., R.S., F.W., M.Y., and C.P. carried out the experiments and collected the data. F.W. and M.W. assembled the long-term abiotic data. F.R.B., J.V., and M.W. ran the statistical analyses. F.W. and M.W. archived the data. All co-authors contributed to the manuscript writing.

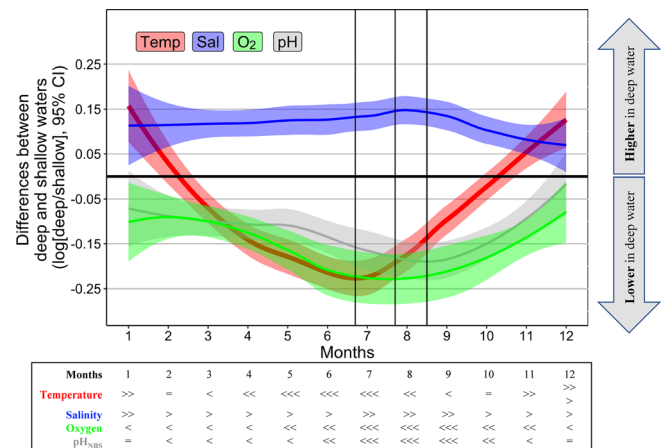
between complexity and feasibility (Boyd et al. 2018; Wake 2019). The number of drivers included in a single experiment must be selectively limited to avoid overstretching infrastructural and analytical resources. The most relevant drivers for coastal marine organisms may be the predicted changes in temperature, current and wave regimes, stratification, nutrient loads, oxygen levels, salinity, fishing, constructions, and chemical, noise and light pollution (Bindoff et al. 2019). In addition, each environmental driver may fluctuate with different frequencies and amplitudes (Vasseur et al. 2014; Gunderson et al. 2016). The temporal match or mismatch between fluctuations in stress intensity (defined by the timing, amplitude and duration of stressful events) and the biology of species will determine their survival and potential for acclimation and adaptation (Kroeker et al. 2019; Rilov et al. 2019).

Ocean warming (“warming” hereafter) is considered the paramount driver of many global change scenarios (Bates and Johnson 2020; Wahl et al. 2020). Its influence on metabolic rates exerts universal ecological shifts across levels of biological organization in marine systems (Brown et al. 2004; Schramski et al. 2015; Provost et al. 2017). Warming will—in a seasonally variable manner—interact with the setting of further environmental parameters. The ecologically most relevant parameters in coastal areas are salinity, oxygen, and—to a lesser extent and variable among functional groups—pH and nutrient levels (Kwiatkowski and Orr 2018). For instance, ocean warming promotes aquatic deoxygenation in several ways (Rabalais et al. 2009, 2014) by reducing the solubility of oxygen in water, enhancing thermal stratification, and accelerating microbial remineralization, ultimately resulting in oxygen depletion in subthermocline waters (Alvisi and Cozzi 2016; van Helmond et al. 2017; Breitburg et al. 2018). Conversely, at a regional and local scale, warming may be substantially mitigated by wind-driven coastal upwelling of cooler bottom waters (Varela et al. 2018; Suursaar 2020). This interaction between warming and upwelling is the focus of the current study. Upwelled cool waters can mask extreme heating events offering temporary thermal refugia to coastal communities, when occurring simultaneously (Chollett et al. 2010; Paalme et al. 2019). Upwelling may additionally modify nutrient concentrations, salinity, pH, and/or oxygen of surface waters. Since water temperature, primary production, stratification, and salinity all vary throughout the year with different frequency, periodicity, and amplitude, we can expect the resulting abiotic characteristics of the upwelled water to differ from one upwelling event to the other. In addition, these parameters are predicted to further shift with global change over the coming decades. Increased eutrophication trends in coastal surface waters (Andersen et al. 2017) may weaken the formerly beneficial fertilizing effect of upwelling through spring and summer. Ocean acidification may enhance the corrosive nature of upwelled water in summer and autumn (Melzner et al. 2013). However, the most alarming may be the

spreading of deoxygenated subsurface waters in shallow coastal systems worldwide (Diaz 2001). Upwelling of this deoxygenated deep water may cause severe mortalities in fishes and benthic invertebrates such as crabs (Grantham et al. 2004). We can presume that warming and upwelling may both be beneficial and detrimental depending on the timing of occurrence (Wahl et al. 2020), and when they co-occur their interaction can be expected to be anywhere on the gradient from antagonistic to synergistic.

Species differentially respond to environmental shifts driven by stressors such as warming and upwelling based on their traits and life histories. The sensitivity of a given organism may also depend on the stress history it has experienced within its lifetime (Walter et al. 2013) or across a selection process (Pansch et al. 2014; Al-Janabi et al. 2019). If the sensitivities of different ontogenetic stages and species to a given environmental setting differ, changes in the nature and strength of biological interactions may change, and ultimately lead to compositional shifts in the community.

Warming, deoxygenation, and increasing wind-driven upwelling intensity seems to progress particularly fast in the Baltic Sea (Carstensen et al. 2014; Gammal et al. 2017; Reusch et al. 2018). In this shallow, a tidal and rather land-locked sea (Medvedev et al. 2016) with a somewhat dampened current regime, physico-chemical properties may differ strongly between surface and bottom water bodies in summer due to a pronounced thermohaline stratification and notoriously high nutrient loads. In this season, subsurface waters tend to be more saline, colder, richer in nutrients, and poorer in oxygen (Lehmann et al. 2012; Paalme



Box 1. Mean multiyear differences (monthly mean, confidence level of 95%) between deeper and shallower waters in Kiel Fjord. Temp = temperature, Sal = salinity, O₂ = oxygen. When stratification starts in late spring, the deep water progressively turns cooler, more saline, richer in nutrients and more hypoxic as compared to surface waters. Upwelling effects differ among seasons, being inconspicuous in winter and inflicting increasing shifts in surface water conditions toward late summer (direction and strength of expected shifts are shown below the graph). The three simulated upwelling events are indicated by vertical black lines.

et al. 2019; Suursaar 2020) (Box 1). In winter, however, waters are well mixed and upwelling will hardly alter the physicochemical water properties in shallow habitats.

In the Baltic Sea, the communities associated to the foundation species *Fucus* spp. are among the most diverse and ecologically valuable (Kautsky et al. 1992). These communities are exposed to increasing environmental stress in the course of global change (Werner et al. 2016; Barboza et al. 2019), as are many productive and diverse macroalgae-based communities worldwide (Koch et al. 2013; Wahl et al. 2015b).

To appreciate the potential biological effects of multifactorial seasonal fluctuations of warming and intermittent upwelling, one must consider the width and location of species-specific physiological comfort zones and how far and for how long a given parameter deviates from optimal conditions (Sinclair et al. 2016; Vajedsamiei et al. 2021). The majority of the species in the investigated benthic community have immigrated from the North Sea into the Baltic Sea several millennia ago. The broad tolerance range with regard to most physicochemical water conditions allowed these species to persist in the extreme and highly fluctuating environmental conditions of this marginal sea (Pansch et al. 2014; Paalme et al. 2019), but with decreasing performance rates when environmental parameters lie below or above their optima (Wahl et al. 2020; Vajedsamiei et al. 2021). For *Fucus vesiculosus*, and most other organisms interacting with it, the physiological optima are found (with considerable variation) in a temperature range between 10°C and 20°C, a salinity range between 20 and 33, a pH range between 7.5 and 9, and an oxygen range between 6 and 10 mg L⁻¹ (Barboza et al. 2019; Wahl et al. 2020) (more information on species-specific requirements are presented in Supporting Information Table S1).

In an effort to assess the seasonally variable and interactive effects of warming and upwelling today and as projected for the future, we subjected natural temperate macroalgal communities to a set of warming scenarios and to artificially induced “upwelling” events in early summer, midsummer, and late summer. The latter consisted of replacing the surface-water flow-through by a flow-through with water pumped from 14 m depth, that is, from below the summer thermocline, for several days. This treatment will be called “simulated upwelling” in the following sections as previously done in similar studies (Taucher et al. 2017). Given the species-specific comfort zones, we hypothesized that the most important interacting taxa of this system, macroalgae, epiphytes, and mesograzers (Jormalainen et al. 2008), would respond differently to the upwelling events in early summer, midsummer, or late summer, and that these respective impacts would vary among warming scenarios (Box 1). Specifically, we predicted that: (1) warming may have beneficial effects when the ambient temperature is at suboptimal levels (in early summer or late summer), but is stressful to most organisms when levels are close to or higher than the species-specific thermal optima (in midsummer); (2) upwelling of cooler water may mitigate warming in warmest part of summer, but may be stressful to many but not all species

when the upwelled water is hypoxic in late summer; (3) differential responses of interacting species (macroalgae, grazers, foulers) may lead to interaction shifts and modulation of the direct impacts of warming or upwelling, or both; and (4) the compound impact of warming and upwelling changes across the different events within the summer season but is generally negative.

Methods

Detailed method on tank monitoring, fjord depth profiling, microfouling quantification, macroalgae-grazer interaction assessment can be found in the Supporting Information Data S1.

Experimental set-up and design

The experiment on community-level impacts of warming and intermittent upwelling events ran from the beginning of May to mid-September 2018 in the Kiel Outdoor Benthocosms (KOB) facility (see details in the Supporting Information Data S1 and in Wahl et al. 2015a). Briefly, this experimental facility consists of 12 insulated 1500-L tanks positioned on an aluminum float in the Kiel Fjord (54.330119°N, 10.149742°E, Southwestern Baltic Sea, Germany). Computer-controlled heaters and chillers allowed the maintenance of temperature offset levels of 0°C, 1°C, 2°C, 3°C, 4°C, and 5°C above the naturally fluctuating fjord water sea surface temperature (SST). These warming levels covered the plausible range of warming scenarios over the coming eight decades in the Baltic Sea (BACC 2015). The expected effects of seasonal upwelling are based on many years of water column profiling (Supporting Information Fig. S1). Pumps ensured that unfiltered fjord water was continuously flowing through each tank at a rate of approximately 7 L min⁻¹, that is, the complete volume of each tank was exchanged seven times per day. Upwelling events were simulated by switching between two intake pipes, pumping in fjord water from: (1) 1 m depth for the non-upwelled treatment level and phases between upwelling events, and (2) 14 m depth, which is well below the thermocline in summer (mostly at 3–6 and 8–11 m in the past 10 years; see Supporting Information Fig. S2). The crossed treatments (one of the six temperature levels, with or without intermittent upwelling) were distributed randomly among the 12 tanks. The warming treatments operated throughout the 4.5 months of the experiment. Simulated upwelling events were imposed in half of the tanks on 03 July–09 July (upwelling 1, “early summer”), 04 August–11 August (upwelling 2, “midsummer”), and 28 August–03 September (upwelling 3, “late summer”). In the upwelling-simulating tanks, after switching the intake pipes, surface water was replaced by the upwelled water at a rate of 7 tank volumes per day, recreating a gradual transition from surface to bottom conditions within 12–24 h (Fig. 1).

Assemblage of tank communities

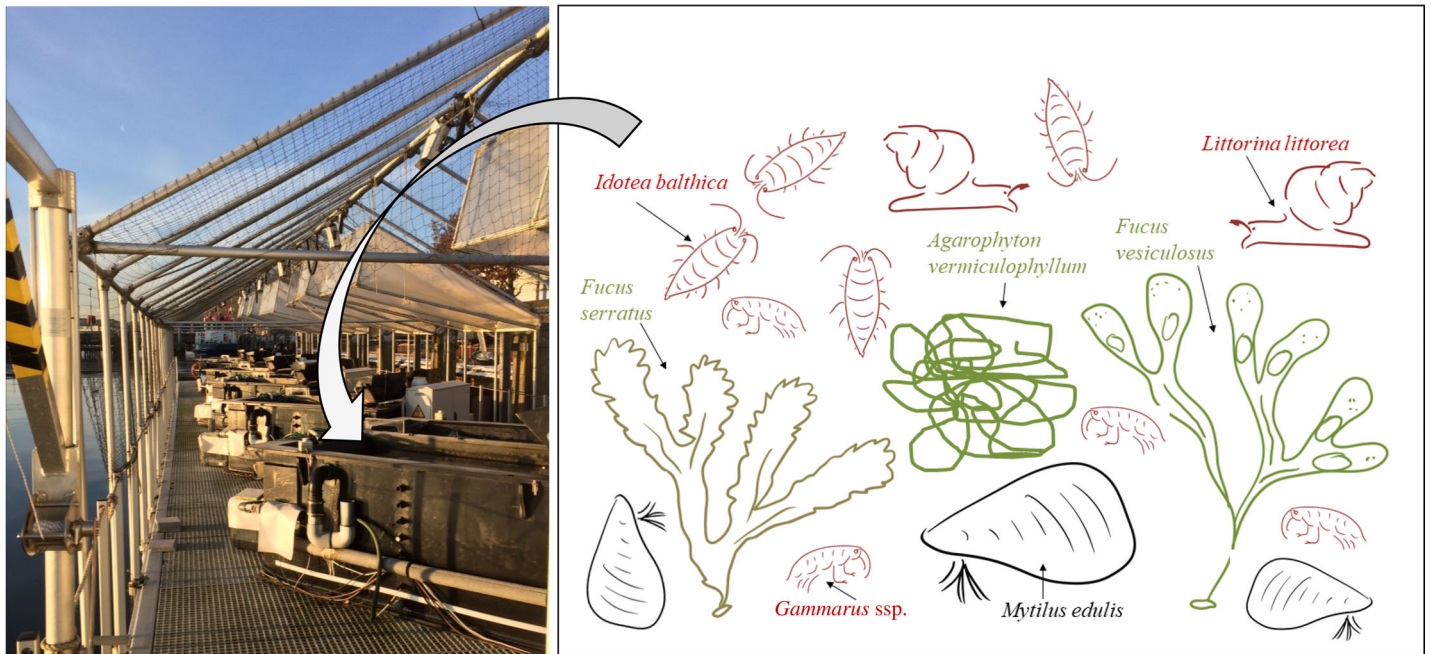
On 02 May 2018, we collected the native brown macroalgae *F. vesiculosus* (Bülk, 54.453976°N, 10.196955°E) and *Fucus serratus* (Kiekut, 54.449711°N, 9.8853131°E) together with their

Warming (°C) and simulated upwelling (black frames) treatments in the 12 tanks

| | | | | | |
|----|----|----|----|----|----|
| +4 | +0 | +3 | +2 | +2 | -5 |
| +5 | +3 | +4 | +0 | +1 | +1 |

“KOB2018”

Starting community in each tank (qualitative)



12 tanks on a floating platform

Fig 1. Experimental design of the study in the Kiel Outdoor Benthocosms in 2018 (KOB2018) showing the treatments (top left panel) in the 12 tanks (low left panel) and the components of the start community (low right panel) which slightly shifted during the experiment due to natural recruitment via the continuous inflow of unfiltered fjord water.

associated mesograzers, the isopod *Idotea balthica*, amphipods of the genus *Gammarus*, and the snail *Littorina littorea*. In this season, the algae are still free of macroepiphytes. Three individuals of each algal species were wet-weighted and placed in each tank, constituting similar wet weight biomasses in all tanks. The macroalgae were individually marked with colored cable ties and nonfertile thallus tips were tagged 22 mm below the terminal meristem with a fluorescent fishing line (i.e., “growth tag”) for growth assessment (see Wahl et al. 2020). The mesograzers were introduced in each tank recreating the mean densities found on the collected macroalgae on the day of sampling. Due to its lagging growth season, the invasive red macroalga, *Agarophyton vermiculophylla*, was collected on 20 June 2018 (close to Heiligenhafen, 54.377341°N, 10.994967°E), wet-weighted, and equally distributed in the tanks in mesh bags on the same date. Additional algal material was added (equally to all tanks) after the second upwelling for an alga-grazer-interaction experiment performed during the third upwelling event (see further details below). An overview of the added or sampled biomasses is given

in Supporting Information Table S2. As the incoming water was not filtered, additional species recruited naturally in the tanks during the experiment. Macroepiphytes that recruited despite the activity of the mesograzers were not removed since this phenomenon reflects quite closely the community dynamics under in situ conditions.

Algal performance and abundance of mesograzers

Algal growth was assessed weekly by: (1) measuring the distance between the growth tag and the thallus tip in marked individuals of *F. vesiculosus* and *F. serratus* using a caliper rule and (2) by measuring the wet weight of tagged *A. vermiculophylla* samples.

The change in population size of mesograzers was estimated before and after UPW2 and UPW3 by submerging a black mosquito net (50 × 50 cm, 1 mm² mesh) in each tank for 24 h and counting the attached motile organisms, upon retrieval of the net.

Macroalgae–grazer interaction assays

From 27 August (prior to upwelling 3) to 04 September (after upwelling 3 ended), we tested how the performance of the potentially competing benthic macroalgal species, *A. vermiculophylla* (invasive red algae) and *F. vesiculosus* (native brown algae), was impacted by warming and upwelling. Specifically, we evaluated how their relative performance (growth, O₂ metabolism) and, thus, the presumed competitive ability (for light and limiting nutrients) may be affected by the (1) the presence of the other competing algal species in the same compartment, (2) the presence of mesograzers, and (3) the physicochemical conditions simulated by the warming and upwelling treatments. Mesograzer survival in response to warming and the hypoxic upwelling 3 was tested by enclosing (separately for each species) three individuals of *L. littorea*, *I. balthica*, and *Gammarus* sp., and six *Rissoa* sp. (which had recruited into the tanks) together with a piece (1 cm²) of *F. vesiculosus* as food in PVC tubes (200 mL) closed at both ends by a net (mesh size 1 mm²). One tube per species was exposed to each tank before the onset of upwelling 3. Survival was assessed 6 d after the upwelling event.

Algal performance was measured as: (1) metabolic rates (net primary production, respiration, and nutrient uptake) at ambient and +4°C using short incubations under light and dark conditions in gas tight translucent chambers and (2) growth rates in all treatment combinations. Metabolic rates (standardized by algal wet weight) were measured by incubating the algae at the start and end of the experiment and quantifying the change in oxygen concentration in the water under dark and light conditions.

Because we suspected that grazing impacts could not be effectively assessed in a short-term experiment inside the big buckets with relatively large algal biomass, we also tested grazing effects inside 50-mL tubes (opening closed by a 1-mm mesh) where a piece of algae and two *I. balthica* individuals were placed together for a duration of 8 d. The algae were wet-weighted and photographed before and after the experiment to evaluate grazing effects. The change in surface area was assessed by image analysis (ImageJ).

Fouling pressure

The formation of microfouling communities was investigated on glass slides (76 × 26 × 0.8 mm, Thermo Fisher Scientific). The slides were submerged vertically at a depth of 5 cm in separate containers fed by water (flow-through of 9500 L d⁻¹) coming from each tank for 10 d during upwelling 3. Three slides for each treatment combination were used. At the end of the experiment, slides were removed and air dried.

Macrofouling accrual under the various treatment combinations was assessed by exposing one 12 × 12 cm PVC panel with a slightly oblique inclination (30° from horizontal) in each tank at a depth of 60 cm. At the end of the experiment, the established fouling community was quantified by the proportion (in %) of the panel occupied by foulers.

Statistical analysis

For all data prior to analysis, the normality of distribution and the homogeneity of variances were explored by graphical means and by appropriate tests (Shapiro, Levine, Fligner). Depending on the characteristics of the data, for the comparisons of responses to discrete factors we used Kruskal–Wallis or ANOVA followed by Tukey's honest significant difference. Relationships between warming and a given response, stratified by upwelling and/or species were modeled as follows.

Before modeling, pseudo-replicated data were averaged, for example, growth measurements performed on different algal individuals included in a given experimental unit (tank). The main and interactive effects of warming and upwelling on the performance of different taxa were evaluated using generalized additive models (GAMs). The modeling and post hoc comparison of trends were done using the *mgcv* and *itsadug* packages in R (Wood 2017). Multivariate dissimilarities among the assemblages of grazers exposed to the different warming and upwelling treatments, in three sampling events (beginning and after UPW2, and after UPW3), were visualized using nonmetric multidimensional scaling (nMDS) plots. The dissimilarities between assemblages were calculated based on species counts using the Bray–Curtis index. The best ordinations were defined through 2000 random iterations and the comparison of stress values, using the function *metaMDS* from the R package *vegan* (Oksanen et al. 2019). Final plots were produced using the package *ggplot2* (Wickham et al. 2019). Further analyses of structural differences among grazer communities were performed using multivariate generalized linear models (mGLMs) through the function *manyglm* from the R package *mvabund* (Wang et al. 2020).

Compiling the effects

We used z-scores or log response ratios to categorize impacts from strongly beneficial (+3) to strongly detrimental (−3) by steps of 1, to facilitate an integrative overview of warming and/or upwelling effects on different community components and traits investigated (Table 1). Warming effects were categorized in the absence of upwelling. Upwelling effects were categorized in the absence of warming. The combined effect was estimated by evaluating by how much and in which direction the warming effect was modified by the upwelling.

Results

Seasonal upwelling-driven shifts of surface water conditions

The parameters of both surface water and deep water changed substantially during the experimental period (Supporting Information Section S8; Figs. S3, S4). The simulated upwelling of natural deep water provoked important changes in the

Table 1. Summarizing heat map about the impacts of warming (“OW,” without upwelling) and upwelling (“UPW,” at ambient temperature) as well as the combination of warming and upwelling (warming + upwelling) in different phases (early summer, midsummer, and late summer) on different response entities. Impact strength was ranked from strongly negative (“-3” = decrease by a factor < 0.4, red) to strongly positive (“3” = increase by a factor > 2.5, green) based on the z-differences or the log-effect-ratios depending on response variable. The “integrated” effect is either the mean (no carryover) or the sum (cumulative, with carryover) effect over the three seasons. Note that the heat map colors were allocated for the time-integrated effects separately from the effects in single phases and that for macrofoulers only integrated mean effects are available. Fv = *Fucus vesiculosus*, Fs = *Fucus serratus*, Av = *Agarophyton vermiculophylla*, “Macrofoulers” are mainly composed of the functional group of filamentous epiphytic algae. “Upwelling” designates the imposed replacement of surface waters by sub-thermocline waters (-14 m) in some of the tanks. The cell colouring illustrates the ranked effects from strongly positive (dark green) to strongly negative (dark red).

| Organisms | Responses | Traits | Early summer | | | Midsummer | | | Late summer | | | Integrated (mean) | | | Integrated (sum) | | | |
|------------|----------------|-----------------|--------------|-----|----------|-----------|-----|----------|-------------|-----|----------|-------------------|------|----------|------------------|-----|----------|------|
| | | | OW | UPW | OW + UPW | OW | UPW | OW + UPW | OW | UPW | OW + UPW | OW | UPW | OW + UPW | OW | UPW | OW + UPW | |
| Macroalgae | Fv | Biomass change | 3 | 1 | 1 | -3 | 1 | -2 | 0 | -1 | 0 | 0.0 | 0.3 | -0.3 | 0.0 | 1.0 | 1.0 | -1.0 |
| | | Photosynthesis | | | | -1 | 0 | -2 | | | | | | | | | | |
| | | Nutrient uptake | | | | 3 | 2 | -3 | | | | | | | | | | |
| Fs | Biomass change | | -3 | -1 | 1 | 1 | -1 | 1 | -1 | 1 | -1.0 | -0.3 | 0.3 | -3.0 | -1.0 | 1.0 | 1.0 | |
| | | | 2 | 1 | -2 | -1 | -1 | 2 | 1 | 1 | 1.0 | 0.3 | -0.7 | 3.0 | 1.0 | 1.0 | -2.0 | |
| Grazers | All | Photosynthesis | | | | | | | 1 | 2 | -2 | | | | | | | |
| | | Nutrient uptake | | | | | | | 3 | -1 | 0 | | | | | | | |
| | | Numbers | 0 | 3 | -3 | -2 | 3 | -3 | -1 | 1 | 0 | -1.0 | 2.3 | -2.0 | -3.0 | 7.0 | -3.0 | -6.0 |
| Isopods | Numbers | | 0 | 1 | -2 | -2 | 0 | -2 | -1 | 2 | -3 | -1.0 | 1.0 | -2.3 | -3.0 | 3.0 | -3.0 | -7.0 |
| | | Feeding | | | | | | | 3 | 3 | -1 | | | | | | | |
| Amphipods | Numbers | | -1 | 3 | -2 | -2 | 0 | 0 | 0 | 1 | 1 | -1.0 | 1.3 | -0.3 | -3.0 | 4.0 | -1.0 | |
| | | Gastropods | 0 | 3 | -2 | -1 | 3 | -3 | -1 | 0 | -1 | -0.7 | 2.0 | -2.0 | -2.0 | 6.0 | -2.0 | -6.0 |
| Foulers | Bacteria | | | | | | | | -3 | -1 | 1 | | | | | | | |
| | | Diatoms | | | | | | | 1 | 0 | 2 | | | | | | | |
| | | Macrofoulers | | | | | | | 1.0 | 1.0 | 2.0 | | | | | | | |

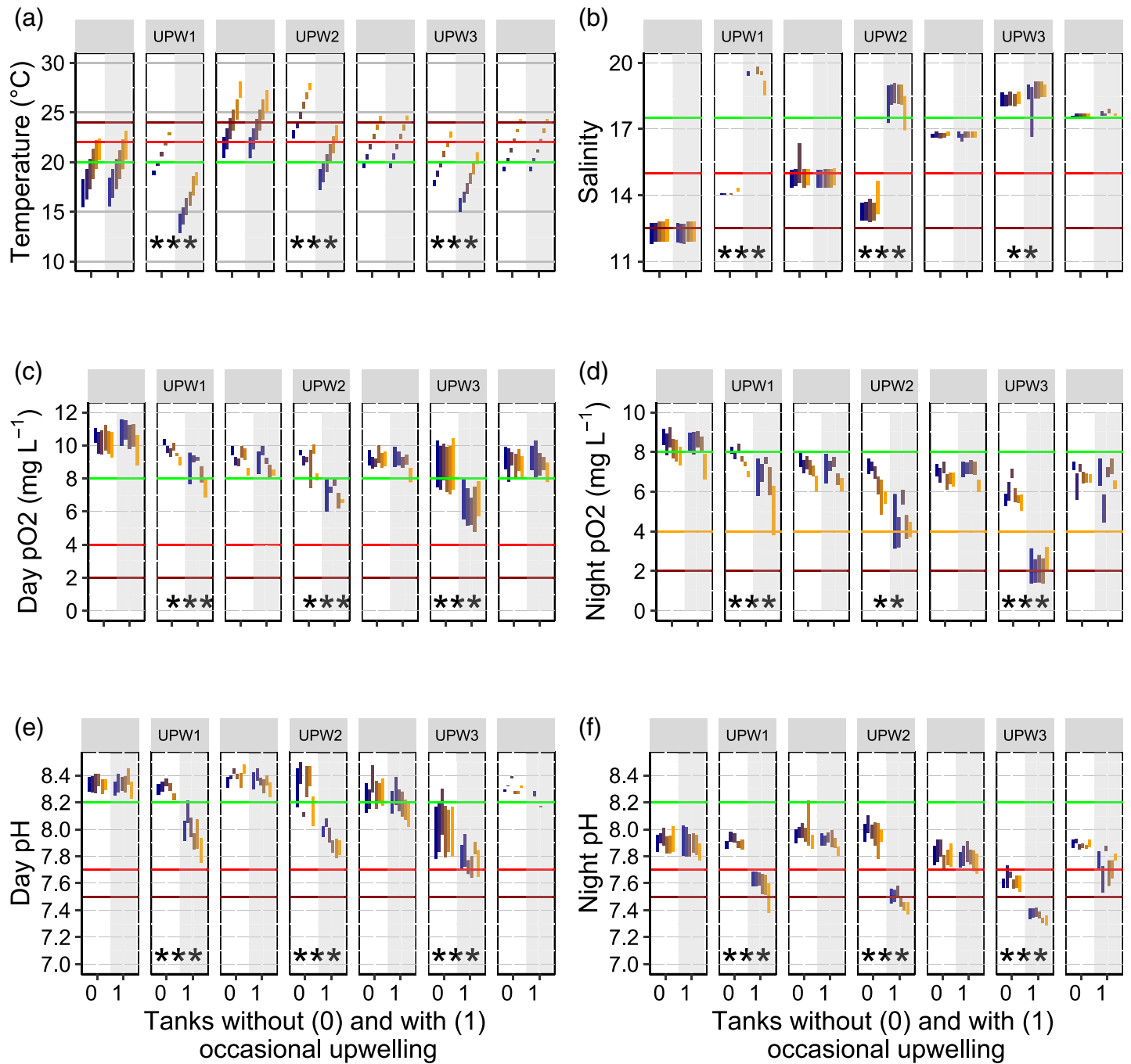


Fig 2. Ranges of temperature (a), salinity (b), daytime oxygen (c), nighttime oxygen (d) daytime pH_{NBS} (e) and nighttime pH_{NBS} (f) in the mesocosm tanks at different warming × upwelling treatments throughout the 4.5 months experiment. Significances of differences between tanks without (0) and with (1) occasional upwelling events (“UPW1,” “UPW2,” UPW3”) are indicated by asterisks (***p* < 0.001, ***p* < 0.01). Horizontal lines indicate no stress (green), onsets of moderate (red) and severe (dark red) stress for most species in the system (based on the literature data cited in the text). The shade of the bar colors indicate the warming level from blue (+0°C) to orange (+5°C). The significance of the upwelling effects in each event was assessed by nonparametric ANOVA (using *r*-Adonis). “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (−14 m) in some of the tanks.

environmental conditions in experimental tanks (Figs. 2, 3), all of them being significant except NO_x change during upwelling 3.

The early-summer upwelling (#1) event led to a temperature drop (means across all warming levels) of 6°C (from 22°C to 16°C, Fig. 2a), a salinity increase of 5 units (from 14 to

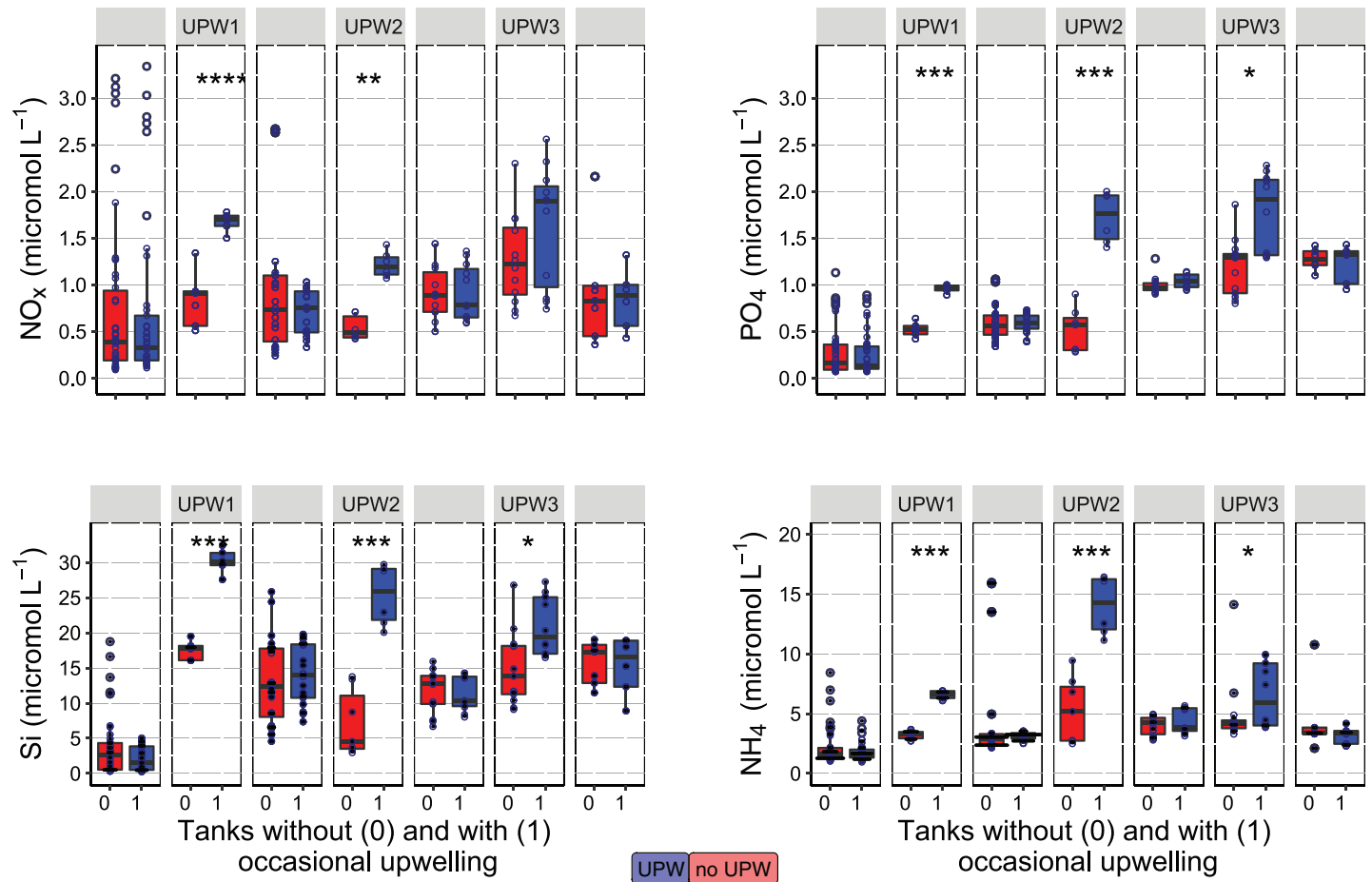


Fig 3. Nutrient concentrations during the three upwelling events (UPW1–UPW3) and during the phases between upwelling events. Significance levels of concentration differences between upwelled and not-upwelled tanks are identified by asterisks (nmANOVA, r-Adonis). “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (–14 m) in some of the tanks.

19, Fig. 2b), a night acidification by 0.35 pH_{NBS} units (from 7.9 to 7.55, Fig. 2f), and a temperature-dependent nighttime deoxygenation of 0.5 mg L^{-1} (under ambient temperature) to $> 2 \text{ mg L}^{-1}$ (at 5°C warming, Fig. 2d). In most species of the experimental community, performance could be improved by the upwelling-driven cooling and salination, while the drop in pH and in nighttime oxygen levels (under warmed conditions) may have an opposite but weaker effect (Fig. 2d–f).

Daytime pH declined from approximately 8.3 to around 8.1 at warming levels of $0\text{--}2^\circ\text{C}$ and to around 7.9 at warming levels $3\text{--}5^\circ\text{C}$ (Fig. 2e). Daytime oxygen decreased from levels around 10 at the surface, to 9.5 in the coolest, and to 7 mg L^{-1} in the warmest tanks (Fig. 2c). All monitored nutrients significantly doubled (mean factor of 1.98) during upwelling 1 as compared to surface waters (Fig. 3) from approximately 0.9 to 1.8, 0.6 to 1, 17 to 32, and 3 to $7 \mu\text{mol L}^{-1}$ for NO_x , PO_4 , Si, and NH_4 , respectively.

The midsummer upwelling (#2) led to a cooling of 4°C (across all warming levels, Fig. 2a) from more stressful levels (from 22°C to 27°C) as compared to early summer. Salinity

levels improved (for all organisms of marine origin) from 13 to 18 (Fig. 2b), while nighttime pH dropped from 8 to below 7.5 units (Fig. 2f). Oxygen at night, even in the absence of upwelling, decreased with warming from 7.5 mg L^{-1} at ambient temperature to between 5 and 6 mg L^{-1} in the warmest treatments. From these levels, upwelling 2 caused a further decline by roughly 2 mg L^{-1} , which led to nighttime oxygen below 4 mg L^{-1} in the warmer treatments (Fig. 2d), and daytime oxygen between ca. 8 and 6 mg L^{-1} in coolest and warmest treatments, respectively (Fig. 2c). Again, as in upwelling 1, the presumably beneficial effects of cooling and salination may at least partly be obscured by the stressful drops in pH and oxygen. Nutrients increased by a mean factor of 3.7 from approximately 0.6 to 1.4, 0.6 to 2, 5 to 30, and 5 to $17 \mu\text{mol L}^{-1}$ for NO_x , PO_4 , Si, and NH_4 , respectively (Supporting Information Fig. S3). Thus, the fertilizing effect in upwelling 2 was even stronger than in upwelling 1.

The late-summer upwelling (#3) caused much weaker shifts in temperature or salinity (Fig. 2a,b) than the earlier two upwelling events, since a weaker natural upwelling co-

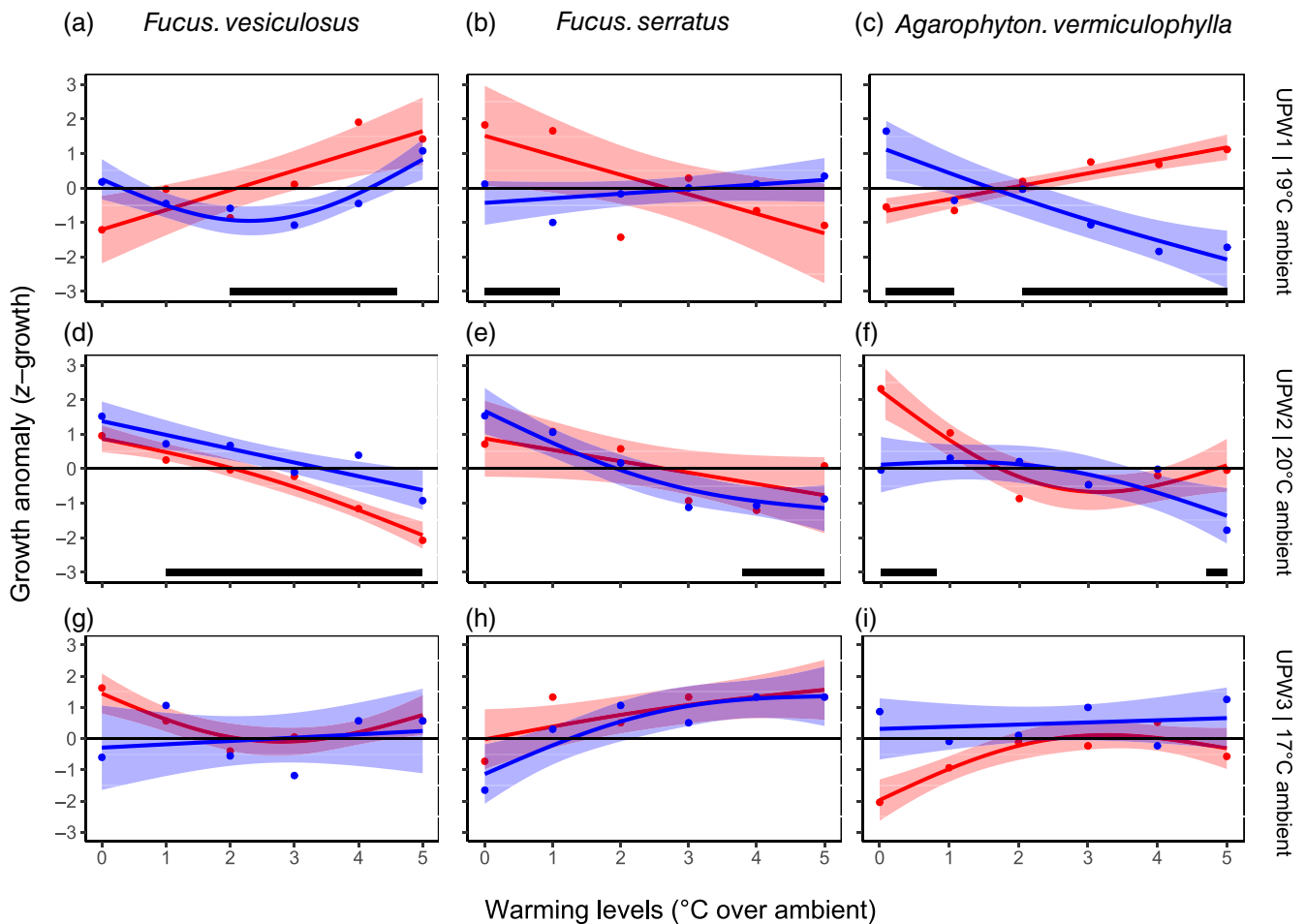


Fig 4. Performance anomalies of the three macroalgal species *Fucus vesiculosus*, *Fucus serratus*, and *Agarophyton vermiculophylla* under upwelled (blue) and non-upwelled (red) conditions during the three upwelling events (upwelling 1 to upwelling 3) over six temperature treatment levels (0–5°C) expressed as z-growth (i.e., the standardized difference to the mean growth of a given species and week under all treatment combinations). Black horizontal bars at the bottom of the panels indicate areas of significant difference as identified by GAM. “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (–14 m) in some of the tanks.

occurred (mentioned earlier). However, substantial drops in night pH (to 7.4, Fig. 2f) and oxygen (approximately 6 mg L⁻¹ at noon, and around or below 2 mg L⁻¹ at night, Fig. 2c,d) to supposedly stressful levels were found at least transiently during the night under the influence of the simulated upwelling. In this case, the stressful effects of hypoxia at night could be expected to dominate the overall impact on organisms. Nutrients during upwelling 3 increased by a mean factor of 1.6 from approximately 1.2 to 1.8, 1.3 to 2, 13 to 19, and 4 to 8 μmol L⁻¹ for NO_x, PO₄, Si, and NH₄, respectively (Fig. 3).

Biological responses to warming and seasonal upwelling events

Macroalgal responses

Overall, there was no substantial net growth in all three macroalgal species over the entire course of the summer (Supporting Information Fig. S5, inter-species ANOVA:

$p > 0.1$). The growth effects of warming on these temperate species are illustrated by the general trend of declining net growth rates with increasing intensity of warming which was marginally significant ($p = 0.055$) and seen similarly in all three species (warming × species: $p > 0.05$). Sporadic upwelling of cooler waters had no direct significant effect on the species’ growth.

Differences in growth rate anomalies with respect to the overall mean of all treatments (z-score, Fig. 4) were mainly driven by warming, and to a lesser extent by upwelling in the absence of warming (only *F. serratus* in upwelling 1 and *A. vermiculophylla* in upwelling 1 and upwelling 2; GAM, Supporting Information Table S3). The effect of warming on growth differed among species and upwelling events. In upwelling 1, warming without upwelling seems to favor the growth of *F. vesiculosus* and *A. vermiculophylla* while it hinders the growth of *F. serratus* (Fig. 3a–c). Upwelling in this seasonal

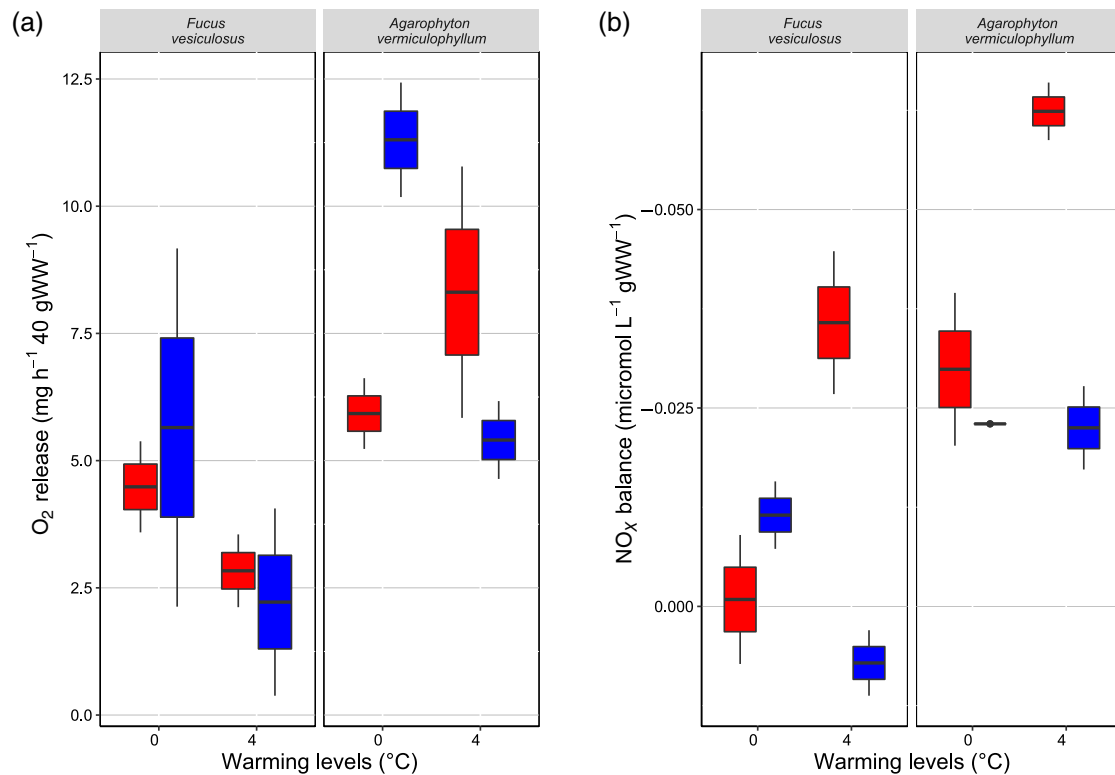


Fig 5. Effects of warming (by 4°C) and the third upwelling event on gross primary production (expressed as gross oxygen production over 24 h **(a)** and nutrient balance (expressed as change in NO_x concentration **(b)**) in tanks without (red) and with (blue) upwelling during upwelling 3. “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (−14 m) in some of the tanks.

phase favors *A. vermiculophylla* growth, relative to growth in the absence of upwelling, at low temperatures (warming 0–1°C), but decreases the growth of *F. serratus* in the low warming levels (warming 0–1°C), as well as the growth of *F. vesiculosus* and *A. vermiculophylla* in high warming levels (warming 3–4°C and 3–5°C, respectively). The apparent competitive disadvantage (i.e., hampered growth) of *F. serratus* in a warming scenario relative to the two other macroalgae may, consequently, be attenuated by early-summer upwelling. In upwelling 2, all algal species feature progressively reduced growth rates with increasing warming. This warming-induced stress was partially mitigated by upwelling in *F. vesiculosus*, but enhanced in *F. serratus* and *A. vermiculophylla* in the warmest levels (Fig. 4). In *A. vermiculophylla*, upwelling also reduced growth in the coolest warming levels (warming 0–1°C). In upwelling 3, ambient temperatures had declined to be low-stress levels (Supporting Information Fig. S3a) and all algae species showed a slight increase in growth performance with warming. During this period, upwelling had no effects on growth responses to warming independently of the algal species, presumably because this simulated upwelling coincided with a natural upwelling event, and consequently, did not lead to substantial cooling or salination of the surface waters compared to deep water as had happened during the earlier

events. The drop of oxygen and pH associated with upwelling 3 does not seem to affect growth of the three algal species. In that phase, *A. vermiculophylla* tended (not significantly) to have a higher GPP rate compared to *F. vesiculosus* (Fig. 5a). In both species, upwelling tended to enhance GPP in the absence of warming, while GPP was reduced by upwelling under warming. Also, during upwelling 3 both species showed an increased uptake of NO_x as a proxy of nutrient balance, with warming in the absence of upwelling and a decrease with upwelling under warming (Fig. 5b). A NO_x balance above zero (net release of nutrients) as seen for *Fucus* spp. under warming and upwelling may be indicative of (partial) decay. However, these apparent effects of warming and upwelling on GPP and nutrient balance were not statistically tested because of the low replication level.

In late summer, the relative growth of *A. vermiculophylla* and *F. vesiculosus* was affected negatively by experimental warming (Fig. 6a) in the absence of hypoxic upwelling (upwelling 3). This detrimental effect was significant only for *A. vermiculophylla* (ANOVA, $p < 0.001$, Supporting Information Table S4a) and was significantly stronger at the highest warming levels (GAM, $p < 0.05$). Upwelling did not have any significant direct effect on either alga but decreased relative growth of *F. vesiculosus* at low warming levels (warming 0–1.5°C) relative to *A. vermiculophylla* (GAM, $p < 0.05$).

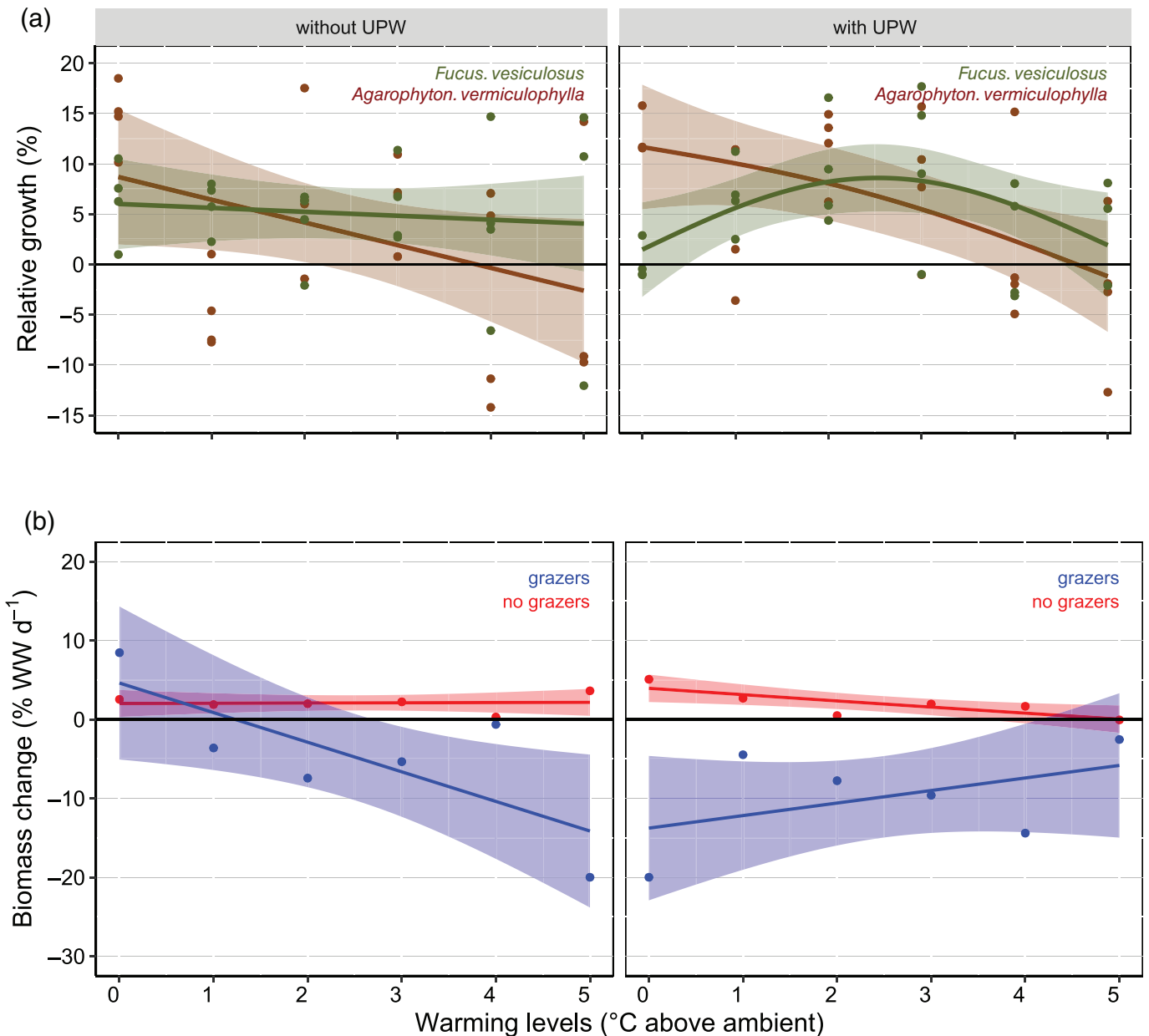


Fig 6. Relative growth (in % change of wet weight = WW per 6, **(a)**) in the absence of grazers by *Fucus vesiculosus* (green) and *Agarophyton vermiculophylla* (red). Biomass change (% WW, **(b)**) of *F. vesiculosus* in the presence (blue) or absence (red) of the mesograzer *Idotea balthica*. Six temperature treatment levels (0–5°C) were applied in tanks without and with upwelling (“UPW”) in late summer. Black horizontal bars at the bottom of the panels indicate areas of significant difference as identified by GAMs. “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (–14 m) in some of the tanks.

The presence of grazers significantly increased the loss of biomass in *F. vesiculosus* (GAM, $p < 0.05$, Supporting Information Table S4b), independently of upwelling. The presence of grazers interacted (marginally significantly) with warming in the absence of upwelling (interaction GAM, $p = 0.052$), as the thallus loss due to grazing increased with warming intensity. This interaction was not evident in the presence of upwelling. However, upwelling itself had no impact on the intensity of grazing (GAM, $p > 0.05$).

Mesograzer community responses

During upwelling 3, the survival of the four tested taxa of mesograzers responded differently to warming and upwelling (Fig. 7). Survival of *I. balthica* was not affected by warming in the absence of hypoxic upwelling, that is, upwelling 3, but declined under hypoxia linearly with warming to reach 100% mortality at the highest warming levels (warming 4–5°C). *Gammarus* spp. survival declined slightly with warming in the absence of hypoxic upwelling.

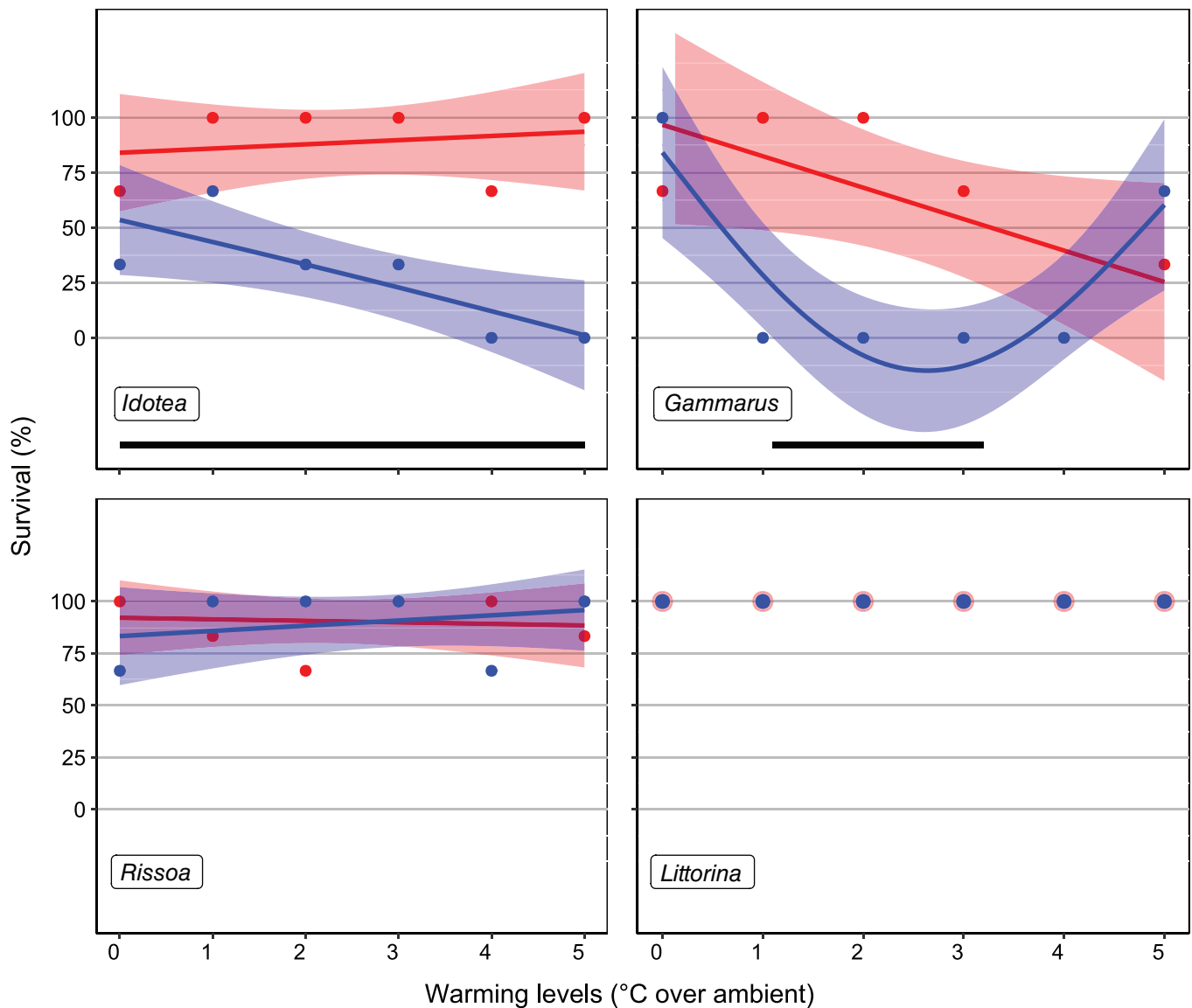


Fig 7. Survival in % during upwelling 3 in the absence (red) and presence (blue) of hypoxic upwelling of the four major mesograzers *Idotea balthica* (a), *Gammarus* spp. (b), *Rissoa* spp. (c), and *Littorina littorina* (d). “Upwelling” designates the imposed replacement of surface waters by subthermocline waters (−14 m) in some of the tanks.

Hypoxic upwelling, in contrast, led to total mortality in most warming levels between (warming 1–4°C), and to a weaker reduction of survival at the highest warming level (warming 5°C). The survival of *Rissoa* sp. and *L. littorea* was not affected by warming or upwelling. Mesograzers population size, mainly composed of isopods (e.g., *I. balthica*, *Jaera albifrons*), amphipods (e.g., *Gammarus* spp., *Calliopius laeviusculus*) and gastropods (e.g., *Rissoa* sp., *Hydrobia* spp., *L. littorea*), tended to shrink with intensified warming (Supporting Information Fig. S6) at all three time points tested. Both the upwelling 1 and upwelling 2 led to significantly higher mesograzers numbers in the cooler warming levels (warming 0–2°C, GAM, $p < 0.05$).

The overall structure of the mesograzers community was significantly shifted by the different warming levels (warming: $p < 0.001$), but not by the three sporadic upwelling events (upwelling: $p = 0.19$; Supporting Information Table S5; Fig. S7) or their interaction with warming (warming \times upwelling: $p = 0.164$). Major drivers for the compositional shifts during the experiment were, thus, tank temperature (represented by the interdependent vectors “ow” and “ttemp”) and time (“week”: $p < 0.001$). The components that contributed most (10%–25% decrease) to the community shifts in response to warming were in decreasing order: juvenile *Gammarus* (23%), *Gammarus locusta* (19%), *C. laeviusculus* (16%), *Rissoa membranacea* (13%), and *J. albifrons* (12%). Other species, such as *I. balthica*,

G. salinus, *Rissoa parva*, were less affected by warming and increased over time. Thus, in opposition to the two other snail species, *R. parva* seemed quite insensitive to warming. Likewise, *G. salinus* was not strongly affected by warming in contrast to the other amphipod species *G. locusta*, juvenile *Gammarus* and *C. laeviusculus*. Cumulatively, however, these specific responses to warming led to the observed (Supporting Information Fig. S6) overall decrease in mesograzers in the system with intensifying warming levels between midsummer to late summer.

Microfouling and macrofouling

Although not significant in the absence of upwelling, bacterial fouling during upwelling 3 tended to decrease with warming. However, upwelling seemed to strongly intensify bacterial fouling under warming conditions (Supporting Information Fig. S8a). Diatom fouling tended to increase under warmer conditions with and without upwelling, but particularly so in the presence of upwelling 3 (Supporting Information Fig. S8b).

The cumulative settlement of macroorganisms on artificial substrata during the entire experimental duration (“fouling pressure”) was higher in the presence of sporadic upwelling ($p < 0.05$) and increased with warming ($p = 0.05$), particularly so under both warming and upwelling, although this interaction was not significant ($p = 0.17$, Supporting Information Table S6; Fig. S8c). The macrofouler community was composed mainly (mean coverage $>1\%$ in decreasing order of dominance) by the encrusting red alga *Hildenbrandia* sp., the barnacle *Balanus* sp., the branching green alga *Cladophora rupestris*, the branching red alga *Aglaothamnion* sp. and the mussel *Mytilus edulis*.

Discussion

On top of the ambient climatology we implemented various aspects of predicted Climate Change, that is, five levels of ocean warming and sporadic upwelling in different phases of the summer. As in nature, these manipulations of single “factors” interacted with each other and with further environmental properties. The results were various environmental scenarios possibly representing plausible situations in the coming decades.

The imposed warming slightly reduced oxygen concentration relative to ambient temperature, particularly so during the night. This may be attributable to two independent processes. (1) Gas solubility decreases with increasing temperature (Bendtsen and Hansen 2013). (2) Likely, warming enhanced the physiological processes causing biogenic day–night fluctuation of oxygen (Brown et al. 2004), which mitigated the negative effects of warming-driven reduction in oxygen saturation during daytime but exacerbated it during nighttime—up to the species-specific optimal temperature (T_{opt}) beyond which metabolic rates should decline.

The three simulated sporadic upwelling events in early-summer, midsummer, and late summer (Fig. 1, upwelling 1–upwelling 3) produced very disparate physicochemical mosaics (sensu

Kroeker et al. 2016). In summary, given the fluctuating environmental conditions in combination with the simulated warming upwelling 1 should be moderately beneficial, upwelling 2 strongly beneficial and upwelling 3 detrimental to the majority of species in the *Fucus* community, but the strength and direction of these effects were likely to differ among the species. Below we discuss the species-specific responses.

F. vesiculosus benefited from warming in the colder period, and was harmed from it in the warmer phase. Upwelling decreased *F. vesiculosus* growth at the higher warming levels in early summer, enhanced growth at all warming levels (except ambient) in midsummer, and had no effect in late summer. This closely matches the expectations based on the thermal requirements of *F. vesiculosus* (Graiff et al. 2015; Al-Janabi et al. 2019). In an Irish Sea study (Brooks and Crowe 2018), no warming impact on *F. vesiculosus* was detected. Possibly thermal stress in this study was lower because the baseline temperature (on which warming levels were imposed) was further below the optimal temperature of *F. vesiculosus* than in the Baltic, or because T_{opt} of this population was higher, or the stress was applied for a shorter period. The second native macroalga, *F. serratus*, generally suffered from warming except in the cooler late-summer period. A more pronounced sensitivity to warming *F. serratus* as compared to *F. vesiculosus* was described earlier (Brooks and Crowe 2018) with substantial thermal impacts beyond 22°C in all populations studied (Martinez et al. 2012). Jueterbock et al. (2014), however, describe substantial differences among European populations of *F. serratus* with regard to their sensitivity to heat pulses.

Upwelling had weak or no effects on growth in all phases of the experiment. The invasive species, *A. vermiculophylla*, seemed to benefit from warming, except in midsummer. Upwelling decreased its growth at higher warming levels except in the cooler late summer. Since *A. vermiculophylla* is capable of living at extremely low nutrient concentrations (Jensen et al. 2007), it may not have benefitted from the nutrient-enrichment caused by upwelling.

Only in late summer, upwelling did not modulate the warming effects. The cumulative effect of the three upwelling events tended to mitigate the detrimental effects of warming on the 4.5-month growth of all three species.

The observed decrease of macroalgal growth with actual summer warming and simulated future warming has been predicted and observed before at regional (Graiff et al. 2015; Graba-Landry et al. 2018) and global (Harvey et al. 2013; Koch et al. 2013; Wahl et al. 2015b) scales. In the present experiment, the negative growth effect was presumably a direct impact rather than indirect effect caused by an increase of grazing rates. Since the lowest temperature in the tanks without imposed warming during all three upwelling events (19°C , 20°C , and 17°C , respectively) was above the optimal temperatures (T_{opt}) for *Idotea* spp. (14°C) and *Littorina* spp. (17°C) (Wahl et al. 2020), all warming levels should have decreased the grazing activities of these two mesograzers groups. Only

amphipod activity ($T_{opt} = 21^{\circ}\text{C}$) could have been enhanced by moderate warming (Gilson et al. 2021). However, it is likely that such warming-induced increase in grazer activity was partially or completely suppressed by the hypoxia stress experienced during upwelling 3 as seen in the incubation experiments. This effect was particularly conspicuous at higher warming levels where the absence of upwelling increased grazing activity and algal biomass loss (in this cooler part of the season), while in the presence of hypoxic upwelling, the grazing effect decreased. In addition, warming led to a decrease in grazer numbers. This shrinking of the grazer population is likely to have (over-) compensated any hypothetical increase of per capita grazing which in addition was limited to the amphipods. The shrinking of mesograzer biomass with warming has been suggested to reflect a mismatch between the warming-driven increase of metabolic rates (Brown et al. 2004) and a finite digestive tract limiting any compensatory feeding (Gilson et al. 2021). The observed detrimental impact on juvenile grazers may hint at a potential carryover effect, since a decrease in the abundance of juveniles under heat stress will translate to a decrease in the abundance of adults even when the stress ceases. Hypoxic upwelling in late summer will exacerbate and slightly redirect these structural shifts in the mesograzer community since it causes substantial mortality in crustacean grazers whereas gastropods seem less sensitive to low oxygen levels (Larade and Storey 2007). Grazing pressure on particular macroalgal species may have changed not only due to the general decrease in mesograzer numbers but also to the restructuring of the mesograzer community, since the different consumer species differ with regard to their feeding preferences. Such preferences may (Nejrup et al. 2012) or may not (Barboza et al. 2019) differ among populations. The Kiel Bight population of *F. vesiculosus* is preferred over co-occurring *A. vermiculophylla* by the isopod *I. balthica* (Weinberger et al. 2008), while *A. vermiculophylla* seems to be the preferred feed of the snail *Littorina littorea* relative to *F. vesiculosus* and *F. serratus* (C. Bommarito, GEOMAR, pers. comm.). If hypoxic upwelling in late summer leads to a decrease in crustacean mesograzer numbers (including *Idotea* spp.) and a proportional increase in gastropod mesograzers (including *L. littorea*), grazing pressure may shift from *F. vesiculosus* to *A. vermiculophylla*. This could partially compensate for the direct negative effect of (hypoxic) upwelling which strongly reduces recruitment of the bladder wrack (M. Wall GEOMAR, pers. comm.). Such a decline in recruitment could be the result of selection under multiple sequential drivers where the bladder wrack population selected under thermal stress exhibits enhanced sensitivity to hypoxia as was shown in a previous study (Al-Janabi et al. 2019).

The tentative ranking of effect size and direction in Table 1 was intended to help compare the single and combined impacts of warming and upwelling in different phases over the summer. Warming outside the hottest phase of the year (mid-July to mid-August) was neutral or

beneficial to most species of the community and tended to benefit more the macroalgae than their grazers or foulers. In the absence of experimental warming, all upwelling events had rather weak effects on macroalgae and were rather beneficial for grazers (except when hypoxic). The combination of warming and upwelling was predominantly stressful, except for foulers. Integrated over the entire summer and assuming intermittent recovery (i.e., mean of effects), warming without upwelling was slightly negative, upwelling without warming was neutral (macroalgae) to positive (grazers), but the combination of both was mostly negative. In contrast to this pattern, macrofoulers (mainly filamentous algae) benefitted from warming and upwelling and, particularly so, from their combination. Assuming carryover effects, the additive effects were strongest (Table 2).

The observation that hypoxic upwelling generally turns particularly detrimental under warmed conditions represents a synergism. Thus, with progressive global change (warmer, wetter, more eutrophicated) the pressure on benthic communities will likely increase. More and more benthic habitats become transiently or permanently exposed to hypoxia (Diaz 2001; Breitburg et al. 2018; Fennel and Testa 2019). This development is particularly conspicuous in the Baltic Sea (Carstensen et al. 2014; Jokinen et al. 2018; Reusch et al. 2018). Most benthic organisms including microbes (Broman et al. 2017) are impacted by hypoxia (Diaz and Rosenberg 1995; Wu 2002), which results in community restructuring and biodiversity loss (Gammal et al. 2017). Species in fluctuating environments as is the Baltic Sea and particularly its shallow subtidal (Pansch et al. 2014; Reusch et al. 2018) may have evolved some degree of robustness towards environmental stress including hypoxia (Gedan et al. 2017), or to another potential stressor associated with hypoxic upwelling, that is, acidification (Thomsen and Melzner 2010). This may be due to selective mortality during phases of enhanced stress (Rilov et al. 2019) because fluctuations per se do not necessarily decrease the overall mean stress (Clark and Gobler 2016). Hypoxia, as do other stressful drivers, has the potential to inflict indirect effects such as shifts or disruptions of biotic interactions including grazing (Young and Gobler 2020). Equivalent to heat stress intensity commonly measured as degree heating days (or weeks) (Kayanne 2016), the severity of hypoxia stress should depend on the duration and distance to optimal oxygen concentration, that is, the integral of suboptimal conditions in time. With regard to the responses to thermal and hypoxia stress in the present investigation, one must also keep in mind that all species considered are of marine origin and, thus, performed under suboptimal osmotic, that is, brackish, conditions in this experiment. Independently of this, an absolute limit to marine life is suggested to be reached when a PO_2 of 1 kPa (ca 0.5 mg L^{-1}) persists for an extended period (Seibel and Childress 2013).

Conclusions

The three ecologically most relevant abiotic parameters, temperature, salinity and oxygen, fluctuate in time and may reach stressful levels synchronously or sequentially. This leads to a stress regime that we have termed “pulsed pressure.” Whether a stress is considered pulse or pressure depends on its duration relative to an organism’s lifespan. Thus, in the brackish Western Baltic, chronically reduced salinity constitutes a pressure to all species of marine origin and a warm summer of several weeks may be experienced as pressure for short-lived gammarids and as pulsed by perennial seaweeds. Short excursions from benign conditions as happening during a few days of heat wave or hypoxic upwelling represents a stress pulse to most macroorganisms. In a fluctuating stress scenario, directional selection could be enhanced by mortality of sensitive genotypes during high stress (Vajedsamiei et al. 2021), and recovery or even reproduction of robust genotypes during low stress (Rilov et al. 2019). However, when sensitivities to different drivers reversely correlate, selection under one stressor may render the surviving population more sensitive to the second stressor (Al-Janabi et al. 2019). This underscores the importance to consider fluctuations and sequence of multiple drivers (Brooks and Crowe 2019). The present study highlights the complexity of coastal environments and the challenge of a pulsed pressure regime biota have to cope with. Therefore, not warming or hypoxia alone but rather the whole array of environmental drivers, and particularly their interplay in time and space, may determine community structural changes in the future ocean.

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Conflict of interest

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