

Warming and parasitism impair the performance of Baltic native and invasive macroalgae and their associated fauna

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Abstract

Global warming, bioinvasions, and parasitism affect single-species performances and species interactions, substantially impacting the structure and stability of marine ecosystems. In light of accelerated global change, the information derived from studies focusing on single species and single drivers is insufficient, calling for a multi-stressor approach under near-natural conditions. We investigated the effects of warming (+3°C) on the performance of a benthic community composed of native and invasive macroalgae, consumers and a trematode parasite in a mesocosm setting. We also assessed the effects of warming and parasitism on the survival and growth of gastropods and mussels and the thermal dependency of trematode performance. Our findings show that warming and grazing by infected gastropods had a large detrimental effect on the invasive macroalga growth. Furthermore, the single and interactive effects of parasitism and warming were detrimental to intermediate host survival and growth, especially to large mussels. Finally, cercarial emergence positively correlated to the natural peaks of summer temperatures, while infection intensity in mussels was higher in larger individuals. Our findings suggest that grazing and warming will be detrimental to the invasive macroalga, favoring the native alga. Moreover, parasitism will enhance grazing, especially in summer, when higher temperatures trigger parasite development. However, parasite-enhanced grazing may be buffered by higher mortality or a shift in the size of infected intermediate hosts under warming. Our findings demonstrate how complex effects of ocean warming can be on food webs and how they can be mediated by parasitism and, as a result, influence native and invasive macroalgae differently.

Global warming increasingly acts as a major ocean stressor, posing profound threats to marine ecosystems, from individuals to communities (Harley et al. 2006; Wernberg

et al. 2016). Subsequently, species distributions and abundances are shifting, although the extent and direction of these shifts depend on the species, their traits, and life histories (Viitasalo and Bonsdorff 2022). Most previous studies investigating global warming effects limited their scope to test the direct effects of temperature on single species (Connell and Russell 2010; Kroeker and Sanford 2022). Nevertheless, current evidence suggests that the effects of global warming on species depend not only on direct physiological responses but also on indirect effects mediated by interspecific interactions, such as consumption and competition (Hawkins et al. 2008; Kordas et al. 2011), and parasitism (Altizer et al. 2013; Sures et al. 2023). These interactions can be enhanced or reduced by warming, and they can also moderate the response to warming. The role of consumers as top-down controllers of primary producer assemblages under warming conditions has been especially highlighted (Gilson et al. 2021). In contrast,

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

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our current knowledge of how climate change effects may mediate parasitism and competition with newly introduced species is still scarce.

Climate change often facilitates bioinvasions by providing the introduced species an earlier start through warmer temperatures and increasing their growth and recruitment (Stachowicz et al. 2002; McKnight et al. 2021), and by putting at a disadvantage native species, no longer experiencing the range of environmental factors to which they are adapted (Byers 2002). According to the enemy release hypothesis, this success might also be attributed to the tendency of native generalist enemies to avoid non-native species when having a choice (Gollan and Wright 2006; Monteiro et al. 2009; Tomas et al. 2011). Another biotic driver favored by climate change is spreading diseases which in the case of aquatic ecosystems, particularly marine ones, has previously been overlooked (Byers 2021). Among parasites, trematodes have become of particular interest in the context of global warming due to their complex life cycle, which involves different parasitic stages and intermediate and final hosts (Galaktionov and Dobrovolskij 2013). The parasitic stages usually include free-living and motile stages, such as miracidia and cercariae, as well as several stages living inside their hosts (i.e., sporocysts, rediae, metacercariae, and adults). The hosts of the different parasitic stages belong to different groups of consumers (Supporting Information Fig. S1) and are all potentially affected by abiotic drivers. Therefore, predicting the effects of global warming on the transmission of trematodes and the subsequent effects on food webs is not a trivial task. For instance, an increase in temperature can trigger trematode cercariae emergence and infectivity (Thieltges and Rick 2006). However, the general assumption of global warming favoring higher trematode transmission was recently reviewed by studies showing how the effect of temperature on trematode performance depends on a complex of different other drivers, such as the sensitivity to temperature of intermediate hosts (i.e., their thermal tolerance upper limits; Selbach et al. 2020; Selbach and Poulin 2020). Furthermore, other biotic factors such as functional traits of the host itself might contribute to the trematode transmission success. For instance, the transmission of cercariae to the bivalve second intermediate host might depend on the host size, with larger bivalves having higher filtration rate than smaller ones (Nikolaev et al. 2006; Thieltges and Reise 2007; Galaktionov et al. 2015).

The effects of climate change and newly introduced competitors and diseases on a community differ from the global to the regional scale (Wahl et al. 2015a). We used a typical macrophyte community in the Baltic Sea to investigate the combined effects of global warming and biotic drivers on the performance of different food web components. Since 1980, a warming trend of up to 0.4°C per decade has occurred in the southern Baltic Sea, exceeding the global average prediction by a factor of ~ 3 (Lehmann et al. 2011; Reusch et al. 2018).

One of the foundation species in the coastal zones of the southwestern Baltic Sea is the brown alga *Fucus vesiculosus*. This macroalga provides habitat and nursery for numerous species, the substratum for micro- and macrofoulers—important food components for many grazers—and other ecosystem functions (Wikström and Kautsky 2007; Kersen et al. 2011). In the last decades, the distribution of *F. vesiculosus* in the Baltic Sea has decreased, probably due to eutrophication and epibiosis (Rohde et al. 2008; Raddatz et al. 2017) and the increasing appearance of competitors such as the invasive red alga *Gracilaria vermiculophylla* (Hammann et al. 2013). *G. vermiculophylla*, native to the Northwest Pacific, was detected for the first time in the Baltic in 2005, east of the Danish Belt in Kiel (Schories and Selig 2006). Its traits make this macroalga a perfect candidate to compete with *F. vesiculosus* (Weinberger et al. 2008; Hammann et al. 2013). *G. vermiculophylla* can grow in shallow waters and is highly adaptable to environmental drivers, such as high irradiance and heat stress (Weinberger et al. 2008; Hammann et al. 2016). On the other hand, this invasive species possibly represents a habitat for native invertebrates due to its intricate three-dimensional structure (Thomsen et al. 2013). One of those invertebrates is the gastropod *Littorina littorea*, widespread in the Atlantic Ocean and the southwestern Baltic Sea and resistant to extreme warming events (Pansch et al. 2018). *L. littorea* is the first intermediate host of different trematode species, such as *Himasthla elongata*, belonging to the Echinostomatidae family (Supporting Information Fig. S1). Despite the high tolerance of *L. littorea* to elevated temperatures, a recent study by Díaz-Morales et al. (2022) provides evidence of higher mortality rates of *L. littorea* provoked by warming when combined with trematode infection. While trematode infections are widely known to provoke mortality episodes in the first intermediate hosts (Jokela et al. 1999; Fredensborg et al. 2005), mortality is rarer in the second intermediate hosts, which in the case of *H. elongata* is the bivalve *Mytilus edulis* (Werding 1969). However, the few studies available argued a combined effect of temperature and trematode infection in determining bivalve mortality (Mouritsen et al. 2018; Selbach et al. 2020).

Understanding the different pathways in which warming may impose stress on such complex biotic systems still needs investigation. So far, most experiments on this topic have been performed in constant laboratory conditions, neglecting natural environmental fluctuations (Gattuso et al. 2014; Wahl et al. 2015a). To overcome this limitation, ecologists lately agreed on the necessity of upscaling experiments and using more natural settings such as mesocosm to better predict future climate change effects (Wahl et al. 2015b).

Hypotheses

To investigate those complex interactions under warming in near real-world conditions, we tested the survival and growth of the main rocky benthic components of the

southwestern Baltic Sea: *F. vesiculosus* and *G. vermiculophylla*, *L. littorea*, and *M. edulis*, as well as the emergence and infectivity of *H. elongata* in a mesocosm experiment (Fig. 1). We hypothesized that: (1) warming will be more detrimental to *F. vesiculosus* than *G. vermiculophylla*, due to its high tolerance to environmental stressors and its avoidance by native generalist grazers; (2) trematode infection will amplify the negative warming effect on growth and survival of the intermediate hosts, *L. littorea* and *M. edulis*; (3) parasitism will indirectly affect macroalgae performance by affecting grazers performance; (4) warming will induce higher *H. elongata* emergence; (5) the metacercarial intensity in *M. edulis* tissue will depend on temperature and host size, with larger individuals being more susceptible to infection.

Methodology

General set-up

The experiment was performed in July–August 2020, for 7 weeks, including a first week of acclimation. The infrastructure used was the Kiel Outdoor Benthocosm (KOB) system at GEOMAR Helmholtz Centre for Ocean Research, Kiel. This facility is a floating platform with 12 (1500 L each) thermally insulated tanks opened at the top, allowing the application of “delta treatments,” that is, the possibility of shifting one or more environmental factors while allowing them to fluctuate with natural frequency and amplitude (Wahl et al. 2015b). Over the entire duration of the experiment, each tank received a constant flow of unfiltered seawater from the Fjord. In total, 12 tanks were used, of which 6 were kept at the ambient temperature of the Kiel Fjord, and 6 were warmed by 3°C above

the ambient temperature (following SSP5-7.0 partial mediation prediction for 2100, Allan et al. 2021). The temperature was controlled by a GHL system (Profilux 3.1T), using heaters and chillers independently in each main tank (Wahl et al. 2015b; for temperature data in the 12 tanks, see Supporting Information Fig. S2). In each tank, three transparent plastic buckets of 10 L each, representing the experimental units, were located on a grid suspended 15 cm below the water surface, with the water covering the buckets until their lid. Each bucket was provided with a hole positioned 2 cm below the lid where it was inserted a plastic tube of around 15 cm to guarantee the water outflow. One unit included one individual of *G. vermiculophylla* and one individual of *F. vesiculosus* (control treatment). Two units included one individual of *G. vermiculophylla*, one individual of *F. vesiculosus*, eight *L. littorea*, three large (50–60 mm) and three small (20–30 mm) uninfected *M. edulis*. In one of these full-community units, the *L. littorea* were infected with *H. elongata* (see below for the details on the screening for the infection status), and in the other unit—uninfected, in a fully crossed design (see Supporting Information Fig. S3). On top of each tank, an additional transparent bucket (header tank) was installed, receiving an inflow of unfiltered seawater, transferred to each of the three experimental units via a silicon tube at a rate of 20–30 mL min⁻¹. The outflow hole of the transparent tank was covered with a 1 mm plastic mesh to avoid incoming unwanted grazers (e.g., gammarids and isopods). The buckets were also scanned throughout the experimental period and no recruitment of grazers was found. To ensure a constant flow, the flow-through rate was measured every other day for the entire duration of the experiment, and the tubes were cleaned

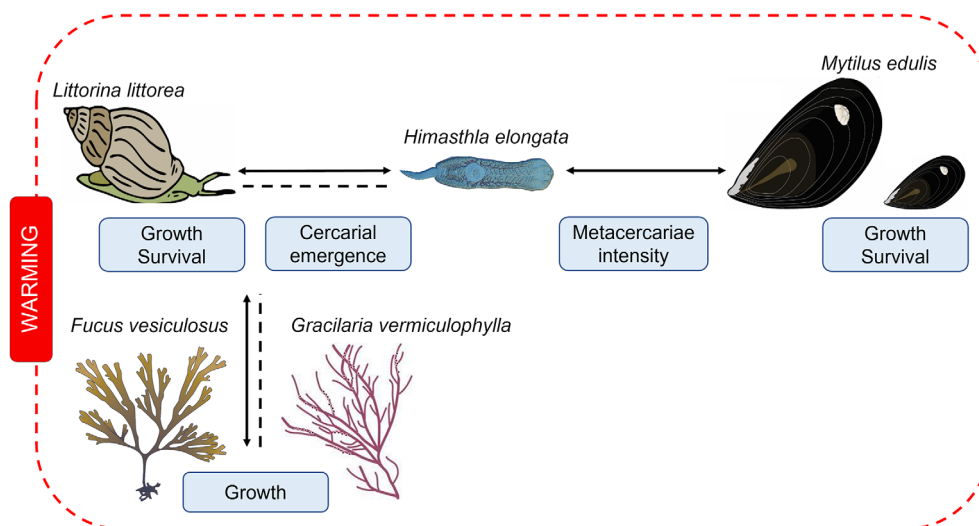


Fig. 1. The experimental community and performance measures. The studied community consists of the native macroalgae *Fucus vesiculosus*, the invasive macroalgae *Gracilaria vermiculophylla*, the periwinkle *Littorina littorea*, the trematode *Himastha elongata* and the blue mussel *Mytilus edulis*. Solid arrow indicates direct interactions between macroalgae species and their grazer (*L. littorea*) and between *H. elongata* and its intermediate hosts (i.e., *L. littorea* and *M. edulis*). Dashed lines indicate indirect interactions between the parasite, grazers, and macroalgae. The green boxes indicate the response variables analyzed.

or replaced when the flow decreased due to growing microalgae. To ensure that the algal individuals received similar nutrient concentrations, nutrients were measured at the start, middle, and end of the experiment (for nutrients sampling methodology and data, see Supporting Information Fig. S4).

Macroalga, grazer, and suspension-feeder collection

Thirty-six individuals of each algal species, *F. vesiculosus* (attached to stone) and *G. vermiculophylla*, with similar biomass, were collected from around 0.5 m depth in Falckenstein (54°23'41.064"N, 10°11'25.655"E) at the mouth of the Kiel Fjord. These two species naturally co-occur at this site. Individuals of *L. littorea* (range of initial size: 18–24.5 mm) were collected from Årøsund, Denmark (55°15'49.2"N, 9°42'30.5"E). *M. edulis* (range of initial size: 21–30 mm for small and 50–63 mm for large *M. edulis*) were collected from the Kieler Meeresfarm, a marine aquaculture facility in the inner Kiel Fjord (54°22'55.2"N, 10°09'43.6"E). During multiple parasitological assessments we found that the mussels in this facility are free from trematode parasite infection. The algae were transferred to a large cooler and transported to the GEOMAR climate chambers set to 16°C. Each *F. vesiculosus* and *G. vermiculophylla* individual was gently dried with a tissue and weighed twice: once with the stone and once after placing the stone near the scale and weighing again to assure accuracy. The initial weight of *F. vesiculosus* individuals ranged between 70 and 125 g. This wide range of initial weight was unavoidable since detaching the algae from the stone or cutting off pieces and further manipulating the individuals would incur stress. Since, unlike *F. vesiculosus*, *G. vermiculophylla* lives unattached, no manipulation was needed, and the weight of each experimental individual was 100 ± 1.1 (SD) g (wet weight). To determine their infection status, *L. littorea* individuals were placed wells of six-well plates (one snail per well) filled with aerated filtered seawater and exposed to heating lamps to induce cercariae shedding for around 3 h, not to cause additional stress to the host. Subsequently, the wells were checked under the dissection microscope, and *L. littorea* infected with *H. elongata* were identified based on released cercariae. *L. littorea* and *M. edulis* individuals were weighed (Denver MAXX-412, precision: 0.01 g), measured with analog calipers (precision: 0.2 mm), and labeled with small bee plastic tags glued to the apex of their shells before setting up the experiment. After labeling, the organisms that were designated for the warming were transferred to two 400 L tanks located in a climate chamber (room temperature of 16°C), for the acclimation to the warm treatment. One tank included half of the algal individuals and the infected *L. littorea* and the other included the other half of the algal individuals, the uninfected *L. littorea* individuals and the *M. edulis* individuals. The tanks were equipped with a constant flow-through originating from the Fjord and provided with LED light bars (LEDaquaristik UG) simulating natural light condition. The temperature was increased by 1°C every other day until

reaching the target temperature (19°C, ambient temperature +3°C). The other half of individuals destined to the ambient treatment was transferred to large plastic tanks in the KOB facility at ambient conditions (16°C), with constant flow-through originating from the Fjord. For the acclimation to both treatments, snails and mussels were kept in nets located inside the tanks, to prevent grazing or loss of individuals in the large tanks.

Cercarial emergence

To measure cercarial emergence during the experiment, 4 d a week from Monday to Thursday for six consecutive weeks, two labeled *L. littorea* were taken from the uninfected unit and two from the infected unit. The same individuals were incubated in the same daily order in the following weeks. The two *L. littorea* were individually placed in 50 mL polypropylene tubes filled with seawater from the header tank for 24 h. The four tubes per tank were sealed with a net, aerated through silicon tubes and then placed on a floating sponge in the main tank to maintain the temperature. The following day, the individuals were placed back in their respective buckets, and the water from the tube was collected (see Supporting Information Fig. S6). Tubes were placed at 4°C for 10 min to allow cercariae settlement at the bottom. Then, 25 out of 50 mL of surface water were discharged, and 10 mL of ethanol 99% were added to the remaining water volume (35 mL in total). Trematode abundance in the water samples was quantified under a stereo microscope (Nikon, SMZ1000 body, C-PS160 stand). The water of uninfected *L. littorea* was also checked to ensure no cercariae were present.

Final measurements

Mortality of *L. littorea* and *M. edulis* was assessed checking the marked individuals every other day and removing them if their body was not responding to any stimuli or if it was already degrading. To assess growth and infection levels at the end of the experiment, macroalgae, periwinkles and mussels were collected, and their wet weight (for macroalgae) and size (i.e., maximal shell length, for periwinkles and mussels) were recorded. The maximal shell length for *L. littorea* was defined as the distance from the aperture to the apex of the shell (Eschweiler and Buschbaum 2011). *L. littorea* and *M. edulis* individuals were dissected to verify the infection status (i.e., *H. elongata* prevalence for *L. littorea* and prevalence and infection intensity for *M. edulis*). The individuals found to be infected in the “uninfected” experimental units (ca. 15%) and those found to be uninfected in the “infected” experimental units (ca. 3%) were removed from the datasets for the analyses.

Statistical analysis

Growth and survival analyses

Relative growth rate of the macroalgae species was calculated according to Lüning (1990) using a logarithmic formula for wet weight: $RGR (\%d^{-1}) = 100 \times \left(\frac{\ln x_2 - \ln x_1}{t_2 - t_1} \right)$, where x_1 is

wet weight (g) at time 0, x_2 is wet weight (g) at time 1, t_0 and t_1 is time in days (d). We decided to include all algal individuals in the analysis and discussion of the results despite some *G. vermiculophylla* individuals were found decaying, since *Littorina* are known to feed on macroalgae individuals regardless of whether it is fresh or decaying (Shumway et al. 1993; Wilhelmssen and Reise 1994). Relative growth rate of *L. littorea* and *M. edulis* individuals was calculated according to Wahl (1996), who used the Bertalanffy growth coefficient: $K(d^{-1}) = \left(\frac{dH}{dt}\right)$, where dH is the maximal difference between final maximal length and initial maximal length, and dt is the time interval in days.

Daily survival rates (DSR) of *L. littorea* and *M. edulis* were assessed by using the formula of van der Toorn (1997): $DSR = 1 - \frac{\sum_{i=1}^K (y_i)}{\sum_{i=1}^K (x_i)}$, where K is the total number of individuals in the sample, y_i is “1” if individual i died during the experimental period and, “0” if individual i is still alive at the end of the experimental period, x_i is the number of survival days for individual i .

All statistical analyses were performed in R (version 4.0.2), 2009–2018. Relative growth rate for macroalgae (RGR, % d^{-1}), *L. littorea* and *M. edulis* (K , d^{-1}) were analyzed using generalized linear mixed models (GLMM) for all groups. The temperature levels, the infection status of the *L. littorea*, and the size (for *M. edulis* survival analysis only) were used as fully crossed fixed categorical factors, the factor “tank” was used as a random factor. For the RGR of macroalgae, the “control” treatment (no *L. littorea*) and the “ambient” temperature level were used as reference categories. For the RGR of *L. littorea* and *M. edulis*, and DSR of *M. edulis*, the “uninfected” and “ambient” levels were used as reference categories. For the DSR of *M. edulis*, the category “size small” was also included as reference category. We decided to include the size treatment as a factor in *M. edulis* DSR and not in *M. edulis* RGR since growth rates differ for *M. edulis* of such different size classes. When running the models, the individual DSR of *L. littorea* and *M. edulis* individuals were averaged across all periwinkle/mussel replicates in each unit (eight for *L. littorea*, three for small, three for large *M. edulis*).

Cercarial emergence and intensity in infected *M. edulis*

The sum of cercariae that emerged over the entire duration of the experiment, averaged by the eight infected *L. littorea* in each experimental unit, was analyzed using a generalized linear model (GLM) with a negative binomial distribution, using the average sum of cercarial emergence as the dependent variable and the temperature treatment as a fixed categorical factor. Before running the analysis, the numbers of cercariae released by *L. littorea* that did not survive for the entire experimental duration were removed from the dataset.

Further analysis was applied to the average daily cercarial emergence in relation to naturally increasing summer temperature. For this analysis, the number of *H. elongata* cercariae that

emerged from the two *L. littorea* incubated daily from each experimental unit was used as the dependent variable and the daily temperature of the KOB tanks as a fixed factor, pooling the daily temperatures of the ambient and warming treatment. A GLMM assuming a negative binomial distribution of residuals and log-link function was applied. In this analysis, the number of cercariae that emerged during the first week was omitted to avoid bias caused by other factors that might have triggered cercarial emergence at the start of the experiment (i.e., location in the experimental units, presence of the second intermediate host). The intensity of metacercariae in small and large *M. edulis* within the infected units was also analyzed using a GLMM with a Poisson distribution, with metacercariae intensity as the dependent variable and temperature and mussel size levels as fixed factors.

For all models, marginal and conditional R^2 were detected using the “r.squaredGLMM” function of the “MuMIn” package (Nakagawa and Schielzeth 2013). Model suitability was evaluated using the residual diagnostics tool from the “DHARMA” package, including quantile–quantile plots with KS test, outlier and dispersion tests (Hartig 2018).

Effect size calculation

To compare the different responses (i.e., growth and survival) in ambient and warming conditions across the different functional groups (i.e., primary producers, grazers, and filter feeders), effect sizes were calculated using Hedge’s g (Hedges 1981) corrected for small sample size. For these calculations, the ambient treatment was used as the reference or “control.”

We decided to discuss the outcomes of both kinds of analysis (GLMM and Hedge’s g), considering their differences in scope: while GLMMs show the significant correlation between all included fixed factors and the analyzed response variable, the Hedge’s g gives insights into the effect sizes of the results. Furthermore, the GLMM analyses the interactions among our fixed factors, while the Hedge’s g is used to compare the performance of each single species in ambient vs. warming conditions.

Results

Growth—Macroalgae

No significant differences were detected among all categories by the GLMM analysis when including the single and interactive effects of warming and presence of uninfected/infected *L. littorea* (GLMM, $p = 0.16$, 0.60 and 0.87 , Supplementary Table S1). Moreover, no significant interactive effects between temperature and *L. littorea* treatments were observed (GLMM, $p = 0.85$ and 0.73 , Supplementary Table S1; Fig. 2a, variance explained = 14%). Generally, *G. vermiculophylla* showed a negative, yet highly variable, growth over all treatments. Compared to the control treatment (ambient condition and no *L. littorea* present), the growth rate of *G. vermiculophylla* was, slightly insignificantly, lower in the treatment with uninfected *L. littorea* (GLMM,

$p = 0.07$, Supplementary Table S2) and significantly lower in the warming treatment and presence of infected *L. littorea* (GLMM, $p < 0.001$, Supplementary Table S2; Fig. 2b, variance explained = 68%).

Survival—*L. littorea* and *M. edulis*

GLMM analysis revealed a slight insignificant interactive effect of infection and temperature on periwinkle survival (GLMM, $p = 0.07$, Supplementary Table S3; Fig. 3a, variance explained = 50%). Survival was significantly lower in large *M. edulis* in the warming treatment compared to the small *M. edulis* and the ambient treatment and slightly higher in large *M. edulis* in the warming treatment with uninfected *L. littorea* (GLMM, $p = 0.005$ and 0.08 , Survival was significantly lowe Table S4; Fig. 3b,c, variance explained = 27%).

Growth—*L. littorea* and *M. edulis*

The GLMM did not reveal significant differences in *L. littorea* growth among all treatments or their interactions

(GLMM, $p > 0.1$ in all levels, Supplementary Table S5). Interestingly, when examining the plots (Fig. 4a), warming resulted in a bimodal distribution in both infected and uninfected *L. littorea*. The GLMM analysis revealed that none of the treatments affected the mean growth of the small *M. edulis* (GLMM, $p > 0.1$ in all levels, Supplementary Table S6; Fig. 4b, variance explained = 1.5%). In contrast, warming significantly reduced the mean growth of large uninfected *M. edulis* (GLMM, $p = 0.003$, Supplementary Table S7; Fig. 4c, variance explained = 29%). Interestingly, in this analysis, as the one of *Littorina*, warming revealed a bimodal distribution in the uninfected small *M. edulis* (Fig. 4b).

Cercarial emergence and metacercarial intensity

The GLM results showed no significant difference in *H. elongata* mean cercarial emergence between the ambient and warming treatments (GLM, $p = 0.8$, Supplementary Table S8; Supporting Information Fig. S6a). Nonetheless, the GLMM analysis of cercarial emergence as a function of

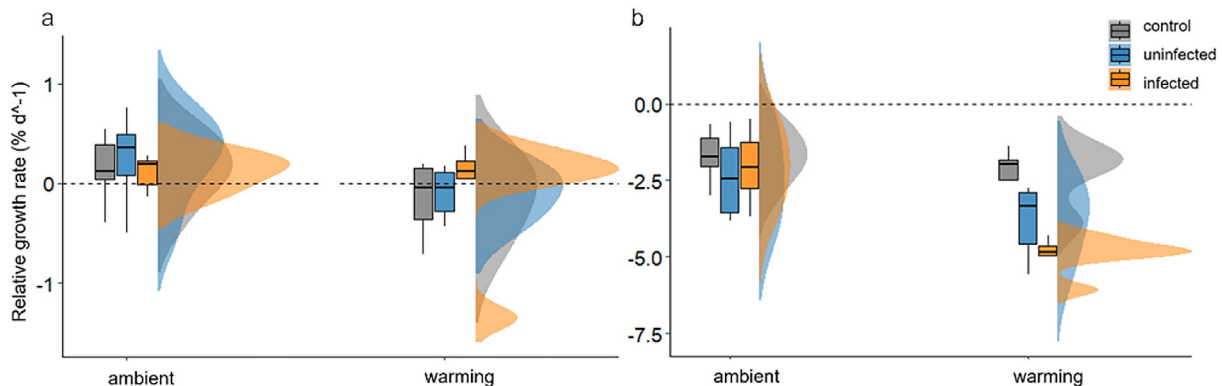


Fig. 2. Raincloud plots of (a) *Fucus vesiculosus* and (b) *Gracilaria vermiculophylla* individual growth expressed as relative growth rate (RGR, % d⁻¹) at the different treatment levels: control treatment without *Littorina littorea* (gray), with uninfected (blue) and *Himasthla elongata*-infected *L. littorea* (orange) treatments, at the ambient and warming treatment, respectively. Each raincloud plot consists of a distribution curve of growth on the right side and boxplots on the left side. Note the different y-axes in figures a and b.

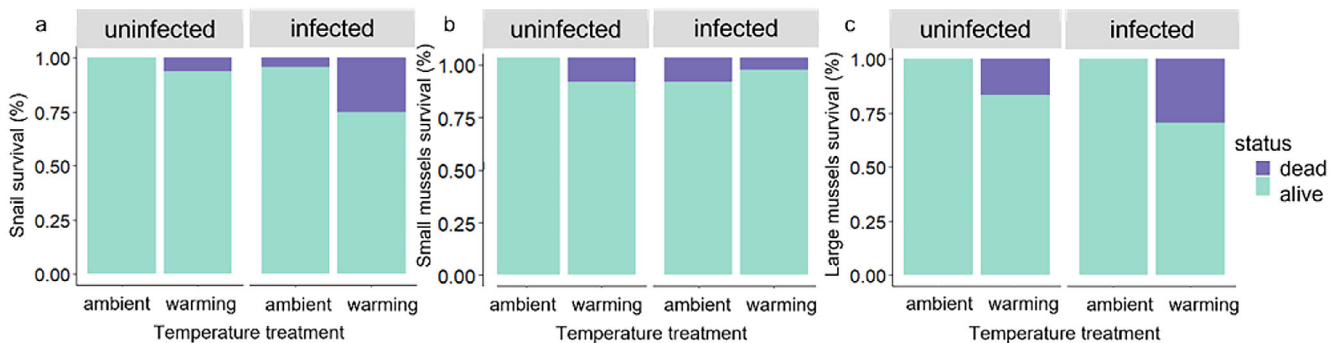


Fig. 3. Survival proportions of (a) infected and uninfected *Littorina littorea* ($n = 96$ of uninfected and $n = 96$ of infected, respectively) in the warming and ambient temperature treatments and (b) infected and uninfected small *Mytilus edulis* ($n = 36$ of uninfected and $n = 36$ of infected, respectively) in the warming and ambient treatments and (c) infected and uninfected large *M. edulis* ($n = 36$ of uninfected and $n = 36$ of infected, respectively) in the warming and ambient treatment. The proportion of survived individuals appears in green and the proportion of dead individuals dead appears in purple.

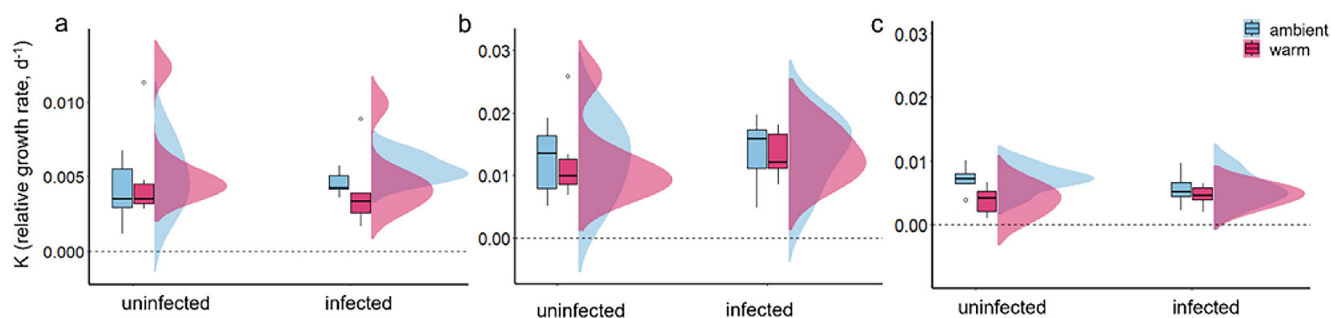


Fig. 4. Raincloud plot of (a) *Littorina littorea* (mean growth of eight individuals replicates per experimental unit), (b) *Mytilus edulis* small individuals, and (c) *M. edulis* large individuals mean growth (mean growth of three individuals replicates per experimental unit) expressed as relative growth rate (K), where growth rate is the length increase (mm) over the whole experimental period (50 d, expressed as t), at the different treatments' levels: uninfected and infected, at ambient (blue) and warm (pink) temperature' levels. Each raincloud plot consists of a distribution curve of growth on the right side and boxplots on the left side.

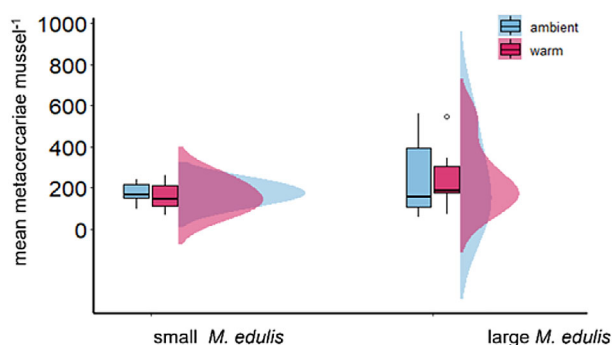


Fig. 5. Raincloud plot of mean *Himasthla elongata* metacercariae intensity in the tissue of a mussel individual in small and large size *Mytilus edulis* in the ambient (light blue) and warming (pink) temperature levels. Each raincloud plot consists of a distribution curve of mean metacercariae on the right side and boxplots on the left side.

temperature revealed a significant positive correlation, with cercarial emergence increasing with increasing natural summer temperature (GLMM, $p < 0.001$, Supplementary Table S9; Supporting Information Fig. S6b). However, the variance explained by the model was extremely low (4%). GLMM analyses of mean metacercariae density in *M. edulis* showed a positive effect of size, with significantly more metacercariae in large *M. edulis* compared to the small ones (GLMM, $p < 0.001$, Supplementary Table S10; Fig. 5, variance explained = 17%).

Summary plot of growth and mortality in response to warming: Hedges' g

Effect size analysis showed a slight negative effect of warming on *F. vesiculosus* growth, while *G. vermiculophylla* growth was significantly and negatively impacted by warming, with the strongest effect in the presence of infected snails (Fig. 6). The impact of warming on the growth of animals was much milder except for the negative effect on uninfected *M. edulis* growth. A more pronounced detrimental effect of

warming was found on periwinkle and mussel's survival, which was exuberated in infected *L. littorea* and large infected *M. edulis* but reduced in small, infected *M. edulis*.

Discussion

This study demonstrated several novel indirect impacts of climate change through species interactions, and specifically the host–parasite pathway. As a single stressor, warming negatively affected the growth and survival of large *M. edulis*. Warming and grazing by infected *L. littorea* negatively and significantly affected the growth of *G. vermiculophylla*, while the growth of the native alga *F. vesiculosus* remained unaffected. Finally, warming enhanced parasite transmission through a higher rate of cercarial emergence during the natural peak of summer temperatures and higher infectivity of larval stages to large *M. edulis*. The variable responses of the different functional groups are further discussed, and potential future lines of research are suggested.

Warming and parasitism combined effects on algal performance

Warming and grazing by infected and uninfected *L. littorea* did not significantly affect *F. vesiculosus* growth. This closely matches previous findings, reporting no warming impact on *F. vesiculosus* (Brooks and Crowe 2018) or an exacerbation of growth only when warming is combined with feeding pressure or other abiotic drivers, such as upwelling events (Wahl et al. 2021). However, considering the slower response of structural measures such as growth, we suggest that future studies also consider physiological responses, as those might respond faster to heat stress (see for instance, Takolander et al. 2017). In contrast to what was expected, the growth of *G. vermiculophylla* was negative in all treatments, including the controls, with some individuals decaying, especially in the warming treatment. Unfortunately, no data are available on the thermal performance curve of *G. vermiculophylla* in its invasive range, but experimental studies by Hammann et al.

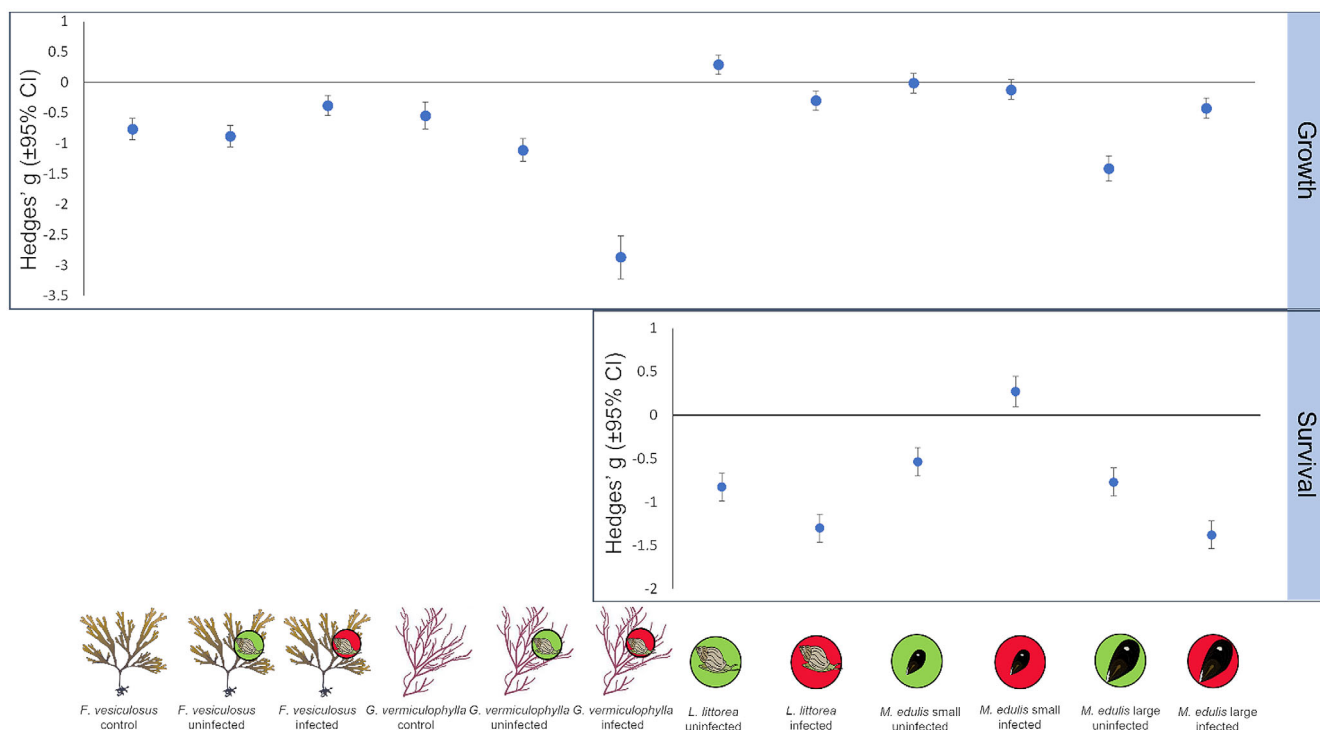


Fig. 6. Effect sizes corrected for small sample size (bias-corrected Hedges' g) and CI ($\pm 95\%$) of the growth of *Fucus vesiculosus* (brown alga) and *Gracilaria vermiculophylla* (red alga) without *Littorina littorea* (control) and with uninfected (green) and infected (red) *L. littorea* with *Himasthla elongata*, and growth (relative growth rate) and survival of uninfected (green) and infected (red) *L. littorea* and uninfected and infected small and large *M. edulis*, in response to warming (ambient temperature $+3^\circ\text{C}$). Positive values indicate an enhancement of growth and survival with warming, and negative values a reduction. An effect is considered significant when the CI bars do not cross the zero line.

(2016) and Sotka et al. (2017) showed that the average climatic niche of *G. vermiculophylla* non-native populations is warmer than that of native populations in Japan, which would suggest a higher thermal resistance than the one we observed in our experiment. However, both studies verified their hypotheses by exposing non-native and native individuals to extreme temperatures (submerged at 40°C) for 2–3 h. It might be that *G. vermiculophylla* displays lower tolerance to long-term exposure to temperatures above 20°C (in Hammann et al. 2016, the ambient conditions for this macroalga species were $15\text{--}20^\circ\text{C}$), which was the case in our experiment in both ambient and warming treatment.

Contrary to the expectations, the growth of *G. vermiculophylla* was negatively, although slightly insignificantly, affected by *L. littorea* feeding. Studies on the invasion success of *G. vermiculophylla* suggested that common grazers of the Baltic Sea (i.e., *Idotea baltica*, *Gammarus* spp., and *L. littorea*), while often associated with this invasive macroalgae, avoid feeding on it in the presence of other food sources such as *F. vesiculosus* (Weinberger et al. 2008; Nejrup et al. 2012). However, in the case of *L. littorea*, Weinberger et al. (2008) reported a slight preference for *G. vermiculophylla* compared to *F. vesiculosus* during the summer season, which aligns with our results. The impact of grazing on *G. vermiculophylla* intensified when combined with warming and snail infection by *H. elongata*. The direction of the effect that

trematodes have on gastropod grazing rates seems to differ among host–parasite combinations with infected snails presenting higher, lower, or similar grazing rates as compared to uninfected snails (Wood et al. 2007; Ayala-Díaz et al. 2019). The studies that align to the results of the present study (i.e., reporting higher grazing rates in infected snails compared to uninfected ones) hypothesize that the trematode poses an energetic burden on the host and might prompt it to increase feeding rates in order to compensate (Ayala-Díaz et al. 2019; Díaz-Morales et al. 2022). The authors suggest that this compensatory feeding might be the result of hijacked energy resources (e.g., glycogen) by the parasites and chronic and energy-costly immunological responses. Moreover, trematode infections can trigger a discrepancy between energy demand and metabolic products in the gastropods (Sokolova and Pörtner 2003), which might stimulate feeding. This result suggests a beneficial effect of parasitism on *F. vesiculosus* which, however, might shift from beneficial to detrimental in the long term. Infection by trematodes could lead to a net reduction of invasive macroalgae consumption by directly affecting the intermediate host survival, especially in warmer seasons. One must keep in mind that this scenario is not limited to *L. littorea* and their trematode parasites, and it remains unclear what would be the responses to warming of other potential grazers of *G. vermiculophylla* (i.e., as gammarids or isopods, see Nejrup et al. 2012).

Warming and parasitism combined effects on survival and growth of *L. littorea* and *M. edulis*

Although slight, the survival of *L. littorea* was afflicted by the imposed warming combined with trematode infection. In the warming treatment, the *L. littorea* were constantly exposed to temperatures above 20°C, and in the last 3 weeks of the experiment, the temperature increased, reaching 25°C. This high-temperature range can occur even today in shallow waters (water depth < 1.8 m) of the Baltic Sea during summer (Wolf et al. 2020). However, trematode infection has been found to enhance the mortality of *L. littorea* even at 22°C (Díaz-Morales et al. 2022). The development of trematodes can explain the mechanism underlying the enhanced host mortality in ectothermic hosts, which is temperature-dependent (Ataev 1991). Hence, infection by trematodes is well-known to heavily affect the first intermediate host by excessive energy demand, tissue damage, and castration (Fredensborg et al. 2005), often leading to host mortality. A previous study suggests that trematode species with rediae as the first larval stage inside the intermediate host, such as *H. elongata*, pose greater damage to their hosts than species using sporocysts (Sorensen and Minchella 2001). In the case of the mussels, we detected a significant detrimental effect of warming and weakly significant interaction of warming and infection status effects on the survival of large *M. edulis*. Interestingly, when warming was combined with infection, its effects on survival were less detrimental. The mechanism underlying this positive effect might be an infection-induced expression of biomarkers, which in turn allow mussels to better cope with heat stress, as hypothesized by Selbach et al. (2020). Different from the effect on the first intermediate host, the effect of trematodes on the second intermediate host is known to be less detrimental. Nevertheless, when the metacercariae number inside the host reaches high levels or when the infection is combined with other drivers, such as increased temperature, it might foster individual- and population-level effects (Mouritsen and Jensen 1997).

According to the analysis, neither infection status nor warming had a significant effect on the growth of *L. littorea*, despite warming being marginally beneficial for uninfected individuals and detrimental for infected individuals. According to Wahl (1996), *L. littorea*'s growth rates range from 0.2 to 14 $\mu\text{m d}^{-1}$. Considering 14 $\mu\text{m d}^{-1}$ as the fastest growth, *L. littorea* could have grown a maximum of 0.5 mm over the course of the experiment (but probably less), possibly too low to be significantly detected. In contrast to *L. littorea*, the imposed warming exerted a stronger negative effect on mussel growth than the effect of trematode infection. However, the negative influence was significant only in large uninfected *M. edulis*, whereas the effect on large infected and small *M. edulis* (regardless of infection) was smaller and insignificant. *M. edulis* is distributed over a wide range of temperatures (Read and Cumming 1967; Seed and Suchanek 1992). However, the optimal temperature (T_{opt}) for the growth of

M. edulis was reported to be around 20°C in the Atlantic Ocean and Baltic Sea (Almada-Villela et al. 1982), which was the minimum temperature reached in the warming treatment. Also, Hiebenthal et al. (2012) reported a temperature of 25°C to negatively affect *M. edulis* growth and survival (at an ambient salinity of 15 psu). The larger effect of warming on large vs. small *M. edulis* might be explained by the interaction of high temperature with low nutrition levels (Kossak 2006). Kossak (2006) found that when high temperatures occur in the Baltic or the North Sea, mussel shell size increases only at a very high phytoplankton load. Although using a flow-through system, our flow rate was relatively low, and nutrition levels in our experimental units might have been suboptimal for *M. edulis*. This possibly resulted in lower growth in such large individuals of 50–60 mm. Considering that the filtration rate in *M. edulis* of 5–6 cm is much higher than that of 2–3 cm *M. edulis* (Pleissner et al. 2013), high temperatures and low nutrients might stump the growth of large *M. edulis*.

An interesting outcome of the results on consumers' growth was the bimodality of the data distribution under warming conditions. These results could imply that under heat stress, genotypic, and phenotypic differences between more vulnerable and more robust individuals may be important, and that the latter might be selected in the future. A recent study by Leicht et al. (2017), for instance, showed that in the freshwater snail *Lymnaea stagnalis* individuals subjected to heat stress tend to be larger.

Parasite transmission

Unexpectedly, we did not detect a significant difference in cercarial emergence between the ambient and imposed warming treatments. However, cercarial emergence significantly increased with naturally increasing summer temperatures from around 20°C to 25°C in the KOB tanks. This range of temperatures perfectly aligns with Díaz-Morales et al. (2022), who reported a wide optimal temperature for cercarial emergence, between 19°C and 25°C, with a peak at 22.7°C. Overall, our findings align with recent studies suggesting that cercariae display a wide tolerance window for emergence from the first intermediate host, usually dependent on the tolerance of the host itself and the adaptability of the trematode species to changes in the environment (Byers 2021; Díaz-Morales et al. 2022). Metacercarial intensity in *M. edulis* was only slightly affected by imposed warming. Instead, mussel size had a major role, with a substantially higher number of metacercariae in larger *M. edulis*. The size of the second intermediate host has been previously demonstrated as a contributing factor to metacercarial intensity, and it is likely the result of (1) accumulation of metacercariae throughout the mussel life (Nikolaev et al. 2006); and (2) a higher filtration rate in larger *M. edulis* that enhance the probability of infection (Mouritsen et al. 2003; Nikolaev et al. 2006). In the present study, since the *M. edulis* were collected from an aquaculture site known to be trematode-free, the second hypothesis more likely explains

our results. A change in size of the second intermediate host in the future could therefore represent a bottleneck for increasing parasitism. In the near future, drivers other than warming, such as freshening of the Baltic Sea along the western coast, might lead to a decrease in mussel size, as it has already been occurring on the eastern coast (Kautsky 1982). This shift in mussel size could hamper the transmission of trematode species such as *H. elongata*, yet favor the transmission of smaller-size trematode species such as *R. roscovita*, having smaller chances of being detected by mussel sensory organs (i.e., mantle margins) (Frenkiel 1980).

Conclusions

Overall, our study showed that warming and parasitism might have single or interactive effects on the Baltic community investigated, with direct effects on the survival of the intermediate hosts and indirect effects on macroalgae growth, especially on the invasive macroalga *G. vermiculophylla*. These effects might initially benefit populations of the native *F. vesiculosus* over the populations of *G. vermiculophylla*.

Our findings demonstrate the complex direct and indirect mechanisms by which climate change, bioinvasions, and parasitism can interact and influence the structure and function of communities. To our knowledge, this is the first study examining these complexities at the community level, along with the direct effects of parasitism. It highlights the need to consider parasites as fundamental players of community biodiversity, indirectly influencing habitat formers such as *F. vesiculosus*. The insights provided by our study would benefit from more research on host and parasite traits as well as their capacity to adapt to various environmental drivers in a rapidly changing environment.

Data availability statement

Data from this article will be available at the PANGEA database.

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Conflict of Interest

None declared.

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