



Co-occurrence of native and invasive macroalgae might be facilitated under global warming

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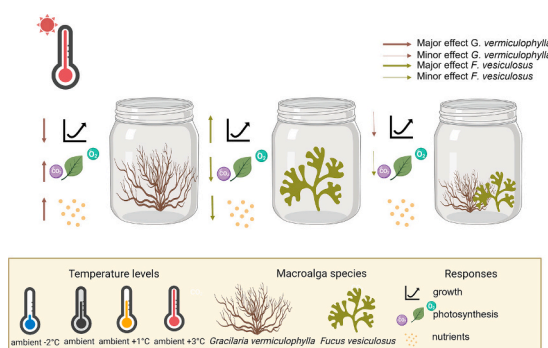
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HIGHLIGHTS

- The RCP8.5 scenario significantly affects both *Fucus vesiculosus* and *Gracilaria vermiculophylla*.
- Warming is detrimental for *G. vermiculophylla* growth while beneficial for *F. vesiculosus* growth.
- The macroalgae appear to benefit from the presence of the other species.
- The differences in nutrients demand of the two macroalgae suggest resource partitioning.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change is driving compositional shifts in ecological communities directly by affecting species and indirectly through changes in species interactions. For example, competitive hierarchies can be inverted when competitive dominants are more susceptible to climate change. The brown seaweed *Fucus vesiculosus* is a foundation species in the Baltic Sea, experiencing novel interactions with the invasive red seaweed *Gracilaria vermiculophylla*, which is known for its high tolerance to environmental stress. We investigated the direct and interactive effects of warming and co-occurrence of the two algal species on their performance, by applying four climate change-relevant temperature scenarios: 1) cooling) 2 °C below ambient – representing past conditions), 2) ambient summer temperature (18 °C), 3) IPCC RCP2.6 warming scenario (1 °C above ambient), and 4) RCP8.5 warming (3 °C above ambient) for 30 days and two compositional levels (mono and co-cultured algae) in a fully-crossed design. The RCP8.5 warming scenario increased photosynthesis, respiration, and nutrients' uptake rates

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of mono- and co-cultured *G. vermiculophylla* while growth was reduced. An increase in photosynthesis and essential nutrients' uptake and, at the same time, a growth reduction might result from increasing stress and energy demand of *G. vermiculophylla* under warming. In contrast, the growth of mono-cultured *F. vesiculosus* significantly increased in the highest warming treatment (+3 °C). The cooling treatment (−2 °C) exerted a slight negative effect only on co-cultured *F. vesiculosus* photosynthesis, compared to the ambient treatment. Interestingly, at ambient and warming (RCP2.6 and RCP8.5 scenarios) treatments, both *F. vesiculosus* and *G. vermiculophylla* appear to benefit from the presence of each other. Our results suggest that short exposure of *F. vesiculosus* to moderate or severe global warming scenarios may not directly affect or even slightly enhance its performance, while *G. vermiculophylla* net performance (growth) could be directly hampered by warming.

1. Introduction

Coastal ecosystems are increasingly threatened by a combination of climate change, local human impacts (e.g., Lotze et al., 2006; He and Silliman, 2019; Gissi et al., 2021), and bioinvasions (Davidson et al., 2018). One of the most important and threatened coastal ecosystems are macroalgal forests that have already been affected by global change in many regions (Wernberg et al., 2011; Monserrat et al., 2022). Macroalgae play essential ecological roles, acting as ecosystem engineers and providing valuable ecosystem services (Graham, 2004; Hawkins et al., 2009). Their sessile nature, which does not allow them to translocate to deeper waters during heat events, and their limited propagule dispersal, make macroalgae particularly prone to abiotic and biotic stress (Wahl et al., 2015).

Among the abiotic drivers affecting macroalgae the most, shifts in temperature play a main role by directly altering photosynthesis, respiration, growth, reproduction, and survival (Capdevila et al., 2019; Liu et al., 2020). The magnitude and direction of these effects depend on the life history and biology of the respective macroalgal species and the ambient diurnal, seasonal, and annual temperature fluctuations it experiences (Wahl et al., 2020). In addition, warming might indirectly affect macroalgal performance by impacting other species with whom they interact (Wahl et al., 2015) or modifying traits that can alter their interactions (Raddatz et al., 2017). Specifically, warming can change the competitive ability to acquire resources with newly introduced macroalgae. Bioinvasions are normally considered problematic, but, in fact, they can have both positive and negative consequences on the native biodiversity and ecosystem functioning (Maggi et al., 2015; Guy-Haim et al., 2018). Algal growth depends on resources—substrate availability, essential nutrients, micronutrients, and light—all of which can become limited in the presence of alien competitors (Wahl et al., 2015). Ephemeral autotrophs, for instance, are able to uptake nutrients more efficiently than slow-growing algae (Pedersen and Borum, 1996), but they may become beneficial for basiphytes (i.e., anchored host algae for epiphytes) under specific stressors. For example, Guy-Haim et al. (2020) found that epiphytes can facilitate the calcification of coralline algae by altering the carbonate chemistry in the diffusive boundary layer of the coralline under ocean acidification scenarios. In general, all primary producers, epibiotic or neighbouring macroalgae, are potential competitors, but the intensity of the competition varies with their individual performance in a specific environmental setting (Wahl et al., 2011, 2015).

Our study focused on the combined effect of ocean warming and potential competitive interactions with alien species on a foundation member of the Baltic Sea macrophyte communities. The Baltic Sea is one of the fastest-changing water bodies in the world (Reusch et al., 2018). Since 1985, the Baltic Sea has experienced an increase in temperature of up to 0.4 °C per decade (Lehmann et al., 2011), and the latest published warming scenarios predict an increase of additional 3 °C sometime between 2069 and 2098 (RCP8.5 scenario; Meier et al., 2022). In general, benthic species in the Baltic Sea are well adapted to changes in temperature and other environmental factors due to the high level of natural fluctuations they experience (Pansch et al., 2014; Paalme et al., 2020). Among the common Baltic species, the brown alga *Fucus vesiculosus*

(Linnaeus 1753) is a foundation species, displaying dioecy but able to hybridise with hermaphrodite *Fucus* species such as *Fucus spiralis* (Cánovas et al., 2011; Hatchett et al., 2022). This macroalga is found along most of the Baltic coasts, occurring in both protected and wave-exposed shores and providing substratum, food, and shelter for numerous associated species of micro- and macroalgae, sessile and motile invertebrates, and fishes (Voipio, 1981; Kautsky et al., 1992; Rohde et al., 2008). The Baltic Sea areas populated by this macroalga are considered marine forests (Rönnbäck et al., 2007) that, in the past decades, have been subjected to pronounced shoaling (Törn et al., 2006). This has been mainly attributed to the direct and indirect effects of eutrophication, which causes decreased light availability and an increased abundance of filamentous algae (Eriksson et al., 1998; Berger et al., 2003, 2004). Although eutrophication remains one of the principal stressors, a recent review highlights that other factors, such as the increase in Baltic Sea surface water temperature and competition with invasive algae, likely contributed to the decline of *F. vesiculosus* (Viitalo and Bonsdorff, 2022).

A potential prominent competitor of *F. vesiculosus* is the alien red alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss 1967. It is considered one of the most successful invaders out of 23 macroalgae species introduced to the European coasts (Nyberg, 2007). This macroalga originates from the Northwest Pacific and was detected in Europe for the first time in 1996 on the French Atlantic coast (Rueness, 2005) followed by its detection on the Danish coast in 2005 (Schories and Selig, 2006), although Krueger-Hadfield et al. (2017) reported that its introduction in the European coasts might have taken place much earlier than documented based on the genetic structure of native and non-native *G. vermiculophylla* populations. *G. vermiculophylla* has an isomorphic life cycle (male and female gametophytes and tetrasporophytes have similar morphologies). Its high tolerance to environmental stress and greater rates of uniparental reproduction in introduced relative to native populations have allowed *G. vermiculophylla* to spread rapidly in the last decades (Yokoya et al., 1999; Rueness, 2005; Nyberg, 2007; Krueger-Hadfield et al., 2016). *G. vermiculophylla* is an ecosystem engineer that, once established, competes for space with native macroalgae and affects the community structure (Byers et al., 2012; Kollars et al., 2016). Weinberger et al. (2008) reported a decline of *F. vesiculosus* in habitats where *G. vermiculophylla* has spread, like the Kiel Fjord. Recent studies by Hammann et al. (2016) and Sotka et al. (2018) reported that non-native populations of *G. vermiculophylla* are tolerant to temperatures up to 40 °C when submerged in water. Its high tolerance for environmental stressors might also enable this invasive macroalga to spread over the Baltic coast down to salinities of 5.5 (Weinberger et al., 2008) and, thus, possibly compete with the native *F. vesiculosus* across its entire distribution. However, whether the effects of this co-occurrence are detrimental or beneficial for either macroalgal species and whether warming can alter this interaction have not been investigated experimentally so far.

1.1. Aims and hypotheses

The effects of climate change on individual species have been widely investigated; however, predictions on climate change consequences for

species interactions are still understudied (Gilman et al., 2010; Vandvik et al., 2020) despite their large ecological relevance. Davis et al. (1998), for instance, showed how strongly the response to temperature of a single species can change when other species are present. Novel species interactions imposed by alien species can strongly affect species fitness since the native species do not share a coevolutionary history with the newly occurring species (Reznick and Ghalambor, 2001). The combination of ocean warming and competition with alien consumers, for example, can lead to the collapse of populations of native key consumers (Yeruham et al., 2019). Our study aimed to compare the effects of global warming on the performance of native and invasive macroalgae species, *F. vesiculosus* and *G. vermiculophylla*, separately and when occurring together. Furthermore, we assessed the presence and magnitude of competition between the two species, which share the same benthic habitat in the Baltic Sea. Specifically, we exposed different combinations (mono-cultured vs. co-cultured) of the two macroalgae species to temperature treatments following scenario projections provided by the Intergovernmental Panel on Climate Change (IPCC, 2019). We also added a cooling treatment to simulate summer conditions when *G. vermiculophylla* was initially introduced (according to the IPCC, 2014, the Baltic Sea Surface Temperature (SST) has increased by 0.35 °C per decade from 1950 to 2009). To assess the algal response, we measured photosynthetic and respiration rates, nutrient uptake, and growth. Since *Gracilaria*'s invasive populations are known to be highly tolerant to heat stress (Sotka et al., 2018), we hypothesized that warming would be beneficial to the invasive alga *G. vermiculophylla*, both when cultured singly and in the presence of the native alga *F. vesiculosus*. As fieldwork and laboratory experiments suggest that this invasive species might cause habitat loss for *F. vesiculosus* (Weinberger et al., 2008), we also hypothesized that *G. vermiculophylla* would have a (warming-enhanced) negative impact on *F. vesiculosus* performance.

2. Methods

2.1. Collection of macroalgae, weighing and acclimation

Fucus vesiculosus and *Gracilaria vermiculophylla* were randomly collected on June 14, 2021, at the Kitzberg Beach in Heikendorf, Germany (54°21'25.6"N 10°10'45.3"E). Individuals presenting high amounts of reproductive vesicles (ca. >50 % algae-surface area coverage) were avoided. *Gracilaria vermiculophylla* thalli (see Krueger-Hadfield et al., 2023 for the use of "thallus/thalli" term instead of "individual" for *G. vermiculophylla*) collected were a mix of floating and

attached thalli. Between June 14 and 17, all collected thalli were kept at ambient temperature in two large tanks of 400 L in the Kiel Indoor Benthocosm (see Pansch and Hiebenthal, 2019 for more information), provided with flow-through and natural light conditions. On June 17, the collected individuals were weighed (LC221s, Sartorius, Germany) after blotting them individually. Subsequently, macroalgae were gradually acclimatised for three days to the different temperature treatments, changing the temperature by 1 °C each day. This rate of change was not greater than the diurnal temperature range at the collection site during that period (Wolf et al., 2020).

2.2. General experimental setup

The experiment was conducted in the Kiel Indoor Benthocosms (KIBs, Pansch and Hiebenthal, 2019) and lasted four weeks, from June 21 until July 22, 2021. The setup included two factors in a fully crossed experimental design: 1) temperature scenarios consisting of four levels: average summer ambient temperature in Kiel Fjord (18 °C), cooling (ambient −2 °C) RCP2.6 warming scenario (ambient +1 °C), RCP8.5 warming scenario (ambient +3 °C) and 2) macroalgae groups consisting of three levels: a) *F. vesiculosus* mono-cultured, b) *G. vermiculophylla* mono-cultured, c) *F. vesiculosus* and *G. vermiculophylla* co-cultured (see Fig. 1). Temperature scenarios were selected according to the predicted future scenarios for global oceans (IPCC, 2019). The experiment was carried out in eight mesocosm tanks equipped with LED light bars (LEDAquaristik UG., Schierbusch, Germany), two tanks per temperature treatment level (see Fig. S1a and b in Supplementary material). The respective target temperatures of each tank were maintained by the use of heaters (300–500 W, Aqua Medic). Each tank contained 10 independent (fed individually from the header tank) experimental units (1.5 L glass jars). One of the 10 experimental units contained seawater only as procedural control for the measurements of photosynthetic, respiration, and essential nutrients' (NO₃, NO₂, PO₄, SI) uptake rates. Three experimental units contained one individual of *F. vesiculosus* each (10 g, wet weight), three units contained one thallus of *G. vermiculophylla* each (10 g, wet weight), and three units contained one individual of *F. vesiculosus* and one thallus of *G. vermiculophylla* each (5 g for each species, wet weight) as the co-culture treatment. All temperature-species combination treatments were thus replicated six times. Seawater was pumped from the Kiel Fjord, sand-filtered, and distributed into 60-L header tanks located above each tank (Pansch and Hiebenthal, 2019). Water was constantly supplied to each jar via a flow-through system from the header tanks through individual silicone tubes, renewing the

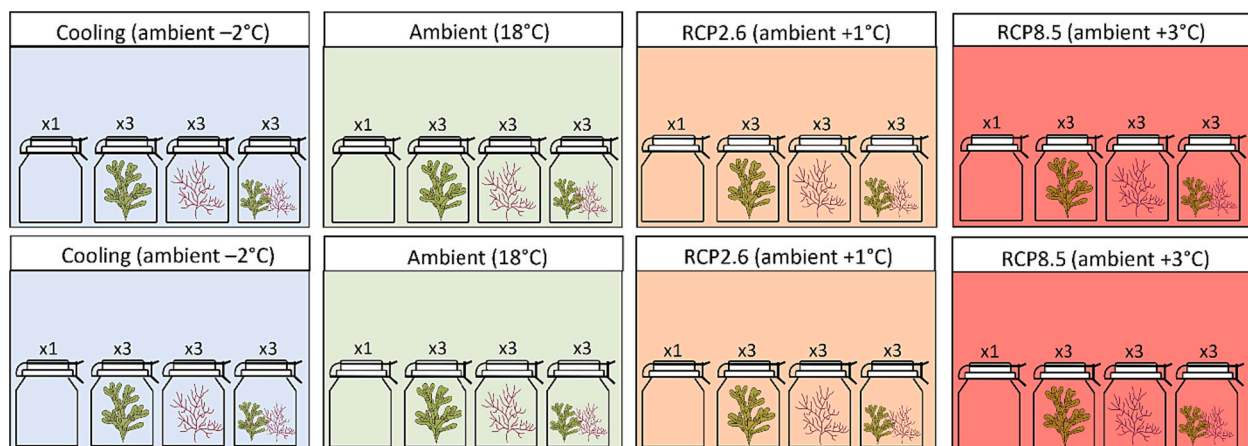


Fig. 1. Experimental setup. The experiment was conducted in eight Kiel Indoor Benthocosm tanks. Two replicate tanks set per each treatment: 2 °C below ambient (cooling, in light blue), ambient ± 0 °C (ambient, in green), 1 °C above ambient (RCP2.6, in orange), and 3 °C above ambient (RCP8.5, in red). The ambient level corresponded to the average summer temperature in the Kiel Fjord (18 °C). The temperature levels were kept constant throughout the entire duration of the experiment. In each tank, ten glass jars closed with glass lids were deployed, one jar as control, three with an individual of *Fucus vesiculosus* of 10 g, three with thalli of *Gracilaria vermiculophylla* of 10 g and three with two thalli together of *F. vesiculosus* and *G. vermiculophylla* of 5 g each, respectively.

seawater within each jar every 3–4 h. Each jar had a glass lid with a 1 cm hand-drilled hole through which a silicone tube was inserted to supply the jar with water. Since the lid of the jar was not sealed, the water from each jar overflowed through the opening of the jar into the tank. The benthocosm's water level was about 3 cm below the jar opening, acting as a water bath to maintain the desired temperatures while preventing the water from flowing back into the jar (see Fig. S1c in Supplementary material).

2.3. Monitoring abiotic parameters

The flow rate in each jar was maintained at 50 mL min⁻¹ for the entire duration of the experiment and checked on a daily basis. Each control jar was equipped with a temperature sensor (GHL, Germany). Temperature readings were automatically logged every 10 min. Furthermore, manual temperature measurements were done every other day with a multimeter (WTW 3630 IDS). Light intensities of the LED bars were measured in a random subset of experimental units in each tank at the beginning of the experiment and then weekly to ensure that light intensity was maintained. The measurements were done with an Apogee Light Meter (MQ-510 Quantum Meter). The light intensities (80–120 mmol m⁻² s⁻¹) were within the range of natural light conditions within *F. vesiculosus* stands in summer (authors pers. obs.).

2.4. Incubations for assessing photosynthetic and respiration rates

During the last week of the experiment, photosynthetic performances were measured to test the response of the single and combined macroalga species to temperature, using short incubations (2 h) by measuring changes of dissolved oxygen (DO) with a hand-held optode WTW 3630 IDS. The incubations were performed on single individuals in gas-tight 1.5 L glass jars. For that, individuals of the “co-cultured” experimental units were separated and their performance parameters were measured individually. Net photosynthesis (P_{net}) and respiration (R) rates were assessed during daytime and nighttime incubations, respectively.

As water reservoir for the incubations, one bucket of 50 L was placed beside each mesocosm tank and filled with running seawater coming from the header tank. Oxygen concentrations and temperature in the water reservoir bucket were constantly measured with a multimeter (WTW 3630 IDS). For net photosynthesis (P_{net}) incubations, each macroalga individual was transferred to a cleaned glass jar with a hermetic lid. The jar was then submerged in the source water bucket to fill it up with water and then closed hermetically. Each jar was then immediately placed in the main mesocosm tanks. Jars were incubated under the light for 2 h. Afterwards, each jar was carefully tilted several times to ensure oxygen mixing, the lid was carefully opened, the water was gently mixed using the multimeter and the oxygen concentration and temperature were recorded. The same method was used to measure respiration (R), after 2 h incubation in complete darkness (0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), which was confirmed by using an Apogee Light Meter (MQ-510 Quantum Meter).

Net production (P_{net} in $\mu\text{mol O}_2 \text{g}^{-1} \text{WW h}^{-1}$) in terms of oxygen production was calculated by the difference between initial and final DO concentration (ΔDO) per wet weight (WW) divided by the duration of the incubation (Δt).

$$P_{net} = \Delta\text{DO}/(\text{WW} \times \Delta t)$$

Respiration rates, (R in $\mu\text{mol O}_2 \text{g}^{-1} \text{WW h}^{-1}$) in terms of oxygen consumption, were calculated in the same way. Gross photosynthetic rate (P_g in $\mu\text{mol O}_2 \text{g}^{-1} \text{WW h}^{-1}$) was inferred as:

$$P_g = P_{net} + R \quad (2)$$

2.5. Nutrient measurements

During the light incubation, seawater was subsampled from three

randomly chosen jars with freshly renewed water for nutrient analysis into 10 mL plastic tubes ($n = 3$) using a 50 mL syringe equipped with a 40 μm filter (Sartorius). After the two-hour incubation, another set of nutrient samples was collected from each jar, with the method described above for the control samples, while oxygen and temperature measurements were performed. The samples were stored at -20°C pending analysis. The analyses were performed using a colourimetric segmented flow analyzer (QuAatro, Seal analytical).

2.6. Growth measurements

At the end of the experiment, macroalgae were collected, blotted and weighed. The relative growth rate of the macroalgae species was calculated according to Lüning (1990) using a logarithmic formula for wet weight:

$$\text{RGR} (\% \text{d}^{-1}) = 100 * \left(\frac{\ln x_2 - \ln x_1}{t_1 - t_0} \right) \quad (3)$$

where x_1 is the wet weight (g) at time 0 (beginning of the experiment), x_2 is the wet weight (g) at time 1 (end of the experiment), t_0 and t_1 are time in days (d).

2.7. Statistical analyses

Statistical analyses were performed with R (version 4.0.2) and Rstudio v.1.3.1073 (2009–2020 RStudio, PBC). Generalized Linear Mixed Models (GLMMs) assuming a Gaussian residual distribution, using the function “lmer” from the “lme4” package, were fitted to test for the significance of main and interactive effects of temperature levels (ambient, cooling, RCP2.6 and RCP8.5) and macroalgal species (*F. vesiculosus* mono-cultured, *G. vermiculophylla* mono-cultured, *F. vesiculosus* co-cultured, *G. vermiculophylla* co-cultured) as fixed categorical factors affecting macroalgae P_{net} , R , P_g , nutrient uptake and RGR ($\% \text{d}^{-1}$) (dependent variables). The “ambient” level and the “*G. vermiculophylla* mono-culture” level were included as reference levels. After running the models, a post-hoc test was applied for each model to verify the significant differences in performance among the macroalgae groups within each temperature level and the differences in performance of each macroalga group among the different temperature levels. Post hoc tests based on Estimated Marginal Means (Searle et al., 1980) were run to assess the significance of differences between pairs of group means, using the function “emmeans” (adjusted as “tukey” by default) from the “emmeans” package for lmer. The Goodness-of-fit of the model was verified by calculating the R^2 through the function “performance” (package MuMIn, version 1.46.0). 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). To analyse P_g , P_{net} and NO_3 and PO_4 uptake, a log-transformation was applied to adjust the data's skewness.

3. Results

The average values of RGR of mono-cultured *F. vesiculosus* were between 1.12 (ambient -2°C , cooling level) and 0.79 (ambient $+3^\circ\text{C}$, RCP8.5). In contrast, the ones of mono-cultured *G. vermiculophylla* were negative, between -0.78 (cooling level) and -2.95 (RCP8.5) (Table 1). For the co-cultured *F. vesiculosus*, values ranged between 1.21 and 1.14, while for co-cultured *G. vermiculophylla* between 0.14 and -1.14 (Table 1). The gross and net photosynthetic and respiration rates show similar patterns, but the difference between P_g and P_{net} under RCP8.5 is higher for mono- than co-cultured *G. vermiculophylla* (Table 1). The nutrient uptake rates showed high variability between species and treatment (Table 1).

Table 1

Average values (\pm standard deviation) of gross photosynthesis (P_g), net photosynthesis (P_{net}), respiration (R_{O_2}), growth (RGR), nutrients' uptake (NO_2 , NO_3 , PO_4 , SiO_4) of the different macroalgal groups 1) mono-cultured *Fucus vesiculosus*, 2) co-cultured *F. vesiculosus*, 3) mono-cultured *Gracilaria vermiculophylla* and 4) co-cultured *G. vermiculophylla*.

	Mono-cultured	Co-cultured	Mono-cultured	Co-cultured
	<i>F. vesiculosus</i>	<i>F. vesiculosus</i>	<i>G. vermiculophylla</i>	<i>G. vermiculophylla</i>
P_g ($\mu\text{mol g}^{-1} \text{h}^{-1}$)				
Cooling	3.40 \pm 0.44	3.97 \pm 0.43	5.77 \pm 1.75	5.64 \pm 1.64
Ambient	3.95 \pm 0.97	5.92 \pm 0.88	5.07 \pm 1.32	6.51 \pm 1.30
RCP2.6	4.29 \pm 0.75	6.69 \pm 1.14	5.17 \pm 1.06	6.77 \pm 0.56
RCP8.5	5.46 \pm 0.50	6.68 \pm 0.86	9.45 \pm 3.19	6.68 \pm 3.14
P_{net} ($\mu\text{mol g}^{-1} \text{h}^{-1}$)				
Cooling	2.84 \pm 0.45	3.47 \pm 0.45	4.72 \pm 1.34	5.12 \pm 1.80
Ambient	3.31 \pm 0.87	5.26 \pm 0.69	4.35 \pm 1.31	5.88 \pm 1.10
RCP2.6	3.76 \pm 0.84	6.15 \pm 1.07	4.64 \pm 1.05	6.21 \pm 0.52
RCP8.5	4.42 \pm 0.67	5.62 \pm 0.84	6.66 \pm 2.95	6.66 \pm 2.78
R_{O_2} ($\mu\text{mol g}^{-1} \text{h}^{-1}$)				
Cooling	-0.55 \pm 0.20	-0.50 \pm 0.13	-1.05 \pm 0.80	-0.52 \pm 0.17
Ambient	-0.64 \pm 0.16	-0.66 \pm 0.24	-0.72 \pm 0.14	-0.63 \pm 0.31
RCP2.6	-0.53 \pm 0.23	-0.54 \pm 0.20	-0.53 \pm 0.32	-0.56 \pm 0.16
RCP8.5	-1.03 \pm 0.18	-1.05 \pm 0.28	-1.73 \pm 0.78	-1.40 \pm 0.61
RGR (% d⁻¹)				
Cooling	1.12 \pm 0.90	1.21 \pm 0.49	-0.78 \pm 3.14	0.14 \pm 2.64
Ambient	0.77 \pm 0.49	1.47 \pm 0.25	-0.20 \pm 1.80	0.49 \pm 1.50
RCP2.6	0.71 \pm 0.67	1.41 \pm 0.40	-1.15 \pm 2.65	0.32 \pm 2.09
RCP8.5	0.79 \pm 0.48	1.14 \pm 0.38	-2.95 \pm 2.21	-1.14 \pm 2.37
Nutrients' uptake ($\mu\text{m g}^{-1} \text{h}^{-1}$) - NO_2				
Cooling	$1.4 \times 10^{-3} \pm 0.2 \times 10^{-3}$	$0.7 \times 10^{-3} \pm 0.6 \times 10^{-3}$	$-1.5 \times 10^{-3} \pm 1.9 \times 10^{-3}$	$0.6 \times 10^{-3} \pm 1.7 \times 10^{-3}$
Ambient	$0.9 \times 10^{-3} \pm 0.6 \times 10^{-3}$	$1.6 \times 10^{-3} \pm 0.7 \times 10^{-3}$	$1.4 \times 10^{-3} \pm 2.6 \times 10^{-3}$	$2.2 \times 10^{-3} \pm 2.1 \times 10^{-3}$
RCP2.6	$0.9 \times 10^{-3} \pm 0.9 \times 10^{-3}$	$3 \times 10^{-3} \pm 0.1 \times 10^{-3}$	$3.9 \times 10^{-3} \pm 3.8 \times 10^{-3}$	$2.1 \times 10^{-3} \pm 2.2 \times 10^{-3}$
RCP8.5	$-0.1 \times 10^{-3} \pm 1.3 \times 10^{-3}$	$-0.2 \times 10^{-3} \pm 1.9 \times 10^{-3}$	$-0.4 \times 10^{-3} \pm 5.5 \times 10^{-3}$	$-0.8 \times 10^{-3} \pm 5.9 \times 10^{-3}$
Nutrients' uptake ($\mu\text{m g}^{-1} \text{h}^{-1}$) - NO_3				
Cooling	-0.05 \pm 0.01	-0.07 \pm 0.02	-0.19 \pm 0.11	-0.20 \pm 0.12
Ambient	-0.06 \pm 0.02	-0.08 \pm 0.01	-0.14 \pm 0.03	-0.17 \pm 0.03
RCP2.6	-0.06 \pm 0.02	-0.09 \pm 0.02	-0.16 \pm 0.13	-0.16 \pm 0.05
RCP8.5	-0.08 \pm 0.00	-0.11 \pm 0.02	-0.35 \pm 0.21	-0.31 \pm 0.20
Nutrients' uptake ($\mu\text{m g}^{-1} \text{h}^{-1}$) - PO_4				
Cooling	$-3 \times 10^{-3} \pm 2 \times 10^{-3}$	$-3 \times 10^{-3} \pm 3 \times 10^{-3}$	$-1.4 \times 10^{-2} \pm 0.12 \times 10^{-3}$	$-0.1 \times 10^{-3} \pm 7 \times 10^{-3}$
Ambient	$-2 \times 10^{-3} \pm 0.000$	$-2 \times 10^{-3} \pm 2 \times 10^{-3}$	$-0.007 \pm 2 \times 10^{-3}$	$-6 \times 10^{-3} \pm 6 \times 10^{-3}$
RCP2.6	$-2 \times 10^{-3} \pm 1 \times 10^{-3}$	$-1 \times 10^{-3} \pm 1 \times 10^{-3}$	$-0.005 \pm 1 \times 10^{-3}$	$-5 \times 10^{-3} \pm 4 \times 10^{-3}$
RCP8.5	$-4 \times 10^{-3} \pm 1 \times 10^{-3}$	$-0.006 \pm 3 \times 10^{-3}$	$-0.19 \times 10^{-3} \pm 0.16 \times 10^{-3}$	$-0.19 \times 10^{-3} \pm 0.17 \times 10^{-3}$
Nutrients' uptake ($\mu\text{m g}^{-1} \text{h}^{-1}$) - SiO_4				
Cooling	-0.05 \pm 0.03	-0.034 \pm 0.03	-0.204 \pm 0.13	-0.162 \pm 0.10
Ambient	-0.01 \pm 0.02	0.004 \pm 0.02	-0.033 \pm 0.09	-0.057 \pm 0.06
RCP2.6	0.01 \pm 0.03	0.061 \pm 0.03	0.005 \pm 0.05	0.042 \pm 0.08
RCP8.5	-0.01 \pm 0.05	-0.044 \pm 0.03	0.280 \pm 0.52	-0.100 \pm 0.18

3.1. Gross, net photosynthetic and respiration rates

The gross photosynthesis of mono-cultured *G. vermiculophylla* was significantly higher at +3 °C (RCP8.5 treatment) than in the other temperature levels (GLMM, $p < 0.001$, Table S1, Fig. 2), while the gross photosynthesis of co-cultured *G. vermiculophylla* was slightly insignificantly lower than the mono-cultured thalli at +3 °C (RCP8.5) (GLMM, $p < 0.02$, Table S1, Fig. 2). Net photosynthesis showed similar results than gross photosynthesis (see Fig. S1 and Table S3 in Supplementary material). Similarly, also the respiration of mono-cultured *G. vermiculophylla* was significantly higher at +3 °C (RCP8.5) than in the other temperature levels (GLMM, $p = 0.015$, Table S5, Fig. 3), while this was not the case for co-cultured *G. vermiculophylla* (Table S5, Fig. 3). As shown by the post hoc test results at ambient and +1 °C treatment, the gross photosynthesis of mono-cultured *F. vesiculosus* was

significantly lower than co-cultured *F. vesiculosus* (Estimated Marginal Means; $p = 0.01$ and $p = 0.005$, respectively, Table S2). Overall, the photosynthetic and respiration rates of *G. vermiculophylla* showed a higher variance as compared to *F. vesiculosus*.

3.2. Growth rates

Mono-cultured *G. vermiculophylla* grew significantly less at the warmest treatment level (RCP8.5) than in other temperatures, while the mono-cultured *F. vesiculosus* showed a slightly significant growth at that level (GLMM, $p = 0.01$ and $p = 0.045$, respectively, Table S7). Similar to photosynthesis, respiration and nutrient uptake, the variability in growth of *G. vermiculophylla* was again much higher than of *F. vesiculosus* (Fig. 4).

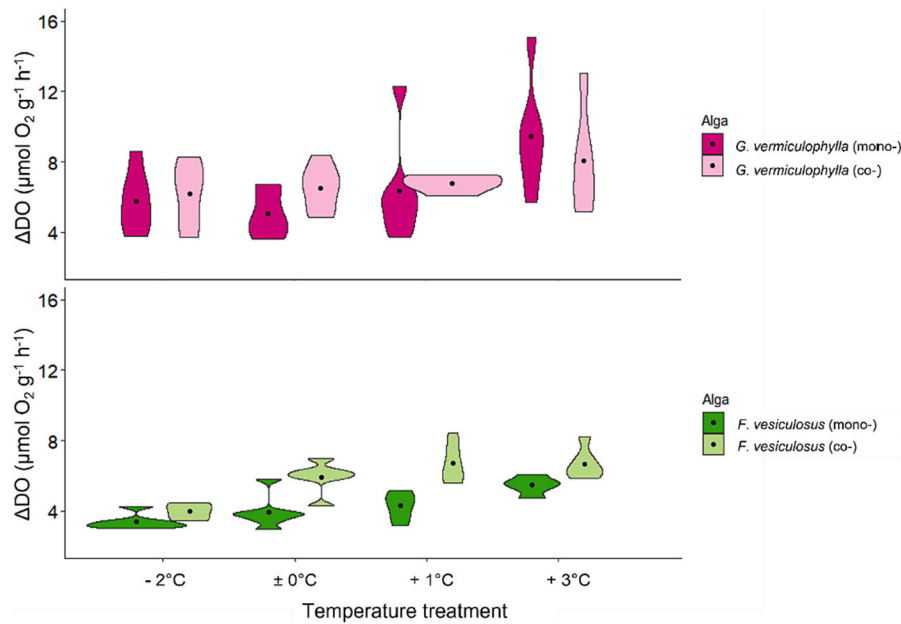


Fig. 2. Violin plots for P_g (gross photosynthesis rate) of the four macroalgae groups a) *Gracilaria vermiculophylla* mono-cultured (in dark pink), b) *G. vermiculophylla* co-cultured (in light pink), c) *Fucus vesiculosus* mono-cultured (in green) and d) *F. vesiculosus* co-cultured (in light green) exposed to cooling (ambient -2°C), ambient ($\pm 0^\circ\text{C}$, 18°C), RCP2.6 (ambient $+1^\circ\text{C}$), and RCP8.5 (ambient $+3^\circ\text{C}$). Black dots indicate the mean.

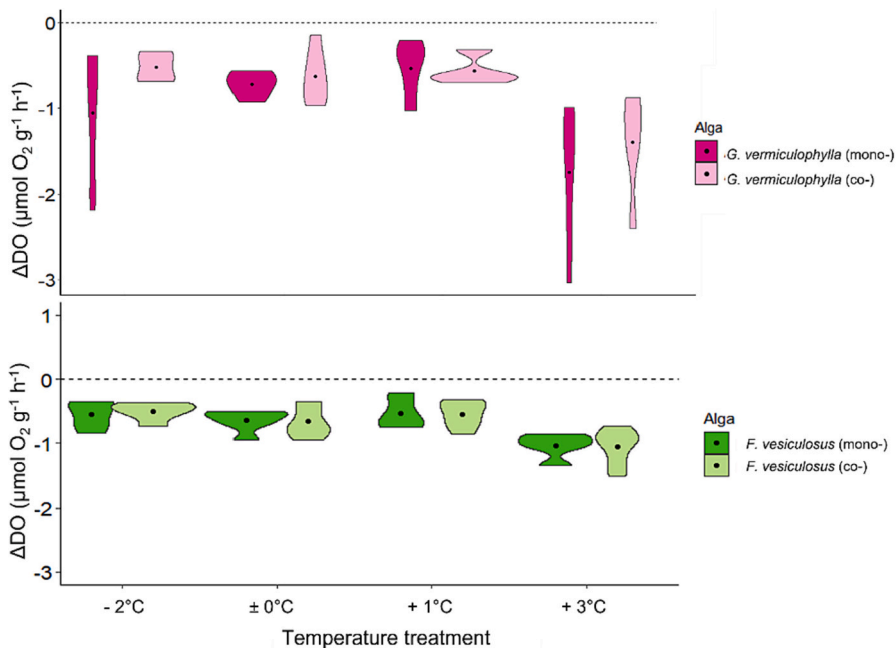


Fig. 3. Violin plots for R_{o2} (respiration) of the four macroalgae groups a) *Gracilaria vermiculophylla* mono-cultured (in dark pink), b) *G. vermiculophylla* co-cultured (in light pink), c) *Fucus vesiculosus* mono-cultured (in green) and d) *F. vesiculosus* co-cultured (in light green) exposed to cooling (ambient -2°C), ambient ($\pm 0^\circ\text{C}$, 18°C), RCP2.6 (ambient $+1^\circ\text{C}$), and RCP8.5 (ambient $+3^\circ\text{C}$). Black dots indicate the mean.

3.3. Nutrients' uptake rates

The nitrate uptake of mono-cultured *G. vermiculophylla* was significantly higher than that of mono and co-cultured *F. vesiculosus* (GLMM, $p < 0.0001$ and $p = 0.01$, respectively; Table S11). Moreover, the nitrate uptake of mono-cultured *G. vermiculophylla* was higher at the warmest temperature level (RCP8.5) than at the other temperature levels (GLMM, $p = 0.01$; Table S11). The phosphate and silicate uptake by mono-cultured *G. vermiculophylla* was significantly higher than by mono-cultured *F. vesiculosus* (GLMM, $p = 0.01$ and $p = 0.008$, respectively;

Tables S13 and S15, Fig. 4). Similarly, as with photosynthesis, *G. vermiculophylla* the nutrient uptake was more variable as compared to *F. vesiculosus* (Fig. 5).

4. Discussion

4.1. Overview and general summary of our findings

We experimentally investigated the combined effects of global warming and species interaction within a native-invasive macroalgal

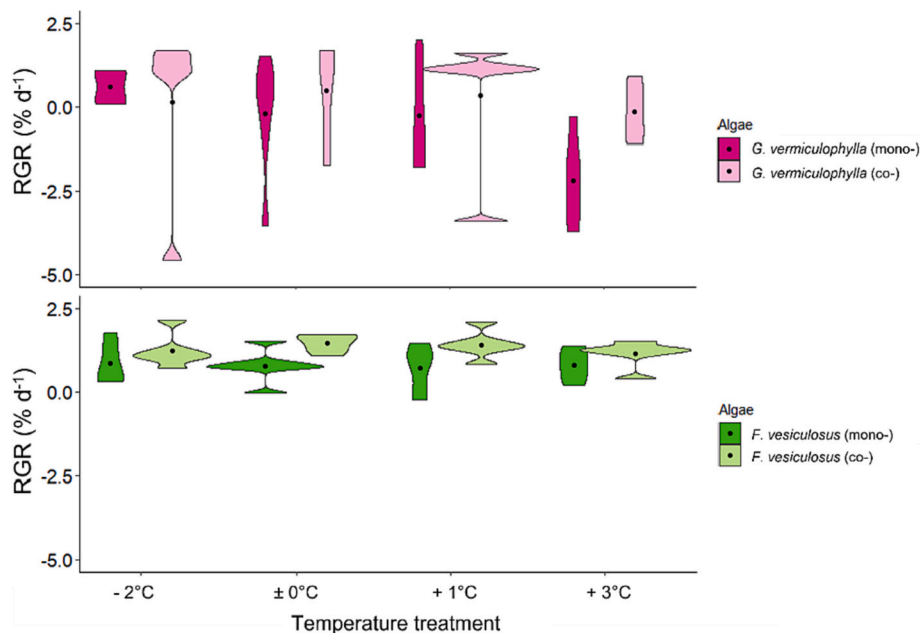


Fig. 4. Violin plots for RGR (Relative Growth Rate, calculated using wet weight) of the four macroalgae groups a) *Gracilaria vermiculophylla* mono-cultured (in dark pink), b) *G. vermiculophylla* co-cultured (in light pink), c) *Fucus vesiculosus* mono-cultured (in green) and d) *F. vesiculosus* co-cultured (light green), exposed to cooling (ambient -2°C), ambient ($\pm 0^{\circ}\text{C}$, 18°C), RCP2.6 (ambient $+1^{\circ}\text{C}$), and RCP8.5 (ambient $+3^{\circ}\text{C}$). Black dots indicate the mean.

system. Such studies are timely considering the fast spread of non-native species and their impact on biodiversity and ecosystem functions. There is a general dread of non-native species; their effects are assumed to be mostly detrimental to biodiversity. Bioinvasions, however, might also have beneficial effects, or their effects might be counteracted by properties of the native species. In the present study, warming by 3°C was found to be detrimental to invasive *Gracilaria vermiculophylla* when mono-cultured, as it caused higher respiration without increasing net photosynthesis to the same extent, resulting in reduced algal growth. In contrast, the growth of the native *Fucus vesiculosus* benefited from warming. When comparing the performance of mono- and co-cultured individuals, *G. vermiculophylla* presence appeared to enhance *F. vesiculosus* photosynthetic rate at ambient temperature and slightly at warmer temperatures. The detrimental effect of warming on *G. vermiculophylla* growth was also buffered, even if not significantly, by the presence of *F. vesiculosus*. The beneficial effects of the interspecific co-occurrence are surprising and offer interesting insights into their future interaction in a warmer ocean.

4.2. Photosynthesis and respiration

The gross photosynthesis of mono-cultured *G. vermiculophylla* significantly increased at the warmest temperature (ambient $+3^{\circ}\text{C}$, RCP8.5). This increment might result from a high respiration rate of *G. vermiculophylla* at high temperatures. A similar trend could also be observed in the gross photosynthesis of *F. vesiculosus*, which on average (but not significantly) increased with higher temperatures. High respiration can result from high microbial activity at elevated temperatures during incubations, indicating the start of necrosis and lower performance. Previous studies indicated that the net photosynthetic production in macroalgae seems less affected by increasing temperature than respiration (Tait and Schiel, 2013; Martins et al., 2020). This might be attributable to a thermal acclimation of respiration and implies a potential decoupling of temperature and gross photosynthesis at high temperatures/under heat stress (Necchi, 2004).

The absence of significant differences in *F. vesiculosus* gross photosynthesis along temperature treatments reflects the wide range of the temperature comfort zone of *F. vesiculosus*, which ranges from 5 to 26°C

(Graiff et al., 2015; Takolander et al., 2017a). Algal photosynthetic rate can quickly acclimatize to increasing temperatures (Davison, 1991). This is especially true in Baltic Sea algae, where a wide annual range of thermal fluctuations occurs (Eggert, 2012; Takolander et al., 2017b). Still, as reported by Graiff et al. (2015), the optimum temperature for Baltic *F. vesiculosus* photosynthesis is around 24°C . This explains the slight increase in *F. vesiculosus* photosynthesis toward the highest experimental temperature in our study (21°C).

The effect exerted by *G. vermiculophylla* on *F. vesiculosus* photosynthesis in the co-cultured treatment at ambient and $+1^{\circ}\text{C}$ treatments can be related to the lower tendency of the small *F. vesiculosus* individuals used in the experiment (relative to the mono-culture individuals) to self-shade. Self-shading limits the PAR received by *F. vesiculosus* blades (Graiff et al., 2020). Baltic *F. vesiculosus* blades are known to expand distally while growing (Russell et al., 1998). Therefore, a larger individual (like the ones in our mono-cultured treatments) might be more prone to self-shading than a smaller one. Since we used smaller individuals (or lower amount of thalli in the case of *G. vermiculophylla*) in the co-culture compared to the mono-culture (5 vs. 10 g, respectively) to maintain equal total biomass across treatments, the increase in photosynthesis in the presence of *G. vermiculophylla* might be due to reduced self-shading of *Fucus vesiculosus* rather than the effect of *G. vermiculophylla* itself. Moreover, in the field and at low abundances, *G. vermiculophylla* is often found on the bottom, intertwined with the basal part of the *F. vesiculosus* individuals (Bommarito and Díaz-Morales pers. obs.). The same pattern was observed in our experimental jars, and therefore, the invasive macroalgae may have interfered less with the photosynthesis reaction of co-cultured *F. vesiculosus*. In other words, a larger individual of *F. vesiculosus* may be more at risk of self-shading than a smaller one co-cultured with *G. vermiculophylla*. The apparent beneficial impact of *G. vermiculophylla* could hence rather be attributable to treatment-caused size differences, but further experiments should test this hypothesis. Considering our results and the findings by Graiff et al. (2015), reporting *F. vesiculosus* growth reduced when temperatures exceed 20°C , under a warming scenario, the native macroalgae *F. vesiculosus* could be less impacted than the invasive *G. vermiculophylla* in terms of photosynthesis, and could even benefit from the presence of *G. vermiculophylla*, especially when considering small size individuals.

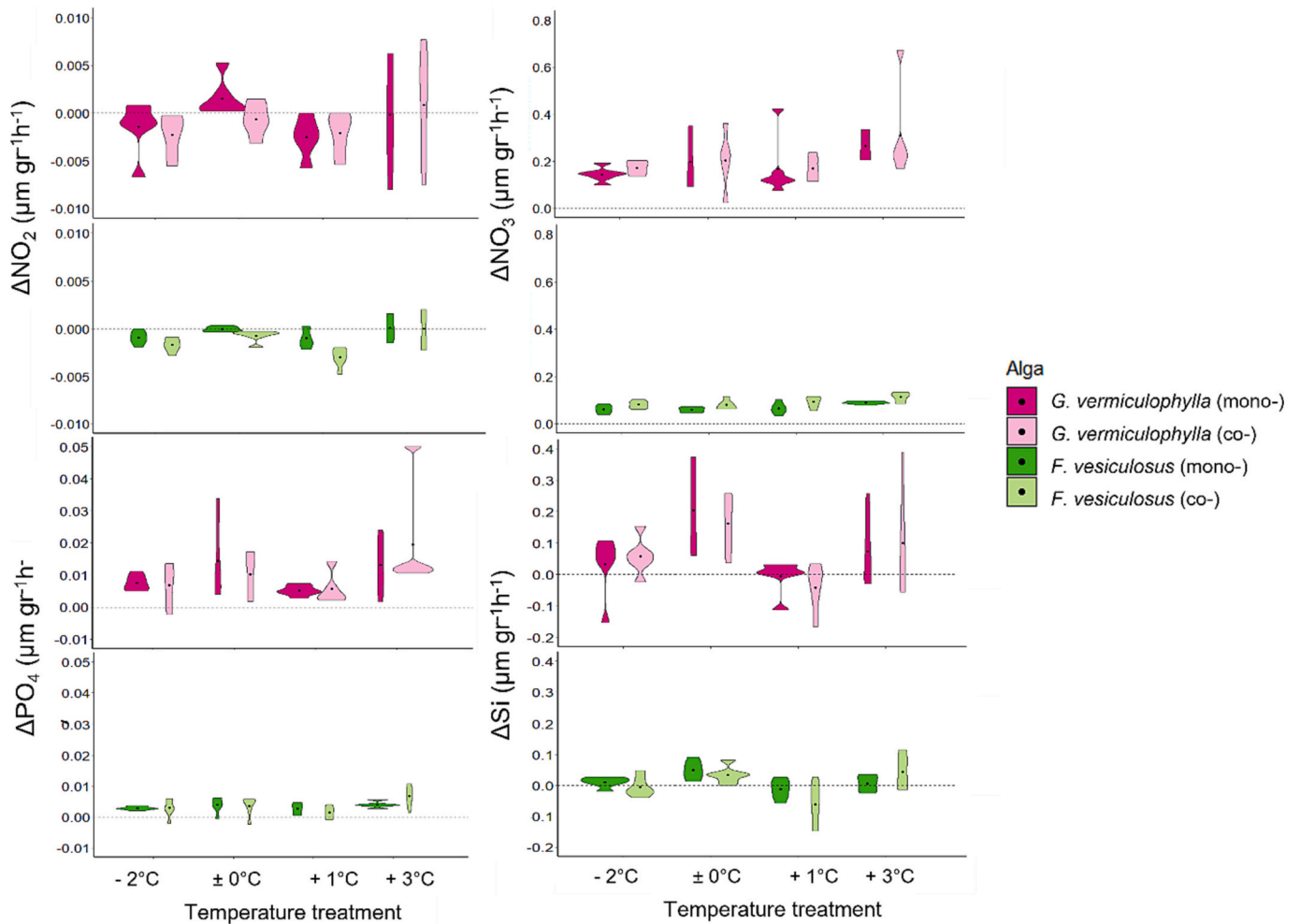


Fig. 5. Violin plots showing a) NO_2 uptake b) NO_3 uptake c) PO_4 uptake and d) Si uptake by the four experimental group of macroalgae a) *Gracilaria vermiculophylla* mono-cultured (in dark pink), b) *G. vermiculophylla* co-cultured (in light pink), c) *Fucus vesiculosus* mono-cultured (in green) and d) *F. vesiculosus* co-cultured (in light green) exposed to cooling (ambient -2°C), ambient ($\pm 0^\circ\text{C}$, 18°C), RCP2.6 (ambient $+1^\circ\text{C}$), and RCP8.5 (ambient $+3^\circ\text{C}$). Black dots indicate the mean.

4.3. Growth

Contrary to our hypothesis, warming ($+3^\circ\text{C}$) was beneficial for the growth of *F. vesiculosus* and detrimental for *G. vermiculophylla*. Yet, the presence of *F. vesiculosus* seemed to buffer the negative effect of warming on the growth of *G. vermiculophylla*, although the effect was not significant. The optimum of *F. vesiculosus* growth in the South Western Baltic Sea ranges between 10 and 24°C , with a peak at 20°C (Graiff et al., 2015). This value lies between the two highest temperatures used in our experiment ($+1$ and $+3^\circ\text{C}$, respectively). Therefore, our results support previous observations that the growth of *F. vesiculosus* from the South Western Baltic seems to be favoured by slighter higher temperatures than other strains inhabiting other regions of the Baltic Sea (Nygård and Dring, 2008) or other seas such as the North Sea (Pearson et al., 2000). These differences in the thermal tolerance among populations have been attributed to genotypic differences (See Pearson et al., 2000; Nygård and Dring, 2008; Graiff et al., 2015).

As opposed to former studies (Nejrup et al., 2013; Gorman et al., 2017), our results showed that warming is likely to hamper the growth and, consequently, the distribution of *G. vermiculophylla*. These results align, however, with the findings of Wahl et al. (2020), who reported a detrimental impact of warming on the growth of *G. vermiculophylla* collected from the same zone as the thalli in our experiment.

In its native range, the shallow waters of the Pacific Ocean, *G. vermiculophylla* is well-adapted to wide environmental fluctuations (i.

e., temperature, salinity, and light) at the regional and seasonal scales (Phooprong et al., 2008; Hammann et al., 2016; Sotka et al., 2018), making it a perfect candidate for spreading in other oceans. Hammann et al. (2016) and Sotka et al. (2018) found non-native populations of *G. vermiculophylla* responding well to heat stress. However, the duration of the exposure to heat stress in these two studies was a maximum of 4 h, way shorter than in our study, which could explain the discrepancy in the findings. Few studies have investigated the influence of temperature on *G. vermiculophylla* growth in the alga's invasive range. Investigating the distribution of *G. vermiculophylla* on the West coast of Sweden, Nyberg et al. (2009) identified temperature and ice cover as growth-limiting factors. On the Danish coast of the Baltic Sea, Nejrup et al. (2013) found that *G. vermiculophylla* was able to grow at 5°C and reach the optimum growth at 20°C (with a light intensity of $225 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), assuming the success of the introduced species in Scandinavian coasts all over the year. In contrast, Weinberger et al. (2008), investigating the growth of *G. vermiculophylla* in the Kiel Fjord, observed a decreasing resistance toward low salinities in summer when the temperature exceeded 15°C . All these results, combined with our findings, are partially contradictory and lead to the conclusion that a combination of local drivers affects the performance of different *G. vermiculophylla* populations and sometimes in contrasting ways.

4.4. High variability among *G. vermiculophylla* thalli

An explanation for the negative effect of temperature on *G. vermiculophylla* growth in our study might be attributed to the high variability in responses found among the *G. vermiculophylla* thalli used. Some thalli were degrading, while others were healthy and fast-growing. This variability might be due to the haploid-diploid ratio in the populations and, in turn, within the thalli we collected for the experiments. Krueger-Hadfield et al. (2016) reported that the majority of introduced *G. vermiculophylla* populations are highly dominated by diploid thalli, usually floating above soft-sediment mudflats. However, among the sampled populations along the German coast (Heikendorf, in Kiel Fjord) also gametophytes were found (Krueger-Hadfield et al., 2017). This suggests that the Kiel population used in our experiment could be characterized by a mix of haploid and diploid thalli, which are known to respond differently to stress conditions (Guillemin et al., 2013).

The success of *G. vermiculophylla* performance is also linked to the strain to which the investigated thalli belong (i.e., ecotype). Phooprang et al. (2008) found that the optimal temperatures of different Japanese populations of *G. vermiculophylla* differed according to the local temperature regimes. The variation in *G. vermiculophylla* performance caused by different ecotypes is also supported by Ruess (2005) and Nejrup et al. (2013). Another important factor for *G. vermiculophylla* health is the intimate link with its microbiome. Lachnit et al. (2011) showed that *G. vermiculophylla* is closely associated with specific bacteria displaying antibacterial activity. The disruption of this link, caused by environmental stress, can result in a drop in the host defences (Egan and Gardiner, 2016; Li et al., 2022). Qiu et al. (2019), who investigated the effects of warming and acidification on the kelp *Ecklonia radiata* and its microbiome, found that microbial community of bleaching and degrading thalli differed from the one of healthy thalli. Their results suggest a relevant role of temperature in the algae microbiome, which might have played a role also in our experiment.

4.5. Nutrient uptake

Temperature did not affect the nutrient uptake of *F. vesiculosus*. This result corroborates previous studies, reporting a correlation between nutrient uptake and temperature for other algal species, but not for *F. vesiculosus* (Topinka Bigelow, 1978). *F. vesiculosus* is a slow-growing alga, which makes this species less susceptible to nutrient limitation than fast-growing species that, for instance, have a higher P-demand (Pedersen et al., 2010). The lower susceptibility of slow-growing algae derives from their capability to use internal nutrient reserves stored during winter and early spring and from their ability to satisfy their nutrient requirements by exploiting lower external concentrations compared to fast-growing algae (Pedersen and Borum, 1996). Therefore, temperature variations might not affect nutrient uptake of *F. vesiculosus* at noteworthy levels.

As opposed to *F. vesiculosus*, the highest temperature level applied (i.e., RCP8.5 scenario, 21 °C) appeared to increase the NO₃ uptake by *G. vermiculophylla*. Furthermore, the nutrient uptake by *G. vermiculophylla* was generally higher than by *F. vesiculosus*, especially in the mono-cultured treatment. Previous studies investigating nutrient kinetics showed that the nutrient uptake by *G. vermiculophylla* is generally rapid and that its maximum uptake can even exceed its immediate requirements (Tyler et al., 2005; Abreu et al., 2011). Pedersen and Johnsen (2017) compared the nutrient dynamics of *G. vermiculophylla* with the ones of other algal species that are native to Scandinavian waters. They showed that *G. vermiculophylla*'s N and P quotas were higher than those of *F. vesiculosus*, which aligns with our results and relates these differences to the medium- (*G. vermiculophylla*) and slow-growing (*F. vesiculosus*) natures of the two algal species. An increase in nutrient uptake following an increase in temperature has already been observed in other seaweeds (Hanisak and Harlin, 1978; Du

et al., 2013) and can be explained by the increased metabolic rates (photosynthesis and respiration) at higher temperatures (Brown et al., 2004). These differences in nutrient demands between the slow-growing *F. vesiculosus* and the rapid-growing *G. vermiculophylla* might indicate resource partitioning, where each species utilizes different nutrient pools and avoids direct competition (Duarte, 1995).

Bracken and Stachowicz (2006) tested the hypothesis of multivariate complementarity by evaluating the effect of seaweed diversity on the nitrogen flux, which is the major limiting nutrient in most marine ecosystems (Ryther and Dunstan, 1971). Their results showed that different functional groups can co-occur if they prefer nitrogen in different forms (i.e., ammonium or nitrate). Hence, niche partitioning might reduce competition. Although our nutrient measurements were performed when the macroalgae individuals/thalli were separated, which excludes the possibility of directly relating our nutrient uptake results with the multivariate complementarity theory, we can argue that this multivariate complementarity might have occurred in our *Fucus-Gracilaria* system, favouring the growth of the two species in the co-cultured treatment.

5. Conclusions

In conclusion, our study showed that the RCP8.5 scenario (+3 °C) exerted none or very slight, at least during the relatively short exposure of four weeks during summer, effects on the native mono- and co-cultured *F. vesiculosus*. As opposed, the RCP8.5 scenario exerted two contrasting effects on the performance of mono- and co-cultured *G. vermiculophylla*. Based on these contrasting responses of *G. vermiculophylla* in terms of metabolic and growth rates, clear predictions on the spreading of this alga are difficult, especially when considering the high variability in the responses among thalli, leading to the hypothesis that ecotypes play an essential role in shaping species response to climate change. Nevertheless, our findings suggest that the presence of *G. vermiculophylla* has either beneficial or no effects on the performance of *F. vesiculosus*. Under a slight warming scenario (RCP2.6), the presence of *G. vermiculophylla* could enhance the photosynthesis of the native alga, especially of small size *F. vesiculosus* individuals. Under the worst warming scenario (RCP8.5), however, the beneficial effect of *G. vermiculophylla* on *F. vesiculosus* photosynthesis could be nullified, possibly due to the detrimental effect of warming on *G. vermiculophylla* itself. However, in the long term, the warming detrimental effect could be buffered by the co-presence and consequent resource portioning of the two species. As shown by our results, a negative impact of an introduced species on co-occurring and potentially competing native species should not always be assumed. The slight beneficial effect of the invasive alga on the native one at the medium temperatures and the beneficial effect of the native alga on the invasive one could trigger a cascading effect, with *G. vermiculophylla* becoming a potential refuge for other benthic species and, consequently, increasing the diversity and the ecosystem functions and services.

CRedit authorship contribution statement

C. Bommarito: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **S. Noè:** Conceptualization, Investigation, Writing – review & editing. **D.M. Díaz-Morales:** Investigation, Methodology, Writing – review & editing. **I. Lukić:** Methodology. **C. Hiebenthal:** Methodology, Conceptualization, Writing – review & editing. **G. Rilov:** Methodology, Writing – review & editing. **T. Guy-Haim:** Formal analysis, Investigation, Methodology, Writing – review & editing. **M. Wahl:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal

relationships which may be considered as potential competing interests: Martin Wahl reports financial support was provided by Bundesministerium für Bildung und Forschung.

Data availability

The data will be uploaded to PANGAEA.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169087>.

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