**Title**

The role of mutualism in marine benthic communities: Key species are affected by predicted warming but show resistance to ocean acidification

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**Running head**

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## Abstract

The effects of climate change on coastal biodiversity are a major concern because altered community compositions may change associated rates of ecosystem functioning and services. While responses of single species or taxa have been studied extensively, it remains challenging to estimate responses to climate change across different levels of biological organisation. Studies that consider the effects of moderate realistic near-future levels of ocean warming and acidification are needed to identify scope for adaptation and evolution. Also, studies including different levels of biological complexity may reveal opportunities for amelioration or facilitation under changing environmental conditions. To test experimentally for independent and combined effects of predicted near-future warming and acidification on key benthic species, we manipulated three levels of temperature (ambient, +0.8 °C, +2 °C) and two levels of pCO2 (ambient at 450 ppm, elevated at 645 ppm) and quantified their effects on mussels and algae growing separately or together (to also test for inter-specific interactions). Warming increased mussel clearance and mortality rates simultaneously, which meant that total biomass peaked at + 0.8 °C. Surprisingly, however, no effects of elevated pCO2 were identified on mussels or algae. Moreover, when kept together, mussels and algae had mutually positive effects on each other’s performance (i.e. mussel survival and condition index, mussel and algal biomass, and proxies for algal productivity including relative maximum electron transport rate [rETRmax], saturating light intensity [Ik], and maximum quantum yield [Fv/Fm]), independent of warming and acidification. Our results show that even moderate warming affected the functioning of key benthic species, and we identified a level of resistance to predicted ocean acidification. Importantly, we show that the presence of a second functional group enhanced the functioning of both groups (mussels and algae), independent of changing environmental conditions, which highlights the ecological and potential economic benefits of conserving biodiversity in marine ecosystems.

## Introduction

The fate of coastal biodiversity is a major concern in changing climate conditions (Cooley et al., 2022; IPCC, 2022; Pörtner et al., 2021). Climate change adds to other anthropogenic drivers of biodiversity change, such as habitat modifications, exploitation or pollution, and can intensify their effects on the distribution, functioning and production of marine species (Bowler et al., 2020; Gissi et al., 2021; O’Hara et al., 2021). Additionally, species interactions can be modified by climate change, and climate change effects can be enhanced or mitigated by direct or indirect species interactions, increasing the uncertainty around future coastal biodiversity (Brooks and Crowe, 2018). Coastal regions are particularly exposed to the cumulative effects of multiple stressors, which puts the ecosystem services they provide at risk, e.g. their potential to provide food, regulate coastal erosion, recycle nutrients, sequester carbon, support recreational activities and sustain cultural identity (Bowler et al., 2020; Cooley et al., 2022). Predicting the cumulative impacts of multiple stressors on coastal biodiversity is crucial for managing and protecting vulnerable ecosystem services (Cooley et al., 2022; Gissi et al., 2021; Keyes et al., 2021; Turschwell et al., 2022).

Climate change and its effects on marine benthic species have been studied extensively, yet impacts are highly variable across taxonomic groups and up-scaling results to communities or ecosystems remains challenging (Hoppit and Schmidt, 2022; Turschwell et al., 2022). Warming directly affects metabolic rates and physiological processes along thermal performance curves (Dell et al., 2011; Pörtner, 2010; Roma et al., 2021). Typically, performance first increases with warming, as metabolic costs are more efficiently met by the rate of supplied energy, until it culminates at an optimum temperature, beyond which costs outbalance any achievable supply and performance declines rapidly (Clarke and Gaston, 2006; Gillooly et al., 2001; Lemoine and Burkepile, 2012; Pörtner, 2010). Whether localised warming enhances or impairs performance is determined by the temperature range on the thermal performance curve to which an organism’s phenology is acclimatised in its habitat (Vasseur et al., 2014). The biological mechanisms underlying the effects of ocean acidification are not yet understood fully (Doney et al., 2020 and references therein; Doo et al., 2020a; Lutier et al., 2022). Calcifying species, such as shellfish, tend to respond to ocean warming and acidification with increased metabolic costs, reduced growth, reproduction and calcification (Doo et al., 2020a; Hoppit and Schmidt, 2022; Lemasson et al., 2018; Lutier et al., 2022; Sadler et al., 2018). Fleshy algae, on the other hand, tend to show resistance and may even benefit from warmer and acidified conditions because of increased CO2 available for photosynthesis at accelerated metabolic rates (Hoppit and Schmidt, 2022; Mooney-McAuley et al., 2016; Stewart et al., 2013). Other ecosystems dominated by fleshy macroalgae, however, suffer from extreme heat events (Smale et al., 2019), increased grazing, competition or impaired reproduction (Veenhof et al., 2022), which may alter community compositions and even cause shifts from complex macroalgal habitats to degraded algal turf communities (Provost et al., 2017). Shellfish and macroalgae are important habitat-forming components of coastal marine ecosystems (O’Connor and Crowe, 2007; Wear et al., 2023), where altered community compositions may profoundly change ecosystem functioning and provisioning (Cooley et al., 2022; Hoppit and Schmidt, 2022; Lemasson et al., 2017). Understanding the effects of warming and acidification on these key species, including interactions with other species closely associated to these biogenic habitats, is therefore a research priority (Turschwell et al., 2022). Furthermore, greater understanding is required to predict how species’ interactions and ecosystem structures may change in future oceans (Hobday et al., 2016; Tagliarolo et al., 2018; Wernberg et al., 2012).

Marine macrophytes, such as seaweeds and seagrass, have the potential to mitigate negative acidification effects on calcifiers, such as shellfish, by removing CO2 from the water and increasing pH, thus, acting as a local buffer to acidification (Doo et al., 2020b; Jiang and Fang, 2021; Jiang et al., 2022; Young et al., 2022). In addition to increasing mean pH with increasing macrophyte biomass, diurnal pH fluctuations become more pronounced, which offers shellfish (e.g. mussels, oysters) temporal refuge from acidification stress that can be used for increased calcification activity (Edworthy et al., 2023; Ricart et al., 2021; Wahl et al., 2018). Integrated multi-trophic aquaculture was first established to utilise surplus nutrients produced by cultivated finfish through co-cultivation with detritivores, filter-feeding shellfish and macroalgae (Mooney-McAuley et al., 2016). More recently, the commercial potential of co-culturing shellfish and seaweeds to enhance shellfish production has been recognised (Hamilton et al., 2022). Seaweed aquaculture is a rapidly growing industry with demands for bioenergy, food, pharmaceutical and fertiliser industries, producing ca. 35 million tonnes of algal biomass annually (FAO, 2022; Mooney-McAuley et al., 2016). Approximately 18 million tonnes of marine molluscs, mainly bivalves, are produced per year, which represents half of coastal and marine animal aquaculture (FAO, 2022). The impact of climate change on aquaculture production is largely unknown and predictions of ecological and economic impacts vary tremendously (Forbes et al., 2022; Gubbins et al., 2013; Hengjie et al., 2023; Theuerkauf et al., 2022; Troell et al., 2022). Therefore, understanding the mechanisms driving the combined effects of warming and acidification on co-cultures of shellfish and seaweed, including adaptation and mitigation of a changing climate, is of ecological and commercial interest (Duarte et al., 2017; Jiang and Fang, 2021; Young et al., 2022).

Much research has been conducted on single species where the effects of ocean warming and acidification were based on or exceeding the worst case scenarios of IPCC climate change predictions (Armstrong et al., 2022; Geraldi et al., 2020; Knights et al., 2020; Navarro et al., 2016; Zhang et al., 2022). These studies help understand population dynamics and community structures under extreme predicted future conditions (Lemoine and Burkepile, 2012; Rall et al., 2010). Incorporating more moderate near-future experimental treatments, however, is required to identify how species and ecosystems may respond within the next few decades or in moderate climate change scenarios by 2100, and to identify their potential for adaptation (Geraldi et al., 2020).

In the current study, we tested empirically for effects of increased temperature and/or ocean acidification on blue mussels (*Mytilus edulis*) and sugar kelp sporophytes (*Saccharina latissima*) grown together and separately with a fully factorial experimental design. Temperature (ambient; +0.8 °C; +2 °C) and pCO2 (ambient, 450 ppm; elevated, 645 ppm) were manipulated based on predicted sea surface temperature and atmospheric pCO2 of the Irish Sea under a moderate climate change scenario by the year 2100, or sooner in the case of a more extreme scenario (IPCC, 2014, 2013; Jacob et al., 2014). We quantified effects of these abiotic experimental treatments (temperature, pCO2) on several proxies for the functioning of mussels and algae including: mussel mortality, mussel biomass, mussel condition index, clearance rates, mussel shell and byssus strength, algal biomass and photosynthetic performance (i.e. relative maximum electron transport rate [rETRmax], saturating light intensity [Ik], light harvesting efficiency [α], and maximum quantum yield [Fv/Fm]). Additionally, we tested whether the functioning of mussels and algae differed in the presence or absence of each other. We hypothesised that both species would respond to warming with increases in all processes quantified, except mussel mortality, which we expected to decrease, because the experiment took place in winter, i.e. at the lower end of the temperature range seasonally encountered by our study organisms. Simultaneously, we expected acidification to have a negative effect on mussels and a positive effect on algal production. Additionally, we hypothesised that the presence of the algae would strengthen positive effects of warming, and act as a local buffer to mitigate negative effects of acidification on mussels, while the presence of mussels would enhance the productivity and photosynthetic performance of the algae. As a consequence, we expected the total accumulated biomass of mussels and algae to be greater in the treatments where they were kept together compared to the sums of biomass of treatments containing just mussels or just algae.

## Methods

### Experimental design

The experiment comprised of two analogous sets of treatments to simultaneously test the single and combined effects of the abiotic factors warming and acidification on mussels or algae separately, in addition to testing for effects of mussels and algae on each other (Figure 1). Specifically, we tested whether the presence of a second functional group (mussels or algae) would alter the effects of the abiotic factors on either group. Water temperature was manipulated at three levels: ambient, +0.8 °C, and +2 °C. pCO2 was manipulated at two levels to simulate acidification with the corresponding pH: ambient (450 ppm) and elevated (645 ppm). Each experimental set consisted of twelve treatments, of which six overlapped. In total, 18 treatments (*n* = 5) were distributed randomly across 90 mesocosms and the factorial design enabled the testing of the independent and combined effects of all factors and their respective levels. The abiotic treatments simulated predicted conditions in Ireland in a moderate climate change scenario in the year 2100, or conditions that might prevail sooner approaching an extreme business-as-usual scenario (IPCC, 2014; Jacob et al., 2014). Six additional mesocosms that contained only seawater but no biota (that can influence pH [Lowe et al., 2019]) were established to monitor variation in the abiotic conditions at each combination of temperature and pCO2 levels. Mussels and algae were collected locally and acclimatised to laboratory conditions at ambient temperature and pCO2 for one week before temperature and pCO2 manipulations started (Kong et al., 2019). Response variables were taken after 6-7 weeks at manipulated abiotic conditions.

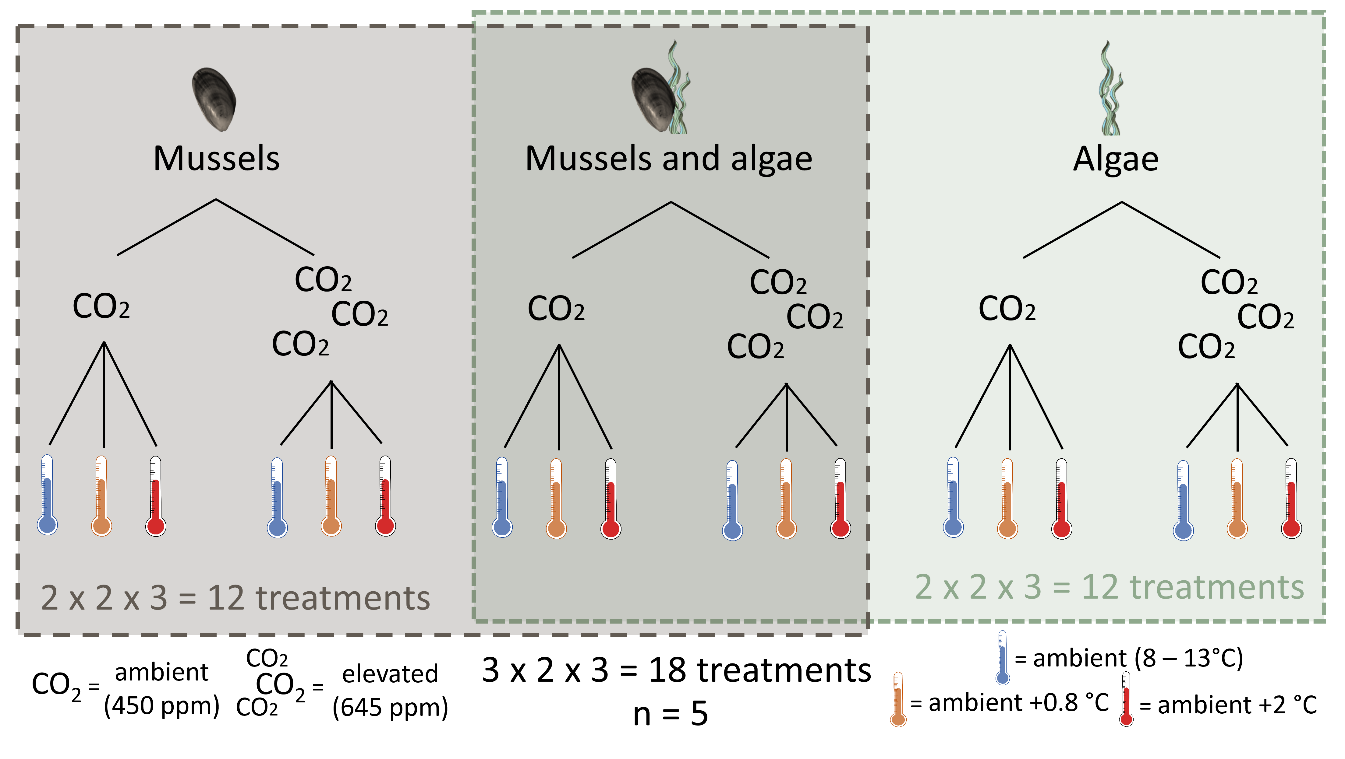


Figure Experimental design for testing the effects of warming and acidification on mussels and on algae separately, in addition to testing for effects of mussels and algae on each other.

### Experimental set-up

The experiment was carried out using the experimental mesocosm platform QIMS (Quantifying the Impacts of Multiple Stressors; Schertenleib, 2023) at Trinity College Dublin, Ireland, from 28/10/2020 to 18/12/2020. The set-up comprised of 96 independent mesocosms that were opaque polypropylene boxes (40 x 60 x 28 cm) filled with 32 L of seawater. The seawater was collected from 20 m depth at the Irish continental shelf (supplied by Seahorse Aquariums) and had a salinity of 34.3. In each mesocosm, the water was continuously recirculated at 130 L/h using small aquarium pumps (OptiMax 500, Oase Living Water), which ensured homogenous mixing. The seawater flow returned into each mesocosm at an angle opposite the pumps to maximise mixing and increase surface gas exchange. Mesocosms were aerated at 15.5 mL/min via aquarium sponge filters (PK200 for < 200 L, Xinyou Aquarium) that ensured nutrient cycling by providing a settlement surface for microorganisms, such as denitrifying bacteria. Lids of transparent polypropylene (Foliarex UV4 Greenhouse Film) were attached to the mesocosms and captured the individual, ambient or pCO2-enriched atmospheres in 16 L headspaces above the seawater. Illumination of 50±4 µmol/m²s (mean ± standard deviation; penetrating through the lids) was provided by LED lights with standard artificial daylight colour (Radium RaLED DAMPPROOF; 6500 Kelvin), set to a 10:14 hour light:dark cycle, reflecting average Irish autumn daylight conditions. Oxygen levels were measured weekly and remained saturated > 8.2 mg/L. Halfway through the experiment, the water was drained and replaced with fresh seawater to maintain high water quality. During this process, mussel faeces and biofilm were removed from the mesocosm bottoms. Mussels and algae, which can both occur in the intertidal in the wild, were disturbed as little as possible and exposure to air minimised to 60 minutes.

### Temperature manipulation

Mesocosm water temperature was manipulated using a separate, facility-wide cooling water circuit with individual heat exchangers at each mesocosm. When recirculating the mesocosm water, the recirculation tubes passed in opposite current direction through cooling water tubes. Three different temperature levels were set with valves leading the recirculation tubes through different lengths of heat exchangers. Three parallel-connected beer chillers (MF Refrigeration Ltd, Midi 6 Coil R290 Hydrocarbon Cooler, 2 kilowatts capacity each) continuously cooled approximately 2000 L of fresh water, circulated through the facility at a rate of 8200 L/h.

After temperature manipulation started, target temperatures were reached in 4-6 hours. Room temperature decreased owing to outside temperatures over the course of the experiment and the coldest (‘ambient’) temperature level ranged between 8.5 °C ± 0.07 and 12.4 °C ± 0.07 (means ± se). The medium temperature level was warmer by 0.8 °C ± 0.0 and the warmest level by 2.0 °C ± 0.1 (means ± se). Temperature was logged every 10 minutes in 42 mesocosms using HOBO pendants (type MX2201, Temperature/Light 64K; two randomly deployed per treatment, one per mesocosm without biota for manipulation monitoring) and measured weekly in all mesocosms using a handheld digital thermometer (Fisherbrand Traceable Kangaroo Thermometer).

### pCO2 manipulation and pH

pCO2 was manipulated through the air lines aerating each mesocosm. Ambient air (450 ppm, from Dublin City) was distributed to mesocosms using large blower pumps, while an alternative air line provided a CO2-enriched air mixture. Valves on each mesocosm controlled which of the two air lines were supplied. To elevate pCO2, pure CO2 was injected into a mixing vessel prior to distribution in the facility. The concentration was controlled using a gas analyser (LI-COR, LI-830) in combination with a professional aquarium computer (GHL, ProfiLux 3) and logged every second. Ambient pCO2 was monitored every minute using a CO2 data logger (Driesen-Kern, DK660).

Ambient pCO2 was 452 ± 0.12 ppm, while elevated pCO2 was 645 ± 0.04 ppm (mean ± se). The corresponding pH in the mesocosms without biota was (mean ± se) 8.09 ± 0.004 at ambient pCO2 and 7.97 ± 0.003 at elevated pCO2, which was confirmed twice weekly. The elevated pCO2 level was reached in the air mixture within minutes of starting the treatment manipulation, while the pH in the seawater adjusted in less than 18 hours.

### Study organisms

One-year-old mussel spat (*Mytilus edulis*) was obtained from seeded rope at 1 m depth in Killary Fjord (Killary Fjord Shellfish; http://killaryfjordshellfish.com/who.html) in October 2020 (*in situ* water temperature 11.2 °C, pH 8.24) and kept moist and cool for transport until placed in 13 °C aerated seawater in Trinity College Dublin. After five days, 3.01 g ± 0 (mean ± se) of live mussel spat wet biomass, made up of 30-40 mussels with an average individual wet biomass of 0.096 mg ± 0.001 (mean ± se) and shell lengths between 7 and 16.5 mm, were assigned randomly to mesocosms. In the mesocosms, the mussels were placed on garden mesh tiles (15 x 15 cm polypropylene with 7 mm single mesh diameter), 2 cm above the bottom and close to the recirculation return to ensure similar hydrodynamic conditions. After two weeks, all had attached either to the mesh or to other mussels. Empty mesh was similarly deployed in all other mesocosms.

Mussels were fed daily with a concentrated marine microalgal mix (Reed Mariculture Shellfish Diet 1800; 0.7 ml Shellfish Diet per gram live spat) to ensure starvation was not the underlying cause for any putative effects in response variables (Thomsen et al., 2013). The total amount of Shellfish Diet per mesocosm during the first week of the experiment was 2 ml, which was increased to 2.5 ml in week two and three, and to 2.75 ml in week four, anticipating growth of the mussels. After week 3.5 the mussels no longer cleared the water, possibly because of mortality, thus, the food dosage was reduced to 1.7 ml daily per mesocosm containing mussels until the end of the experiment.

Algal sporophytes were obtained on seeded aquaculture string from the Queen's University Marine Laboratory (QML) in Portaferry. The string had been sprayed with a *Saccharina latissima* (kelp, brown macroalgae) gametophyte culture and was grown following standard operation procedure hatchery conditions (Gorman, 2014) for eleven weeks prior to addition to the mesocosms. Both in the mesocosms and in the hatchery, the kelp sporophytes grew slowly and at low density compared to previous trials, possibly compromised following reduced care in the hatchery during the 2020 Covid-19 pandemic lockdowns (e.g. hatchery room lights had been kept switched off, instead of adding to the culture light, reducing light availability for the juvenile kelp). As a result, kelp individuals were microscopic when seeded string was deployed into the mesocosms but were expected to grow rapidly.

In the treatments that included algae, 65 cm of seeded string were weighed and randomly assigned to one of the 60 respective mesocosms. To establish this experimental treatment, the seeded string was wrapped around 60 cm long polypropylene header ropes (10 mm diameter), which were fastened 1 cm below the water surface diagonally to the bottom area after soaking in seawater for two days. A freshly prepared solution of premixed f2 powder (Varicon Aqua, 0.5 ml f2 solution L-1 seawater) was added to the mesocosms with seeded string weekly because we expected the kelp to grow and deplete the nutrients over a week.

### Data collection

#### Mussel mortality

Every two to four days, the mesocosms were checked for dead mussels, which were identified by their shells gaping open and no closing response to physical stimulation or by lack of attachment. Mussels that died during the acclimatisation period were replaced prior to the temperature and pCO2 manipulation, using similar-sized live individuals that had been kept at similar lab conditions. After abiotic manipulations had started, dead mussels were removed and recorded to quantify mortality. The total amount of dead mussels per mesocosm was used for data analyses. Mortality was independent of mussel size (Supplementary Material A.1), which enabled averaging and standardising mussel response variables that were measured per mesocosm (e.g. clearance rate, accumulated biomass) according to individuals.

#### Mussel biomass and condition index

The mussels were retrieved on their mesh tiles from the mesocosms after 51 days to measure total accumulated wet mussel biomass, which was then standardised by the number of alive mussels. Accumulated biomass per mussel was calculated as the difference between initial and final mean individual wet biomass (mg). To calculate the condition index, a subsample of five mussels of similar shell length was selected per mesocosm and dissected into shells and flesh, which were then weighed and dried at 80 °C until dry weight remained constant. Following Lucas and Beninger (1985), the condition index was calculated to assess the bivalves’ physiological state, as the shell is a product of cumulative growth while the flesh represents recent metabolic activity that may be reduced under stress:

#### Mussel clearance rates

Clearance rate samples were taken on the 35th and 36th day of manipulated temperature and pCO2 conditions. On the previous day, the mussels had received a reduced feeding dosage of 1 ml shellfish diet per mesocosm. To measure clearance rates, mussels were given 1.7 ml Shellfish Diet per mesocosm. After allowing 10 minutes for homogenous dispersal, the first of three 50 ml samples was drawn from each mesocosm to determine the initial cell concentration (T0). Two (T1) and 17 hours (T2) after feeding, additional water samples were taken. The samples were stored at 4 °C and stirred before four coulter counter cell counts were conducted from a 20 ml subsample (Beckman Coulter Counter Z Series, aperture 100 μm, Kd: 59.29, sampling volume: 0.5 ml, count of particles between 6 and 19 μm). Each first count was discarded (to ensure the coulter counter tubes were flushed and only contained the current sample) and the mean taken from the subsequent three counts.

Clearance rates were calculated following Coughlan (1969):

Where M is the volume of the suspension, n is the number of animals per mesocosm, concT0 and concT1 are the concentrations of the suspension at the start (T0) and after time t. Samples from the mesocosms that contained no experimental organisms, and were used for monitoring the manipulated abiotic factors, confirmed low background particle load and continuous counting accuracy throughout the measurements.

#### Shell strength

To analyse shell strength, the force needed to break them was determined using a materials testing machine for compression tests (ZwickRoell zwickiline Z2.5) at the Department of Mechanical, Manufacturing & Biomedical Engineering, Trinity College Dublin. Three mussels of each mesocosm were collected on the last day of the experiment and stored for five days at 4 °C before they were dissected into shell valves and flesh. Visibly intact right shell valves were placed individually into the machine with the shell valve openings lying flat on the machine in similar orientation (Mackenzie et al., 2014). A load cell of 20 N was used for smaller shells and 200 N for the largest. Force was applied from the top at a speed of 200 mm/min until shell failure occurred. The force applied was logged at 0.01 s intervals using testXpert II software (ZwickRoell) that determined the maximum applied force (Fmax). 60 shells broke visibly during dissection and were discarded, and 19 tested shells were excluded from analysis because they cracked multiple times instead of showing one clear failure event. A total of 101 shell breaking tests were available for data analysis, with shells from all but five (each from different treatments) of the 60 mesocosms and seven to eleven shells per treatment. Shell length (Supplementary Material A.1) was used to standardise Fmax and the average applied force per mm (N/mm) was calculated for each mesocosm and used for data analysis.

#### Byssus strength

After recording wet biomass, mussels were cut off the mesh tiles at the byssus stem, leaving the byssus threads as intact as possible. Areas where the byssus threads clearly belonged to one single mussel were marked and the mesh tiles were returned to their mesocosms for intermediate storage. Four days later, the mesh tiles were individually fastened to a materials testing machine for traction tests (ZwickRoell zwickiline Z2.5; load cell: 20 N; Department of Mechanical, Manufacturing & Biomedical Engineering, Trinity College Dublin) in the centre below the byssus cluster and parallel to the bottom of the machine. A plastic-wrapped wire was fed centrally through the cluster so that the cluster stem was positioned in a bend of the wire, with approximately equal amounts of byssus threads on each side (exact numbers could not be determined). The wire ends were clamped into the top machine end, which pulled the wire vertically away from the mesh at 5 mm/min (Bouhlel et al., 2017), exerting traction on the byssus cluster until all the byssus threads on one side of the wire ruptured. All tests were conducted in air. The applied force was logged at 0.1 s intervals using testXpert II software (ZwickRoell), recording the succession and magnitude of applied tensile force and load drops over time. In adult *Mytilus californianus*, large drops in loads can be assigned to single threads breaking and the sum of individual load drops exceeds the maximum force applied to a whole byssus cluster (Bell and Gosline, 1996). The many and delicate byssus threads of the juvenile *M. edulis* used in this study did not allow us to link load drops to individual observed thread ruptures. Analyses of all load drops that were recorded showed that load drops < 0.01 N occurred more than five times as often as the next force range. This indicates the background noise of the tests and justifies the load drop limits considered for analysis as > 0.01 N. The average load drop > 0.01 N was used as a proxy for byssus strength. A total of 43 tests were conducted on byssus clusters from 34 mesh tiles. Test results from the same mesh tile were averaged and data of three random mesocosms per treatment were used for analysis, except for the two acidified mussel-only treatments at increased temperatures, for which only two mesh tiles were available for byssus strength testing.

#### Algal biomass

The kelp sporophytes on the seeded strings grew unexpected slowly, presumably because of unusual hatchery conditions due to pandemic lockdowns (described previously). Over time we observed that microphytobenthos (primarily benthic diatoms and, to a lesser extent, green algae) grew on the seeded string, resulting in a microscopic, mixed algal assemblage on the seeded strings. Instead of quantifying biomass of individuals of kelp at the end of the experiment as planned, the total accumulated biomass of algae associated with seeded string was quantified. Final abundance of kelp individuals, which had reached up to 1.4 mm in length at the end of the experiment, was counted using a dissection microscope.

#### Photosynthetic performance

Photosynthetic performance of the algae present in the mesocosms was tested using a pulse amplitude modulation (PAM) fluorometer (DIVING-PAM-II, Walz) on the 39th day at manipulated abiotic conditions. A leaf clip (DIVING-LC, Walz GmbH) was connected to the seeded string to eliminate light and ensure consistent spacing of the optic fiber with the algae. Rapid light curves (RLCs) were taken on ambient-light acclimated algae to assess differences in potential photosynthetic performance. Prior to starting the RLCs, tissue was quasi-dark adapted for a few seconds to allow re-oxidization of the primary electron acceptor (Randall et al., 2019; Schreiber, 2004). Relative electron transport rates were determined at steps of increasing actinic light intensity, from which the DIVING-PAM-II calculated the relative maximum electron transport rate, i.e. photosynthetic capacity rETRmax, as well as the saturating light intensity Ik, and the initial slope of the RLC, i.e. the light harvesting efficiency α (Randall et al., 2019). After 15 minutes of dark acclimation, a different section of the seeded string was then used to measure the maximum quantum yield Fv/Fm, calculated as where Fm represents the maximal fluorescence after a saturating light pulse and F0 the steady-state fluorescence under weak initial illumination before the light pulse (Miranda et al., 2019). The higher the yield, the more suitable the conditions (Bilger et al., 1995).

#### Total accumulated biomass

Total accumulated biomass for mussels and algae that were kept in the same mesocosm was calculated by adding the accumulated algal biomass to the accumulated mussel biomass. To compare between the total accumulated biomass of mussels and algae that had been kept together and the sum of accumulated biomass of mussels kept on their own and algae kept on their own in the same abiotic treatments, each possible combination of accumulated biomass per mesocosm of mussels kept on their own (n = 5) and algae kept on their own (n = 5) was calculated (for analysis n = 5\*5 = 25).

### Data analyses

To test hypotheses, three-way Analyses of Variance (ANOVAs) were performed using temperature (three levels), pCO2 (two levels) and the presence of a second functional group (two levels; i.e. mussels vs. mussels and algae; or algae vs. mussels and algae) as fixed orthogonal factors and including all possible interactions. Data of rETRmax and Ik were log transformed to meet the assumptions of ANOVA. Normality of errors was confirmed by plotting histograms of the residuals and applying Shapiro-Wilks-tests. Homogeneity of variances was tested using Levene’s tests and by plotting the residuals as a function of the fitted values. To test for autocorrelation in the residuals, Durbin-Watson tests were conducted, and the presence of influential data points was assessed using Cook’s distance. Data of mussel shell strength and mussel byssus strength were slightly unbalanced, hence ANOVA type 3 sums of squares were considered. When the ANOVA indicated differences between more than two treatment levels, Tukey’s Honest Significance Differences were calculated as post-hoc tests. To assess whether the final amount of kelp sporophytes differed among treatments, a generalised linear model of the family quasipoisson was applied. To test for differences in total accumulated biomass when mussels and algae were kept together and the sums of accumulated mussel and algal biomass when kept separately, the sums of all possible biomass combinations of mesocosms that had only mussels and only algae were calculated for each abiotic treatment (temperature levels crossed with pCO2 levels), which yielded 25 samples per abiotic treatment. Variances were heterogeneous between these groups and the corresponding five samples of mesocosms in which mussels and algae had been kept together at the same abiotic treatments, thus the Scheirer-Ray-Hare test was used for analysis, followed by the Dunn test for post-hoc comparisons (Mangiafico, 2016).

All statistical analyses and data visualisation were conducted in R version 4.2.1 (R Core Team, 2022) using R Studio version 2022.07.2 (RStudio Team, 2022) and the packages tidyverse version 1.3.2 (Wickham et al., 2019), car version 3.1.1 (Fox and Weisberg, 2019), Hmisc version 4.7-2 (Harrell Jr, 2022), rcompanion version 2.4.34 (Mangiafico, 2023), and FSA version 0.9.5 (Ogle et al., 2023). Byssus strength test files were prepared and the average load drop > 0.01 N calculated in Microsoft Excel.

## Results

### Mussel responses

No interactions were identified among any of the factors on mussel response variables. We did find an effect of temperature on mussel mortality (F2, 48 = 6.382; p = 0.004) and post-hoc tests indicated significant differences (p = 0.002) between the ambient and the warmest (+2 °C) temperature level (Figure 2). pCO2 had no effect on mussel mortality (F1, 48 = 0.37; p = 0.549). Fewer mussels died when algae were present (F1, 48 = 8.403; p = 0.006).

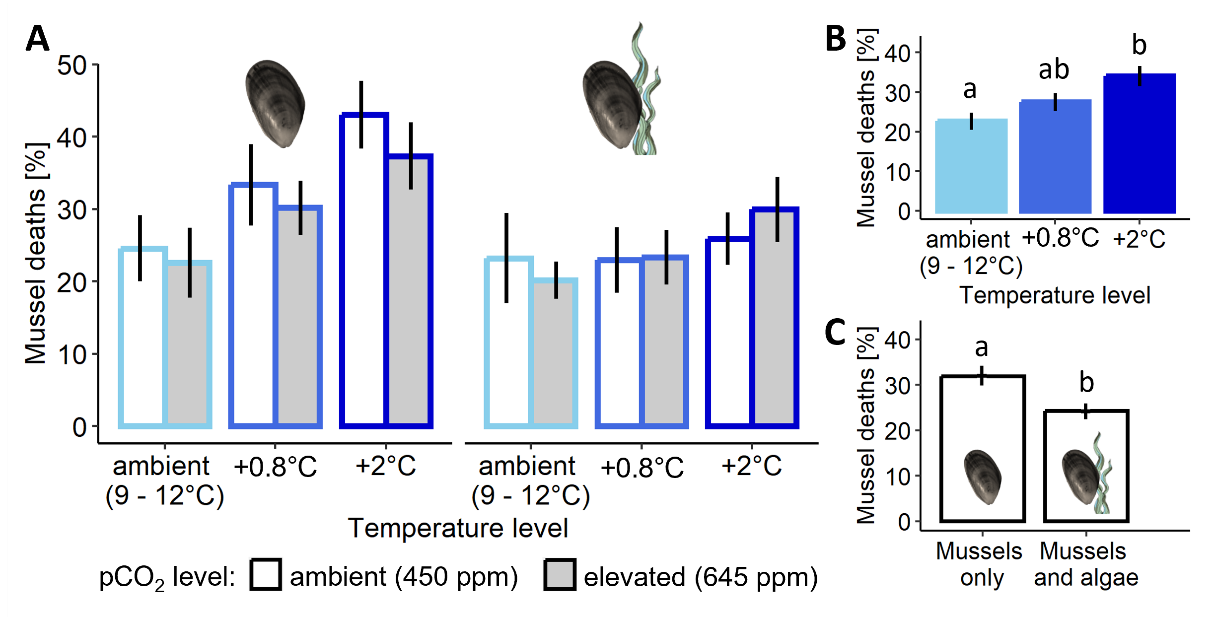


Figure Mean (± standard error) mussel deaths in A (all treatments) at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature and at ambient (white bars) and elevated (grey bars) pCO2, in the absence (left panel in A) or presence (right panel in A) of algae, n = 5; in B at different temperatures (significant main effect); and in C without and with algae (significant main effect). Significant differences among groups of means are indicated by lower case letters (p < 0.01).

Temperature had no effect on mussel biomass (F2, 48 = 2.398; p = 0.102), nor on the condition index (F2, 48 = 0.086; p = 0.917), nor did pCO2 (F1, 48 = 0.821, p = 0.369 and F1, 48 = 0.093; p = 0.862; Figure 3). The presence of algae, however, had a positive effect on mussel biomass (F1, 48 = 22.073; p < 0.001) and condition index (F1, 48 = 18.437; p < 0.001; Figure 3). Mussel biomass almost doubled in the presence of algae compared to treatments without algae and mussel condition index was almost 20 % greater in the presence of algae compared to their absence (Figure 3A).

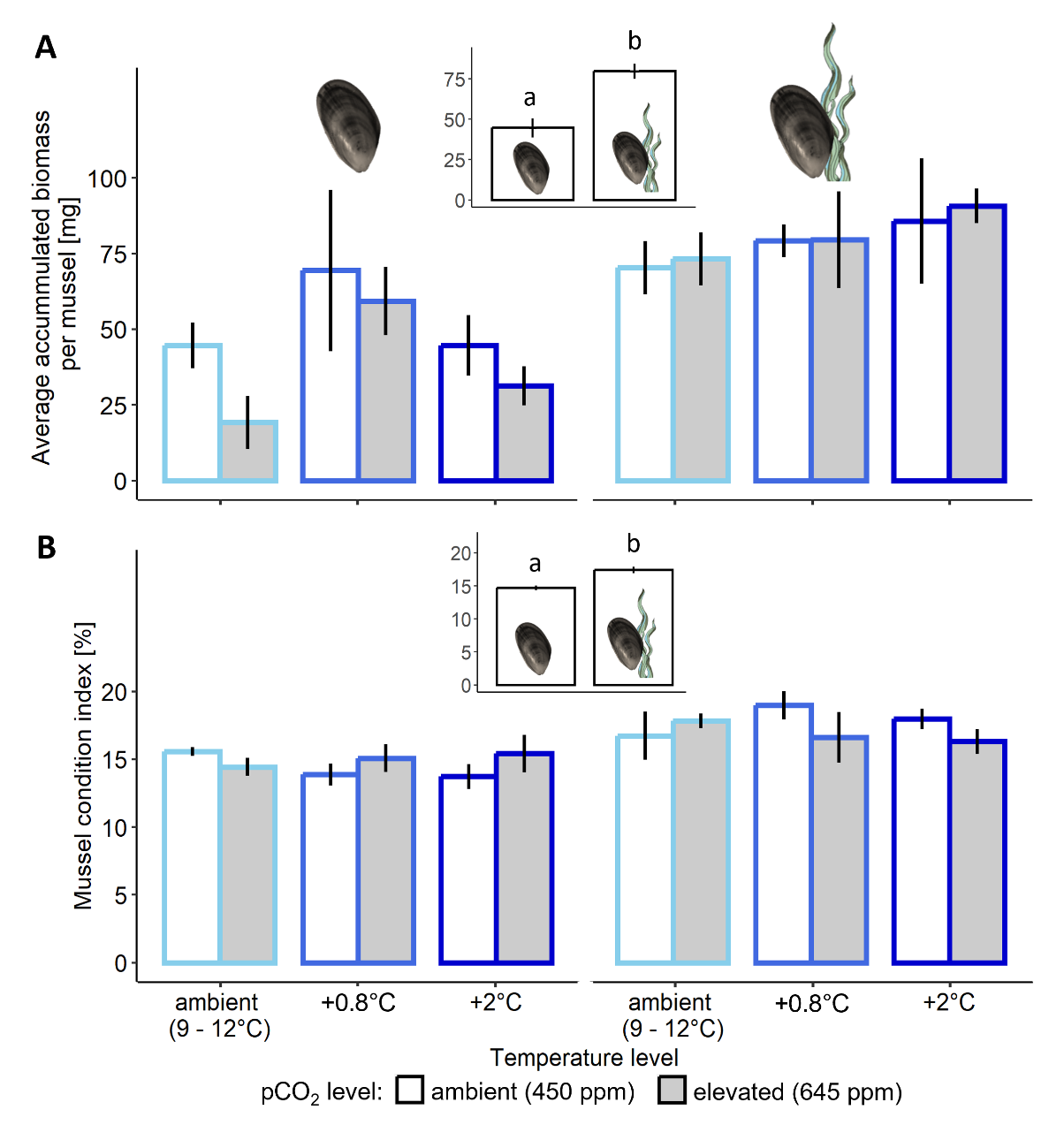


Figure . Mean (± standard error) accumulated biomass per mussel in A and condition index of mussels in B at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, and at ambient (white bars) and elevated (grey bars) pCO2, in the absence (left panel) or presence (right panel) of algae, n = 5. Insets show significant differences among groups of means without and with algae, also indicated by lower case letters (p < 0.001).

No differences among treatments were found in clearance rates after 2 hours of feeding (temperature: F2, 48 = 2.213, p = 0.120; pCO2: F1, 48 = 3.156, p = 0.082; algae: F1, 48 = 0.750, p = 0.391), however, after 17 hours, a significant effect of temperature on mussel clearance rates was identified (F2, 48 = 3.556; p = 0.036), with an almost 40 % greater rate in the warmest temperature level compared to the ambient temperature level (Figure 4). No effects of pCO2 (F1, 48 = 0.708; p = 0.404) nor the presence of algae (F1, 48 = 1.870; p = 0.178) were identified after 17 hours.

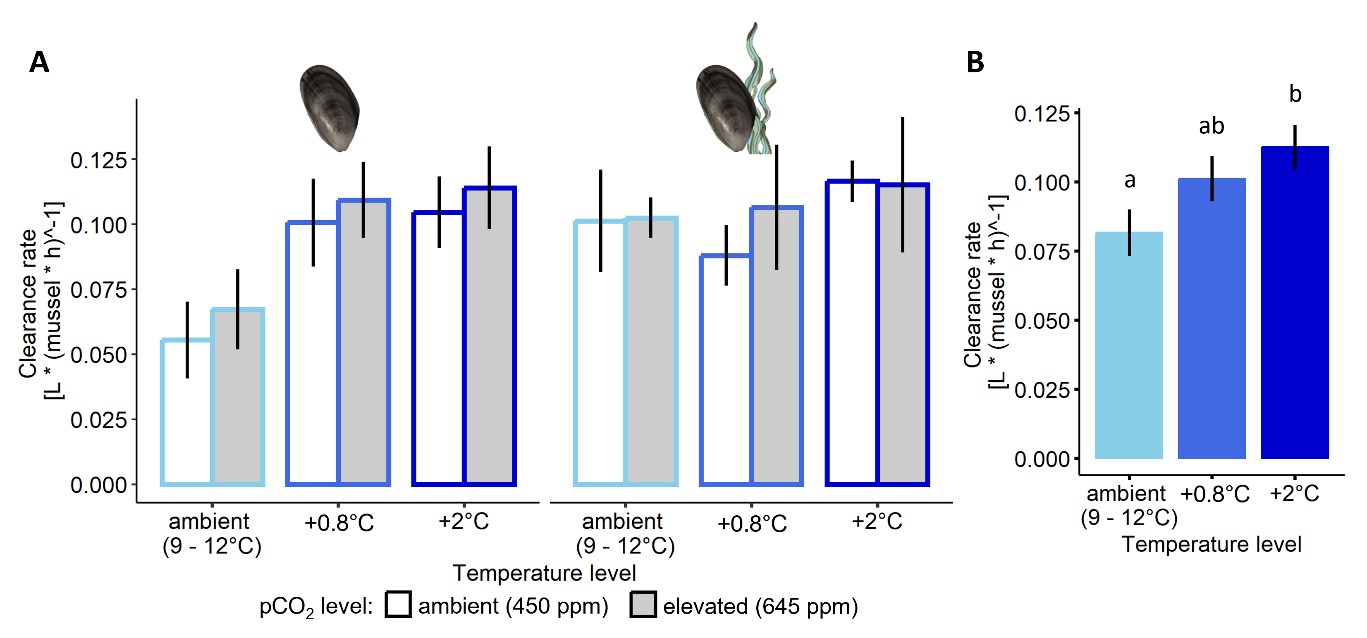


Figure . Mean (± standard error) mussel clearance rates in A (all treatments) at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, and at ambient (white bars) and elevated (grey bars) pCO2, in the absence (left panel) or presence (right panel) of algae, n = 5; and in B (significant main effect) at different temperatures with significant differences among groups of means indicated by lower case letters (p < 0.05).

No effects of temperature, pCO2 nor the presence/absence of algae on mussel shell strength (temperature: F2, 43 = 0.454, p = 0.638; pCO2: F1, 43 = 0.000, p = 0.995; algae: F1, 43 = 0.774, p = 0.384) or byssus strength (temperature: F2, 22 = 0.058, p = 0.944; pCO2: F1, 22 = 0.685, p = 0.417; algae: F1, 22 = 0.201, p = 0.658) were found.

### Algal responses

No interactions were identified among any of the factors on algal response variables. Neither temperature (F2, 48 = 0.014; p = 0.986) nor pCO2 (F1, 48 = 0.734; p = 0.396) affected the accumulated biomass of algae in the mesocosms. In the presence of mussels, however, 20 % more algal biomass accumulated than in the absence of mussels (F1, 48 = 17.156; p < 0.001; Figure 5).

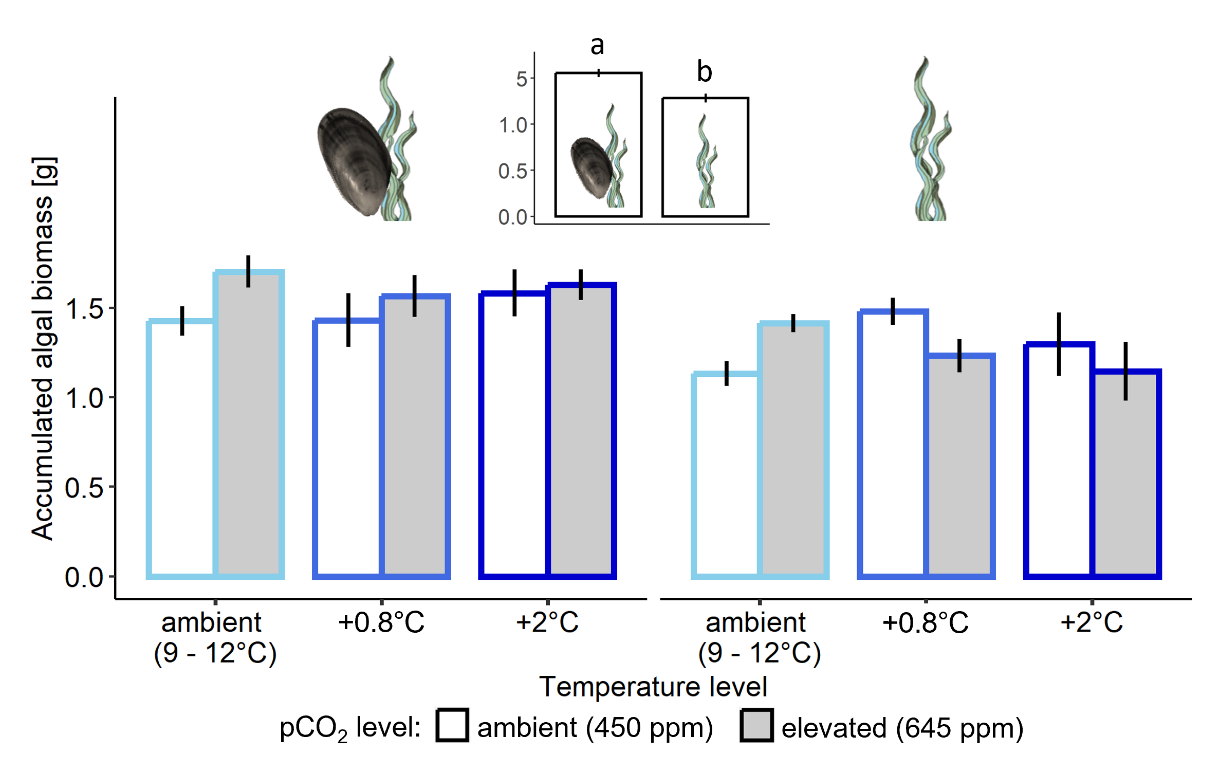


Figure . Mean (± standard error) accumulated biomass of algae at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, and at ambient (white bars) and elevated (grey bars) pCO2, in the presence (left panel) or absence (right panel) of mussels, n = 5 per bar. Inset shows significant differences among groups of means with and without mussels, also indicated by lower case letters (p < 0.001).

At the end of the experiment, no effects of temperature (F2, 29 = 5.161; p = 0.527) nor pCO2 (F1, 29 = 0.000; p = 1.000) on the abundance of kelp individuals were identified, however, sporophytes could only be counted in the treatments without mussels.

Results of the rapid light curves revealed no effects of temperature nor pCO2 on the relative maximum electron transport rate rETRmax (temperature: F2, 48 = 0.324; p = 0.725; pCO2: F1, 48 = 2.130; p = 0.151) or on the saturating light intensity Ik (temperature: F2, 48 = 1.459; p = 0.243; pCO2: F1, 48 = 0.774; p = 0.383) of algae in these treatments (Figure 6). The presence of mussels, however, significantly affected rETRmax (F1, 48 = 10.107; p =0.003) and Ik (F1, 48 = 31.966; p < 0.001; Figure 6). rETRmax increased by 30 % in the presence of mussels and Ik by 45 %. The light harvesting efficiency α did not show any differences among experimental treatments (temperature: F2, 48 = 1.400, p = 0.257; pCO2: F1, 48 = 2.790, p = 0.101; mussels: F1, 48 = 3.234, p = 0.078).

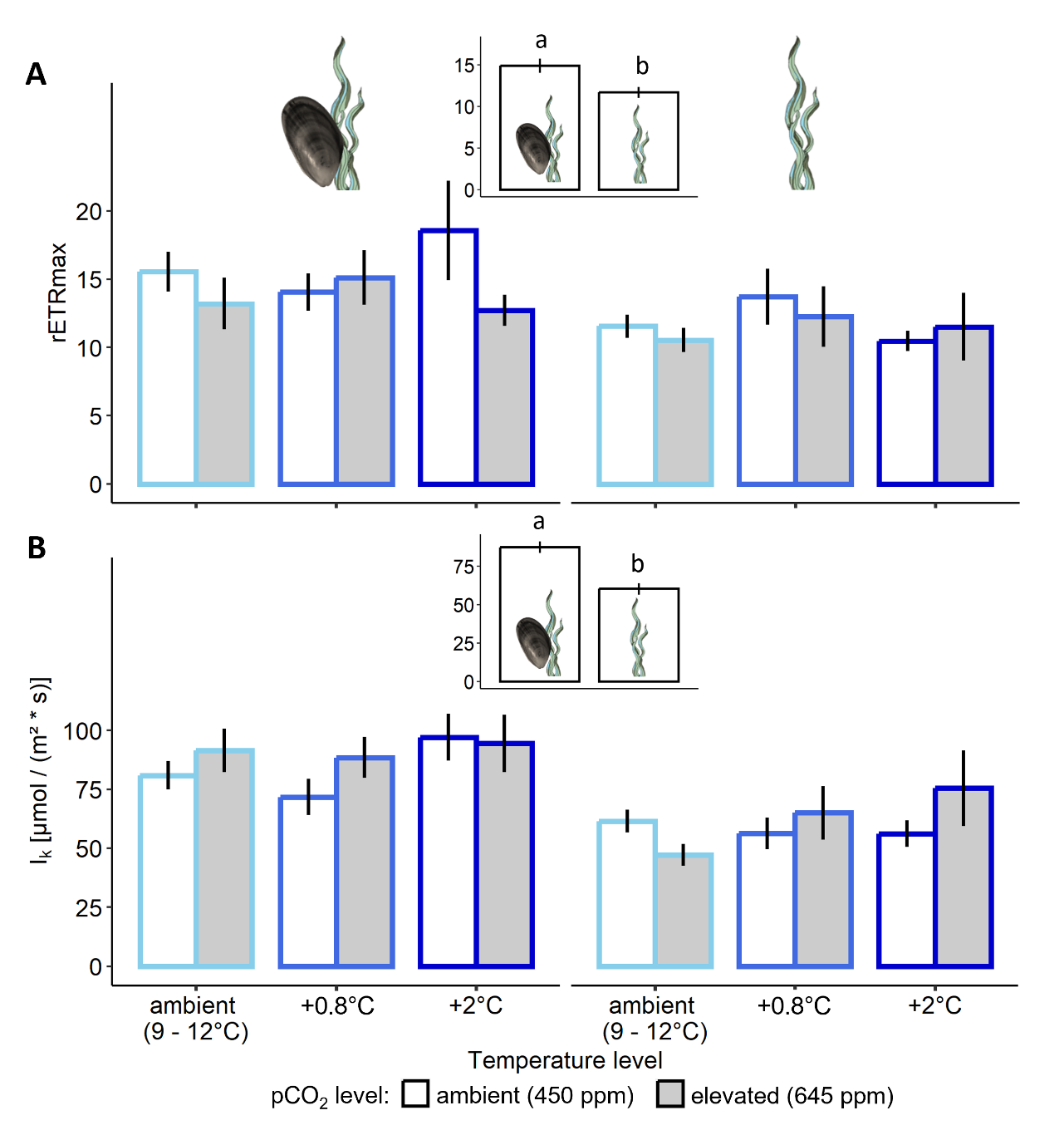


Figure . Mean (± standard error) relative maximum electron transport rate in A and saturating light intensity in B at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, and at ambient (white bars) and elevated (grey bars) pCO2, in the presence (left panel) or absence (right panel) of mussels; n = 5. Insets show significant differences among groups of means with and without mussels, also indicated by lower case letters (p < 0.001).

The maximum quantum yield Fv/Fm was significantly affected by temperature (F2, 48 = 3.261; p = 0.047), but not by pCO2 (F1, 48 = 0.972; p = 0.329) nor the presence or absence of mussels (F1, 48 = 1.602; p = 0.212). Post hoc tests were inconclusive (Table B.1) but we can suggest tentatively that the medium temperature level differed from the ambient and the warmest level (Figure 7).

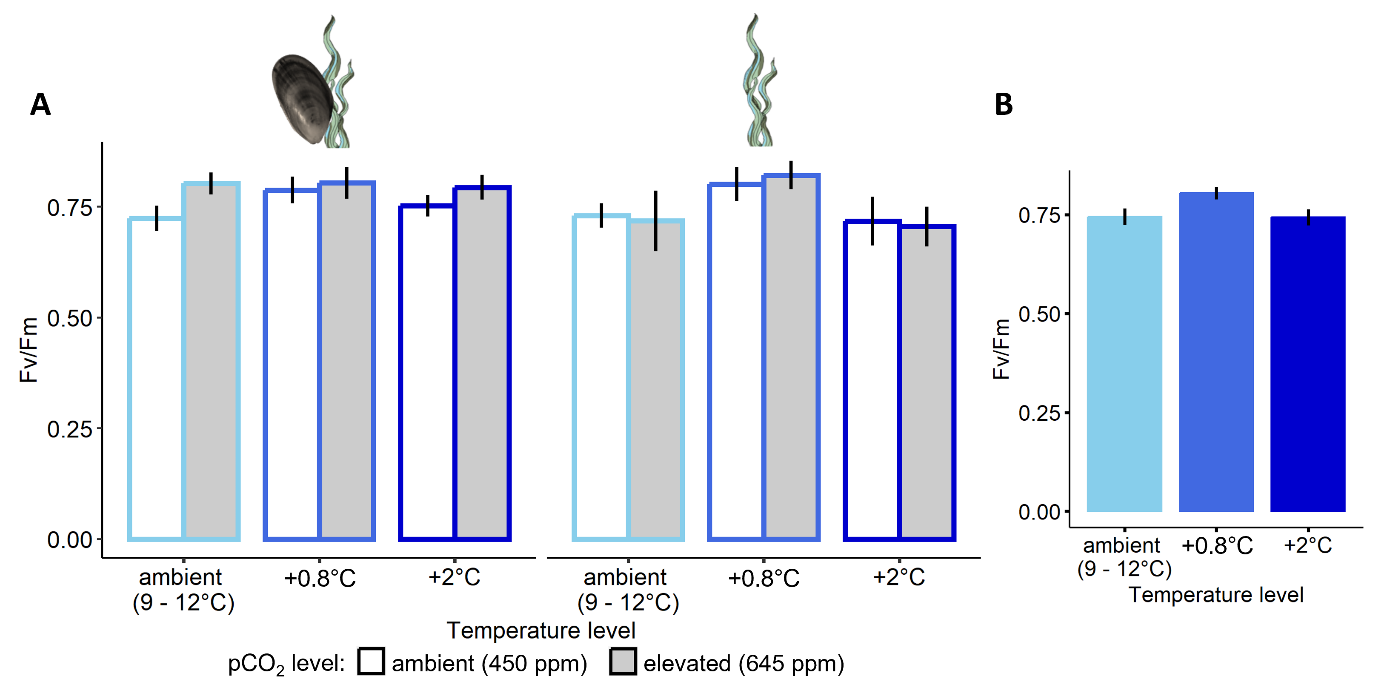


Figure . Mean (± standard error) maximum quantum yield of algae in A (all treatments) at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, and at ambient (white bars) and elevated (grey bars) pCO2, in the presence (left panel) or absence (right panel) of mussels, n = 5; and in B (significant main effect) as groups of means at different temperatures.

### Total accumulated biomass

No factors interacted when comparing the total accumulated biomass of mussels and algae in treatments where they were kept together to the sums of biomass in treatments that contained just mussels or just algae. Whether mussels and algae were kept separately or together affected the total accumulated biomass significantly (F3, 228 = 135.902; p < 0.001), which was 54 % higher when kept together compared to their sums when kept separately (Figure 8). Temperature had an effect on the total accumulated biomass (F2, 228 = 16.314; p < 0.001) and post-hoc tests indicated significant differences between the ambient and the medium (+0.8 °C; p = 0.003) and the medium and the warmest (+2 °C; p < 0.001) temperature level. pCO2 had no effect on the total accumulated biomass. Differences in total accumulated biomass were mainly driven by mussels (Figure 5; Figure 8).

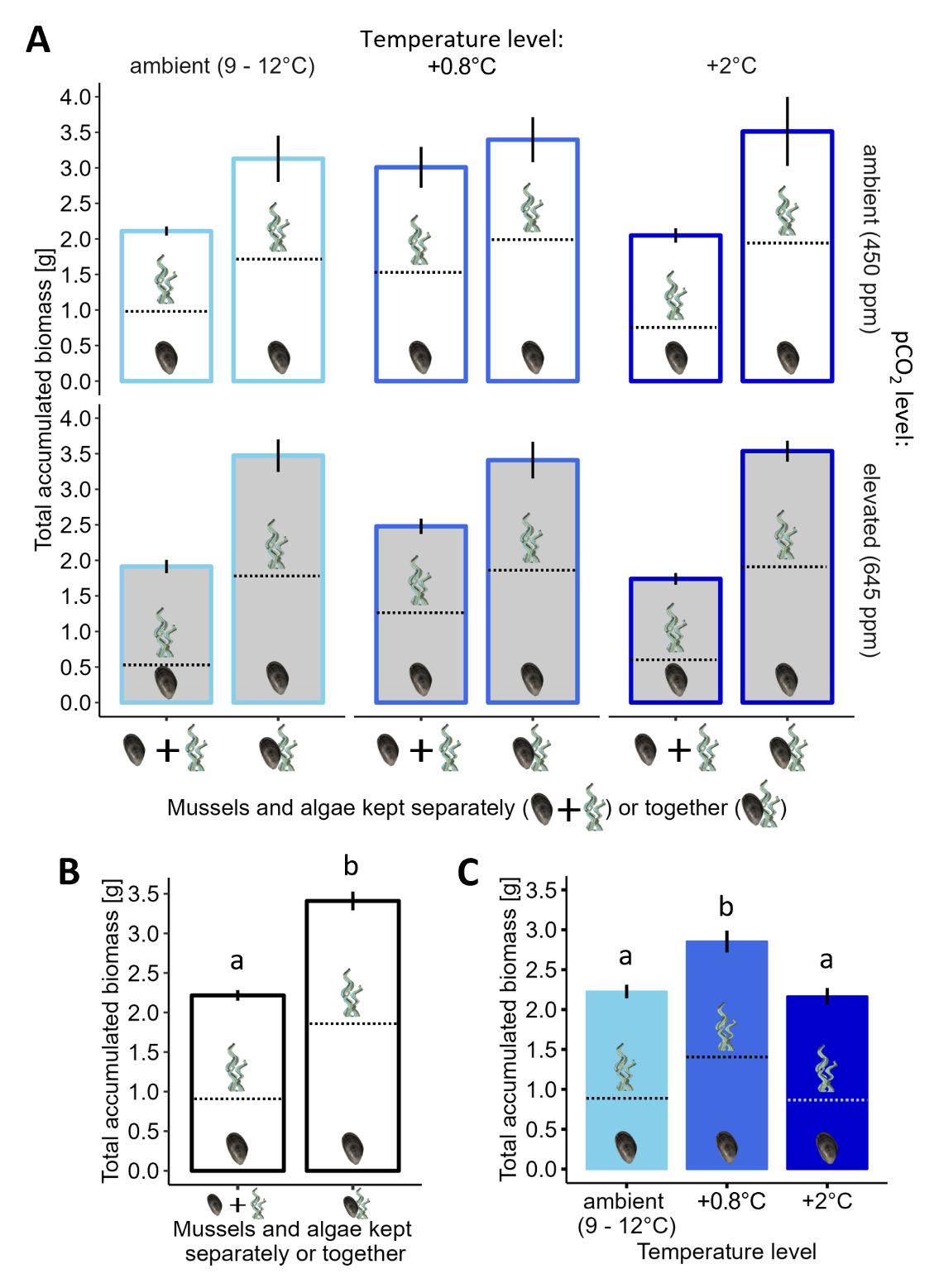


Figure Mean (± standard error) total accumulated biomass per mesocosm in A (all treatments) for the sum of mussel and algal biomass kept in separate treatments (n = 25) compared to the total accumulated biomass of mussels and algae kept together (n = 5). Proportional contributions of mussels or algae to total biomass accumulation are indicated by dashed lines. The panels show means at ambient (light blue), +0.8 °C (blue) and +2 °C (dark blue) temperature, the rows at ambient (white bars) and elevated (grey bars) pCO2. Significant main effects of functional group (mussels and algae kept separately vs. together) in B and of temperature in C with significant differences among groups of means indicated by lower case letters (p < 0.05).

## Discussion

Understanding how species interact when exposed to multiple stressors associated with climate change is crucial to estimate future ecosystem structure and the provisioning of ecosystem services. Here, we show that moderate predicted warming, but not acidification, affected the functioning of mussels and algae and that culturing them together enhanced both their performances compared to treatments that contained only mussels or only algae.

Mussel clearance rates were greater at warmer temperatures as we hypothesised. Contrastingly, mussel mortality was also greater, which was contrary to our expectations. This indicates that the mussels were not able to maintain their fitness despite increasing their energy intake. Average accumulated biomass of individual mussels and condition index were not affected by temperature. The fact that marine ectotherms, including bivalves and algae, adapt their metabolic rates and directly related traits, such as feeding rates in the case of mussels, according to the prevailing water temperature within their thermal range is well understood (e.g. Gao et al., 2019; Kittner and Riisgård, 2005; Pörtner, 2010; Roma et al., 2021). When food supply is high, biomass in *M. edulis* usually increases accordingly, while the condition index can decrease in response to warming when food is limiting (Mackenzie et al., 2014; Thomsen et al., 2013). When mussels died, the relative availability of food increased for the remaining mussels, which may have served to compensate increased energy demands at higher temperatures, e.g. required for byssus production, and may explain the absence of temperature effects on individual biomass and condition index (Roberts and Carrington, 2023).

The absence of pCO2 effects on mussel responses may be because coastal ecosystems experience large daily and seasonal fluctuations in pCO2 and respective pH conditions (Duarte et al., 2013; Fernández et al., 2019; Lutier et al., 2022; Vargas et al., 2017). When the mussel spat used in our experiment was collected in October 2020, a snapshot measurement of in-situ pH of 8.24 was taken, i.e. 0.15 logarithmic units higher than in the ambient treatment in the presented experiment, which is a greater interval than between the ambient and elevated pCO2 level applied. Long-term, continuous seasonal monitoring data of pH of Killary Fjord is not available. Between 2007 and 2009, however, summer pH ranged from 7.87 to 8.30 (O’Boyle et al., 2013), reflecting the influences of groundwater from surrounding calcerous limestone, nutrient inputs and biological activity (Duarte et al., 2013; McGrath et al., 2016). Therefore, the experimental pCO2 level of 645 ppm with an associated decrease in pH of 0.1 units compared to the ambient level of 450 ppm, or pH 8.09, respectively, lies within the range that the mussels experience and are likely adapted to in their natural habitats (Melzner et al., 2013; O’Boyle et al., 2013; Thomsen et al., 2013). It is currently unknown if natural carbon chemistry fluctuations will simply shift according to future mean background acidification, or if fluctuations will become more extreme. The effects of both possibilities should be included in future acidification research, given that increased temperature variation may be more harmful to ectotherms than increased mean temperature (Pansch and Hiebenthal, 2019; Vasseur et al., 2014). Furthermore, biological processes, such as growth and calcification, in juvenile *M. edulis* are mainly driven by food abundance, and are not impacted by pCO2 levels of up to 3350 ppm when food supply is high (Melzner et al., 2011; Thomsen et al., 2013). Similar to our results, increased clearance rates were found in individual juvenile *Mytilus chilensis* at +4 °C of warming, whereas acidified conditions of 700 ppm did not have any effects compared to ambient (380 ppm) conditions (only highly acidified conditions at 1000 ppm reduced the clearance rates independent of temperature; Navarro *et al.*, 2016).

We found no effect of any of the experimental treatments on shell strength. Other studies found evidence of shell dissolution in morphometric analyses and/or weakened shell strength in crushing tests after 6 – 9 months of exposure to strong acidification (> 2400 ppm or > -0.4 pH units) when mussels were kept at poor food supply (Mackenzie et al., 2014; Melzner et al., 2011). New shell material grown under acidified conditions has repeatedly proven to be more brittle in its microstructure, thus mechanically weaker than shells grown in ambient conditions (Fitzer et al., 2015a, 2015b), especially when food supply was low (Melzner et al., 2011). Our results show that 1-year-old spat can resist shell degradation under moderate ocean acidification for at least 6 weeks when kept at a favourable food supply.

During this study, byssal thread production was not affected by any of the experimental treatments. Previous studies suggested that byssus strength is highly size-dependent and that the attachment strength of juvenile life stages may be less affected by ocean acidification than that of larger adults (Clements and George, 2022). The absence of any effects of all applied treatments aligns with other recent conclusions that byssus production is generally prioritised over other energy expenditure, such as growth, in mussels in stressful conditions (Roberts and Carrington, 2023).

Similar to the pattern found in mussels, algal energy uptake as Fv/Fm depended on temperature but not pCO2, and there was no temperature effect on accumulated algal biomass. This may indicate that either the maximum quantum yield potential was not fully exploited, or that other cellular maintenance was prioritised over biomass and growth despite favourable temperatures.

Total accumulated biomass of mussels and algae combined was significantly higher at +0.8 °C than at ambient or the warmest (+2 °C) temperature. The proportional contributions of mussels to total accumulated biomass and the absence of a temperature effect on accumulated algal biomass suggest that differences in total accumulated biomass were driven by the mussels. Mussel clearance rates and mortality were significantly higher at +2 °C than at ambient temperature, indicating an increase with temperature. At the medium temperature level of +0.8 °C warming, mussels apparently still managed to fulfil their increased energy demand and, therefore, died less often than at the highest temperature level of +2 °C warming, resulting in the highest total accumulated biomass. While total accumulated biomass at +2 °C resembled that of ambient temperature, the underlying mussel population contained fewer individuals. This shows that small intervals of warming between 0.8 and 2 °C, even at the lower end of seasonally experienced temperatures, can have significant effects on community composition, which may have profound ecological consequences.

A key finding of this study was that the presence of algae enhanced mussel performance by decreasing mussel mortality and increasing mussel biomass and condition index. Concurrently, the presence of mussels also enhanced algal performance by increasing algal biomass and strengthening photosynthetic adaptation (relative maximum electron transport rate rETRmax and the saturating light intensity Ik). This mutual facilitation is exemplified in particular by comparing the total accumulated biomass in treatments where both mussels and algae were present to the sums of biomass in treatments comprised of only mussels and only algae. We have identified a synergistic interaction here where the total biomass of mussels and algae grown together exceeded the sums of biomass from treatments in which only mussels and only algae were grown by up to 54 %, which could be considered a form of complementarity or transgressive overyielding (Schmid et al., 2008). We know that benthic diatoms dominate the biofilms that produce extracellular polymeric substances binding particles together, and play an important role as a resuspended food source for filter feeders including mussels (Kang *et al.*, 2006; Evrard *et al.*, 2012; Andriana *et al.*, 2021). In turn, the mussels enrich the biofilms with nutrients by depositing ammonium, faeces and pseudofaeces, which fuels benthic primary production and diatom growth, and eventually benefits mussels e.g., by increasing sediment surface stability and sedimentation (Lindström Swanberg, 1991; Andriana *et al.*, 2021). In the present study, it remains unclear if mussel mortality decreased in the presence of algae because of additional food available through re-suspended microphytobenthos, or by an improved environment for decomposing microorganisms that metabolised waste products, such as ammonia, and, therefore, increased water quality. The microalgae in the treatments with mussels and algae were fed both with f2 medium and through mussel faeces and pseudofaeces, which led to increased algal biomass accumulation compared to treatments in which mussels were absent. Simultaneously, however, the microalgae in these treatments seem to have outcompeted the juvenile kelp sporophytes, presumably owing to their ability for faster growth. Our results of algal photo physiology align with Rugiu *et al*. (2020) who exposed 1-year-old *Saccharina latissima* to mussel farm effluent and found increased rETRmax and Ik (but no effect on the light harvesting efficiency α) compared to control treatments.

#### Conclusion

Our study showed that short-term metabolic processes related to energy intake (mussel clearance rates or algal maximum quantum yield) increased with moderately elevated temperature, while moderately elevated pCO2 did not have any effect on the response variables. Simultaneously, mussel mortality increased with warming, resulting in highest total accumulated biomass (of mussels and algae combined) at the medium temperature level of ambient +0.8 °C. We show that, depending on species’ positions on their thermal performance curves and in their thermal ranges, future marine communities in a warmed ocean are likely to undergo severe changes in their structure and functioning, even if changes in temperature are 0.8 – 2 °C and may seem small. The tolerance of mussels towards elevated pCO2 and lowered pH when food is abundant highlights the importance of considering ecosystem dynamics and trophic interactions under global change. Furthermore, considering that 645 ppm CO2 did not impact the performance of juvenile mussels negatively, and that marine organisms will be exposed to more frequent and more intense environmental fluctuation extremes, there is potential for cross-generational adaptation to more acidic conditions in the future.

Mussels and algae mutually facilitated their performance, including overall productivity and energy budgets (mussel condition index, both mussel and algal biomass, algal electron transport rate and light sensitivity). Considering that the total biomass of mussels and algae grown together substantially exceeded the biomass of sums of treatments with only mussels and only algae present, and that mussel mortality was significantly reduced where algae were present, efforts to increase and conserve biodiversity in marine ecosystems may provide noticeable ecological and economic benefits.

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# Appendix – Supplementary Material

## Shell length determination and size-independent mortality

At the start and the end of the experiment, the mussels from each mesocosm were photographed on graph paper for subsequent shell length determination. Initial and final individual mussel shell lengths were determined from a random half of the mesocosms (*n* = 30) by measuring the maximum anterior-posterior axes (Seed, 1968) using image analysis (ImageJ 1.53q; Rasband, 1997). Mussel lengths were comparable within photos but not across photos because the camera was readjusted several times when photos were taken. As a consequence, no absolute length growth rates could be determined. However, Kolmogorov Smirnov tests confirmed that in 29 of the 30 examined mesocosms the lengths distributions remained the same throughout the experiment, i.e. mussel mortality was independent of size (Table A.2.2). Accordingly, mussel individuals of a mesocosm were treated as similar on average and clearance rate samples that were taken before mussel retrieval at the end of the experiment were standardised by the number of alive mussels per mesocosm.

Shell lengths of mussels used in shell strength tests were determined separately with the same methodology and without camera readjustments to ensure comparability of the lengths.

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## Supplemental Tables

Table . TukeyHSD test on the effect of temperature (3 levels: Ta – ambient, T+ – ambient +0.8 °C, T++ – ambient + 2°C) on the maximum quantum yield Fv/Fm.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Diff | Lower 95% CI | Upper 95% CI | *P (adj)* |
| T++-T+ | -0.062 | -0.128 | 0.005 | 0.074 |
| Ta-T+ | -0.060 | -0.126 | 0.007 | 0.085 |
| Ta-T++ | 0.002 | -0.065 | 0.068 | 0.998 |

Table . Two-sample Kolmogorov-Smirnov tests comparing the initial and final mussel length distributions in 30 of 60 mesocosms

|  |  |  |
| --- | --- | --- |
| Mesocosm ID | D | *P* |
| B1 | 0.200 | 0.723 |
| B6 | 0.217 | 0.559 |
| B9 | 0.179 | 0.812 |
| C1 | 0.400 | 0.048 |
| C4 | 0.110 | 0.998 |
| C5 | 0.140 | 0.952 |
| E2 | 0.133 | 0.962 |
| E6 | 0.125 | 0.970 |
| E9 | 0.173 | 0.807 |
| F3 | 0.153 | 0.906 |
| F4 | 0.242 | 0.358 |
| F6 | 0.110 | 0.998 |
| G1 | 0.122 | 0.984 |
| G8 | 0.162 | 0.964 |
| G9 | 0.230 | 0.571 |
| H1 | 0.163 | 0.736 |
| H3 | 0.259 | 0.249 |
| H7 | 0.138 | 0.989 |
| H8 | 0.186 | 0.761 |
| I1 | 0.130 | 0.957 |
| I4 | 0.212 | 0.585 |
| I5 | 0.236 | 0.600 |
| J2 | 0.167 | 0.893 |
| J4 | 0.264 | 0.453 |
| J5 | 0.125 | 0.980 |
| J7 | 0.137 | 0.973 |
| J9 | 0.176 | 0.862 |
| K3 | 0.250 | 0.441 |
| K5 | 0.208 | 0.436 |
| K9 | 0.208 | 0.637 |