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# Coral-macroalgal competition under ocean warming and acidification

Lena Rölfer [a,b,*,1], Hauke Reuter [a,b], Sebastian C.A. Ferse [a,b], Andreas Kubicek [c], Sophie Dove [c], Ove Hoegh-Guldberg [c], Dorothea Bender-Champ [c]

[a] Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstraße 6, D-28359 Bremen, Germany
[b] Faculty of Biology & Chemistry (FB2), University of Bremen, D-28359 Bremen, Germany
[c] Global Change Institute and School for Biological Sciences, University of Queensland, 4072 Brisbane, Australia

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ABSTRACT

Competition between corals and macroalgae is frequently observed on reefs with the outcome of these interactions affecting the relative abundance of reef organisms and therefore reef health. Anthropogenic activities have resulted in increased atmospheric $CO_2$ levels and a subsequent rise in ocean temperatures. In addition to increasing water temperature, elevated $CO_2$ levels are leading to a decrease in oceanic pH (ocean acidification). These two changes have the potential to alter ecological processes within the oceans, including the outcome of competitive coral-macroalgal interactions. In our study, we explored the combined effect of temperature increase and ocean acidification on the competition between the coral *Porites lobata* and on the Great Barrier Reef abundant macroalga *Chlorodesmis fastigiata.* A temperature increase of +1 °C above present temperatures and $CO_2$ increase of +85 ppm were used to simulate a low end emission scenario for the mid- to late 21st century, according to the *Representative Concentration Pathway 2.6* (RCP2.6). Our results revealed that the net photosynthesis of *P. lobata* decreased when it was in contact with *C. fastigiata* under ambient conditions, and that dark respiration increased under RCP2.6 conditions. The Photosynthesis to Respiration (P:R) ratios of corals as they interacted with macroalgal competitors were not significantly different between scenarios. Dark calcification rates of corals under RCP2.6 conditions, however, were negative and significantly decreased compared to ambient conditions. Light calcification rates were negatively affected by the interaction of macroalgal contact in the RCP2.6 scenario, compared to algal mimics and to coral under ambient conditions. Chlorophyll *a*, and protein content increased in the RCP2.6 scenario, but were not influenced by contact with the macroalga. We conclude that the coral host was negatively affected by RCP2.6 conditions, whereas the productivity of its symbionts (zooxanthellae) was enhanced. While a negative effect of the macroalga (*C. fastigiata)* on the coral *(P. lobata)* was observed for the P:R ratio under control conditions, it was not enhanced under RCP2.6 conditions.

## 1. Introduction

Macroalgae are important organisms on coral reefs, contributing significantly to primary production (Gattuso et al., 1998) and nitrogen fixation (Heil et al., 2004). On a healthy reef, corals generally predominate the benthic community and are generally competitively superior to macroalgae (Chadwick and Morrow, 2011). However, in recent years reef ecosystems experienced dramatic declines in coral cover due to anthropogenic impacts such as global climate change, ocean acidification, eutrophication, sedimentation and overfishing as well as disease outbreaks (Hoegh-Guldberg et al., 2007; Hughes et al., 2010, 2007). Between 2014 and 2017 a 36 month global heatwave led to multiple bleaching events on coral reefs and on the Great Barrier Reef to a loss of shallow water corals of 22–30% with even 50% in the northern parts (Hughes et al., 2017; Eakin et al., 2018).

The free space on the reef created by high coral mortality can be taken up by other sessile benthic organisms such as macroalgae, corallimorpharians and sponges (Aronson and Precht, 2001; Norström et al., 2009). Competition between benthic, sessile organisms is one of the main factors shaping the community composition on reefs (Dayton,

*Abbreviations:* RCP2.6, Representative Concentration Pathway 2.6; $P_{net}$, net oxygen production (net photosynthesis); $R_{dark}$, dark respiration rate; P:R, Photosynthesis per Respiration ratio.

* Corresponding author at: Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstraße 6, D-28359 Bremen, Germany.
*E-mail address:* lena@roelfer.de (L. Rölfer).
[1] Present address: Climate Service Center Germany (GERICS), Helmholtz-Zentrum Geesthacht, Fischertwiete 1, D-20095 Hamburg, Germany.

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1971). Macroalgae are competing for space in different ways, including physical abrasion of coral tissue (Coyer et al., 1993), shading (Hughes, 1994) or allelochemicals (i.e. harmful chemicals) to induce bleaching or death in corals (Longo and Hay, 2017; McCook, 2001; Nugues et al., 2004). Furthermore, macroalgal exudates can lead to microbe-induced mortality of adjacent corals (Clements et al., 2020; Smith et al., 2006). Corals that are weakened by anthropogenic impacts are not able to invest energy in spatial competition as their energy is needed for various maintenance functions (Diaz-Pulido et al., 2011; Foster et al., 2008; Rinkevich and Loya, 1985). Additionally, changes in the reef environment such as high nutrient availability (eutrophication) and overfishing of herbivores can result in enhanced growth rates of macroalgae as well as their release from predation pressure (Hughes et al., 2007, 1987; Shenkar et al., 2008). As a consequence, macroalgae become the stronger competitor and proliferate over the reef environment (Done, 1992; McCook, 1999), which may lead to a phase shift from a coral to an algal dominated state (Anton et al., 2020; Done, 1992; Hughes et al., 2010; Norström et al., 2009).

Ocean warming and acidification, combined with disturbances such as overfishing and nutrient enrichment, have a high potential to also decrease resilience of coral reefs (Anthony et al., 2011; Dove et al., 2013) and may change the outcome of competition (Chadwick and Morrow, 2011; Diaz-Pulido et al., 2011; Hoegh-Guldberg et al., 2007). Thus, on many reefs worldwide macroalgae are the winners in the competition for space on coral reefs (Gardner, 2003; McCook, 1999; Mumby et al., 2013; Scheffer et al., 2001).

Corals are particularly vulnerable to ocean acidification (Pörtner et al., 2019), resulting in a significant reduction in calcification rate through a decreased aragonite saturation, which controls coral calcification (Doney et al., 2009; Kleypas and Langdon, 2006; Langdon, 2002). With an increase of dissolved $CO_2$, however, productivity may be enhanced, as $CO_2$ is often a limiting factor in the marine realm. Enhanced productivity under elevated $CO_2$ levels has been shown for both, macroalgae (Gao et al., 1993, 1991; Wu et al., 2008) and zooxanthellae (Al-Moghrabi et al., 1996; Leggat et al., 1999).

Under current conditions, corals are already at their thermal limits, and with temperatures continuing to rise, corals will be pushed more frequently beyond their thermal tolerance threshold, as oceans warm (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; Anton et al., 2020). This was last observed in the longest and most severe coral bleaching event 2014–2017, when global monthly sea surface temperature maxima increased to 30–31 °C (Lough et al., 2018), which led to a mass mortality of shallow water corals (Heron et al., 2016; Hughes et al., 2017).

Investigations about coral-algal interactions have strongly increased during the last decade, monitoring interactions both in situ and in tank experiments (Bender et al., 2012; Birrell et al., 2008; Brown et al., 2019; Del Monaco et al., 2017; Diaz-Pulido et al., 2010; Diaz-Pulido and Barrón, 2020; Jompa and McCook, 2003; McCook, 2001; Rasher et al., 2011; Rasher and Hay, 2010; Vieira et al., 2016)However, information on the impacts of global and climate change on ecological interactions are still underrepresented in the literatura.

In order to explore the interaction of the macroalgae and corals under climate change, we used the macroalgae *Chlorodesmis fastigiata* (C. Agardh) S.C.Ducker and the coral *Porites lobata* (Dana, 1846) from Heron Island on the southern Great Barrier Reef. Both species are abundant and interactions between each are frequently observed (Jompa and McCook, 2003). *C. fastigiata,* a siphonous green macroalga, has been shown to have mostly negative impacts on corals, such as inducing bleaching (Bonaldo and Hay, 2014), decreased photosynthesis (Rasher et al., 2011; Rasher and Hay, 2010), polyp retraction by abrasion (Jompa and McCook, 2003), reduced tissue recovery (Bender et al., 2012), and reduced coral settlement (Birrell et al., 2008). *P. lobata* is a massive, colonial coral from the order Scleractinia and constitutes one of the most important and occurring reef-building corals on Pacific coral reefs (Budd, 1986).

The combined effect of elevated $CO_2$ and temperature on the interaction between *P. lobata* and *C. fastigiata* was tested against ambient seawater as control, to provide further insights into coral-algal interactions under changing environmental conditions. Temperature of the treatment water was increased by 1 °C (compared to today; +2 °C compared to preindustrial times) and the CO2-concentration by +85 ppm according to the RCP2.6 scenario for the mid- to late 21st century (IPCC, 2013). We hypothesized that the coral would be negatively affected by both, the interaction with macroalgae and RCP2.6 conditions, and that the interaction with live algae would induce stronger effects than mimics because of biological/chemical in addition to mechanical effects (e.g. shading or abrasion).

## 2. Materials and methods

### 2.1. Study site and collection of corals and macroalgae

This study was done between October and December 2016 (late spring/Australian summer) at Heron Island Research Station (HIRS), located in the southern section of the Great Barrier Reef. Organisms were collected with permission from the Great Barrier Reef Marine Park Authority (permit number G16/38942.1). Colonies of *P. lobata* (approximately 30 cm in diameter) were collected at the reef flat of Heron Reef (four colonies, 23°26′S, 151°54′E) and the adjacent Wistari Reef (two colonies, 23°27′S, 151°52′E). From the colonies, 90 coral cores (further referred to as corals) of 5 cm diameter were drilled using a core saw, cut to a height of 1.5 cm and put into tanks with constant flow-through of seawater for a recovery time of 5 days.

Thirty specimens of *C. fastigiata* of approximately the same size as coral cores were collected with a small amount of substrate (Bonaldo and Hay, 2014) at the reef flat of Heron Reef. Care was taken not to injure holdfast or other tissue to avoid leaking of chemical compounds. Macroalgal substrate was cleaned of crabs and other organisms that lived and fed on the macroalgae were removed. Macroalgae were put into tanks with corals, with care not to touch the corals (or other macroalgae). After the recovery time of five days, seawater in all tanks was slowly switched to treatment water over another five days in order to let corals and algae acclimatize to the new conditions. Macroalgae mimics were made from 13 cm long pieces of fibre rope (0.7 cm in diameter), which were bent once in the middle, tied at the base and separated into its fibres (Edgar and Klumpp, 2003), and pieces of substrate were attached to the bottom. After the acclimatization time, mimics and specimens of *C. fastigiata* were tied to coral cores using rubber bands (without touching coral tissue) (Bonaldo and Hay, 2014) to avoid mimics from floating and to assure that macroalgae stayed with the same coral for the time of the experiment.

### 2.2. Experimental set-up, maintenance and monitoring

To assess the effect of elevated temperature and ocean acidification on a coral-algal interaction, organisms were subjected to ambient conditions and the Intergovernmental Panel on Climate Change (IPCC) scenario RCP2.6 conditions (Dove et al., 2013). Data collected at a reference site in the Wistari Channel (adjacent to Heron Reef) was used as a baseline for ambient temperature and $CO_2$. Sea water was pumped from the reef flat to a holding tower at Heron Island Research Station and redistributed into two sumps, in which $CO_2$ and temperature treatment conditions were established (as described by Dove et al., 2013). From these sumps the experimental tanks were supplied with the respective treatment water. Temperature and pH feedback sensors in experimental tanks were connected to a system controller, which then adjusted the conditions in the sumps at intervals of two hours to guarantee exact diurnal and seasonal conditions within the experimental tanks (Fig. 1). See Dove et al. (2013) for details. Both water treatments (ambient and RCP2.6) were applied to nine tanks each (18 tanks in total). Per treatment condition, three tanks each contained five

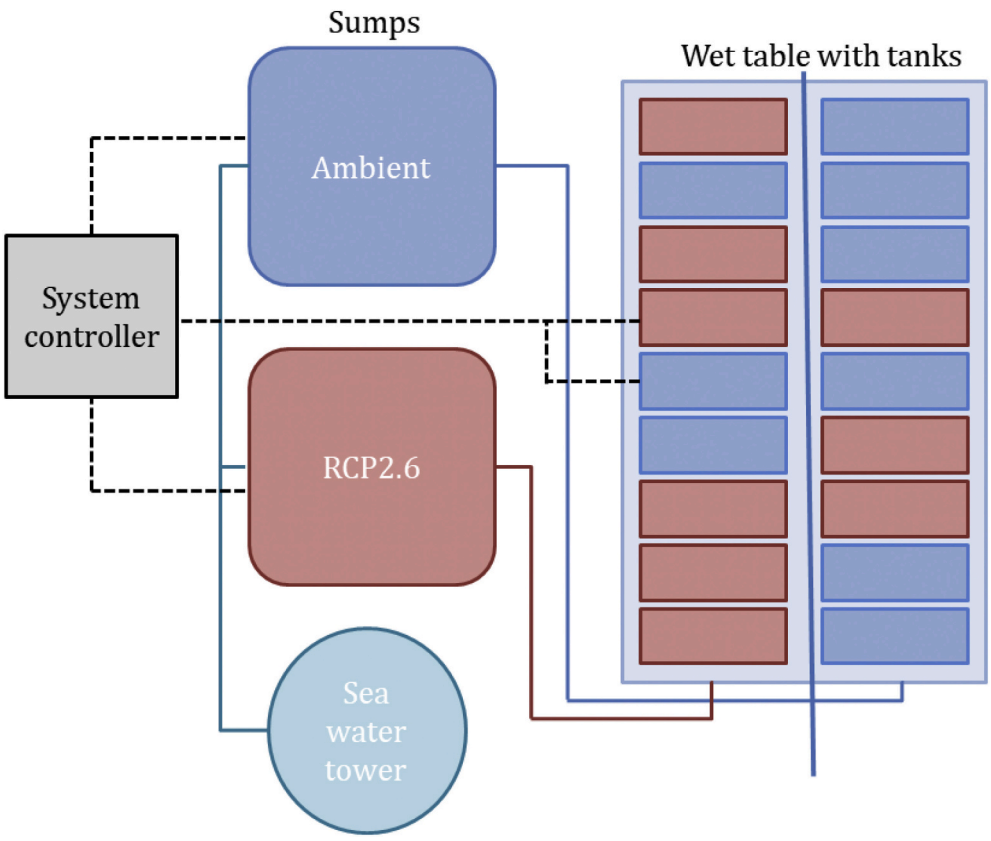


**Fig. 1.** Schematic of sumps and wet table set up with partial pressure of $CO_2$($pCO_2$)/ temperature control system. Seawater from the tower (light blue) is pumped into sumps (dark blue, red), treatment conditions are applied and tanks ($n = 3$ per interaction treatment) on wet table are connected to sumps. System controller (grey) with feedback loop (dotted line) to adjust conditions in a two hour interval. AMB: ambient seawater; RCP2.6: treatment seawater with increased temperature and $pCO_2$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

replicates of either a) only corals, b) corals with interacting macroalgae, or c) corals with macroalgal mimics (Fig. 2), summing up to 15 coral replicates per contact treatment. Organisms were kept under treatment conditions for a period of 22 days and physiological measurements were performed subsequently.

Experimental tanks (60*20*38 cm; ~ 35 l) containing corals and macroalgae were covered with Lee-filters (*Old Steel Blue, 725*) on the sides and lids to imitate light intensity at a water depth of 3–6 m on the reef flat. They were exposed to natural sun irradiance with a constant flow-through of seawater (0.8–1 l*min$^{-1}$). Pumps (*Clearpond Infiniti 800*) were installed to agitate seawater in order to avoid the forming of a boundary layer. Tanks were cleaned from fouling organisms every three days, with macroalgal mimics being washed in freshwater to remove biofouling, and settled substrate was carefully cleaned off corals with toothbrushes. At the same time, tanks were rotated to avoid confounding of light and temperature differences.

To monitor the abiotic conditions within tanks (Table 1), we installed four light loggers (*PAR Sensor, Odyssey, Dataflow Systems, New Zealand*) and five temperature loggers (*HOBO Data Loggers, Onset*) as well as four pH-probes (*Mettler Toledo, Port Melbourne, Victoria, Australia, InPro4501VP X* connected to an *Aquatronica Aquarium Controller ACQ110*). pH was measured on the scale $pH_{sw}$ and the pH probes were calibrated every second to third day by a two point calibration. The loggers and probes were randomly swapped between tanks every three days to monitor every tank throughout the experiment. Temperature and $pCO_2$ contents of sumps were recorded additionally (Table 1). $pCO_2$ was measured in the sumps (logged continuously every 3 min) and calculated in CO2SYS (developed by E. Lewis and W.R. Wallace) based on twice daily alkalinity and salinity sampling, and continuous temperature and pH monitoring at 10 min intervals (see Dove et al. (2013) for more detail). The total alkalinity of each tank was sampled once a week at midday and midnight (Table 1) and measured using a *Mettler Toledo* titrating system (T50) by Gran titration after Dickson et al. (2003) using the method with a precision of ±3 μmol Kg$^{-1}$ or better as described in Kline et al. (2012). RCP2.6 conditions of ~1 °C increase and a $CO_2$ level of +85 ppm compared to ambient conditions could be maintained during the experimental period.

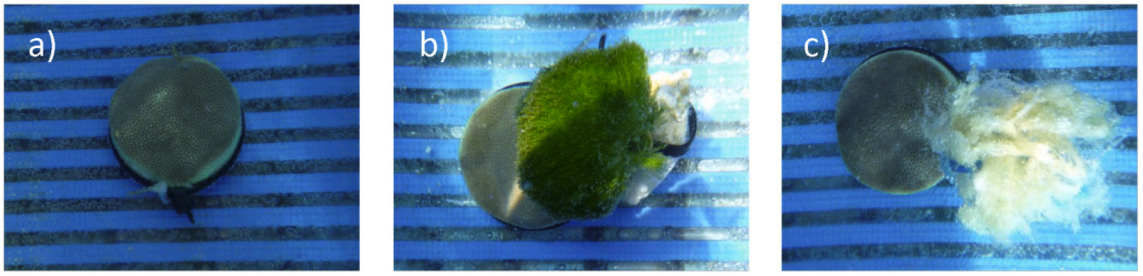


**Fig. 2.** Pictures of interaction treatments: a) coral *P. lobata*, b) coral *P. lobata* with interacting alga *C. fastigiata*, and c) coral *P. lobata* with algal mimic (made out of plastic fibre rope). Ambient and RCP2.6 water treatments were applied to each 3 tanks with 5 replicates each per interaction treatment.

**Table 1**
Summary of values of water chemistry data for scenario conditions.

| | Ambient | RCP2.6 |
|---|---|---|
| Temperature [°C] tanks | 25.95 ± 0.65 | 26.88 ± 0.75 |
| $pH_{SW}$ tanks | 8.07 ± 0.03 | 7.96 ± 0.03 |
| Temperature [°C] sumps | 25.38 ± 0.44 | 26.29 ± 0.57 |
| $pCO_2$ [ppm] sumps | 465.27 ± 53.48 | 550.58 ± 49.52 |
| Total alkalinity day [μmol Eq. $L^{-1}$] | | |
| Day | 2289.65 ± 12.23 | 2287.18 ± 11.86 |
| Night | 2269.11 ± 26.18 | 2271.64 ± 25.18 |
| $pCO_2$ [μppm] CO2Sys | | |
| Day | 268.17 ± 30.32 | 282.13 ± 25.32 |
| Night | 311.26 ± 26.52 | 331.45 ± 21.68 |
| $HCO_3^-$ [μmol Kg $SW^{-1}$] | | |
| Day | 1706.37 ± 43.74 | 1723.38 ± 36.09 |
| Night | 1744.8 ± 35.13 | 1767.53 ± 31.80 |
| $CO_3^{2-}$ [μmol Kg $SW^{-1}$] | | |
| Day | 234.64 ± 15.85 | 226.79 ± 11.60 |
| Night | 210.61 ± 10.87 | 202.61 ± 7.98 |
| ΩAragonite | | |
| Day | 3.66 ± 0.25 | 3.54 ± 0.18 |
| Night | 3.28 ± 0.17 | 3.16 ± 0.12 |

Temperature, pH, $pCO_2$ values are means over experimental period, continuously measured over the experimental period (22 days). High standard deviation is due to daily variability. Total alkalinity, $pCO_2$, $HCO_3^-$, $CO_3$ and ΩAragonite of treatments are given as means over experimental period, measured once a week at midday and midnight in tanks and were estimated using CO2SYS software. Kg SW, kilogram of seawater.

### 2.3. Measurement of respiration and calcification rates

In order to investigate treatment effects on the metabolism of corals and macroalgae, the net oxygen production ($P_{net}$) and dark respiration rates ($R_{dark}$) were measured following the methodology of Crawley et al. (2010) at the end of the experiment (i.e. after 22 days in treatment conditions). Organisms ($n_{coral} = 12$ per treatment, $n_{macroalgae} = 6$ for RCP2.6 and 8 for ambient) were dark adapted for 45 min prior to dark respiration measurements. For $P_{net}$ measurements the light intensity was adjusted by modifying the distance of a metal halide lamp (Ocean Light T5 MH combo 150 W, with 2 × 24 Ocean Blue Actinic, Aqua-Medic of North America, LLC) from the specimens. The average light intensity within the experimental tanks matched that measured at midday of the previous week (694.5 μmol photons $m^{-2}\,s^{-1} \approx h = 32.5$ cm). Oxygen flux was recorded using high-precision optical oxygen sensors (optodes) connected to a logging system (Oxy-10, PreSens, Germany) for 12 and 20 min for macroalgae and corals, respectively, and was normalized to the surface area of corals (see below) and fresh weight of macroalgae. All measurements were conducted in the respective treatment water ($t_{ambient} = 25.9$ °C, $t_{RCP2.6} = 26.9$ °C) calculated as a mean for the previous week. The photosynthesis per respiration (P:R) ratio was calculated by dividing $P_{net}$ by $-R_{dark}$.

The light and dark calcification rates were measured in addition to the photosynthetic/respiratory rates of the corals. To do this, alkalinity samples ($n = 5$ per treatment) were taken from respirometry incubations and the changes in the calcification of corals measured using the alkalinity anomaly technique using bulk water samples as blanks. Alkalinity samples were stored in a fridge at 4 °C, and within eight weeks after collection (Huang et al., 2012), were measured using a *Mettler Toledo* titrating system (T50) by Gran titration after Dickson et al. (2003) with a precision of ±3 μmol $Kg^{-1}$ or better using the method described in Kline et al. (2012). The calcification rate was then calculated from the total alkalinity after Zundelevich et al. (2007), corrected by $10^{-3}$ for unit conversion and divided by two as molar amount of dissolved $CaCO_3$ equals only half of observed $A_T$ increase (Chisholm and Gattuso, 1991). Calcification rates were normalized to time and surface area and expressed in μg $CaCO_3$ $cm^{-2}\,h^{-1}$.

### 2.4. Growth measurements

To examine possible differences in growth rates of organisms between treatments, buoyant weight of corals (Jokiel and Maragos, 1978) ($n = 15$ per treatment) and fresh weight of macroalgae ($n = 15$ per treatment) were measured before the tank period and after respirometry measurements were conducted (i.e after 26 days). Fresh weight of macroalgae was calculated by subtracting the weight of the substrate (measured by buoyant weight) from the total weight. To minimize inaccuracy of measurements, macroalgae were blotted with paper tissue prior to weighing. Weight differences were calculated as percentage change of buoyant weight and fresh weight for corals and macroalgae, respectively. After weighing, all samples were frozen at −20 °C pending further analysis.

### 2.5. Tissue analysis of corals

Tissue samples were taken from same corals used for respirometry measurements ($n = 12$ per treatment), by removal with a seawater jet (Johannes and Wiebe, 1970). Samples were poured into a *Falcon* tube and then vortexed and centrifuged at 4500 rpm for 5 min at 4 °C. The supernatant was poured into a 2 ml *Eppendorf* tube for protein analysis. To dilute the pellet left in the tube, 10 ml of filtered seawater was added and vortexed. From this dilution, 1 ml was pipetted into two tubes for zooxanthellae count and chlorophyll *a* analysis.

The population density of zooxanthellae was measured using a *Neubauer* hemocytometer (*Neubauer-improved, Marienfeld GmbH*), counting cells within three squares of four replicate grids. Chlorophyll *a* was measured by adding 2 ml of 100% acetone to the 1 ml pellet dilution. Samples were sonicated in an ice bath for 10 min to extract the pigments and then centrifuged at 4500 rpm for 5 min at 4 °C to separate the pellet from the pigment solution. The supernatant was poured into a new *Falcon* tube and frozen and the extraction was repeated twice until supernatant was clear. After the extraction, tubes with supernatants were centrifuged again to remove debris (Hellebust and Craigie, 1978). Samples were measured in a spectrophotometer (*SpectrostarNano*) at wavelengths of 663 nm and 645 nm and blanks of acetone were measured after every ten samples and subtracted directly. The amount of chlorophyll *a* was then calculated after Arnon (1949) and expressed in g $l^{-1}$. As a quantitative indicator for the thickness of the tissue, the protein content was measured. Subsamples were measured as triplicates in the spectrophotometer at wavelengths of 235 nm and 280 nm. Protein content was calculated after Whitaker and Granum (1980) and expressed in g $l^{-1}$. To normalize tissue properties, respirometry measurements and calcification rates, the corals' surface area was measured using the paraffin wax technique (Stimson and Kinzie III, 1991).

### 2.6. Data analysis

Before statistical analysis of data was performed, all variables were tested for a possible tank effect by using the *lmne* package in R Studio, which compares Gaussian linear and nonlinear mixed-effect models. The test was performed for models with and without tank as a random factor. Since the tank factor was non-significant for all variables ($p > 0.25$) (results in supplementary table S2), specimens were used as replicates (Underwood, 1997), hence increasing the power of the analysis.

All response data of corals were tested using a two-factor analysis of variance (ANOVA) with "scenario" (ambient; RCP2.6) and "contact" (coral; coral-algal interaction; coral with algal mimic) as fixed factors, including the interaction term. Response data of macroalgae were tested using a one-way ANOVA with "scenario" as factor. To account for multiple comparisons of physiological parameters for *P. lobata* a Bonferroni correction was applied reducing the α-level of significance to 0.005. When significant effects of factors occurred, ANOVAs were followed by a Tukey multiple comparisons test to identify significant groups. Data were tested for homogeneity of variance (visual inspection

of residuals vs. fitted values), and normality of residuals was tested using Shapiro-Wilk normality test. Non-normally distributed data were log or power transformed to correct for right- or left skew, respectively. Statistical analysis of data was performed using *R Studio Version 1.0.143* (R Core Team, 2015) and results were expressed as boxplots using the *ggplot* package. Some samples of chlorophyll *a* and protein content of corals were lost throughout the analysis, reducing the degrees of freedom in the analysis.

## 3. Results

### 3.1. Corals

Coral growth, reported as percentage change in buoyant weight, was not significantly affected by the RCP2.6 or macroalgae treatment, or a combination of both. However, slightly negative growth was observed in the RCP2.6 coral treatment with an average of −0.34% change in buoyant weight (see supplementary TableS1).

The technique used for the respirometry measurements allowed the quantification of calcification rates under treatment conditions in the presence and absence of light for a particular point in time. The response of light calcification was dominated by an interaction of "scenario" and "contact". In the absence of macroalgae or mimics, corals showed significantly higher light calcification under ambient conditions with $48.7 \pm 10.3$ $CaCO_3$ [$\mu g\, h^{-1}\, cm^{-2}$] as compared to $15.1 \pm 5.9$ $CaCO_3$ [$\mu g\, h^{-1}\, cm^{-2}$] in the RCP2.6 scenario (Table 2, Fig. 3a). Corals in the ambient treatment also performed significantly different compared to corals in interaction with macroalgae in the RCP2.6 treatment. Dark calcification was significantly greater in the ambient scenario, with negative dark calcification in the RCP2.6 scenario for all contact treatments (Table 2, Fig. 3b).

$P_{net}$ was significantly influenced by "contact" (Table 2, supplementary material Fig.S1A) and lower in the coral-algal interaction treatment compared to only corals, while there was no difference of both treatments to the mimics treatment. $R_{dark}$ was significantly affected by "scenario" (Table 2, supplementary material Fig.S1B), with higher respiration under RCP2.6 compared to ambient conditions. For the P:R ratio there was a highly significant effect of "contact" (Fig. 3c, Table 2), with differences among all treatments. P:R ratio was highest for the mimics treatment, followed by the coral treatment and lowest for the coral-algal interaction treatment. While the P:R ratio was higher under ambient conditions for only corals and corals with mimics compared to RCP2.6 scenario conditions, there was an opposite trend for the coral-algal interaction. However, the interaction term of "scenario" and "contact" was not significant (Anova, $p = 0.03$, Table 2).

Chlorophyll *a* (Fig. 4d and Protein content (Fig. 4a) were significantly different among "scenarios" (Table 2). The mean value of chlorophyll *a* content in the coral-algal interaction under RCP2.6 conditions was more than two times higher than for the interaction under ambient conditions (Fig. 4d). There was a slight trend of a higher zooxanthellae population density in the RCP2.6 compared to the ambient scenario, irrespective of the contact treatment (Table 2, Fig. 4b).

### 3.2. Macroalgae

The macroalga at the centre of this study was very sensitive, and began to die after eight days of exposure to treatment conditions. Macroalgae that died were replaced once by 'back-up' macroalgae, which were acclimated and kept in additional tanks with ambient and RCP2.6 conditions, respectively. However, due to permit limitations no more macroalgae could be replaced after that. Over the remainder of the experiment another 14 macroalgae died, some of which were 'back-up' macroalgae, summing up to a total of 30 dead macroalgae ($n = 13$ in ambient, $n = 17$ in RCP2.6). Only 16 macroalgae survived throughout the whole experimental time ($n = 9$ in ambient, $n = 7$ in RCP2.6), reducing the degrees of freedom in the analysis.

Due to differences in size of macroalgae, growth was expressed as percentage change in fresh weight. Growth of individuals was positive and negative in both of the scenarios, with negative values resulting from a loss of filaments, explaining a high standard deviation. However, total change in fresh weight was positive in both treatments, with no significant difference between treatments (Table 3). There was also no significant difference in $R_{net}$ between the scenarios (Table 3). $R_{dark}$ was slightly higher in the RCP2.6 compared to the ambient scenario, resulting in a non-significant difference of P:R ratios between scenarios (Table 3).

**Table 2**
ANOVA output of different variables for *P. lobata* with bold values indicating significant effects on the variable.

| Variable | Source of variation | df | F | p |
|---|---|---|---|---|
| Bouyant weight | Scenario | 1 | 0.279 | 0.599 |
| | Contact | 2 | 1.633 | 0.202 |
| | Scenario x Contact | 2 | 1.587 | 0.211 |
| | Residuals | 81 | | |
| Light calcification | Scenario | 1 | 4.354 | 0.048 |
| | Contact | 2 | 2.878 | 0.076 |
| | Scenario x Contact | 2 | 7.480 | **0.003** |
| | Residuals | 24 | | |
| Dark calcification | Scenario | 1 | 36.792 | **<0.001** |
| | Contact | 2 | 5.007 | 0.013 |
| | Scenario x Contact | 2 | 2.843 | 0.078 |
| | Residuals | 24 | | |
| Zooxanthellae | Scenario | 1 | 7.031 | 0.010 |
| | Contact | 2 | 0.821 | 0.445 |
| | Scenario x Contact | 2 | 0.034 | 0.967 |
| | Residuals | 66 | | |
| Chlorophyll a | Scenario | 1 | 13.909 | **<0.001** |
| | Contact | 2 | 0.068 | 0.934 |
| | Scenario x Contact | 2 | 3.434 | 0.039 |
| | Residuals | 54 | | |
| Protein | Scenario | 1 | 12.448 | **<0.001** |
| | Contact | 2 | 0.848 | 0.433 |
| | Scenario x Contact | 2 | 2.228 | 0.117 |
| | Residuals | 60 | | |
| $P_{net}$ | Scenario | 1 | 2.390 | 0.127 |
| | Contact | 2 | 5.893 | **0.004** |
| | Scenario x Contact | 2 | 3.485 | 0.036 |
| | Residuals | 66 | | |
| $R_{dark}$ | Scenario | 1 | 8.749 | **0.004** |
| | Contact | 2 | 3.631 | 0.032 |
| | Scenario x Contact | 2 | 0.156 | 0.856 |
| | Residuals | 66 | | |
| P:R | Scenario | 1 | 2.899 | 0.093 |
| | Contact | 2 | 13.466 | **<0.001** |
| | Scenario x Contact | 2 | 3.693 | 0.030 |
| | Residuals | 66 | | |

df = degrees of freedom; F = F-value; p = *p*-value (significance <0.005).

## 4. Discussion

We investigated the important issues as to how ecological competition may vary under climate change. To do so, we investigated the interactions between the coral *P. lobata* and the potential competitor, the fleshy alga *C.fastigiate*, under low rates of future ocean warming and acidification. Corals and macroalgae were exposed to a temperature increase of +1 °C and a $CO_2$ increase of +85 ppm above ambient, which is close to the RCP2.6 scenario of the IPCC at mid- to late 21st century (IPCC, 2013). This corresponds to $CO_2$ levels expected if action is taken globally in accordance with the *Paris Agreement* and refers to the best-case scenario. We found that both, interaction with macroalgae and the combined effect of temperature and $CO_2$ affected the coral, whereas no significant impact of treatment conditions was detected for the macroalgae.

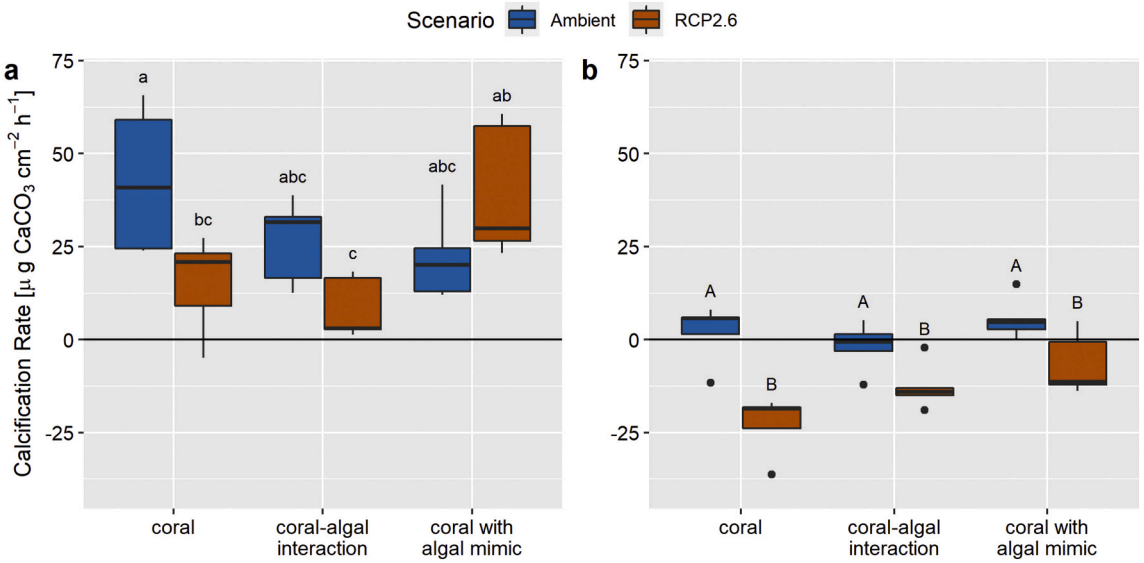


**Fig. 3.** Calcification rates of *P. lobata* under a light ($n = 5$), and b dark conditions (n = 5), measured during respirometry incubations. Letters indicate significant differences between interactions (a) or among scenarios (b).

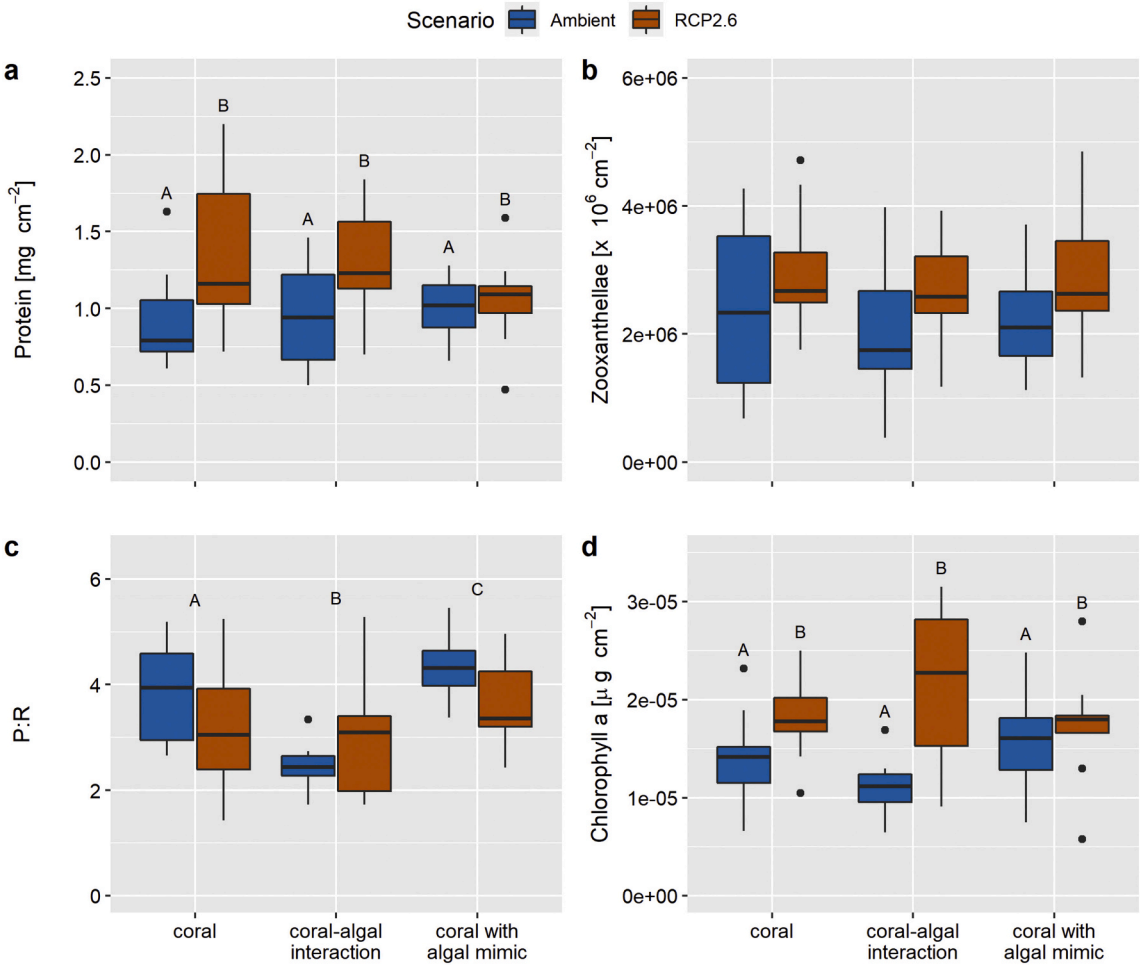


**Fig. 4.** a Protein content ($n = 11$), b Zooxanthellae density ($n = 12$), c Photosynthesis/Respiration (P:R) ratio (n = 12), d Chlorophyll *a* content ($n = 10$), protein content (n = 11) for *P. lobata*. Letters indicate significant differences among scenarios (a,d) or contact (c).

**Table 3**
ANOVA output of different variables for *C. fastigiata*.

| Variable | Source of variation | df | F | p |
|---|---|---|---|---|
| Fresh weight | Scenario | 1 | 1.470 | 0.244 |
| | Residuals | 15 | | |
| $P_{net}$ | Scenario | 1 | 1.852 | 0.197 |
| | Residuals | 13 | | |
| $R_{dark}$ | Scenario | 1 | 0.336 | 0.572 |
| | Residuals | 13 | | |
| P:R | Scenario | 1 | 0.341 | 0.569 |
| | Residuals | 13 | | |

df = degrees of freedom; F = F-value; p = *p*-value (significance >0.05).

### 4.1. Calcification under low rates of warming and acidification

The calcification of massive species such as *P. lobata* can be slow, as compared to faster growing corals such as branching species (Lough et al., 1999). In this study, percentage change in buoyant weight (~deposited calcium carbonate) was close to zero in all treatments. It is very likely, however, that the period of our tank experiment (22 days) was too short, as well as the increase of $pCO_2$ too small, to lead to a detectable effect in buoyant weight. Anthony et al. (2008) measured growth of *P. lobata* over a period of eight weeks and reported slightly reduced growth rate at 520–700 ppm and a ~ 40% decrease at 1000–1300 ppm. Diaz-Pulido et al. (2011) found that the linear extension of the fast growing coral *Acropora intermedia*, measured over eight weeks, was also strongly negatively affected by $CO_2$ treatments, but showed no significant difference between treatments with or without competition with the seaweed *Lobophora papenfussii*.

While a change in buoyant weight was not detected, measurements of dark calcification rates were significantly decreased under conditions similar to RCP2.6 for all interaction treatments, as well as for the coral treatment under light conditions. This is in agreement with other studies on coral of the genus Porites, including *P. lobata* (Anthony et al., 2008); *P. lutea* (Ohde and Hossain, 2004); *P. compressa* (Marubini et al., 2003) and supports the sensitivity of corals to elevated $CO_2$ (Kleypas and Langdon, 2006). In the present study, negative calcification (i.e. decalcification) was observed in all treatments under RCP2.6 conditions in the dark. $CaCO_3$ dissolution even exceeded light calcification in the coral and coral-algae interaction treatment which would lead to negative growth rates in these treatments if measured over a longer period. While the amount of energy available from photosynthesis (P:R) was stable among scenario conditions in the coral-algal interaction, dark calcification was reduced under RCP2.6 conditions. This suggests that resources were used for processes other than calcification that demanded higher energy expenditure under RCP2.6 conditions in the dark while in contact with the alga.

Calcification under illuminated conditions in the RCP2.6 scenario was significantly reduced in the interaction with the macroalgae compared to algal mimics and to coral under ambient conditions. Those results suggest that macroalgal mimics benefitted the light calcification of corals through shading by reducing irradiance and therefore light stress (Anthony et al., 2008), while this positive effect could not be detected for live algae.

### 4.2. Photosynthesis and respiration: evidence of a $CO_2$ fertilization effect?

Contrary to the results for the calcification rates, we found that RCP2.6 conditions significantly increased chlorophyll *a* and protein content. The increase in chlorophyll *a* coincides with an increased net photosynthesis under RCP2.6 conditions and might be explained by a '$CO_2$ fertilization effect' due to the greater availability of $CO_2$ to photosynthesize. An increase in chlorophyll *a*n under future conditions was also found in the branching corals *Stylophora pistillata* under raised temperature (Reynaud et al., 2003) and *Acropora formosa* under elevated $CO_2$ (Crawley et al., 2010). Crawley et al. (2010) used an increase of >200 ppm, but interestingly, a $CO_2$ increase of only +85 ppm in this study was sufficient to lead to an increase in chlorophyll *a*. This is comparable to another study, which found an increase in productivity at an intermediate $CO_2$ scenario (520–705 ppm), while the positive effect was mitigated at high $CO_2$ (1010–1350 ppm) (Anthony et al., 2008). The positive effect of $CO_2$ on chlorophyll *a* found in this study facilitates the slight increase of zooxanthellae and therefore protein content, which is an indicator for the nutritional condition of the coral (Ferrier-Pagès et al., 2003). However, the positive effect of $CO_2$ on the chlorophyll *a* content could be mitigated when $CO_2$ concentrations reach a higher level, as more energy is needed to maintain base functions of the coral host. This negative effect may be further enhanced by other anthropogenic stressors, which weaken the competitive strength of corals over macroalgae (Diaz-Pulido et al., 2011; Foster et al., 2008).

While a decrease in photosynthesis of corals in contact with various macroalgae is documented (Rasher et al., 2011; Rasher and Hay, 2010), the interacting effects of $CO_2$ and temperature on the interaction have scarcely been considered yet. Our study showed that there was a significant decreased P:R ratio of corals in interaction with macroalgae compared to no contact and the mimics treatment irrespective of the temperature/$CO_2$ regime the corals were under. RCP2.6 conditions had a lesser negative effect that was only visible as a trend in the coral only and mimics treatment. *C. fastigiata* caused a significant decrease of photosynthetic efficiency in the corals *Montipora digitata, Acropora millepora* and *Pocillopora damicornis* under ambient conditions, which was more severe compared to the effect of seven other common macroalgae (Longo and Hay, 2017; Rasher et al., 2011). In our study, however, corals were not actually in contact with macroalgae during the physiological measurements, because each species' metabolic rate was measured separately. Negative carry-over effects of macroalgae on the coral photosynthesis and respiration found in our study might be even more enhanced if measured whilst in contact.

### 4.3. Physical impacts of competitors

Impacts of macroalgae can harm corals by various mechanisms including shading and abrasion (McCook et al., 2001) as well as biochemical reactions, e.g. the induced bleaching due to harmful chemicals (Longo and Hay, 2017; McCook, 2001; Nugues et al., 2004). Indeed, *C. fastigiata* has been shown to produce allelochemicals that can suppress photosynthesis (Rasher et al., 2011) and cause bleaching (Rasher and Hay, 2010). A study by Del Monaco et al. (2017) investigated the impact of allelochemical extracts from *C. fastigiata* on corals over the same time scale as our project and Diaz-Pulido and Barrón (2020) tested the release of dissolved organic carbon, which can promote bacterial metabolism on corals surface and subsequent mortality, under future $CO_2$ conditions. Both studies conclude that the effects of *C. fastigiata* were not more harmful to corals under future climatic conditions (Del Monaco et al., 2017; Diaz-Pulido and Barrón, 2020).This is in agreement with our results, which show an effect of *C. fastigiata* on the P:R ratio, which however was not enhanced under RCP2.6 conditions.

A recent study by Brown et al. (2019) suggests that coral-algal interactions are temporally variable across seasons. Photosynthetic rates of the coral *A. intermedia* in contact with *H. heteromorpha* were reduced in winter and increased in summer, while calcification rates in summer reduced in contact with the algae. Even though photosynthetic activity was increased in contact with the algae, negative effects of a high-end ocean acidification and warming scenario (RCP8.5) reduced overall performance of corals (Brown et al., 2019), which is comparable to the results of our study.

The impacts of competitors can vary strongly among coral-algal interactions. *C. fastigiata* is a siphonous macroalga and therefore lacks discrete cell walls (Rasher et al., 2011). For that reason, handling such as collection or tank cleaning might have had a significant impact on the health of the organisms, resulting in a high mortality rate of the

macroalgae. Additionally, cycles of periodic loss and reappearance are known to occur in *C. fastigiata,* but the timing is unknown (Jompa and McCook, 2003). As the mortality rate was higher in the RCP2.6 scenario, temperature and $CO_2$ increase might have affected algal health and led to a die-off. However, measurements are hardly comparable between treatments, as time in treatment differed between minimum 13 days and maximum 22 days, due to the mortality. Furthermore, only 9 corals in the ambient and 7 corals in the RCP2.6 treatment had an algal partner at the end of the study. Despite the early die off of macroalgae, we still measured their effects on corals, which, however, might have been more visible in the absence of algal mortality, especially in the RCP2.6 scenario, where macroalgae died relatively early in the experiment.

## 5. Conclusions

*P. lobata* has a 'massive 'coral morphology, and has previously been shown to be less affected by the interaction with competing macroalgae compared to other coral species. The negative impact of *C. fastigiata* was only visible in the decrease of the P:R ratio, but the study shows no enhanced impact under RCP2.6 conditions. The energy budget of the coral in this study, however, was very likely negatively influenced by RCP2.6 scenario conditions. Calcification, which is directly linked to the aragonite saturation, was probably negatively affected by the increase in $CO_2$ as shown in earlier studies. We hypothesize that the productivity of zooxanthellae might be enhanced under the RCP2.6 scenario due to elevated $CO_2$ availability ($CO_2$ fertilization effect), leading to an increase of chlorophyll *a*. The coral host, however, was rather stressed, resulting in higher respiration and decreased calcification.

*C. fastigiata* is known for its strong allelopathy, but also very sensitive under experimental conditions. While the impacts of the algae on the coral were small, a temperature and $CO_2$ increase of more than 1 °C and 85 ppm respectively over longer periods, whether due to global warming or warm water periods (e.g. El Niño), might have significant impacts on coral-macroalgal interactions. Hence, further studies with less sensitive macroalgae are needed to investigate the likelihood of interaction shifts for *P. lobata* under future climatic regimes.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151477.

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