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ORIGINAL PAPER

Differential responses in recovery, growth and survival between intertidal and subtidal corals after acute thermal stress

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Abstract

Sea temperature increases may compromise ecological restoration as a tool for recovering degraded coral reefs. A potential solution may lay within using corals with naturally higher thermal resilience, such as intertidal corals. This study aimed at comparing thermal resilience, growth and survival between intertidal and subtidal corals in a reciprocal transplant experiment. Sixty coral nurseries were installed in a shallow coral reef area in Kenya: half were placed in the intertidal zone and half in the subtidal zone. At both zones, intertidal and subtidal *Pocillopora cf. damicornis* coral fragments were cultured in equal proportions, resulting in 15 replicate nurseries for four treatments. After an initial culture phase of 1 month in situ, six nurseries per treatment were thermally stressed ex situ by exposing corals for 5 days to a temperature of 32 °C (3 °C above summer maximum), after which they were returned in situ to recover. Fragment brightness was measured as the response variable to thermal stress. Intertidal and subtidal corals increased brightness (i.e., bleached) at a similar rate, but during recovery intertidal corals returned quicker to their original brightness in both culture environments. Coral growth was highest for intertidal corals in the intertidal zone during cooler months and was highest for subtidal corals in the subtidal zone during peak temperatures. Intertidal corals transplanted to the subtidal zone registered the lowest survival. Thus, intertidal corals display higher thermal resilience through quicker recovery, but potential trade-offs require further investigation before these corals can be used as a climate-proof broodstock for reef restoration.

Keywords Climate change · Coral bleaching · Coral gardening · Coral reef restoration · Heat stress · *Pocillopora damicornis* · Thermal resilience · Trade-offs

Introduction

Contemporary increases in ocean temperatures and heat wave frequency and intensity have been major causes for coral reef degradation worldwide (Hughes et al. 2018). In face of persisting temperatures that are 1–2 °C higher than local maximum summer averages, corals are prone to bleach (Glynn 1991). When corals bleach, they lose the symbiotic algae that provide most of the energy they require (Muscatine and Hand 1958). Bleached corals expose their bright calcium carbonate skeletons through a thin layer of translucent coral tissue, display reduced metabolism, growth and fecundity and are vulnerable to starvation, diseases and competitors: a fragile state that can often lead to death (Glynn 1983; Hoegh-Guldberg 1999; Jokiel and Coles 1990). This phenomenon has been increasing in severity in recent years, causing widespread coral cover declines in all three major ocean basins (Hughes et al. 2017a, b). Thermal bleaching is a large threat to reef recovery and should therefore be taken into consideration when designing strategies for conservation and reef restoration (Boström-Einarsson et al. 2020).

Current reef restoration is mostly done through coral gardening, an approach where coral fragments are first grown in nurseries and then out planted onto degraded reef areas (Rinkevich 1995). This approach has proven quite effective in culturing a large number of coral species and transplantation of cultured fragments (Hein et al. 2021; Rinkevich

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2019; Vaughan 2021). However, these cultured and outplanted corals are still prone to bleaching in the face of further temperature increases (Edwards et al. 2010; Vaughan 2021). Thus, to ensure a future for reef restoration it has become necessary to look for methods to produce corals that can face the current and foreseen increases in ocean temperatures (Rinkevich 2014; Van Oppen et al. 2015). Recently, a breakthrough has been reported in establishing thermo-resilient corals through a combination of selective breeding and assisted evolution (Buerger et al. 2020; Quigley and van Oppen 2022). Although very promising, these techniques may not be readily available for large-scale application worldwide. An alternative approach is to obtain thermo-resilient broodstocks by culturing corals that are naturally thermal resilient (Rinkevich 2019; Caruso et al. 2021).

Corals with a naturally superior thermal resilience can be found in environments where they are daily exposed to highly variable conditions, such as reef flats or back reef areas (Oliver and Palumbi 2011; Schoepf et al. 2015). These shallow habitats are heavily influenced by the daily tidal variations and the inhabiting corals can face periods of air exposure during spring low tide (Rivest et al. 2017). Surviving in these areas exposes corals to intense and stressing regimes of multiple abiotic factors for short periods of time, which allows them to develop a naturally higher resilience to extreme environmental conditions (Richards et al. 2015; Camp et al. 2018; Safaie et al. 2018). Particularly, the exposure to high and variable temperature regimes has been shown to improve the capacity of the corals to resist (Middlebrook et al. 2008; Bellantuono et al. 2012; Bay and Palumbi 2015) and recover from thermal stress (Schoepf et al. 2020; Jung and Schoepf 2021; Speelman et al. 2023).

The variable conditions felt in these extreme environments is contrasting with what most corals experience (Schoepf et al., 2023). Being commonly found in the reef slope area and submerged during high and low tides, most corals thrive under more stable and mild conditions (Whitfield and Elliott 2011). The stable subtidal conditions make these corals more sensitive to higher temperatures and less thermally resilient (Safaie et al. 2018). As coral mariculture practices usually target subtidal habitats for restoration, a key question is whether corals from thermally variable environments are able to keep their superior thermal resilience when transplanted to milder conditions (Rivest et al. 2017). Various findings have been reported in this respect. Corals from environments with warm and variable conditions that were transplanted to cooler and stable regimes kept their superior thermal resistance (Palumbi et al. 2014; Morikawa and Palumbi 2019; Schoepf et al. 2019), even though there was a reduction in bleaching resistance when compared to corals from the high and variable temperature regimes that stayed in their native habitat (Palumbi et al. 2014). On the other hand, corals from stable environments that were transported to variable and warmer conditions were reported to increase (Palumbi et al. 2014; Thomas et al. 2018) or keep (Barshis et al. 2018; Klepac and Barshis 2020; Barott et al. 2021) their natural thermal resistance, depending on whether these corals were branching or massive forms, respectively. Furthermore, corals may show decreased survival and growth when transplanted to new environments (Howells et al. 2013). Given the variation in retention of thermal resilience and the potential of associated trade-offs, site and species-specific evaluations of thermal resilience and coral performance remain crucial to determine the potential of using corals from extreme environments for reef restoration.

The aim of this study was to evaluate the possibility to use corals from a lower littoral area with a variable temperature regime (hereafter referred to as "intertidal zone") as a thermo-resilient broodstock for active reef restoration in Kenya. The study focused on the coral *Pocillopora cf. damicornis* (hereafter referred to as *P. damicornis*). The first objective was to assess whether intertidal corals were more resilient to heat stress when compared to their conspecifics from the subtidal zone and how the culture in different environments would affect their thermal resilience. To do so, intertidal and subtidal *P. damicornis* corals were exposed to a short and acute heat wave to mimic a thermal stress scenario that induced bleaching, similarly to the "classic" experiment described by (Voolstra et al. 2020). After exposure to heat, corals were allowed to recover and their responses to and after thermal stress were compared. The second objective of this study was to assess whether intertidal corals could be cultured under subtidal conditions and vice versa, which was investigated through a reciprocal transplantation experiment and by assessing the growth rates and percentage of living tissue of coral fragments through time.

Materials and methods

Study area

This study was conducted between October 2019 and March 2020 in Shimoni, Kenya, focusing on the patchy coral reefs on the coastal side of Shimoni (Fig. 1).

The area is characterized by a semidiurnal tidal regime, with a tidal range between 0.1 m (LAT - Lowest Astronomical Tide: Elevation of the lowest tide expected to occur at site under average meteorological conditions (NOAA 2020) to 4.1 m (HAT - Highest Astronomical Tide: Elevation of the highest tide expected to occur at a site under average meteorological conditions (NOAA 2020) (KPA 2020). The climate is influenced by two alternating seasons: the southern and northern monsoons. From November to March the

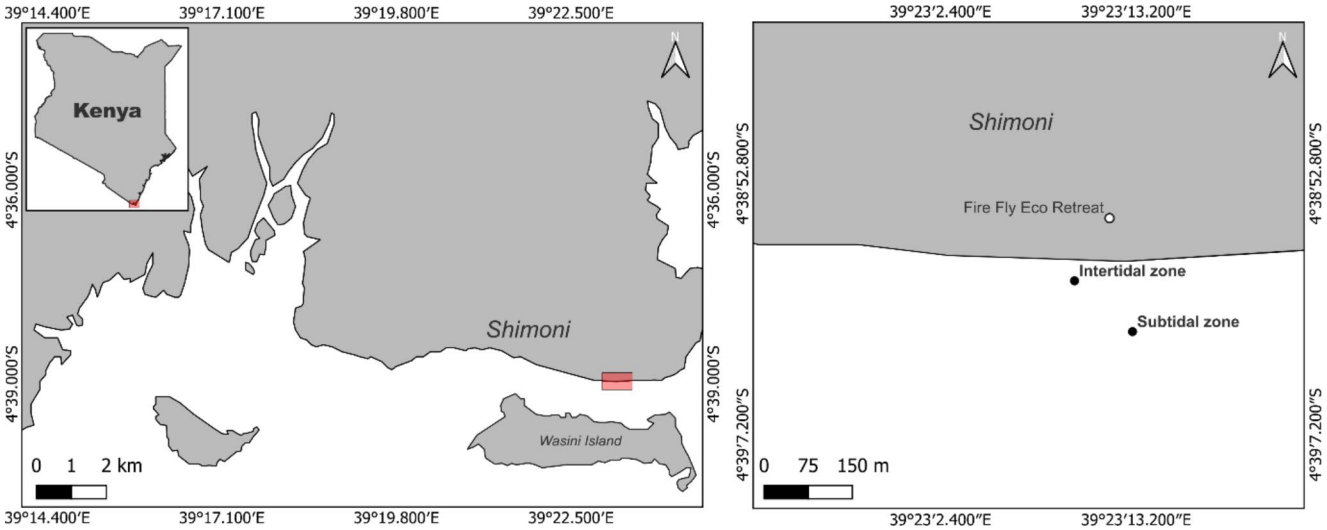

Fig. 1 Study location site. Left – Map of Shimoni in relation to Kenya. Right – Studied intertidal and subtidal zones. Maps created with © 2023 QGIS version 3.32.1

NE monsoon is the prevailing wind and is associated with the southern hemisphere summer, or dry season. From April to May comes the rainy season. From June to October there is a complete reversal in wind direction and the SE monsoon wind prevails, associated with the southern hemisphere winter (Richmond 2002). According to the National Oceanic and Atmospheric Administration (NOAA), during the course of this study the daily sea surface temperature varied on average between 26.9 and 30 °C in the study region (Fig. S1) (NOAA 2022).

An intertidal (4°38’58.7"S 39°23’09.8"E) and a subtidal (4°39’01.5"S 39°23’13.0"E) zone were studied. HOBO Pendant UA-002-08 loggers were placed between February and March 2020 in both zones to register temperature (Fig. S2) and light intensity (Fig. S3). Light intensity was measured in Lux and converted to PAR (Valiela, 1984). The intertidal zone registered a high daily temperature variability with a daily average of 30.3 °C, minimum average temperatures during dark hours registering 28.0 °C and maximum values during light hours reaching 32.5 °C. The intertidal reef was patchy and characterized by a low number of coral species, where most specimens developed wide, short and thick colonies. Among these coral colonies it was common to find coral rubble, macroalgae and sea urchins. Additionally, small reef fishes (e.g. families Labridae, Pomacentridae and Ostraciidae) were present with a high incidence of juveniles. The most abundant coral species were massive corals, namely *Porites spp*., *Pavona spp*., *Dipsastraea spp*., *Favites spp.* and *Galaxea spp*., but branching forms were also present, namely *Pocillopora spp.* and *Stylophora spp*. During spring low tides, some corals would experience air exposure for maximum 1 h.

The subtidal zone registered more stable temperature regimes and a daily average temperature of 30.0 °C, with average minimum temperatures during dark hours registering 28.0 °C and maximum average temperatures during light hours reaching 31.0 °C. The subtidal reef had a higher abundance of coral species, with seagrass meadows interspersed between coral patches. Sea urchins were also common in this area and there were more fish species (other than the families mentioned above, e.g. Acanthuridae, Chaetodontidae, Diodontidae, Pomacanthidae, Scarinae, Scorpaenidae, Serranidae, Siganidae, Tetratodontidae and Zanclidae) and a higher proportion of adult individuals. Other than the aforementioned coral species, in the subtidal zone it was also possible to find more branching species such as *Acropora spp.* and *Seriatopora spp.* as well as other massive species belonging to the family Faviidae. The reef-building hydrozoan *Millepora spp.* and the feather hydroid *Aglaophenia spp.* were also commonly found. See Knoester et al. (2022) for additional details on this subtidal reef.

Experimental design

Experimental units

P. damicornis coral fragments (Fig. S4) were cultured in small coral nurseries that contained eight fragments each (mean length ± SD = 4.2 cm ± 0.7, $n = 480$), collected from either the intertidal or the subtidal zone. Each nursery was considered an experimental unit. Nurseries consisted of PVC pipes mounted onto 1.5-L glass bottles that were anchored into a round concrete disk of 40 cm in diameter. Four plastic PVC pipes were welded in a cross shape: two measuring

22 cm and two measuring 26 cm, connected to each other and to the bottle by T-joints. One of the joints was screwed on the opening of the bottle and tightly secured with tie wraps. Per PVC pipe, two coral fragments were hung in a slipknot made with a fishing line with 12 cm between the two fragments (Fig. S5).

Corals from the intertidal zone were collected from depths between − 1.42 to -0.15 m and corals from the subtidal zone between 0.66 and 1.67 m, all depth values with reference to MLLW (Mean Lower Low Water: Average elevation of the lowest tide recorded at a site under average meteorological conditions (NOAA 2020). No more than three fragments were collected from the same colony to ensure that the cultures were genetically diverse and to avoid over-harvesting of donor colonies. Fragments from the same environment were pooled together before being used to fill nurseries, thereby mixing donor colonies randomly across the experiment. Coral fragment collection and nursery filling occurred simultaneously from 14th until 17th October 2019. A graphic timeline summarizing all steps of this study is available in Fig. S6. In total, 480 coral fragments were collected and 60 nurseries were constructed and deployed, half in the subtidal zone and the other half in the intertidal zone, with adjacent structures separated by 1 m. Nurseries were placed adjacently (within 20 m) to donor coral colonies. Thus, four different treatments were prepared (Fig. 2) ($n = 15$ each), of which two control treatments: intertidal corals cultured in the intertidal zone (intint) and subtidal corals cultured in subtidal zone (subsub) and two transplant treatments: intertidal corals cultured in the subtidal zone (intsub) and subtidal corals cultured in the intertidal zone (subint).

Acute thermal stress response and recovery

Twenty-four nurseries (six nurseries per treatment) containing eight coral fragments each were exposed to an acute thermal stress. The remaining thirty-six nurseries (nine nurseries per treatment) were kept in the culture environment as control without receiving thermal stress. No additional nurseries were subjected to thermal stress due to time constraints. An outdoors ex-situ setup (Fig. S7) was prepared at the Pilli Pipa dive base at Fire Fly Eco Retreat in Shimoni, Kenya. Six light-blue plastic basins were filled with approximately 65 L of natural seawater and each was equipped with a Dophin WP3000 Wave Pump to maintain water movement and a Sunsun 300-Watt submersible heater to control the temperature. The basins were covered by a

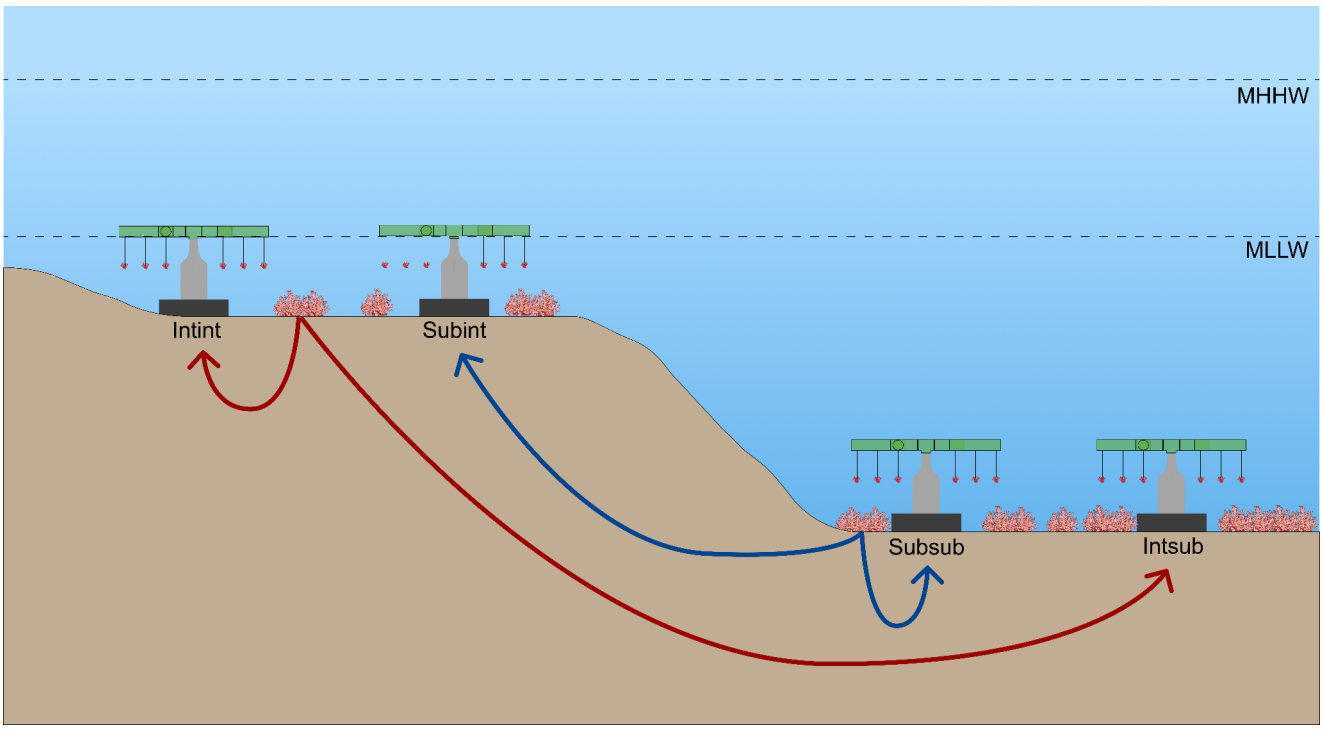

Fig. 2 Schematic diagram of the four treatments prepared for the reciprocal transplant experiment. Per treatment the corals in 6 structures were thermally stressed. Red arrows indicate the direction of transplant of intertidal originated corals and blue arrows indicate the direction of transplant of subtidal originated corals. Treatments ($n = 15$): Intint – intertidal corals cultured in the intertidal zone. Intsub – intertidal corals cultured in the subtidal zone. Subint – subtidal corals cultured in the intertidal zone. Subsub – subtidal corals cultured in the subtidal zone. MHHW – Mean Higher High Water: Average elevation of the highest tide recorded at a site under average meteorological conditions. MLLW – Mean Lower Low Water: Average elevation of the lowest tide recorded at a site under average meteorological conditions (NOAA 2020). Model created with © 2024 Figma Desktop App version 124.0.2

small mesh mosquito net so they would not be affected by debris falling from nearby trees. For additional protection against direct sunlight, wind and rainfall, an overlaying canvas was placed above the basins. No artificial light was supplied to the coral fragments, but the overlaying canvas allowed for indirect sunlight to enter from the sides. Light intensity on the basis was generally lower than the values registered on the natural culture environment but reached similar values with the subtidal zone during cloudy days (Fig. S8). No flow through or water exchange occurred while the corals were kept in the basins, but water flow was induced with an aquarium wave pump. Water temperature was monitored with a DIGIFLEX digital fish aquarium thermometer.

Corals had been in culture in the nurseries for approximately one month in situ before being thermally stressed ex situ. The thermal stress procedure began by setting the water temperature in the basins at ambient temperature in the nursery area (27–28 °C). The PVC crosses with coral fragments were unscrewed from the in situ bottle nursery and transported to the ex situ basins so that each basin contained one PVC cross with eight fragments. A series of incubations was done sequentially (i.e. four series of six incubations within a month) and per incubation all corals shared the same culture environment, but half were originated from the intertidal zone and the other half from the subtidal zone. After 24 h of acclimatization to the water in the basins, the temperature was increased at a rate of 0.5–1 °C per hour until it reached 32 °C. The coral fragments were kept at this temperature for five days. Pictures of fragments were taken daily using a Nikon Coolpix W300, approximately at 1600 h, to track the progress of fragment brightness increment induced by thermal stress. Hence, fragment brightness was used as indicator for the coral bleaching response to the applied acute thermal stress.

After the five-day period of exposure to 32 °C, the heaters were turned off so the water could cool down for 24 h. The PVC crosses with coral fragments were then transported back to the in-situ culture settings so they could start to recover. Pictures of the recovering coral fragments were taken every other day for a period of two weeks. Between consecutive incubations, the basins were cleaned and water was changed.

Additional control treatments (hereafter referred to as "ex-situ control") were run to understand whether the conditions of the ex-situ setup alone were affecting coral coloration. Two additional PVC crosses were filled with intertidal and subtidal corals, collected separately from the ones used in the experimental design, as these were intended for subsequent studies. Each cross was placed in a seawater filled basin where the water was kept at ambient temperature for five days. The coloration of these coral fragments while on the ex-situ setup was studied by following the same procedure as described above but it was not assessed during the recovery period, as no changes in colour were observed.

Measurements and data preparation

Coral fragment brightness

ImageJ software version 1.52 (Ferreira and Rasband 2012) was used to quantify brightness by estimating the pixel intensity of each picture. Pixel intensity is measured in bits per pixel (bpp) and describes brightness from 0 (black) to 255 (white), averaged across red, green and blue channels. (Ferreira and Rasband 2012). This method is based on the relation between coral colour and chlorophyll content, where a healthy coral with darker coloration is expected to have higher chlorophyll density than a stressed coral with lighter colours (Winters et al. 2009).

The average brightness of each coral fragments was obtained by using the "Polygon selections" tool on ImageJ, which allows to manually select the whole area of a coral fragment. Then, the "mean grey value" of each selected area was measured to obtain the brightness value on each coral fragment (Chow et al. 2016; Mclachlan et al., 2021). To account for natural variations in light, all pictures used to track brightness during the acute thermal stress trials were taken with a coral health chart from the University of Queensland as colour reference (Siebeck et al. 2006). On the first day that pictures were taken, one of the squares from the health chart (D4) was selected to be the colour reference and its brightness value was quantified as described above. On subsequent measurements, a new assessment of brightness of the same square was done. The reference value obtained on the first day would then be divided by the value obtained on successive measurements. The result would be multiplied by the brightness value obtained from each coral fragment to obtain the final coral fragment brightness value:

$$Coral\ fragment\ brightness = Polygon\ selection\ value \times \frac{Reference\ colour\ square\ value}{Colour\ quare\ value}$$

Coral growth and live tissue cover

Additional pictures of each coral fragment under in situ conditions were taken in October 2019, December 2019 and March 2020 to measure growth rates and the percentage of live tissue cover. Growth rates were calculated for the October – December and December – March periods to account for the environmental differences due to seasonal

temperature increases. Maximum length (l), maximum width (w_1) and perpendicular width (w_2) were determined for all coral fragments in the beginning (t_0) and end (t_1), of both periods using a ruler and ImageJ. With this data, Ecological Volume (EV) in cm^3 – the total volume of coral fragment and water between branches – was calculated for t_0 and t_1. From these EV values, Specific Growth Rate (SGR) was obtained for each fragment (Knoester et al. 2019):

$$EV = \pi \left(\frac{w_1 + w_2}{4}\right)^2 \times l$$

$$SGR/d = ln\left(\frac{EV_{t_1}}{EV_{t_0}}\right) / (t_1 - t_0)$$

Live tissue cover was assessed for the October 2019 – March 2020 period, since no seasonal differences were verified for these measurements. Live tissue cover was assessed as a measure of coral fragment condition and was calculated by dividing the percentage of living tissue visually estimated at the end of the experiment by the percentage of live tissue estimated in the beginning.

Data analysis

Data on each coral fragment for brightness, growth and live tissue cover were averaged per nursery tree so that each nursery was considered an independent replicate to avoid pseudo-replication. All data was analysed with RStudio software version 2023.9.1.494 (Posit team 2023). In all statistical analyses, the assumptions of normality and homogeneity of variances were confirmed by plotting the residuals against fitted values in QQ plots and scatterplots, respectively.

During the initial thermal stress trials, the stress provided was too intense - a rate of temperature increase higher than 1 °C per hour until 32 °C were reached - for the coral fragments in ten nurseries (5/15 nurseries for both intsub and subsub treatments) and these were not able to survive. This procedure was not further used and it was adjusted as described in the materials & methods section. To maintain a balanced dataset for growth and live tissue cover analysis, these structures were filled with replacement coral fragments from the same environment. Data from the coral fragments on the nurseries that did not survive the first thermal stress trials was not further used. The replacement corals were integrated in the control pool and were not subjected to acute thermal stress. As the replacement corals were only added on the 4th of December, only 4/15 nurseries could be used to assess growth in intsub and subsub treatments during the October – December 2019 period. From December onwards, all four treatments had again 9/15 control nurseries (see also the timeline in Fig. S6). Throughout the whole experiment, the number of nurseries for the acute thermal stress response were constantly 6/15.

Coral brightness differences

Differences in coral brightness caused by the different culture settings alone were assessed through the brightness values registered in the different treatments after one month in culture and prior to any temperature increase by performing a One-way ANOVA followed by a Tukey's post-hoc.

To assess for differences on how coral brightness changed over time, Linear Mixed Models obtained from the lnme package (Pinheiro et al. 2023) were used. Two separate models were prepared, one to analyse the response to acute thermal stress and another for recovery. In both models the significance of the fixed effects was assessed with an ANOVA and no post-hoc analysis was required. Furthermore, in both models data was transformed with the natural logarithm to deal with positive skews. Coral fragment brightness was considered the response variable. For the analysis on response to thermal stress, 6/15 nurseries were analysed for all treatments, so that $n = 6$. The fixed effects of the model were considered the interaction between treatment (intint, intsub, subsub and subint) and time (number of days in thermal stress 1–5). The random effects were considered the interaction between nursery, time and series (1–4, where 1 is referent to the first nurseries being thermally stressed and 4 the last structures being thermally stressed), as the brightness values associated with each nursery were expected to vary differently with time. To assess for differences in the ex-situ control treatments, an additional Linear Mixed Model was applied, following the same method as described above, but by using origin (intertidal and subtidal) interacting with time for the fixed effects portion of the model and without integrating the series component. Additionally, since the two treatments were represented by only one nursery, differences were assessed by comparing the brightness values between the eight coral fragments of each treatment, so that $n = 8$.

For the recovery from acute thermal stress analysis, the differences in response were assessed between the different origins of the corals (intertidal and subtidal) and not according with the different treatments. Due to time constraints, it was not possible to gather a balanced dataset for recovery on all coral treatments and there was an underrepresentation of treatments for the entire 13-day recovery period. Particularly, for the treatments intsub and subsub there is no data available from the 7th day of recovery onwards. For the recovery analysis 12/30 nurseries were analysed for each origin, so that $n = 12$. The differences in recovery from acute thermal stress with time were assessed as described above.

The considered fixed effects were the interaction between origin and time (number of days in recovery 1, 3, 5, 7, 9, 11, 13). The random effects were the same as for the thermal stress response model.

Coral growth and live tissue cover

Growth rate and live tissue cover were analysed separately for fragments that did and did not receive the heat shock treatment. For fragments not receiving the heat shock (i.e., unstressed), differences in growth rate in the different treatments for the periods October – December 2019 (57 days) and December 2019 – March 2020 (92 days) were assessed by performing a One-way ANOVA followed by a Tukey's post hoc for each period. Since 5/15 structures for the treatments intsub and subsub had to be replaced and 6/15 nurseries were thermally stressed, only 4/15 nurseries could be used for these treatments to estimate growth during the period October – December 2019, so that $n=4$, whereas for the treatments subint and intint 9/15 nurseries were available for growth analysis during this period, so that $n=9$. For the December 2019 – March 2020 period. The growth rate of fragments that had been thermally stressed were analysed for the period December 2019 – March 2020 (i.e., after the thermal stress) and potential differences were assessed as mentioned above. As 6/15 nurseries per treatment were thermally stressed, $n=6$ was used for this analysis. Growth data in stressed fragments was transformed with the square root since it was negatively skewed.

Differences in live tissue cover were assessed with the same tests for the full period October 2019 – March 2020. Data in both measurements was transformed with arcsin since it was negatively skewed. Since this analysis included the full duration of this study, it was possible to use the data from 9/15 nurseries that were not thermally stressed, so that $n=9$ on all treatments.

Results

Acute thermal stress and recovery

Differences in brightness of coral fragments before any thermal stress were detected between treatments (ANOVA, F (3,20) = 8.96, $P<0.001$; Fig. S9; Table S1). When cultured in their place of origin, intertidal and subtidal corals display almost identical values for brightness. However, when transplanted to a different setting than their original one, intertidal corals cultured in the subtidal zone became brighter, displaying a significant difference with the control intertidal treatment (Tukey HSD, t = 0.41, $P=0.02$; Table S2).

Change in brightness during the five-day exposure to thermal stress were not significantly different among treatments over time (ANOVA, F (12,74) = 1.044, $P=0.419$; Fig. 3; Table S3).

The ex-situ control treatments revealed no significant differences in brightness between coral fragments with different origins over time (ANOVA, F (4,35) = 2.214, $P=0.088$; Table S5).

Changes in brightness during the thirteen-day recovery period revealed a significant difference among origins over time (ANOVA, F (6,57) = 2.401, $P=0.039$; Fig. 4; Table S6). Intertidal coral brightness decreased again while subtidal corals continued to become brighter. Brightness in intertidal corals started to consistently decrease after the third recovery day. On the other hand, the brightness of subtidal corals kept increasing until nine days after the heat shock. Recovery has also been plotted according to the different treatments and can be consulted on Fig. S10 and Table S7.

Coral growth and live tissue cover

Significant differences were verified in growth among unstressed coral treatments for the October – December period (ANOVA, F (3,22) = 3.871, $P=0.023$; Fig. 5; Table S9) and for the December – March period (ANOVA, F (3,32) = 4.402, $P=0.011$; Fig. 6; Table S10).

In unstressed coral fragments, a trend was visible during the first growth period for higher growth of control intertidal corals compared to control subtidal corals (Tukey HSD, t = −0.004, $P=0.09$; Table S11). Whereas for the second period, intertidal corals had a significantly lower growth rate than subtidal corals, when both were cultured in their place of origin (Tukey HSD, t = 0.005, $P=0.026$; Table S12). The intertidal corals that were transplanted to the subtidal zone started by showing a significant decrease in growth during the October – December growth period, when compared with the control intertidal treatment (Tukey HSD, t = −0.005, $P=0.036$; Table S11) but these treatments featured similar growth rate in the December – March period (Table S12). Conversely, the subtidal corals moved to the intertidal zone did not present a significant difference with the control subtidal treatment at first (Tukey HSD, t = −0.003, $P=0.415$; Table S11) but displayed a marked decrease for the latter growth period (Tukey HSD, t = 0.006, $P=0.014$; Table S12).

Significant differences in growth rate were verified for the heat-stressed coral fragments for the December 2019 – March 2020 period (ANOVA, F (3,19) = 5.623, $P=0.006$; Fig. 7; Table S13). A clear difference in growth rates can be seen between corals with an intertidal origin and corals with a subtidal origin, where intertidal corals display higher

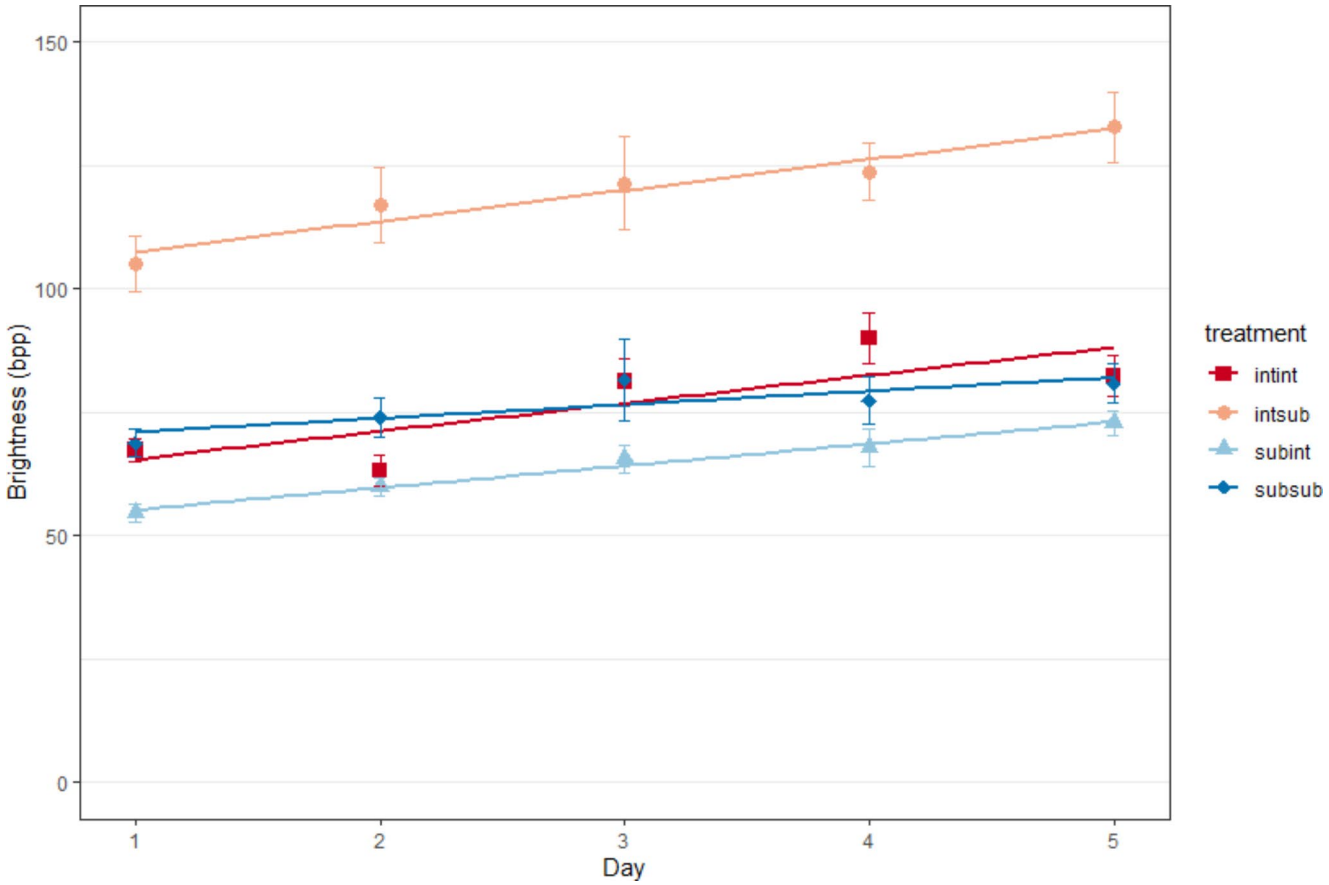

Fig. 3 Average brightness of *Pocillopora cf. damicornis* coral fragments per treatment during the five-day acute thermal stress at 32˚C. Treatments ($n=6$): intint – intertidal corals cultured in the intertidal zone. intsub – intertidal corals cultured in the subtidal zone. subint – subtidal corals cultured in the intertidal zone. subsub – subtidal corals cultured in the subtidal zone. Brightness is measured in bits per pixel (bpp) and ranges from 0 (black) to 255 bpp (white). Bars represent mean ± 2 Standard Error. Information on trend lines is present on Table S4

growth rates after being thermally stressed regardless of the culture environment (Table S14).

Significant differences among treatments were verified for live tissue cover (ANOVA, F (3,31) = 11.07, $P<0.001$; Fig. 8; Table S15) in the October 2019 – March 2020 period for unstressed coral fragments. All treatments display a very similar percentage of tissue cover, except for the intsub treatment. The intertidal corals moved to the subtidal zone present remarkably low values that are significantly different with all other treatments for live tissue cover (Table S16).

No significant differences in live tissue cover were found among stressed coral fragment treatments in the December 2019 – March 2020 period (ANOVA, F (3,20) = 2.547, $P=0.0848$; Fig. S11; Table S17).

Discussion

The objective of this study was to assess the viability of using coral fragments from the intertidal zone to produce resilient cultures for reef restoration that can withstand increasing sea surface temperatures. To do so, it was assessed whether intertidal *P. damicornis* coral fragments are more resistant to and recover faster from thermal stress than their subtidal conspecifics. Also, it was explored how intertidal and subtidal coral cultures differ in growth rates and live tissue cover. Our results indicated no differences in thermal resistance, but a stronger recovery capacity of intertidal compared to subtidal coral fragments. A contrasting trend was found for growth, as the intertidal zone appeared to provide better growing conditions during the season with lower temperatures, whereas the subtidal zone seemed to be the best culture environment when temperatures are highest. Additionally, a low live tissue coverage and paling was found for intertidal corals that had been relocated to the more constant conditions of the subtidal zone. The reasons for this reduced

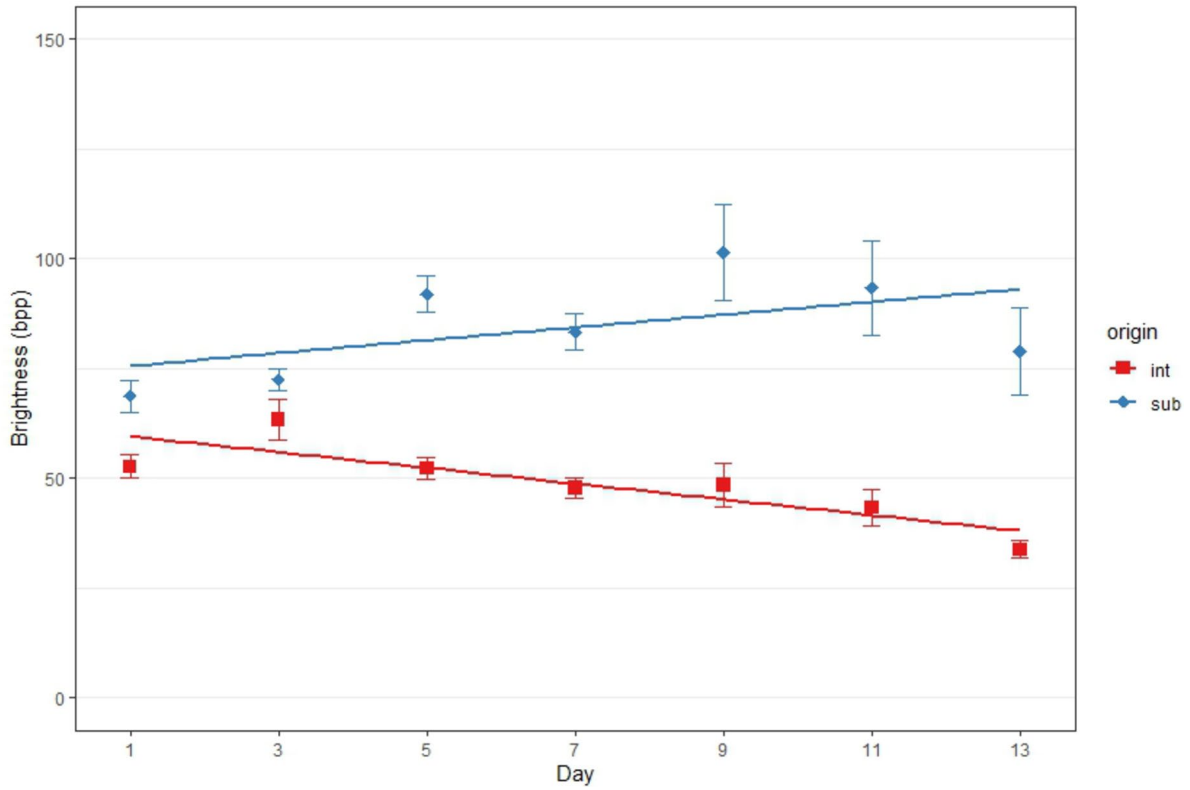

Fig. 4 Average brightness of *Pocillopora cf. damicornis* coral fragments per treatment during the 13-day recovery period at ambient temperature after a 5-day acute thermal stress. Treatments ($n = 12$ for days 1–7 and $n = 6$ for days 9–13): int – Intertidal corals. sub – Subtidal corals. Coral brightness data was averaged according to the different origins of the coral fragments, so that intsub and intint treatments compose the int origin, while subint and subsub treatments compose the sub origin. Brightness is measured in bits per pixel (bpp) and ranges from 0 (black) to 255 bpp (white). Bars represent mean ± 2 Standard Error. Information on trend lines is present on Table S8

performance of intertidal corals in the subtidal zone remain unclear and would need to be resolved in order to assess the practical usage of intertidal corals as climate proof solutions in future coral reef restoration practices.

Methodological considerations

The ex situ setup prepared for this study aimed at exploring the potential of using a short-term experiment to study the differences in thermal stress response in corals with different origins, similarly to the CBASS method but over a 5-day stress and following a 1 month acclimation versus a 6 h stress with no acclimation (Voolstra et al. 2020; Evensen et al. 2023). The thermal stress method presented in this study was attempted in 2019, before the CBASS method was published. Both methods allowed to gather rapid and exact results from direct observation on a small scale, using equipment that can easily be acquired and applied on a modest budget in remote regions. The experimental setup in this study presented a more practical and less technical solution than the CBASS method. The colour quantification method presented in this study is less biased than using different colour categories describing bleaching intensity and does not imply sacrificing coral fragments to quantify tissue thickness, zooxanthellae number or chlorophyll density. No direct comparison has been made between the method described in this study and other methods using a quantitative grey scale image calibration to calculate chlorophyll content (Chow et al. 2016; Mclachlan et al., 2021; Winters et al. 2009). However, the method presented here aimed at providing a 'rough' estimate on how chlorophyll changes in different treatments over time after an acute thermal stress, not at calculating an estimate for chlorophyll content and how this compares to other methods. The control treatments revealed no significant coloration loss for the corals kept at ambient temperature in ex situ setup conditions. Still, the method described in this study came with its limitations. A mismatch between the last day of thermal stress and the first days of recovery is visible, likely due to the photos for the thermal stress response being taken on land and the recovery photos being taken underwater and mostly in different times of the day, which may have influenced the obtained values. Further standardization of bleaching experiments and measurements will reduce such discrepancies.

The ex situ heat exposure test design applied in this study did reveal differences among subsequent in situ treatments

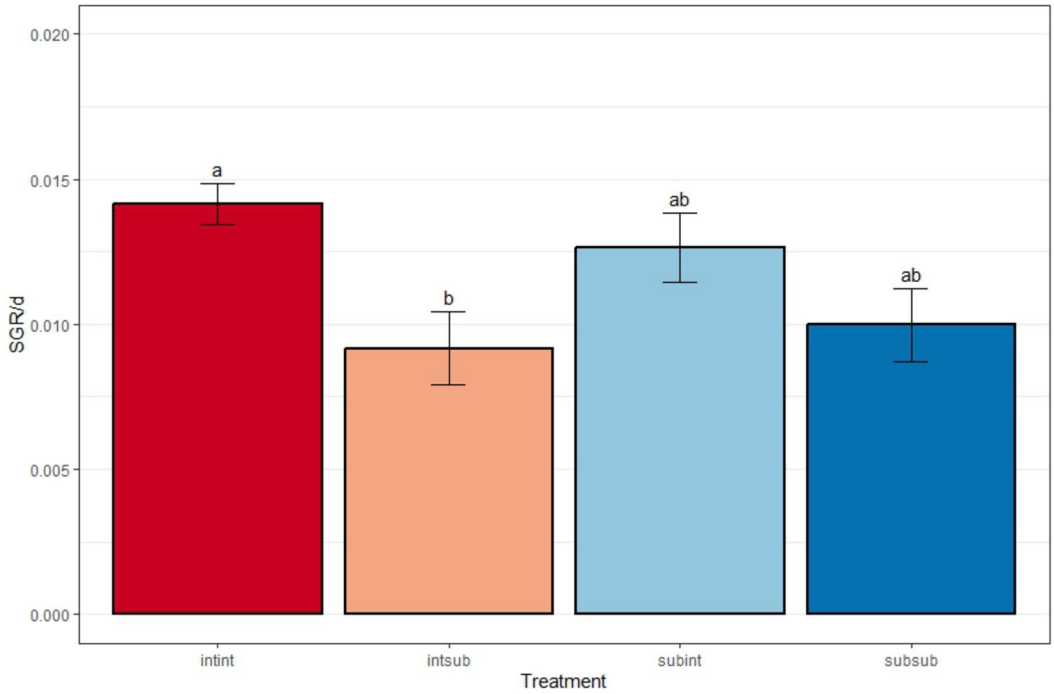

Fig. 5 Average Specific Growth Rate per day of unstressed *Pocillopora cf. damicornis* coral fragments for the period October – December 2019. Treatments: intint ($n=9$) – intertidal corals cultured in the intertidal zone. intsub ($n=4$) – intertidal corals cultured in the subtidal zone. subint ($n=9$) – subtidal corals cultured in the intertidal zone. subsub ($n=4$) – subtidal corals cultured in the subtidal zone. Bars represent mean ± 2 Standard Error. Different lower-case lettering represents significant differences between treatments ($p<0.05$)

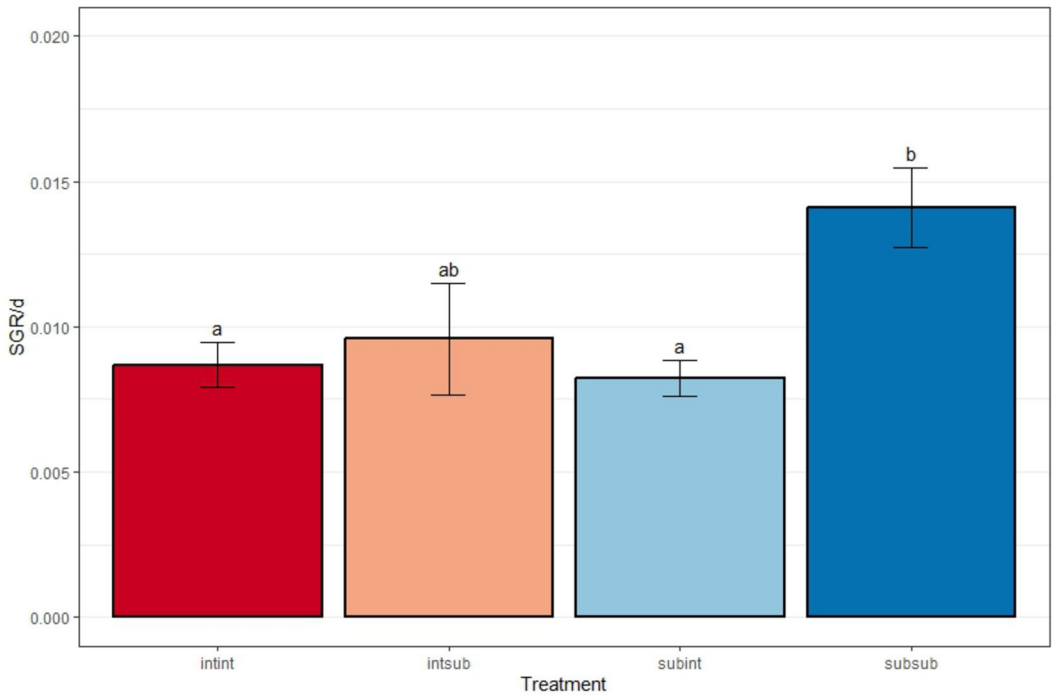

Fig. 6 Average Specific Growth Rate per day of unstressed *Pocillopora cf. damicornis* coral fragments for the period December 2019 – March 2020. Treatments ($n=9$): intint – intertidal corals cultured in the intertidal zone. intsub – intertidal corals cultured in the subtidal zone. subint – subtidal corals cultured in the intertidal zone. subsub – subtidal corals cultured in the subtidal zone. Bars represent mean ± 2 Standard Error. Different lower-case lettering represents significant differences between treatments ($p<0.05$)

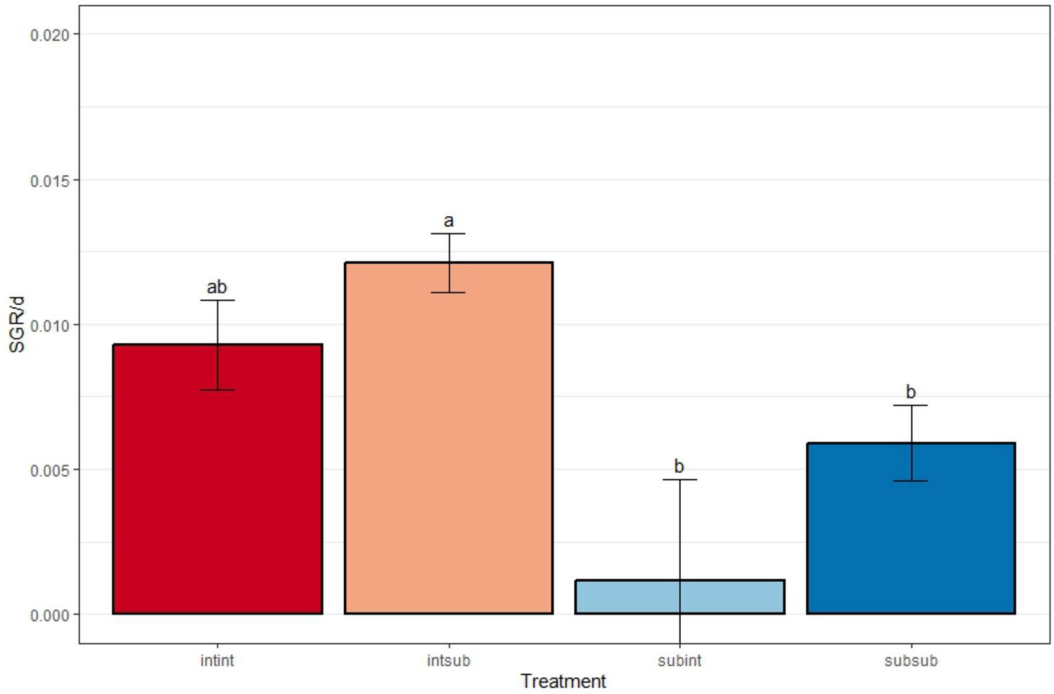

Fig. 7 Average Specific Growth Rate per day of thermally stressed *Pocillopora cf. damicornis* coral fragments between December 2019 – March 2020. The consecutive thermal stress trials started approximately 3 weeks before the fragments were measured. Treatments ($n = 6$): intint – intertidal corals cultured in the intertidal zone. intsub – intertidal corals cultured in the subtidal zone. subint – subtidal corals cultured in the intertidal zone. subsub – subtidal corals cultured in the subtidal zone. Bars represent mean ± 2 Standard Error. Different lower-case lettering represents significant differences between treatments ($p < 0.05$)

that could be related to presumed differences in thermotolerance. This promising result expresses the need for further validation of this test design. Future studies should compare the current five-day test to other heat stress tests such as the short-term (6-hour exposure) CBASS method(Voolstra et al. 2020) and longer-term heat stress assays that better resemble natural summer heat waves (Wijgerde et al. 2020). Whereas CBASS is rapid and cost-effective on a large scale, it may reflect responses to acute thermal stress rather than responses to the more gradual heat stress that typically causes coral bleaching. Classic bleaching experiments, on the other hand, require time and resources that are not always available in remote coral reef locations. The test design presented here may represent a useful intermediate approach, which is corroborated by recent work (Drury et al. 2022). In their study, a constant five-day exposure to a temperature of 3.5 °C higher than local ambient temperature caused a significant, but genotype-specific improvement in the subsequent heat tolerance in the coral *Montipora capitata*. Hence, the heat-stressed corals may exhibit a better heat tolerance after recovery than the untreated controls. This aspect will be further evaluated in a follow-up study of this current work.

Differences in resistance and recovery from thermal stress

Previous research on corals inhabiting environments with highly variable environmental conditions have attributed them a superior thermal resilience. These corals have been demonstrated to display a more moderate bleaching response (Oliver and Palumbi 2011; Kenkel et al. 2013, 2015b; Pineda et al. 2013; Palumbi et al. 2014; Schoepf et al. 2015). In the present study, intertidal and subtidal *P. damicornis* had an almost identical response to thermal stress, as they lost coloration at a similar rate during the five-day thermal stress experiment. These results suggest that the studied habitat conditions of *P. damicornis* do not affect their resistance to acute thermal stress. Morikawa and Palumbi (2019) studied the differences in response to a natural thermal stress between corals with different origins in a common culture setting. Even though they reported a significantly higher thermal resistance for corals (*Acropora gemmifera* and *Acropora hyacinthus*) from a location with more temperature variability, they too did not report significant differences among *P. damicornis* coral fragments. *P. damicornis* has been shown to be sensitive to thermal stress (McClanahan et al. 2004; Dias et al. 2019), which may hinder the capacity to distinguish different responses to

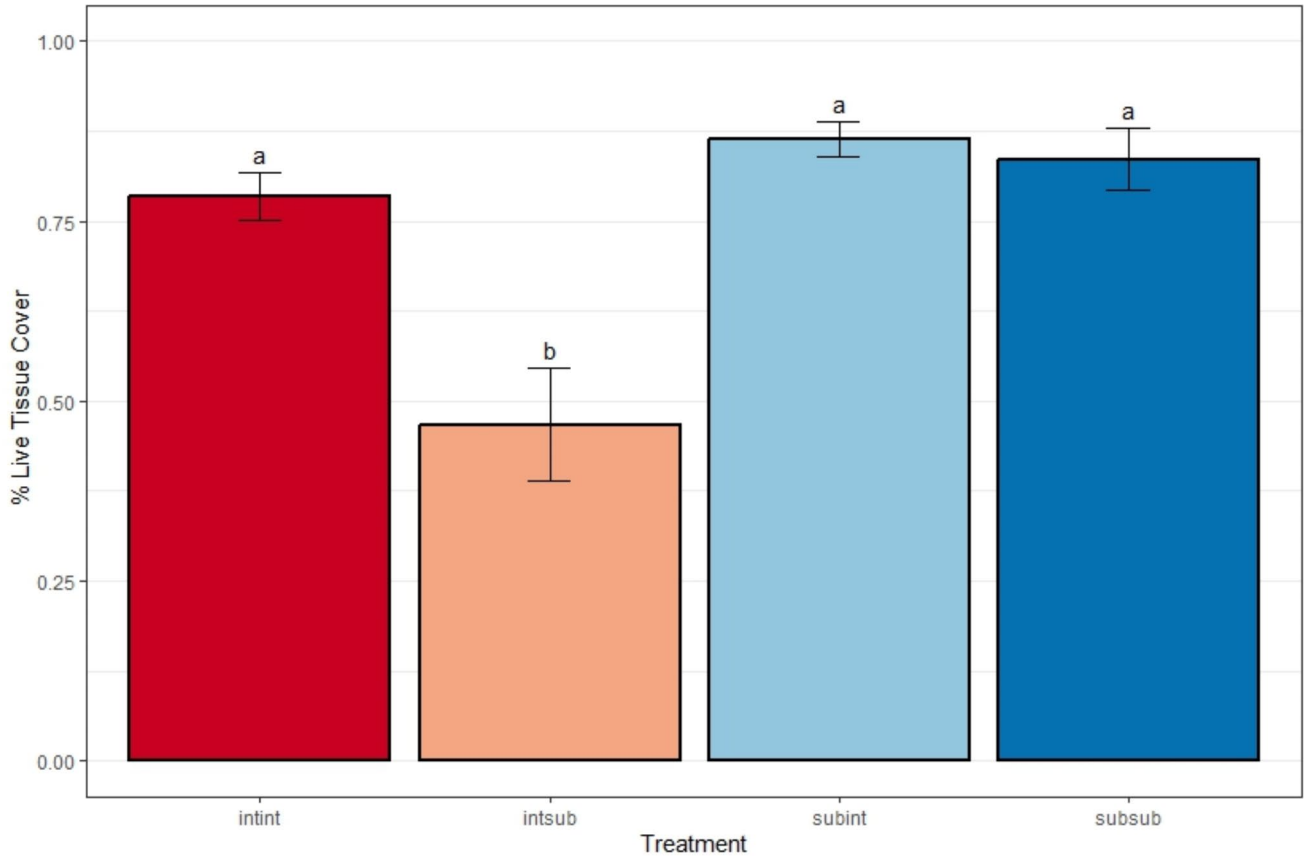

Fig. 8 Live tissue cover of unstressed *Pocillopora cf. damicornis* coral fragments between October 2019 – March 2020. Treatments ($n = 9$): intint – intertidal corals cultured in the intertidal zone. intsub – intertidal corals cultured in the subtidal zone. subint – subtidal corals cultured in the intertidal zone. subsub – subtidal corals cultured in the subtidal zone. Bars represent mean ± 2 Standard Error. Different lower-case lettering represents significant differences between treatments ($p < 0.05$)

stressful temperatures. Hence, the intensity and especially the rate of thermal stress applied in this study may have been strong enough to hide potential differences among the different *P. damicornis* coral fragment treatments. A more conservative approach to the thermal stress (Schoepf et al. 2019; Voolstra et al. 2020) or using different stress regimes, such as a pulse heat stress (Palumbi et al. 2014), may be explored to assess for different responses in *P. damicornis* coral fragments to thermal stress.

The enhanced thermal resilience of corals from highly variable environments has been supported in this study by their faster recovery capacity to a healthy state and by a faster reestablishment of a normal growth rate after being thermally stressed. The faster return to a healthy state could reflect either adaptation or acclimation to the demanding conditions in the intertidal zone. When reacting to and recovering from thermal stress, intertidal corals may exhibit differential molecular responses when compared to subtidal conspecifics, as has been reported for corals (*A. hyacinthus*) from environments with highly variable conditions (Barshis et al. 2013; Bay and Palumbi 2014). Intertidal *P. damicornis* may possess and express a higher number of beneficial alleles for highly variable conditions (Bay and Palumbi 2014). Alternatively, intertidal *P. damicornis* may exhibit an increased expression due to a faster response or a reduced expression due to an attenuated response, indicating acclimatization processes at the phenotype level (Barshis et al. 2013, 2018). Either way, a quicker reestablishment of what pre-stress gene expression levels would be, would confer intertidal corals with a higher capacity to survive successive thermal stress scenarios (Thomas et al. 2019).

The higher thermal resilience of intertidal *P. damicornis* may also be influenced by the composition of the coral microbiome. This may be verified in the identity of the zooxanthellae, as subtidal fragments may be associated with the genus *Cladocopium*, which is common in cooler and more stable environments, while intertidal fragments may be associated with *Durusdinium*, a more thermally resistant genus (Thomas et al. 2018; Manzello et al. 2019). However, no major differences in growth rates were found between corals with different origins and corals harbouring *Durusdinium* symbionts were reported to have slower growth rates

(Bay et al. 2016; Morikawa and Palumbi 2019). Alternatively, intertidal and subtidal *P. damicornis* may differ in the prokaryotic portion of their microbiome, namely in bacterial composition (Nika Alina and Rachmawati 2022). It has been shown that the bacterial community in *P. damicornis* can differ between reef slope and flat environments(van Oppen et al. 2018) and some pocilloporids are able to maintain the original bacteria community after thermal stress (Ziegler et al. 2019). Moreover, corals surviving in demanding environments have bacteria that can withstand harsh conditions without losing function (Reigel et al. 2021). To support these hypothesis, future studies on this topic should focus on the characterization of *P. damicornis* microbiome and on the differences in coral fragments with different origins.

Differences in growth rate and live tissue cover

P. damicornis growth has been reported to increase with sea surface temperature until about 27 °C, where it stabilizes and remains fairly constant until 30 °C (Anderson et al. 2017). In the current study, two growth periods were analysed, one with cooler (October – December 2019) and one with warmer temperatures (December 2019 – March 2020). Contrasting patterns in growth rates were noted between the different periods. For the period with cooler temperatures, it is visible that the intertidal corals transplanted to the subtidal zone had a marked decrease in growth rate when compared to the controls. During this period, the temperature and light conditions in the intertidal zone may have reached optimum values that allowed *P. damicornis* intertidal control fragments to grow faster without suffering physiological stress. By being exposed to milder conditions in the subtidal zone, the transplanted intertidal corals may have met sub optimal conditions which did not allow them to grow as fast as the controls. For the period with warmer temperatures, a marked decrease in growth rate happened for the subtidal corals transplanted into the intertidal zone when compared to the controls. During this period, the temperature and light conditions in the intertidal zone may have been high enough to inhibit the growth of *P. damicornis* coral fragments, which would be closer to stressful conditions. Conversely, during this period the subtidal zone may act as a buffer for the excessive temperature and light, providing the subtidal controls with the best culture conditions.

No major differences in live tissue cover were found between intertidal and subtidal corals, except for a marked low tissue cover in intertidal corals cultured in the subtidal zone. This is contrasting with results of past studies, where corals from environments with highly variable temperatures were reported to have higher survival than corals from environments with more stable temperatures, regardless of the culture environment (Bay and Palumbi 2017). Additionally, results from other reciprocal transplant studies have indicated that corals adapted to more variable conditions were able to maintain their superior thermal resilience when moved to stabler conditions without relevant fitness trade-offs (Barott et al. 2021; Marhoefer et al. 2021; Morikawa and Palumbi 2019). For the present study, intertidal *P. damicornis* corals transplanted into the subtidal zone displayed signs of cold-water bleaching (Howells et al. 2013; Schoepf et al. 2019), as indicated by their initial brighter coloration and reduced growth rate and live tissue cover. These effects may persist and affect the corals capacity to survive in the long term but may also diminish as the intertidal corals progressively acclimatize to subtidal culture conditions (Schoepf et al. 2019). This response can be due to a trade-off between enduring higher and more variable temperatures and supporting more stable and lower temperature regimes (Howells et al. 2013; Kenkel et al. 2015a). Since they are adapted to withstanding warmer and more variable temperatures, intertidal *P. damicornis* may not be able to acclimatize to stable and milder conditions, which is reflected in a markedly low percentage of live tissue cover (Baumann et al. 2021; Kenkel et al. 2015a). This low survival capacity may hinder the usage of intertidal *P. damicornis* corals in subtidal restoration efforts, as higher mortality may deem these cultures inviable even when superior thermal resilience is maintained, which is evidenced here by their faster recovery capacity and higher specific growth rate after thermal stress (Kenkel et al. 2013, 2015b). Other fitness trade-offs may also affect the long-term viability of these coral fragments and should be further studied, as changes in e.g. reproductive capacity accompanying changes in culture environment may also occur (Barott et al. 2021).

Differing environmental variables may have affected the survival of intertidal *P. damicornis* in the subtidal zone and a more thorough characterization of both culture environments would be necessary to fully understand what caused the intertidal coral fragments to have a low survival in the subtidal zone. Future studies in this topic should measure and compare between both zones not only temperature, but also other environmental factors such as UV radiation, oxygen content, salinity, pH, sedimentation, quantity of suspended particulate matter, water flow and a description of the reef community.

Conclusion

Though this study could not show that *P. damicornis* corals from an environment with more variable conditions have lower bleaching susceptibility than their conspecifics from more stable regimes, it does demonstrate that intertidal *P. damicornis* corals are more resilient than their subtidal

conspecifics due to their faster recovery capacity after being thermally stressed. Intertidal *P. damicornis* could therefore produce viable and resilient cultures and could be a solution for coral reef restoration to face higher sea surface temperatures in the near future. Nevertheless, attention should be paid to intertidal corals cultured in the subtidal zone, as the process of translocation between zones can have unforeseen negative effects on corals. Both zones need to be further characterized to understand what environmental factors may affect the long-term persistence of *P. damicornis* coral fragments.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Luís Almeida, Ewout Knoester and Ronald Osinga. The first draft of the manuscript was written by Luís Almeida and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets and code used for analysis are available as a Github repository on: https://github.com/luisalmeid/intertidal-subtidal.

Declarations

Competing interests The authors declare that the research was conducted in the absence of any commercial or financial relationships that could become a potential conflict of interest.

Ethics approval No approval of research ethics committees was required for this study. Applicable international guidelines for monitoring on coral reefs were followed. This study was performed under the research license NACOSTI/21/8896.

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