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ORIGINAL PAPER

# Mild *in situ* warming altered community structure, increased growth, and decreased survival in New Zealand subtidal encrusting ascidian and bryozoan assemblages

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## Abstract

To better understand the ecological consequences of ocean warming on marine ecosystems, experimental manipulation of ecologically relevant parameters is essential. Here, we employed short-term (3 months) *in situ* heated settlement panel experiments over four seasons to assess the effects of warming on shallow-water (3–5 m depth) encrusting invertebrate communities in a temperate marine ecosystem in New Zealand. Moderate warming (+1 °C above ambient) was generally associated with increases in growth, while the effects of greater warming (+2 °C above ambient) were more variable and seasonally dependent. Growth rates under a heatwave treatment were often reduced relative to the other heated treatments, with little difference from ambient. Notably, a non-native colonial ascidian, *Lissoclinum perforatum* emerged as the dominant species in warmed treatments, suggesting its potential to dominate future encrusting communities in this region, even after short-term warming events. For many taxa, increased growth rates did not equate with higher survival probabilities, with some species exhibiting decreased survival even under +1 °C of warming, despite enhanced growth. Spatial competition within these encrusting communities also shifted in response to warming, with reduced density and complexity observed under +2 °C of warming. Our experiment shows that even moderate warming, at temperatures already being experienced in marine ecosystems, can substantially alter growth and survival within these assemblages over short time periods and, by extension, benthic community processes and composition. Our findings highlight shifts in spatial competition dynamics that are anticipated to intensify with further ocean warming.

**Keywords** Climate change · *In situ* manipulation · Temperature · Encrusting community · Growth · Competition

## Introduction

Anthropogenic climate change has been documented as a primary driver of elevated local extinctions (Nikolaou and Katsanevakis 2023), thereby posing a substantial threat to global biodiversity and ecosystem functioning (Nikolaou and Katsanevakis 2023; IPCC 2023). This threat stems from the ability of temperature shifts to influence biological processes at multiple levels, from cellular processes to survival, growth, reproduction, and behaviour, which ultimately exert a significant impact on population dynamics (Hochachka and Somero 2002; Clarke 2017). With ocean temperatures projected to increase by over 3 °C by the end of this century, understanding community responses to warming is crucial to successfully protect marine biodiversity and manage resources (IPCC 2023; Weiskopf et al. 2020).

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The mechanisms driving community change in response to environmental shifts include direct physiological and behavioural responses, as well as indirect effects mediated by altered species interactions, such as intensified predator-prey dynamics due to increased metabolic rates (Gilman 2017; Gunderson et al. 2017). When temperatures exceed a species physiological optimum, sublethal effects often precede declines in survival potential (O'Connor et al. 2007). In addition, marine encrusting communities, which are often space-limited due to constraints on primary substrate availability (Richmond and Seed 1991), are likely to be significantly affected by ocean warming due to species-specific responses to temperature changes (Clark et al. 2019). The different temperature optima of species can drive shifts in growth and survival rates, altering competitive advantage and thereby resulting in significant compositional changes within these communities (Kroeker et al. 2013), while competitive encounters, particularly under resource-limited conditions, play a crucial role in community structure, succession, and function (Barnes and Neutel 2016; Lord 2017b). In space-limited encrusting marine communities, temperature impacts the outcome of spatial competition by influencing the ability that species have to maintain space. For example, in bryozoans, growth responses to temperature change can depend on competitive interactions within the community they occupy (Smith 2014). Changes in energy budgets in response to environmental stress will influence growth rates, reproductive success, and survival probability, while also negatively impacting the organism's ability to compete (Lord 2017b), with the outcome dependent on the timescales considered (Ashton et al. 2017; Clark et al. 2019). The differential impact of environmental shifts on the fitness of benthic species can have transitional effects throughout the wider community, leading to wide-scale changes within ecosystems (Wisz et al. 2013). For instance, the mass mortality of the foundational mussel species, *Brachidontes pharaonis*, during a heatwave led to a functional reordering of the community by disrupting filtration services, demonstrating how benthic assemblage shifts can have cascading effects on ecosystem structure and function, particularly when specific functional traits are minimised or lost (Sarà et al. 2021). Laboratory studies on warming effects are often limited in their applicability to natural systems, as growth responses to temperature can differ significantly *in situ* (Amui-Vedel et al. 2007; Ashton et al. 2017). This can be attributed to the complexity of environmental and biotic interactions within the ocean influencing species responses, resulting in growth, survival, and competitive outcomes not detected in laboratory studies. Such discrepancies highlight the need to concurrently study marine ectotherm physiological responses in natural settings, rather than laboratory experiments alone. Linking field observations of community changes with experimental temperature manipulations under realistic conditions is essential for predicting future impacts of ocean warming (Wernberg et al. 2012; Thompson et al. 2013; Bass et al. 2021). This approach is particularly relevant for species residing near their physiological threshold, as they may be at increased risk of local extinction and potential replacement by more heat-tolerant species (Sunday et al. 2012). With the observed impact of temperature on the biodiversity and function of sessile marine communities (Barnes et al. 2021; Montie and Thomsen 2023b), competition for space is predicted to intensify under modelled warming scenarios (Lancaster et al. 2017; Ladd et al. 2019; Barnes et al. 2021). However, accurate predictions are difficult to make, as spatial competition is influenced by various factors, including the timing, intensity, frequency, and type of stressor. Furthermore, the strength of interactions among species are spatially and temporally dependent (Liu and Gaines 2022). In general, heat-tolerant species are predicted to maintain physiological performance and compete more effectively under moderate warming (Diamond et al. 2017; Barnes and Neutel 2016). Hence, competition for space in encrusting communities is projected to increase under moderate levels of warming, while more extreme warming is expected to generate varied responses (Barnes and Neutel 2016; Lord et al. 2017). Shallow-water benthic encrusting communities are ideal model systems for studying the effects of climate change on marine community structure and function, due to their high rates of colonisation and sensitivity to small temperature fluctuations. Furthermore, community structure changes occur across multiple levels of biological organisation, influencing succession, development, reproductive timing, and food web processes (Cattano et al. 2020; Lennon and Sealey 2023). Besides their physiological responses to temperature fluctuations, encrusting invertebrate communities are further ideal model systems as their sessile nature facilitates standardised experimental designs through settlement panels, thereby enabling the monitoring of whole community dynamics, including succession and community development in a way rarely possible with other assemblages. In this study, we employed heated settlement panels developed by Ashton et al. (2017) to simulate ocean warming *in situ*. We assessed the growth, survival, and competitive dynamics of shallow-water (3–5 m depth) ascidian and bryozoan species across seasons under three warming treatments. The experiment was conducted under environmentally relevant warming conditions, according to current modelling forecasts based on the RCP8.5 high emission scenario (Law et al. 2018). By evaluating these processes, this study aims to enhance our understanding of how benthic encrusting communities may respond to ocean warming and, ultimately, provide essential insights for successful management and conservation of marine biodiversity in a changing climate.

## Materials and methods

### Experimental design

We deployed heated settlement panels between September 2021 and June 2022 (following Ashton et al. 2017; supplementary 1). Panels were attached to concrete pavestones (50 × 50 cm) on the seafloor of Otago Harbour (Portobello Marine Laboratory; Otago, New Zealand) at a depth of approximately 3 to 5 m (Fig. 1). Onshore-powered heated settlement panels allowed for controlled manipulation of temperature at the panel surface and the overlying boundary layer of water (Ashton et al. 2017). These panels create a uniform heated layer between 2 and 10 mm, but never smaller than 2 mm (Moffitt 2024; Supplementary 1), which is maintained under tidal flow conditions generally experienced in the Otago Harbour (mean flow of 12.8 cm s$^{-1}$). The present study focused on encrusting invertebrates which were maintained within the heated boundary layer for the duration of the experimental period.

Panels were connected to a shore-based control unit, allowing for a continuous power supply to the panels. Panels were held in place using elastic cord, with the micro-abraded settlement surface (9.8 × 9.8 cm) face down, maintaining a 2 cm gap from the pavestone surface (Fig. 1; Supplementary 1).

A total of 16 heated panels were deployed across four replicate blocks (Fig. 1b). Each replicate block consisted of a single concrete slab containing one of each experimental treatment randomly allocated to one of the four possible positions (Supplementary 1, +1 °C above ambient, +2 °C above ambient, heatwave and ambient; 16 panels total). The four replicate blocks were evenly spaced and rested against wharf pillars for the duration of the experiment (Fig. 1b). The +1 °C and +2 °C above ambient treatments were held at their respective elevated temperatures throughout the experimental period, while the ambient treatment represents our experimental control. These temperature treatments were selected based on warming predicted for New Zealand's coastal waters (Law et al. 2018; IPCC 2023). We also established a heatwave treatment in which a community was developed for a month at ambient temperatures before being subjected to a month of increasing warming (+1 °C for two weeks, followed by two weeks at +2 °C). Globally, heatwaves are characterised by a period of warming, within the 90th percentile of temperatures, that last for at least five consecutive days (Hobday et al. 2016). In Otago Harbour the historical temperature recordings and upper 90th percentiles (ranging from +0.9 °C to +1.4 °C above the long-term mean) suggest that prolonged warming of +2 °C above ambient is sufficient to simulate heatwave conditions (Table 1; Supplementary 2). Therefore, the temperature regime used here fell within the accepted definition of marine heatwaves for this region (Table 1).

Four independent deployments were undertaken over the course of a year (hereafter referred to as season) each involving the deployment of panels for three months that

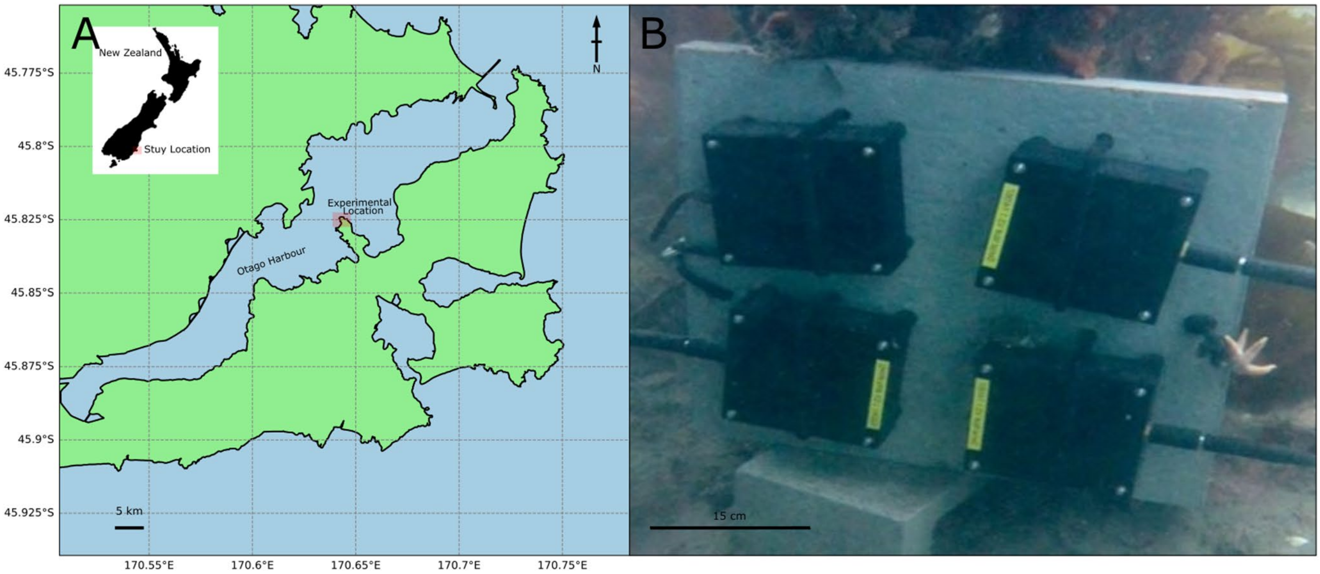


**Fig. 1** Experimental Layout: **A**) Otago Harbour map indicating the experimental location (red square, Portobello Marine Laboratory; -45°49'39.32"S, 170°38'28.24"E), and its location within New Zealand indicated in the top left corner. **B**) Experimental set-up *in situ* of one replicate block of heated-settlement panels. Heated settlement panels were evenly spaced on the concrete slab, that is positioned vertically against the marine lab wharf piling

**Table 1** Long-term average and range of sea temperatures for the experimental period (2021–2022) for each seasonal deployment period, and the long-term mean temperature and upper 90th percentile for the baseline period (1953–1980)

| | Spring | Summer | Autumn | Winter |
|---|---|---|---|---|
| Mean | 13.35 ± 2.11 | 16.9 ± 0.9 | 14.0 ± 2.1 | 8.6 ± 0.9 |
| **Minimum** | 6.4 | 14.4 | 8.9 | 6.9 |
| **Maximum** | 15.5 | 19.1 | 16.9 | 10.1 |
| **Median** | 11.2 | 16.5 | 13.5 | 8.3 |
| **95% Range** | ± 0.3 | ± 0.2 | ± 0.3 | ± 0.3 |
| **Long-term mean** | 11.4 ± 2.03 | 15.6 ± 1.5 | 12.0 ± 2.4 | 7.3 ± 1.1 |
| **Long-term upper 90th percentile** | + 1.2 | + 1.3 | + 1.4 | + 0.9 |

spanned the Austral seasons (Spring: Sep – Nov 2021, Summer: Dec 2021 – Feb 2022, Autumn: Mar – May 2022, Winter: Jun – Aug 2022). Fresh panels were deployed for each experimental period; hence newly established colonisers were examined.

Heated settlement panels were sampled monthly for the duration of the experiment using high-resolution photography. For this, individual settlement panels were brought to the surface by SCUBA divers and immediately submerged in tanks containing filtered ambient seawater. The submerged panels were photographed using a Nikon D100 DSLR camera fitted with an AF-S Nikkor macro 60 mm lens. Camera exposure settings were standardised across photographs (Aperture: 1/16; ISO: 1600; Shutter speed: 1/40; Format: RAW). Thirty-five overlapping images of each panels surface were captured using a metal sliding frame and corresponding Ikelite underwater housing. Pictures were merged into a single image of the panels surface using Adobe Photoshop (Version 23.3). The final image was cropped to the 96 mm$^2$ heated settlement region. Our methodology resulted in high image resolution, allowing for the identification of specimens as small as 0.2 mm. The photographing of settlement plates took approximately 5 min, after which panels were returned to the experimental location (with minimal air exposure, < 30 s over the entire procedure).

## Growth measurements and survival probability

We focused on responses of six target species: three bryozoans: *Calloporina angustipora*, *Disporella* sp., and *Rhynchozoon zealandicum*, and three ascidians: *Lissoclinum perforatum*, *Asterocarpa humilis*, and *Corella eumyota*. Species selection was based on the abundance and occurrence of individuals on the heated settlement panels, alongside the relative importance of their contribution to the difference in community assemblage (Moffitt 2024). Individuals or colonies were identified in 'endpoint' photos and traced back in time, with size measured using ImageJ *v* 1.53 (Schneider et al. 2012). A small number of individuals/colonies that sustained damage during handling were excluded from analyses. In addition, two bryozoan colonies showed no incremental growth between initial and final measurements. After further examination, these colonies were considered non-viable and excluded from growth analysis.

Size was based on the average surface area (mm$^2$) after three replicate measurements. Growth rate (mm$^2$ day$^{-1}$) was calculated between sampling months using the following equation:

$$growth\ rate = \frac{\Delta A}{\Delta t} = \frac{A_2 - A_1}{t_2 - t_1}$$

where $A_1$ and $A_2$ are the mean of the surface area for the relevant specimen at time point $t_1$ and $t_2$, respectively, with $\Delta t$ representing the time between measurements in days (Hoffmann and Poorter 2002; Burgess and Bueno 2021).

Survival rates were measured for the duration of the three-month experiment. Survival was determined based on the number of observed individuals of each of the target species after one month of deployment. Individuals still present in subsequent timeframe images were identified, while individuals that were no longer present were recorded as a mortality. New individuals and colonies were marked separately on each successive time point image.

## Percentage coverage and dominant space holder

The total coverage of any individual on each heated settlement panel was calculated using *ImageJ* (Schneider et al. 2012). Coverage of benthic organisms was distinguished from the background of each panel (blank space) by selecting pixels with the pixel-select tool. Each identified species was mapped with a specific colour corresponding to its species or family, indicating that the specimen had been counted. This process enabled the measurement of the area occupied by each species. The overall percentage cover on each plate was determined by setting a colour threshold that selected and measured all pixels distinct from the settlement surface. With the exact size of the settlement surface known, and standardised image capture conditions, the number of pixels per mm$^2$ was calculated, enabling the occupied area for each species to be quantified in mm$^2$. Dominant space holders on each heated settlement panel were determined by ranking species based on the area of space they occupied.

## Competitive encounters

Common metrics used to describe changes in contest competition include encounter probability, complexity, and density (Barnes and Neutel 2016; Barnes et al. 2021; Koch et al. 2023). For this study, these metrics were defined as follows:

*encounter probability* refers to the likelihood that any individual within the community will experience competition; *encounter complexity* denotes the number of distinct interacting pairs within the community; and *encounter density* represents the number of competitive encounters per mm$^2$. The probability, density, and complexity of spatial competition were calculated for each settlement panel. Competitive encounters were identified from endpoint images using the count tool in ImageJ (Schneider et al. 2012), with an interaction classified as competitive only when the competitive boundary exceeded 5% of the individual's outer edge (Barnes et al. 2021).

## Statistical analysis

All statistical analyses were undertaken in R version 4.3.1 (Team 2020; R Core Team 2021). Measurements were tested for normality and equal variance using the Shapiro–Wilk test for normality and Levene's test for equal variance among treatment groups.

*Growth*: As the assumptions for parametric tests were violated for growth rate data, we conducted a PERMANOVA analysis using the adonis2 function in vegan *v 2.6.4* (Oksanen et al. 2022). Post-hoc pairwise PERMANOVA analyses (function: pairwiseadonis2) were conducted to determine between-group differences in growth. The number of growth measurements collected for each species was limited by the species occurrence on the panels (ranging from 29 to 420 total occurrences). Thus, the number of measurements available for analysis and their degrees of freedom varied among species, treatment, and season. Within-group dispersions were assessed using a robust permutation test on the absolute deviations from the group's median, as this test was suitable for unequal samples sizes. Given that no significance was detected using this permutation test, the PERMANOVA results for growth were seen to be robust (supplementary 1).

*Survival*: For each group, survival probability was calculated as the number of surviving specimens divided by the total number of initial individuals. Further, a nested-dichotomies logistic regression (NDLR) model was run on categorical data: survival data for six species; total survival of ascidian and bryozoan groups; and overall total survival. Fitted values were then obtained using the '*predict()*' function. NDLR was used to model categorial survival outcomes across the three-month study period as it allowed for the inclusion of individuals who settled during the second experimental month. Survival was further analysed to quantify treatment and season effects using likelihood Chi-square tests, based on the observed combined deviance across the NDLR (i.e., survival through the entire nested model), compared to a null model (i.e., no treatment or seasonal effects).

*Percentage coverage and dominant space holder*: Percentage cover data was analysed using chi-square tests to assess if the observed percentage cover under heated treatments differed from ambient coverage (null hypothesis). Frequencies of occupied versus unoccupied space were compared across season and treatment, with $\alpha = 0.05$.

*Competitive encounter*: Data, that violated the assumptions of ANOVA were transformed, with the specific transformation method dependent on the variable (Supplementary 3). Following transformation, two-way ANOVAs were performed to assess the impact of season and treatment, as well as their interaction; these were included as fixed factors. A Tukey's HSD post hoc test was then used for pairwise comparisons.

# Results

## Growth rates

Warming of +1 °C was associated with increased growth rates during summer or spring for all six target species (Fig. 2, Supplementary 3). The observed increase in growth rates during the experiment was significant in four of the target species under +1 °C of warming (Supplementary 4; Table S4.2). However, the growth response showed high species-specific and seasonal variability. *Lissoclinum perforatum*, for example, showed increased growth during autumn under +2 °C warming, while the slower growing *Calloporina angustipora* showed less clear seasonal patterns in growth and in response to temperature treatments.

Overall, PERMANOVA indicated that both temperature treatment and season factors significantly influenced growth rates for five of the target species, while only the growth rate of *Asterocarpa humilis* did not respond significantly throughout the experiment (Fig. 2; Table 2; PERMANOVA, pseudo-F = 0.9, $R^2 = 0.06$, $P = 0.497$). In the heatwave treatment, growth rates tended to be slightly elevated compared to the ambient treatment, but they were only significantly in *Lissoclinum perforatum* and *Calloporina angustipora*, in autumn and *Rhynchozoon zealandicum* during summer (post-hoc pairwise PERMANOVA: F = 3.07, $R^2 = 0.10$, $P = 0.009$; F = 11.8, $R^2 = 0.07$ $P = 0.001$; and F = 0.307, $R^2 = 0.09$, $P = 0.05$, respectively).

Species-specific response among treatments and seasons are outlined below and detailed in Supplementary 4. The factor 'season' differentially influenced the impact of temperature treatment on growth rate for *C. angustipora*, *Disporella* sp., and *L. perforatum* (Table 2; Fig. 2). For *C. angustipora* growth rates were enhanced under the +1 °C treatment in summer, where growth was on average 0.08 mm$^2$ day$^{-1}$ ($n = 22$) faster than the ambient treatment, while

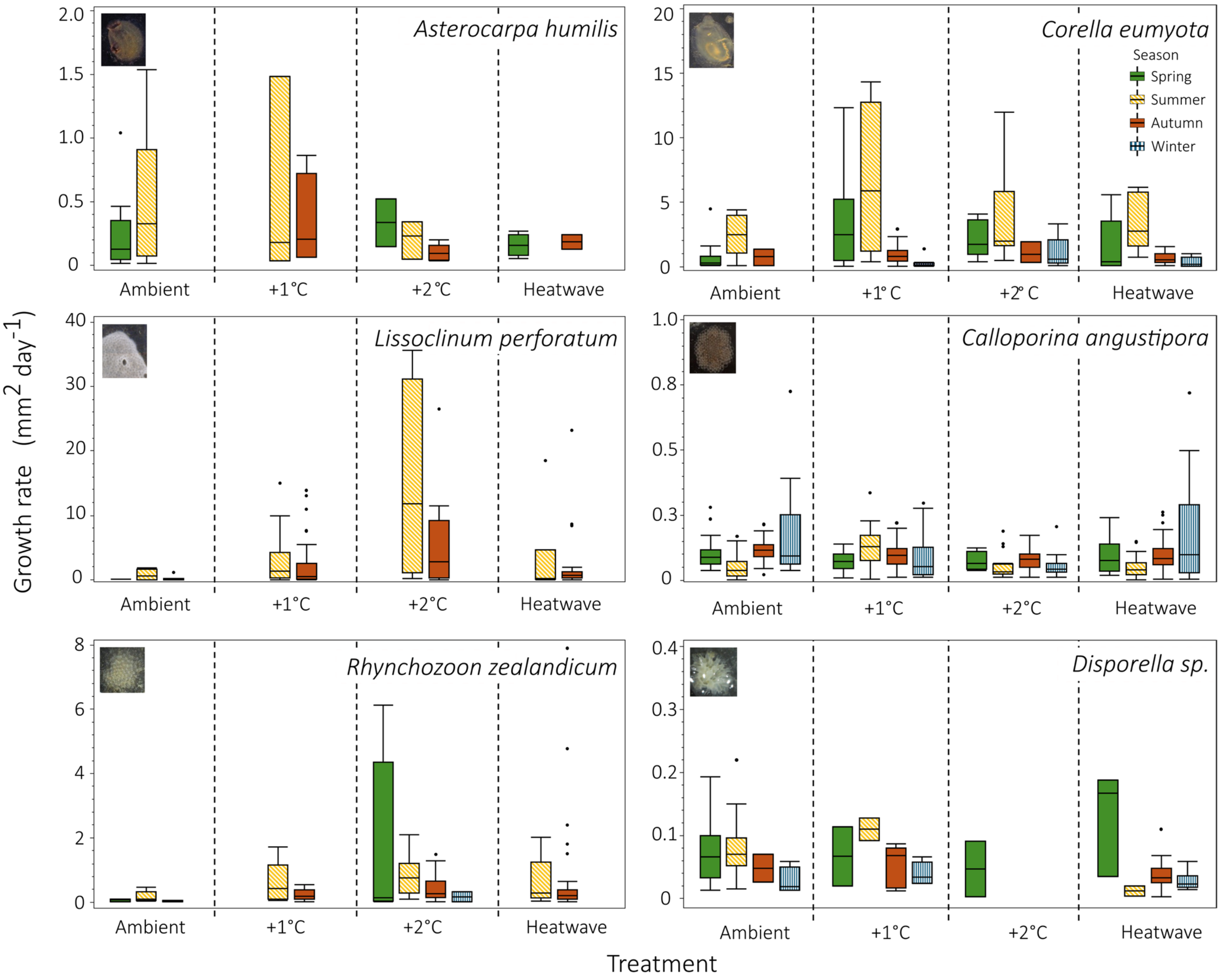


**Fig. 2** Box and whiskers plots for species-specific growth rates (mm$^2$ day$^{-1}$) among four seasons for *Asterocarpa humilis*, *Corella eumyota*, *Lissoclinum perforatum*, *Calloporina angustipora*, *Rhynchozoon zealandicum*, and *Disporella* sp., respectively. Note the Y-axis differs among species. Black dots represent outliers. For specific n values see supplementary information 3

the same warming resulted in growth rate reductions during the other seasons (Fig. 2). For instance, *C. angustipora* colonies grew significantly slower under heated (+1 °C and +2°C) treatments during winter than in the ambient treatment, with growth 0.112 mm$^2$ day$^{-1}$ slower in winter under +2°C (post-hoc pairwise PERMANOVA: F = 19.91, $R^2 = 0.26$, $P = 0.001$). For *Disporella* sp. growth rates in summer were reduced when exposed to the heatwave treatment when compared to ambient growth rates (post-hoc pairwise PERMANOVA: F = 9.33, $R^2 = 0.18$, $P = 0.004$). While slight increases in growth of *Disporella* sp. under the heatwave treatment were observed during spring, they were not significantly faster than the ambient treatment (Fig. 2; post-hoc pairwise PERMANOVA: F = 0.87, $R^2 = 0.07$, $P = 0.41$).

*Lissoclinum perforatum* displayed significant growth differences across seasons (PERMANOVA, pseudo-F = 2.68, $R^2 = 0.04$, $P = 0.007$) and treatments (PERMANOVA, pseudo-F = 5.63, $R^2 = 0.12$, $P = 0.0001$). Furthermore, the effect of treatment on growth rates for *L. perforatum* was seasonally dependent, with rates of growth 9.52 ± 7.43 mm$^2$ day$^{-1}$ higher in summer when subjected to +2°C warming (post-hoc pairwise PERMANOVA: F = 2.16, $R^2 = 0.18$, $P = 0.09$). Despite similar patterns produced across summer and autumn, growth rates in autumn were always slower than the summer growth rates (Fig. 2; Table 2). The heatwave treatment was associated with non-significant moderate increases in growth rates of *L. perforatum* (2.21 ± 4.29 mm$^2$ day$^{-1}$ and 0.51 ± 2.62 mm$^2$ day$^{-1}$ faster for summer and autumn, respectively).

*Rhynchozoon zealandicum* growth rates differed significantly among ambient and heated treatments, with maximum growth observed in spring. During summer, under

**Table 2 Comparison of growth rates among season and treatment for six taxa.** PERMANOVA tables, gathered from the ADONIS 2 function in the Vegan program in R, for growth rate ~ Treatment * Season, accounting for the variation attributed to block, for the six target species considered here. Where alpha = 0.05 and significance is indicated in bold

| | Treatment | Season | Treatment * Season | Residual (ε) | Total | Treatment | Season | Treatment * Season | Residual (ε) | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | *Asterocarpa humilis* | | | | | *Corella eumyota* | | | | |
| **DF** | 3 | 2 | 3 | 38 | 46 | 3 | 3 | 8 | 140 | 154 |
| **Mean Squares** | 6.67 | 11.11 | 7.50 | 6.07 | 6.32 | 2.22 | 0.65 | 4.94 | 5.96 | 4.95 |
| **$R^2$** | 0.06 | 0.03 | 0.06 | 0.86 | 1 | 0.04 | 0.15 | 0.05 | 0.76 | 1 |
| **F** | 0.90 | 0.54 | 0.80 | | | 2.67 | 9.13 | 1.2 | | |
| **Pr(>F)** | 0.497 | 0.727 | 0.58 | | | **0.02** | **0.001** | 0.28 | | |
| | *Lissoclinum perforatum* | | | | | *Calloporina angustipora* | | | | |
| **DF** | 3 | 2 | 3 | 108 | 116 | 3 | 3 | 9 | 775 | 790 |
| **Mean Squares** | 1.29 | 0.98 | 6.15 | 6.14 | 5.48 | 1.46 | 0.33 | 1.48 | 10.09 | 8.41 |
| **$R^2$** | 0.12 | 0.04 | 0.06 | 0.78 | 1 | 0.02 | 0.10 | 0.07 | 0.82 | 1 |
| **F** | 5.63 | 2.68 | 2.90 | | | 6.93 | 30.3 | 6.82 | | |
| **Pr(>F)** | **0.001** | **0.007** | **0.001** | | | **0.001** | **0.001** | **0.001** | | |
| | *Rhynchozoon zealandicum* | | | | | *Disporella* sp. | | | | |
| **DF** | 3 | 3 | 4 | 213 | 223 | 3 | 3 | 6 | 111 | 123 |
| **Mean Squares** | 1.29 | 0.98 | 6.15 | 6.14 | 5.48 | 1.89 | 2.48 | 5.22 | 9.10 | 7.59 |
| **$R^2$** | 0.06 | 0.08 | 0.02 | 0.85 | 1 | 0.09 | 0.08 | 0.07 | 0.76 | 1 |
| **F** | 4.78 | 6.30 | 0.99 | | | 4.81 | 3.65 | 1.75 | | |
| **Pr(>F)** | **0.001** | **0.001** | 0.46 | | | **0.001** | **0.001** | **0.05** | | |

+2°C warming, *R. zealandicum* colonies exhibited growth rates 0.68 $mm^2$ $day^{-1}$ faster than under ambient conditions and 0.20 $mm^2$ $day^{-1}$ faster than under the +1 °C warming treatment (post-hoc pairwise PERMANOVA: F = 21.14, $R^2$ = 0.236, *P* = 0.001 and F = 6.68, $R^2$ = 0.117, *P* = 0.003 for ambient compared to +2°C and +1 °C, respectively). Both *L. perforatum* and *R. zealandicum* exhibited consistent growth rate increases that correlated with temperature, reaching peak growth rates in summer and spring, respectively, when subjected to +2°C warming, while showing slower growth and reduced presence during cooler periods (Fig. 2).

*Corella eumyota* growth rates were also correlated with temperature such that during winter growth rates were significantly lower than in the other seasons (Supplementary 4). *Corella eumyota* also grew faster under warming, with growth rates on average 1.06 $mm^2$ $day^{-1}$ faster under the +2°C treatment when considering all seasons (post-hoc pairwise PERMANOVA: F = 4.67, $R^2$ = 0.083, *P* = 0.005). The heatwave treatment also resulted in growth rates 0.79 and 1.08 $mm^2$ $day^{-1}$ faster than ambient treatments during spring and summer respectively, however these differences were not significant.

## Survival probability

Species-specific survival rates were recorded for five of the six target species, with newly settled individuals of *R. zealandicum* unable to be distinguished from other bryozoan species. The temperature treatments significantly influenced survival across the remaining five species, with season and the interaction between season and treatment significant in three target species (Table 3). Overall, survival rates tended to be lower during summer, irrespective of heated treatments (Fig. 3). For example, the survival probability of *C. angustipora* decreased under the +2 °C warming treatment in summer (2-fold lower than ambient) and spring (1.6-fold lower than ambient) but increased during winter (1.85-fold higher than ambient), while survival did not differ among treatments for this species during autumn.

The survival of *C. eumyota* was reduced under heated treatments (+1 and 2 °C treatments when compared to the ambient treatment) during summer and autumn, although initial survival (from months 1 to 2) was on average higher under the +2 °C treatments in this species, end point survival was reduced by 0.22 and 0.13, during summer and autumn, respectively. Survival of *C. eumyota* was, however, increased under +2 °C treatments in spring compared to end-point survival in other treatments. Furthermore, the heatwave treatment resulted in increased survival of *C. eumyota* individuals relative to other heated treatments in both summer and winter.

The survival probability of *L. perforatum* increased under heated treatments in both summer and autumn, with survival probabilities being 6.9-fold higher under the +2 °C warming treatment in summer compared to ambient conditions. Conversely, *Lissoclinum perforatum* exhibited low survival under cooler temperatures, with no colonies surviving longer than one month in winter and none surviving under ambient conditions in autumn.

**Table 3** Likelihood chi-squared charts for survival among treatment and season. Pr(>Chisq) based on the observed combined deviance across the NDLR (i.e., survival through the entire nested model), compared to a null model, (no treatment or seasonal effects) for each species. Alpha = 0.05 and significance is indicated in bold

| | Treatment | Season | Treatment * Season | Treatment | Season | Treatment * Season |
|---|---|---|---|---|---|---|
| | *Asterocarpa humilis* | | | *Corella eumyota* | | |
| **LR Chi Sq** | 23.84 | 17.56 | 21.74 | 25.06 | 69.7 | 95.19 |
| **DF** | 11 | 11 | 14 | 12 | 12 | 34 |
| **Pr(>Chi Sq)** | **0.031** | 0.092 | 0.084 | **0.014** | **0.001** | **0.001** |
| | *Lissoclinum perforatum* | | | *Calloporina angustipora* | | |
| **LR Chi Sq** | 31.51 | 74.55 | 42.23 | 217.97 | 87.76 | 42.26 |
| **DF** | 12 | 12 | 25 | 12 | 12 | 34 |
| **Pr(>Chi Sq)** | **0.002** | **0.001** | **0.016** | **0.001** | **0.001** | 0.156 |
| | *Disporella* sp. | | | | | |
| **LR Chi Sq** | 33.86 | 65.69 | 27.41 | | | |
| **DF** | 8 | 12 | 17 | | | |
| **Pr(>Chi Sq)** | **0.001** | **0.001** | **0.05** | | | |

## Percentage cover and dominant space holder

The observed percentage of occupied space varied significantly among seasons (Chi-squared, $\chi^2(3) = 18.68$, $P < 0.001$), which was driven by the overall reduction in percentage cover across all treatments in winter (i.e. 10.9 ± 1.9% (Winter), 27.8 ± 11% (Spring), 40.9 ± 12.4% (Summer), and 35.3 ± 12.9% (Autumn), $n = 4$). Temperature treatment was not a significant factor in determining the observed overall percentage cover on the settlement panels (Chi-squared, $\chi^2(3) = 1.92$, $P = 0.59$). However, percentage cover scaled with temperature such that cover increased with the average temperature experienced throughout the experiment, regardless of the treatment group.

Warming resulted in a shift in the dominant spatial occupier present on the heated settlement panels, with the dominant spatial occupier never the same between the heated (+1 and +2) and ambient treatments (Supplementary 5 & Fig. 4). For instance, *Lissoclinum perforatum* was the dominant spatial occupier in all three heated treatments in summer and autumn, but never on the ambient panels, with the dominant space occupier in ambient treatments being the bryozoan, *Calloporina angustipora.* When further examined the space occupied by *L. perforatum* varied significantly among seasons (ANOVA, $F_{(3,12)} = 4.48$, $P = 0.001$) and treatment (ANOVA, $F_{(3, 12)} = 4.11$, $P = 0.003$), with the impact of treatment being seasonally dependent (two-way ANOVA, interaction factor: $F_{(6, 48)} = 3.8$, $P = 0.003$; Fig. 4). In contrast, the space occupied by *C. angustipora* was significantly reduced under 2 °C of warming during summer (ANOVA, $F_{(3,12)} = 3.29$, $P = 0.03$; Fig. 4). The dominant occupier also shifted between ambient and the heatwave treatment, with *L. perforatum* emerging as the dominant occupier under summer and autumn seasons, while *C. eumyota* emerged during spring, replacing *C. angustipora* as the spatial dominant. When considered across season, *L. perforatum* was the spatial dominant under all temperature manipulated treatments (Fig. 4).

## Competitive response

The probability of encountering spatial competition differed significantly among seasons (ANOVA, $F_{(3,120)} = 12.1$, $P = 0.001$). The probability of spatial competition occurring tended to be higher under the +2 °C treatment, however this was only statistically significant during spring (Table 4). Encounter density also differed significantly with season (ANOVA, $F_{(3,12)} = 60.5$, $P < 0.001$; Fig. 5). Density was generally lowest in the +2 °C treatments, apart from the increase seen in both heated treatments in winter and the lower density observed in the +1 °C treatment during spring. Encounter complexity varied with season, where complexity decreased in winter compared to all other seasons. While treatment was not a significant factor, the influence it had varied with season (ANOVA, $F_{(3,12)} = 2.491$, $P = 0.02$; Fig. 5), which was evident through the significant interaction factor between these variables. This difference is apparent through the slight loss of competitive complexity under the +2 °C treatment in spring, summer, and autumn, while this was moderately increased in winter (Fig. 5).

# Discussion

Using *in situ* temperature manipulation experiments we found that small, environmentally relevant increases in sea temperature impacted growth and survival of encrusting taxa, altering the structure and composition of the studied communities. This was particularly evident through analysis of spatial dominance, where we found that the dominant occupier was never the same species between ambient and heated panels.

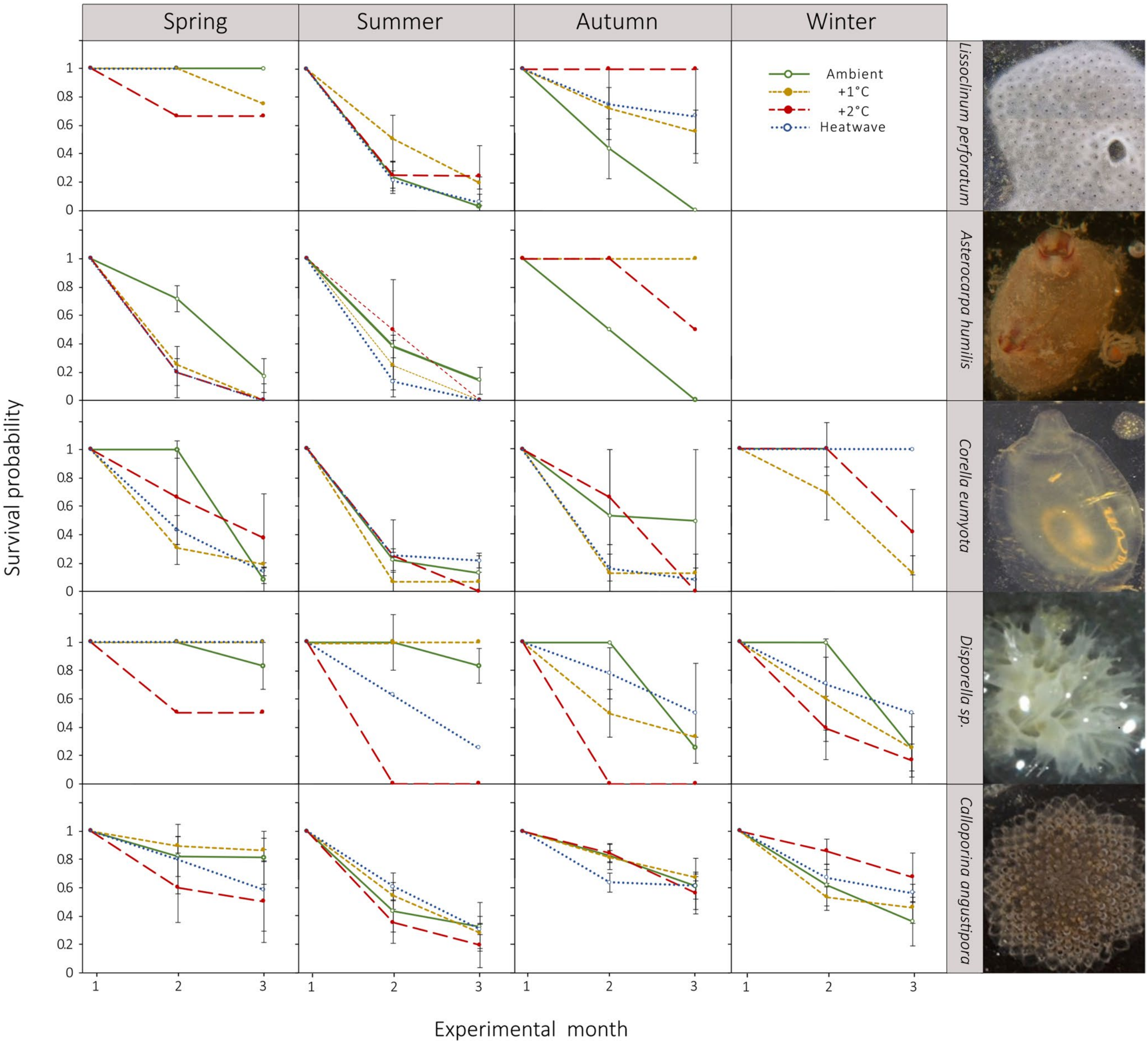


**Fig. 3** Species-specific survival probability. Survival probability of five species, using the raw survival data (*L. perforatum*, *A. humilis*, *C. eumyota*, *Disporella* sp., and *C. angustipora*) as rows for each season *(columns)* for the duration of the experiment. Error bars represent between replicate standard error, *n* = 4

## Linking species-specific responses with potential community shifts

We observed that species-specific changes in growth rate resulted in significant changes to the encrusting invertebrate communities. The ability to increase growth rates was observed under moderate (+1 °C) temperature increases, which in conjunction with increased survival or occurrence, can provide species with the advantage to gain and retain space. This response was seen in *L. perforatum and Corella eumyota* for example, where the ascidians increased in abundance under warming as a result of improved relative fitness. These observations are consistent with prior studies, which have indicated an increase in growth and coverage within marine encrusting invertebrate communities under moderate warming from both field observations and temperature manipulations (Wernberg et al. 2012; Lord 2017a; Ashton et al. 2017; Salama et al. 2018). Moderate warming has also been linked to increased percentage cover within marine encrusting communities (Maughan and Barnes 2000; Schiel et al. 2004; Lord 2017b; Khosravi et al. 2019). Although we anticipated increased total coverage of encrusting communities under warmed treatments, the observations from this study were not strong enough to

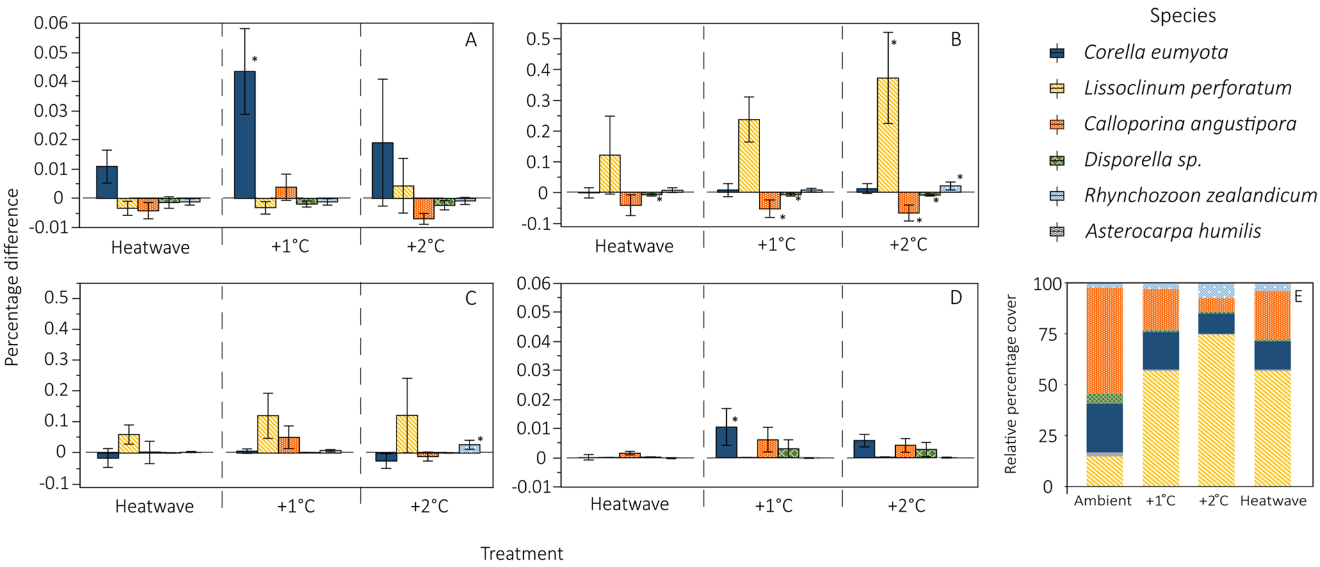


**Fig. 4** Change in percentage cover. Percentage cover change relative to coverage in ambient treatments of each target species in spring (**A**), summer (**B**), autumn (**C**) and winter (**D**), where significant difference from the ambient treatment is indicated by * and the error bars represent standard error. $N=4$ (**E**) indicates the relative assemblage of each species averaged across season for each treatment, indicating the change in dominant spatial occupier between ambient and heated treatments. Note that the Y-axis is different for each plot in this figure, due to seasonal differences in coverage

support this hypothesis. In this respect, we only observed total percentage cover increases in warming treatments of less than 1% above the ambient treatment. The duration of our experiments (3 months) meant that we only captured the early development of the encrusting communities, and longer observations would likely have produced more distinct changes in coverage in the warming treatments.

Species-specific shifts in growth rates will have the largest impact where species have the potential to increase growth rapidly under warmed conditions. Such traits can allow species to take advantage of conditions, which adversely or neutrally impact competitor species, to gain and maintain space. Our results indicate that encrusting communities in the Otago region may be vulnerable to overgrowth by species that can take advantage of warming through increased growth and competitive ability; several of these species will be non-native, such as *L. perforatum*. These results are consistent with previous documentation of the dominance of *L. perforatum* in an intertidal coral reef community (Kelmo et al. 2014), where an increased density of *L. perforatum* was observed during an extended heat event, lasting one year with temperatures approximately 1.5–1.7 °C warmer that previous periods. (Kelmo et al. 2014). While Kelmo et al. (2014) noted that a stable benthic community was re-established, it varied significantly from initial assemblages, with *L. perforatum* noted as influential in this shift. Assemblage-level shifts which persist after warming events can be linked to increased coverage of species that would normally be outcompeted by native or more specialised species (Michaud et al. 2022). We observed a shift in the dominant space occupier on our panels, from a native bryozoan species *Calloporina angustipora*, to an exotic ascidian species *Lissoclinum perforatum* during the two warmest seasonal experiments. Interestingly, the reductions in *C. angustipora* are consistent with similar observations of reductions in abundance within the Otago Harbour, which have been documented alongside an increase in non-native 'weedy' ascidian and bryozoan species (Feary and Smith 2024). These abundance changes coincided with a 0.1 °C ± 0.047 °C decadal ocean warming measured in the Otago Harbour (Shears and Bowen 2017), and suggest changes in wild communities predicted by our experiments are already underway.

## Heatwave treatment responses

Marine heatwaves are now seen as having important impacts on communities (Capotondi et al. 2024), and with changes that can differ from long-term warming. For New Zealand coasts, marine heatwaves have been documented as drivers in community and assemblage level shifts, which often persist long after the event (Thomsen et al. 2019; Montie and Thomsen 2023a; Bell et al. 2024 ; Spyksma et al. 2024). Our study demonstrates the differential impact that shorter term warming (as seen in a marine heatwaves) has on growth and survival within encrusting communities. Here, we found growth rates post-heatwave exposure were reduced when compared to the constant warming treatments, such that increased growth or survival under continuous warming treatments did not always translate to increases under the heatwave treatment. Heatwave events can be the cause

**Table 4** ANOVA tables for competitive interactions. ANOVA results for competitive probability, density, and complexity for the combined data (Total) and each seasonal period (Columns). Where alpha = 0.05 and significance is indicated in bold and residuals is represented by ε

| Encounter probability | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Total | | | | Spring | | Summer | | Autumn | | Winter | |
| | Treatment | Season | Treatment * Season | ε | Treatment | ε | Treatment | ε | Treatment | ε | Treatment | ε |
| **Df** | 3 | 3 | 9 | 48 | 3 | 12 | 3 | 12 | 3 | 12 | 3 | 12 |
| **Sum Sq** | 0.12 | 0.54 | 0.13 | 1 | 0.138 | 0 | 0.07 | 0 | 0.03 | 0 | 0.01 | 0 |
| **Mean Sq** | 0.04 | 0.18 | 0.01 | 0 | 0.046 | 0 | 0.02 | 0 | 0.01 | 0 | 0 | 0 |
| **F** | 2.61 | 12.1 | 0.97 | | 3.289 | | 1.19 | | 0.97 | | 0.19 | |
| **P** | 0.06 | 0.001 | 0.48 | | 0.05 | | 0.36 | | 0.44 | | 0.89 | |
| Encounter density | | | | | | | | | | | | |
| | Total | | | | Spring | | Summer | | Autumn | | Winter | |
| | Treatment | Season | Treatment * Season | ε | Treatment | ε | Treatment | ε | Treatment | ε | Treatment | ε |
| **Df** | 3 | 3 | 9 | 48 | 3 | 12 | 3 | 12 | 3 | 12 | 3 | 12 |
| **Sum Sq** | 0.07 | 11.17 | 1.06 | 3 | 0.42 | 1 | 0.31 | 1 | 0.23 | 1 | 0.16 | 0 |
| **Mean Sq** | 0.02 | 3.72 | 0.12 | 0 | 0.14 | 0 | 0.1 | 0 | 0.08 | 0 | 0.05 | 0 |
| **F** | 0.35 | 60.45 | 1.91 | | 2.97 | | 1.04 | | 1 | | 2.36 | |
| **P** | **0.79** | **0.001** | **0.07** | | 0.07 | | 0.41 | | 0.43 | | 0.12 | |
| Encounter complexity | | | | | | | | | | | | |
| | Total | | | | Spring | | Summer | | Autumn | | Winter | |
| | Treatment | Season | Treatment * Season | ε | Treatment | ε | Treatment | ε | Treatment | ε | Treatment | ε |
| **Df** | 3 | 3 | 9 | 48 | 3 | 12 | 3 | 12 | 3 | 12 | 3 | 12 |
| **Sum Sq** | 2.98 | 127 | 21.31 | 46 | 8.35 | 21 | 8.47 | 12 | 6.47 | 11 | 1 | 2 |
| **Mean Sq** | 0.99 | 42.25 | 2.37 | 1 | 2.78 | 2 | 2.82 | 1 | 2.16 | 1 | 0.33 | 0 |
| **F** | 1.04 | 44.45 | 2.49 | | 1.59 | | 2.87 | | 2.42 | | 1.85 | |
| **P** | **0.38** | **0.001** | 0.02 | | 0.24 | | 0.08 | | 0.12 | | 0.19 | |

of major physiological stress resulting in conditions which exceed physiological tolerances and result in local mortality events (Pansch et al. 2018; Bell et al.2024 ), supporting the conclusion that acute thermal stress and temperature variation are important contributors to physiological responses to warming (Stoks et al. 2017). This pattern was particularly evident during spring and winter, where ascidian survival as a group was reduced under the heatwave treatment when compared to the ambient and constant warming treatments. Thus, despite a seemingly positive impact on growth under a continuous warming scenario, acute heat stress during colder months may result in increased mortality, and the opportunity for dominance of warm affiliated species (Atkinson et al. 2020). While continuous and prolonged warming, which does not exceed a species physiological threshold, can enhance growth (Smale et al. 2017; Ashton et al. 2017), it should be noted that thermal thresholds can be very low, even in 1˚C or less in *in situ* warming trials lasting well in excess of 1 year (Clark et al. 2019). Acute heat stress which is unanticipated can drive short-term declines in growth, survival and competitive ability, even when temperatures do not exceed summertime maxima (Atkinson et al. 2020).

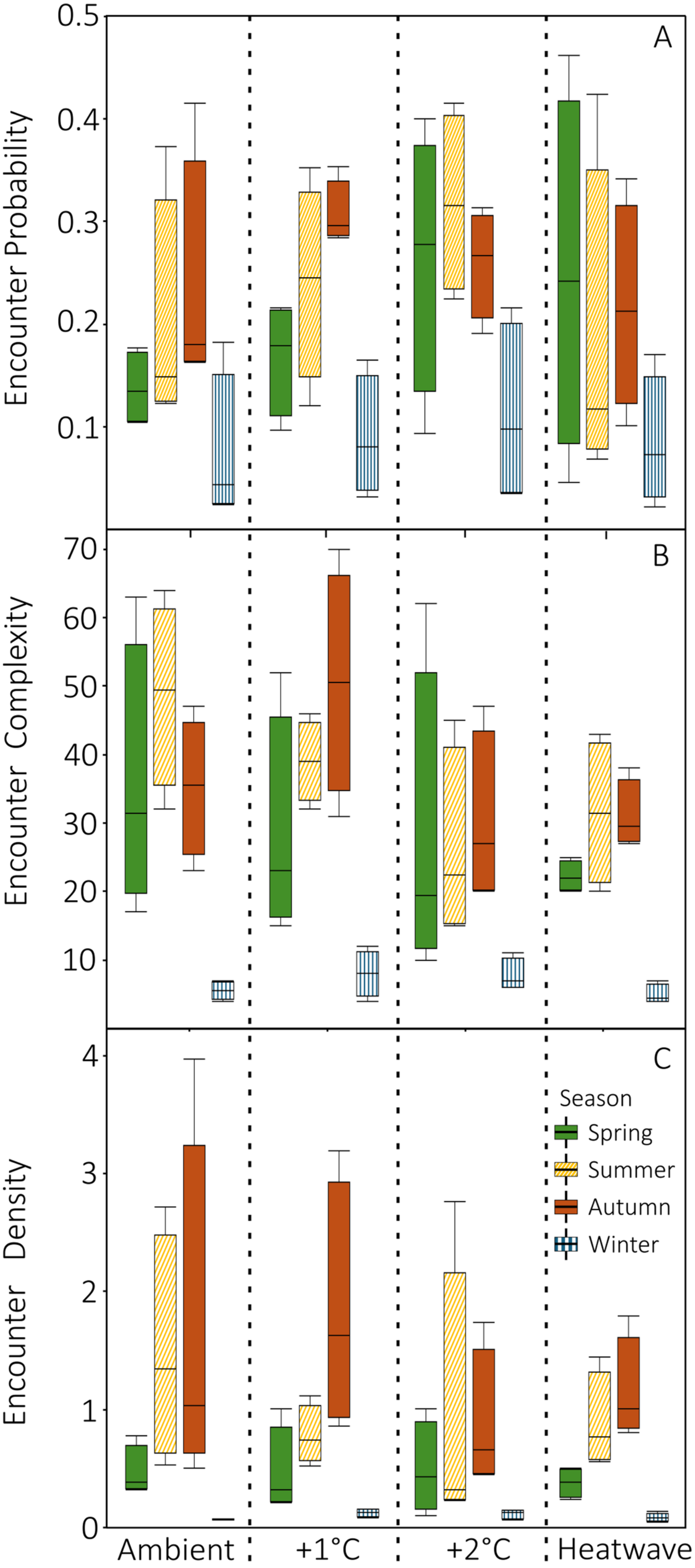
Short-term warming, such as heatwave conditions can have more immediate influences on marine shallow-water encrusting communities. For example, our results indicate that dominance shifts can occur after heatwaves within the Otago Harbour region. With a year-round increase in intensity and duration of marine heatwaves anticipated in New Zealand (Behrens et al. 2022), such dominance shifts are becoming increasingly likely. The dominance of warm-affiliated species after heatwave events can lead to persistent changes within encrusting communities (Davis et al. 2018; Vicente et al. 2021; Lennon and Sealey 2023). Such responses have already been observed after heatwave events in other areas of New Zealand, for instance the increase of an invasive ascidian, *Symplegma brakenhielmi* during the 2021/2022 marine heatwave (Spyksma et al. 2024). This inference suggests that changes in community composition and dominance within shallow water encrusting communities may move towards more warm affiliated assemblages in response to short-term thermal events. This emphasises the vulnerability of these near-shore encrusting communities to near future heatwave events. The loss of foundation species, shifts in dominance, and community reshuffling are emerging as real-time responses to marine heatwaves (Thomsen et al. 2019; Montie and Thomsen 2023b; Bell et al. 2024), and understanding the differential responses of species to such events is required for adequate mitigation and protection of vulnerable species. In addition, wintertime heatwaves, even those that do not exceed summertime temperatures, may have lasting negative impacts on encrusting ascidian species in this region. The impact of wintertime heatwave events has often been overlooked, but the frequency of these events has increased in our study area, as well as in multiple other locations around New Zealand (De Burgh-Day et al. 2022; Montie et al. 2024).

## Overgrowth and dominance

A change in spatially dominant species is expected to have widescale impacts on community composition and ecosystem function, given that ecological communities are generally made up of a small number of dominant species, and a large number of rare species (Magurran and Henderson 2003). Such a shift is particularly relevant if the replacement species alters the functional roles within the community (Gómez-Gras et al. 2021). Furthermore, if a dominant space occupier influences settlement or survival of other taxa within the community, it can result in impacts on the evenness and hence stability of the community. Indeed, the early dominance of a colonial species, such as *L. perforatum* can switch the mechanisms which maintain biodiversity, leading to an increased importance in primary space occupation (Dijkstra and Harris 2009). For example, some solitary ascidians facilitate settlement as their tunic provides a suitable settlement surface for smaller organisms. In contrast, flat colonial ascidians have considerably softer outer tunics, and as a result do not provide a suitable settlement surface (Claar et al. 2011). Within the encrusting communities observed in the present study, *Corella eumyota*, a solitary ascidian, often had early settlers on its tunic (settlers included bryozoans and spirorbid worms), which was not observed on *L. perforatum.* The increased importance of primary space occupation in this instance may result in increased spatial competition later as the amount of suitable habitat is reduced (Ladd et al. 2019).

There are many examples of facilitation coinciding with shifts in dominance within marine communities (Davis et al. 2018; Vicente et al. 2021; Lennon and Sealey 2023). For instance, the invasive solitary ascidian *Pyura doppelgangera*, forms dense beds that have competitively displaced native communities of the northern tip of New Zealand (Davis et al. 2018). The dominance of *P. doppelgangera* facilitates the development of a completely different community, indicating the cascading impact that a dominant superior competitor can have (Davis et al. 2018). This response can be amplified in such cases, where dominance alters the value of the community to higher trophic levels. In a more broad example, a switch from sponge/coral-dominated benthos to a sponge/algal-dominated system occurred as a result of anthropogenic influences, negatively impacted associated fish assemblages in nearshore marine systems in the Florida Keys (Lennon and Sealey 2023). Changes in species

**Fig. 5** Shifts in competitive encounters across four seasons. Box plots of competitive probability (A), complexity (B), and density (C) for each experimental treatment, where season in represented by colour.



associated with benthic communities, including abundance, composition and community succession, has been observed in fouling communities (Vicente et al. 2021).

### Climate change and spatial competition

As space becomes increasingly limited, the intensity and occurrence of competitive encounters are predicted to increase (Lord et al. 2015; Barnes et al. 2021). Our results are consistent with this statement, with the probability of encountering spatial competition increasing with increasing percentage cover of the heated settlement panels. Furthermore, as seasonality was the major driver in determining the percentage cover on the heated settlement panels, this translated to a strong seasonal impact seen in the probability, density, and complexity of competitive encounters. It has previously been suggested that competitive encounters are of increased importance in seasonal environments (Lord et al. 2015; Gastaldi et al. 2020). Maughan and Barnes (2000) found that competition was more intense during summer in biofouling communities in Lough Hyne, Ireland when recruitment was highest. More broadly this indicates that competitive encounters followed a seasonal pattern alongside patterns of percentage cover and recruitment (Maughan and Barnes 2000).

There has been increasing evidence that the impact of species interactions under changing conditions may be a driving factor in determining community composition (Gunderson et al. 2017). A moderate increase in growth across multiple species present within a community, as seen under the + 1 °C treatment here, translates to a higher demand on available space potentially leading to more intense and frequent levels of competition (Barnes and Neutel 2016; Barnes et al. 2021). In a similar study, Barnes et al. (2021) determined that warming of 1 °C above ambient increased the probability that an individual within the community would encounter spatial competition, a result which was not evident under late-century levels of warming (Barnes et al. 2021). Therefore, the present study anticipated that both density and probability of competition would increase under future ocean temperatures. However, despite a slight increase in encounter probability under the + 2 °C, treatment, warming was not a significant factor in determining the probability of competitive encounters. This may reflect the short duration of our experiments (3 months), which may be insufficient for strong competitive interactions to develop. Despite little evidence to support this hypothesis here, our data (such as increased growth rates) suggest that spatial competition would be anticipated to shift under future warming, particularly when considering competition complexity, although the anticipated increase in competitive encounters associated with increased growth rates could be balanced by the increased failure of some species seen in heated treatments here. The effects and implications of this change are likely to be more readily detectable under longer-term experimental studies.

The dynamics of competitive encounters are highly dependent on the assemblage of competitors, their levels of physiological tolerances, and how species within the community allocate energy (i.e. to growth, competition, or repair etc.) as ocean warming progresses. Given the high probability that warming will alter community composition within encrusting communities, alongside changes in growth, it is clear that strategies for maintaining space within sessile marine communities will shift with warming (Ladd et al. 2019; Barnes et al. 2021). Thus, spatial competition will continue to be an influential factor in community stability.

## Conclusions

The implications of temperature on physiological function are likely to have cascading effects on species interactions and community assemblages (Gunderson et al. 2017). The results presented here indicate that ocean warming can shift the growth and survival of species under moderate warming with increasingly variable impacts under further temperature increases. In particular, responses observed indicate that warming of 2 °C in the Otago Harbour may lead to increased sub-lethal stress in species less equipped to cope with increased temperatures, resulting in reduced growth and ultimately survival rates, with likely implications for competitive success in such species. Temperate encrusting reefs provide a complex habitat structure, the loss of which, through the dominance of flat colonial ascidians, for example, may shift the epifaunal use of these communities, resulting in similar outcomes to the simplification of macroalgae and coral-dominated systems (Sunday et al. 2017; Cattano et al. 2020; Fraser et al. 2020; Agostini et al. 2021).

Our results ultimately indicate that assemblage-level shifts and wider ecosystem-level consequences are becoming increasingly probable in these communities. As a whole, this study suggests that warming of as little as 1–2 °C will have strong but variable influences on encrusting marine invertebrates, which will in turn influence the community composition and likely the resulting function of these systems. Our experiments also suggest short-term warming events (i.e. marine heatwaves) can have strong effects on encrusting taxa, but which can differ from effects of constant increases in sea temperature. Given the increase in the occurrence and duration of marine heatwaves, community level shifts may occur earlier than expected, given average warming alone. Of particular importance when considering community changes is the apparent advantages of warming given to non-native taxa. As the pool of competitors can influence how interactions shape communities (Lord 2017b), the introduction of non-native species is anticipated to become an important aspect of understanding competitive encounters under future ocean conditions.

While the experimental design used here provides a step forward in understanding responses *in situ*, it is important to note that these experiments do have limitations. Of note, these experiments only manipulate temperature while climate change impacts multiple environmental and biological variables (IPCC 2023). Although other factors, such as the solubility of carbonates and oxygen, will also vary within the micro-environment created by the warmed boundary layer, this was not actively measured here. Lastly, our experiments were of short durations (3 months) which does not capture changes that occur beyond settlement and early establishment of encrusting species, nor responses to warming once these communities have fully developed.

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**Author contributions** This study was conceptualised by Lloyd Peck, Miles Lamare and Jessica Moffitt, the experimental design was developed by Lloyd Peck and the specific methods used here were designed and by Jessica Moffitt, Tom Massué and Miles Lamare. Jessica Moffitt completed the investigation, data collection and was responsible for data visualisation. Gert- Jan Jeunen, Ceridwen Fraser, Neil Gemmell and Miles Lamare supervised the research process. Jessica Moffitt wrote the original draft of the manuscript; all authors contributed to editing the manuscript.

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**Data availability** Data relating to this paper has been deposited to Mendeley data and can be found at DOI: https://doi.org/10.17632/mkfntxpx43.1.

## Declarations

**Competing interests** The authors declare that we have no known conflicts of interest that have influenced the work presented in this paper.

**Compliance with ethical standards** The authors declare that we have complied with ethical standards.

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