Projected warming disrupts temperate serpulid communities, key engineers of benthic ecosystems: Evidence from *in situ* thermal experiments

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Running page head*:* Temperate serpulid responses to warming

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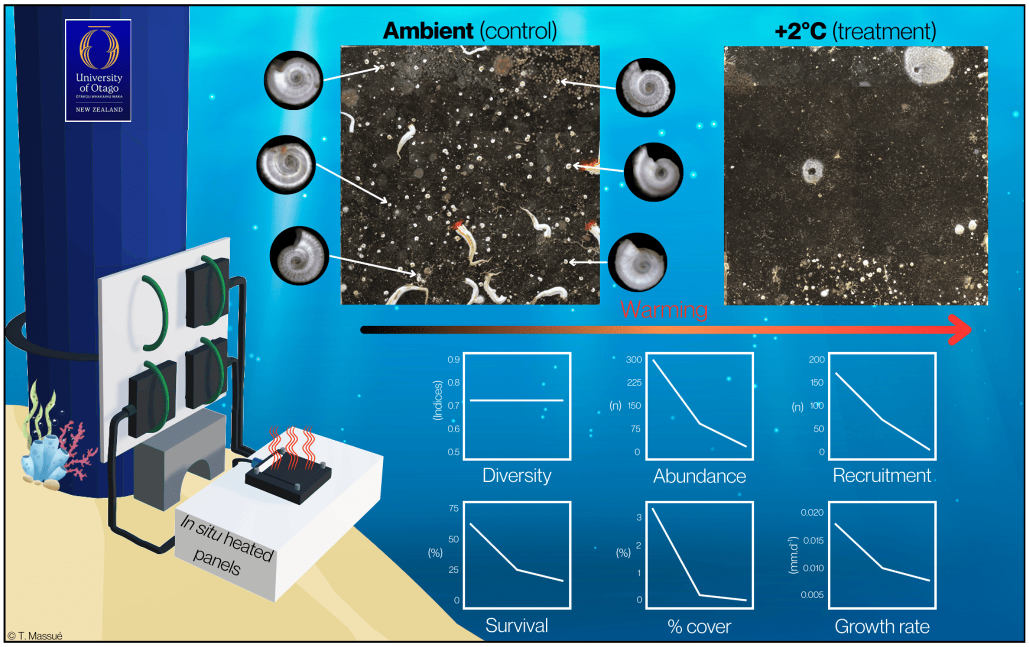
ABSTRACT

Global ocean warming is reshaping marine communities, with consequences for species- and community-level functioning. Serpulid polychaetes are a key component of benthic ecosystems that may be particularly vulnerable to rising temperatures, yet their responses remain poorly studied. Using *in situ* bespoke heated recruitment panels, we investigated the effects of warming (mid- and end-of-century temperature projections, i.e. +1 °C and +2 °C above ambient temperature, as well as short-term warming heatwave events) on the abundance, diversity, recruitment, survival, percentage cover, and growth rate of eleven morphologically distinct serpulid taxa in southern New Zealand. Seasonal variability strongly influenced serpulid responses. No differences in community structure or growth rate were detected under warming treatments in winter. In contrast, negative responses became more pronounced as seasonal temperatures increased. While diversity remained stable across treatments, the most significant changes occurred under +2 °C in late summer: abundance decreased 10-fold, recruitment six-fold, survival and cover three-fold, and growth rate was halved, resulting in smaller individuals. The +1 °C and heatwave treatments had intermediate effects, indicating a progressive response to warming. While some serpulids exhibited greater short-term resilience, our observations suggest that warming may favour thermally tolerant taxa, including invasive species. This work is the first *in situ* experimental study investigating the response of temperate serpulid communities to ocean warming. Our findings highlight their vulnerability to climate-driven changes and underscore the need for further research into their ecological role in a rapidly warming ocean.

GRAPHICAL ABSTRACT



Keywords*:* Serpulidae, ecosystem engineer, climate change, marine benthos, community disturbance, growth rate, recruitment panels, temperate habitat

1. INTRODUCTION

Climate change-induced modifications to benthic marine ecosystems, particularly through ocean warming, will have important ecological consequences in temperate coastal regions (Scheffers et al. 2016). The physiological effects of warming and thermal stress, including reduced fitness and survival, and altered reproductive capacity, will directly impact the stability and dynamics of benthic communities (Buckley & Huey 2016). Ocean warming has also led to important phenological responses, impacting life histories, and the timing and magnitude of seasonal productivity (Alter et al. 2024). Key factors driving these changes include direct effects of warmer sea temperatures, water column stratification, salinity, and alterations in thermal stability duration (Scheffers et al. 2016).

Individual responses to temperature change will be species-specific and influenced by the duration of temperature modification, geographical location, and organism physiology (Whiteley & Mackenzie 2016). At the community level, meta-analyses across global marine ecosystems show a drastic decline in community abundance for 80% of studied systems, aligning with climate change predictions (IPCC 2023). Assemblage structure and species composition of marine benthic organisms, therefore, provide strong indicators of environmental conditions, offering valuable insights into the impact of warming temperatures.

Environmental shifts are equally important for benthic suspension feeders, altering their abundance, distribution, survival, recruitment and growth rates (McGarrigle & Hunt 2024). The growth and development rates of benthic invertebrates are typically positively correlated with environmental temperature to an optimal point, after which either growth rate or survival decrease (e.g. Lamare et al. 2014, Stanwell-Smith & Peck 1998). However, in certain temperate and tropical habitats, these organisms exhibit a decline in growth for some species under warming conditions (Alter et al. 2024).

One key group of marine benthic species are serpulid (Polychaeta) tube worms, sedentary benthic suspension-feeders organisms inhabiting calcareous tubes. In their habitats, these animals act as pioneer organisms and ecosystem engineers, play a vital role in habitat recolonisation, contribute to increasing local habitat complexity, and serve as high-latitude biodiversity hotspots (Montefalcone et al. 2022). These benthic marine communities are also crucial for oxygenation, bioturbation, nutrient cycling, and pollutant processing (Martins & Barros 2022), while serpulid aggregations locally influence water flow, sedimentation, water quality, and carbon fluxes (Chapman et al. 2012). Despite their essential ecological function, some serpulid species are also known for their invasive potential. Forty six invasive species have been reported in the Serpulidae family, with non-native species notable for their potential to reshape food webs, introduce diseases, and alter habitat structures, accompanied by significant economic costs (Çinar 2013). Rising sea temperatures are also considered a facilitating factor for the survival and expansion of alien polychaete species (Seebens et al. 2018).

Previous research on serpulid marine tube worms reveal varied responses to rising temperatures. On the Antarctic Peninsula, faster growth rates were observed in a community of spirorbin tube worms under warming conditions (i.e. +1°C and +2°C above ambient temperature) during the summer season, and varied responses emerged in the autumn when temperature and food availability declined (Ashton et al. 2017). In contrast, Ni et al. (2018) observed ontogenetic and seasonal growth effects on *Spirorbis spirorbis* in the Baltic Sea, with no significant difference between ambient and elevated temperatures. To date, no studies have investigated the effects of warming on the abundance, diversity, recruitment, survival, and percent cover of temperate serpulid assemblages, despite their key ecological roles.

Here, we employed *in situ* warming experiments in a New Zealand temperate serpulid worm assemblage to investigate the impacts of warming on this key group. Serpulid worms are a major component of New Zealand's coastal benthic biodiversity, with at least 471 tube worm species described (Glasby & Read 1998), and only one considered invasive (Read & Gordon 1991). New Zealand is expected to undergo significant sea temperature increases, with regional models projecting a rise of 0.8–1°C by mid-century (2036–2055) and up to 2.5°C by 2081–2100 under various emissions scenarios (Law et al. 2018). This regional warming reflects broader trends in Southern Hemisphere oceans, where average sea surface temperatures (SST) are rising faster than the global average (IPCC 2023). Within this context of long-term warming, the Southern Hemisphere is also experiencing more frequent and intense marine heatwaves (Oliver et al. 2018), which contribute to ecological changes such as kelp and sponge losses and shifts in species distributions (Bell et al. 2024; Smale 2020). These heatwaves are part of the ongoing warming process, amplifying temperature fluctuations and their associated impacts. In December 2023, La

Niña triggered a marine heatwave in New Zealand waters, with SST anomalies of +1.1˚C to +1.8˚C, impacting taxa from fish to benthic invertebrates (Cook et al. 2024). These heatwaves are projected to further increase in frequency and duration, intensifying pressures on marine ecosystems already vulnerable to warming (Domeisen et al. 2023).

Current research on the effects of warming on benthic species has primarily relied on controlled laboratory studies, mesocosm experiments, or long-term correlational analyses based on historical collections (e.g., Nguyen et al. 2011; Peck et al. 2009, 2014). However, these approaches often fail to capture the natural complexity and variability of marine ecosystems (Wernberg et al. 2012). To address these limitations, we used *in situ* heated recruitment panels—a well-established method extensively used in Antarctic field experiments to reproduce realistic ocean warming directly in the environment (Ashton et al. 2017; Clark et al. 2019).

In this study, we deployed these panels to test the effects of three warming treatments (+1°C and +2°C above ambient for three months, and a short-term acute warming mimicking a heatwave) on a temperate serpulid assemblage across three distinct seasons. The +1°C and +2°C treatments were applied as constant temperature increases relative to ambient temperature, meaning that panel temperatures fluctuated naturally through time while remaining consistently elevated. The short-term heatwave treatment was designed to reproduce, as closely as possible, the magnitude and duration of marine heatwaves observed in temperate coastal systems. Although these two fixed and one fluctuating constant temperature increases do not reproduce the full temporal variability projected under future warming scenarios, this approach provides a controlled and reproducible way to assess chronic warming effects under realistic field conditions. Moreover, the selected temperature increases correspond to near- and long-term regional projections for coastal New Zealand (Law et al. 2018; IPCC 2023), making them ecologically relevant for anticipating species and community responses to sustained ocean warming.

We hypothesised that elevated temperatures would reduce serpulid recruitment, survival, and growth—particularly under +2°C and heatwave conditions—due to increased metabolic stress, while favouring thermally tolerant serpulid taxa and altering community composition. We also expected seasonal variability to modulate these responses, with stronger impacts during periods of naturally higher thermal stress. By quantifying the effects of warming on serpulid abundance, diversity, recruitment, survival, percent cover, and growth rate, this study provides the first experimental assessment of climate change impacts on these critical benthic ecosystem engineers.

2. MATERIALS AND METHODS

2.1. Study site and materials

Bespoke heated recruitment panel experiments, using novel *in situ* technology designed by the British Antarctic Survey (Ashton et al. 2017), were deployed in June 2021 in Otago Harbour at the Portobello Marine Science Laboratory, Dunedin, New Zealand (Figure 1A–B, Figure A2, Video S1) (Lat. 45°49’S; Long. 170°38’E). The system consisted of a shore-based 240V power supply (Figure A3), 100 m power cables, and experimental panels composed of PVC blocks (15 × 15 × 5 cm). Panels were micro-abraded and etched to create a 9.8 × 9.8 cm central recruitment surface, which was evenly heated via an embedded heating element when powered. Panels were held at either

+1°C or +2°C above ambient for two constant warming treatments. A third heatwave treatment mimicked short-term warming by maintaining ambient temperature for four weeks, then increasing to +1°C for two weeks, +2°C for another two weeks, before returning to ambient for the final four weeks. This one-month period of elevated temperatures reflects the magnitude and duration of moderate marine heatwaves observed in New Zealand and similar temperate regions (Oliver et al. 2018). Although this experimental treatment does not strictly conform to the percentile-based definition of a marine heatwave (i.e. temperatures exceeding the 90th percentile for at least five consecutive days; Hobday et al. 2016), it allows assessment of the biological responses to short-term warming events while maintaining experimental control and reproducibility. Control panels remained unpowered at ambient sea temperature. Heating calibration, developed by the British Antarctic Survey, ensured uniform warming with a water layer 2–10 mm thick above the panel and ±0.03°C accuracy. In this study, no serpulids settled beyond the minimum 2 mm heated layer throughout the three seasons experiments. This observation aligns with typical growth patterns in serpulid species, which exhibit limited vertical growth due to their tube-dwelling behaviour. Studies on spirorbins have shown that growth beyond 2 mm in height is uncommon under natural conditions, as environmental and physiological constraints limit upward expansion (e.g., Glasby & Read 1998; Ippolitov & Rzhavsky 2014).

2. Plate deployment and image analysis

Four cement slabs (50 × 50 cm) were positioned vertically at depths of 3–5 m (depending on tide), 30 cm above the seafloor (Figure 1A–B, Figure A4), each holding one replicate of the three heated treatments and one control panel attached in a randomised block design using elastic cords.

Although each treatment was represented once per block, model validation indicated no violation of model assumptions or evidence for block × treatment interaction effects (checked using DHARMa residual diagnostics). Heated panels were spaced 2 cm off the concrete using PVC cylinder spacers, with four replicates per treatment and 16 panels total per deployment. Panels were deployed in three independent seasonal trials (winter, spring, summer 2021-2022), not to test for seasonal effects per se, but to assess the temporal consistency of treatment responses under varying ambient conditions (Table A1). Ambient sea temperatures were recorded hourly using loggers fixed to each slab (Figure A5). Serpulid communities were monitored monthly via high-resolution digital photography using a Nikon D100 with a NIKKOR 60 mm macro lens inside an IKELITE 200FL TTL underwater housing. A custom sliding frame enabled 35 overlapping photos (6043 × 6043 pixels) per panel at a fixed distance, later stitched in Adobe Photoshop 2021 to create full panel images (Figure 1C), then cropped to the 9.8 × 9.8 cm treatment area for analysis. Only one image set was obtained in winter due to poor visibility (Figure 1D), and a clean set of panels was used for each season. All tube worms visible on the final image set (month three) were marked and tracked backward onto previous images to monitor individuals through time. Because serpulid tubes are firmly attached to the substrate and exhibit distinctive morphological features that persist as they grow (Ippolitov & Rzhavsky, 2014), individuals could be reliably matched across time. Eleven morphospecies were recorded based on external tube morphology and confirmed with 18S rDNA barcoding (Massué et al. in review).

2.3. Size and growth rate measurements

When possible, up to five individuals per morphospecies group that settled during each seasonal experiment were measured per panel across sampling events using ImageJ v1.53 (Schneider et al.

2012), for a total of 20 individuals per group per treatment. Two tube morphologies were observed: a longitudinal serpulin form (Serpulinae) and a conispiral spirorbin form (Spirorbinae). Only spirorbin worms were measured, using radius (from coil centre to tube aperture), as serpulin numbers were too low across all seasons. Growth rate was calculated following standard approaches (see also Ashton et al. 2017 for recent applications):

$$\mathrm{R}ate\ (mm\ d^{-1}) = \frac{(Radius\ at\ T2 - Radius\ at\ T1)}{(T2 - T1)}$$

2.4. Assemblage comparisons

All individuals observed across the three-month sampling period of each panel in spring and summer were marked and numbered under a microscope for identification. Individuals present only in the last two months, the first two months, or a single month were marked differently to assess recruitment. Survival was determined by tracking all individuals observed continuously from the first to the last month of the experiment. Predation was not monitored in this study, as visual identification of predation events on serpulid individuals is challenging without clear evidence. Growth and survival data were used to calculate percentage cover over time per panel, with calculations separated into early- and late-recruitment stage individuals due to size differences. Early settlers were present for at least two months, and late settlers were observed in only one month. Early-stage area was calculated from average radius measurements, while late-stage area (0.196 mm^2) was based on the mean of ten individuals per panel. Pielou’s evenness, Simpson’s diversity, and species richness were calculated from morphospecies counts collected at the end of each experimental period, corresponding to the biologically relevant peak of community development. Because diversity was assessed once per season, ‘Season’ is confounded with sampling date. Accordingly, Season was not analysed as a biological effect of interest but was included as a temporal blocking factor to account for broad-scale environmental variability among deployments rather than to estimate seasonal effects.

2.5. Statistical analysis

Assemblage responses (community-level abundance, morphospecies-level abundance, recruitment, survival, and percentage cover), size, and growth rate data, were analysed using mixed-effects models in R environment for statistical computing version 4.4.0 (R Core Team 2024), with the DHARMa package (Hartig et al. 2024) on RStudio version 2023.06.2+561 (RStudio Team 2023). The reference model included ‘CROP’ (i.e. cement slabs), ‘Treatment’, and ‘Season’ as nested random effects, accounting for repeated measurements, using the glmmTMB package (Brooks et al. 2017). ‘Season’ was included as a random factor to account for broad-scale temporal variability among deployments rather than to test for fixed seasonal effects.

A negative binomial distribution was applied to the abundances and recruitment datasets, a beta distribution, suitable for percentage data, was applied to the survival and percentage cover datasets in their respective models. For the size data set, a gamma distribution was applied through months, and a Gaussian distribution applied for the last month event accounting for the Winter season. For the growth rate data, the Tweedie power parameter was determined empirically based on model fitting and applied using the glmmTMB package allowing selection of the most suitable distribution ($p = 1.68$), resulting in a Compound Poisson-Gamma distribution. Assumptions for each model were checked using residual diagnostics with the Goodness-of-Fit

(GOF) test, verifying dispersion, quantiles, outliers, and uniformity of residuals. The ANOVA function from the car package (Fox et al. 2023) was used to test for non-significant effects, and models were adapted accordingly based on Q-Q plots and residual plots of random effects. The reference model was as follow:

```
> count_glmmT <- glmmTMB(Value ~ (CROP + Season + Treatment + Month)^3 - CROP:Season:Treatment + (1|CTS_ID), family=nbinom2(), data=count)
```

For the size and growth rate models, control parameters for model convergence were adjusted using the glmmTMBControl() function, with maximum iterations (iter.max) and evaluations (eval.max), both set to 5000 to ensure model convergence. Additionally, the dispersion parameter was modelled as a function with two-way interactions using the nested random effects and the month variable using the dispformula argument. These adjustments were made to improve model fit and ensure stable convergence.

Models were adapted to 2-way interactions when necessary. Model selection was guided by Akaike’s Information Criterion (AIC), with the aim of identifying the most parsimonious model that best explained the data. Among models that met diagnostic criteria, the one with the lowest AIC was selected. If removing non-significant interactions resulted in a lower AIC, the last model was chosen; otherwise, non-significant interactions were retained to preserve model simplicity and interpretability. This stepwise approach ensured a balance between goodness-of-fit and model parsimony. Significant interaction effects within each model were quantified using the emmeans package (Lenth et al. 2023). To account for multiple comparisons, p-values were adjusted using the Tukey method.

Diversity indices were calculated for each season using the vegan package in R (Oksanen et al. 2023), including species richness, Shannon's index, Simpson's Diversity Index (D), and Pielou's evenness index (J). Linear models (LM) were fitted to test the effect of the warming treatment on each diversity index. Two complementary approaches were used. First, models were run separately for each season to examine treatment effects within seasons. Second, full models including 'Season' as a factor were fitted to account for overall seasonal variation and to ensure that treatment effects were not confounded by seasonal differences. Model assumptions were checked using residual diagnostics. When a significant effect of treatment was detected, pairwise differences were assessed using estimated marginal means (*emmeans*) with Tukey-adjusted tests.

3. RESULTS

3.1. Sea Temperatures

Ambient sea temperatures ranged from 8.8°C in winter to 12.5°C in spring, and reached 16.9°C in summer (Figure A5). Temperature variability was lowest in the winter deployment (ranging from 6.6 to 9.4°C), while the spring deployment showed the greatest range (7.9 to 16.8°C). Across all three experimental periods, temperatures showed relatively rapid changes in temperature on daily time scales.

3.2. Species-level abundance and diversity responses

Across the study, a total of eleven morphospecies groups were recorded within the heated areas of the experimental panels (Figure 2.E). To assess the taxonomic and thus ecological relevance of these morphologically defined groups, we verified whether they corresponded to distinct genetic lineages through a barcoding analysis based on the 18S rRNA gene (Massué et al. in review). Visual differences in both general and tube-worm-specific assemblages were evident on the recruitment plates under the warming treatments compared to the control for each experimental season (Figure 1.D).

The abundance of serpulid taxa varied significantly among treatments ($\chi^2 = 65.13$, df = 33, $p < 0.001$) and across seasons ($\chi^2 = 169.25$, df = 22, $p < 0.001$). However, most morphospecies groups did not exhibit significant differences in abundance among seasons, with the exception of the morphospecies group 9, 2, and 6, being more abundant in winter, spring, and summer, respectively (Figure 2). Some morphospecies groups were absent during specific seasons or in certain treatments. For example, Serpulinae sub-family groups (i.e. morphospecies groups 8, 9, and 10) were rarely observed, and almost exclusively detected in winter, with only a small number of individuals detected in spring for the morphospecies groups 8 and 9. Similarly, the morphospecies group 11, belonging to the Spirorbinae sub-family, was rarely observed, and not detected in winter or in control treatments. In terms of treatment effects, most morphospecies groups were significantly more abundant in the control treatment compared to the warming treatments, with the most pronounced reductions observed under the +2°C treatment above ambient temperature (Figure 2).

Despite changes in the abundance of individual in morphospecies groups, no significant differences in overall species richness or diversity indices (e.g., Pielou's evenness index, Simpson's Diversity Index) were observed across treatments for the three experimental seasons (Figure 3). In spring, the heatwave treatment showed significantly lower species richness than all other treatments, including the control (t = 5.06, df = 12, p = 0.0014) and both warmed treatments (+1 °C and +2 °C; t = −3.37, df = 12, p = 0.0248 for each contrast). However, this effect was not retained when season was included as a factor in the full model, indicating that the initial result was sensitive to seasonal variability. Overall, both single-season and full linear models consistently showed no treatment effect on diversity metrics. The limited sample size (n = 4) likely reduced the ability to detect subtle effects.

3.3. Assemblage responses

The overall abundance of serpulid tube worms (i.e. morphospecies groups and late-recruitment stages not identifiable) on panels did not show any significant differences among treatments in winter (Figure 4.A). In spring, treatment effects became evident at the end of the season, with tube worm abundance being approximately three times higher on the control treatment compared to the +2°C and heatwave treatments (Figure 4.A). While the abundance on the +1°C treatment was significantly higher than on the +2°C treatment, it was also lower than on the control, although not significantly. In summer, abundance on the +1°C treatment was at least twice as high as on the +2°C treatment, this trend remained consistent throughout the season. In contrast, abundance on the control treatment increased over time, becoming approximately 10-fold higher than on the +2°C treatment and four-fold higher than on the +1°C treatment by the end of the season (Figure 4.A). During the second month of the summer experiment, when the heatwave treatment was sequentially warmed to +1°C and +2°C over a period of two consecutive weeks, a decrease in abundance was observed compared to the control, although not statistically significant.

Recruitment of new serpulid individuals followed similar trends to overall abundance in spring and summer (Figure 4.B). In spring, by the end of the three months, recruitment was significantly higher in control treatments compared to all warming treatments, while in summer, tubeworm recruitment decreased distinctly during the active phase of the heatwave treatment compared to the control.

Serpulid survival rate was significantly higher on the control treatment compared to warming treatments in both spring and summer seasons. In summer survival rate on the control more than doubled compared to warming treatments (Figure 5.A), while in spring, survival on the +1°C treatment was significantly higher than on the +2°C and heatwave treatments, though still significantly lower than on the control.

Due to differences in recruitment and survival, the percentage cover on the panels varied considerably in spring and summer. Tube worm coverage was at least twice as high on control panels compared to warming treatments in spring and three-fold higher in summer (Figure 5.B). The +1°C treatment had significantly greater coverage than the +2°C treatment at the end of the spring season and throughout the summer season. The heatwave treatment displayed variable percentage cover over time in spring and exhibited a similar declining trend to the +1°C treatment in summer, although significantly higher throughout the season (Figure 5.B). No significant differences in serpulid coverage were observed between treatments in winter.

3.4. Size and growth rate responses

Size and growth rate analyses were conducted exclusively on Spirorbinae tube worms, as Serpulinae individuals were largely absent across the three experimental seasons. Due to the low number of individuals per morphospecies in each treatment, data were pooled across morphospecies for statistical analyses. This reduced problems associated with sparse data and improved the robustness of the models. While this approach limits interpretation at the morphospecies level, it allows assessment of the overall assemblage response to warming among ecologically similar taxa.

Spirorbin tube worms size and growth rate responses to warming varied across warming treatments among seasons, while those on control plates displayed relatively constant responses (Figure 6). In both the spring and summer seasons, the average size of spirorbins on control plates had a slightly larger average size than those on warming treatments, with these differences becoming significant only at the end of the experimental seasons (Figure 6.B). At the start of the summer season, spirorbins exposed to warming treatments were significantly larger than those on control plates, although the difference in size under the +2°C treatment was not statistically significant compared to the control (Figure 6.B). No significant size differences were observed among warming treatments over time during either season, except in the second month of the spring season, where spirorbins under the +2°C treatment were significantly smaller compared to those on other warming treatments (Figure 6.B).

The growth rate of spirorbins generally declined over time on all plates and in each season, but the rate of decline varied among treatments (Figure 6.A). In spring, spirorbins on the heatwave and +1°C warming treatments initially had growth rates similar to those on control plates, but by the end of spring, growth rates on warming treatments were significantly slower than on control plates (except for +2°C). The reverse trend was observed in summer, where spirorbin growth rates were significantly slower at the start of the season for all warming treatments compared to the control, and by the end of summer, growth rates on warming treatments were slower than on control plates, but not significantly so (Figure 6.A). In winter, no significant differences in spirorbin size were detected among treatments at the end of the season, although average sizes on warming treatments tended to be larger than those on control plates (Figure 6.C).

4. DISCUSSION

This study examined the impact of simulated ocean warming on the structure and dynamics of temperate serpulid communities in New Zealand. Simulating mid- and end-century warming scenarios (+1°C and +2°C above ambient) and a short-term heatwave, we observed significant responses in abundance, recruitment, survival, percentage cover, and growth rate. The strongest effects occurred under the +2°C treatment, with seasonal variability further influencing outcomes. In winter, when ambient temperatures were lowest, no significant differences were detected across treatments, suggesting that thermal tolerance and sub-lethal functioning were not exceeded, thus maintaining similar ecological patterns and indicating that winter warming may have limited impact. Significant effects appeared by late spring and persisted through summer, suggesting that thermal stress becomes relevant as ambient temperatures rise. The typical spawning time for serpulid species occurs in late spring and summer (Potswald 1965), aligning with the observed periods of increased thermal stress and ecological impact. Seasonal variability underscores thus that warming impacts are not uniform year-round but intensify when environmental temperatures approach or exceed species' upper thermal limits.

4.1. Abundance and diversity

The abundance of serpulids was significantly influenced by both warming treatments and seasonal changes, leading to shifts in community composition under elevated temperatures. The morphospecies group 6 was abundant during summer under ambient conditions, suggesting strong species-specific thermal tolerances to natural fluctuations. However, when temperatures exceeded seasonal norms, as under future warming scenarios, overall serpulid abundance declined sharply, despite some species showing greater resilience. Morphospecies groups 8, 9, and 10 (Serpulinae sub-family) were notably absent during the warmer spring and summer months, indicating lower thermal tolerance within this sub-family. In contrast, the persistence of morphospecies group 11 (Spirorbinae sub-family) in heated treatments suggests greater resilience to thermal stress.

Several studies have shown species-specific thermal limits in serpulids, beyond which physiological stress and mortality increase. For example, *Ficopomatus enigmaticus* shows reduced survival in both larval and adult stages under elevated temperatures (Peria & Pernet 2019), while *Hydroides elegans* displays variable thermal tolerance across generations and developmental stages, with evidence of transgenerational acclimation (Genovese 2024).

Despite species-specific declines in abundance, overall diversity indices did not significantly decrease under warming. This suggests shifts in the proportional representation of morphospecies, with seasonal changes influencing dominance patterns and altering community composition.

4.2. Recruitment, survival, and percentage cover

Recruitment, survival, and percentage cover of serpulid worms were significantly affected by warming, with marked seasonal variation. Recruitment peaked in summer under ambient conditions but declined notably under elevated temperatures; by two- to three-fold under +1°C and three- to four-fold under +2°C. These reductions align with findings that serpulid recruitment depend on environmental factors like temperature, salinity, and microbial biofilms (Breaux et al. 2023). Even mild thermal deviations can impair larval development and metamorphosis (Lavajoo & Amrollahi Biuki 2015), while altered biofilm composition may disrupt larval recruitment cues, limiting colonisation (Lau & Qian 2001).

Survival showed similar patterns, with increased mortality under warming. Elevated temperatures affect early stages by increasing embryonic abnormalities and reducing larval survival (Sánchez-Ovando et al. 2023), and also lower gamete quality and fertilisation success in adults (Kupriyanova & Havenhand 2005). These sublethal stressors can compromise population persistence, especially with repeated or prolonged exposure. Adult survivorship also drops under sustained thermal stress, as observed in *Serpula vermicularis* (Hughes et al. 2008), likely due to impaired respiration and higher metabolic demands (Wang et al. 2021).

Warming also reduced percentage cover, despite natural summer peaks under ambient conditions. Cover declined by late summer under elevated temperatures, likely due to physiological constraints on calcification or increased energetic costs (Clark et al. 2019; Gold & Vermeij 2023). Reduced cover may shift competitive balances in favour of faster-growing or thermally tolerant fouling species (e.g. bryozoans, ascidians; Pansch et al. 2018), leading to overgrowth or exclusion of serpulids and threatening their structural and ecological role in benthic communities.

4.3. Size and growth rate

Growth rates of Spirorbinae tube worms showed a clear response to warming, with significantly slower growth under elevated temperatures. In both spring and summer, growth declined under future warming scenarios (+1°C and +2°C above ambient), either early in the season or as it progressed. Under ambient conditions, newly settled spirorbins exhibited faster initial growth and reached maturity rapidly, consistent with observations in other temperate serpulids (Lucey et al. 2018). In contrast, warming reduced both growth rate and final size, likely due to metabolic constraints or trade-offs between calcification and maintenance under thermal stress (Li et al. 2014). While warming accelerates growth in Antarctic spirorbins (Ashton et al. 2017), our results suggest that in temperate species, it may exceed optimal physiological limits, reducing growth over seasonal timescales.

Serpulid physiology is strongly affected by physical factors such as temperature, salinity, and acidification, which regulate calcification, reproduction, and survival (Montefalcone et al. 2022). Rising sea temperatures, along with shifts in carbonate chemistry, may impair tube formation and maintenance, leading to weaker structures and increased mortality (Ni et al. 2018). Furthermore, phenological shifts in planktonic food availability due to climate change may constrain growth if warming disrupts the timing of primary production (Calbet 2024).

4.4. Serpulid responses to marine heatwaves

In contrast to constant elevated temperature treatments, the heatwave scenario (simulating short-term warming events) also reduced serpulid recruitment, survival, percentage cover, and growth rate. While summer abundance was unaffected at the community level, recruitment declined during the warming phase and partially recovered once temperatures returned to ambient, suggesting that early serpulid development is sensitive to short-term thermal fluctuations. Survival and growth trends mirrored those of constant warming, though percentage cover under heatwave conditions was higher than in +1°C and +2°C treatments, yet still below control levels.

These findings align with studies showing that marine heatwaves can exceed species' physiological thresholds (Pansch et al. 2018), including in New Zealand (Cook et al. 2024), as our observed declines in serpulid recruitment, survival, and growth under heatwave conditions suggest similar stress responses. Heatwave effects vary with warming rate and function, as some processes like righting in sea urchins are more thermally resilient than others like feeding (De Leij et al. 2022). Heatwaves are also recognised as major stressors to marine biodiversity and ecosystem function (Smale et al. 2019), and are linked to mortality events (Bell et al. 2024), shifts in community structure, and interactions with other pressures such as pollutants (Vellani et al. 2024). In serpulids, including reef-forming *Ficopomatus enigmaticus*, heatwaves may alter biomarkers and impact key life history traits, particularly during early stages (Vellani et al. 2024). These results suggest that short-term thermal events may be as or even more influential than chronic warming in shaping the structure and persistence of benthic assemblages, including foundation species like serpulids.

4.5. Ecological role and invasive potential of serpulids

This study has important implications for the future of temperate benthic communities under climate change. As key ecosystem components, serpulids contribute to habitat formation, nutrient cycling, and biodiversity (Montefalcone et al. 2022). Declines in abundance, recruitment, survival, cover, and growth under warming suggest that these organisms may struggle to maintain their ecological roles. Serpulid reefs, like those of *Serpula vermicularis*, support high biodiversity (Chapman et al. 2012), and their loss could trigger cascading effects on associated species and functions. Shifts in species composition and dominance, with some morphospecies persisting in warmer treatments, may lead to community restructuring and altered interactions (Brundu & Magni 2021). Losing less thermally tolerant species could reduce functional diversity, impair carbon cycling, and simplify habitats, ultimately threatening ecosystem resilience.

Thermal stress may also increase vulnerability to opportunistic serpulids, known to expand in disturbed or warming environments (Çinar 2013). While no invasive species were observed in Otago Harbour (Massué et al. in review), other studies link warming to their spread and negative impacts (Schwindt et al. 2001). Introduced serpulids can dominate space, displace natives, and alter interactions (Schwan et al. 2015), while causing economic harm through biofouling (Çinar 2013). Environmental stress may further aid their establishment via facilitation by native species

(Uyà et al. 2020). Given these risks, ongoing monitoring is essential to detect and mitigate future invasions.

4.6. Conclusions

The impact of future warming scenarios and short-term heat events on temperate serpulid assemblages, especially in summer, was evident. While some serpulid groups exhibit a degree of thermal tolerance, overall declines in all ecological indices highlight the vulnerability of their ecological roles in benthic habitats. The short-term nature of this study limited scope for adaptation, though some species may persist via phenotypic plasticity or selection of thermally tolerant genotypes, a critical mechanism for marine taxa under rapid climate change (Reusch 2014). Yet, how much these responses can offset wider ecological disruptions remains unclear. While our experimental treatments (+1°C and +2°C constant temperature increases and short-term heatwaves) do not capture the full range of natural temperature variability or strictly meet the statistical definition of marine heatwaves, they provide controlled, reproducible, and ecologically relevant conditions to assess how serpulid assemblages respond to both chronic and acute warming.

Our experimental approach, despite these limitations, accounted for natural variability and potential interactions with other environmental factors. Although treatments were unreplicated within blocks, model validation indicated no lack of fit or interaction effects, suggesting that the block structure adequately captured local variability without biasing treatment responses. This consideration of natural variability is essential, as abiotic stressors like oxygen, pH, salinity, and food availability interact with warming and influence serpulid dynamics. These stressors may further impair resilience across life stages by affecting key processes such as larval development and recruitment under hypoxia (Leung et al. 2013), osmoregulation under altered salinity (Peria & Pernet 2019), and calcification under acidification (Díaz-Castañeda et al. 2019). Fluctuating pH also impacts mortality and fecundity in calcifiers (Shi & Li 2024), while food and hydrodynamics affect feeding and larval viability (Bolton & Havenhand 2005). These interacting pressures suggest that warming alone may not solely drive shifts in serpulid assemblages and that a broader range of environmental variables should be considered under future trajectories of temperate serpulid communities.

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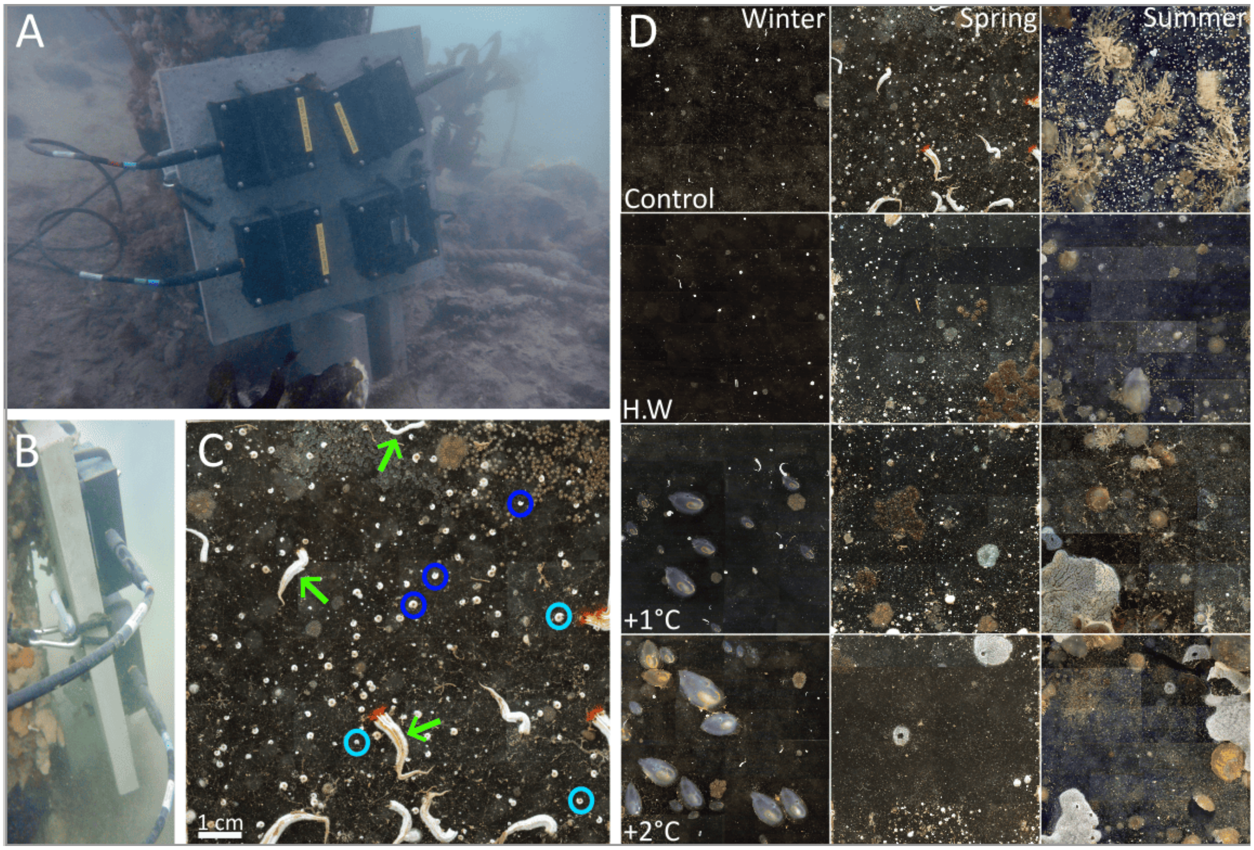


Figure 1. (A) Four experimental plates attached to a cement paving slab (50 cm x 50 cm), 3 m depth in the Otago Harbour. Note the array is kept 20 cm off the seafloor and is attached to a wharf piling. The elastic cords holding the panels in place are evident. Note that the heated area is between the inner surface of the panels and the concrete slab. (B) A side-view of the paving slab with panels attached. (C) A single panel showing a serpulid assemblage. The serpulin organisms are pointed by green arrows, and the

spirorbin organisms are circled by blue circles (anticlockwise in dark blue and clockwise in light blue). (D) Examples of *in situ* heated panels at the end of each season studied. Each season (Winter 2021, Spring 2021, and Summer 2021/2022) was deployed over three months under a control and warming treatments (+1°C and +2°C above ambient, and heatwave[H.W]). Each image (for C and D) shows an entire experimental recruitment surface (9.8 x 9.8 cm).

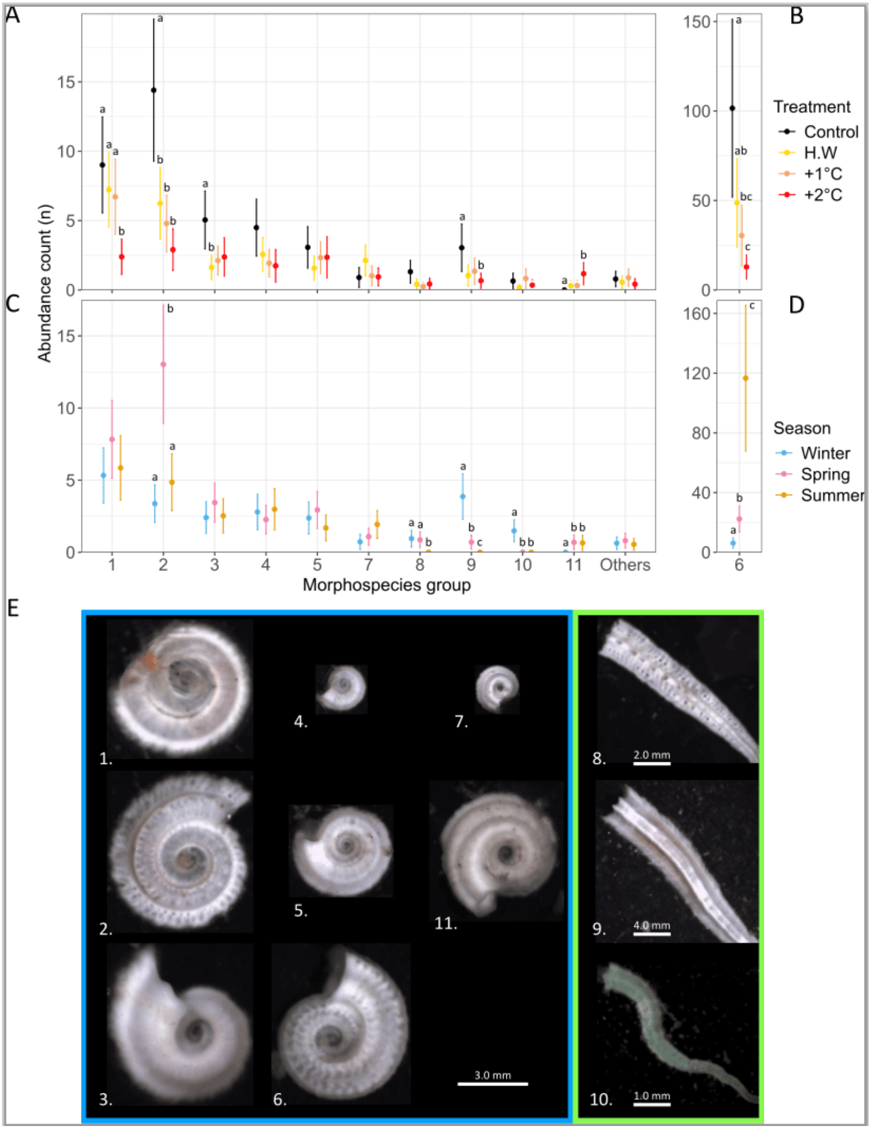
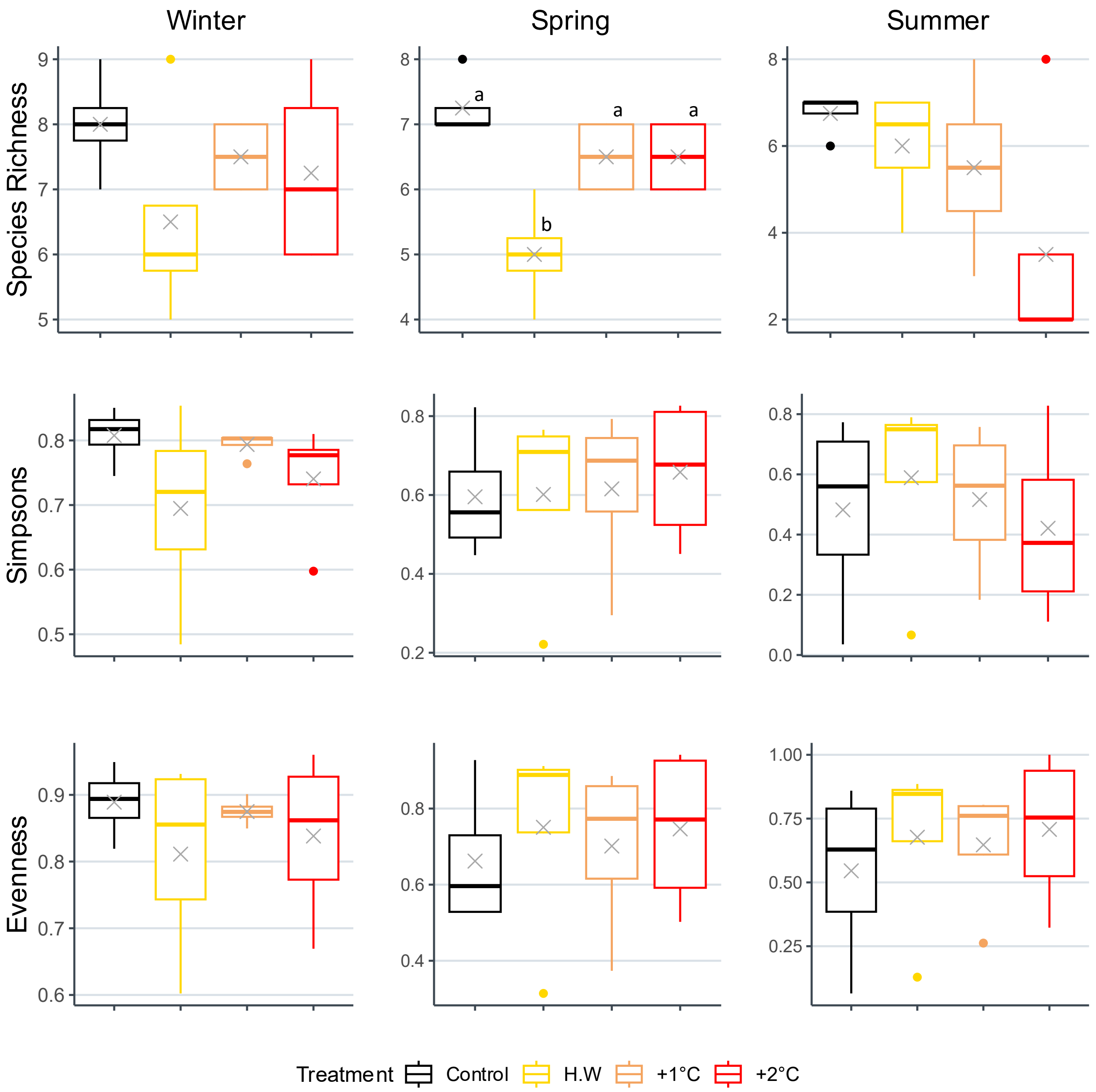


Figure 2. Abundance count per morphospecies group presented in Massué et al. in review: (A) and (B) averaged across the level of season under warming treatments. (C) and (D) averaged at the level of treatment per experimental seasons. Due to its high abundance, the morphospecies group 6 is displayed in separate graphs (B and D) for clarity. Data show the estimated marginal means (EMMs) and 95% confidence intervals (CIs), accounting for the effects of other variables in the model. The morphospecies group "Others" regroups unidentified early-stage individuals. Differences of lowercase letters indicate significant differences of

694 abundance within each morphospecies groups ($p < 0.05$). H.W = Heatwave treatment. (E) Illustration of the morphospecies groups

695 from the Spirorbinae sub-family (blue rectangle), and the Serpulinae sub-family (green rectangle).



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697 **Figure 3.** Diversity indices (species richness, Simpson's diversity index, and Pielou's evenness index) under warming and control

698 treatments at the end of each seasons. Boxplots show the median and interquartile range, while the grey crosses indicate the

699 means, and the solid symbols the range. Differences among treatments were only detected for species richness in spring, where

the heatwave (H.W) treatment showed lower values than all other treatments ($p < 0.05$; letters indicate significant pairwise contrasts). However, this effect did not persist when season was included as a factor in the full model.

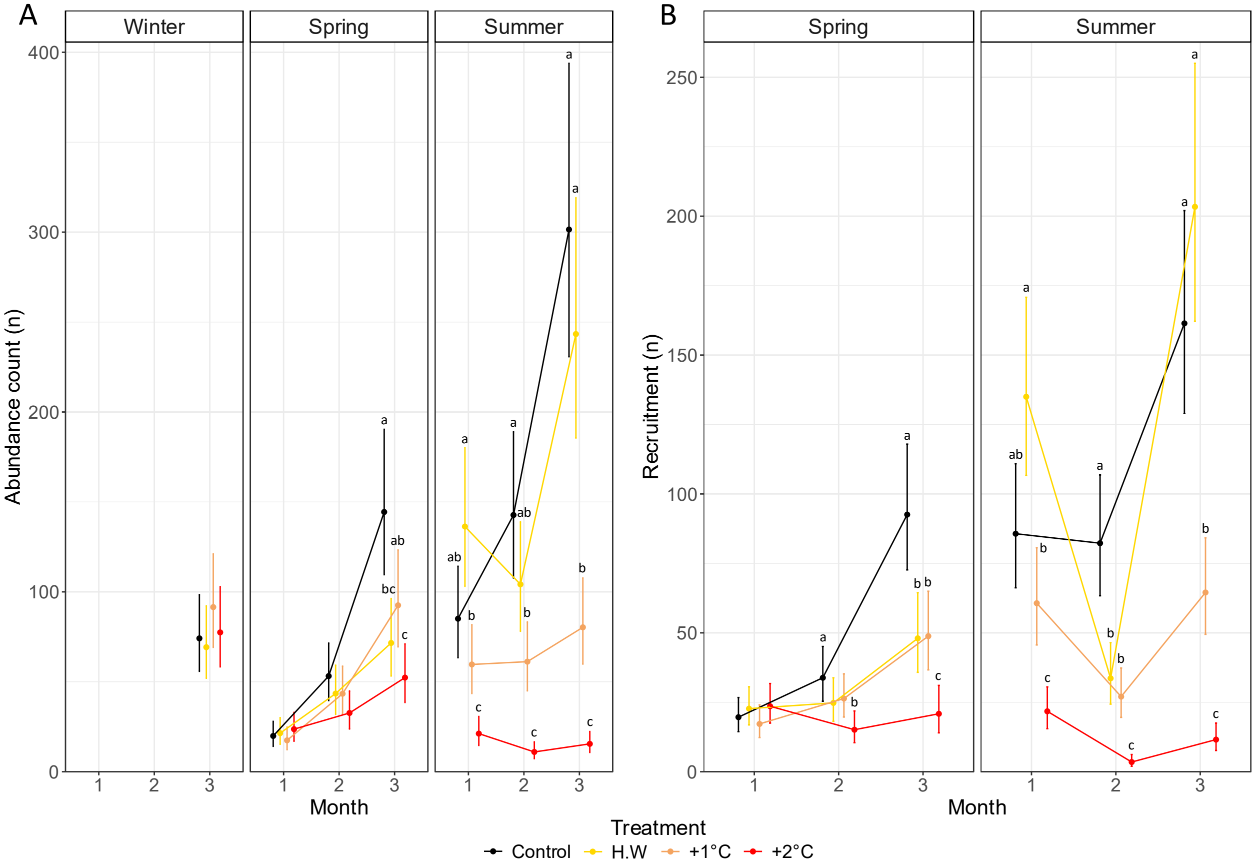

Figure 4. Abundance count of the overall serpulid tube-worms assemblage (A), and recruitment count (B) through time under warming and control treatments per seasons. The points signify the estimated marginal means (EMMs) and the error bars are for the 95% confidence intervals (CIs), accounting for the effects of other variables in the model. Different lowercase letters indicate significant differences between treatments for each month of each season ($p < 0.05$). H.W = Heatwave treatment.

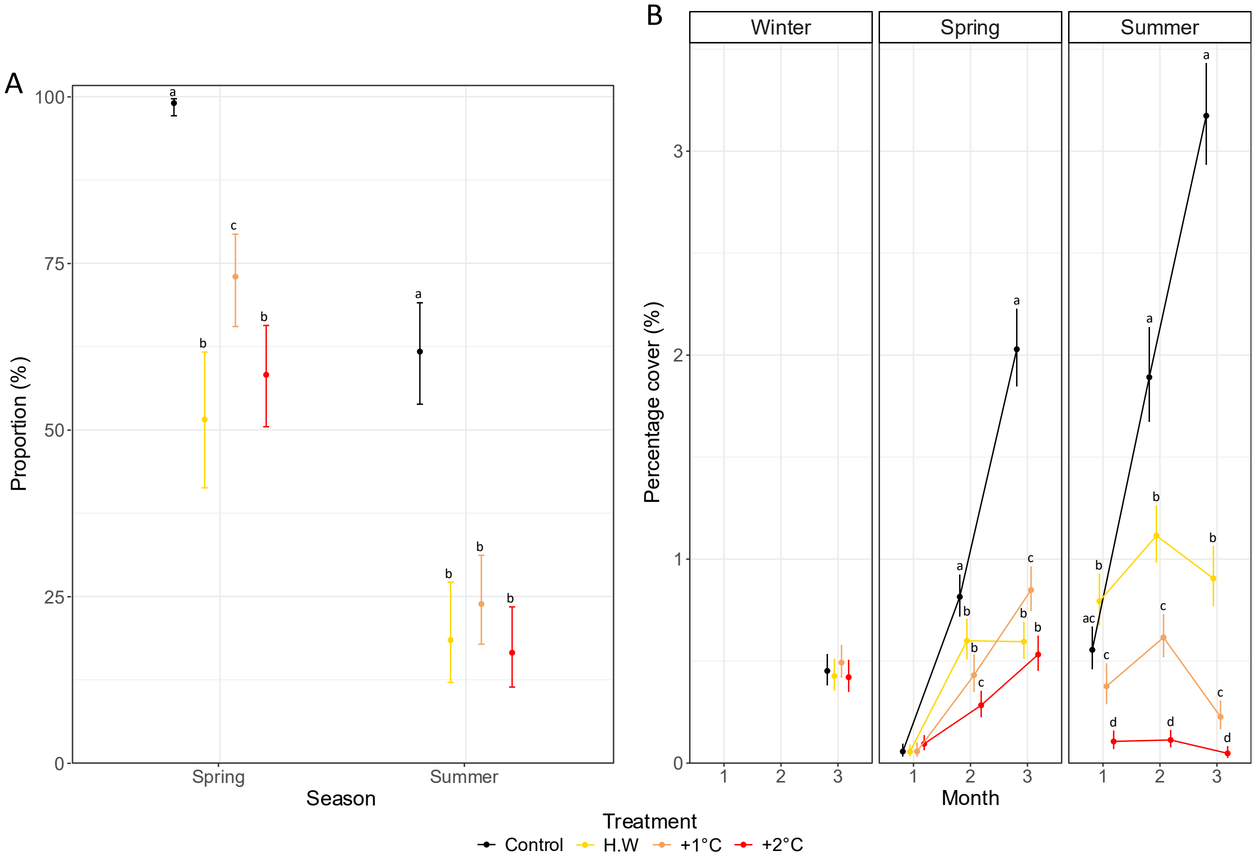

Figure 5. Survival proportion (A), and percentage cover through time (B), of serpulid tube-worms under warming and control treatments per seasons. The points signify the estimated marginal means (EMMs) and the error bars are for the 95% confidence intervals (CIs), accounting for the effects of other variables in the model. Different lowercase letters indicate significant differences between treatments for each season, or for each month of per season ($p < 0.05$). H.W = Heatwave treatment.

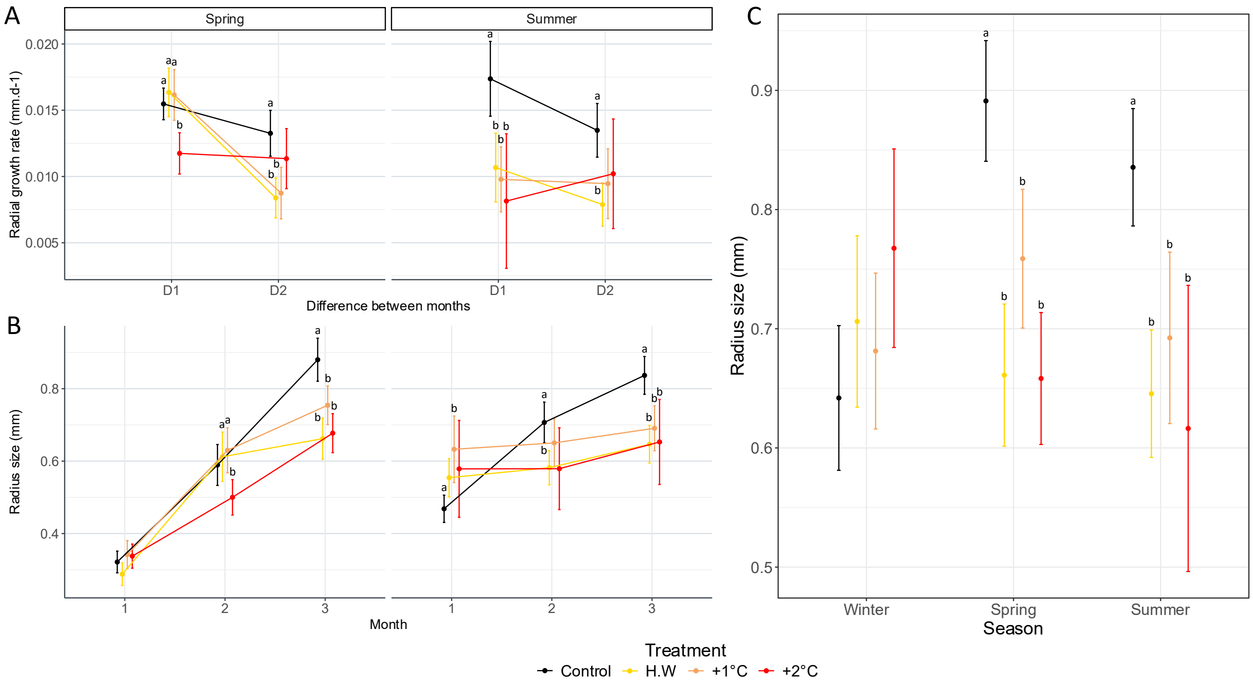

Figure 6. Growth rate (A) and size (B) responses of spirorbin tube-worms through time under warming and control treatments per seasons. (C) Size responses of spirorbin tube-worms under warming and control treatments only at the end of the experimental seasons including winter. For all graphs, the points signify the estimated marginal means (EMMs) and the error bars are for the 95% confidence intervals (CIs), accounting for the effects of other variables in the model. Different lowercase letters indicate significant differences between treatments for each months or differences of each season for (A) and (B), and for each season for (C) ($p < 0.05$). H.W = Heatwave treatment.

APPENDICES

Table A1. Deployment, photography, and retrieval dates of heated panels at the Portobello Marine Science Laboratory, by season.

Deployment Season	Deployment Date	Photographed	Retrieved and Sampled	Days - Weeks duration
Winter	2021-06-11	2021-09-10	2021-09-10	91 days - 13 weeks
Spring	2021-09-14	2021-10-14&15 2021-11-08 2021-12-06	2021-12-06	83 days - 12 weeks
Summer	2021-12-07	2022-01-11 2022-02-02 2022-03-01	2022-03-01	84 days - 12 weeks

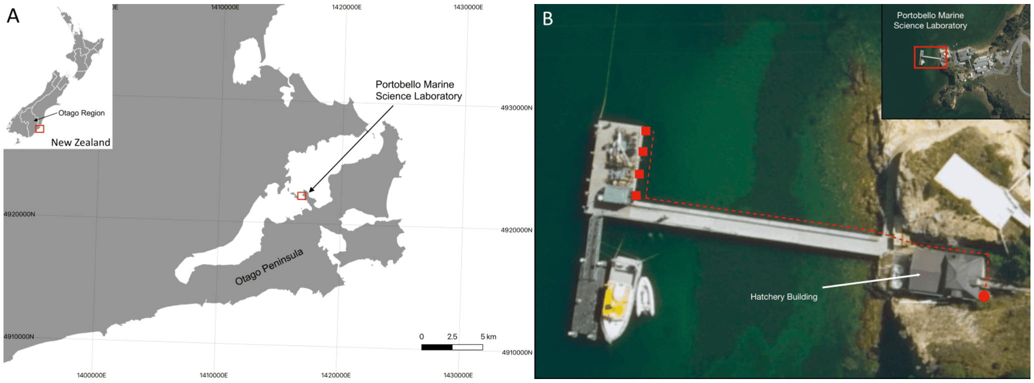

Figure A2. (A) Deployment site of the heated panels at the Portobello Marine Science Laboratory, outlined by a red square, on the Otago Peninsula, Dunedin, New Zealand. (B) Map of the Portobello Marine Science Laboratory and its wharf. The red square indicates the location of the four concrete slabs attached to the wharf columns. The red dot marks the power supply unit behind the hatchery building. The red dashed line shows the cables connecting the panels to the unit. Image retrieved from Google Earth (2022).

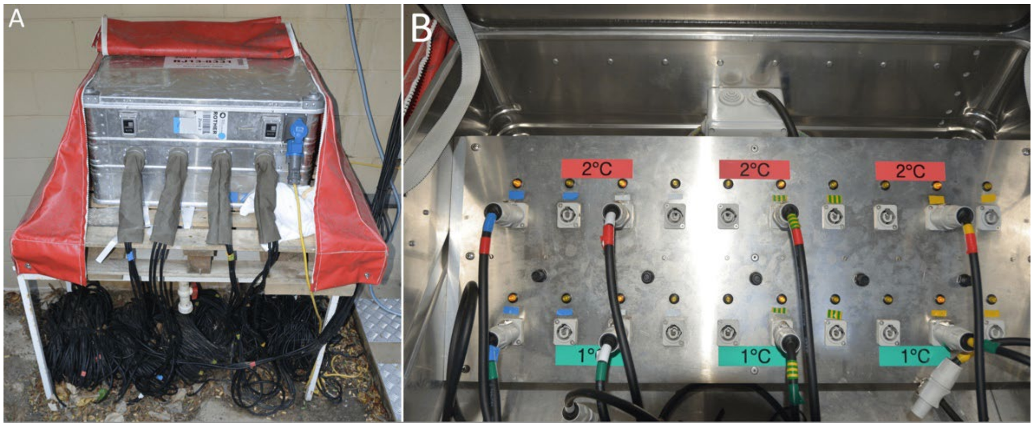

Figure A3. (A) Illustration of the power supply and the twelve cables (three per replicate) connected to it. Each cable is 100 m long. (B) Illustration of the inside of the power supply unit, where cables are connected either to a +1°C or a +2°C outlet.

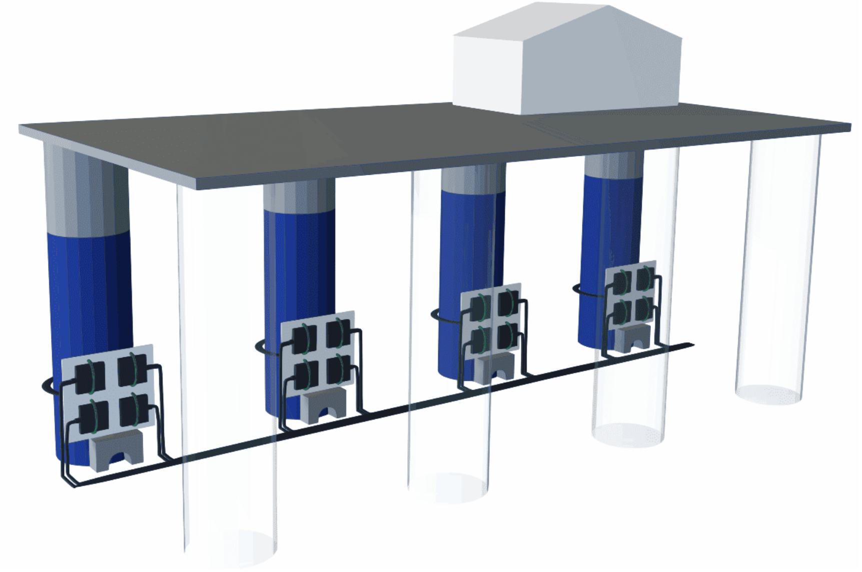

Figure A4. Three-dimensional model of the heated panel experiment beneath the wharf at the Portobello Marine Science Laboratory, Dunedin, New Zealand. Four cement slabs are elevated on concrete blocks at the base of each wharf column. All panels are secured to the slabs with elastic cords and connected by cables to the power supply unit located behind the hatchery building (see Figure A2, A3).

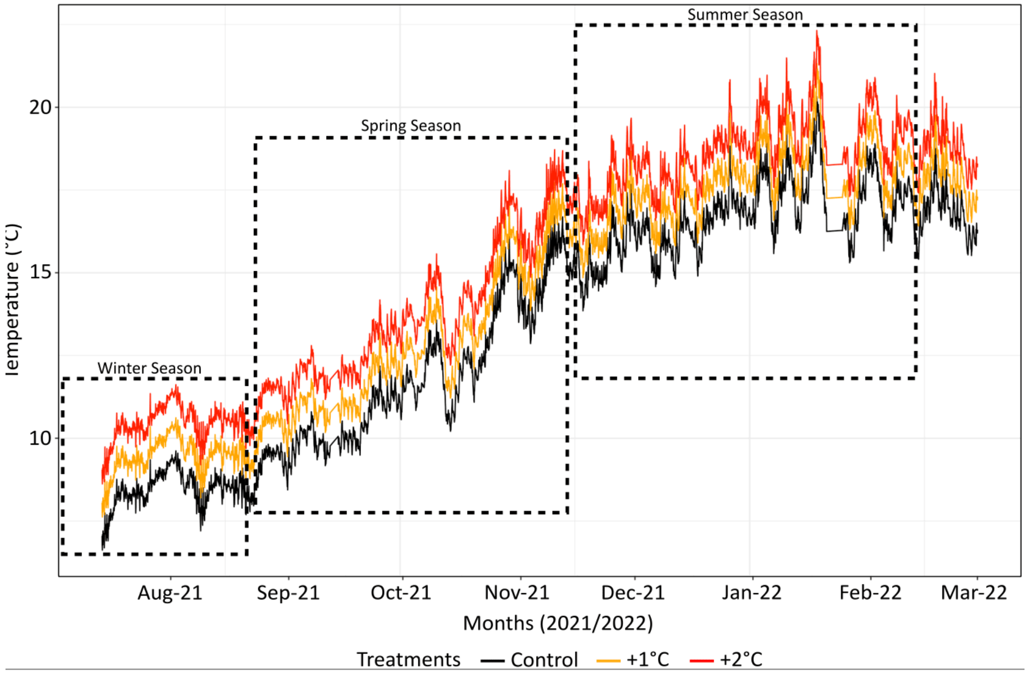

Figure A5. Ambient sea surface temperatures at the Portobello Marine Science Laboratory during the three seasons studied, from July 2021 to March 2022. Note the +1°C or +2°C treatment temperatures were not measured directly, but are plotted as temperatures +1°C or +2°C above the reported ambient temperatures. Boxes represent temperature ranges for each season.

Video S1. Visualisation of the four cement slabs, each supporting four heated panels elevated on concrete blocks at the base of each wharf column at the Portobello Marine Science Laboratory, Dunedin, New Zealand. Cables connected the heated panels to the power supply and lay on the seafloor for a short distance before being secured under the wharf to reach the power unit.