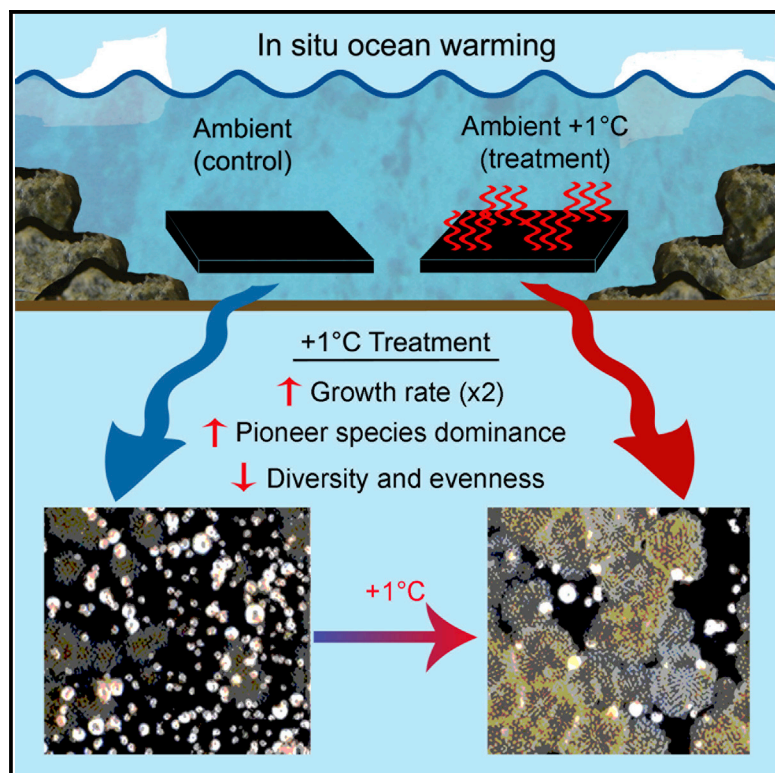


# Current Biology

## Warming by 1°C Drives Species and Assemblage Level Responses in Antarctica's Marine Shallows

### Graphical Abstract



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### In Brief

Ashton et al. describe population to assemblage level responses to the most realistic in situ warming of marine life to date, implemented in Antarctica. These include surprising increases in growth rate with a 1°C rise in sea temperature and domination of the benthic community by a pioneer species that dramatically altered community structure.

### Highlights

- Unexpected growth increases in response to experimental in situ ocean warming are shown
- A 1°C rise in sea temperature nearly doubled growth of Antarctic seabed life
- A 2°C rise produced divergent responses with resultant high assemblage variability
- A single *r*-strategist pioneer dominated cover, diversity, and evenness response



# Warming by 1°C Drives Species and Assemblage Level Responses in Antarctica's Marine Shallows

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## SUMMARY

Forecasting assemblage-level responses to climate change remains one of the greatest challenges in global ecology [1, 2]. Data from the marine realm are limited because they largely come from experiments using limited numbers of species [3], mesocosms whose interior conditions are unnatural [4], and long-term correlation studies based on historical collections [5]. We describe the first ever experiment to warm benthic assemblages to ecologically relevant levels in situ. Heated settlement panels were used to create three test conditions: ambient and 1°C and 2°C above ambient (predicted in the next 50 and 100 years, respectively [6]). We observed massive impacts on a marine assemblage, with near doubling of growth rates of Antarctic seabed life. Growth increases far exceed those expected from biological temperature relationships established more than 100 years ago by Arrhenius. These increases in growth resulted in a single “*r*-strategist” pioneer species (the bryozoan *Fenestrulina rugula*) dominating seabed spatial cover and drove a reduction in overall diversity and evenness. In contrast, a 2°C rise produced divergent responses across species growth, resulting in higher variability in the assemblage. These data extend our ability to expand, integrate, and apply our knowledge of the impact of temperature on biological processes to predict organism, species, and ecosystem level ecological responses to regional warming.

## RESULTS

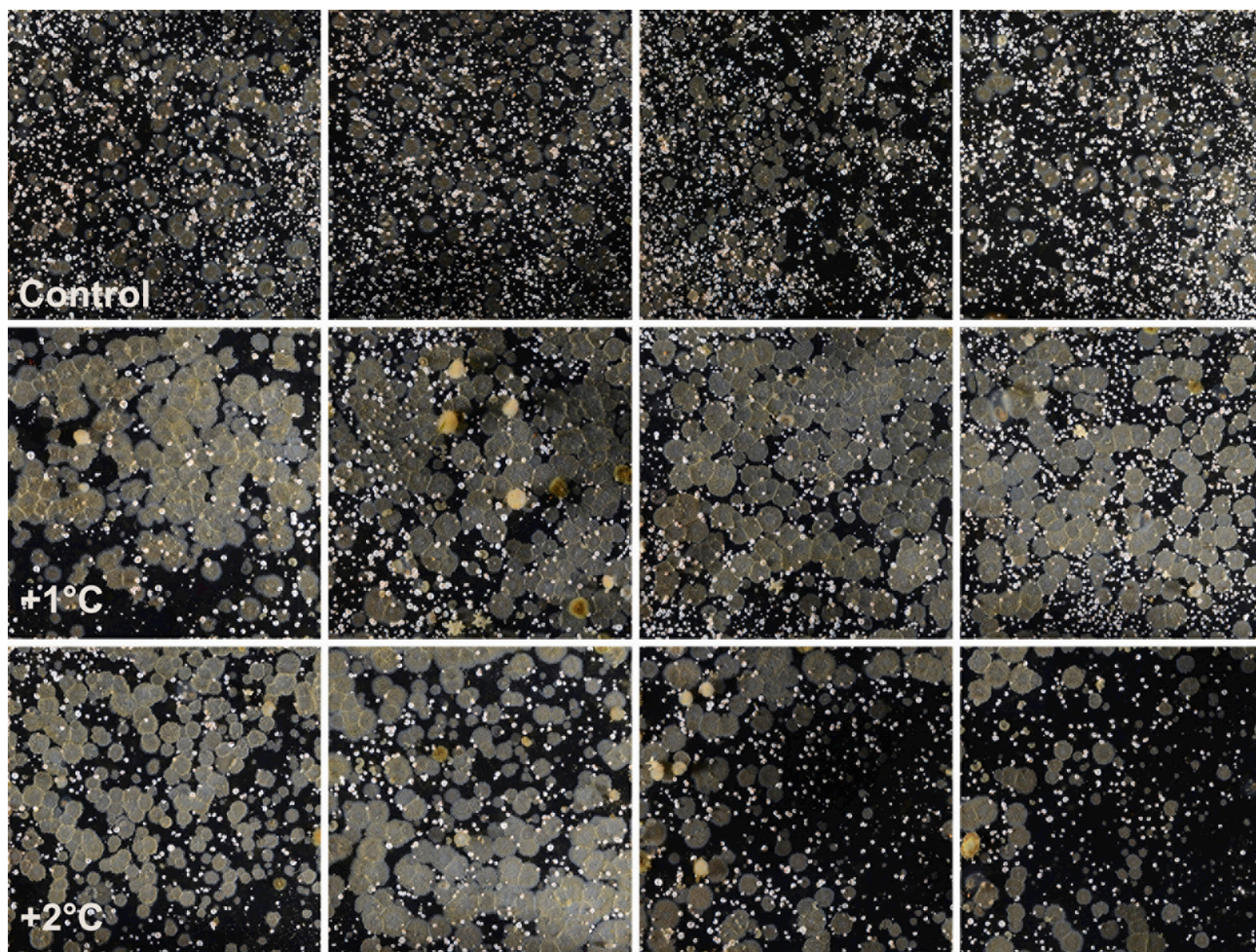
The hard substratum colonizers that developed under 1°C and 2°C warming conditions were visibly different from those observed on un-heated controls (Figure 1). We evaluated growth across six spatially dominant species, with growth rates in the +1°C treatments increasing in all and more than doubling in some species (Figure 2). Individuals of two key space occupiers were significantly larger in the +1°C treatments after 2–3 months (Figure 2A;  $F_{(1,9)} > 14.4$ ,  $p < 0.01$ ); colonies of the spatially dominant bryozoan *Fenestrulina rugula* grew to more than twice the

surface area after just 2 months, and individuals of the spirorbid worm *Romanchella perrieri* were on average 70% larger than controls (Figure 2A).

Growth-rate responses to warming were different among species, ages, and seasons (month). Growth rates in all species were higher in warmed treatments through the summer (December through February; Figure 2B), but different responses among species were observed in March, when both food availability for suspension feeders and ambient temperature declined (Figure S1). March growth rates of two spirorbid species with 1°C of warming remained higher than those at ambient temperatures. In one species, however, growth rate in March declined in all treatments, including controls (*R. perrieri*), whereas growth of *Protolaeospira stalagmia* continued to increase (Figure 2B). The growth rates of two bryozoans (*F. rugula* and *Celleporella antarctica*) at +1°C declined toward the end of summer, more so than those living on ambient temperature plates. Growth rates of other bryozoans (*Micropora notialis* and *Ellisina antarctica*), however, increased with 1°C of warming but remained within the variance of those held at ambient temperatures.

Warming of 2°C above ambient produced more variable growth responses among species. The responses varied among the two spatially dominant species, resulting in larger colonies of the bryozoan *F. rugula* than those grown at ambient temperatures ( $F_{(1,9)} > 14.4$ ,  $p < 0.01$ ) but smaller than those at 1°C above ambient. In contrast, the spirorbid *R. perrieri* showed a similar size increase in all heated treatments (Figure 2). Similar growth rates were also observed in both warming treatments (+1°C and +2°C) of two bryozoans *C. antarctica* and *E. antarctica* (Figure 2B). Two species (the bryozoan *M. notialis* and the spirorbid *P. stalagmia*) showed an additional 20%–30% increase in growth rate at +2°C compared to +1°C. The magnitude of the differences among growth rates also changed through the season.

After 9 months in situ, the spatial composition of species was significantly different under 1°C of warming compared to controls (analysis of similarity [ANOSIM],  $R = 0.33$ ,  $p = 0.03$ ; Figures 3B and 3C). Assemblage differences were detectable under 2°C of warming (see Figure 1), but these were not significantly different from either the control or +1°C treatments (ANOSIM,  $R = 0.396$ ,  $p = 0.06$ ; Figures 3B and 3C). The spatially dominant bryozoan *F. rugula* and the availability of free space explained the similarity of compositions within treatments (contributing up to 50% of the total; Figure 3E), whereas multiple rarer species were responsible for differences between treatments.



**Figure 1. Panel Assemblages after 9 Months In Situ Illustrating the Visibly Distinct Communities**

End-point photographs of all control (top), +1°C (middle), and +2°C (bottom) panels. Each image shows an entire experimental settlement surface (9.8 × 9.8 cm). Note the two +2°C panels on the bottom right, which appear uniquely uneven in their recruitment. See also [Figure S2](#).

Overall, 23 taxa were identified on the panels, with species assemblages dominated by bryozoans and spirorbid polychaetes but also including ascidians, hydroids, and sponges. Eight taxa colonized all panels. Species responded differently to the treatments in assemblage metrics. For example, percent cover responses included (1) increase with 1°C of warming but less so with 2°C of warming (e.g., *F. rugula*; [Figure 3E](#)); (2) decrease with 1°C of warming but less so with 2°C of warming (e.g., *Protolaeospira stalagmia*; [Figure 3E](#)); and (3) decrease with increased temperature (e.g., *Romanchella perrieri*; [Figure 3E](#)). The greater index of multivariate dispersion (IMD) values revealed that spatial assemblages on control panels were more similar to each other than those within either heated treatment (i.e., the assemblages on panels in either treatment were more variable; [Figures 3B and 3D](#)). In comparison, the dispersion within and among the heated treatments was similar (IMD = -0.167; [Figure 3D](#)).

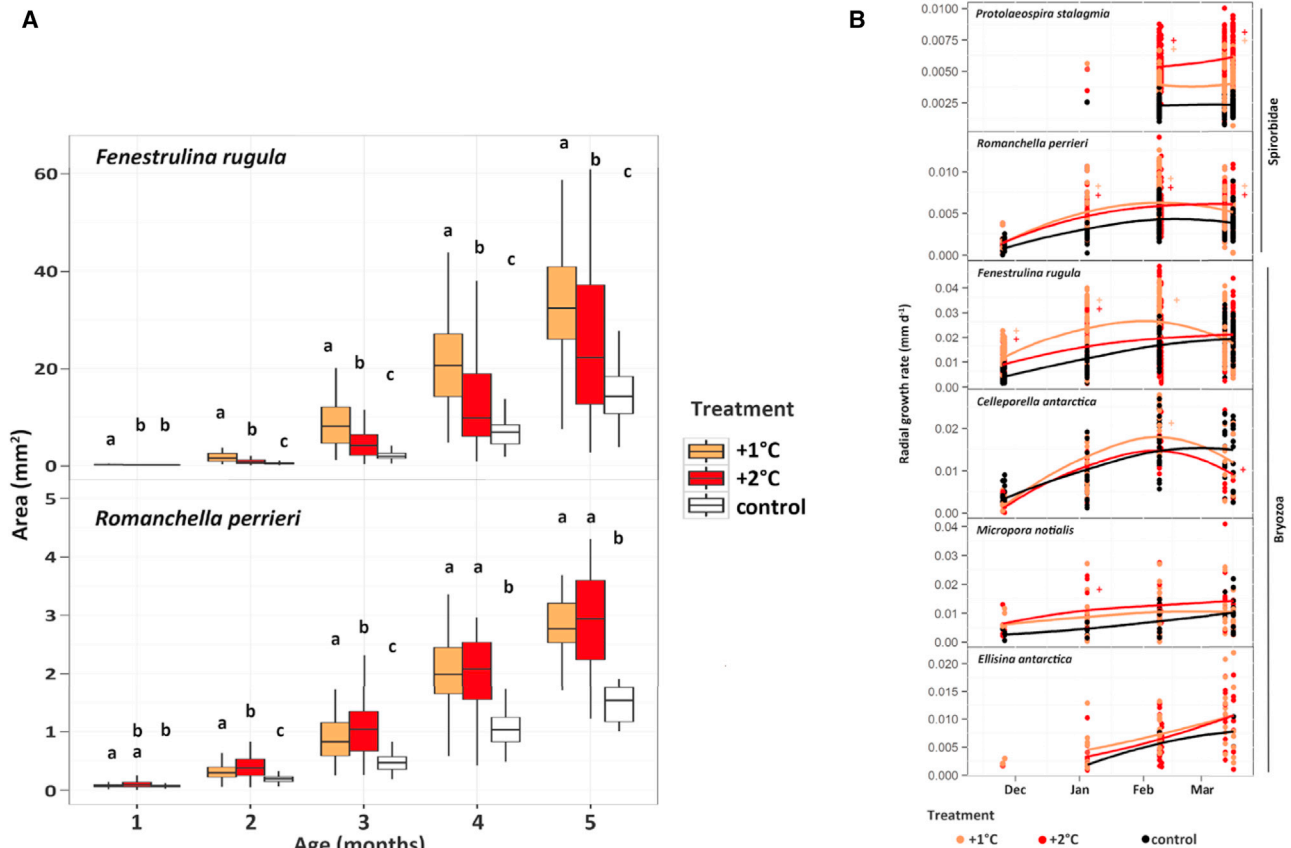
Species richness was similar across all treatments, but the control panels were more diverse, even in terms of species percent cover ([Figure 3A](#);  $p < 0.05$ ). In contrast, when the

spatially dominant *F. rugula* was removed from diversity indices, diversity and evenness on heated panels increased above that of the control panels, but not significantly so ([Figures 3A and S2A](#)). This (and [Figure 1](#)) illustrates how contrasting and complex the effect of making a small change in just a single variable (temperature) can be on an assemblage.

Percentage cover on the panels varied considerably, between 20% and 80%. Control panels were most sparsely covered (mean = 39%), whereas panels in the +1°C treatment experienced the highest coverage (mean = 68%). The availability of bare space was directly correlated with the cover of *F. rugula*, almost on a 1:–1 ratio ([Figure S2B](#)). Panels in the +2°C treatment were intermediate in terms of coverage and also had high variability in spatial coverage ([Figures 1 and S2B](#)).

## DISCUSSION

This study aimed to examine temperature effects on organisms living in one of the regions where climate is altering fastest and on the seabed where most polar species live. To do this, we



**Figure 2. Different Growth Rate Responses among Species Were Observed in the Three Treatments: Control, +1°C, and +2°C**

(A) Area covered by the spatially dominant bryozoan (*Fenestulina rugula*) and spirorbid (*Romanchella perrieri*) under warming and control treatments. Data show the mean and interquartile range of panel surface area covered by a single colony (top) or individual (bottom). Different letters indicate significantly different areas per age ( $F_{(1,9)}$  with  $p < 0.01$ ).

(B) Growth-rate response of six spatially dominant species to warming treatments. Data are individual (spirorbid polychaete) or colony (bryozoan) growth rates since the previous sampling [calculated as  $(\text{radius at T}_2 - \text{radius at T}_1) / (\text{T}_2 - \text{T}_1)$  mm d<sup>-1</sup>]. Lines are loess smoothed trends in growth rates during the 2014/2015 summer season in Antarctica.

See also Figure S1.

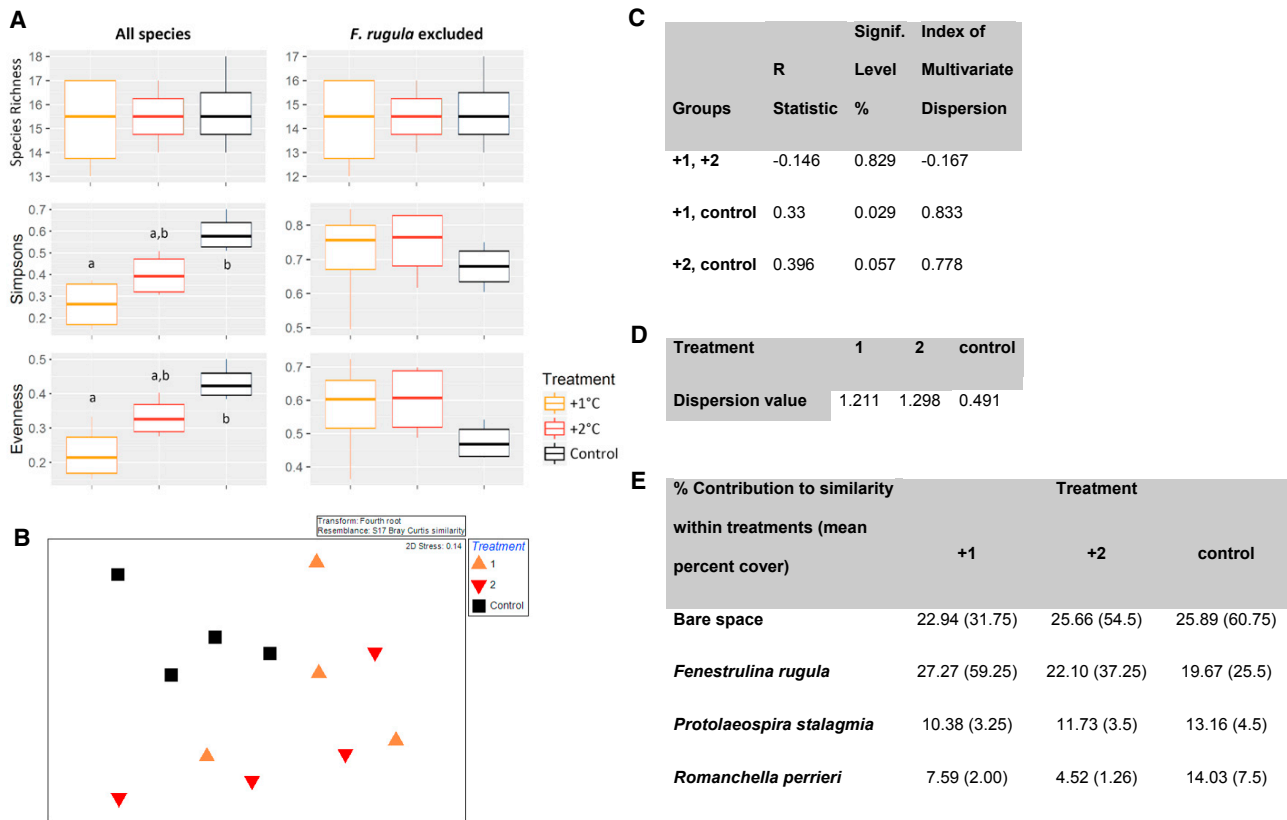
investigated in situ warming effects on an Antarctic marine encrusting benthic assemblage over a nine month period. Just 1°C of warming (the approximate shallow sea temperature rise projected over the next 50 years [6]) substantially changed the recruiting hard substratum assemblage, with likely consequences for the developing epibenthic assemblage and further through benthic-pelagic coupling. Growth rates and bare space colonization increased, and species diversity and evenness in the recruiting assemblage were reduced. If ocean warming projections are realized, these results point to extensive future changes in shallow water Antarctic benthic assemblages with implications for the whole ecosystem.

### Growth-Rate Response

The increases in growth rate observed on the panels were far beyond expectations. Based on long established Arrhenius relationships and literature reports [7–9], biological reactions, enzyme activity, development, and growth rates should increase 7%–12% per 1°C warming ( $\times 2$ – $\times 3$  increase per 10°C rise). In the +1°C treatments, growth rate in some species doubled

with a 1°C temperature rise (giving maximum  $Q_{10}$ s around 1,000). These very large effects of temperature on biological processes at polar temperatures critically change our thinking of how polar benthic communities might respond to ocean warming in the next 50–100 years and make them likely to respond very differently from lower latitude faunas or from current predictions. Although we have a good understanding of the impact of temperature on biochemical processes, our ability to expand, integrate, and apply this knowledge to the organism level is still limited [7, 10]. The differing magnitude and pattern of responses among organisms highlights the complexity of this challenge [11].

Projected warming of 1°C–2°C could be particularly significant to Antarctic marine biota, which typically experience annual temperature ranges of <4°C [12]. Antarctic benthic taxa are perceived as vulnerable to environmental shifts [13], being considered sentinels for monitoring the effects of climate change [14]. Over the last 50 years, the Bellingshausen Sea west of the Antarctic Peninsula has been one of the fastest warming globally [15], and both polar oceans are forecast to remain among the



**Figure 3. Assemblage Response to Warming**

(A) Biofouling panel community diversity indices. Data show the mean and interquartile range of three diversity measures (species richness, Simpson's diversity index, and Pielou's evenness index) calculated using percentage cover as abundance; panels on the right have the abundance of *Fenestulina rugula* excluded from the calculations. Letters depict significant differences between treatments when all species were included in the analyses ( $p < 0.05$ , Kruskal-Wallis with Tukey's post hoc); no differences were significant when *F. rugula* data were excluded ( $p > 0.05$ ).

(B) Non-metric multi-dimensional scaling (nMDS) plot illustrating differences in species composition of assemblages recruiting to panels after 9 months in situ. Biofouling assemblages established on heated panels ( $+1^{\circ}\text{C}$ ) were significantly different from those on control panels ( $p = 0.029$ ), whereas assemblages on panels heated a further degree ( $+2^{\circ}\text{C}$ ) were also different, but not significantly so ( $p = 0.057$ ; C).

(C) Portions of bare space and the three top space occupiers contributing to the similarity of community compositions within treatments.

(D and E) Analysis of similarity (D) and dispersion statistics (E). Biofouling assemblages established on panels heated to  $+1^{\circ}\text{C}$  were significantly different and more variable than those on control panels ( $p = 0.029$ ). Assemblages heated a further degree ( $+2^{\circ}\text{C}$ ) were also variable and more similar to those warmed to  $+1^{\circ}\text{C}$ , but not significantly different from control panels ( $p = 0.057$ ).

See also Figure S2.

areas most impacted by climate change. Many biological reactions proceed much more slowly at polar temperatures than would be predicted from the effect of temperature on these functions in temperate and tropical species or from standard Arrhenius relationships [16]. A steeper gradient in the relationship between temperature and growth, early development, and meal processing rates at cold temperatures would align with the greater than expected response to warming observed here in polar species.

Antarctic species are perceived to have reduced acclimation abilities [3] probably resulting from long-term adaptation to stable cold environments. The observed tolerance and in most cases increased growth rates of species under warming treatments in the current study suggests that sessile benthic invertebrates are well adapted to deal with predicted warming over the next 50 years. Furthermore, our in situ manipulations subjected the organisms to rapid warming (especially in the  $+2^{\circ}\text{C}$  treatment)

that excluded physiological or genetic adaptation; these species should be capable of adapting to gradual warming over 50 years. Rapid growth rate is advantageous in benthic biofouling communities where space is limiting [17, 18] and when many measures of success are related to growth rate (e.g., age to reproduction, reproductive output, and competitive ability). The associated consequences for colonization and assemblage recovery after disturbance would be great, possibly counteracting the increased disturbance expected with climate change associated reduction in sea ice and increased glacial retreat [13, 19]. Increased growth would also impact carbon accumulation in benthic systems, recently demonstrated as a negative feedback mechanism to carbon driven climate change [20, 21].

### Assemblage Response

The temperatures used here are within the thermal window of most Antarctic benthic species [3], but different species

responses could critically impact the resulting assemblage composition [17]. Species diversity, both richness and composition, directly influences ecosystem function [22, 23]; thus, our understanding of the likely impacts of future climate change relies on our ability to predict responses at this practical and/or pragmatic level. Most experimental studies in the marine environment have observed declines in overall species richness among benthic communities subjected to artificial warming [24, 25], mirroring observations from terrestrial environments [26, 27].

In the Antarctic shallows, increased iceberg disturbance driven by ocean warming has already been suggested as a likely driver of change in ecosystem structure [19]. Our results indicate that ocean warming will also directly influence species composition of shallow benthic assemblages, possibly amplifying secondary effects, including iceberg groundings. Both stressors seem to favor the opportunist *F. rugula*.

Species contributing most to the differences among treatments were pioneer species, i.e., those colonizing bare space. Such species dominate encrusting Antarctic shallow benthic assemblages up to 3 years old (see [28, 29]). Shifts in *r*-strategists also dominate changes in hurricane-impacted forest assemblages [30] and in streams affected by wildfire disturbance [31]. Succession is a variable process, but, as demonstrated here, ocean warming is likely to alter the balance of facilitation, competition, and inhibition among species [32], changing the resultant community.

Ecological succession could be further altered by different effects or by different intensities of effects on physiological processes among species. For example, growth rates of some species are directly increased under warming ([33]; this study) and development rates of marine invertebrates are markedly affected by warming [34, 35], whereas onset of reproduction may be more closely related to other stimuli: light or food availability, for example [26, 36]. With these various effects, changes in ambient temperature will most likely have complex effects on the end result of ecological succession [37, 38].

Species diversity and evenness in this study were reduced because of the increase in pioneer species growth on heated panels. Although metabolic rates generally increase with rising temperature, other factors, including nutritional status, food processing time, and thermal tolerance, may limit increases in biological processes [39]. We could not observe later stages of succession, but we suggest that rare species may be impacted by the overwhelming response of common pioneers (*F. rugula* here). Effects of keystone species can amplify across biotic relationships through networks of interactions to alter the structure and dynamics of ecosystems [28]. In this assemblage, *F. rugula* appears as the pivotal species.

Assemblage growth on the panels increased under warming treatments. A similar increased cover response was observed in short-term (36 days) heated panels deployed in Perth, Australia [40]. In that study, an ascidian, *Didemnum perlucidum*, dominated the increase in cover, even though it rapidly grew out of the heated conditions. In laboratory experiments, growth increased in three ascidian species settled on panels and subsequently warmed to between 5°C and 9°C above ambient [33]. Ascidians were a minor component of the Antarctic recruiting assemblage in our study, where the response of the dominant bryozoan species, *F. rugula*, outweighed all others.

Compared to the +1°C panels, warming on the +2°C panels produced divergent responses across species, leading to a further different assemblage after 9 months. The assemblage growth response (as area covered) was more variable across the +2°C treatments, with two panels exhibiting similar growth to the +1°C panels and two panels with less growth (similar to or less than that of controls). The increase in variability is somewhat unsurprising given the nonlinearity of thermal performance curves [41]. The panels with reduced growth had large areas of non-colonized surface (rather than evenly distributed bare patches; Figure 1). Panel construction, warming, and surface texture were identical, and there was no evidence of predation. Reduced recruitment is the most likely contributing factor to the low spatial cover on these panels. Reduction of recruitment success in benthic species under future warming would severely impact the marine ecosystem.

Understanding different species responses to warming is critical to modeling likely community change under ocean warming scenarios. Shifts in abundance, phenology, and spatial organization (distribution and dispersion) should be expected [39]. However, it is difficult to isolate the relative importance of warming on physiological-, population-, and community-level responses. The response will be complicated further by the interaction of warming with other stressors, e.g., ocean acidification, sea-ice loss, and iceberg impact frequency [42, 43]. The observed increase in spatial cover in this experiment could be explained by the physiological response of one species, *F. rugula*, which doubled under 1°C of warming. But the resulting alterations in species composition and impact on later stages of succession are harder to predict. Community and ecosystem processes are often dominated by a few strong interactions against a background of many weak interactions [25, 44, 45]. In this Antarctic environment, *F. rugula* may provide a benthic indicator of ecological response to environmental change.

A reduction in diversity was observed in benthic communities associated with artificial warming at temperate latitudes (e.g., [24, 25]). Similar trends have been observed in terrestrial experiments, with warmed communities developing lower species richness and evenness in both tundra and alpine communities [27, 46]. The evidence from multiple biotopes suggests that a projection of global decline in species diversity may not be an exaggeration. However, larger-scale studies and models based on biogeography tend to predict richness increases driven by range expansion from neighboring areas (e.g., [47]). There is an apparent discrepancy between results from short-term, small-scale experiments (<5 years, <10 km) and long-term large scale models, which are generally based on overall distributions of species at larger scales. Short-term experiments do not allow the timescales necessary for population expansion [24], but models ignore the potential changing biological interactions between species already in the community, as well as those between natives and newcomers.

### Advances

New technologies are improving our ability to simulate future scenarios on land and in the ocean [48, 49]. Studies of responses beyond the species level are critical to understand assemblage,

community, and ecosystem function responses [50, 51]. By placing the panels on the seafloor (near to natural hard substrate habitat and assemblages), creating constant warming above ambient temperature, and measuring actual growth rates from individuals contained within the warmed area throughout the experiment, we significantly improved upon previous efforts to experimentally dissect the effects of in situ heating in marine environments. We observed that warming projected for the next 50–100 years strongly accelerates invertebrate growth and colonization rates. Increased benthic assemblage growth may be a positive ecosystem function response; nutrients would be more quickly available for higher trophic levels, further increasing carbon cycling. The observed maintenance of species richness under warming scenarios is also reassuring, although reductions in assemblage diversity and evenness might concern some.

Limitations still exist; for example, the abundance and timing of food availability as well as water chemistry were probably not influenced by the panels. Communities that settle and grow on panels in the short term differ somewhat from natural communities ([52] and references therein), and the less than 12 month experiment duration precluded studying longer-term growth and assemblage development over multiple annual cycles. However, the approach represents a major advance in simulating future oceanic climate change projections. The different species responses underscore the need to move beyond single species experiments, to realistic ocean-warming community level studies to better parameterize and validate predictive modeling of future ecosystem dynamics. Replication of this experiment in temperate and tropical environments presents challenges because of faster organism growth rates and the need to deploy panels over multiple seasons. However, in situ manipulative marine experiments are probably the best available technologies to inform global assessments of marine assemblage responses to future ecosystem change.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR RESOURCE SHARING
- METHOD DETAILS
  - Experimental design
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Data acquisition
  - Statistical analysis

## SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.07.048>.

## AUTHOR CONTRIBUTIONS

Conceptualization and Funding Acquisition, L.S.P., S.A.M., D.K.A.B., and M.S.C.; Methodology and Writing, G.V.A., S.A.M., D.K.A.B., M.S.C., and L.S.P.; Formal Analysis and Investigation, G.V.A.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
R: A language and environment for statistical computing.	Foundation for Statistical Computing, Vienna, Austria	<a href="https://www.R-project.org/">https://www.R-project.org/</a>
nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128	[57]	<a href="http://CRAN.R-project.org/package=nlme">http://CRAN.R-project.org/package=nlme</a>
lsmeans: Least-Squares Means. R package version 2.26-3	[59]	<a href="https://CRAN.R-project.org/package=lsmeans">https://CRAN.R-project.org/package=lsmeans</a>
Vegan: Community Ecology Package. R package version 2.4-0.	[61]	<a href="https://CRAN.R-project.org/package=vegan">https://CRAN.R-project.org/package=vegan</a>
PRIMER v6	Plymouth Routines In Multivariate Ecological Research	<a href="http://www.primer-e.com">http://www.primer-e.com</a>

### CONTACT FOR RESOURCE SHARING

Further information and requests may be directed to, and will be fulfilled by, the Lead Contact, Gail V. Ashton ([ashtong@si.edu](mailto:ashtong@si.edu)).

### METHOD DETAILS

#### Experimental design

Bespoke heated settlement panels were deployed on the benthos close to the British Antarctic Survey's Rothera Research Station (Lat. 67°34'S; Long. 68°07'W). Metal heat trace was embedded in a PVC block such that the temperature on the panel surface could be increased using power supplied to the panel. As the specific heat capacity of seawater is a constant  $4.186\text{J g}^{-1}\text{°C}^{-1}$ , by keeping the power supply constant, the quantity of water is constant and therefore the resultant temperature increase is also constant. Power necessary to generate a uniform constant warming across the experimental panel surface was calibrated prior to deployment (14.2V and 20.1V for 1°C and 2°C of warming, respectively). The degree of warming was accurate to within 0.2°C at a distance of 1mm from the panel surface at flow rates up to  $2\text{cm sec}^{-1}$  (Figure S3). This created a water layer of > 2mm from the surface with uniform heating  $\pm 0.03\text{°C}$  (no animal grew beyond the 2mm layer for the duration of this experiment). The extent and evenness of warming was rigorously verified both in a flow flume during the design phase, in aquaria after the deployment, and in trial shallow in situ deployments where a panel set at +1°C gave a warming of  $1.01\text{°C} \pm 0.029\text{°C}$  (SE, n = 50 measurements). Panels were connected to a shore-based (mains supplied) control unit via a 100 m cable. The power supply to each cable (and thus panel) was controlled using resistors within the unit and verified using an inline voltmeter. Indicator lights within the control unit were monitored 1-2 times per week, up to once a month depending on weather conditions, to confirm continuance of the power supply.

Each panel was micro-abraded and etched to create a 9.8x9.8 cm central settlement surface. A PVC spacer was secured to the four corners of each panel such that with the experimental surface facing down it would be held 2cm from the substrate. Panels were deployed using SCUBA at a depth of 15 m. One replicate of each treatment (ambient, +1°C, +2°C) was deployed on each of 4 concrete slabs in a random block design, secured in place using elastic cord (n = 12 panels total). Panels were deployed during June 2014. Antarctic weather precluded monitoring the panels until October 2014, after which they were monitored on an approximately monthly basis. The experiment was stopped at the end of March 2015 when iceberg impact damaged power supply cables.

### QUANTIFICATION AND STATISTICAL ANALYSIS

#### Data acquisition

Panels were monitored in situ by SCUBA divers via photography using a Nikon D7000 with a 60mm macro lens. The elastic cord securing the panel to the sea bed was removed and the panel was turned over so that the experimental surface was facing up. A sliding frame was used to keep the camera lens at a constant distance from the panel to ensure images were captured on optimum settings and to assist with image analysis. Each image captured approximately 3.5x2.5 cm of the panel; more than 25 overlapping images of each panel were taken on each sampling event so that the entire panel surface was captured at least once. The sampling took approximately 5 min for each panel, after which time the panel was turned over and secured in place using the elastic cord.

Images were imported into Photoshop CS5, merged to a single image and cropped to the central 9.8x9.8cm area of each panel. Images could then be stacked over successive sampling events such that individuals or colonies could be followed through the duration of the experiment. The area of the image was set to 9.8x9.8 cm<sup>2</sup> (the area of the experimental surface) and calculations of area were recorded using the built-in Analysis tools. Organisms recruiting to the panels were identified using Hayward [53] for bryozoans, and Knight-Jones & Knight-Jones [54, 55] for spirorbid polychaetes. Thirty individuals per plate of *Romanchella perrieri* and *Proto-laeospira stalagmia* and colonies of *Fenestrulina rugula* were identified and measured over successive sampling events in this manner. Individuals/colonies that showed incremental growth were selected to exclude those that may have been dead. For other bryozoans, 30 representatives per plate were not available and all available colonies were used (total n > 41 for each species). The radius of each area projected as a circle was calculated (the bryozoans and spirorbids studied here grow in an approximately circular manner). Growth rates were then calculated as:

$$\text{Rate (mm d}^{-1}\text{)} = \frac{(\text{Radius at T2} - \text{Radius at T1})}{(\text{T2} - \text{T1})}$$

The end-point photographs were used to assess the spatial composition of the assemblage. A 10x10 grid was added to each image and the species at each cross-hair was identified using taxonomic keys ([53], and subsequent primary literature). The plate was checked under a microscope to confirm the identity where characters were unclear on the images. A species list for each panel was created using both the photographs and a search of the whole live panel under the microscope (capturing species that had not been counted in the point count).

### Statistical analysis

Area and growth rate data were analyzed using mixed effects models in the R environment for statistical computing [56] using the *nlme* package [57]. The reference model included colony ID, plate and block as nested random effects, and treatment, age and an interaction term between treatment and age as fixed effects:

```
>lme(Area~factor(Treatment)*factor(Age),random=~1|Block/Plate/Colony_ID,data=FrugGrow,method="REML")
```

The best-fit model was determined in a backward-stepwise fashion using a chi-square test to compare models with the null hypothesis that the model with fewer terms was sufficient [58]. The best-fit model for area included random effects Plate and Colony ID, and both fixed effects with the interaction term. Because variance increased with Age, we included a weighting of the standard deviation reliant on Age, giving the best model:

```
>lme(Area~factor(Treatment)*factor(Age),random=~1|Plate/Colony_ID,weights=varIdent(form=~1|Age)
```

The fit of the model was validated using plots of Q-Q, residual versus fitted, and residuals versus Treatment and Age. The significance of differences between treatments was assessed using the *lsmeans* package [59]:

```
>(mod.pairs=contrast(lsmeans(lme,~Treatment|Age),"pairwise"))
>inter.con=contrast(mod.pairs,"pairwise",by=NULL)
>test(inter.con,joint=TRUE)
```

P values were adjusted for multiple comparisons using the Tukey method. F statistics were calculated as t2.

For growth rate, we were interested in the interaction between Treatment and the three fixed effects (Age, Month and Species), the full model was thus:

```
>lme(radgrowrate~factor(Treatment)*Age+factor(Treatment)*factor(Month)+factor(Treatment)*factor(Spp),random=~1|Block/Plate/Colony_ID,data=master,method="REML")
```

Following the same backward-stepwise exclusion of terms, and weighting of standard deviation according to Age, the final model was:

```
>lme(radgrowrate~factor(Treatment)*Age+factor(Treatment)*TimeStep+factor(Treatment)*factor(Spp),random=~1|Plate/Colony_ID,weights=varIdent(form=~1|Age)
```

Trends in the radial growth rate data were illustrated using loess smoothed plots.

Species and total percent cover for each panel was calculated from the point count data. In addition, each species that was present on the panel, but not recorded in the point count was given a nominal percent cover of 0.01. Differences in assemblage composition between treatments were assessed using ANOSIM analyses on fourth root transformed data. The between-panel resemblance matrix was presented using MDS plots. SIMPER analysis was used to determine the contribution of each species to the dissimilarity between treatments. The MVDISP algorithm was used to quantify the variability in spatial composition within each treatment and to compare the variability between treatments using the Index of Multivariate Dispersion (IMD). IMD is a score between +1 and -1 and is most extreme when dispersion within a treatment is most different from that between two treatments. An IMD of zero implies no

difference between two samples in terms of variability in multivariate structure. All these analyses were performed using the PRIMER6 package [60].

Using the percent cover data from each panel to indicate spatial dominance, the following indices were also calculated using the package Vegan in R [56, 61]: species richness, Simpsons Diversity Index (D) and Pielou's evenness index (J). Differences in the indices between treatments were assessed using Kruskal-Wallis, with Tukey post hoc tests where differences were indicated.

As settlement panels and statistical analyses were dominated by a single species, analyses were repeated with this species removed to better understand the changes in the assemblage driven by rarer species.