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Extreme climatic event drives range contraction of a habitat-forming species

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Species distributions have shifted in response to global warming in all major ecosystems on the Earth. Despite cogent evidence for these changes, the underlying mechanisms are poorly understood and currently imply gradual shifts. Yet there is an increasing appreciation of the role of discrete events in driving ecological change. We show how a marine heat wave (HW) eliminated a prominent habitat-forming seaweed, *Scytothalia dorycarpa*, at its warm distribution limit, causing a range contraction of approximately 100 km (approx. 5% of its global distribution). Seawater temperatures during the HW exceeded the seaweed's physiological threshold and caused extirpation of marginal populations, which are unlikely to recover owing to life-history traits and oceanographic processes. *Scytothalia dorycarpa* is an important canopy-forming seaweed in temperate Australia, and loss of the species at its range edge has caused structural changes at the community level and is likely to have ecosystem-level implications. We show that extreme warming events, which are increasing in magnitude and frequency, can force step-wise changes in species distributions in marine ecosystems. As such, return times of these events have major implications for projections of species distributions and ecosystem structure, which have typically been based on gradual warming trends.

1. Introduction

Global warming has caused many species to shift their geographical range towards cooler environments [1,2]. As such, the poleward redistribution of species is emerging as a significant biological response to increased global temperatures in both marine and terrestrial ecosystems [3–5]. While range shifts have been detected across decadal time-scales, by comparing historical and contemporary data, there have been few direct observations of the processes that drive population change at the range edge. Moreover, there have been far fewer observations of climate-driven range contractions compared with expansions, and, as such, the mechanisms and velocities of change at the 'trailing edge' are poorly understood [6]. These issues have major implications for understanding and predicting the dynamics of range shifts [2].

The current paradigm implies that species ranges change continuously with warming [7], yet this perception cannot be reconciled with recent observations of no [8,9] or abrupt [10,11] ecological change in response to gradual warming. Alternatively, range shifts are incremental, being driven by discrete extreme events. In nature, it is likely that species exhibit a combination of both gradual and sudden, and extensive distribution shifts in response to climate when physiological thresholds are exceeded. The distinction between gradual and abrupt range dynamics has important implications for climate change mitigation because of the implied threshold dynamics and the difficulties of predicting (as well as reversing) any undesirable changes. Event-driven changes also prevent accurate estimation of the velocity of range contractions, leading to errors in projections of future impacts. Extreme climatic events are increasing in frequency and intensity as a consequence of anthropogenic climate change [12,13]. These events are likely to have major implications for natural resources, and understanding and predicting biological responses to 'events', rather than to 'trends',

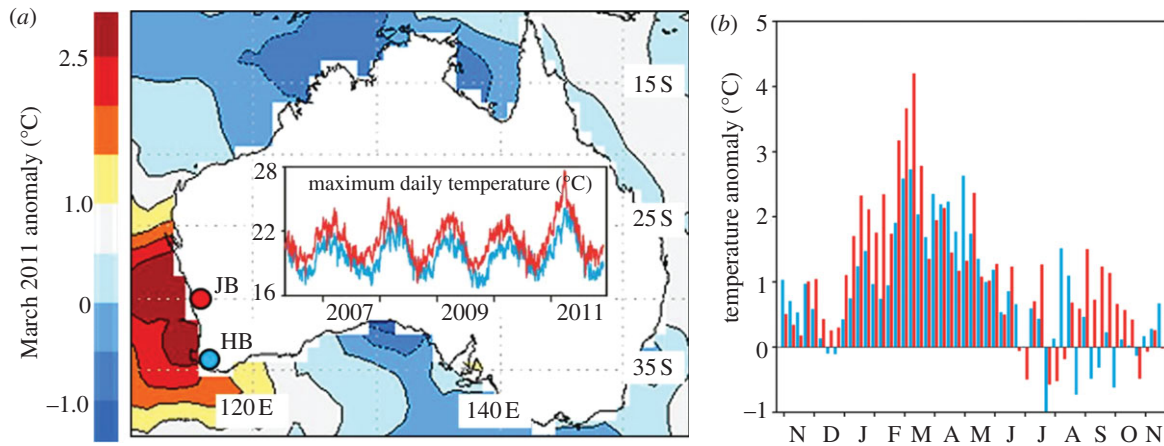


Figure 1. (a) Satellite-derived SST anomaly map for March 2011 (relative to a 1971–2000 baseline of monthly means for March) and *in situ* temperatures (inset) in Jurien Bay (JB, red) and Hamelin Bay (HB, blue). (b) Weekly temperature anomalies throughout 2011 (relative to a 2006–2010 baseline), measured *in situ* at the reef surface (~ 10 m depth) at both monitoring locations in Western Australia.

have become increasingly important [14]. Evidence for species range shifts in terrestrial ecosystems, in response to both gradual warming and discrete warming events, far exceeds evidence from marine ecosystems [15,16]. As the velocity of warming in the sea is similar to that on land [17] and most coastal ecosystems have warmed significantly in recent decades [18], it is very likely that the poleward redistribution of marine biota has been severely under-reported.

Southern Australia supports rich assemblages of marine life, and represents a global hotspot of endemism and biodiversity [19,20]. Coastal waters encompass extensive rocky reef habitat, which supports a wealth of seaweed, invertebrate and fish life, making it the world's most biodiverse temperate marine ecosystem. Canopy-forming seaweeds perform a variety of critical functions in this ecosystem, including provision of food and shelter, and amelioration of environmental stressors. *Scytothalia dorycarpa*, a large (greater than 1 m) perennial furoid (brown alga) endemic to southern Australia, is one of the most prominent habitat-forming species across more than 3000 km of temperate coastline, at depths of approximately 3–30 m (T. Wernberg 2003–2013, personal observation). Having evolved during cool, climatically stable conditions [20], *S. dorycarpa* is thought to be sensitive to high and increasing temperatures, and has been proposed as a potential indicator of ocean warming [21,22].

In early 2011, the coastal waters of Western Australia experienced an unprecedented 'marine heat wave' (HW), where sea temperatures soared to up to 5°C above normal for several weeks [23–25]. Here, we show how this extreme warming event caused *S. dorycarpa* to retract its range some 100 km (approx. 5% of its entire global distribution), and how extirpation of this habitat-former at the range edge might have far-reaching implications for the structure and functioning of benthic communities and the wider ecosystem.

2. Material and methods

(a) Temperature during the 2011 marine heat wave

Satellite-derived sea surface temperatures (SSTs) were used to compare temperatures in March 2011, the peak of the warming event [25], against a baseline of 1971–2000 (using monthly means generated from the MODIS aqua dataset to derive the

anomaly). An SST anomaly map was generated from the NOAA Operational Model Archive Distribution System (NOMADS), hosted by NOAA's Environmental Monitoring Center. *In situ* temperature measurements were collected at two long-term monitoring locations in Western Australia—Jurien Bay (JB; approx. 30° S) and Hamelin Bay (HB; approx. 34° S)—where regular sampling of *S. dorycarpa* was also conducted (figure 1). Sea-water temperatures at 9–12 m depth over subtidal rocky reefs were continuously measured by Onset Stowaway loggers (model TBI32-05 + 37, accuracy $\pm 0.2^\circ\text{C}$) since 2006 (see [26] for detailed climatology of the region).

(b) Biological surveys

The response of *S. dorycarpa* to the HW was assessed in two ways. First, repeated fine-resolution surveys were conducted at both JB and HB, to quantify the percentage cover of *S. dorycarpa* on subtidal rocky reefs. In November 2005, before the HW, the 'transect-scale' cover of *S. dorycarpa* was estimated by scuba divers along 40 transects (25 m in length) at each location. Ten random transects were conducted at three rocky reef sites, separated by 2–10 km, at 8–12 m depth. The same sites were resurveyed in November 2011 after the HW [21]. 'Quadrat-scale' cover of *S. dorycarpa* was monitored more frequently (in November 2006, 2007 and 2010 before the HW, and again after the event in November 2011), by quantifying percentage cover in 12 haphazardly placed quadrats (0.5×0.5 m), six at each of two sites. These survey data were analysed by two-way analysis of variance (ANOVA) between years and locations, using $\ln(x + 1)$ -transformed percentage cover data. Where a significant main effect or interaction term was detected (at $p < 0.05$), post hoc pair-wise Student–Newman–Keuls (SNK) tests were performed. During the quadrat-scale benthic surveys, the percentage cover of other canopy-forming species (e.g. the kelp *Ecklonia radiata*) and understory taxa (e.g. encrusting coralline algae, turf-forming algae, sponges) was also quantified. Shifts in understory community structure associated with changes in the cover of *S. dorycarpa* were examined with multivariate analyses (using PRIMER v. 6 [27]).

Second, spatially extensive data on the percentage cover of *S. dorycarpa* were collated from a number of benthic surveys both before and after the warming event. Survey sites were spread across a latitudinal gradient of approximately 6°, which encompassed the known equator-ward range edge of *S. dorycarpa* (figure 2). Survey data were obtained from various sources, including a state-funded marine park monitoring programme, unpublished studies and by resurveying a suite of 'historical'

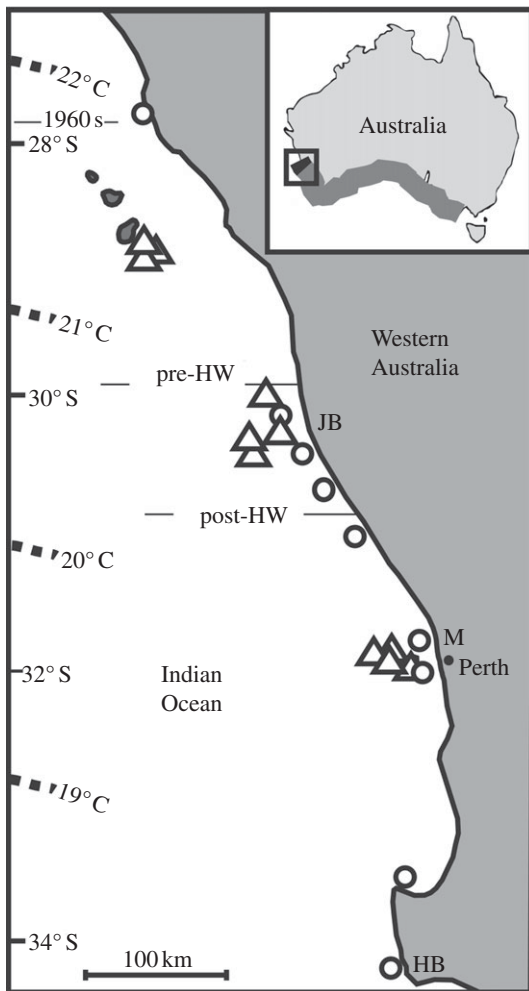


Figure 2. Locations surveyed by scuba divers (circles) and by AUV (triangles) along the Western Australian coastline. Each location symbol represents at least three survey sites within that location, with each site separated by at least 2 km. Dotted lines indicate approximate annual SST isotherms. The estimated equator-ward range edges for *Scytothalia dorycarpa* during the 1960s (derived from herbarium records), during the 2000s before the warming event ('pre-HW', range edge derived from surveys) and from late 2011 onwards following the warming event ('post-HW', this study) are shown. The continuous monitoring locations of JB and HB, as well as the collection site for the physiological assays, Marmion (M), are also shown. Inset map depicts the approximate distribution of *S. dorycarpa* in southern Australia (grey shading) and the equator-ward range edge (black shading) within the current study region (black box).

sites with previously confirmed abundances of *S. dorycarpa*. In all cases, scuba divers conducted multiple transect (more than five) surveys to collect quantitative percentage cover estimates and also performed extensive random swim searches for presence/absence information. 'Pre-HW' survey data were collected between 2000 and 2010, and 'post-HW' data were collected between November 2011 and April 2012. Survey sites all comprised suitable rocky reef habitats (5–18 m depth) and were moderately to fully exposed to wave action. In total, 27 sites were surveyed both before and after the warming event, and an additional eight sites were surveyed only after the event, covering a total of more than 24 000 m² subtidal reef. Additionally, multiple surveys at 12–50 m depth were undertaken with an autonomous underwater vehicle (AUV) at three monitoring locations (The Houtman Abrolhos Islands, 28.9° S; JB, 30.5° S; Rottnest Island, 32.0° S; figure 2). These surveys were completed in April 2010, before the HW, and again in April 2011, one month after the peak of the event

(see [28] for AUV survey design and rationale). In total, over 7000 AUV images (more than 10 000 m²), captured across 40 hard-bottom sites, were examined for *S. dorycarpa*. Raw data are available through the Integrated Marine Observing System (IMOS; <http://imos.aodn.org.au/webportal>).

The three survey techniques described earlier (i.e. quadrat-scale, transect-scale and AUV-derived habitat scale) varied in sample 'grain size' and therefore generated estimates of per cent cover that were not directly comparable. Datasets were analysed separately because the proportion of unsuitable microhabitat surveyed (e.g. patches of sand, steep-sided reef edges), and the likelihood of sampling a patch of *S. dorycarpa* varied between sampling techniques.

(c) Physiological assays

The physiological performance of *S. dorycarpa* in response to short-term thermal stress was determined from the rates of net photosynthesis of epiphyte-free sections of tissue (2.42 ± 0.36 g fresh weight, mean \pm s.e., $n = 6$) from the upper third of the thallus (see [29] for expanded methodology). Seaweeds were collected from reefs at approximately 8 m depth in Marmion (32° S; approx. 100 km south of the current range edge) in March 2012. Measurements were made within a few hours of collection using a temperature-controlled incubation unit, which allowed measurements of oxygen exchange to be taken from light-exposed algal material ($530 \mu\text{E m}^{-2} \text{s}^{-1}$; corresponding to open-canopy light levels at the collection site [30]). All algal material was cooled to 10°C and allowed an acclimation period of 30 min prior to commencing measurements of photosynthesis. Experiments were conducted from 12°C to 30°C to incorporate the thermal range found below and within the species range (12–24°C), as well as temperatures matching and exceeding those measured during the HW (25–30°C). Changes in oxygen concentrations were measured using an OxyGuard Handy Polaris (OxyGuard International, Birkerød, Denmark) oxygen probe, at the beginning and at the end of each incubation period, which had a duration of 60 min at 10–20°C and 30 min for each of the remaining temperatures (slow metabolic rates at low temperatures necessitated longer incubations; all measurements were standardized for incubation period [29]). The electrode was calibrated regularly. Differences in oxygen metabolism between temperature treatments were tested by one-way ANOVA by permutation (999 unrestricted permutations of the raw data) followed by pair-wise comparisons to ascertain which treatments differed ($p < 0.05$) from one another [31].

3. Results

(a) Temperatures during the 2011 marine heat wave

The southeast Indian Ocean region experienced a significant warming event in early 2011. By March 2011, a SST warming anomaly of more than 2.5°C affected more than 2000 km of coastline (figure 1a). *In situ* loggers recorded peak temperatures of 27.8°C at JB and 24.1°C at HB (figure 1a). Compared with the preceding 5 years, temperatures were up to 4°C above normal, and a warming anomaly of greater than or equal to 2°C persisted for approximately 10 weeks at both locations (figure 1b), which resulted in the highest thermal stress anomalies on record, some 50 per cent greater than previous maximums [25]. The event was driven by unusually strong La Niña conditions, which increased the flow of the region's major ocean current (the Leeuwin current) and the transfer of warm tropical water polewards [32]. Simultaneously, air–sea heat flux was anomalously high and both processes were superimposed onto a decadal-scale warming

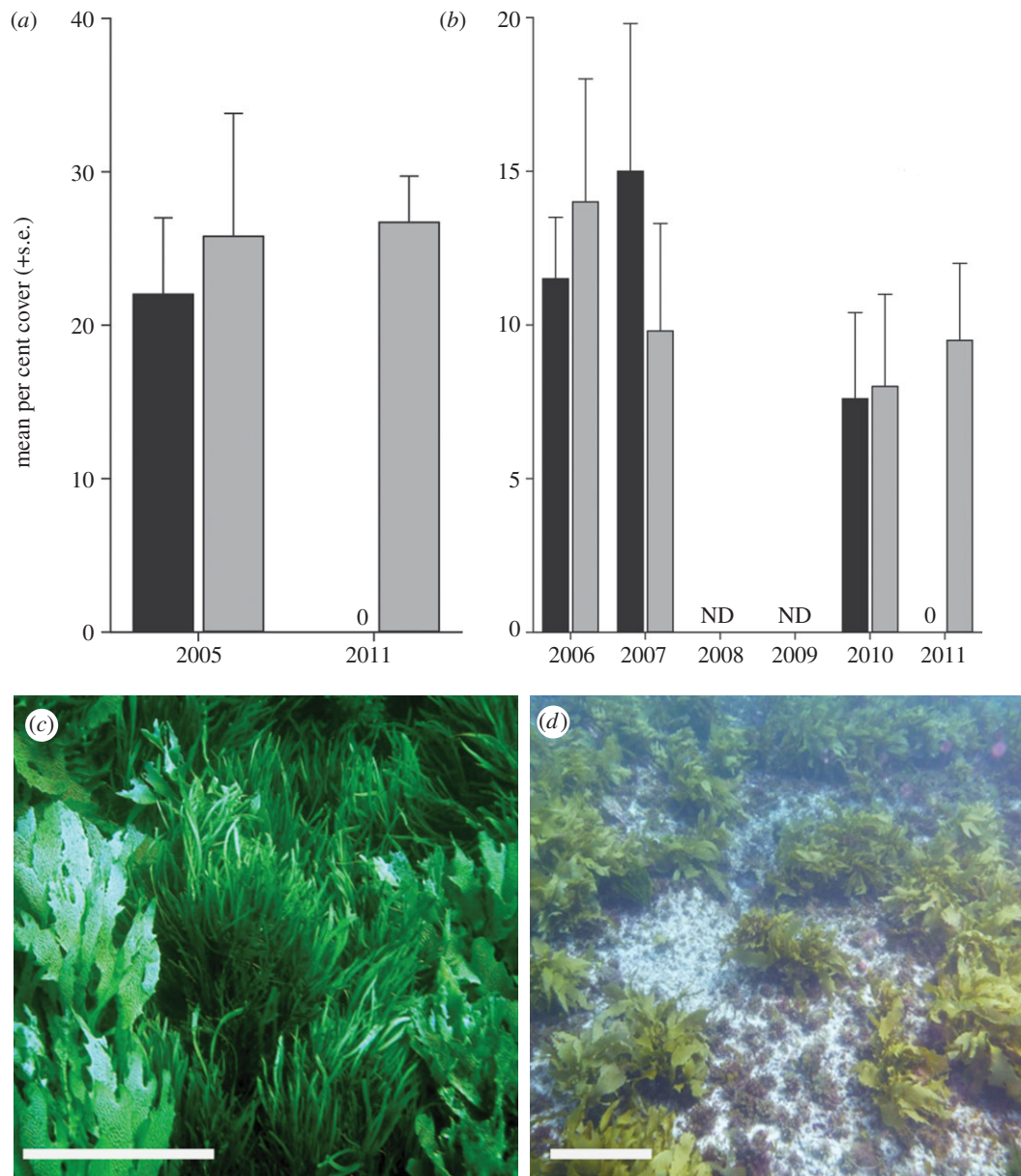


Figure 3. Mean (+ s.e.) (a) transect-scale and (b) quadrat-scale covers of *Scytothalia dorycarpa* at both monitoring locations in Western Australia. Note differences in scale on the y-axis between plots. Black bar, JB; grey bar, HB; ND, no data. (c) Also shown is a representative patch of mixed canopy comprising the kelp *Ecklonia radiata* and *S. dorycarpa* (centre) JB prior to the HW, and (d) habitat structure at the same site after the HW showing large gaps where *S. dorycarpa* was eradicated from the previously closed canopy. *S. dorycarpa* is now completely absent from JB. Scale bars represent approximately 0.5 m.

trend, as the southeast Indian Ocean has warmed at a rate above the global average over the past 50 years [32,33].

(b) Biological surveys

Transect-scale surveys (covering approx. 750 m² of subtidal reef) at the two monitoring locations showed that *S. dorycarpa* covered approximately 25 per cent of reef surfaces at 8–12 m depth in 2005, prior to the HW (figure 3a). In 2011, following the event, *S. dorycarpa* was completely absent from JB, whereas no change was observed at the cooler location, HB (figure 3a and table 1). Quadrat-scale surveys at the same reefs confirmed that *S. dorycarpa* completely disappeared from JB between November 2010 and 2011, whereas, again, no differences were recorded at HB (figure 3b and table 1). Loss of this habitat-former from JB, where the seaweed canopy was formerly dense (figure 3c), has resulted in extensive gaps in the canopy (figure 3d). In the JB region, widespread searches,

including AUV mapping of 3750 m² reef between 12 and 50 m depth, did not return a single *S. dorycarpa* individual, even ruling out a depth refuge. Furthermore, regular targeted surveys at multiple sites, where the species was formerly abundant, in the 16 months since the peak of the HW have yielded no individuals. This period includes two recruitment episodes for *S. dorycarpa*, where recruits have been observed at cooler locations (e.g. HB, 34° S).

Data on the coverage of *S. dorycarpa* were obtained from approximately 1000 km of coastline, representing a gradient of SST (annual mean) of 18–22°C (figure 2). Prior to the HW, the equator-ward limit of *S. dorycarpa* was approximately 50 km north of JB (approx. 30.1° S); following the HW, extensive surveys indicated that the range edge was situated between Grey (approx. 30.8° S) and Lancelin (approx. 31.0° S). As such, we conservatively estimate that the warming event caused the equator-ward range edge to shift some 100 km south (0.8° S), in less than 1 year (figure 2). Analysis

Table 1. (a) Results of two-way ANOVA to test for differences in transect-scale cover of *Scytothalia dorycarpa* between sampling years and locations. (b) One-way examinations of the effect of year within each location (JB, Jurien Bay; HB, Hamelin Bay) were also performed at this spatial scale. (c) Similarly, two-way ANOVA tests were conducted to test for differences between years and locations in *S. dorycarpa* cover at the quadrat-scale and (d) within the significant interaction term. In all cases, percentage cover data were $\ln(x + 1)$ -transformed.

source	d.f.	MS	F	p	pair-wise
(a) two-way global (transect scale)					
year	1	8.15	54.90	< 0.001	
location	1	6.46	43.50	< 0.001	
year \times location	1	8.15	54.87	< 0.001	
residual	8	0.15			
(b) one-way within location (transect scale)					
JB—year	1	14.56	260.9	< 0.001	2005 > 2011
HB—year	1	0.049	0.20	0.676	n.s.
(c) two-way global (quadrat scale)					
year	4	8.14	7.97	< 0.001	
location	1	3.12	3.07	0.083	
year \times location	4	3.89	3.82	0.007	
residual	87	1.02			
(d) one-way within location (quadrat scale)					
JB—year	4	10.92	25.78	< 0.001	2006, 2007, 2010 > 2011
HB—year	4	0.63	0.414	0.798	n.s.

Table 2. Results of two-way ANOVA to test for differences in the percentage cover of *Scytothalia dorycarpa* before and after the HW, within latitudinal bins. Post hoc pair-wise comparisons (SNK tests) to examine differences before ('b') and after ('a') the HW within each latitudinal bin are also shown. Data were $\ln(x + 1)$ -transformed prior to analysis but failed tests for normality and homogeneity of variance.

source	d.f.	MS	F	p	latitude ($^{\circ}$ S)	pair-wise
latitude	4	12.52	30.72	< 0.001	27.0–29.9	b = a
HW	1	4.19	10.30	0.002	30.0–30.9	b > a
latitude \times HW	4	3.85	9.46	< 0.001	31.0–31.9	b > a
residual	50	0.40			32.0–32.9	b = a
					33.0–34.9	b = a

of transect-scale percentage cover data from across the *S. dorycarpa* range edge provided further evidence of the range contraction. Prior to the HW (surveys conducted between 2000 and 2010), *S. dorycarpa* covered 11.9 ± 2.9 per cent of the rocky reefs surveyed between 30.0 and 30.9 $^{\circ}$ S, whereas surveys of the same reefs (and additional sites) following the HW did not return a single individual within this latitudinal range (table 2 and figure 4). Between 31.0 $^{\circ}$ S and 31.9 $^{\circ}$ S, *S. dorycarpa* was significantly less abundant following the HW, whereas no differences were detected at higher latitudes (table 2 and figure 4). At the AUV sites, *S. dorycarpa* was not recorded at the Abrolhos (28.9 $^{\circ}$ S), was present before (at approx. 1% cover) but not after the HW at JB (30.5 $^{\circ}$ S), and covered approximately 10 per cent of rocky reefs at Rottnest (32.0 $^{\circ}$ S) both before and after the event (note that AUV-derived estimates of *S. dorycarpa* cover at JB were considerably lower than those derived from scuba-based transects because of the greater range of depths and habitat characteristics covered by the AUV surveys, which were used to investigate possible depth refugia for marginal populations).

Monitoring data from JB were also examined for community-level responses associated with the loss of *S. dorycarpa* as a dominant habitat-former. First, quadrat-scale percentage cover data for all understorey taxa were square-root-transformed, and replicates were pooled for each site per year. A multi-dimensional scaling (MDS) ordination, based on a Bray–Curtis similarity matrix, was then generated to visualize community structure before and after the HW. The MDS ordination showed a clear partitioning between understorey community structure after the 2011 HW compared with previous years (figure 5), and a cluster analysis showed that samples before and after the HW formed distinct groups at 70 per cent similarity (figure 5). A SIMPER analysis [27] was conducted to determine which understorey taxa were the major contributors to community-level differences before and after the HW. Key discriminatory taxa were turf-forming algae, which increased in cover after the warming event, and encrusting coralline and non-coralline algae, which both decreased in cover after the HW (figure 5 and table 3).

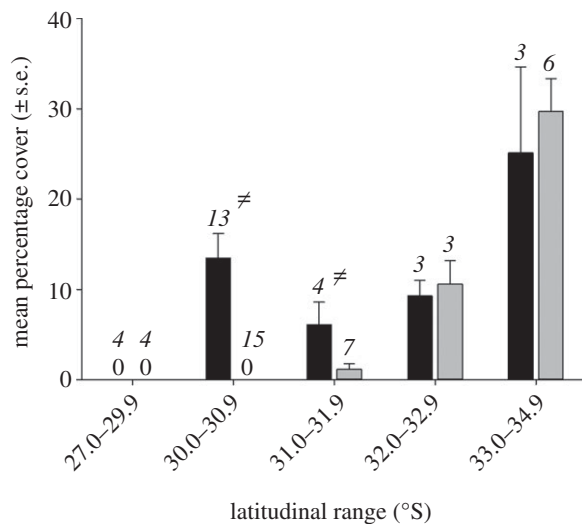


Figure 4. Mean (\pm s.e.) percentage cover of *Scytothalia dorycarpa* within latitudinal bins both pre- (black bars) and post-HW (grey bars). Italicized numbers denote the number of independent sites (n) surveyed by scuba divers within each latitudinal bin; multiple transects were conducted at each site (transects pooled for analysis). A significant difference in *S. dorycarpa* cover before and after the HW, as determined by post hoc pair-wise tests within each latitudinal bin (table 2), is shown by the 'not equal to' symbol (\neq). Note different latitudinal ranges within northernmost and southernmost bins.

Table 3. Results of SIMPER analysis to determine the contributions of coarse taxonomic groups to the overall observed difference in understorey community structure, before and after the 2011 HW, at JB. The overall dissimilarity between pre- and post-HW communities was 30.6%. turf, turf-forming algae; ECA, encrusting coralline algae; ENC, encrusting non-coralline algae; red, red macroalgae; AC, articulate coralline algae; spon., sponges. Mean percentage cover (square-root-transformed) for each major group before and after the HW is shown. 'diss/SD' is a measure of the variation in contribution to dissimilarity, 'contrib%' is the contribution of each group to total dissimilarity and 'cum%' is the cumulative contribution to dissimilarity.

taxon	pre-HW mean cover	post-HW mean cover	diss/SD	contrib%	cum%
turf	1.13	3.42	2.81	18.39	18.39
ECA	5.90	3.80	2.91	16.38	34.77
ENC	3.26	1.46	3.95	14.28	49.05
red	5.03	6.45	1.99	11.14	60.19
AC	2.59	1.89	1.18	9.00	69.19
spon.	1.45	0.85	1.62	6.92	76.10

The loss of the habitat-former was 'scaled-up' to the ecosystem level by estimating the total reduction of canopy biomass at the range edge. In 2006, the identity and wet weight of all macroalgal species within 30 replicate 0.25 m² quadrats were quantified, across five subtidal reefs, in JB (see [34] for sampling details and study rationale). These data showed that prior to the HW the biomass of *S. dorycarpa* was, on average, 166 tonne km⁻² (or 166 g m⁻²), which accounted for approximately 5 per cent of total canopy biomass. As suitable subtidal rocky reef habitat is abundant in the range contraction region (between 30.1° S and 30.9° S; there is more than 180 km² of suitable habitat between 2 and 20 m depth; data from various sources, including Department of Environment and Conservation, and Department of Planning and Infrastructure), we conservatively estimate that the extirpation of marginal populations has resulted in a reduction of biogenic habitat of least 31 000 tonnes. This clearly represents a substantial loss of benthic primary producer

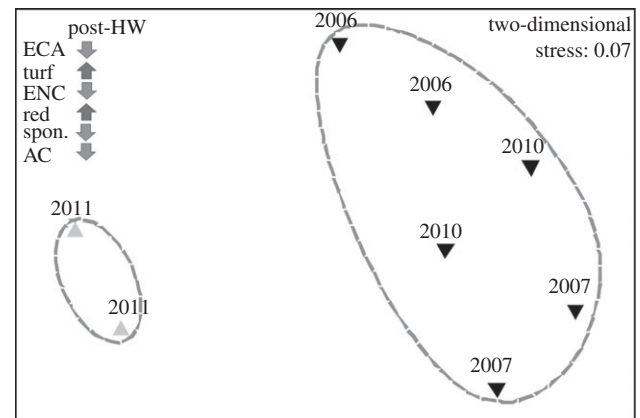


Figure 5. MDS ordination of understorey community structure at JB, before and after the warming event, based on a Bray–Curtis similarity matrix generated from square-root-transformed percentage cover data. Centroids represent understorey community structure at two independent study sites within JB for each survey year (averages of six replicate quadrats per year per site combination). Also shown is the response of key discriminatory taxonomic groups to the HW (i.e. increased or decreased per cent cover) based on SIMPER analysis (see table 3 for results and taxa abbreviations). Grey triangle, post-HW; inverted black triangle, pre-HW.

biomass, even though such up-scaling, back-of-the-envelope calculations should be treated cautiously.

(c) Physiological assays

Physiological assays showed that oxygen metabolism varied significantly with incubation temperature ($MS = 0.0738$, $F_{6,35} = 9.24$, $p = 0.001$; figure 6). However, there was a considerable variability in net primary productivity within temperature treatments, possibly reflecting variation among individuals in acclimation to reef microclimates. Still, the short-term incubations indicated that net productivity increased from approximately 10°C to approximately 24°C, before rapidly declining at higher temperatures (figure 6). Photosynthesis rates under HW conditions at JB were significantly lower than peak rates observed under 'normal' field conditions (figure 6). Crucially, net photosynthesis was negative at experimental temperatures, similar to those observed

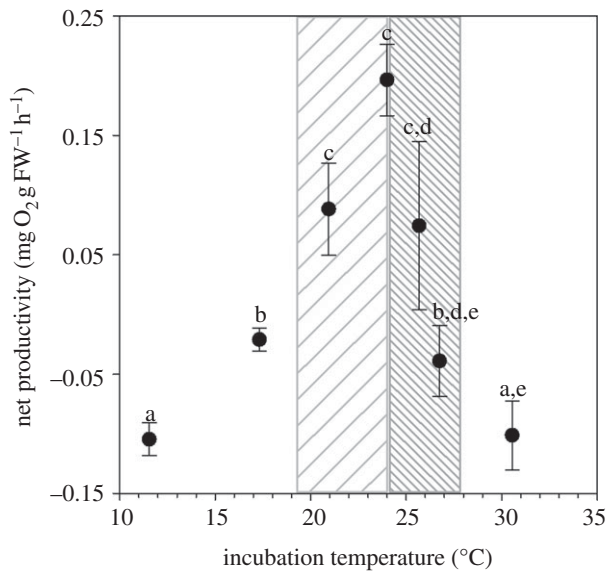


Figure 6. Mean (\pm s.e., $n = 6$) net photosynthesis at $530 \mu\text{E m}^{-2} \text{s}^{-1}$ rates for *Scytothalia dorycarpa* tissue under short-term incubation at different temperatures. The sparsely hatched lightly shaded box indicates temperatures normally experienced on subtidal reefs at JB (2006–2010) and the densely hatched dark box indicates extreme temperatures recorded at JB during the HW of 2011. Points with shared letters are not significantly different ($p > 0.05$).

in JB during the HW. At HB, the cooler study location, temperature peaked at 24.1°C during the HW, which was below the physiological threshold for photosynthesis for some of the most ‘warm-adapted’ individuals (figure 6).

4. Discussion

HWs are discrete, extreme warming events that are likely to increase in frequency and magnitude as a result of anthropogenic climate change [13]. In marine ecosystems, physical drivers of HWs are complex and vary between regions, but ecological responses include physiological stress [23,35], mass mortalities [36,37], and changes in the structure of communities and entire ecosystems [25,38]. Here, an extreme warming event caused the extirpation of marginal populations of an important habitat-forming species, resulting in an approximately 100 km contraction of the warm-water range boundary. Our experimental results provide evidence to suggest that the extreme temperatures exceeded the lethal threshold of individuals within marginal *S. dorycarpa* populations, as a key physiological process could not be maintained under prolonged HW conditions. Although the absolute values of our short-term incubation experiment should be interpreted with some caution, to take into account the possibility of local acclimation and long-term responses, the fact that net photosynthesis was negative at temperatures experienced at JB, but not HB, during the HW provides support for physiological mechanisms driving the range contraction.

Extensive losses of canopy-forming macroalgae (giant kelp, *Macrocystis pyrifera*) have previously been recorded during extended warm-water episodes along the west coast of the Americas [36]. Rapid recovery of these kelp beds was probably facilitated by their ‘seed’ bank of microscopic life stages [39], long-range dispersal of both zoospores [40] and floating adults [41], and source populations being located

upstream of the main ocean currents [42]. Recovery of *S. dorycarpa* populations, by contrast, depends on the proximity of fertile adults as the species has direct development, no flotation and large propagules with short dispersal distances. These attributes, as well as the fact that potential source populations are located downstream of the main ocean current [21], make a full recovery unlikely and point to a persistent range contraction.

The loss of *S. dorycarpa* at JB was associated with a shift in understory community structure, which was most likely to be driven by the indirect effects of loss of canopy cover rather than the HW *per se*. As canopy-forming seaweeds generally out-compete turf-forming algae, by reducing light and sediment levels on the seafloor and by inhibiting the settlement of recruits [43,44], it is likely that a reduced cover of *S. dorycarpa* and the kelp *E. radiata* [25] led to a proliferation of turf-forming algae. Conversely, the cover of encrusting algae and sponges (which are adapted to low light and sediment conditions, and are facilitated by canopy-forming seaweeds [44]) decreased. This shift from structurally complex canopy-dominated habitat to open turf habitat is characteristic of a degraded system [45]. Furthermore, the substantial loss of seaweed biomass from the range edge will have major implications for ecosystem-scale processes, at least in the immediate term. Large seaweeds provide habitat and food, both directly and as a spatial subsidy, for a diverse range of marine organisms [46,47]. As such, loss of *S. dorycarpa* will alter benthic productivity and energy transfer, as well as biogenic habitat provision, along more than 100 km of warm temperate coastline. Loss of benthic primary production could also impact secondary production and, ultimately, the amount of energy available for important commercial species in the region [48]. Over time, it is possible that other habitat-formers, such as warm-water-adapted corals or seaweeds, will fill the void and serve a similar function to *S. dorycarpa* [21], as part of a regional transition from a warm temperate to a more subtropical ecosystem. In the immediate term, however, loss of cool-affinity habitat-formers from the transition zone will be most likely to adversely impact ecosystem structure and functioning.

Extreme climatic events are superimposed onto longer-term changes in climate or human activities. There is mounting evidence from terrestrial ecosystems to suggest that discrete climatic events (e.g. HWs, floods and droughts) interact with chronic stressors (e.g. warming and nutrient input) to reach and exceed ecological tipping points that cause abrupt, step-wise shifts in populations and communities [49,50]. For the habitat-former *S. dorycarpa*, historical herbarium records suggest that, over the five decades prior to the HW, its equator-ward range edge retracted at an average rate of 3.2 km yr^{-1} [1], probably in response to a combination of both gradual warming (approx. 0.6°C off southwest Australia over the same period; see [33]) and historical discrete warming events (albeit lower in magnitude than the 2011 event; see [25]). In 2011, the equator-ward range edge contracted approximately 100 km in response to a discrete warming anomaly of approximately $2\text{--}5^\circ\text{C}$, which equates to approximately 5 per cent contraction of this species’s global distribution. Crucially, *S. dorycarpa* and other components of the marine flora of southern Australia cannot sustain their geographical extents through range expansions at the poleward edge, as there is no available habitat south of the Australian continental shelf.

Previous studies on the influence of discrete extreme climatic events on species range dynamics in marine ecosystems have focused on intertidal organisms [51,52] or tropical

coral species [53]. These studies have demonstrated that biogeographic changes to climate are 'ratchet-like' [51] and are defined by punctuations of population responses to extreme events. The loss of *S. dorycarpa* from its equator-ward range edge following the 2011 'marine heat wave' provides further direct evidence for how discrete, climatically extreme events can drive abrupt range shifts in marine ecosystems through local extinctions of marginal populations. A philosophical problem in climate change biology is that attribution of observed changes to climatic forcing generally occurs post hoc from events spanning long time-scales confounded by other drivers such as changes in land use, urbanization or harvesting [54]. The evidence presented here is particularly compelling because the observed changes were predicted *a priori* [21,22] and follow likely range changes in response to general warming over the past 50 years [1]. Extreme climatic events are increasing in frequency and magnitude as a consequence of human activities, and in the last 30 years alone the

number of days of anomalously high seawater temperatures has increased along 38 per cent of the world's coastlines [18]. Understanding how these discrete disturbances drive abrupt ecological change is of fundamental importance to climate change mitigation and adaptation.

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