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An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot

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Extreme climatic events, such as heat waves, are predicted to increase in frequency and magnitude as a consequence of global warming but their ecological effects are poorly understood, particularly in marine ecosystems[1-3]. In early 2011, the marine ecosystems along the west coast of Australia—a global hotspot of biodiversity and endemism[4,5]—experienced the highest-magnitude warming event on record. Sea temperatures soared to unprecedented levels and warming anomalies of 2–4 °C persisted for more than ten weeks along >2,000 km of coastline. We show that biodiversity patterns of temperate seaweeds, sessile invertebrates and demersal fish were significantly different after the warming event, which led to a reduction in the abundance of habitat-forming seaweeds and a subsequent shift in community structure towards a depauperate state and a tropicalization of fish communities. We conclude that extreme climatic events are key drivers of biodiversity patterns and that the frequency and intensity of such episodes have major implications for predictive models of species distribution and ecosystem structure, which are largely based on gradual warming trends.

Ecosystems around the world have responded to climate change and climate variability, with major implications for humanity's use of ecological goods and services[6]. Links between increasing mean temperatures and changes in populations, communities and ecosystems have been documented convincingly across many regions[1,6]. Concurrent with these observations, predictions of how biodiversity will respond to further climate change have been developed, largely based on climate-envelope modelling approaches using projected mean temperatures[7]. There is growing recognition, however, that ecological change is often driven by discrete events, as well as continuous gradual change[3], as extreme events affect species' distributions and, ultimately, ecosystem structure and functioning[8]. Storms, tropical cyclones, droughts, floods, cold spells and heat waves, which are likely to increase in frequency and magnitude as a consequence of climate change[9], have been widely documented to have catastrophic effects on terrestrial ecosystems[3]. In contrast, the influence of extreme events, rather than gradual warming trends, on marine ecosystems is poorly understood, as almost all knowledge has been gained from only a few events, such as the 1983 and 1998 El Niño episodes[10,11] and the Mediterranean heat wave of 2003 (ref. 12). Recent analysis has shown that the frequency of anomalously high seawater temperatures has increased along 38% of the world's coastlines[13], and although our understanding of how temperature anomalies affect coral reefs, in particular, is increasing[14], empirical evidence of how extreme warming events shape marine ecosystems in general remains scant.

The coastal margins along the west coast of Australia form a transition zone between tropical and temperate biota and represent a global hotspot of biodiversity and endemism[4,5]. In the austral summer of 2010/2011, the southeast Indian Ocean experienced a discrete warming event, where seawater temperatures were the highest since satellite-derived records began some three decades ago[15]. Warming anomalies of 2–4 °C persisted for more than two months along the expansive coastline (Supplementary Fig. S1). In January 2011, an anomaly of 2.5 °C developed off northwest Australia, adjacent to the Ningaloo coral reef ecosystem (Supplementary Fig. S1). By March 2011, the anomaly had migrated polewards towards the kelp-dominated coastal habitats of southern Australia (Fig. 1a and Supplementary Fig. S1). The event was driven by unusually strong La Niña conditions, which increased the flow of the region's main ocean current (the Leeuwin current) and the transfer of tropical warm water polewards[15]. Simultaneously, air–sea heat flux was anomalously high and both processes were superimposed onto a decadal scale warming trend (Supplementary Fig. S2a), as warming rates in the southeast Indian Ocean are above the global average[15,16]. Here, we document the response of the temperate marine ecosystem to the heat wave by examining interannual variability in the community structure of rocky-reef-associated macroalgae, sessile invertebrates and fish over six years. Biodiversity patterns were examined in two regions, >500 km apart, which support a rich, endemic marine biota that is representative of temperate Australia[17,18]. In both regions, the warming event peaked in March 2011, when anomalies of up to 5 °C were recorded on rocky reefs at ∼10 m depth (Fig. 1b,c). This heat wave represented the most extreme warming event in the region in the past 140 years; for two consecutive months, thermal stress anomalies[14] exceeded the previously recorded maximum by >43% (Supplementary Fig. S2b).

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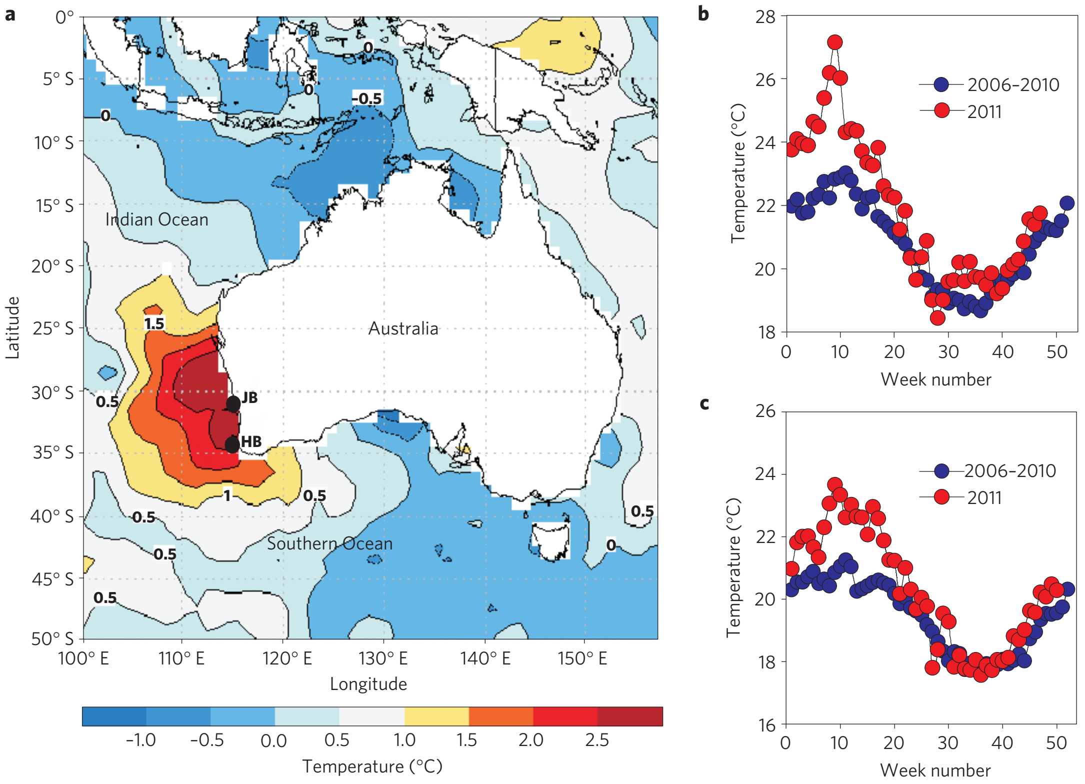

Figure 1 | The 2011 heat wave in the southeast Indian Ocean. a, Blended sea surface temperature anomaly map for March 2011 (relative to a 1971–2000 baseline), indicating a warming anomaly of >2.5 °C along the warm temperate western coast of Australia. The Jurien Bay (JB) and Hamelin Bay (HB) study regions are also shown. **b**,**c**, Weekly temperature anomalies during 2011 (relative to means of the preceding five years) generated from *in situ* measurements at ~10 m depth at the sites where community data were collected: Jurien Bay (**b**) and Hamelin Bay (**c**).

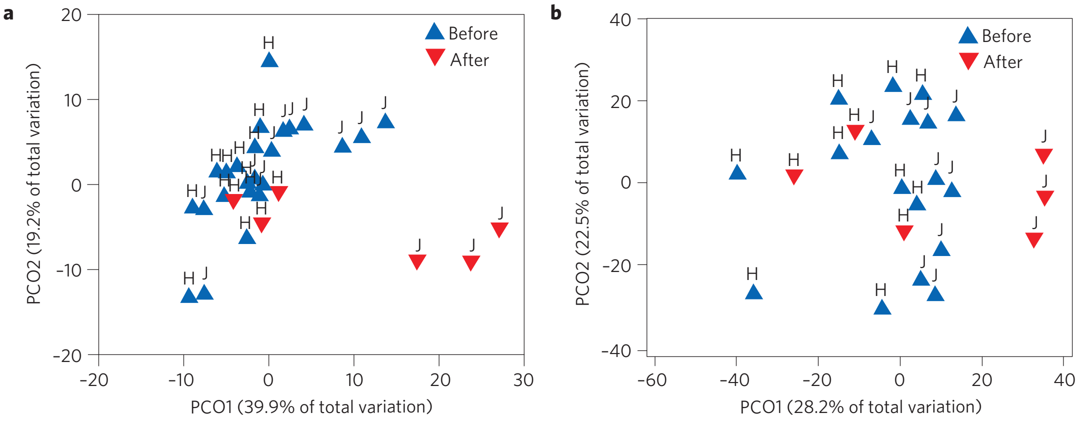

Figure 2 | The ecological structure of marine communities before and after the heat wave of 2011. a,**b**, Principal coordinates analysis of benthic (invertebrates and macroalgae; **a**) and fish (**b**) community structure on rocky reefs at each study location (J, Jurien Bay; H, Hamelin Bay) before and after the 2011 warming event. PCO1 and PCO2 are the first and second principal coordinates axes, indicating percentage of variation explained by each axis.

Reef-associated communities exhibited variable responses to the extreme event (Fig. 2 and Supplementary Table S1). In our warm temperate study region, Jurien Bay (30° S), the community structure of benthic organisms and fish was significantly different in November 2011, eight months after the heat wave, compared with November in preceding years (Fig. 2). After the heat wave, both benthic and fish communities were markedly distinct from preceding years, although fish communities exhibited greater spatiotemporal variability (Fig. 2 and Supplementary Tables S2 and S3). Conversely, communities at the cooler region, Hamelin Bay (34° S), did not exhibit a response to the heat wave (Fig. 2 and Supplementary Tables S2 and S3).

Shifts in the benthic community structure at Jurien Bay were attributed to a reduced cover of the dominant kelp (*Ecklonia radiata*) and encrusting coralline algae, and an increased cover of turf-forming algae (Fig. 3 and Supplementary Table S4). Furthermore, total cover of the macroalgal canopy (that is, kelps and large fucoids) significantly decreased following the heat wave (Fig. 4 and Supplementary Table S5). Most of these habitat-forming seaweeds are temperate species that persist near the warm edge of their respective distributions at the study area[19]. A warming anomaly of ~5 °C would have resulted in thermal stress that exceeded anything previously experienced at these locations for several decades (Supplementary Figs S2 and S3). This thermal stress

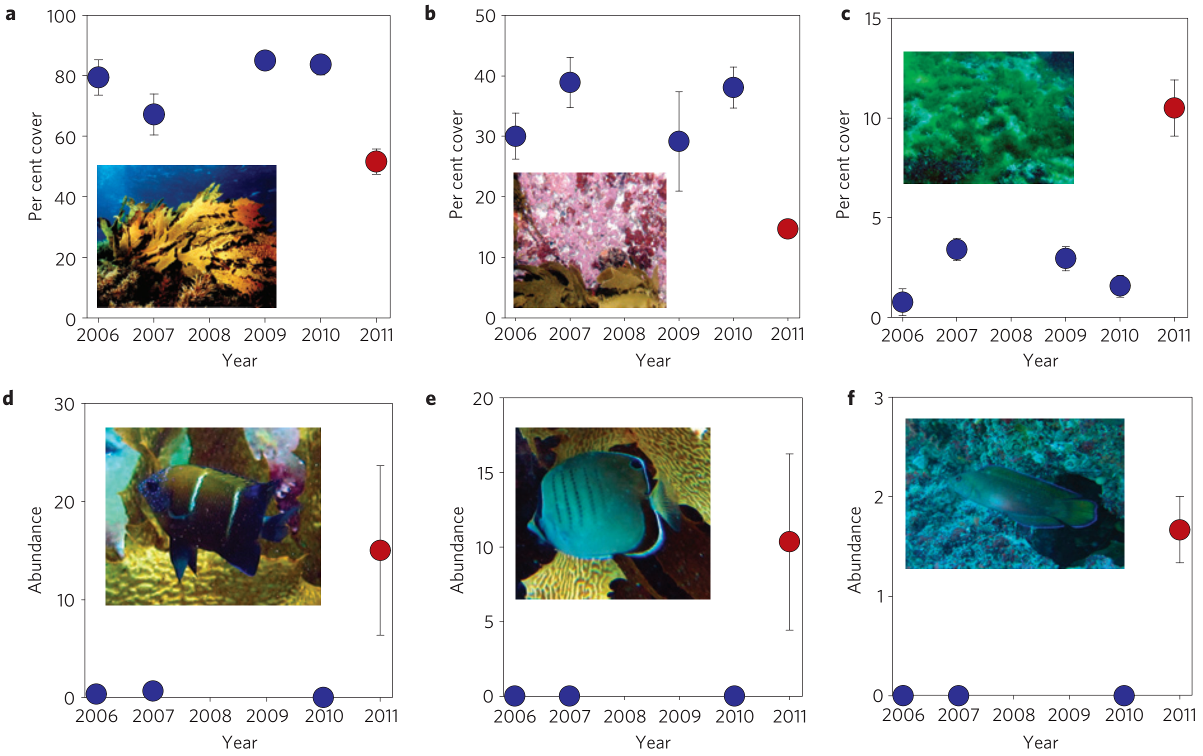

Figure 3 | The response of macroalgae and fish to the marine heat wave of 2011. a–c, Mean percentage cover (±standard error of the mean (s.e.m.), *n* = three sites with six pooled quadrat samples) during each year of sampling of the kelp *E. radiata* (**a**), encrusting coralline algae (**b**) and turf-forming algae (**c**) (sampling not conducted in 2008). **d–f**, Mean abundances (±s.e.m., *n* = three sites with three pooled transects) of fish species that were major contributors to differences in community structure before and after the heat wave are also shown; *P. occidentalis* (**d**), *C. assarius* (**e**) and *L. lineatus* (**f**) (sampling was not conducted in 2008 or 2009).

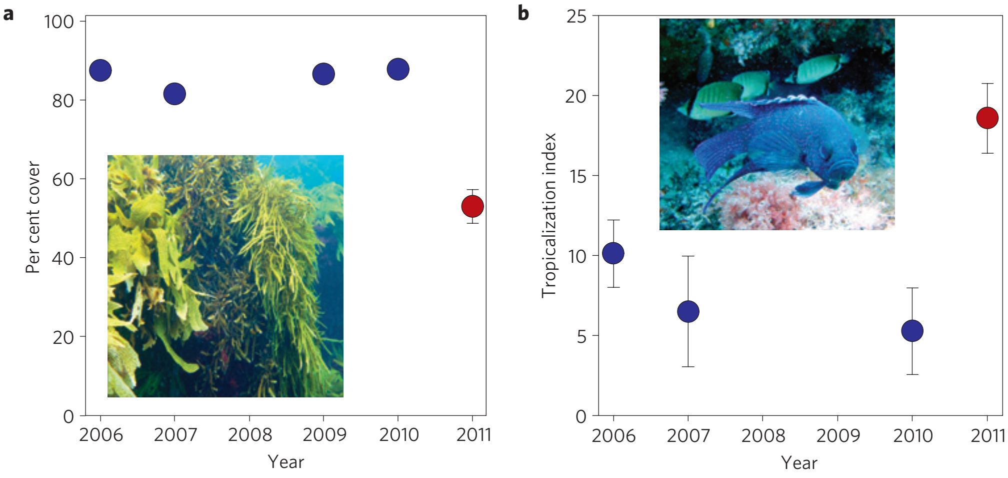

Figure 4 | Changes in seaweed canopy cover and tropicalization index for fish communities following the marine heat wave of 2011. a, Mean precentage cover (± s.e.m., *n* = three sites with six pooled quadrat samples) of the entire macroalgal canopy (that is, kelps and fucoids) and **b**, mean contribution (± s.e.m., *n* = three sites with three pooled transects) of tropical species to overall fish community composition during each year of sampling (temperate Western Blue Devil (*Paraplesiops meleagris*) with tropical *C. assarius* in the background).

would almost certainly have exceeded physiological thresholds for primary productivity, growth and, in some cases, survival[19,20] and was most probably the causative agent behind the loss of seaweed canopy cover. The depletion of macroalgal canopies on temperate reefs has major implications for local biodiversity, by altering species interactions (for example, competition and facilitation) and habitat and food for associated organisms[21,22]. Subtidal habitat-forming seaweeds generally outcompete turf-forming species by inhibiting the settlement of turf-forming algae and by reducing sedimentation and light on the reef surface[23,24]. At Jurien Bay, a reduction in canopy cover following thermal stress would have released resources (for example, space and light), allowing the proliferation of turf-forming algae. Conversely, the cover of encrusting coralline algae and sponges decreased, again an indirect consequence of the loss of kelp that facilitates these taxa[24]. This shift in community structure from a structurally diverse kelp bed to simple mats of algal turfs represents a shift towards a depauperate ecological state[22,23].

Compositional changes in fish communities at Jurien Bay following the heat wave were largely driven by the sudden appearance of warm-water species, such as *Parma occidentalis* (western scalyfin), *Chaetodon assarius* (west Australian butterflyfish) and *Labracinus lineatus* (lined dottyback). The abundances of these species were significantly greater in 2011 than in years before the heat wave (Fig. 3 and Supplementary Table S5). For example, only three *P. occidentalis* individuals were observed at these sites at Jurien Bay during sampling spanning five years before the warming event, whereas 45 individuals (mostly juveniles) were recorded in 2011. An influx of warm-water fish species was most evident at the community level, as the tropicalization index (ratio of tropical to all species) increased after the heat wave, from 5–10% to ~20% (Fig. 4 and Supplementary Table S6). This tropicalization of fish communities probably reflects a stronger poleward flow of the Leeuwin current increasing the likelihood of tropical fish larvae reaching warm temperate zones[25]. Furthermore, prolonged increased temperatures and a shorter, milder winter is also likely to have favoured the development, survival and local reproduction of these warm-water species[26]. A combination of these processes would have led to an increase in the diversity and abundance of fish with a warm-water affinity in Jurien Bay eight months after the extreme event. There was no evidence of a decline in temperate fish species following the heat wave, despite nearby observations of mass mortalities of fish and abalone during peak warming[15]. Persistence of colder-water species in the face of warming while warmer-water species are expanding has also been seen for marine species in Europe[8].

Community-level responses to the heat wave were observed only at the warm region, not at the cooler region, despite similar warming profiles. Marginal populations of both temperate and tropical species co-exist in Jurien Bay[17,18] to form a diverse, transitional biota. Soaring temperatures would have exceeded the physiological thresholds of sessile cool-affinity species without the ability to seek temporary refuge, and proved favourable for warm-affinity species, thus driving community-level change. In contrast, Hamelin Bay supports a typical temperate biota with few marginal populations[17,18], so that cool-water species were not subjected to conditions exceeding their absolute physiological thresholds and the influx of warm-water species did not occur because of lower actual temperatures and greater dispersal distances from their warm-water source populations. These contrasting patterns highlight the importance of biogeographic context and absolute thermal thresholds in determining community responses to climatic events and add another element of complexity to understanding and predicting ecosystem responses to abrupt warming.

An unanswered question concerns the rate and trajectory of community recovery at Jurien Bay following the heat wave. Studies conducted in other marine ecosystems have highlighted marked variability in ecological responses to, and recovery rates following, discrete warming events, probably reflecting system-specific idiosyncrasies. For example, El Niño–Southern Oscillation-mediated warming events in Californian waters represent major disturbances to kelp forests, causing widespread losses in canopy cover and subsequent shifts in community structure[11]. Post-disturbance recovery, however, can be rapid and is facilitated by the biological traits of key habitat-forming species (for example, dispersal potential, life history) and local oceanography[27]. Conversely, the ecological consequences of the 2003 heat wave in the Mediterranean, which included range expansions and mass mortalities, have persisted with little sign of recovery towards a preperturbed state[12]. The persistence and trajectory of recovery of the perturbed state in southwest Australia depends on the resilience of marginal seaweed populations and the long-term survival of warm-water fish populations. Physiological adjustment may allow habitat-forming macroalgae, such as kelps, to persist during periods of warming, but at an ecological cost in terms of their competitive ability and recruitment rates[28]. Intervening periods of cooling could enable some species to bounce back; however, once mats of turf-forming algae become established they can inhibit the recovery of habitat-forming macroalgae for many years[23]. For fish, the survivorship of warm-water juveniles over the winter will be a key limiting factor in determining whether populations become established and community tropicalization persists. Empirical evidence from east Australia suggests that the ability of tropical fish to overwinter in temperate waters—and thus undergo a range expansion—is increasing in line with seawater warming and we would predict a similar pattern in west Australia[26].

Extreme climatic events can affect the distribution and abundance of organisms both directly, through physiological stress, and indirectly, through altered species interactions[3]. We suggest that the 2011 heat wave in the southeast Indian Ocean had both direct physiological effects on temperate macrophytes and warm-water fish species, and indirect effects relating to knock-on consequences of macroalgal canopy loss. The extreme climatic event caused a step-change in biodiversity patterns in an important tropical–temperate transition zone. So far, observed and predicted ecological responses to gradual climatic trends have received far more attention than those associated with discrete events[3]. Although conceptually challenging, the frequency, magnitude and geographical extent of extreme events needs to be considered in conjunction with mean warming trends for accurate prediction and mitigation of climate change effects on marine ecosystems.

Methods

Ecological surveys were conducted by scuba divers at Jurien Bay (30° 18′ 38 S, 114° 58′ 9 E; average temperature, ~20.7 °C) and Hamelin Bay (34° 14′ 18 S, 115° 0′ 54 E; average temperature, ~19.4 °C). At each location, three rocky reef sites (9–12 m depth, >2 km apart) were surveyed in November/December (austral summer) during each sampling year. For benthos, six haphazard 0.25 m^2 quadrats (>5 m apart) were sampled at each site by quantifying the cover of macroalgae, sessile invertebrates and bare substrata. For fish, underwater visual censuses were conducted along triplicate 25 m transects at each site[29]. Benthic communities were not surveyed in 2008; fish communities were not surveyed in 2008 or 2009. For analysis, replicate quadrats/transects were pooled for each site and variability in multivariate community structure between regions (fixed factor) and years (fixed factor) was examined with permutational multivariate analysis of variance[30]. Permutations were based on a Bray–Curtis similarity matrix generated from either square root transformed per cent cover data for benthos (13 variables, Supplementary Table S7) or presence/absence data for fish (33 species and six genera, Supplementary Table S8). In both cases, a significant ($P < 0.05$) location × year interaction was recorded (Supplementary Table S1) and so each location was analysed separately, using a one-way permutational multivariate analysis of variance (between years) with pre-planned single degree of freedom contrasts[31], to test the hypothesis that communities in 2011 (that is, after the heat wave) were distinct from previous years (Supplementary Tables S2 and S3). Differences in multivariate structure between factors were visualized with principal coordinates analysis[30]. A similar statistical approach was used to examine the response of individual taxa/functional groups to the event, using similarity matrices based on Euclidian distance of untransformed data. Temporal trends in the percentage contribution of tropical species to entire fish communities (a tropicalization index) were also examined. Blended sea surface temperature anomalies for March 2011 (relative to a 1971–2000 baseline) were provided by the National Weather Service and were plotted using GrADS. *In situ* loggers (Onset TidbiT +5−37) deployed ~5 cm above the reef surface collected continuous temperature data since 2005.

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Author contributions

T.W. conceived the research programme and secured financial support. D.A.S. and T.W. contributed equally to the conceptualization and development of the paper. D.A.S. wrote most of the paper, with assistance from T.W., and carried out most analyses, with assistance from T.W. and T.J.L. Fieldwork was orchestrated by T.W. and conducted by T.W., F.T., T.d.B., M.S.T., S.B., T.J.L. and D.A.S. Analysis of temperature data was carried out by C.S.R. and T.W., with assistance from D.A.S. All authors discussed the results.

Additional information

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Competing financial interests

The authors declare no competing financial interests.