Climate-driven regime shift of a temperate marine ecosystem

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Ecosystem reconfigurations arising from climate-driven changes in species distributions are expected to have profound ecological, social, and economic implications. Here we reveal a rapid climate-driven regime shift of Australian temperate reef communities, which lost their defining kelp forests and became dominated by persistent seaweed turfs. After decades of ocean warming, extreme marine heat waves forced a 100-kilometer range contraction of extensive kelp forests and saw temperate species replaced by seaweeds, invertebrates, corals, and fishes characteristic of subtropical and tropical waters. This community-wide tropicalization fundamentally altered key ecological processes, suppressing the recovery of kelp forests.

Broad-scale losses of species that provide the foundations for habitats cause dramatic shifts in ecosystem structure, because they support core ecological processes (7–9). Such habitat loss can lead to a regime shift, in which reinforcing feedback mechanisms intensify to provide resilience to an alternate community configuration, often with profound ecological, social, and economic consequences (4–7). Benthic marine regime shifts have been associated with the erosion of ecological resilience through overfishing or eutrophication, altering the balance between consumers and resources, rendering ecosystems vulnerable to major disturbances (1, 2, 6, 7).

Now, climate change is also contributing to the erosion of resilience (8, 9), because increasing temperatures are modifying key physiological, demographic, and community-scale processes (8, 10), driving species redistribution at a global scale and rapidly breaking down long-standing biogeographic boundaries (11, 12). These processes culminate in novel ecosystems where tropical and temperate species interact, with unknown implications (13). Here we document how a marine heat wave caused the loss of kelp forests across ~2300 km² of Australia’s Great Southern Reef, forcing a regime shift to seaweed turfs. We describe a rapid 100-km range contraction of kelp forests and a community-wide shift toward warm-water species, with ecological processes suppressing kelp forest recovery.

To document ecosystem changes, we surveyed kelp forests, seaweeds, fish, mobile invertebrates, and corals at 65 reefs across a >2000-km tropical-to-temperate transition zone in western Australia (14). Surveys were conducted between 2001 and 2015, covering the years before and after an extreme marine heat wave affected the region. The Indian Ocean adjacent to western Australia is a “hot spot” where the rate of ocean warming is in the top 10% globally (15), and isotherms are shifting poleward at a rate of 20 to 50 km per decade (16). Until recently, kelp forests were dominant along >800 km of the west coast (8), covering 2266 km² of rocky reefs between 0 and 30 m depth south of 27.7°S (Fig. 1). Kelp forests along the midwest section of this coast (27.7° to 30.3°S) have experienced steadily increasing ocean temperatures since the 1970s, recently punctuated by three of the warmest summers in the past 215 years. In December 2010, immediately on July 8, 2016
midwest were similar to those of the temperate southwest (~500 km farther south) and clearly distinct from those of tropical reefs in the (~500 km farther north) (Fig. 3, A and B, and fig. S3) (17).

By early 2013, only 2 years later, our extensive surveys found a 43% (963 km²) loss of kelp forests on the west coast (Fig. 1). Previously dense kelp forests north of 29°S had disappeared (Fig. 2 and fig. S1) or been severely reduced (~90% loss, Fig. 1), representing a ~100-km range contraction and functional extinction from 370 km² of reef (a reduction in abundance severe enough to delete ecological function). Instead, we found a dramatic increase in the cover of turf-forming seaweeds (Fig. 2) and a community-wide shift from species characteristic of temperate waters to species and functional groups characteristic of subtropical and tropical waters [Figs. 3 and 4 and fig. S3, mean square contingency coefficient (φ²) = -0.70, P < 0.001]. Compared to the composition of the heavily affected midwest reef communities in Kalbarri before the 2011 marine heat wave, differences in community structure (Bray-Curtis dissimilarity) from reefs in Perth in the temperate southwest decreased by 32 and 16%, respectively. This broad-scale community-wide reef transformation reflected consistent decreases in the abundance of taxa characteristic of temperate reefs, coinciding with increases in the abundance of species characteristic of subtropical and tropical reefs, for both seaweeds (Fig. 3C and table S2, φ² = -0.68, P < 0.001) and fishes (Fig. 3D and table S3, φ² = -0.64, P = 0.008). Similar changes were seen for sessile and mobile invertebrates in the southern part of the midwest region, where small hermatypic coral colonies increased almost sixfold in abundance and doubled in species richness (Fig. 4 and table S5), while the abundances of sea urchins and gastropods also increased and decreased in accordance with their thermal affinities (Fig. 4 and tables S4 and S5, φ² = -0.68, P < 0.045).

Even though the acute climate stressor has abated (Fig. 2 and fig. S1), as of late 2015, almost 5 years after the heat wave, we have observed no signs of kelp forest recovery on the heavily affected reefs north of 29°S. Instead, concurrent with an 80% reduction in standing seaweed biomass (Fig. S2), we have recorded subtropical and tropical fish feeding rates on canopy seaweeds that are three times higher than on comparable coral reef systems. Similarly, we have found a 400% increase in the biomass of scraping and grazing fishes, a functional group characteristic of coral reefs, which now display grazing rates on seaweed turfs that are comparable to those observed on healthy coral reefs worldwide (table S6) (10). High herbivore pressure now suppresses the recovery of kelp forests by cropping turfs and kelp recruits (10).

We deduce that extreme temperatures beginning in 2011 exceeded a physiological tipping point for kelp forests north of 29°S, and now reinforcing feedback mechanisms have become established that support a new kelp-free state. Similar ecosystem changes have not been observed in the south-west, where heat wave temperatures remained within the thermal tolerance of kelps (17), and the greater distance to tropical bioregions limited the incursion of tropical species. Threshold temperatures for kelp forests appear close to 2.5°C above long-term summer maximum temperatures, consistent with other seaweeds in the region (20). However, the partial loss of kelp forests on reefs between 29° and 32°S suggests that there is variation in threshold temperatures within and between kelp populations.

The consistent responses of both cool- and warm-water species clearly illustrate the important role of temperature. However, the transition in community structure and subsequent persistence of the new regime would have been augmented...
Fig. 3. Changes in seaweed and fish communities on affected reefs after the 2011 marine heat wave. Ordinations (nonmetric multidimensional scaling) of seaweed (A) and fish (B) communities show how community structure on reefs north of 29°S shifted from a close resemblance to temperate reefs farther south to a greater resemblance to tropical reefs to the north. Dark blue = Kalbarri before (2005–2007), light blue = Kalbarri before (2005–2007), light blue = Kalbarri after (2013–2015), red = Ningaloo Reef (2010) (table S1). Each symbol represents an individual reef. Ordinations are based on Bray-Curtis dissimilarities calculated from ln(x + 1)–transformed data. (C and D) Change in ln(x + 1)–transformed abundance of seaweeds (C) grams of fresh weight per 1.5 m² and fish (D) individuals per 2500 m² in Kalbarri (2005–2007 versus 2013–2015) clearly show the decline in cool-water species (blue bars) and concurrent increase in warm-water species (red bars), with several species not previously recorded (+) or now absent from the samples (−). Each bar represents an average across six reefs for an individual species. White bars indicate taxa with ambiguous distributions. Species are listed in tables S2 and S3.

Fig. 4. Changes in benthic invertebrate abundances in the midwest after the 2011 marine heat wave. (A and B) Change in ln(x + 1)–transformed abundance of common mobile invertebrates (inverts) [(A) individuals per 30 m²] and small (<6 cm) hermatypic corals [(B) colonies per 1000 m²]. Colors and symbols are as in Fig. 3. Each bar represents an average across 6 and 23 reefs for an individual species of mobile invertebrates and corals, respectively. Mobile invertebrates were counted in Jurien Bay (2005, 2011 versus 2013 and 2014), and corals were counted between Cervantes and Dongara (30.6° to 29.3°S) (2005–2006 versus 2013) (table S1). Species are listed in tables S4 and S5.
Structural basis for membrane anchoring of HIV-1 envelope spike

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HIV-1 envelope spike (Env) is a type I membrane protein that mediates viral entry. We used nuclear magnetic resonance to determine an atomic structure of the transmembrane (TM) domain of HIV-1 Env reconstituted in bicelles that mimic a lipid bilayer. The TM forms a well-ordered trimer that protects a conserved membrane-embedded arginine. An aminoterminal coiled-coil and a carboxy-terminal hydrophilic core stabilize the trimer. Individual mutations of conserved residues did not disrupt the TM trimer and minimally affected membrane fusion and infectivity. Major changes in the hydrophobic core, however, altered the antibody sensitivity of Env. These results show how a TM domain anchors, stabilizes, and modulates a viral envelope spike and suggest that its influence on Env conformation is an important consideration for HIV-1 immunogen design.

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IV-1 envelope spike (Env; trimeric (gp160)3, cleaved to (gp120/gp41)3) fuses viral and host cell membranes to initiate infection (1). Binding of gp120 to receptor (CD4) and co-receptor (e.g., CCR5 or CXCR4) trigger large conformational changes, leading to a cascade of refolding events in gp41 and ultimately to membrane fusion (2–4). Mature Env spikes, harboring charged residue (usually arginine) near the middle of the TMD suggests functions other than just spanning a bilayer. TM helices of many cell surface receptors are not merely inert anchors but play essential roles in receptor assembly and signal transduction. For example, we have shown that CT truncation affects the antigenic surface of the ectodomain of HIV-1 Env on the opposite side of the membrane (15). Thus, understanding the physical coupling (conformation and/or dynamics) between the CT and the ectodomain mediated by the TMD may guide design of immunogens that mimic native, functional Env and induce broadly neutralizing antibodies (bnAbs).

To characterize the TMD structure by nuclear magnetic resonance (NMR), we used a fragment of gp41 (residues 677 to 716; HXB2 numbering, fig. S1), derived from a clade D HIV-1 isolate 92UG024.2 (14). This construct, gp41HIVD(677-716), contains a short stretch of MPER (residues 677 to 683); the TM segment (residues 684 to 705), deuterated gp41HIVD(677-716) protein was purified and reconstituted into bicelles (fig. S2, A and B) (17–19) with an expected lipid-bilayer diameter of ~44 Å (fig. S2C) (20, 21), thereby incorporating the refolded gp41HIVD(677-716) into a membrane-like environment. The bicelle-reconstituted gp41HIVD(677-716) protein migrates on SDS–polyacrylamide gel electrophoresis (SDS-PAGE) with a size close to that of a trimer (theoretical molecular mass 14.1 kDa) (fig. S2D), suggesting that the protein was trimeric and resistant to SDS denaturation. The reconstituted gp41HIVD(677-716) protein in bicelles generated an NMR spectrum with excellent chemical-shift dispersion (fig. S3A). The equivalent protein constructs from isolates 92BR025.9 (clade C) and 92RU131.16 (clade G) gave similar NMR spectra (fig. S3, B and C), suggesting that the TMDs of most HIV-1 Envcs have similar structures when reconstituted in bicelles. We completed the NMR structure of gp41HIVD(677-716) using a previously described protocol (figs. S4 and S5) (22, 23). The final ensemble of structures converged to a root mean square deviation of 0.7 Å for all heavy atoms.
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Editor's Summary

No turning back?

Ecosystems over time have endured much disturbance, yet they tend to remain intact, a characteristic we call resilience. Though many systems have been lost and destroyed, for systems that remain physically intact, there is debate as to whether changing temperatures will result in shifts or collapses. Wernburg et al. show that extreme warming of a temperate kelp forest off Australia resulted not only in its collapse, but also in a shift in community composition that brought about an increase in herbivorous tropical fishes that prevent the reestablishment of kelp. Thus, many systems may not be resilient to the rapid climate change that we face.

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