Coral Reefs
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REPORT

The state of Western Australia's coral reefs

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Abstract Western Australia's coral reefs have largely escaped the chronic pressures affecting other reefs around the world, but are regularly affected by seasonal storms and cyclones, and increasingly by heat stress and coral bleaching. Reef systems north of 18°S have been impacted by heat stress and coral bleaching during strong El Niño phases and those further south during strong La Niña phases. Cumulative heat stress and the extent of bleaching throughout the northern reefs in 2016 were higher than at any other time on record. To assess the changing regime of disturbance to reef systems across Western Australia (WA), we linked their site-specific exposure to damaging waves and heat stress since 1990 with mean changes in coral cover. Since 2010, there has been a noticeable increase in heat stress and coral bleaching across WA. Over half the reef systems have been severely impacted by coral bleaching since 2010, which was further compounded by cyclones at some reefs. For most (75%) reef systems with long-term data (5–26 yrs), mean coral cover is currently at (or near) the lowest on record and a full recovery is unlikely if disturbances continue to intensify with climate change. However, some reefs have not yet experienced severe bleaching and their coral cover has remained

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relatively stable or increased in recent years. Additionally, within all reef systems the condition of communities and their exposure to disturbances varied spatially. Identifying the communities least susceptible to future disturbances and linking them through networks of protected areas, based on patterns of larval connectivity, are important research and management priorities in coming years while the causes of climate change are addressed.

Keywords Western Australia · Coral bleaching · Tropical cyclones · Anthropocene · Climate change

Introduction

Surrounding much of Australia's tropical coastline, coral reefs make a significant contribution to the nation's economy and identity through associated fisheries, tourism and recreation. Although not as well studied as those on the east coast, coral reefs along the vast Western Australian (WA) coastline are comparable in extent and diversity. More than 400 coral species have been identified on reefs ranging from the northern oceanic atolls (10°S) to the Abrolhos Islands (to 29°S) 4, 000 km to the south, and thousands of kilometres offshore to Christmas and Cocos Keeling Islands (Veron and Marsh 1988; Richards and Rosser 2012; Richards et al. 2014). Despite their extent and diversity, there are few published accounts of the condition of WA reefs, which are also not well represented in global assessments of coral reefs (Maina et al. 2011; Halpern et al. 2015; MacNeil et al. 2015; Cinner et al. 2016).

The plight of coral reefs globally has led to increased efforts to identify both degraded and healthy reefs, and to understand the pressures causing degradation and the mechanisms promoting resilience. Chronic pressures degrading the world's reefs and impeding their recovery from acute disturbances commonly include overfishing, pollution and poor water quality (Bellwood et al. 2004; Graham et al. 2011; Maina et al. 2013). Current levels of fishing pressure on WA reefs are unlikely to directly or indirectly affect the condition of coral communities (Halpern et al. 2015). Commercial, recreational and indigenous fisheries are managed and typically target carnivorous species (Fletcher 2015; Ryan et al. 2015), rather than the herbivorous species that can aid coral recovery following disturbances (Graham et al. 2015). Water quality varies naturally among Western Australian reefs according to their proximity to the coastline and river systems, their sediment composition and the degree of resuspension by tides, storms and cyclones (Veron and Marsh 1988; Gilmour et al. 2016). However, there are few significant river systems adjacent to WA reefs, many of which are located offshore, so chronic degradation of water quality associated with land use and terrestrial run-off is unlikely. Large-scale dredging operations supporting industrial developments periodically increase turbidity and sedimentation at some Pilbara reefs, but the long-term effects on water quality are unknown (Fisher et al. 2015; Jones et al. 2016). Acute disturbances contributing to the degradation of the world's reefs commonly include outbreaks of coral diseases and predators (Maynard et al. 2015; Walton et al. 2018), tropical storms and cyclones (De'ath et al. 2012; Cheal et al. 2017), and heat stress causing coral bleaching (Eakin et al. 2018; Hughes et al. 2018a, b). There have been few extensive outbreaks of coral diseases or predators on WA reefs. Coral diseases have caused only local impacts at some reefs and have followed high winter temperatures, cyclones and dredging activities (Gilmour et al. 2013; Pollock et al. 2014; Hobbs et al. 2015). High densities of the corallivorous snail *Drupella cornus* have previously (1990s) affected parts of Ningaloo Reef (Black and Johnston 1994; Turner 1994), and local aggregations of the crown-of-thorns starfish *Acanthaster planci* have been reported at some Pilbara reefs (Simpson and Grey 1989; Wilson 2013; Babcock et al. unpublished). However, in WA there have not been repeated outbreaks of coral predators causing significant coral mortality across entire reefs, as has occurred on the Great Barrier Reef and elsewhere (Pratchett 2010; Graham et al. 2011; Baird et al. 2013). Tropical cyclones and coral bleaching are the two most important acute disturbances affecting coral reefs off WA. Seasonal storms and cyclones have shaped the WA coastline and its coral reefs for thousands of years (Wilson 2013; Haig et al. 2014; Drost et al. 2017) regularly affecting mid-latitude ($\approx$ 12–22°S) reefs (Speed et al. 2013; Zinke et al. 2018). More recently, heat stress causing coral bleaching has emerged as a major threat to WA coral reefs. Previously, mass bleaching had been limited to just a few reefs, whereas in the last ten years most WA reefs have experienced recurrent heat stress and some level of bleaching (Thomson et al. 2011; Abdo et al. 2012; Moore et al. 2012; Depczynski et al. 2013; Gilmour et al. 2013; Ridgway et al. 2016). In 2016, the 3rd Global Coral Bleaching Event caused unprecedented heat stress in Australian waters, including those in north-western Australia (Oliver et al. 2017; Benthuysen et al. 2018; Eakin et al. 2018).

Here we present the results of a coordinated monitoring effort assessing the impacts of the 2016 heat stress on Western Australian coral reefs. We quantify the site-specific levels of heat stress and coral bleaching at 401 sites

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spanning 18° latitude, and corresponding changes in coral cover on the reefs worst affected. We then place this 2016 bleaching event in a historical context, by linking the exposure of long-term monitoring sites to damaging waves and heat stress since 1990 to their mean variation in coral cover, to assess the changing regimes of disturbances and condition of WA coral reefs.

Methods

Sea surface temperatures

Sea surface temperatures (SST) and degree heating weeks (DHW) were extracted from NOAA Coral Reef Watch's 5 km global dataset v3.1 (NOAA 2018a). SST and DHW values were extracted for pixels overlying study sites using MATLAB R2017b (http://www.mathworks.com/) and averaged for each reef.

The duration of heat stress was defined as the period when DHW exceeded 4 °C-weeks. At some reefs, there were times during this period when NOAA Coral Reef Watch's HotSpot metric temporarily reduced (e.g. cyclone-related cooling), but then subsequently increased. At these times, NOAA Coral Reef Watch's Bleaching Alert Levels were often downgraded temporarily. As DHW is a cumulative measure of heat stress, it was less affected by short-term cooling, and we present the number of consecutive days where DHW exceeded 4 °C-weeks as an indicator of heat stress for each reef.

Study sites included those where percentage bleaching was estimated in 2016 and where long-term trends in coral cover were quantified. Where in situ temperature data were available, a mean daily temperature value for each reef was first calculated and then compared to the mean SST for pixels containing those sites.

Damaging waves from storms and cyclones

A time series of the height and direction of damaging waves (both cyclonic and non-cyclonic) were extracted for each monitoring site and then averaged across sites. Hourly cyclone-generated wind speeds were reconstructed along cyclone tracks from 1985 to 2015 (McConochie et al. 2004) using data from the International Best Track Archive for Climate Stewardship (IBTrACS—https://www.ncdc.noaa.gov/ibtracs/). To account for the contribution of non-cyclonic winds to sea state, at each time step cyclone-generated winds were blended with synoptic winds obtained from the National Center for Atmospheric Research in Boulder, Colorado (CSFR—Climate Forecast System Reanalysis, downloaded from https://climatedataguide.ucar.edu/climate-data/climate-forecast-system-reanalysis-cfsr). We weighted cyclonic winds by proximity to cyclone centres and weighted synoptic winds by increasing distance beyond 3 radii of the cyclone eye. Following Puotinen et al. (2016), we used these data and fetch to estimate whether the resulting waves were capable of damaging coral colonies, with damaging waves defined as having the top one-third of wave heights $\geq$ 4 m (significant wave height [H_s] $\geq$ 4 m). A lack of high resolution bathymetry and reef/island mapping prevented any adjustment of localised fetch effects using custom-fit numerical wave models. However, for each cyclone from November 2010–May 2018, we used significant wave height and direction extracted from the nearest WAVEWATCH III® global hindcast dataset at $\sim$ 50 km resolution (Tolman 2009, downloaded at: http://polar.ncep.noaa.gov/waves/index2.shtml) and maps of the study sites to assess the exposure of each long-term monitoring site on each reef to damaging waves. Compared to measuring distances from passing cyclones, this method improves accuracy by considering the sheltering effects of reef structures and by explicitly modelling the spatial extent of damaging waves around the cyclone track which is known to vary considerably as a cyclone's size, forward speed and intensity change along its track (Puotinen et al. 2016). This enabled us to more reliably attribute observed changes in coral cover at each site to damaging waves from storms or cyclones. For cyclones from January 1998–December 2013, a finer-resolution assessment was possible using data extracted from an Australia-wide hindcast wave dataset produced by CSIRO and BOM at 11 km resolution using the WAVEWATCH III® model. Finally, we supplemented these assessments by using the WAVEWATCH III® data to characterise the typical exposure of long-term monitoring sites to wave energy during non-cyclone events.

Exposure of reef systems to heat stress and damaging waves

Reef systems across Western Australia were grouped according to their exposure to heat stress and damaging waves from 1990 to 2017 (as above). Several summary statistics that characterised maximum exposure and variation in heat stress (DHW) and damaging waves (significant wave height [H_s] $\geq$ 4 m) were explored, and those highly correlated (> 0.8%) with more informative statistics were excluded. The final statistics used in the multivariate analysis were the number of heat stress events, when DHW $\geq$ 4 °C-weeks, the maximum and standard deviation of DHW, the average and standard deviation of damaging waves attributable to cyclone activity, and the average and standard deviation of damaging waves typical of background conditions and not attributable to cyclone activity. In the software PRIMER, a Bray–Curtis dissimilarity matrix was generated from the normalised environmental statistics, and a CLUSTER analysis performed with groups distinguished using the SIMPROF procedure at a 40% significance levels (Clarke and Warwick 2001). The procedure was repeated using statistics summarising exposure to heat stress, to damaging waves, and heat stress and damaging waves combined.

Bleaching observations, mortality and long-term changes in coral cover

Based on responses to previous extreme El Niño conditions in 1998 (Oliver et al. 2009) and seasonal outlooks for ocean temperatures (NOAA 2018a), coral bleaching was predicted to be most severe at reefs north of 18°S from March to April 2016. Our monitoring around the 2016 bleaching was therefore focused on the reefs from Ningaloo northwards, but with observations extending as far south as the Abrolhos Islands. Bleaching observations were recorded at replicate sites and representative habitats in depths ranging from the reef flat to shallow reef slope (< 12 m). Survey locations, sites and sampling methods are presented in Table 1. At long-term monitoring sites, photographs were compared to assess variation in coral colour over time and among observers. Most observers had previous experience documenting coral bleaching, but to ensure consistency information packs were provided that included datasheets and images of coral taxa and communities in various states of bleaching (healthy, partially bleaching, wholly bleached, and recently dead from bleaching). For the few observers not experienced in documenting coral bleaching, images of bleached communities and colonies were reviewed by authors. The percentage of bleached corals at 401 sites was estimated by observers according to the following categories: < 1%, 1–10%, 11–30%, 31–60%, 61–90% and > 90% bleached (Hughes et al. 2017b). Bleaching estimates were proportions of total coral cover. Colonies wholly or partially bleached, obviously paling, or recently dead (intact skeletons and recent algal growth) were considered bleached in these estimates. Surveys coincided with times of heat stress and coral bleaching in 2016 at all sites but for those at Ashmore Reef. Following extreme heat stress (14.1 °C-weeks) at Ashmore Reef, bleaching was inferred from the percentage of colonies that had recently (≈ 6 months) died and whose skeletons were intact, covered in turf or coralline algae, and showed no signs of physical damage in October 2016, following Depczynski et al. (2013).

The change in percentage cover of hard and soft corals following the 2016 bleaching was quantified only on reefs north of 18°S, given that little or no bleaching (< 10%) was predicted or observed at the more southern reefs. Bleaching-related mortality at replicate sites was derived from the relative change in the percentage cover (Table 2) before and after the period of peak heat stress (March–May 2016). Coupled with our estimates of percentage coral bleaching, decreases in cover following extreme heat stress were assumed to be caused by bleaching-related mortality when no other severe disturbances were recorded, while stable or increasing cover was considered as evidence of no significant bleaching. Survey methods are presented in Table 2.

Long-term (5–26 yrs) changes in percentage cover of hard and soft corals were quantified at replicate sites and averaged for each reef or reef system. The replication of habitats and sites varied among studies, but replicate sites within the leeward reef slope or back reef habitats, in depths from 3 to 10 m, were represented in all studies and were the primary habitat surveyed (Table 2). Changes in coral cover in most studies were quantified from benthic photographs taken at 1-m intervals along permanent transects (Table 2). The sampling design within each study and reef was consistent through time, and sites not replicated during all years were excluded from the data. The changes in coral cover through time were therefore specific to each reef or reef system and could not be compared quantitatively, given variation in survey methods, habitats and site replication among monitoring programmes. Two separate monitoring programmes were conducted at the Cocos Keeling Islands and Ningaloo Reef, and the mean changes in coral cover for each are presented independently.

Results

The 2016 temperature stress and bleaching event

Across Western Australia, heat stress, bleaching and coral mortality varied among reefs in 2016, with the most severe heat stress restricted to northern reefs (10°S–18°S; Fig. 1). Heat stress sufficient to cause coral bleaching (DHW ≥ 4 °C-weeks, Fig. 1) occurred at all northern reefs and was the highest on record for all but Christmas Island (ESM Table 1). Bleaching was not predicted at reefs south of 18°S. SST generally showed good agreement with in situ temperature records (r^2 = 0.71–0.98, RMSE = 0.4–1.7 °C, ESM Fig. 1) and the broad pattern of heat stress was consistent with the observed variation in coral bleaching at 401 sites, with high but variable bleaching recorded at northern reefs and minimal bleaching at the more southern reefs (Fig. 2).

Cocos Keeling Islands

At the Cocos Keeling Islands, heat stress (DHW ≥ 4 °C-weeks) persisted for 104 d and DHW reached a maximum

Table 1 Methods used to quantify coral bleaching at 401 sites at reefs across Western Australia during the period of peaks temperature stress from March to May 2016

Reef system	Latitude (°S)	Survey time	Habitats	Sites	Method
Cocos Keeling Islands	12.1–12.2	April 2016[a]	Reef crest	6	Transect
			Reef slope—deep	6	Transect
Christmas Island	10.4–10.5	April 2016[a]	Reef flat	1	Transect
			Reef crest	8	Transect
			Reef slope—deep	8	Transect
Ashmore Reef	12.2–12.3	April 2016[b]	All habitats		Aerial survey
		October 2016[c]	Reef crest	6	Inferred*
			Reef slope	6	Inferred*
Hibernia Reef	11.9–12.0	November 2017[c]	Reef crest	2	Inferred*
			Reef slope	2	Inferred*
Scott Reef	13.6–14.2	April 2016[c]	Lagoon bommie	6	Transect
(South, North and Seringapatam Reefs)			Lagoon floor	16	Transect
			Reef flat	9	Transect
			Reef crest	11	Transect
			Reef slope	30	Transect
Rowley Shoals	17.1–17.6	April 2016[c]	Lagoon bommie	3	Transect
			Lagoon floor	3	Transect
			Reef flat	3	Transect
			Reef crest	2	Transect
			Reef slope	3	Transect
Inshore Kimberley	13.9–16.6	March 2016[d]	Lagoon	2	Transect
			Reef flat	2	Transect
			Reef slope	2	Transect
		April 2016[e]	All habitats		Aerial survey
		April 2016[f]	Reef flat	3	Random swim
		April 2016[g]	All habitats	4	Aerial surveys
		April 2016[h]	Reef slope	3	Random swim
		April 2016[i]	Reef flat	3	Transect
		May 2016[d]	Reef flat	2	Transect
			Reef crest	3	Transect
Inshore Pilbara	20.3–21.8	March 2016[d]	Reef flat, slope	16	Transect
		March 2016[j]	Reef flat	9	Transect
			Reef slope	6	Transect
Ningaloo	21.7–24.1	March 2016[j]	Lagoon	17	Transect
			Reef flat	5	Transect
			Reef slope	36	Transect
		April 2016[d]	Lagoon	10	2 m survey radius
		April 2016[d]	All habitats		Aerial surveys
Abrolhos	28.2–29.0	April 2016[h]	Not specified	1	Anecdotal observations

Reef habitats were further distinguished by depth, according to: lagoon and lagoon bommie = 0–6 m, reef flat = 0–3 m, reef crest = 3–6 m, and reef slope = 6–12 m. Letters in superscript after survey times indicate the data source

[a]JP Hobbs, [b]Australian Border Force, [c]AIMS, [d]DBCA, [e]D Barrow, [f]D Williams, A Lewis, [g]D Woods, J French, [h]J Fowler, [i]V Schoepf, [j]CSIRO, [h]S Evans

* Surveys were not conducted at Ashmore or Hibernia Reefs during the time of heat stress, and percentage bleaching was inferred from the percentage of recently dead coral colonies with intact skeletons (see "Methods")

Table 2 Methods used to quantify variation in coral cover at reef systems across WA

Location	Latitude (°S)	Method	Depth (m)	Sites	Year/s	Habitat
Cocos Keeling	12.1–12.2	Point intercept;[a] 6 × 50 m	5, 20	5–6	5 surveys; 2005–2017	Reef slope
		Line intercept;[b] 3 × 20 m	10	2	12 surveys; 1999–2018	Reef slope
Christmas Island	10.4–10.5	Point intercept;[a] 6 × 50 m	5, 20	7–8	9 surveys; 2005–2017	Reef slope
Ashmore Reef	12.2–12.3	Photo transects;[c] 6 × 20 m (2010–2016) and 5 × 50 m (2017)	6, 9	6–7	4 surveys; 2010–2017	Reef slope
		Point intercept;[d] 3 × 15 m	9–12	6	1 survey; 2013	Reef slope
		Point intercept;[e] 3 × 50 m	3–10	6	2 surveys; 2005, 2009	Reef slope
Scott Reef	13.6–14.2	Photo transects;[c] 5 × 50 m	6, 9	7	16 surveys; 1994–2017	Reef slope
Inshore Kimberley North	13.9–14.1	Photo transects;[d] 3 × 25 m	3–10	4	2 surveys; 2012–2016	Back reef
Inshore Kimberley South	15.8–16.6	Photo transects;[c] 100 m	3–10	4	2 surveys; 2015–2016	Back reef
		Photo transects;[f] 6 × 15 m	0–2	2	2 surveys, 2016	Reef flat
Rowley Shoals	17.1–17.6	Photo transects;[c] 5 × 50 m	6, 9	3	10 surveys; 1995–2017	Reef slope
Montebello and Barrow Islands	20.4–21.1	Photo transects;[h] 3 × 50 m	1–9	7–14	7 surveys; 2009–2014	Back reef
Ningaloo	21.6–24.1	Photo transects;[h] 3 × 50 m	1–9	7–20	14 surveys; 1991–2017	Back reef, Lagoon
	21.6–24.1	Photo transects;[g] 3 × 25 m	2–6	6–50	8 surveys; 2007–2017	Reef flat, crest
Shark Bay	24.7–26.2	Photo transects;[h] 3 × 50 m	1–9	5–9	4 surveys; 2010–2015	Reef flat, slope

Relative changes in coral cover before and after the bleaching in March/April 2016 were used to estimate mortality

[a]JP Hobbs; [b]J Buckee; [c]AIMS; [d]WAM; [e]Richards et al. (2009); [f]V Schoepf; [g]CSIRO; [h]DCBA

of 10.6 °C-weeks in late April and May (Fig. 1), the highest on record for this location (ESM Table 1). However, in April there was very little (< 1%) bleaching observed at any of 13 sites surveyed in depths from 5 to 20 m (Fig. 2) and only minor bleaching (1–10%) at North Keeling Island. Mean coral cover was similar ($\approx$ 48%) in 2014 and 2017 (Fig. 3).

Christmas Island

At Christmas Island, heat stress (DHW $\geq$ 4 °C-weeks) persisted for 96 d and DHW reached a maximum of 10.1 °C-weeks from mid-April to May (Fig. 1), the second highest on record for this location (ESM Table 1). Severe bleaching (> 60%) was observed in April at all 23 sites in depths from 0 to 20 m, and evident to 60 m depth (Fig. 2). Mortality at sites ranged from 6 to 57%, but for one site where there was little change in cover (Fig. 3). Mean cover decreased from 58% in April 2016 to 40% in July 2017.

Ashmore Reef

At Ashmore Reef, heat stress (DHW $\geq$ 4 °C-weeks) persisted for 205 d and DHW reached a maximum of 14.1 °C-weeks in May (Fig. 1), the highest on record for this location (ESM Table 1). While surveys did not coincide with periods of heat stress, bleaching and mortality were inferred from the percentage of colonies in October that

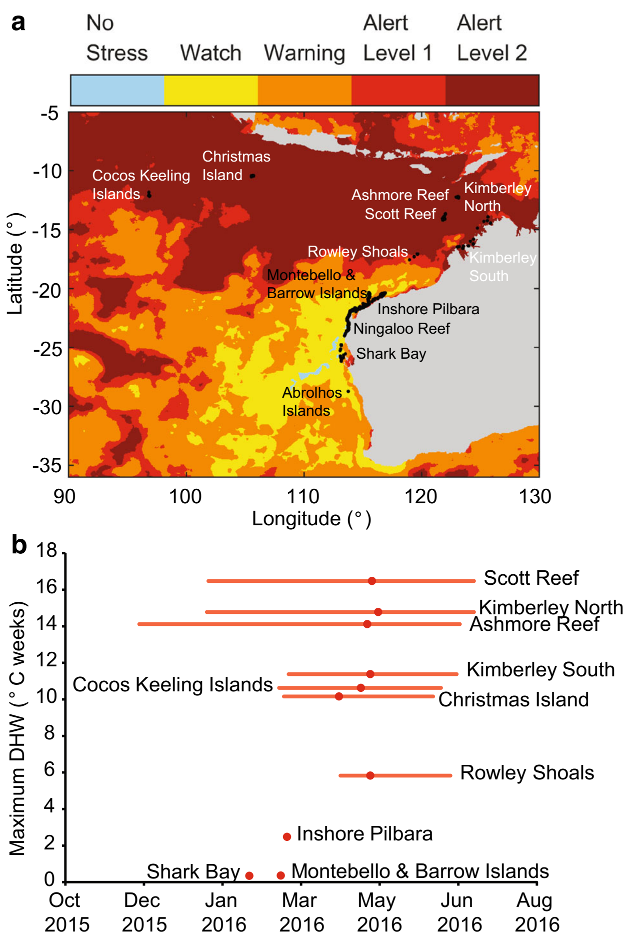


Fig. 1 **a** Annual maximum bleaching alert levels for WA in 2016 (NOAA 2018b). Black dots indicate bleaching observations or coral monitoring sites (see Table 1 and Table 2). **b** Value and timing of maximum degree heating weeks (red dots), and the period of heat stress (DHW ≥ 4 °C-weeks, red lines), at monitoring sites from October 2015 to August 2016. For Ningaloo Reef and Abrolhos Islands, DHW remained at 0 °C-weeks during this time

had recently died and had intact skeletons with no signs of physical damage. At three of 12 sites, between 30 and 60% of colonies were estimated to have recently died from bleaching, in addition to 10–30% mortality at one site, 1–10% mortality at 2 sites and < 1% mortality at the remaining 6 sites (Fig. 2). The following summer, heat stress (DHW ≥ 4 °C-weeks) persisted for a further 86 d and DHW reached a maximum of 8.4 °C-weeks in December 2016. Mortality between October 2016 and October 2017 ranged from 19% to 74% at eight sites, with cover at one site increasing (Fig. 3). Decreases in cover were lower at sites with a southerly exposure and in deeper (6 m) water, than those in shallower (3 m) water on other parts of the reef. Reductions in cover following the first bleaching in March/April were not quantified, but mean cover decreased from 36% in October 2016 to 24% in October 2017. At nearby Hibernia Reef in October 2017, between 30 and 60% of colonies at two reef crest (3 m) sites and 10–30% of colonies at two reef slope (6 m) sites were also estimated to have died from the recent heat stress.

Scott Reef

At Scott Reef, heat stress (DHW ≥ 4 °C-weeks) persisted for 170 d and DHW reached a maximum of 16.5 °C-weeks in early May (Fig. 1), the highest on record for this location (ESM Table 1). The heat stress caused severe and widespread bleaching to 20 m depth (Fig. 2). All 72 sites had > 30% bleaching, with 63 sites having > 60% bleaching. Mortality at sites ranged from 54% to 91% (Fig. 3), with the lowest mortality at sites that were still recovering from severe cyclone impacts in 2012. Mean cover decreased from 48% in January 2016 to 13% in October 2016.

Northern Inshore Kimberley

At the northern inshore Kimberley, heat stress (DHW ≥ 4 °C-weeks) persisted for 171 d and DHW reached a maximum of 14.8 °C-weeks in May (Fig. 1), the highest on record for this location (ESM Table 1). However, no bleaching was observed at eight of the ten sites surveyed in April and May in depths from 0 m to 12 m, with 1–10% bleaching at the remaining two sites (Fig. 2). Relative increases in cover at all sites ranged from 5% to 60%, and mean cover increased from 40% in October 2012 to 55% in September 2016 (Fig. 3).

Southern inshore Kimberley

At the southern inshore Kimberley, heat stress (DHW ≥ 4 °C-weeks) persisted for 109 d and DHW reached a maximum of 11.4 °C-weeks in May (Fig. 1), the highest on record for this location (ESM Table 1). The heat stress caused bleaching of varying severity from March to May, in depths from 0 m to 10 m. Bleaching was observed at all of 13 sites surveyed, with 30–60% bleaching at nine sites and 60–90% bleaching at two sites (Fig. 2). Mortality at sites ranged from 40% to 80%, and mean cover decreased from 36% in October 2015 to 13% in May 2016 (Fig. 3).

Rowley Shoals

At the Rowley Shoals, heat stress (DHW ≥ 4 °C-weeks) persisted for 71 d and DHW reached a maximum of 5.8 °C-weeks in May (Fig. 1), the highest on record at this location (ESM Table 1). However, there was little or no bleaching (< 1%) recorded in late April at seven of 12 surveyed sites from 0 to 15 m depth. At one reef slope

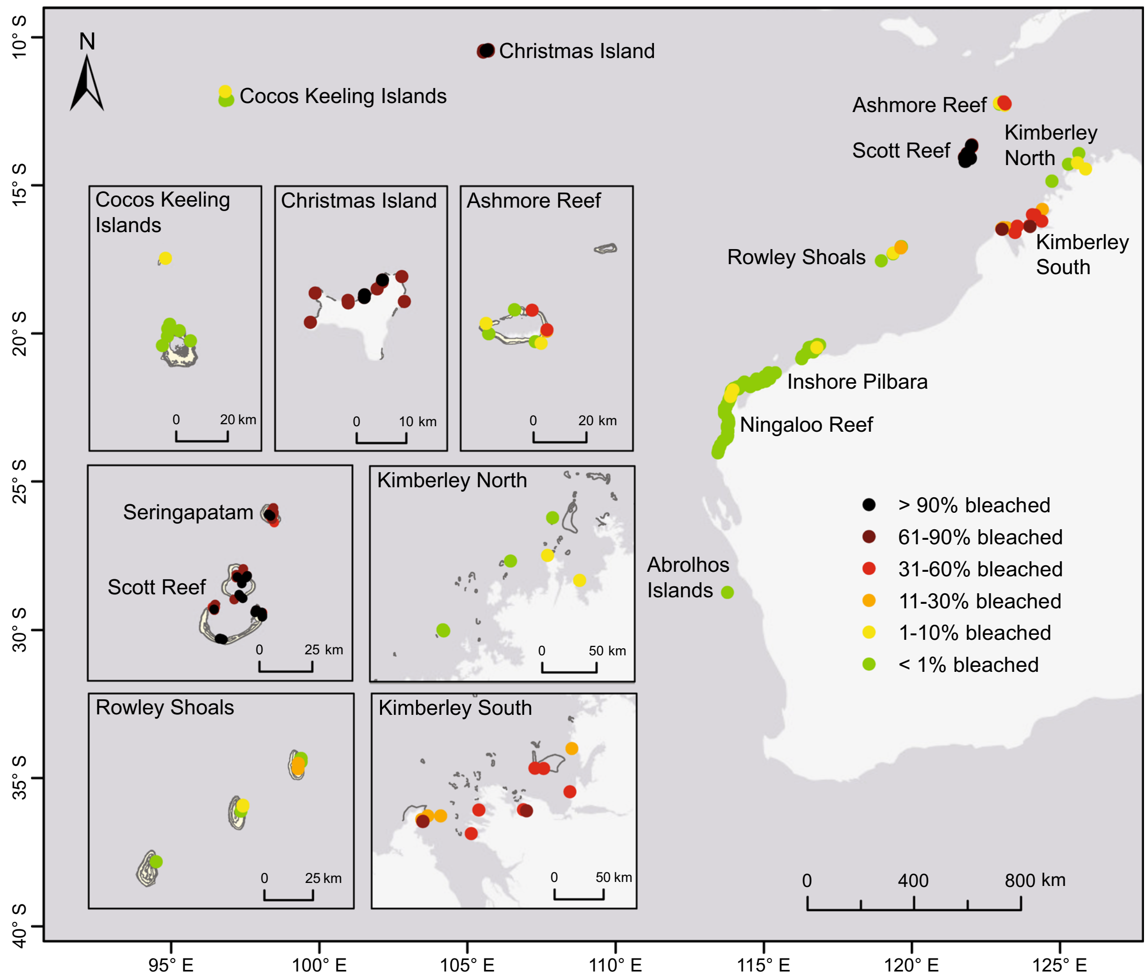
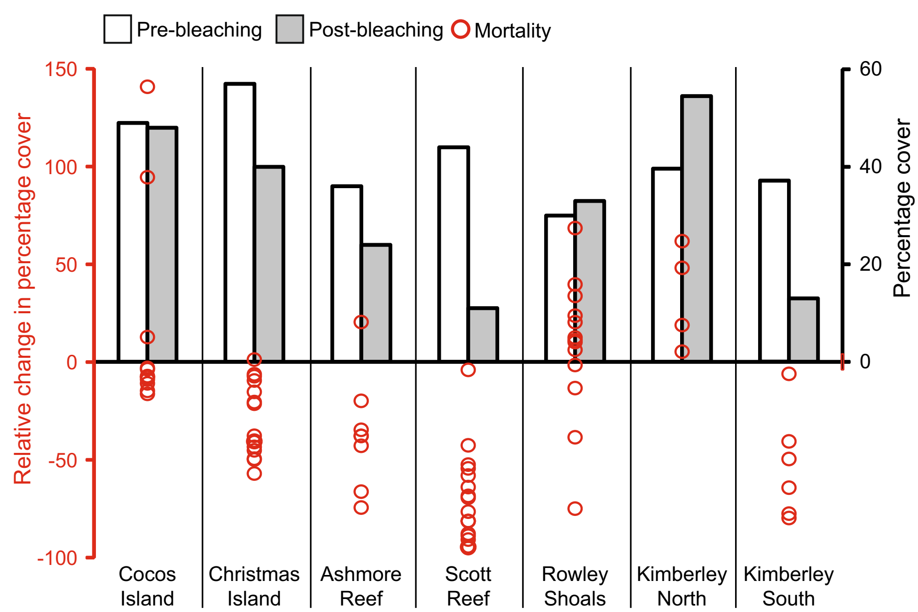


Fig. 2 Percentage bleaching of hard and soft corals at reefs across WA in 2016. Estimates were based on in-water and aerial surveys (see Table 1)

Fig. 3 Mean coral cover at WA reefs north of 18°S before (white bars) and after (grey bars) bleaching in March/April 2016 and the relative changes in coral cover (mortality) at replicate sites within reefs (see Table 2)



(6 m), one reef crest (3 m) and one lagoon site, there were minor bleaching (1–10%) and 11–30% bleaching at two lagoon sites (Fig. 2). Mortality was highest (70% and 38%) at the two lagoon sites worst affected by bleaching. A lower mortality (13%) at another site was likely due to cyclone damage, while all other sites had either changed little or increased in cover (Fig. 3). Following exposure to moderate heat stress and cyclones, mean cover increased from 30% in January 2016 to 33% in October 2017 (Fig. 3).

Long-term changes in coral cover, temperature stress and cyclone exposure

Long-term (5–26 yrs) changes in coral cover at reef systems varied according to their exposure to damaging waves and heat stress, but generally remained stable or increased, had large decreases following severe coral bleaching, or smaller but more frequent decreases following coral bleaching and cyclones (Fig. 4).

Since 1990, all reef systems have been exposed to damaging waves from tropical lows or cyclones, particularly those from Scott Reef to Ningaloo (Fig. 4, ESM Table 2, ESM Fig. 2, ESM Fig. 3). Some reefs (Cocos Keeling, Christmas, Shark Bay) were also routinely exposed to high wave energy as part of their prevailing conditions (ESM Fig. 2, ESM Fig. 3). However, damaging waves rarely caused mean reductions in cover across an entire reef system because impacts were spatially variable and many sites were sheltered from the predominant directions of wave energy (Figs. 2, 4).

Since 1990, all reef systems experienced heat stress sufficient to cause coral bleaching (DHW ≥ 4 °C-weeks), with an increased frequency and severity since 2010 (Fig. 4, ESM Table 1). Although the frequency and severity of heat stress varied among the reef systems (ESM Fig. 3), 88% of those with long-term data have experienced sufficient heat stress to cause mass bleaching and mortality (DHW ≥ 8 °C-weeks) since 2010. Coral bleaching coincided with mean reductions in coral cover across most reef systems one or more times since 1990 (Figs. 2, 4). At 63% of reef systems, mean coral cover in the most recent survey (> 2015) was at, or near, the lowest on record.

Cocos Keeling Islands

At the Cocos Keeling Islands, mean coral cover was 39.6% and ranged between 25 and 57% over 21 yrs (1998–2018). Wave energy was relatively high (average H_s = 2.35 m), and damaging waves were regularly produced during winter storms, and rarely by cyclones (ESM Table 2, ESM Fig. 2), but sites were usually sheltered from the damaging waves. Heat stress (DHW ≥ 4 °C-weeks) occurred four times since 1990, with severe heat stress (DHW ≥ 8 °C-weeks) likely to cause mass bleaching and mortality occurring in 2014 and in 2016, although bleaching was not observed (ESM Table 1, Fig. 2). Neither wave energy nor heat stress caused mean reductions in coral cover across the reef system, which in two monitoring programmes had either remained stable or increased (Fig. 4).

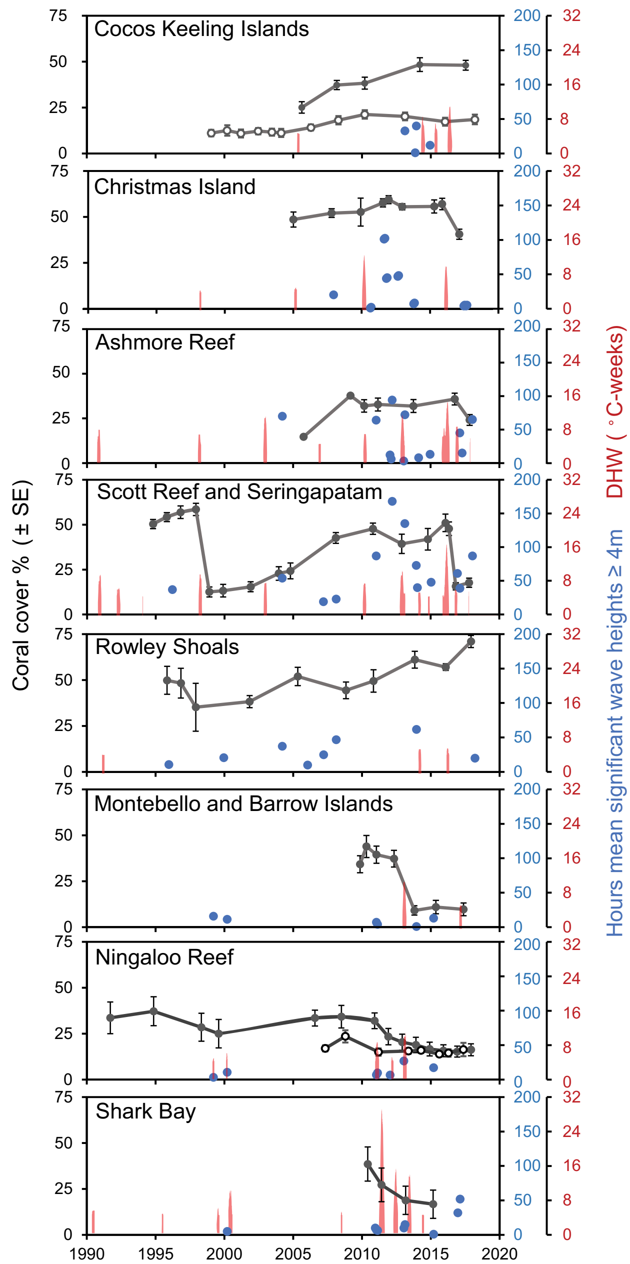


Fig. 4 Long-term changes in coral cover at WA reef systems, and their site-specific exposure to damaging waves (blue dots) and heat stress (red areas) since 1990. At Cocos Keeling Islands and Ningaloo Reef, open and closed circles are used to differentiate two separate monitoring programmes (sources in Table 2)

Christmas Island

At Christmas Island, mean coral cover was 55% and ranged between 40% and 60% over 13 yrs (2005–2017). Mean wave energy was relatively high (average $H_s = 2.17$ m), and damaging waves were regularly produced by seasonal storms and occasionally by cyclones (ESM Table 2, ESM Fig. 2), but did not cause mean reduction in coral cover. Heat stress (DHW ≥ 4 °C-weeks) occurred four times since 1990, including 1998 when widespread bleaching was observed, but changes in coral cover were not quantified (Fig. 4, ESM Table 1). Severe heat stress (DHW ≥ 8 °C-weeks) likely to cause mass bleaching and mortality occurred in 2010 and 2016. Bleaching was observed in 2005 (1–10%) and 2010 (11–30%), but did not cause mean reduction in cover across the reef system (Fig. 4). In contrast, mass bleaching in 2016 affected all sites and caused the most significant mean reduction (18%) in coral cover on record (Figs. 2, 4).

Ashmore Reef

At Ashmore Reef, mean coral cover was 29% and ranged between 14% and 36% over 8 yrs (2010–2017). Mean wave energy was moderate (average $H_s = 1.2$ m), and damaging waves were occasionally produced by seasonal storms and cyclones (ESM Table 2, ESM Fig. 2), but only coincided with mean reductions in coral cover following periods of significant heat stress in 2003 and 2016 (Fig. 4). Heat stress (DHW ≥ 4 °C-weeks) occurred nine times since 1990, and severe heat stress (DHW ≥ 8 °C-weeks) likely to cause mass bleaching and mortality occurred in 2003, 2013, 2016 and 2017 (Fig. 4, ESM Table 1). Widespread bleaching was predicted in 1998 but did not occur (ESM Table 1). Mass bleaching was observed in 2003, and coral cover was the lowest (14%) on record when first quantified in 2005 (Fig. 4). Cover increased to 36% in 2009 and remained relatively stable before decreasing to 24% following mass bleaching and cyclones in 2016/2017 (Fig. 4).

Scott Reef

At Scott Reef, mean coral cover was 36% and ranged from 13 to 51% over 23 yrs (1994–2017). Mean wave energy was moderate (average $H_s = 1.25$ m), and damaging waves were produced by seasonal storms and frequent cyclones (ESM Table 2, ESM Fig. 2). Most cyclones caused significant impacts at the few most exposed sites, but not mean reductions in coral cover across the reef system (Fig. 4). The exception was Cyclone Lua in 2012, whose impacts at a few exposed sites were severe enough to cause a reduction (8%) in mean cover. Heat stress (DHW ≥ 4 °C-weeks) occurred 12 times since 1990, including severe heat stress (DHW ≥ 8 °C-weeks) likely to cause mass bleaching and mortality five times (Fig. 4, ESM Table 1). Mass bleaching in 1998 caused a large reduction (46%) in mean cover to the lowest on record (12%) (Fig. 4). Recovery was slowed by the local effects of cyclones and by further bleaching in 2010, 2011 and 2013, although coral cover increased to 51% by 2016. Mass bleaching in 2016 again caused a large reduction (37%) in mean cover, to 14% in 2017 (Fig. 4).

Rowley Shoals

At the Rowley Shoals, mean coral cover was 50% and ranged between 35 and 70% over 22 yrs (1995–2017). Mean wave energy was moderate (average $H_s = 1.16$ m), but damaging waves were produced by frequent cyclones (ESM Table 2, ESM Fig. 2). Sites were sheltered from the direction of the most damaging waves, but at least eight cyclones caused local impacts and four coincided with mean reductions (4% to 13%) in cover across the reef system (Fig. 4, ESM Table 2). The mean decrease in cover between 2005 and 2008 followed exposure to three cyclones and a moderate bleaching event in 2005 (Fig. 4). Heat stress (DHW ≥ 4 °C-weeks) did not occur in 2005, but did occur on three other occasions since 1990, although severe heat stress likely to cause mass bleaching and mortality (DHW ≥ 8 °C-weeks) did not occur on any occasion (ESM Table 1). A maximum of 5.8 °C-weeks was recorded in 2016, but only minor bleaching was observed (Fig. 2). Since 1997, mean coral cover has increased through periods of impact and recovery from cyclones, reaching the highest (71%) on record in 2017 (Fig. 4).

Montebello and Barrow Islands

At Montebello and Barrow Islands, mean coral cover was 26% and ranged between 9% and 44% over eight years (2009–2017). Mean wave energy was low (average $H_s = 0.7$ m), with damaging waves mostly generated by cyclones (ESM Table 2, ESM Fig. 2), but without causing mean reductions in coral cover (Fig. 4). Heat stress (DHW ≥ 4 °C-weeks) occurred twice since 1990, which included severe heat stress likely to cause mass bleaching and mortality (DHW ≥ 8 °C-weeks) in 2013 (ESM Table 1). Although heat stress (DHW ≥ 4 °C-weeks) did not occur in 2011, bleaching caused a small (2%) reduction in mean cover; a much larger reduction (28%) to the lowest cover on record (9%) followed mass bleaching in 2013 (Fig. 4). Coral cover has since remained low (< 11%), following recent exposure to moderate heat stress (ESM Table 1, Fig. 4).

Ningaloo Reef

At Ningaloo Reef, mean coral cover was 25% and ranged between 15% and 37% over 26 yrs (1991–2017). Mean wave energy was moderate (H_s = 1.43 m), and damaging waves were regularly produced by both seasonal storms and cyclones (ESM Table 2, ESM Fig. 2). Since 1990, seven cyclones have impacted some sites, and four have contributed to decreases in mean cover since 2010, in addition to the impacts from coral bleaching (Fig. 4, ESM Table 2). Heat stress (DHW $\geq$ 4 °C-weeks) occurred five times since 1990, and severe heat stress (DHW $\geq$ 8 °C-weeks) likely to cause mass bleaching and mortality occurred in 2011 and 2013 (ESM Table 1). Mass bleaching was observed in both 2011 and 2013, but mortality varied considerably among sites. The local effects of cyclones and bleaching caused successive reductions in mean cover, from 32% in 2010 to 16% in 2015 in one monitoring programme and from 24% in 2008 to 14% in 2015 in the second monitoring programme (Fig. 4).

Shark Bay

At Shark Bay, mean coral cover was 25% and ranged between 17% and 38% over five years (2010–2015). Mean wave energy was high (H_s = 2.59 m), and damaging waves were regularly produced by seasonal storms and rarely by cyclones (ESM Table 2, ESM Fig. 2). Damaging waves affected the reef system eight times since 1990, of which four coincided with reductions in mean cover since 2010. However, most sites were sheltered from the damaging waves and the decreases in mean cover were more likely a consequence of coral bleaching (Fig. 4). Heat stress (DHW $\geq$ 4 °C-weeks) occurred nine times since 1990, and severe heat stress (DHW $\geq$ 8 °C-weeks) likely to cause mass bleaching and mortality occurred in 2000, 2011, 2012 and 2013 (ESM Table 1). Coral cover was high (38%) when monitoring commenced in 2010, but severe bleaching and mortality at some sites caused mean decreases over several years, while other sites were relatively unaffected. Consequently, there were small but consecutive decreases in mean cover from 38% in 2010 to 17% in 2015 (Fig. 4).

Discussion

Regional variation in heat stress, bleaching and mortality

Heat stress and coral bleaching in Western Australia (WA) during the 3rd Global Coral Bleaching Event peaked between February and May 2016, primarily affecting the reefs north of 18°S. Cumulative heat stress and the scale of coral bleaching across northern WA reefs were greater than at any other time on record (1985–2017). Mass bleaching in 2016 dramatically reduced (70%) coral cover at Scott Reef and caused widespread mortality (> 30%) at Christmas Island, Ashmore Reef and inshore reefs in the southern Kimberley. In contrast, there was little (< 10%) or no bleaching observed at Cocos Keeling Islands, the northern inshore Kimberley, Rowley Shoals, Pilbara and Ningaloo reefs in 2016. Scott Reef was also devastated by coral bleaching during the 1998 El Niño, and since 1998, most (87%) of the northern reefs have bleached one or more times, usually during El Niño phases (Ceccarelli et al. 2011; Gilmour et al. 2013; Hughes et al. 2017b).

Of the reefs least affected by heat stress in 2016, the reefs south of 18°S were previously affected by coral bleaching during a La Niña heatwave in 2010/2011 (Abdo et al. 2012; Moore et al. 2012; Depczynski et al. 2013; Speed et al. 2013), which also disrupted fisheries, devastated temperate macroalgae forests, seagrass meadows and damaged terrestrial ecosystems (Wernberg et al. 2016; Arias-Ortiz et al. 2018; Ruthrof et al. 2018). Within the Pilbara and Ningaloo reefs, the severity of the bleaching and mortality during the 2010/2011 heatwave varied considerably, with some areas being more severely affected in subsequent years (Ridgway et al. 2016; Lafratta et al. 2017; Babcock et al. unpublished). Regardless of the regional patterns in bleaching among ENSO phases, there has been an obvious increase in heat stress and mass bleaching across all WA reefs since 2010, compared to the previous two decades.

Regimes of disturbance and the future of WA reefs

Along with increasing heat stress, storms and cyclones remain a pervasive disturbance affecting most WA reef systems (Carrigan and Puotinen 2011; Zinke et al. 2018). Some reefs (Cocos Keeling, Christmas, Shark Bay) exist within a high energy environment where large waves routinely occur and those generated by cyclones play a minor role. In contrast, large waves were usually generated by tropical cyclones at reefs from Scott Reef to Ningaloo (ESM Fig. 3). The largest reductions in coral cover following cyclones occurred at Scott Reef and particularly the Rowley Shoals, where some monitoring sites were exposed to the direction of waves generated by some cyclones. At other reefs where cyclones are common, coral communities and study sites were often sheltered from the direction of damaging waves. Consequently, storms and cyclones rarely caused mean reductions in coral cover across reef systems and recovery was usually quick ($\approx$ 5 yrs) because it was facilitated by the regrowth of survivors and supply of larvae from nearby communities. Nonetheless, severe or recurrent cyclone impacts can slow recovery after heat stress and bleaching (Thompson and Dolman 2010; Gilmour et al. 2013; Cheal et al. 2017; Torda et al. 2018).

Recovery from previous cyclone and bleaching impacts on WA reefs have been aided by favourable background conditions (e.g. good water quality, high fish abundance) and a lack of chronic pressures. There is little evidence of chronic pressures degrading WA reefs (Maina et al. 2011; Gilmour et al. 2016; Wilson et al. 2018; Zinke et al. 2018), although dredging operations associated with industrial development have periodically affected water quality near some Pilbara reefs (Fisher et al. 2015; Ridgway et al. 2016; Babcock et al. unpublished). Of greater concern for WA reefs is the increased frequency and severity of acute disturbances since 2010. At reefs from the Pilbara southwards, coral cover at Montebello and Barrow Islands decreased dramatically and has remained low following bleaching, cyclones and recent aggregations of crown-of-thorns starfish, while at Ningaloo and Shark Bay there have been smaller but consecutive decreases in coral cover (Holmes et al. 2017; Babcock et al. unpublished). The disproportionate losses of coral groups most susceptible to cyclones and bleaching, which typically accompany overall reductions in coral cover, should not be interpreted as disturbances having diminishing impacts. Instead, these patterns provide evidence of communities persisting in a degraded state, in which coral cover and structural complexity are reduced (Pratchett et al. 2013; Hughes et al. 2018a, b; Torda et al. 2018; Edmunds 2019). Indeed, at most (75%) WA reef systems with long-term ($\geq$ 5 yrs) data, mean coral cover in recent surveys is at, or near, the lowest on record. In coming decades, reefs lacking chronic pressures will face long-term degradation due to the increased frequency and severity of acute disturbances arising from climate change (Heron et al. 2017; Bruno et al. 2018).

The future condition of many WA reefs is threatened by rising ocean temperatures causing recurrent bleaching events and more severe storms, cyclones and outbreaks of coral diseases (Maynard et al. 2015; Ainsworth et al. 2016; Walsh et al. 2016; Hoegh-Guldberg et al. 2017). At some Pilbara reefs, the impacts have been further compounded by aggregations of coral predators (Babcock et al. unpublished). Return times for bleaching events on many of the world's reefs are already less than a decade (Hughes et al. 2018a, b), whereas a full recovery from mass bleaching takes longer than a decade (Glynn et al. 2009; Thompson and Dolman 2010; Gilmour et al. 2013; Johns et al. 2014; Torda et al. 2018). Increasing severity of climate-related disturbances also causes higher mortality over broader spatial scales than in historical events, compromising neighbouring reefs' capacity to aid recovery with a supply of recruits. The implications are particularly significant for WA's offshore reefs, given that there is little exchange of larvae among these reef systems, so recovery and maintenance of species diversity and genotypic diversity depend primarily on local survival of colonies (Gilmour et al. 2009; Underwood et al. 2009; Gilmour et al. 2013; Underwood et al. 2018). In particular, the Scott system of reefs provides a salient example of the fate of many of the world's previously healthy reefs: having been devastated by mass bleaching in 1998 and taken over a decade to recover, the reefs suffered moderate bleaching in 2010, 2011 and 2013 and were again devastated by mass bleaching in 2016. Previously an example of the resilience of even isolated coral reefs (Gilmour et al. 2013), the reef system may now be chronically degraded by climate change.

Not all WA reef systems have suffered severe heat stress and mass bleaching (ESM Fig. 3). The inshore reefs of the Kimberley exist within a particularly remote part of the world, for which there are currently no long-term monitoring data. The southern inshore reefs bleached in 2016, but other northern reefs did not bleach despite the extreme (14.8 °C-weeks) heat stress (Fig. 1) (Le Nohaïc et al. 2017; Richards et al. unpublished). At the Cocos Keeling Islands, coral cover has remained relatively stable or increased over two decades, with this reef system experiencing limited cyclone activity but some historic heat stress. However, the associated bleaching at the Cocos Keeling Islands has not been severe enough to cause mean reductions in cover across the reef system. The Rowley Shoals have also bleached previously without mean reductions in coral cover. Heat stress was typically lower at the Rowley Shoals than at other reefs north of 18°S, with the reef system located near the southern extent of the region worst affected by El Niño heating (Fig. 1). Mean reductions in cover (5–20%) at the Rowley Shoals were caused by cyclones and were followed by a rapid recovery ($\approx$ 5 yrs), with coral cover now higher than at any time on record (23 yrs). The inshore Kimberley, Cocos Keeling Islands and Rowley Shoals are among WA's healthiest reefs, but even they face an uncertain future if ocean temperatures continue to rise. Particularly alarming was the first observations of coral bleaching at the southern inshore Kimberley reefs in 2016, whether in scientific records or indigenous communities' long oral history of sea country (D. Oades pers. comm.), despite these reefs having evolved to cope with extreme environmental conditions (Wilson 2013; Schoepf et al. 2015; Richards et al. 2018). In addition, the severity of the bleaching at the Rowley Shoals in 2016 was likely reduced by the passing of Cyclone Stan, which cooled temperatures by 2 °C (SST) for up to 23 d during the main period of cumulative heat stress, with cooling also evident at Scott Reef (Green et al. 2019). Heat stress on all of these reef systems in 2016 was the highest on record (5 to 15 °C-weeks) and sufficient to cause some bleaching. Further increases in ocean temperatures will likely cause more widespread bleaching on these and other reefs across WA.

While most WA reef systems have undergone large reductions in mean coral cover since 2010, exposure to disturbances and the condition of coral communities varied spatially among and within reefs. The local impacts of cyclones varied according to bathymetry, exposure to damaging waves and the abundance of fragile corals. Local variation in heat stress varied according to current speeds, retention times within lagoons and embayments, upwelling of cool water and atmospheric cooling of water over the reef flat (Woo et al. 2006; Shedrawi et al. 2017; Green et al. 2019; Babcock et al. unpublished). The response of coral communities to this heat stress was also a function of their previous exposure to higher and more variable temperatures (McClanahan et al. 2007; Middlebrook et al. 2008; Safaie et al. 2018), the abundance of susceptible species (Baird and Marshall 1998; Van Woesik et al. 2011; Hoey et al. 2016) and the genomic variation within species (Palumbi et al. 2014; Coles et al. 2018; Thomas et al. 2018). Spatial heterogeneity in exposure and susceptibility to disturbances mean that coral communities at some reefs, and particularly sites within reefs, will maintain a comparatively high cover and diversity through an increasingly severe regime of disturbances. Identifying these communities is a research priority, as they will be critical for maintaining reefs across WA in coming decades.

Future research and management priorities

The current and future degradation of many of the world's reefs has alarming consequences for the organisms that depend on them for food and shelter (Wilson et al. 2006; Pratchett et al. 2018), and the economic and social benefits they provide to humanity (MacNeil et al. 2010; Cinner et al. 2012; Pratchett et al. 2014). Our current inability to manage carbon emissions contributes most significantly to the future degradation of coral reefs, and mitigating this is the most urgent priority for their conservation (Hoegh-Guldberg et al. 2017; Hughes et al. 2017a). But even with immediate emission reductions, climate change and other cumulative pressures will cause ongoing reductions in coral cover and diversity for several years to decades, requiring a fundamental shift in the spatial and temporal scales of research and management (Carpenter et al. 2008; Hoegh-Guldberg et al. 2017; Hughes et al. 2017a; Eyre et al. 2018).

Management strategies for WA reefs must consider their likely condition in coming decades, to manage their transition into the next century. This will require improved integration of research and management along the WA coastline, spanning tropical to temperate reefs. Monitoring programmes have provided a reasonable understanding of the susceptibility of some reefs to emerging disturbances, but for others our current knowledge and resources are insufficient to inform management strategies. A coordinated approach to monitoring that links environmental stressors with changes in community structure, coral life history traits and genomic diversity, and ensures that results are comparable among reefs and regions, would inform which regions, reefs and communities are more or less exposed and susceptible to emerging pressures (Game et al. 2008; Diaz-Pulido et al. 2009; Mellin et al. 2016). The spatial configuration of protected areas should be guided by routine patterns of larval connectivity for both spawning and brooding corals, informed by studies of larval ecology, oceanography and genetic differentiation (Burgess et al. 2014; Kough and Paris 2015; Edmunds et al. 2018). Networks of protected areas at this scale will provide the best opportunity for the maintenance of coral communities over years to decades within reef systems.

To inform management initiatives over much larger spatial and temporal scales, mapping of coral reef distributions should include regions suitable for reef formation into the next century, considering projected changes in disturbance regimes, substrata availability, ocean temperatures, acidity and available light (Greenstein and Pandolfi 2008; Edmunds et al. 2014; Muir et al. 2015; Anthony 2016; van Woesik and Cacciapaglia 2018; Wall et al. 2018). Studies of larval connectivity should also consider the much larger distances over which larvae can occasionally disperse and recruit over decadal time steps, to inform initiatives aiding the exchange of larvae and genotypes across regions of WA (Underwood et al. 2013; Magris et al. 2014; Edmunds et al. 2018). Connectivity patterns along WA's coastline are driven primarily by the southerly flow of major currents along the northwest shelf to North West Cape at Ningaloo Reef and then onto the subtropical and temperate reefs in the Leeuwin Current (Domingues et al. 2007; Pattiaratchi 2007; D'Adamo et al. 2009; Feng et al. 2016). Expansion of corals and other tropical species into temperate regions has already begun on both of the sides of Australia (Wernberg et al. 2016; Tuckett et al. 2017; Booth et al. 2018; Sommer et al. 2018). The capacity of corals to acclimate and adapt to changing environmental conditions is remarkable (Edmunds et al. 2014; Chakravarti et al. 2017; McClanahan 2017; Torda et al. 2017; Coles et al. 2018), but the rate at which these processes will occur remains unknown. Establishing networks of protected areas nested along the WA coastline provides a mechanism for promoting local recovery from recurrent disturbances and aiding natural processes of acclimation, adaptation and range expansion, until the fundamental causes for their decline are addressed.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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