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Recurrent coral bleaching in north-western Australia and associated declines in coral cover

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Abstract. Coral reefs have been heavily affected by elevated sea-surface temperature (SST) and coral bleaching since the late 1980s; however, until recently coastal reefs of north-western Australia have been relatively unaffected compared to Timor Sea and eastern Australian reefs. We compare SST time series with changes in coral cover spanning a period of up to 36 years to describe temporal and spatial variability in bleaching and associated coral mortality throughout the Pilbara–Ningaloo region. Declines in coral cover ranged from 12.5 to 51.3%, with relative declines ranging from 38 to 92%. Since 2013, coral cover throughout the region has declined to historically low levels at four of five subregions, with impaired recovery occurring at two subregions. Observations are consistent with global trends of repeated severe heat waves, coral bleaching and acute declines in coral cover. Locations within this study region have already experienced multiple coral-bleaching events within a period of less than 5 years. There is a high likelihood that reefs in the western Pilbara and northern Ningaloo regions will experience more frequent marine heatwaves, coral bleaching and mortality events in the future. Action, therefore, needs to be taken now to support the resilience of coral reef ecosystems in the region, which is arguably the most important coral-reef province on Australia's western coast.

Keywords: climate change, coral bleaching, coral reef, cyclones, recovery, temperature variation.

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Introduction

Global coral bleaching and threats to coral reefs

Reef-building corals face a wide range of threats directly related to human activities, including changes to water quality, overfishing and coastal development (Wilkinson 2000). Increasingly, warm ocean temperatures are causing widespread coral bleaching and subsequent mortality (Glynn *et al.* 2001; Smith *et al.* 2005, Hughes *et al.* 2017). High ocean temperatures during marine heatwaves (MHW) are caused by intensification of variations in existing global ocean circulation patterns that generate interannual and decadal oscillations in temperature, such as, for example, La Niña, exacerbated by underlying warming trends in the world's oceans (Doi *et al.* 2013; Han *et al.* 2014; Cai *et al.* 2014, 2015). Ocean warming is now recognised as an existential threat to coral reefs globally (Baker *et al.* 2008; Heron *et al.* 2017). Effects of bleaching and associated coral mortality can be long lasting (Hoegh-Guldberg *et al.* 2007; Gilmour *et al.* 2013) and range from altered species composition of coral communities (Perry and Morgan 2017*a*) and their zooxanthellae (Glynn *et al.* 2001; Smith *et al.* 2005), reduced coral abundance (including localised extirpations), to reduced calcification rates and declining structural complexity (Perry and Morgan 2017*b*). The loss of corals is accompanied by changes in the composition and biomass of associated fish (Pratchett *et al.* 2008; Graham 2014) and invertebrates (Przeslawski *et al.* 2008), and an increasing abundance of algae (Graham *et al.* 2014). The decline of coral reefs continues even on reefs that are protected by strong laws and that receive significant management, including the world's largest reef, the Great Barrier Reef (GBR; De'ath *et al.* 2012).

The response of corals to predicted changes in sea-surface temperature (SST) is likely to vary among geographical regions, in part due to regional differences in the background seasonal and year-to-year variation in maximum summer SST (Hoegh-Guldberg 1999). The responses of corals to extreme temperature anomalies can depend on the temperature variability that corals have experienced in the past (Carilli *et al.* 2012). In addition, because the accumulation of heat stress (measured by degree heating weeks, DHW) increases non-linearly, the level, frequency and regularity of accumulated heat stress resulting from a given change in the maximum summer SST is directly affected by the background seasonal and year-to-year temperature variation in the maximum SST (Langlais *et al.* 2017).

Coral bleaching in Australia

On the eastern coast of Australia, the GBR was seriously affected by coral bleaching in 1998, when bleaching was severe globally (Goreau *et al.* 2000). The GBR has been affected by bleaching eight times between 1980 and 2005 (Oliver *et al.* 2009), although bleaching was most widespread in 1998 and 2002. More recently, in 2016 and 2017, the GBR experienced bleaching in consecutive years for the first time (GBRMPA 2017; Hughes *et al.* 2017), as foreshadowed by earlier modelling (Hoegh-Guldberg 1999). In contrast, knowledge of bleaching of coral reefs off the coast of north-western Australia (WA) in 1998 has been limited to the bleaching that occurred in 1998 at oceanic atolls off the Kimberley shelf of north-western WA, principally at Scott and Seringapatam reefs (Skewes *et al.* 1999; Gilmour *et al.* 2013). Bleaching has also been observed, although less extensively documented, in the Dampier Archipelago and reefs in the southern Pilbara in 1998 (Wilkinson 2000; Gilmour 2004) and again in the Dampier Archipelago in 2005 and 2008 (MScience 2008).

Recent north-western Australian marine heatwaves (2011–2016)

In 2010–2011, extreme La Niña conditions resulted in SSTs as much as 5°C above the long-term average off the western coast of Australia, which are the most extreme on record for this area (Feng *et al.* 2015). Coral bleaching during this MHW occurred across 12 degrees of latitude, from the Montebello Islands in the north (19°S) to Rottnest Island in the south (31°S). Mortality of corals was widespread in many areas, with the north-eastern (Bundegi) and central areas of Ningaloo Reef (Coral Bay) and the Houtman-Abrolhos Islands (Depczynski *et al.* 2013; Moore *et al.* 2012) being the worst affected. However, bleaching and mortality was patchy; for example, north-western Ningaloo Reef was barely affected, whereas areas immediately to the south and east were severely affected. A similar picture of patchy bleaching and low levels of mortality was evident in the Montebello and Barrow Islands region (Moore *et al.* 2012). The most intense heating was experienced in the central part of the western coast, where it led to impacts on a wide range of flora and fauna (Wernberg *et al.* 2016; Babcock *et al.* 2019) whereas offshore reefs north of Dampier (20.5°S), including areas affected in the 1998 bleaching event, appeared to be minimally affected (Moore *et al.* 2012).

Heatwave conditions on the WA coast abated in 2012, but anomalously warm waters were again present in 2013 in north-western Australia (21.75°S to 20.3°S), immediately north of the region worst affected by the 2011 MHW. Widespread bleaching and mortality of corals were recorded on reefs across north-western Australia on both nearshore (51–68%, Lafratta *et al.* 2017) and offshore reefs (69.3%, Ridgway *et al.* 2016). The temperature anomaly that caused this bleaching was the result of persistent La Niña conditions and the development of the Ningaloo Niño in the eastern Indian Ocean (Feng *et al.* 2015), bringing warm surface waters along the western coast of Australia (Zhang *et al.* 2017), combined with regional wind patterns that produced localised warming on the western Pilbara shelf. In 2016, the return of El Niño conditions resulted in bleaching further to the north in the Kimberley region of WA (Schoepf *et al.* 2020), as well as on offshore atolls in the Timor Sea.

Historically, coral reefs in WA have been described as being in a state of 'dynamic stability' (Speed *et al.* 2013), with sufficient intervals between disturbances for recovery to occur, and a stable level of coral cover over the recorded past. The GBR and other parts of the world are now seeing consecutive years of bleaching (GBRMPA 2017; Hughes *et al.* 2017). Global warming, through its effects on ocean-circulation patterns and global climate variability, is predicted to increase the frequency and intensity of high-temperature anomalies on Australia's western coast (Feng *et al.* 2015; Cai *et al.* 2015; Doi *et al.* 2013). Since western Australia's MHW of 2011, high-temperature anomalies, bleaching and coral mortality have continued to manifest in the region between Ningaloo and the Dampier Archipelago (Ridgway *et al.* 2016; Lafratta *et al.* 2017), a scenario that may become increasingly common in the near future, threatening the status of dynamic stability of WA coral reefs.

Here, we use historical and recent measures of coral cover throughout north-western Australia, to document the timing and extent of bleaching, mortality and recovery of corals in this region from 1980 to 2016. In particular, we examine the fine-scale spatio-temporal variability in coral bleaching among locations within the Pilbara, in relation not only to SST anomalies but also SST variability, and discuss these observations and rates of recovery in the context of regional and global trends.

Materials and methods

Study area

The Ningaloo and western Pilbara coastal regions of north-western Australia lie just north of the Tropic of Capricorn and

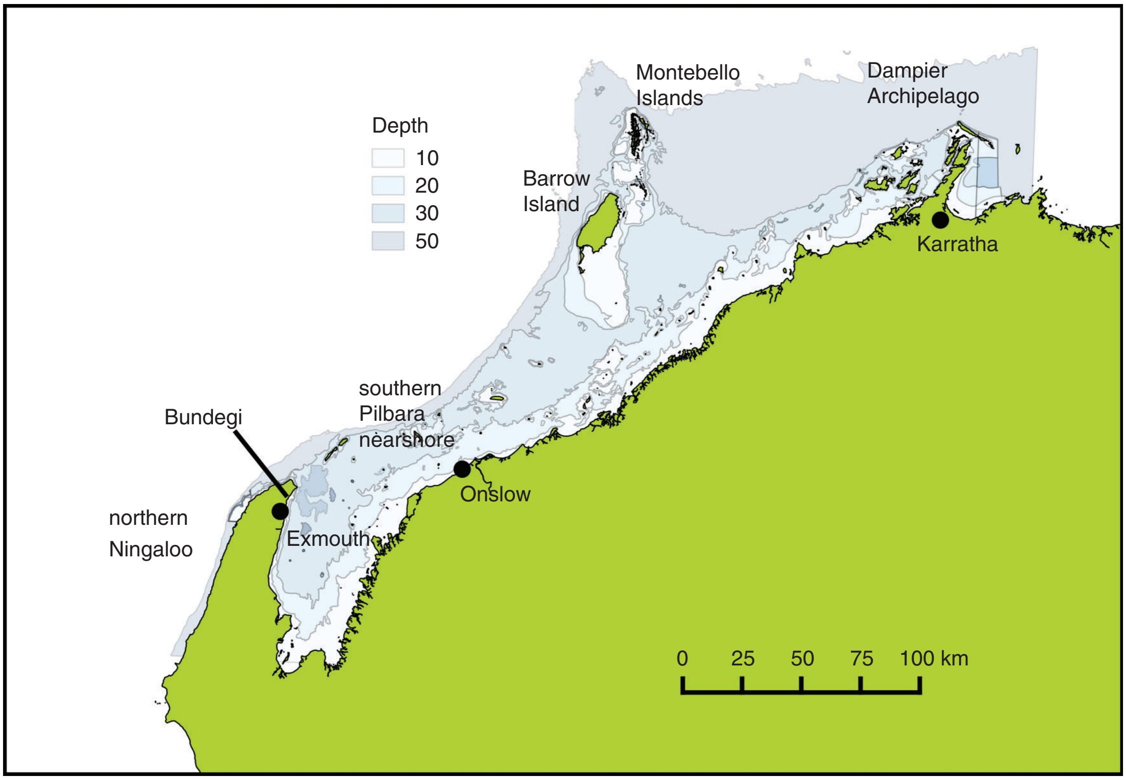

Fig. 1. Western Pilbara and Ningaloo coastal region (centred on 21.4°S, 115.45°E) and continental-shelf depth contours, with Australian mainland shown in green.

are characterised by extensive reef development and diverse coral assemblages (Veron and Marsh 1988). Coastal fringing reefs at Ningaloo comprise some of the most extensive continuous fringing reef systems in the world. The continental shelf is narrow adjacent to northern Ningaloo, but is broader along the north in the western Pilbara coast, between Bundegi and Dampier. The western Pilbara coast is characterised by over 1000 islands and reefs that are exposed at astronomical low tides, notably the Dampier Archipelago, Montebello and Barrow Islands, and the nearshore islands of the south Pilbara off the coast of Onslow (Fig. 1).

Sea-surface temperature

Remotely sensed data were used to produce maps and time-series graphs of SST and degree heating weeks (DHW). Time series were plotted for the following five locations: northern Ningaloo, Bundegi, south Pilbara nearshore, Montebello and Barrow Islands, and the Dampier Archipelago. The data for each location were averages over a 0.1°-square centred on each location. The SST data were from the IMOS GHRSST L3S night-only 1-day, 0.02° IMOS dataset (https://portal.aodn.org.au/), which is the dataset used for the ReefTemp system on the GBR (Garde *et al.* 2014). We calculated DHW by using the methods outlined by NOAA Coral Reef Watch (Liu *et al.* 2006, 2008) and calculated the monthly climatology over the 10-year period from 2002 to 2011 (matching that of ReefTemp). The maximum mean monthly SST of the hottest month (MMM SST) was also calculated from the climatology. The bleaching threshold at each point is 1°C above MMM SST at that point. DHW for each day was calculated as the sum over the 12 weeks ending on that day of SST minus MMM SST, for days when SST was at or above the bleaching threshold.

Degree heating week (DHW) is sensitive to missing SST data, affecting not only average DHW values, but, in our study, also comparisons of relative DHW among years. To address the problem conservatively, we partially interpolated missing data with a weighted running average by using a window of 11 days. Weight declined linearly from one at 0 days, to zero at 6 days. Imputation was performed only when there were at least two data points in the window. This method balanced imputing data with minimising bias from over-extrapolation (e.g. of isolated high SST values). To check for anomalies caused by imputation, DHW time-series graphs were compared with graphs calculated from raw SST data and SST data imputed by loess regression. Significant coral bleaching usually occurs when DHW values reach 4°C-weeks. By the time values reach 8°C-weeks, widespread bleaching is likely and significant mortality is expected (Liu *et al.* 2006, 2008).

To help with interpretation, daily SST anomaly maps were calculated as the difference between the 11-day weighted running average and a daily climatology. The daily climatology was calculated in the same way as monthly climatology, except that a 31-day window centred on each day was used in place of month.

Coral at different locations in the Pilbara experiences the heating represented by DHW in different contexts of temperature norms and variation. To summarise the different contexts of temperature norms and variation, maps representing summer temperature, seasonal variation of temperature and year-to-year variation of summer temperature were calculated. The data period was from July 1994 to June 2017 (23 years). For summer temperature, the long-term 90th percentile of year-round temperature was calculated and, so as to reduce bias owing to missing values, observations were weighted such that each month (over all years) had the same weight. For seasonal variation, we calculated seasonal range from a daily climatology calculated using a 31-day smoothing window. For year-to-year variation, we calculated the standard deviation of the yearly 90th percentile temperature from July to June. Again, observations were weighted to reduce bias owing to missing values; however, the maximum weight was limited to a factor of five to constrain the influence of observations from months with few data points. To examine whether the norms and variation had changed over time, we also calculated them for the first and second halves of the data period (12 years each). To put our study region into context, we also calculated these maps for the Kimberley and GBR regions. To help with interpretation, we note that, in these regions, the 90th percentile SST was similar to MMM SST used for DHW calculation (90% of differences –0.2–0.5°C).

Coral cover

There were three types of data sources considered for inclusion in our study, namely (1) peer-reviewed literature (journal articles), (2) grey literature (reports), and (3), unpubl. data that were collected for research purposes or environmental monitoring programs (Supplementary material File S1). Studies that provided an estimate of percentage cover of hard coral (Scleractinia) from any location in our study region were included, provided they also included other metadata, including depth (or depth range), habitat type(s) surveyed and collection method. Data collected from *in situ* monitoring were used, including still photography, video and *in situ* visual estimates from transects, quadrats, manta-tows, towed video and remotely operated vehicle (cf. Speed *et al.* 2013).

We were primarily interested in coral cover of shallow coastal and offshore areas because of the availability of data, and increased vulnerability to prominent natural and anthropogenic impacts. We, therefore, restricted data collection to surveys that were conducted at depths ≤20 m, with the majority of data being collected at average depths of ≤10 m (80% of surveys). This also reduced potentially confounding results of coral-cover patterns owing to varying depth gradients. Surveys included were also generally restricted to subtidal zones. A complete list of data sources is included in File S1, available at the journal's website.

Analysis

Coral-cover time-series evaluation was performed by using change-point analysis to determine whether and when significant changes in coral cover occurred. This technique uses serial bootstrap sampling to determine when changes in time series values are large enough so that they could not be reasonably explained by chance alone (Sharma *et al.* 2016). Each bootstrap sample was a random re-ordering of the coral cover, which was repeated 1000 times in each analysis. This procedure allowed estimates of variances associated with the changes in the coral cover to be calculated. Analysis then identified break points where substantial deviations from the range of expected values occurred and calculated confidence intervals around breakpoints (Taylor 2000).

Results

Dampier

The long-term average coral cover in the Dampier Archipelago was 27.1 ± 16.5% (mean ± 1 s.d.). Whereas the earliest estimate of coral cover comes from a single site, sampling effort during subsequent years was relatively high, owing to several projects designed to monitor the environmental impacts of dredging, which covered a range of nearshore and offshore sites (Fig. 2). Sampling was undertaken annually between 2003 and 2010, and resumed after a gap of 4 years in 2014. Whereas the coral cover was slightly below the long-term average before 2003, the period of 2003–2010 was generally characterised by above-average coral cover. There was a slight relative dip in the coral cover between 2006 and 2009, corresponding with reports of bleaching and mortality in the region in 2005 and 2008 (MScience 2008); however, this did not affect the longer-term trend in the coral cover (Table 1, Fig. S1, available at the journal's website). Satellite SST indicated heating levels of ~4 DHW in 2008 (Fig. S2) coinciding with reported bleaching. Temperatures in 2005 were characterised by only slightly elevated DHW values (Fig. 3, Fig. S2). By 2014, a significant decline of coral cover, below the long-term average, was evident, and, in 2015, coral cover was at historically low levels. This change is likely to have occurred in 2013, because satellite SST indicated that parts of the Dampier Archipelago experienced >6 DHW in 2013. Although there was no sampling between 2010 and 2014, bleaching was reported anecdotally at high levels in 2013 (https://www.youtube.com/watch?v=HQk3J7p9yWg, verified 29 September 2020). Extensive surveys were conducted in 2014 and although bleaching was observed at low levels, no mortality was observed. The DHW experienced in the Dampier Archipelago in 2014 were about half the levels recorded in 2013 (<4 DHW; Fig. S2), and heating was spatially patchy throughout the archipelago (Fig. 3). Coral cover recovered slightly up to 2016. Of our five study locations, Dampier Archipelago had the highest summer temperature and seasonal range of SST, but the lowest year-to-year variation of summer temperature (Fig. 4).

Barrow and Montebello Islands

Records of coral cover at Barrow Island and the Montebello Islands extend back only to 2005, and have been annual since 2009 (Fig. 2). For the initial part of this period, coral cover was at or above the long-term average of 31.3 ± 12.9%. Coral cover declined from a high of ~45% in 2005 to just above 32% in early 2013. Since 2013, the level of coral cover has declined significantly (Table 1, Fig. S1) to between 8% and 11%, and reached a minimum of 6.7% in 2015 (Table 1, Fig. S1), an overall decline of over 25%. Satellite SST indicated that, in 2011, there was widespread but still moderate warming of ~4 DHW in the Barrow and Montebello islands (Fig. 3, Fig. S2). Conditions were much warmer in early 2013; however, more than 8 DHW were recorded adjacent to Barrow and Montebello islands, coinciding with significant declines in coral cover (Table 1, Fig. S1). In early

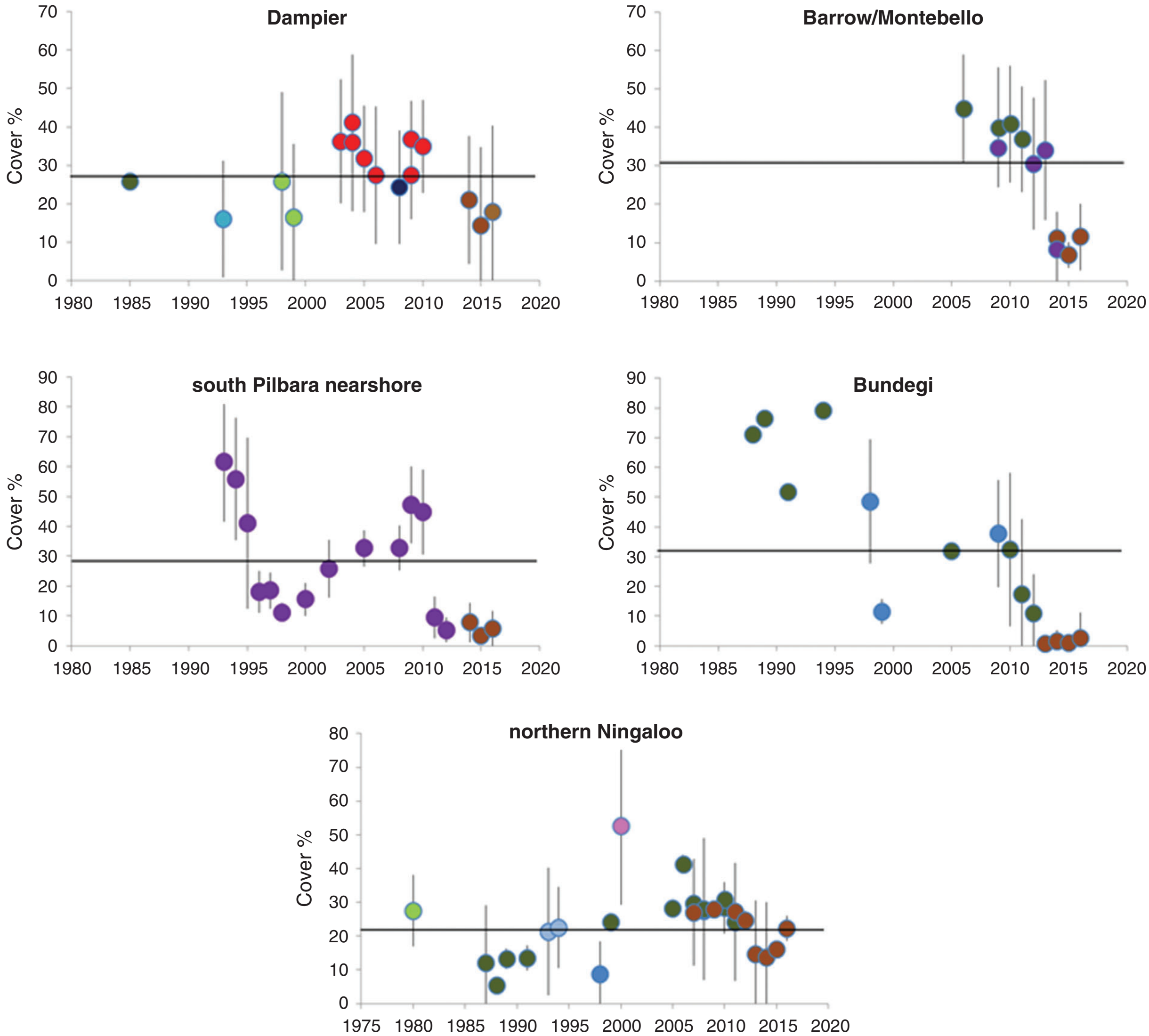

Fig. 2. Coral cover from coastal coral reefs off north-western Australia. Data are means and standard deviations derived from point-intercept transects. Horizontal line shows the long-term average coral cover. Present study (brown symbols), Department of Conservation Biodiversity and Attractions (dark green symbols), Australian Institute of Marine Science (light blue symbols), West Australian Museum (light green symbols), Chevron (purple symbols), MScience (red symbols), and Worley Parsons (dark blue symbols). Black arrows indicate cyclones passing within 100 km of the region, and white arrows indicate years of reported bleaching in the region.

Table 1. Change-point analysis for significant changes in coral cover

Table shows years in which significant change was detected to occur, with confidence level relating to that change having occurred, and the confidence interval around this timing (95%)

Location	Change-point	Confidence interval		Confidence level	
			(%)	From	To
Dampier	2014	2004, 2014	99	29.26	17.79
Montebello and Barrow Islands	2014	2014, 2014	97	37.41	9.45
South Pilbara nearshore	1998	1994, 1998	95	69.6	32.41
	2011	2010, 2011	94	32.41	5.66
Bundegi	1998	1994, 1998	93	69.55	32.41
	2011	2010, 2011	93	32.41	5.66
Northern Ningaloo	1999	1994, 1999	100	15.57	30.16
	2013	2000, 2013	100	30.16	16.67

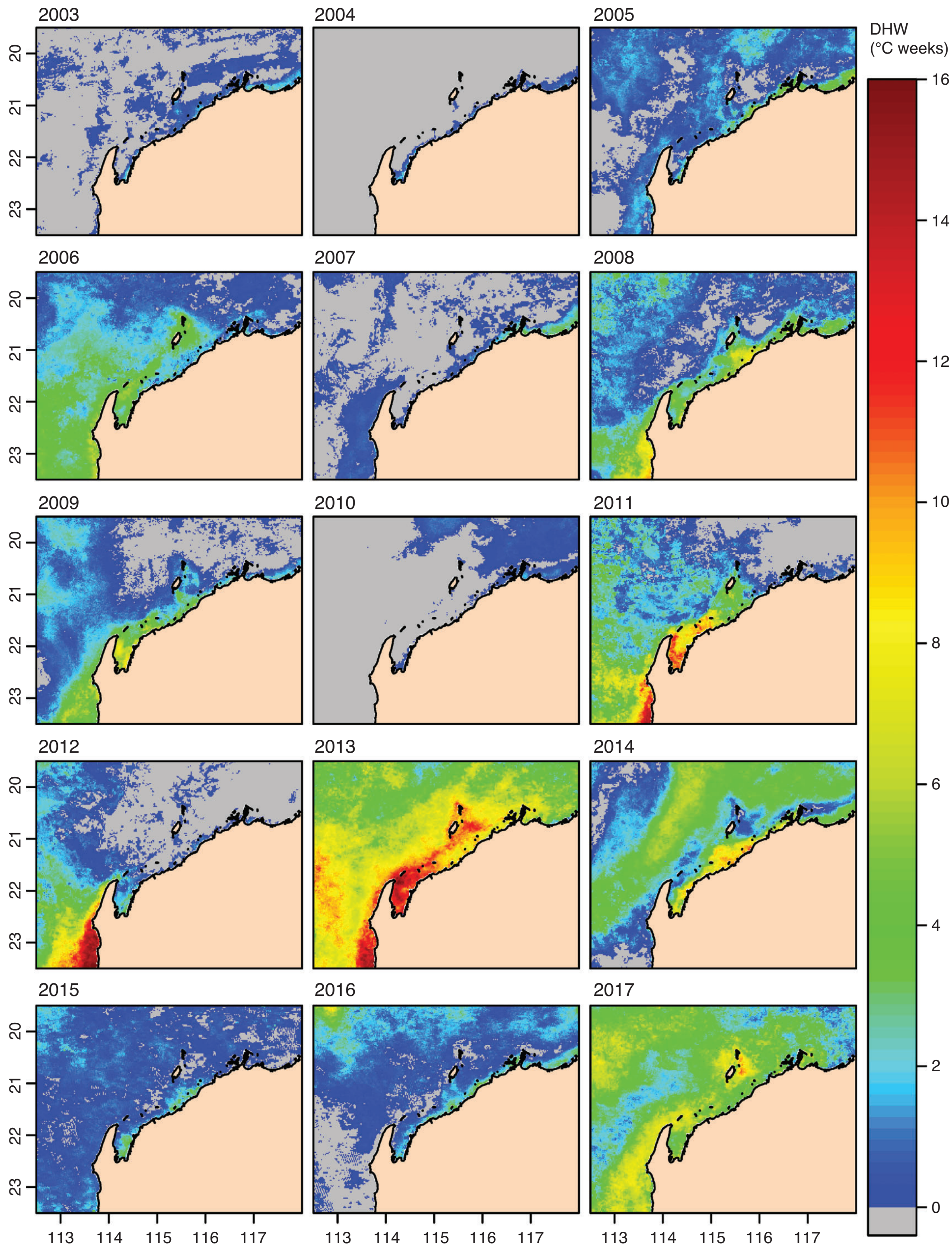

Fig. 3. Sea-surface temperature (SST) degree heating weeks (DHW) in the Pilbara region off Western Australia 2003–2017. The maps show the maximum DHW from December to May. The year is the year in which the summer ended.

2014, anomalous warming of up to 4 DHW was again recorded in parts of the region (predominantly towards the south of Barrow Island; Fig. 3). There was a non-significant increase in the coral cover to 11.5% in 2016, although coral cover remains well below the long-term average of 31.3 ± 12.9%.

South Pilbara nearshore

Average coral cover on southern Pilbara nearshore reefs was 25.7 ± 18.8% between 1993 and 2016. Highest coral cover was recorded in 1993, with an average of 61.5 ± 19.9%, declining to 18.1 ± 6.9% in 1996, and further reducing to 11.3 ± 3.1% in

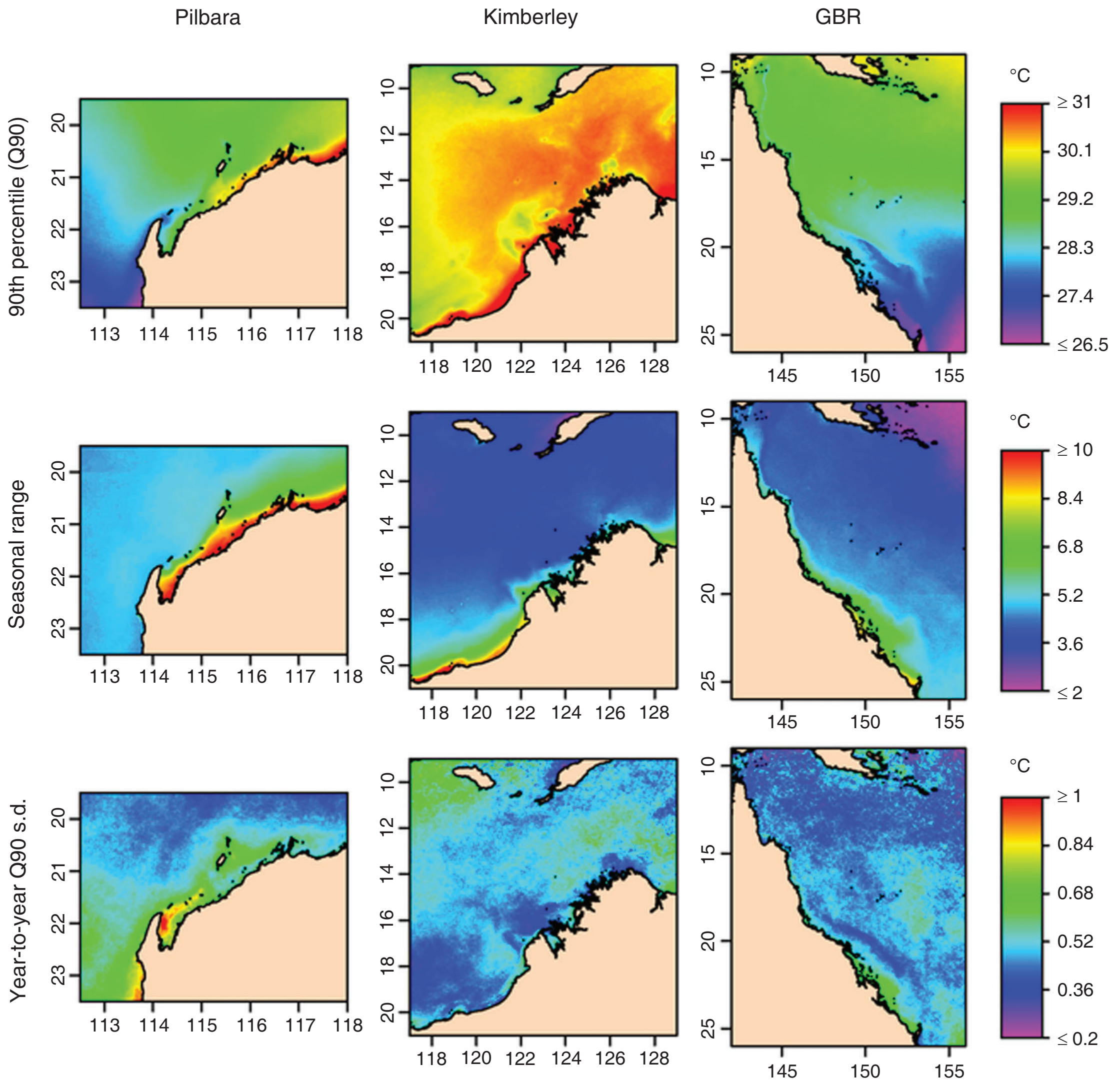

Fig. 4. Temperature norms and variation in the Pilbara, Kimberley (north-western Australia) and Great Barrier Reef (north-eastern Australia) regions for the period 1994–2017. The maps represent typical summer temperature (long-term 90th percentile of year-round sea-surface temperature, SST), seasonal variation (seasonal range of SST) and year-to-year variation of summer temperature (standard deviation of yearly 90th percentile SST).

1998. Low coral cover in 1998 followed successive cyclone impacts on this region in 1995 (tropical cyclone Bobby, Category 3) and 1996 (tropical cyclone Olivia, Category 4) and reports of bleaching in 1998 (Fig. 2). Average coral cover recovered within 4 years of the low point of coral cover in 1998 (Table 1), reaching levels above the long-term average by 2002, which peaked at 47% in 2009 and remained high in 2010 (Fig. 2). Coral cover declined precipitously to an average of 9.6% in 2011, being a decrease of over 37% in absolute terms. There were clear and substantial changes across all nearshore Pilbara sampling sites, which were sampled both before and after the change points in 1998 and 2011 (Table 1). Satellite SST indicated warming of ~9 DHW over much of the area in early 2011 (Fig. 3, Fig. S1). Higher temperatures occurred in 2013 (over 11 DHW) and another warming episode occurred in 2014 (~6 DHW, mainly nearshore). Coral cover continued to decline from 2011 levels of 9.6% and reached a low of 3.4% in 2015. While the bleaching event in 2011 caused a substantial change in the coral cover, subsequent bleaching episodes in 2013 and 2014 resulted in further mortality of the already depleted coral community. In absolute terms, this second reduction in coral cover was not as great as in 2011, because coral cover was so low to start with; however, in relative terms, this represented a further reduction of ~65%. Coral cover increased slightly in 2016, to 5.8%, but remained well below the long-term average of 23% (Fig. 2). Warming in the southern Pilbara nearshore is spatially complex because the location spans steep gradients of MMM SST, seasonal SST variation and year-to-year SST variation (Fig. 4).

Bundegi

Coral cover at Bundegi averaged 30.78 ± 13.3% between 1988 and 2016 (Fig. 2); however, coral cover has been highly variable

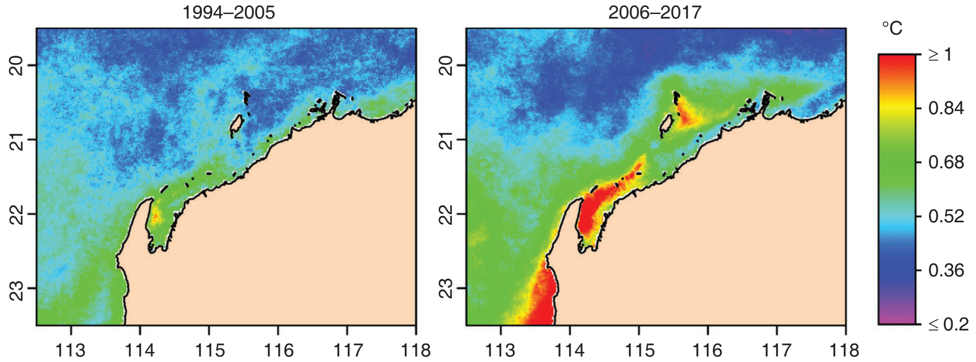

Fig. 5. Year-to-year variation of summer temperature (standard deviation of yearly 90th percentile sea-surface temperature, SST) in the Pilbara coast of north-western Australia in the first and second halves of the period 1994–2017.

over time, with periods of very high coral cover, such as in the late 1980s when it was greater than 70% at times, and periods of very low cover (<3%) in recent years. The early trend of high coral cover declined significantly after 1998 (Table 1, Fig. S1), and levels of cover dropped further in 1999, to 11.6%, as a result of cyclone Vance. Coral recovered rapidly between 1999 and 2005 to ~32%, which was similar to the long-term average, although cover was still significantly lower than between 1988 and 1997. Coral cover remained at about these levels until 2011, when it declined significantly again in 2011, to 17%, and further declined in 2013, to <1% cover. The cumulative decline between 2010 and 2013 was 31.6%. Exmouth Gulf experienced warming of ~11 DHW in 2011 and 15 DHW in 2013, followed by 6 DHW in coastal areas in 2014 (Fig. 3, Fig. S2). Coral cover in 2016 remained at record low levels (2.5%), contrasting with the observed recovery that occurred following 1999. Several cyclones passed near the Bundegi–Ningaloo region between 2011 and 2017, including tropical cyclone Olwyn, which passed almost directly over the site in 2015. Surveys conducted immediately before and following the passage of tropical cyclone Olwyn showed negligible damage to the remaining reef at Bundegi or the western coast in northern Ningaloo (R. Babcock, unpubl. data). Of our five study locations, Bundegi experienced the highest year-to-year variation in summer temperature (Fig. 4).

Northern Ningaloo

Northern Ningaloo coral cover has averaged 21.8 ± 9.3% between 1980 and 2016. At the time the first measurements were made in 1980, coral cover was 27%, but declined gradually to below the long-term average by 1987 (Fig. 2) and remained at similar low levels until the mid-1990s. A significant change point in coral cover was evident from 1999 when the coral cover increased (Table 1, Fig. S1) and remained above average levels until 2012, when it averaged 27% (Table 1, Fig. S1). There was a significant decline in the coral cover of 12.5% in 2013 when coral cover returned to below-average values at 14.5%, recovering slightly to levels equivalent to the long-term average of 21.8 ± 9.3% by 2016 (Fig. 2). The SST warming anomaly at Ningaloo was ~6 DHW in 2011 and 2012, and then ~12 DHW in 2013 (Fig. 3, Fig. S2). Little or no warming was observed in 2014. Although warming in 2011 was moderate, it was sustained over an extended period (above-threshold SSTs occurred in 12 weeks over a 15-week period from January to April). Of our five study locations, northern Ningaloo experienced the lowest summer temperature and seasonal variation, but a moderately high year-to-year variation of summer temperature (Fig. 4).

Geographical patterns of temperature norms and variation

The temperature norms and variation in the Pilbara differed from those in the Kimberley and the GBR (Fig. 4). Among the three regions, the Kimberley was characterised by high summer SST, and the Pilbara and GBR typically experience moderate MMM SST. However, there was a much greater range in MMM SST across the Pilbara region (roughly 3° of latitude) than observed across much larger latitudinal gradients in other regions such as the Kimberley (10° of latitude) or the GBR (15° of latitude). The Pilbara also shows a much greater year-to-year variation in summer temperature and a higher year-to-year variation of summer SST than either the Kimberley or GBR regions (Fig. 5). Seasonal ranges in SST in the Pilbara and Kimberley are much higher than in the GBR, which is mainly evident in the contrast among shallow coastal areas in some parts of these regions, which are absent on the GBR. In summary, compared with the much larger regions such as the GBR, MMM SST in the Ningaloo–Pilbara region appears to transition sharply between cooler, more subtropical waters and very warm summer waters characteristic of the tropical eastern coastal regions of Australia and the Timor Sea. This spatial variability is most likely the driver of the spatial variability in the observed series of bleaching in the region. The western coast of Ningaloo experienced the least bleaching and had generally low MMM SST and low seasonal and interannual SST variability. The worst-affected areas at Bundegi and the south Pilbara nearshore reefs experienced the highest interannual SST variability. The Ningaloo–Pilbara region also showed a higher level of temporal variation in seasonal and year-to-year SST than do other much larger regions such as the GBR. The GBR tended to be moderate in all three attributes.

Within the Pilbara, summer temperature increased from south to north and, in the north, towards the coast (Fig. 5). Cross-shelf variation in seasonal range was much higher in

Pilbara nearshore coastal waters from Exmouth Gulf to Dampier, with a general lower variation in seasonal range at Ningaloo than at Dampier. Year-to-year variation of summer temperature was highest south of North West Cape in the Exmouth Gulf (including Bundegi). This interannual variation was higher in the second half of the period (2006–2017) than in the first half (1994–2005) of the period we examined (Fig. 5). The change in year-to-year variation at Bundegi, (+0.29°C, standard deviation of the yearly 90th percentile) was comparable with the increase in summer temperature (long-term 90th percentile) (+0.27°C). The levels of SST variability experienced over the past decade in the south-western Pilbara and Exmouth Gulf are clearly greater than the region has experienced before that (Fig. 5), reflecting recent MHW conditions and coinciding with historically low levels of coral cover in many parts of the region.

Discussion

Role of bleaching and other factors in regional trends in coral cover

The Dampier Archipelago in the north-western Pilbara region experienced little or no thermal anomaly in 2011 during the MHW in WA, but there were signs of anomalous warming in 2013, when the area experienced 6–8 DHW. Although no coral mortality was reported in the region at the time, trends in coral cover showed ongoing declines between 2010 and 2014, most likely being due to the observed heating. Bleaching and mortality of corals have been reported in Dampier previously in 1998 (Wilkinson 2000; Gilmour 2004), although Gilmour (2004) attributed the mortality in his study to a combination of bleaching, dredging and cyclone activity. Bleaching reported in 2005 and 2008 (MScience 2007, 2008) appears not to have resulted in a change in trend for coral cover, although there may have been some mortality, because average cover did decline immediately after 2005. The Dampier Archipelago, particularly the central part of the archipelago, presently has some of the highest levels of coral cover in the western Pilbara, reflecting the absence of severe bleaching and mortality in the Dampier Archipelago until 2013, in contrast to the multiple bleaching and mortality episodes in 2011 and 2013 in other regions of the Pilbara.

Acute declines occurred in coral cover on reefs of the nearshore southern Pilbara near Onslow in 2011, an area which was similarly affected by thermal stress in 2011 and 2013. It is evident from our data that most bleaching-related coral mortality in this area occurred in 2011, confirming previous inferences (Lafratta *et al.* 2017). Although there was a larger thermal anomaly and significant bleaching was reported in 2013 (Lafratta *et al.* 2017), this appeared to have had little further impact on the overall coral cover. This is most likely to be related to the observation that, before 2011, reefs in the area were dominated by genera sensitive to bleaching, whereas in 2013, the coral genera remaining were more resistant to bleaching (Lafratta *et al.* 2017). Corals in the Onslow area have bleached previously, in 1998 (see Wilkinson 2000), confirming recent reports that a prior history of bleaching does not always provide protection from future bleaching events (Hughes *et al.* 2017).

Thermal stress (DHW) at the Montebello and Barrow islands in 2011 was not as great as that in nearshore reefs of the southern Pilbara, possibly in part because of the cooling effects of several cyclones that passed through the area in early 2011 (Moore *et al.* 2012) and the proximity of relatively deeper waters to Montebello and Barrow islands. Thus, these reefs, which are located less than 100 km from the severely affected nearshore southern Pilbara reefs, escaped major coral mortality in 2011. Even though bleaching of corals did occur in 2011 (Moore *et al.* 2012; Ridgway *et al.* 2016), this did not afford protection from bleaching and mortality (e.g. Guest *et al.* 2012) of reefs at the Montebello and Barrow islands in 2013, because there was a substantial reduction in coral cover following thermal anomalies in 2013. Recovery of coral in this region is likely to have been further impeded by aggregations of the crown-of-thorns starfish at both the Montebello Island and Barrow Island in 2014 and 2015, which may have started as early as 2006 (Haywood *et al.* 2019).

Major declines in coral cover were also recorded at Bundegi, in the north-western part of the Exmouth Gulf in 2011, where temperatures were higher than in other Pilbara coastal waters (11 DHW) and mortality of corals exceeded 80% (Moore *et al.* 2012; Depczynski *et al.* 2013). In 2013, heating was even more extreme, with a peak of 15 DHW, but little bleaching was observed, primarily because so few corals remained to be affected. Coral cover has remained at less than 3% up to the present time, with little indication of any significant recovery. On the basis of the survival of small colonies observed in 2011, recovery might have been predicted at Bundegi, following bleaching in 2011 (Depczynski *et al.* 2013); however, coral cover declined further in subsequent years, suggesting that small colonies detected during post-bleaching surveys in 2011 may have been affected by the MHW in 2013.

In contrast, less than 20 km away on the western side of northern Ningaloo, although some coral bleaching was observed in 2011, coral mortality was reported to be minimal, (Moore *et al.* 2012). Nevertheless, a significant decline in coral cover was detected in 2013. Although thermal anomalies on the northern Ningaloo western coast in 2011 were moderate, they were sustained over a long period. Anomalies were also observed in 2012, and in 2013 strong heating was present, apparently without any further significant reductions in coral cover. Despite reductions in the cover remaining modest between 2012 and 2013, cover remains at historically low levels, below 20%. There appears to be signs of recovery, although further monitoring is required to confirm this trend.

Spatial variability

Our observations draw together data from the western Pilbara and northern Ningaloo, to more completely describe the temporal and spatial variability in the pattern of bleaching-related mortality in the region as a result of repeated temperature anomalies. The first reports of bleaching and mortality in the region were from Dampier in 1998. Since then, bleaching in the Pilbara has been most frequent in the Dampier region, having been recorded five times. In comparison, bleaching has been recorded three times at the southern Pilbara nearshore, twice at the Montebello and Barrow islands and Bundegi and only once at northern Ningaloo. In addition to this trend in the observed frequency of bleaching, there were distinct differences among subregions in the intensity of coral bleaching and mortality, even across distances of as little as 20 km. For example, the MHW of

2011 northern Ningaloo and the Montebello and Barrow islands saw patchy bleaching and there was little mortality, whereas adjacent areas at Bundegi and the southern Pilbara nearshore experienced very severe bleaching and mortality in the same year. In 2013, bleaching at Montebello and Barrow islands was severe, yet bleaching and mortality at Dampier was patchy and moderate, with apparently high levels of variation even within the archipelago. There were no reports of bleaching at northern Ningaloo in 2013.

These subregional scale differences in the occurrence and outcomes of coral bleaching may be due not only to spatial variation DHW (Fig. 3), but also the sensitivity of corals to a given level of DHW, where different sensitivity in responses may result from local seasonal and year-to-year SST variation in temperature that the corals have experienced in the past (Carilli *et al.* 2012). That is, at locations where variability is low, corals will have experienced either fewer or milder heating events (or both), and, potentially, be less well adapted and more sensitive to a given level of DHW. There is little evidence to support this from our observations because Ningaloo, which has the least variable SST regime, experienced minor bleaching and mortality, despite being exposed to 12 DHW in 2013. At locations where variation is high, the following two possibilities arise: (1) the variation matches historical patterns, and the coral may be less sensitive to a given level of DHW or (2) the variation has recently increased, and the coral is under stress. We checked for recent changes by comparing temperature norms and variation between the early and late halves of our 24-year analysis period. The high mortality rates of corals at Bundegi and the southern Pilbara nearshore suggest that the latter hypothesis is more likely because, although these areas are the most variable on a year-to-year basis, they have also experienced the largest increases in interannual SST variability of any part of the region since 2005. This observation increases the level of risk that these areas will experience future impacts from MHW in the future because MHW are expected to intensify and increase in frequency in the future (Oliver *et al.* 2018).

Recovery

Reefs from southern Pilbara nearshore and Bundegi have experienced multiple episodes of disturbance and recovery; however, recovery from recent disturbances has been markedly slower than observed previously. Tropical cyclone Vance in early 1999 caused a drop in hard coral cover at Bundegi to ~15%, and a combination of cyclones, and possibly bleaching, are likely to have caused similar declines in the coral cover in the southern Pilbara nearshore region. Following impacts in the 1990s, Bundegi recovered to levels above the long-term average after just 6 years. Although the timing of impacts in the southern Pilbara nearshore reefs was slightly different, declines in coral cover were of similar magnitude and comparable recovery of coral cover was observed by 2002, just 6 years after tropical cyclone Olivia (1996). On the basis of previous observations, coral cover at Bundegi and the southern Pilbara inshore might have been expected to recover relatively rapidly after bleaching in 2011; however, in both areas, there has been little if any indication of recovery in coral cover as of 2016. The recovery rates of these reefs, therefore, appears to be significantly reduced relative to previous recovery rates at these reefs.

Repeated and severe bleaching impacts across the region have reduced coral cover to historically low levels, with cover being below 5% in the worst affected regions, and may have reduced regional larval supply and the potential for self-seeding of coral populations (e.g. Gilmour *et al.* 2013). Depletion of larval supply would lead to reductions in recruitment and recovery rates. In addition, recurrent MHW and bleaching may have reduced recovery from any remaining colony fragments or small juveniles that survived the initial bleaching, which has been suggested to be important in previous recovery at Bundegi (e.g. Depczynski *et al.* 2013). Reduced rates of recovery from environmental disturbances owing to impacts of rising temperatures on coral growth rates have also been suggested as an explanation for slowing recovery rates (Osborne *et al.* 2017); however, at Bundegi and the southern Pilbara nearshore, the very low levels of coral cover make this explanation less likely. At this point, we cannot rule out any of these factors and they may well act in combination, resulting in an overall decline in resilience of reefs within the region.

MHW frequency

It has been clear for some time that episodes of coral bleaching cannot be viewed as one-off events, but rather as recurring phenomena (Oliver *et al.* 2009; Trapon *et al.* 2011; Guest *et al.* 2012). On reefs off north-western Australia, multiple bleaching episodes have now been recorded in all regions of the western Pilbara, except for northern Ningaloo. In many parts of the region, these events have occurred after very short intervals, between 1 and 3 years, and appear to be increasing in intensity, producing the most severe effects yet recorded in the region. This pattern is similar to that seen on the GBR, which experienced its most severe bleaching ever in 2016, followed by further bleaching in 2017 (GBRMPA 2017; Hughes *et al.* 2017). The apparent lack of adaptation of Bundegi corals to heating patterns such as those experienced in recent years is consistent with the observation that seasonal and interannual patterns of temperature variability off north-western Australia have changed; summer temperature and year-to-year variation of summer temperature were both higher in the past 10 years than they were in the 10 years previously (Fig. 5). The recurrent bleaching episodes reported here and on the GBR are consistent with the observed increase in marine heatwaves globally, including northern Australia (Oliver *et al.* 2018).

Predictions that coral reefs globally, including World Heritage Sites such as Ningaloo, will experience severe bleaching twice per decade as early as 2041 (Heron *et al.* 2017) may appear pessimistic, but evidence presented here indicates that areas within the western Pilbara region have already been exposed to this level of disturbance. Although the western coast of Ningaloo is buffered from bleaching to an extent, owing to upwelling-favourable summer conditions (Xu *et al.* 2015), other reefs of the Pilbara are located further from the shelf edge and are less exposed to seasonal longshore summer winds that drive this upwelling. These areas may be affected even earlier by changes to climate. Action, therefore, needs to be taken now at a local level to increase future resilience of coral-reef ecosystems in the region that is arguably the most important coral-reef province on Australia's western coast. Most importantly, the future of Pilbara reefs, and coral reefs globally, will be assured only by swift and far-reaching action on limiting anthropogenic CO_2 emissions (Hoegh-Guldberg *et al.* 2014).

Conclusions

In developing mitigation strategies for coral bleaching, we need to consider that global warming and extreme climate events can trigger fundamental shifts in ecosystems (van de Pol *et al.* 2017), and that the loss of resilience, being manifested as an increased length of time needed to recover from disturbance, often precedes ecosystem shifts (Scheffer *et al.* 2001). Therefore, management strategies that maintain ecosystem resilience are important. Further, mitigation strategies need to be flexible and adapt to the information gained by monitoring and assessment (Schindler and Hilborn 2015). This requires closely integrating management interventions with ecosystem research and, potentially, the implementation of a range of direct interventions, such as control of *Acanthaster* aggregations and others that are being implemented or considered for the GBR (Anthony *et al.* 2017).

Recent climate simulations have indicated that seasonal and interannual variability in SST maxima may be an important factor in determining bleaching frequency (Langlais *et al.* 2017). Because areas of high and low seasonal and interannual SST variability exist in the western Pilbara, and to coincide with patterns of bleaching in the period between 2011 and 2016, it may be possible to optimise future management strategies by understanding how these patterns may affect the overall system resilience. For example, spatio-temporal refugia provided by such variability, which appears to be greater than that on Australia's other tropical coasts, may interact with ecosystem properties such as regional connectivity to affect resilience (Boschetti *et al.* 2017). An understanding of connectivity regimes among coral populations within the region is emerging on the basis of both hydrodynamic modelling (Feng *et al.* 2016; Boschetti *et al.* 2017) and genetic studies. Particle-track modelling shows that reefs to the north of Barrow Island have a low connectivity with those to the south (Feng *et al.* 2016), which was corroborated in a recent coral population-genetic study of *Cyphastrea microphthalma*, which showed low levels of differentiation among some Pilbara reefs (Evans *et al.* 2019). Other recent genetic studies of a fish (*L. carponotatus*; DiBattista *et al.* 2017) and mangrove (*Avicennia marina*; Binks *et al.* 2019) have shown that the Pilbara region is well mixed along the coast from northern Ningaloo to Dampier, by using Bayesian clustering analyses of single-nucleotide polymorphisms; however, there were low levels of population structure on the basis of F_{ST}, particularly between the northern and southern sites (DiBattista *et al.* 2017). At a larger scale, southern Ningaloo and Shark Bay are isolated from tropical populations to the north on ecological time-scales (DiBattista *et al.* 2017, Binks *et al.* 2019; Evans *et al.* 2019). This recent understanding of the connectivity of the region suggests that larval connectivity is not the sole driver of recovery failures, such as those at Bundegi, but is likely to have been exacerbated by the lack of survivability of new recruits because of repeated disturbance events at intervals too frequent to allow recovery.

Given the likely increase in underlying ocean temperature as a result of global warming, and the projected increase in the intensity and frequency of MHW and other extreme climate events (Oliver *et al.* 2018), there is a high likelihood that reefs in the western Pilbara and even northern Ningaloo regions will experience more frequent bleaching and mortality events in the future. Year-to-year variability in SST in the Pilbara region is increasing, reflecting the higher frequency of MHW in the region and it is also likely that we are already seeing the ecological effects of this trend, with recent changes in the composition of coral assemblages at northern (Thomson *et al.* 2017) and parts of central Ningaloo (Shedrawi *et al.* 2017) and an apparent lengthening of recovery times for coral cover following disturbances. These observations are consistent with trends on the GBR and in other parts of the world, where repeated and severe bleaching impacts have led to changes in the composition of coral-reef species assemblages (Perry and Morgan 2017*a*; Hughes *et al.* 2018).

Conflicts of interest

Datasets from the inshore Pilbara region were made available by consent of Chervron. The authors declare that they have no other conflicts of interest.

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