Global Change Biology

Towards modelling the future risk of cyclone wave damage to the world's coral reefs

Journal:	*Global Change Biology*
Manuscript ID	GCB-19-2295.R1
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	n/a
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Keywords:	coral reef, tropical cyclone, hurricane, typhoon, climate change, disturbance
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Running title: Size matters in models of cyclone reef damage

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Paper type: Primary Research

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Keywords: coral reef; tropical cyclone; hurricane; typhoon; disturbance; climate change

Statement of authorship: MP, JG, RL and BR conceived the original idea for the study with input from all authors. ED analysed and interpreted broad-scale wind and wave models for cyclone Lua. RL analysed and interpreted fine-scale wave transformation over Scott Reef. JG and MD contributed and interpreted field data for Scott Reef. BR and AH contributed field data for the shoals and Scott Reef. MP calculated cyclone return times for coral ecoregions, with key input from BR. MP constructed the figures and tables and wrote the manuscript with input from all authors.

Abstract

Tropical cyclones generate extreme waves that can damage coral reef communities. Recovery typically requires up to a decade, driving the trajectory of coral community structure. Coral reefs have evolved over millennia with cyclones. Increasingly, however, processes of recovery are interrupted and compromised by additional pressures (thermal stress, pollution, diseases, predators). Understanding how cyclones interact with other pressures to threaten coral reefs underpins spatial prioritisation of conservation and management interventions. Models that simulate coral responses to cumulative pressures often assume that the worst cyclone wave damage occurs within ~100 km of the track. However, we show major coral loss at exposed sites up to 800 km from a cyclone that was both strong (high sustained wind speeds >= 33 m s^{-1}) and big (widespread circulation >~300 km), using numerical wave models and field data from northwest Australia. We then calculate the return time of big and strong cyclones, big cyclones of any strength, and strong cyclones of any size, for each of 150 coral reef ecoregions using a global dataset of past cyclones from 1985 to 2015. For the coral ecoregions that regularly were exposed to cyclones during that time, we find that 75% of them were exposed to at least one cyclone that was both big and strong.   Return intervals of big and strong cyclones are already less than 5 years for 13 ecoregions, primarily in the cyclone-prone NW Pacific, and less than 10 years for an additional 14 ecoregions. We identify ecoregions likely at higher risk in future given projected changes in cyclone activity. Robust quantification of the spatial distribution of likely cyclone wave damage is vital not only for understanding past coral response to pressures, but also for predicting how this may change as the climate continues to warm and the relative frequency of the strongest cyclones rises.

Introduction

Coral reef communities around the world are under increasing threat from a range of stressors, with up to one-third of species estimated to be at risk of extinction (Carpenter et al. 2008). Many studies have shown that the incidence of stressors of various types vary spatially across the world's coral reefs (e.g., thermal stress – Hooidonk et al. 2013; coral disease - Maynard et al. 2015; tropical cyclones – Carrigan and Puotinen 2011; human activities – Halpern et al. 2008). Further studies have shown that spatial variation in stressor exposure can inform where to focus management efforts to conserve reefs by focusing conservation effort at reefs least likely to be disturbed frequently (e.g., Game et al. 2008, Beyer et al. 2018, Darling et al. 2019). Tropical cyclones (hurricanes, typhoons) can be a major factor degrading ecological condition of reefs (Great Barrier Reef - De'ath et al. 2012; Caribbean - Gardner et al. 2005; Western Australia - Zinke et al. 2018). However, it is the combination of cyclones with rising exposure to other stressors – most notably thermal stress (Hughes et al. 2017, Hughes et al. 2018) - that is the most significant emerging threat to reefs globally. Unravelling these relative contributions in a way that offers solutions for management can be difficult (Cote et al. 2016). Nonetheless, knowledge of where and how often cyclones damage coral communities on reefs has been vital for understanding past patterns of coral response to pressures (GBR – De'ath et al. 2012, Mellin et al. 2019, Ceccarelli et al., 2019; Western Australia – Zinke et al. 2018, Gilmour et al. 2019; Indo-Pacific – Darling et al. 2019), and can be used to estimate reef resilience into the future.

Extended periods of elevated wave energy and breaking waves generated by tropical cyclones can physically damage coral communities, ranging in severity from broken coral tips to removal of entire sections of the reef structure. Such damage has been widely documented in field surveys (Guam – Ogg & Koslow 1978; Jamaica – Woodley et al. 1981; French Polynesia- Harmelin-Vivien & Laboute 1986; US Virgin Islands – Rogers et al. 1989; Great Barrier Reef (GBR) – Done 1992; Hawaii – Dollar & Tribble 1993; Mexico – Lirman et al. 2001; Netherlands Antilles – Bries et al. 2004; Florida Keys – Gleason et al. 2007). Coral vulnerability to wave damage depends on coral size and growth form, which are highly variable at very local scales (Madin & Connelly 2006). Exposure of corals to damaging waves also depends on their position on a reef, relative to the incoming wave direction and other reefs and islands (Young & Hardy 1993). The resulting patchiness in damage occurs even from strong cyclones (Caribbean –Woodley et al. 1981, GBR – Fabricius et al. 2008, Beeden et al. 2015, NW Pacific – Reyes et al. 2015). Remnant coral populations can provide a key source of local recruitment to stimulate recovery after a cyclone, and many reefs have recovered quickly (southern GBR - Halford et al. 2004; central GBR – Lukoschek et al., 2013, Beeden et al., 2015; Scott Reef, Western Australia – Gilmour et al., 2019). However, a return to the former coral cover does not guarantee recovery of the prior composition of coral and fish communities (Bellwood et al. 2012). This is particularly likely if the structural complexity of the reef remains low even as coral cover increases (Emslie et al. 2014). Further, the combination of repeated impacts from subsequent cyclones and/or other pressures can reduce the structural complexity of a reef to such a low level that the community can no longer be thought of as hard coral dominated. If a loss of hard coral dominance is permanent, the change to the community is termed a phase shift, with associated changes in fish and other organisms from those that are known to inhabit hard coral dominated reefs (Cheal et al. 2010, Mumby et al. 2014). Hard corals are often replaced by macro-algae on degraded reefs (e.g., Caribbean - Hughes 1994; GBR - Done et al. 2007, Diaz-Pulido et al. 2009), but they can also be dominated by other biota like soft corals (Fine et al. 2019) or sponges (Norstrom et al. 2009). Thus, a consequence of hard coral losses from multiple impacts over time is reduced reef resilience (Hughes et al. 2003), particularly if coral cover drops below a threshold level needed to sustain a reef as hard coral dominated (Perry et al. 2013).

At regional scales, the effect of any one cyclone on coral reef communities depends on its strength (measured as maximum wind speed in m/s), duration (hours for which extreme conditions persist near reefs), spatial extent (size, measured as distance from the track to where wind speed drops to gale force – 17 m/s), and translation speed (speed of forward motion of the cyclone, measured in m/s). The likelihood of severe damage is maximised when a cyclone is strong (maximum wind speeds >= 33 m/s), long lasting (gale force winds persist long enough near reefs to build seas capable of causing severe damage to most communities– for at least 12 hours), big (size >= 300 km) and tracks slowly (translation speed <= 5 m/s) past many reefs.

However, the importance of cyclone size to its destructive potential is rarely incorporated into models of cyclone damage risk to coral reefs, which often assume that the key determinant of such risk is cyclone strength (e.g., Cheal et al. 2018) and that severe damage from any strong cyclone is limited to within ~100 km of the track (Manzello et al. 2007, Wolff et al. 2016) or less (i.e., Done 1992, Gardener et al. 2005, Edwards et al. 2011). This approximation is based on early cyclone damage field surveys (e.g. Woodley et al. 1981, Done 1992). It can be a reasonable assumption for strong, medium-sized cyclones, but not for strong cyclones that are either small or big, and/or very fast or very slow moving (Puotinen et al. 2016), for which size and speed can have a major impact on the magnitude and spatial extent of the damaging waves that are generated (Drost et al. 2017). Importantly, strong cyclones range dramatically in size (Chavas et al. 2015) from <100 km (cyclone Tracy – northern Australia) to over 2200 km (Typhoon Tip, NW Pacific) (Knaff et al. 2014), and move at a range of speeds. This variability makes generalisations on expected damage to reefs based on intensity alone problematic. Further, the size, strength and translation speed of a given cyclone can vary considerably along its track. These issues can be avoided by reconstructing the spatial distribution of cyclone –generated winds and waves with models using publicly available meteorological data recorded for cyclones (see methods).

Typically, cyclone wind speeds decrease exponentially with distance away from a peak close to the boundary of the calm region at the centre of the cyclone (Wang et al. 2011). Thus, wind speeds often decrease to below gale force within ~50 km of the centre for small and ~100 km for medium sized (Fig. 1) cyclones.

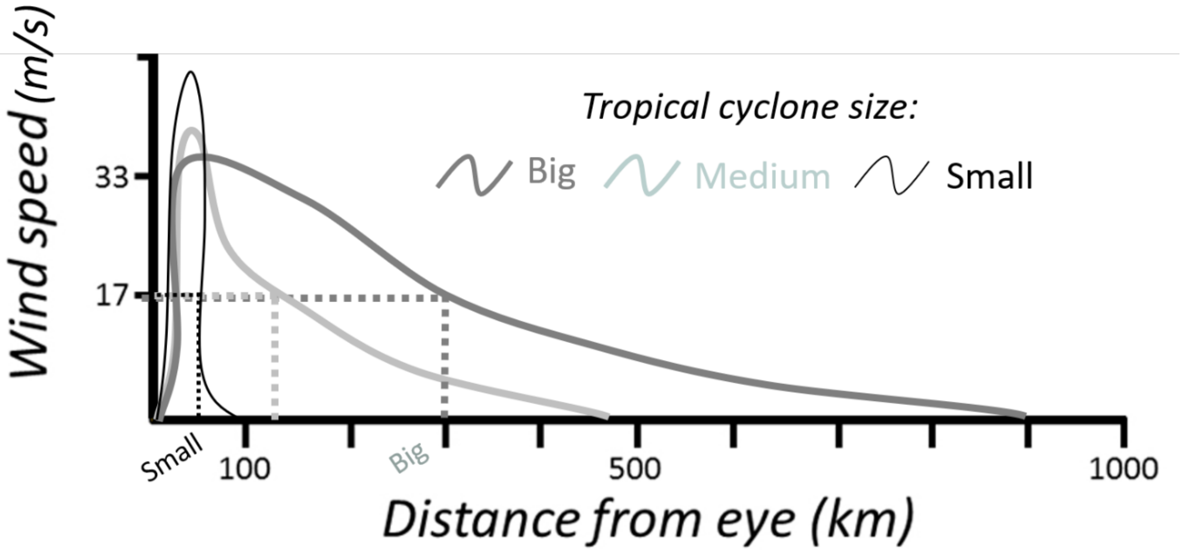


Fig. 1. Schematic diagram showing a typical distance from the cyclone centre over which maximum sustained wind speed declines to gale force for tropical cyclones that are small, medium and big in size. Winds speeds of 17 m s^{-1} and 33 m s^{-1} are gale force and hurricane force, respectively. For small cyclones, wind speeds decline to gale force over much shorter distances than for medium cyclones (within 50 versus 150 km), whereas a similar decline occurs over much larger distances for big cyclones.

Wave generation is driven by a combination of wind speed, duration and the area of water over which winds blow uninterrupted (fetch - Young 2003). Consequently, even the strongest cyclones with the highest wind speeds may cause little damage to coral reefs if the cyclones are small in size. This effect is amplified when small cyclones also move very quickly (i.e. category 5 hurricane Andrew, Caribbean – Flora et al. 1994; category 5 cyclone Larry, GBR – Puotinen et al. 2016). In contrast, big and strong cyclones can damage reefs over a larger area because strong winds extend much further from the cyclone track (Young

2003) (Fig. 1-C), generating rough seas over a greater area (i.e Drost et al. 2017). Also critical is the duration of high winds in a given location, as the time required to transform wind energy into wave energy increases as the wind speed drops. Finally, wave formation from a given wind speed is influenced by where the cyclone tracks and is most likely to reach its full potential when cyclones move slowly over deep water (Drost et al. 2017). Thus, a big and strong cyclone can result in damage to coral reefs across vast areas (i.e., cyclone Yasi - Beeden et al. 2015).

In 2012, cyclone Lua provided a unique opportunity to test the effects of big and strong cyclones on emergent coral reefs and submerged shoals on Australia's northwest shelf. Lua was a strong and big cyclone that moved very slowly over the open ocean across the continental shelf. Here, we use numerical wave modelling and field data of changes to coral communities, surveyed before and after Lua, to test whether the 100 km distance threshold commonly used to define the spatial extent of cyclone damage is appropriate. We test our results against published accounts of other strong cyclones where comprehensive field data exists from around the world. We then calculate the return interval (number of years) of big and strong cyclones, big cyclones of any strength, and strong cyclones of any size, for 150 coral ecoregions (Veron et al. 2016) using a global dataset of past cyclones (Knapp et al. 2010) from 1985 to 2015. Finally, we discuss our findings within the context of how ignoring size when assessing cyclone risk poses a threat to the way in which we adaptively manage the world's coral reef ecosystems now and under future climates.

Methods and materials

Benthic field surveys

Benthic field data was collected by the Australian Institute of Marine Science (AIMS) at Scott Reef (Fig. 2-A) and Barracouta East, Vulcan and Goeree Shoals (the shoals – Fig. 2-B) before (Scott Reef – Oct 2010, the shoals – 2011) and after (Scott Reef – Oct 2012, the shoals – 2013) Lua tracked through Australia's northwest shelf region in March 2012 (Fig. 2). Scott Reef was surveyed using on SCUBA along permanent transects in October 2010 and October 2012 at four locations: SL3, SL4, SL1, and SS1 (Fig. 3). Changes in percentage cover following cyclones depend on community composition. For a given wave energy, communities dominated by fragile corals will have larger reductions in cover than those dominated by robust corals. Similarly, for a given coral group, the relative reduction in cover following disturbances will be inaccurate if the group is rare (<5% cover). To account for these biases, we compare wave damage among communities at Scott Reef by focusing on two common (>10% cover) coral groups with contrasting susceptibilities (Supplementary Material); *Acropora* have a branching growth form and are among the most susceptible to wave damage whereas the massive *Porites* are among the most robust corals (e.g. Madin and Connelly 2006). Images were analysed using point sampling technique and benthic groups identified to the lowest taxonomic resolution achievable by each observer (Jonker et al. 2008).

East Barracouta, Vulcan and Goeree shoals were surveyed in 2011 and 2013 using a combination of towed video (Heyward et al. 2010) and still camera transects at depths from 20 to 60 m (Heyward et al. 2013). Images were also analysed using point sampling technique and benthic groups identified to the lowest taxonomic resolution achievable by each observer (Jonker et al. 2008). The resulting data was then aggregated to estimate the percentage cover of: hard corals, massive corals (including but not limited to *Porites spp*), and *Acropora spp* (branching corals) corals for each shoal as a whole. As at Scott Reef, these coral groups were chosen because they were abundant and had contrasting susceptibilities to wave damage.

Cyclone Lua numerical modelling

As per Drost et al. 2017, data from the Australian Bureau of Meteorology were used to drive a parametric tropical cyclone wind model (McConochie et al. 2004) to evaluate the tropical cyclone wind field during Lua (every 15 minutes from UTC 13 March 2012 0000 to 20 March 2012 0000). Modelled wind speeds were blended with synoptic regional-scale wind data from the Climate Forecast System Reanalysis (CSFR – Wang et al. 2011) provided by the National Center for Environmental Prediction (NCEP) every hour to embed the cyclone vortex within its regional context.

The modelled wind speeds and directions were used to force the SWAN numerical wave model (Simulating Waves Nearshore - Booij et al. 1997) to evaluate the evolution of the surface wave fields across north-western Australia during Lua. See the Supplementary material for further detail. Hourly time series of characteristic wave parameters (H_s, T_p, wave direction) were extracted from the SWAN data for the nearest location in deep water (~200 m depth) west of the field survey locations (Scott Reef; Barracouta East, Vulcan and

Goeree shoals). Significant wave height (H_S) is the mean wave height of the one-third highest waves, and often used as an indicator of sea state (Denny 1988). Wave period (T_p) is the time taken in seconds for a single wave to travel a distance equal to the length of the wave and is useful for distinguishing between locally generated wind-driven sea (T_p <10 s) and swell (T_p <= 10 s). We also compared the magnitude and duration of waves approaching Scott Reef and the shoals to other high energy events over the time period between biological surveys (Scott Reef – 18 Oct 2010 to 1 Nov 2012; the Shoals – 10 Apr 2011 to 17 Apr 2013) using NOAA WaveWatch III global hindcast (spatial resolution - 0.5°, temporal resolution - 3 hours; (Tolman 2009) downloaded at: http://polar.ncep.noaa.gov/waves/index2.shtml).

Waves transform in shallow waters through wave breaking, refraction and diffraction as they interact with the reef bathymetry. Considerable wave energy can dissipate at the leading edge of a reef with respect to incoming waves, creating a wave shadow on the lee side of a reef (Young & Hardy 1993, Madin & Connelly 2006). Thus, the shallow water transformation of cyclone waves approaching Scott Reef was modelled to obtain more realistic estimates of the finer-scale spatial variability in wave heights as indicated by H_s to explain differences in observed damage between the sites. To model this fine-scale wave variability within and adjacent to Scott Reef (Fig. 3), a second SWAN wave model was used with a 50 m grid resolution, based on bathymetry derived from a merged multibeam and LIDAR bathymetry product, as described in the supplementary material. This high-resolution SWAN model was forced at its open boundaries using output (H_s, T_p, wave direction) from the regional SWAN, and simulated the wave conditions for a day centred on peak wave event on 16 March.

We did not model wave transformation across the shoals for two reasons. First, we estimated coral cover for each shoal as a whole instead of at each of a series of sites. Second, wave transformation over the shoals was likely negligible given their submergence in depths ranging from 20 to 80 m.

Interpreting likely exposure to damaging seas

The wave height of a given sea state is characterised based on H_S using the internationally recognised Douglas Sea Scale, ranging from calm (degree 0, Hs = 0 m) to phenomenal (degree 9, Hs = 14+ m). On this scale, sea conditions are termed 'very rough' when H_S = 4m. A 'very rough' sea state is at least one-third more energetic than calm conditions and has been shown to move entire reef blocks onto the reef flat (Goto et al. 2009). Thus, we use H_S = 4m as the threshold to define the spatial boundary of the cyclone footprint. See Supplementary material for more detail.

Global implications of big and strong cyclones for coral reefs

We consider a cyclone to be big when the distance from the calm centre to winds of gale force (17 m/s - radius to gales) is 300 km or more (see supplementary material). The radius to gales of a cyclone is commonly recorded in freely available global databases like Knapp et al. (2010). We rate a cyclone as strong when its maximum sustained wind speed is 33 m s^{-1}

or greater- this equates to a ‘severe tropical cyclone’ on the Australian cyclone ranking scheme or ‘H1’ or above on the Saffir-Simpson scale (Table S1).

To approximate how frequently coral reefs around the world have been exposed to big and strong cyclones and to assess how this varies at a regional scale, we mapped six-hourly positions of all cyclones that tracked within 30°N and 30°S over the period 1985-2015 (see Supplementary material). We calculated the number of years expected between subsequent occurrences (return intervals) of cyclones within each of the world’s 150 ecoregions where corals and coral reefs are known to exist, as provided by Veron et al. (2016) and described in Veron et al. (2015). Within a given ecoregion and its reefs, damage from any given cyclone will be patchy due to local scale factors, so this represents damage potential only. We used the 500 m scale United Nations Environment Program mapping of global coral reefs (UNEP 2010) to calculate the % of global coral reef area found in each ecoregion. To put the frequency of big and strong cyclones into context, we repeated the analyses for: i) all strong cyclones of all sizes and for ii) big cyclones of all intensities.

We define exposure for an ecoregion as being crossed by a cyclone every 5 years or less as ‘very frequent’, and every 10 years or less as ‘frequent’, to reflect typical periods required for full recovery of coral communities from cyclone damage (see Supplementary material, Figure 4 in Puotinen et al. 2016). We further define exposure to cyclones as ‘occasional’ when return intervals are more than 10 and less than 35 years, and as ‘very rare’ when return intervals are 35 years or more or cannot be calculated because no such cyclones occurred over the recent past (1985-2016).

We then use the available literature to assess how current cyclone return times at ecoregions may change under future climates given what is known from global climate models.

Results

Exposure of Australia's north-west shelf to damaging waves from cyclone Lua

Lua tracked across Australia's North West Shelf from 13-19 March 2012 and reached peak strength (maximum 10-minute sustained wind speeds 47 m s^{-1}) while it was big (radius to gale force winds up to 333 km: bold black circles on Fig. 2) and located over deep water. Initially, Lua moved very slowly, but then picked up speed once it intensified. Consequently, a substantial area of extreme winds persisted for nearly a day (17 hours) with virtually unlimited fetch over deep water to the left of the track. This led to the development of a vast area of damaging local wind-sea conditions extending nearly 1,000 km from the storm centre (Fig 2), and swells propagating ahead of Lua which only decayed very slowly (Drost et al. 2017, see Fig S4 for how this progressed over time). The spatial extent of damaging seas (Hs >= 4m) predicted by the numerical model corresponds reasonably well to that predicted using the simpler 4MW model described in Puotinen et al. (2016). However, 4MW underpredicted heavy seas located to the far north-east of the study area likely because it neglects the possibility of swell.

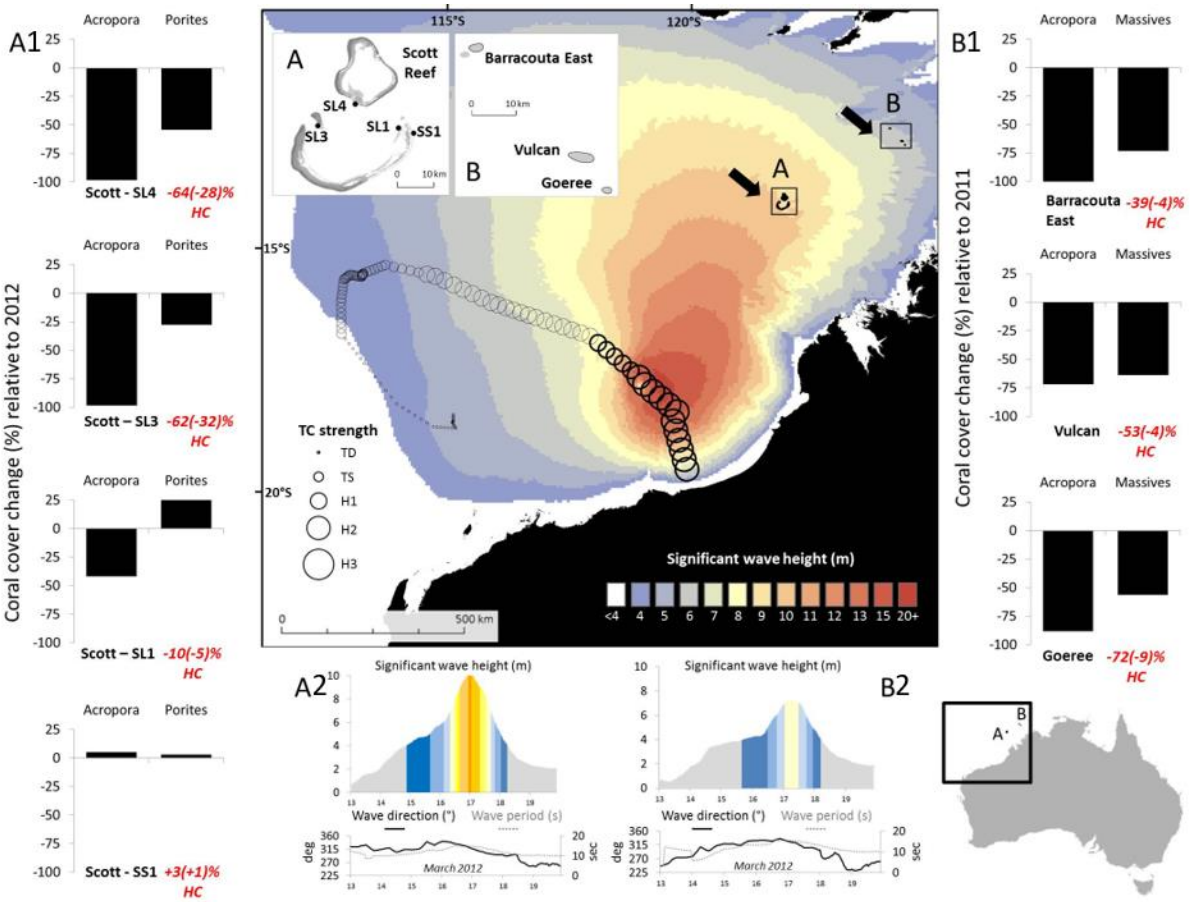


Fig. 2. Extreme conditions generated by big and strong cyclone Lua in March 2012 and their impacts on coral communities along Australia's north-west shelf. The main map shows the maximum significant wave height (Hs) generated by Lua of ≥4m as modelled by SWAN. The black unfilled circles show one-hourly positions of Lua's eye, with the circle width indicating intensity on the Saffir-Simpson scale. Circles are outlined in bold for eye positions with a larger than typical size (radius to gale force winds ≥ 300 km). Black boxes on the map indicate the location of study sites at: A – Scott Reef and B – Barracoutta East, Vulcan and Goeree shoals (the shoals). Bold arrows show the dominant incoming wave direction at the time when sea state was sufficiently energetic to severely damage corals (H_S ≥4 m). Graphs to the left of the main map (A1 – Scott Reef) and to the right of the main map (B1 – the shoals) show the relative change in cover following Lua) for hard corals typically vulnerable

to wave energy (*Acropora*) versus those typically resistant to wave energy (A1 – massive Porites, B1 – all massive corals). The relative change in total coral cover following Lua is shown in red, with the absolute change in brackets. See Fig S2 for more detail. Plots below the main map show hourly values for Hs (top) and wave direction / period (bottom) from 13-19 March 2012 for: A2 – Scott Reef and B2 – the shoals.

We observed severe damage at study sites at Scott Reef (Fig 2A1) and the shoals (Fig 2B1), 500km and 800km away from the closest position of Lua's track (Table S2, S3). Our reconstructed wave data show that Lua generated sufficiently prolonged and energetic wave action to severely damage the study sites ($H_s \geq 4$m). Damaging waves persisted for ~2.5 days at the shoals (Fig. 2-B2, bottom) and for 3.5 days at Scott Reef (Fig. 2-A2, bottom), where H_s exceeded 8 m for one-third of that time.

Field data before and after Lua demonstrates large reductions in hard coral cover. At Scott Reef (Fig. 2-A1, Fig. S2-A, Fig. S4-A, Table S2), hard coral cover was dramatically reduced at the most exposed westerly sites (SL3- 62% to 32%; SL4 – 64% to 28%), with smaller reductions (10% to 5%) in cover of the more fragile corals (*Acropora spp.)* at the less exposed (SL1) site, contrasting with the small increase (41.5% to 42.0%) at the most sheltered site (SS1) on the leeward side of south Scott Reef. At the most exposed sites, coral cover dropped by nearly 100% for *Acropora* colonies (SL4, 3.7% to 0.07%; SL3,12.6% to 0.2%; Fig. S2-B, Table S2), and dropped by up to 50% for massive *Porites* colonies (SL4, 11.7% to 6.5%; Fig. S2-C, Table S2). Similarly, at the submerged shoals (Fig. 2-B1, Table S3), there were considerable losses of hard coral cover in depths of ~18m (Barracouta East: 11.3% to 6.9%), ~20m (Vulcan: 7.7% to 3.6%) and ~25m (Goeree: 12.7% to 3.5%). At

Barracouta East, all (100%) of *Acropora spp.* colonies were lost (12.8% to 0%), while most were lost at Vulcan (9.9% to 2.2%) and Goeree (39.7% to 5.9%). Robust massive corals were initially more abundant than Acropora corals at all three shoals, and their cover dropped considerably (Barracouta East, 25.3% to 6.8%; Vulcan, 28.6% to 10.4%; Goeree, 11.4% to 5%).

Despite the vast extent of Lua's predicted zone of damaging waves (Fig. 2) and the magnitude and duration of the waves that were generated, some corals at Scott Reef remained undamaged due to local sheltering by the reef (site SS1, Scott Reef – Fig. 2-A1, Fig. S1-A, Table S2). We provide a physical basis for this expected patchiness by demonstrating, with high resolution modelling of wave transformation across Scott Reef, that wave heights dropped dramatically as waves encountered the shallow reef topography (Fig. 3). H_s was estimated to exceed 10 m west of Scott Reef, but quickly dropped (Fig. 3-A) as wave energy almost completely dissipated with transit through shallow reef areas (Fig. 3-B). This created a gradient of decreasing wave exposure that matches the observed variation in hard coral cover loss (Fig. S1, Table S2).

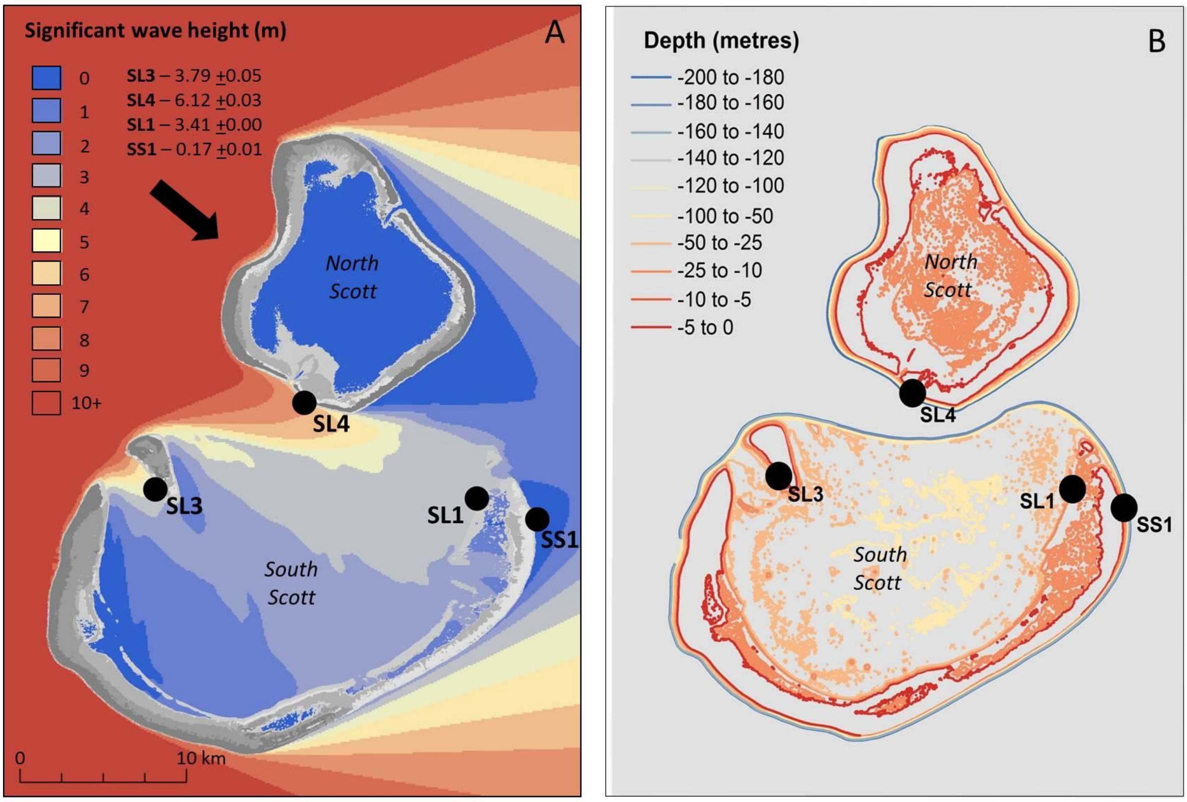


Fig. 3. Transformation of wave energy across Scott Reef from north-west to south-east at UTC 16 March 2012, 2100, as modelled by SWAN (A). Colours indicate significant wave heights from near 0 (dark blue) to 10+ m (red). The large arrow shows the incoming peak wave direction (315 degrees, north-west) during the time of maximum wave conditions. The hard-line reef crest is shaded dark grey. Depth contours (B) are shown by coloured lines, ranging from the deepest in darkest blue (-200 to -180 metres) to the shallowest in red (-5 to 0 metres).

Global implications for coral reefs

Our global analysis shows that cyclones regularly track near most of the world’s coral reefs, except reefs in the equatorial belt (8 degrees N or S latitude) and the South Atlantic Ocean (Fig. 4-A). Indeed, 71% of the world’s total reef area is located within ecoregions that are at least occasionally (every 10 to 31.5 years) crossed by strong cyclones, 56% by big cyclones, and 54% by big and strong cyclones (non-blue colours in Fig. 5-A, 5-B, 5-C). The wave conditions experienced by any particular reef within cyclone-exposed ecoregions depends on local scale factors, including fetch generation time, fetch distance and bathymetry. The degree of exposure of any given coral colony to those waves depends on reef geomorphology, shelf position and depth (see Fig S1). Of the world’s 150 ecoregions, those of the NW Pacific are currently the most frequently exposed to cyclones (grey dots - Fig. 4-A, Fig. 1 in Carrigan & Puotinen 2011), particularly cyclones that are big and strong (red dots - Fig. 4-A, Table 1 (Chavas et al. 2015; Knaff et al. 2014).

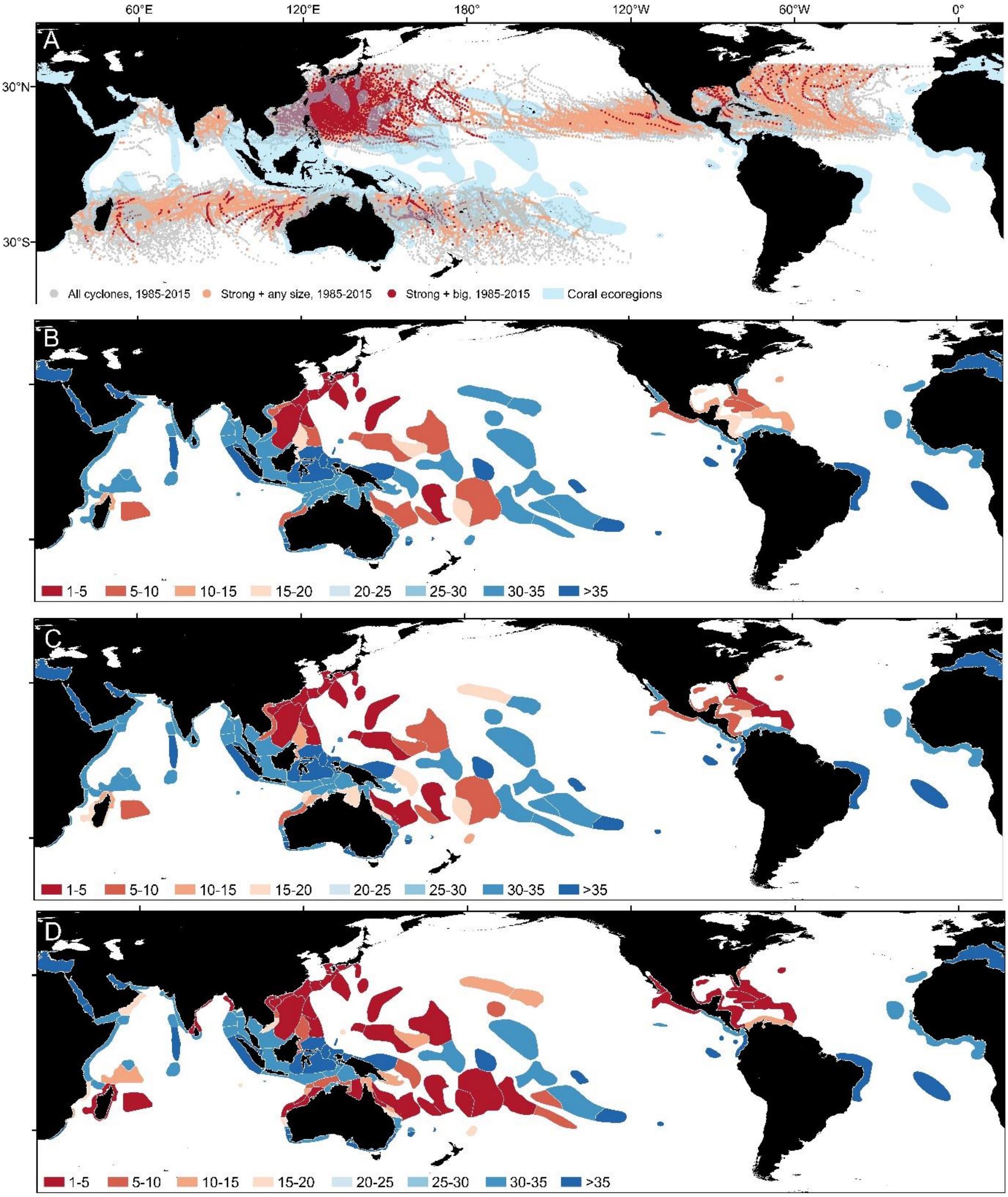


Fig. 4. Global distribution of cyclone return times (in years) within coral reef ecoregions. Panel A compares the prevalence of the 6 hourly recorded positions of all global TCs (grey dots) from 1985-2015 with TCs that are strong (maximum wind speed ≥ 33 m/s - pink dots) and those that big (radius to gales ≥300 km) + strong (red dots). Coral ecoregions are shown with transparent shading that appears blue when no cyclones are present and grey when

cyclones are present. Panels B, C and D show the expected number of years between cyclone occurrences for each ecoregion based on the time period 1985-2015, from the most frequent (1 to 5 years - darkest red) to the least frequent (more than 35 years - darkest blue) for: big and strong cyclones (B), big cyclones of any strength (C), and strong cyclones of any size (D). The total number of cyclone observations in ecoregions from 1985-2015 were: all sizes and strengths, 17,590; big and strong, 2,126; big of any strength, 3,372; strong of any size, 6,116.

Big and strong cyclones frequently (every 5 years or less) transit approximately 9% of coral ecoregions, particularly those in the north-west Pacific but also in the central south Pacific around Vanuatu (dark red areas in Fig. 4-B, Table 1, Table S4). These ecoregions encompass 8% of the world's coral reef area (Fig. 5-A).

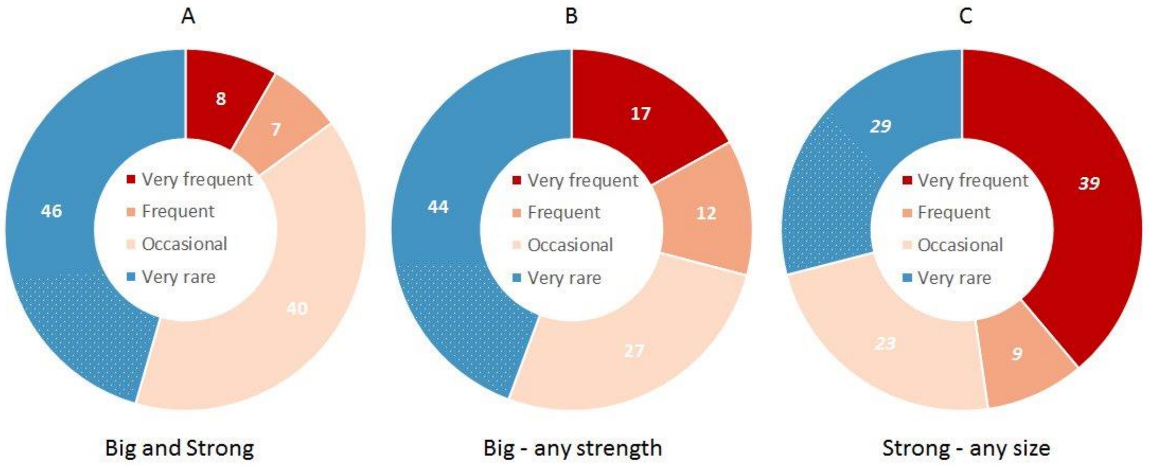


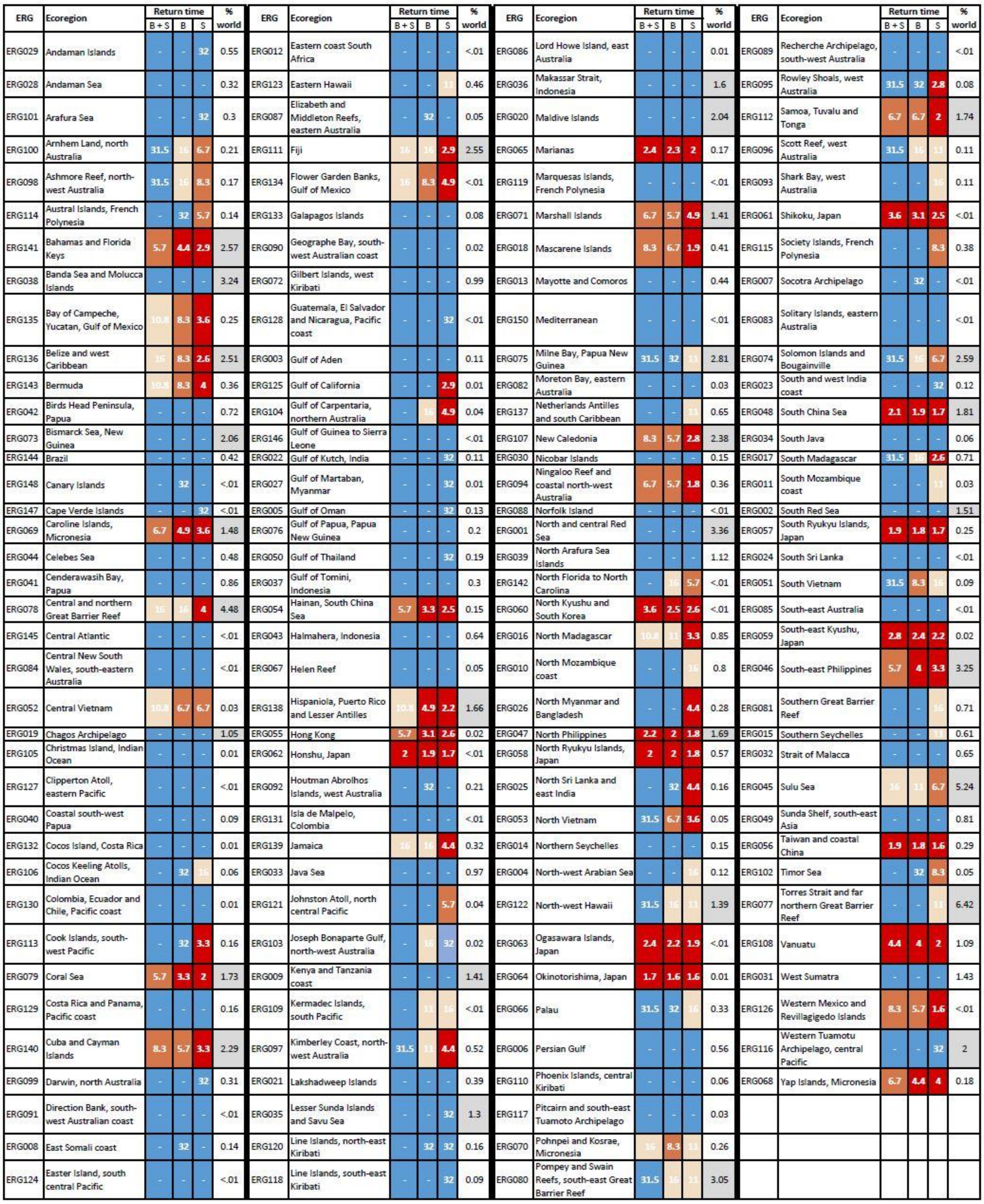
Fig. 5. Percentage of the world's coral reef area with potential exposure to cyclones that are 'very frequent' (red - <= 5 years), 'frequent' (dark orange – 5-10 years),' occasional' (light orange – 10-31.5 years) and 'very rare' (blue - >31.5 years) based on the time series 1985-2015, for cyclones that are: big and strong (A), big of any strength (B), and strong of

any size (C). Cyclones are classed as 'big' when the radius to gales >300km, and as 'strong' when maximum sustained wind speed ≥ 33 m s^{-1}. The white dotted areas within the 'very rare' (blue) segment show the % of coral reef area within 8 degrees north and south of the Equator and unlikely to experience cyclones. Note that each reef's exposure to cyclones within the ecoregion will be patchy due to local scale factors. The total number of cyclone observations in ecoregions from 1985-2015 were: all sizes and strengths – 17,590; big and strong – 2,126; big of any strength – 3,372; strong of any size – 6,116.

A further 9% of ecoregions and 7% of world reef area (Fig. 5-A) are frequently (every 5 to 10 years – dark orange areas in Fig. 4-B) crossed by big and strong cyclones, particularly the Caribbean (i.e., Bahamas and Florida Keys, Cuba and Cayman Islands), parts of the south-west Pacific (i.e., Coral Sea, New Caledonia, Samoa, Tuvalu and Tonga), parts of the north-west Pacific (Marshall Islands, Micronesia, areas adjacent to ecoregions very frequently exposed), the Mascarene Islands near Madagascar, and Ningaloo Reef in western Australia (Table 1).

Table 1. Return intervals (years) in coral ecoregions for i) big and strong cyclones (B+S), ii) all big cyclones (B), and iii) all strong cyclones (S) based on 1985-2015. For cells with a dash (-), no cyclone crossed the ecoregion from 1985-2015. A cyclone was classed as 'big' if radius to gale force winds ≥300 km, and 'strong' if maximum sustained wind speed > 33 m s^{-1}. Cells are shaded to match Figs 4 and 5, such that: dark red = very frequent (return time ≤5 years), dark orange = frequent (return time >5 and ≤ 10 years), light orange = occasional (return time >10 years and <= 31.5 years) and blue = rare (return time > 31.5 years). Grey

shading on the last column shows ecoregions where the percentage of the world's coral reef area located therein is >= 1%. Ecoregions are sorted in alphabetical order. A full sized version of this table is provided in the Supplementary Material (Table S5).



ERG	Ecoregion	Return time			% world
		B + S	B	S	
ERG029	Andaman Islands	-	-	32	0.55
ERG028	Andaman Sea	-	-	-	0.32
ERG101	Arafura Sea	-	-	32	0.3
ERG100	Arnhem Land, north Australia	31.5	16	6.7	0.21
ERG098	Ashmore Reef, north-west Australia	31.5	16	8.3	0.17
ERG114	Austral Islands, French Polynesia	-	32	5.7	0.14
ERG141	Bahamas and Florida Keys	5.7	4.4	2.9	2.57
ERG038	Banda Sea and Molucca Islands	-	-	-	3.24
ERG135	Bay of Campeche, Yucatan, Gulf of Mexico	10.8	8.3	3.6	0.25
ERG136	Belize and west Caribbean	16	8.3	2.6	2.51
ERG143	Bermuda	10.8	8.3	4	0.36
ERG042	Birds Head Peninsula, Papua	-	-	-	0.72
ERG073	Bismarck Sea, New Guinea	-	-	-	2.06
ERG144	Brazil	-	-	-	0.42
ERG148	Canary Islands	-	32	-	<.01
ERG147	Cape Verde Islands	-	-	32	<.01
ERG069	Caroline Islands, Micronesia	6.7	4.9	3.6	1.48
ERG044	Celebes Sea	-	-	-	0.48
ERG041	Cenderawasih Bay, Papua	-	-	-	0.86
ERG078	Central and northern Great Barrier Reef	16	16	4	4.48
ERG145	Central Atlantic	-	-	-	<.01
ERG084	Central New South Wales, south-eastern Australia	-	-	-	<.01
ERG052	Central Vietnam	10.8	6.7	6.7	0.03
ERG019	Chagos Archipelago	-	-	-	1.05
ERG105	Christmas Island, Indian Ocean	-	-	-	0.01
ERG127	Clipperton Atoll, eastern Pacific	-	-	-	<.01
ERG040	Coastal south-west Papua	-	-	-	0.09
ERG132	Cocos Island, Costa Rica	-	-	-	0.01
ERG106	Cocos Keeling Atolls, Indian Ocean	-	32	16	0.06
ERG130	Colombia, Ecuador and Chile, Pacific coast	-	-	-	0.01
ERG113	Cook Islands, south-west Pacific	-	32	3.3	0.16
ERG079	Coral Sea	5.7	3.3	2	1.73
ERG129	Costa Rica and Panama, Pacific coast	-	-	-	0.16
ERG140	Cuba and Cayman Islands	8.3	5.7	3.3	2.29
ERG099	Darwin, north Australia	-	-	32	0.31
ERG091	Direction Bank, south-west Australian coast	-	-	-	<.01
ERG008	East Somali coast	-	32	-	0.14
ERG124	Easter Island, south central Pacific	-	-	-	<.01
ERG012	Eastern coast South Africa	-	-	-	<.01
ERG123	Eastern Hawaii	-	-	11	0.46
ERG087	Elizabeth and Middleton Reefs, eastern Australia	-	32	-	0.05
ERG111	Fiji	16	16	2.9	2.55
ERG134	Flower Garden Banks, Gulf of Mexico	16	8.3	4.9	<.01
ERG133	Galapagos Islands	-	-	-	0.08
ERG090	Geographe Bay, south-west Australian coast	-	-	-	0.02
ERG072	Gilbert Islands, west Kiribati	-	-	-	0.99
ERG128	Guatemala, El Salvador and Nicaragua, Pacific coast	-	-	32	<.01
ERG003	Gulf of Aden	-	-	-	0.11
ERG125	Gulf of California	-	-	2.9	0.01
ERG104	Gulf of Carpentaria, northern Australia	-	16	4.9	0.04
ERG146	Gulf of Guinea to Sierra Leone	-	-	-	<.01
ERG022	Gulf of Kutch, India	-	-	32	0.11
ERG027	Gulf of Martaban, Myanmar	-	-	32	0.01
ERG005	Gulf of Oman	-	-	32	0.13
ERG076	Gulf of Papua, Papua New Guinea	-	-	-	0.2
ERG050	Gulf of Thailand	-	-	32	0.19
ERG037	Gulf of Tomini, Indonesia	-	-	-	0.3
ERG054	Hainan, South China Sea	5.7	3.3	2.5	0.15
ERG043	Halmahera, Indonesia	-	-	-	0.64
ERG067	Helen Reef	-	-	-	0.05
ERG138	Hispaniola, Puerto Rico and Lesser Antilles	10.8	4.9	2.2	1.66
ERG055	Hong Kong	5.7	3.1	2.6	0.02
ERG062	Honshu, Japan	2	1.9	1.7	<.01
ERG092	Houtman Abrolhos Islands, west Australia	-	32	-	0.21
ERG131	Isla de Malpelo, Colombia	-	-	-	<.01
ERG139	Jamaica	16	16	4.4	0.32
ERG033	Java Sea	-	-	-	0.97
ERG121	Johnston Atoll, north central Pacific	-	-	5.7	0.04
ERG103	Joseph Bonaparte Gulf, north-west Australia	-	16	32	0.02
ERG009	Kenya and Tanzania coast	-	-	-	1.41
ERG109	Kermadec Islands, south Pacific	-	11	16	<.01
ERG097	Kimberley Coast, north-west Australia	31.5	11	4.4	0.52
ERG021	Lakshadweep Islands	-	-	-	0.39
ERG035	Lesser Sunda Islands and Savu Sea	-	-	32	1.3
ERG120	Line Islands, north-east Kiribati	-	32	32	0.16
ERG118	Line Islands, south-east Kiribati	-	-	32	0.09
ERG086	Lord Howe Island, east Australia	-	-	-	0.01
ERG036	Makassar Strait, Indonesia	-	-	-	1.6
ERG020	Maldive Islands	-	-	-	2.04
ERG065	Marianas	2.4	2.3	2	0.17
ERG119	Marquesas Islands, French Polynesia	-	-	-	<.01
ERG071	Marshall Islands	6.7	5.7	4.9	1.41
ERG018	Mascarene Islands	8.3	6.7	1.9	0.41
ERG013	Mayotte and Comoros	-	-	-	0.44
ERG150	Mediterranean	-	-	-	<.01
ERG075	Milne Bay, Papua New Guinea	31.5	32	11	2.81
ERG082	Moreton Bay, eastern Australia	-	-	-	0.03
ERG137	Netherlands Antilles and south Caribbean	-	-	11	0.65
ERG107	New Caledonia	8.3	5.7	2.8	2.38
ERG030	Nicobar Islands	-	-	-	0.15
ERG094	Ningaloo Reef and coastal north-west Australia	6.7	5.7	1.8	0.36
ERG088	Norfolk Island	-	-	-	<.01
ERG001	North and central Red Sea	-	-	-	3.36
ERG039	North Arafura Sea Islands	-	-	-	1.12
ERG142	North Florida to North Carolina	-	16	5.7	<.01
ERG060	North Kyushu and South Korea	3.6	2.5	2.6	<.01
ERG016	North Madagascar	10.8	11	3.3	0.85
ERG010	North Mozambique coast	-	-	16	0.8
ERG026	North Myanmar and Bangladesh	-	-	4.4	0.28
ERG047	North Philippines	2.2	2	1.8	1.69
ERG058	North Ryukyu Islands, Japan	2	2	1.8	0.57
ERG025	North Sri Lanka and east India	-	32	4.4	0.16
ERG053	North Vietnam	31.5	6.7	3.6	0.05
ERG014	Northern Seychelles	-	-	-	0.15
ERG004	North-west Arabian Sea	-	-	16	0.12
ERG122	North-west Hawaii	31.5	16	11	1.39
ERG063	Ogasawara Islands, Japan	2.4	2.2	1.9	<.01
ERG064	Okinotorishima, Japan	1.7	1.6	1.6	0.01
ERG066	Palau	31.5	32	16	0.33
ERG006	Persian Gulf	-	-	-	0.56
ERG110	Phoenix Islands, central Kiribati	-	-	-	0.06
ERG117	Pitcairn and south-east Tuamoto Archipelago	-	-	-	0.03
ERG070	Pohnpei and Kosrae, Micronesia	16	8.3	11	0.26
ERG080	Pompey and Swain Reefs, south-east Great Barrier Reef	31.5	16	11	3.05
ERG089	Recherche Archipelago, south-west Australia	-	-	-	<.01
ERG095	Rowley Shoals, west Australia	31.5	32	2.8	0.08
ERG112	Samoa, Tuvalu and Tonga	6.7	6.7	2	1.74
ERG096	Scott Reef, west Australia	31.5	16	11	0.11
ERG093	Shark Bay, west Australia	-	-	16	0.11
ERG061	Shikoku, Japan	3.6	3.1	2.5	<.01
ERG115	Society Islands, French Polynesia	-	-	8.3	0.38
ERG007	Socotra Archipelago	-	32	-	<.01
ERG083	Solitary Islands, eastern Australia	-	-	-	<.01
ERG074	Solomon Islands and Bougainville	31.5	16	6.7	2.59
ERG023	South and west India coast	-	-	32	0.12
ERG048	South China Sea	2.1	1.9	1.7	1.81
ERG034	South Java	-	-	-	0.06
ERG017	South Madagascar	31.5	16	2.6	0.71
ERG011	South Mozambique coast	-	-	11	0.03
ERG002	South Red Sea	-	-	-	1.51
ERG057	South Ryukyu Islands, Japan	1.9	1.8	1.7	0.25
ERG024	South Sri Lanka	-	-	-	<.01
ERG051	South Vietnam	31.5	8.3	16	0.09
ERG085	South-east Australia	-	-	-	<.01
ERG059	South-east Kyushu, Japan	2.8	2.4	2.2	0.02
ERG046	South-east Philippines	5.7	4	3.3	3.25
ERG081	Southern Great Barrier Reef	-	-	16	0.71
ERG015	Southern Seychelles	-	-	11	0.61
ERG032	Strait of Malacca	-	-	-	0.65
ERG045	Sulu Sea	16	11	6.7	5.24
ERG049	Sunda Shelf, south-east Asia	-	-	-	0.81
ERG056	Taiwan and coastal China	1.9	1.8	1.6	0.29
ERG102	Timor Sea	-	32	8.3	0.05
ERG077	Torres Strait and far northern Great Barrier Reef	-	-	11	6.42
ERG108	Vanuatu	4.4	4	2	1.09
ERG031	West Sumatra	-	-	-	1.43
ERG126	Western Mexico and Revillagigedo Islands	8.3	5.7	1.6	<.01
ERG116	Western Tuamotu Archipelago, central Pacific	-	-	32	2
ERG068	Yap Islands, Micronesia	6.7	4.4	4	0.18

Of the ecoregions that are rarely (return time > 31.5 years) crossed by big and strong cyclones (Figs. 4-A; 5-A), ten are frequently (return time 5-10 years) or very frequently (return time $\leq$ 5 years) crossed by strong cyclones of any size (Figs. 4-B; 5-B). This means their likelihood of being crossed by big and strong cyclones will rise if big cyclones become more prevalent near them in future. These include many of the ecoregions in north and north-west tropical Australia (1.43% of world coral reef area: Ningaloo Reef; Rowley Shoals; Kimberley coast; Ashmore Reef; Arnhem Land; Timor Sea; Gulf of Carpentaria) and near Madagascar (1.97% of world coral reef area: North Madagascar; South Madagascar; Mascarene Islands – Table 1). Conversely, ecoregions where big cyclones currently occur frequently (return time 5-10 years), but strong cyclones occur only occasionally (return time 10-31.5 years), may be crossed by more big and strong cyclones in the future as the relative proportion of cyclones that are strong rises. These areas include: South Vietnam; Pohnpei and Kosrae, Micronesia; and to a lesser degree the Joseph Bonaparte Gulf near north-west Australia (Table 1).

Discussion

Our models show that peak significant wave heights during cyclone Lua reached 12 and 10 standard deviations above the mean between field surveys at Scott Reef and the shoals, respectively (Fig. S3). Accordingly, coral losses at the most exposed sites at Scott Reef when Lua was over 500 km away (Fig. 2-A) were worse than those caused by the devastating 1998 mass bleaching event that reduced mean (± SE) hard coral cover across the reef system from 47.6% (± 4.3) to 9.9% (± 2.2) (Gilmour et al. 2013). Comparing this to published data from field surveys of the GBR, we find that severe damage from Lua extended 20 times further than it did for strong cyclones Larry (2006), Ingrid (2014, Fabricius et al. 2008) and Ita (2015) – all of which were stronger at peak intensity than Lua but much smaller in size (Puotinen et al. 2016). For small strong cyclones, a 100 km threshold would overestimate the spatial extent of severe damage by up to 50% (severe damage was limited to within about 50-60 km of the track). A cyclone's size is thus as important to its potential destructiveness as its strength, a fact long recognised by meteorologists (Powell and Reinhold 2007, Knaff et al. 2014, Holland et al. 2019). Also important is how fast a cyclone moves. Yasi, one of the most powerful cyclones affecting north-east Australia since records began, was similar in size to Lua and reached a peak strength that was higher than Lua by almost 10 m/s. Yet Yasi generated severe damage over an area (Beeden et al. 2015) that was only 30% as extensive as Lua (Fig. 2). The key difference was in how quickly the cyclones moved when at peak size and peak intensity. Lua moved very slowly over relatively deep water when at peak intensity and peak size before accelerating towards the coast (Drost et al. 2017). In contrast, Yasi reached peak intensity and peak size when moving relatively quickly over the shallow waters of the GBR Lagoon (Beeden et al. 2015). Through these comparisons, we show that assuming severe coral damage for all strong cyclones occurs within a 100 km distance threshold can both underestimate (for strong and big cyclones) and overestimate (for strong and small cyclones) the extent of damage. Using a 100km damage threshold for strong cyclones from 1985-2015 on a global basis would thus underestimate the extent of damage 35% of the time (when cyclones were strong and big) and overestimate damage 29% of the time (when cyclones were strong and small). Put simply, using a 100km distance threshold for coral damage would be on target for only 36%

of strong cyclone positions from 1985-2015. Underestimating the effects of cyclones can have important consequences for modelling long term trends in coral reef ecosystems even for ecoregions where big and strong cyclones occur only occasionally, such as the Central and northern Great Barrier Reef. For example, the combined effect of strong cyclone Hamish (2009) and big and strong cyclone Yasi (2011) contributed significantly to a 50% decline in coral cover (De'ath et al. 2012) in the ecoregion, despite big and strong cyclones expected to revisit the area only occasionally (every 16 years – Table 1).

The diversity of coral species varies considerably across the globe, with the highest global diversity in the Indo-Pacific region termed the 'Coral Triangle', followed by the Red Sea and northern Madagascar (Veron et al. 2015). Pressures also vary spatially across the world's coral reefs, which can inform where to focus management efforts to conserve reefs (e.g. Game et al. 2008, Beyer et al. 2018, Darling et al. 2019). For example, coral reefs in the southern GBR, parts of Sulawesi, Indonesia, Papua New Guinea and Cuba have been identified as 'temporary refugia' from thermal stress based on models of future thermal stress (van Hooidonk et al. 2015, 2016). Within these potential refugia from heat stress, reefs frequently exposed to cyclones may be less beneficial as refugia – such as the Cuba and Cayman Islands ecoregion that is exposed to strong cyclones every 3.3 years and big and strong cyclones every 8.3 years, and where reefs have a lower species diversity (Veron et al. 2015). In contrast, the Southern Great Barrier Reef ecoregion is currently only intermittently exposed to strong cyclones and has not experienced a big cyclone since 1985 (Fig. 4, Table 1). Further, much of Indonesia and Papua New Guinea are rarely exposed to cyclones (Fig. 4, Table 1), and also host high global diversity (Veron et al. 2015). The value of analyses that map the spatial and temporal distribution of pressures to inform conservation depends on the robustness of the estimates. Our study shows that for cyclones, inferring impacts requires quantification of how strength and size vary along their track, via numerical modelling (e.g. Drost et al. 2017) or empirical methods (e.g. Puotinen et al. 2016). While numerical modelling is often not feasible due to lack of requisite data and computational load, empirical methods are already widely used by risk analysts around the world (Peduzzi et al. 2012). Applying simple distance thresholds alone, even when considering cyclone strength (Puotinen 2004, Edwards et al. 2011, Ban et al. 2015), would underestimate the spatial extent of damage for over one-third of the relevant strong cyclones at the global scale. Spatial datasets of the likelihood of damaging waves generated by reconstructing past cyclone winds and waves have already been used to develop a more rigorous understanding of coral response to disturbance regimes (Western Australia - Gilmour et al. 2018; Great Barrier Reef - Puotinen et al. 2016, Mellin et al. 2018, Ceccarelli et al. 2019, Vercelloni et al. 2020). This regional assessment of the likelihood of damaging waves from past cyclones should be extended to include the rest of world’s reefs where cyclones regularly occur.

Future return times of big and strong cyclones within a given ecoregion depends on how the spatial positioning of cyclone tracks (and how the strength and size and translation speed of each cyclone varies along its track) shifts as the climate warms. Many studies have used global climate models to simulate how cyclone activity, particularly intensity, will change. Despite continuing uncertainty, there is general agreement that a greater proportion of the cyclones that form in future will be strong (Knutson et al. 2010, Walsh et al. 2016, Camargo and Wing 2016, Bacmeister et al. 2018). The overall numbers may not change (Walsh et al. 2015, Camargo and Wing 2016 – but noting Bhatia et al. 2018) because the frequency of cyclones of all intensities may stay the same or drop, as an increase in inhibiting factors such as wind shear make it harder for cyclones to form (Kang & Elser 2015). Little work has been done to predict how cyclone size may change in future climates, though Chavas et al. (2015) suggest a link between cyclone size and higher relative Sea Surface Temperatures (SST) which may lead to simulations of cyclone sizes under warming scenarios using downscaled SST data. Indeed, recent reviews call for more work in this area (Walsh et al. 2016, Parker et al. 2018). Nonetheless, even if big cyclones do not become more prevalent in future, the chance of a cyclone being both big and strong at the same time should rise because a greater proportion of cyclones will be strong.

Knowing which reefs are increasingly impacted by cyclone disturbances is vitally important for developing conservation strategies, yet even less work has been done to examine how the spatial distribution and movement of cyclones may change in future (Parker et al. 2018). Some evidence suggests that where cyclones reach their peak strength has already moved poleward (Kossin et al. 2016), ranging from 7 (± 98) km per decade in the North Atlantic basin to 67 (± 55) km per decade in the South Indian basin (Kossin et al. 2014). If this trend continues, return intervals for strong cyclones of any size may shorten in some ecoregions as cyclones become more prevalent in the higher latitudes where they are currently relatively infrequent. Some examples (Fig. 4-C) include ecoregions near southern parts of Australia (Shark Bay, West Australia; Pompey and Swain Reefs, south-east Great Barrier Reef; Southern Great Barrier Reef), near south-east Africa (South Mozambique coast; Eastern coast South Africa) and near Hawaii (North-west Hawaii; Eastern Hawaii – Table 1). Of these, the South Mozambique coast is a secondary global diversity hotspot (Veron et al. 2015). Most ecoregions where big cyclones currently cross frequently or very frequently

(Fig. 4-B) already experience the crossing of strong cyclones very frequently (Fig. 4-C, Table 1). However, for five ecoregions in the south Pacific (Joseph Bonaparte Gulf, north-west Australia; Scott Reef, West Australia; Pompey and Swain Reefs, south-east Great Barrier Reef; Kermadec Islands, South Pacific and at North-west Hawaii - Table 1), a greater incidence of strong cyclones may also increase the likelihood of big and strong cyclones (Fig. 4-B, C).

Changes in cyclone impacts within ecoregions will be superimposed on rising stress from human activities and climate change, most notably more frequent exposure to higher levels of thermal stress (Henson 2017, Hughes et al. 2017, Hoegh-Guldberg 2017). As the climate continues to warm, the occurrence of stretches of uninterrupted recovery time become shorter, as already documented for the GBR. For example, back to back mass bleaching events in 2016 and 2017 devastated large areas of the GBR (Hughes et al. 2017), which undoubtedly interrupted the recovery of corals previously affected by a spate of recent strong cyclones in the northern parts of the region (Nathan – 2015, Ita – 2014) and central (Yasi – 2011, Hamish – 2009). Clearly there is little we can do to reduce the incidence or severity of cyclones near reefs. However, understanding where and how often cyclone wave action is likely to affect the world’s coral reefs is essential to inform conservation efforts to help them survive the escalating pressures that threaten their continued existence. In this paper, we identified ecoregions potentially at greater future risk from cyclone wave damage (e.g., southern, north-west, northern Australia; Hawaii; south-east Africa) based on current return times of cyclones combined with global predictions of how the distribution and intensity of cyclones may change as the climate warms. This should be modelled in more depth by reconstructing cyclone winds and waves across coral reef regions regularly visited by cyclones using future cyclone tracks generated from a range of global climate models. The resultant estimates of future risk to reefs from damaging cyclone waves (with confidence intervals) would be a key step towards answering the 'call to action' for ecologists to develop robust methods for monitoring and modelling cyclone impacts on both land and marine based ecosystems (Pruitt et al. 2019).

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Acknowledgements:

Data presented for Western Australia includes those from the Scott Reef program supported by Woodside Energy Limited as operator for and on behalf of the Browse Joint Venture (BJV – Woodside Browse Pty Ltd, Shell Australia Pty Ltd, BP Developments Australia Pty Ltd, Japan Australia LNG (MIMI Browse) Pty Ltd and PetroChina International Investment (Australia) Pty Ltd). RJL acknowledges support from an Australian Research Council (ARC) Discovery Project grant (DP140102026) and the ARC Centre of Excellence for Coral Reef Studies (CE140100020). ED acknowledges support from the University of Western Australia postgraduate scholarships (SIRF and UIS). Surveys of the shoals were funded by PTTEP Australasia Ltd.