Coral Reefs
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RESEARCH

Comparing impacts and recovery of locally managed reefs after exposure to extreme waves from a category 5 cyclone

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Abstract As the climate warms, coral reefs face more frequent and severe impacts from thermal stress while a greater proportion of tropical cyclones are expected to reach the strongest categories. Understanding the impacts of extreme cyclone waves and reef recovery dynamics is essential to support projections of reef communities under future climate scenarios. We present an evaluation of 18 sites across two large barrier reef systems in Fiji under varying forms of local management using data collected prior, directly after, and four years following Tropical Cyclone Winston (2016), which generated extreme waves 11 standard deviations above the long-term average. Our study aimed to: (1) determine how storm wave energy links to changes in hard coral cover; (2) quantify the impact and recovery of benthic communities on reefs with different management interventions; and (3) assess fish community trajectories in relation to observed differences in benthic communities and/or management. The cyclone's impact on benthic communities was severe, with a relative loss of 54 ± 8% hard coral cover (primarily branching and plating *Acropora*) and corresponding increases in rubble and turf algae. However, hard coral recovery and reassembly by 2020 was rapid and extensive, indicating high resilience. Fish biomass was consistently high with variable effects of no-take areas, and functional groups were minimally impacted by the cyclone. No-take areas did not promote faster recovery, but all sites were removed from local impacts, known to be highly productive and exposed to strong currents that are expected to facilitate high resilience. Identifying and prioritising resilient sites for management is crucial for the future of coral reefs.

Vakasama Na dikevi ni cakau (na ka e yaco kina kei na nodra bula tale mai) e vakacacani ena cagilabana category 5 Na kena toso cake tiko na katakata ni vuravura koya vakavuna na draki veisau; e sa vakavuna na vakacacani ni veicakau ka namaki talega na kena toso cake na kaukauwa ni cagilaba. Na kena kilai vakamatata na veika ena yaco vei ira na vei tikotiko e voleka ena veicakau ena gauna ni drake veisau; ena gadrevi kina na noda kila vakamatata na ka e kauta mai na toso cake ni kaukauwa ni ua kei na sala era na vakabulabulataki ira ga vakataki ira na cakau. E rua na cakau lelevu e vakadikevi, na vakadidike oqo e tauri mai ena tinikawalu nai wasewase ni cakau ka sa vakayacori tiko kina na kena taqomaki ka maroroi na cakau ena kenai valavala ga vakaitaukei. E wase tolu na kena vakaso kumuni nai tutkutuku me baleta na cagilaba ko Winston (ena yabaki 2016), sebera na cagilaba, oti ga na cagilaba kei oti na va na yabaki ni cagilaba. Na kaukauwa kei na kena tubu cake ni ua e kauta mai na cagilaba ko Winston e se sega ni laurai vakadua ena vei cagilaba sa oti. E tolu nai naki ni vakadidike

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oqo: (1) na noda kila na ka e kauta mai na kaukauwa ni ua ka veisau kina na cakau; (2) na kena vakayagataki nai walewale ni maroroi se taqomaki ni veicakau kei na kena sema ki na nodra vakabulai tale mai na veika era bula tu ena ruku ni veicakau kei na (3) kena sema vakacava na veiwalewale ni maroroi ni cakau kei na veisau e yaco ki vei ira na ika ka ra kana mai na vei lumilumi ena veicakau. Na vakacaca e kauta mai na cagilaba ko Winston e vakamatea na veicakau me rauta e 54 ± 8% vakabibi na laselase gagata kei na laselase tateba. E toso cake talega nai wiliwili ni lase mate kei na lumilumi. Ni oti e va na yabaki na kena yaco na cagilaba e kunei ni totolo sara na kena bula tale mai na lase kei na kena tete. Qo e vakaraitaka na kaukauwa ni nodra rawa ni bula tale mai na cakau ni ra vakacacani ena ua lelevu ni cagilaba. E laurai ni sega ni levu na duidui ni levu ni ika mai na vanua e vakatabui kei na vanua e tubu vou mai kina na lase se na cakau. Na vei cakau e dikevi era tiko ena vanua e kaukauwa kina na kui ka vakasamataki ni qo e dua vei ira na vuna e bulabula kina vakatotolo na lase se na cakau. Na vanua era vakatabui e sega ni levu na duidui ni totolo ni nodra bula cake mai ni oti na cagilaba. Na bulabula ni cakau ena veigauna mai muri e vakatau ena kena kunei kei na kena maroroi na vei cakau era bula totolo mai ni oti na cagilaba, se na veimataqali leqa tale eso e rawa ni tarai ira.

Keywords Benthic communities · Monitoring · Wave energy · Locally managed marine area · Herbivorous fish · Ecosystem recovery

Introduction

As the impacts of global change become more pronounced across diverse ecosystems, there is an escalating need to focus attention on those at the forefront of these changes (Walther et al. 2002; IPCC 2019; Malhi et al. 2020). Examining such ecosystems is crucial for gaining insights into the intricate dynamics of environmental transformation. Coral reefs represent high biodiversity systems that provide critical ecosystem services throughout tropical regions. Globally, coral reefs face mounting pressure from 'press' (chronic) and 'pulse' (acute) disturbances, raising concerns about their continued ability to support these services (Ellis et al. 2019; Vercelloni et al. 2020). Press disturbance is commonly associated with local human activities resulting in extraction of fish and invertebrates or deteriorating water quality, while pulse disturbance is more often associated with natural perturbations, many of which are worsening as a result of global climate change (e.g. increasing intensity of cyclones, elevated heat stress events). Coral reefs have naturally been subjected to sporadic pulse disturbances, followed by periods of recovery (Connell 1997), but this natural disturbance regime has been altered in the Anthropocene (Nyström et al. 2000). As a result of climate change, modern-day reefs are exposed to ever more frequent and intense pulse disturbances (IPCC 2019), with shorter periods for recovery (Hughes et al. 2003, 2018). Simultaneously, most modern reefs are also exposed to increased levels of press disturbance that reduce system resilience, putting the continued persistence of coral-dominated reefs in peril (Anthony et al. 2015; McLean et al. 2016; MacNeil et al. 2019).

Cyclones represent a common pulse disturbance on tropical reefs, particularly those in the Pacific region (Lovell et al. 2004; Marler 2014). While coral reefs in the Pacific have evolved and persisted with periodic cyclone impacts, future projections of cyclones and compromised recovery dynamics are a cause for concern. Cyclones are projected to be further energised by ocean warming under climate change (IPCC 2019). Ocean warming causes its own direct impacts, with widespread bleaching events and subsequent coral mortality (Eakin et al. 2019; Sully et al. 2019). However, following bleaching-associated mortality, the reef structure often remains intact, which could promote favourable recovery rates compared to systems with unconsolidated rubble from broken corals generated by cyclones (Graham et al. 2011). Two key mechanisms underpin this pattern: first, loose rubble is easily mobilised by wave action and can be damaging to new coral recruits (Johns et al. 2018); second, the loss of complexity can have a pronounced negative impact on fish communities (Wilson et al. 2006). Cyclones have been shown to cause extensive regional damage to structurally complex reefs, causing dramatic loss in hard coral cover—for example on Australia's Great Barrier Reef (Beeden et al. 2015; Cheal et al. 2017), Fiji (Mangubhai 2016; Price et al. 2021), French Polynesia (Harmelin-Vivien and Laboute 1986), New Caledonia (Wantiez et al. 2006), and American Samoa (Craig et al. 2005), with some knock-on effects on fisheries and livelihoods documented (Wilson et al. 2006; Thomas et al. 2025). The impact on fish communities, however, is more variable, with large reductions in coral cover accompanied by minor (Price et al. 2021) to severe (Wantiez et al. 2006) impacts on fish biomass and community composition. While cyclones are expected to become less frequent under climate change in most ocean basins (Chand et al. 2022), climate modellers are reasonably confident in projected increases in cyclone intensity (Wu et al. 2022), with greater proportions of Category 4 and 5 cyclones (IPCC 2019). These projections have led to concerns of serious consequences for tropical coral reefs (Cheal et al. 2017), as well as the biodiversity and human populations that they support. At the scale of individual reefs, however, climate models do not yet resolve key cyclone features (intensity, size, forward speed and location of tracks) sufficiently well enough to predict worsening future impacts robustly (Dixon et al. 2022).

The impact of cyclones is highly spatially variable (Puotinen et al. 2016, 2020), determined by a combination of several features, including: the magnitude of the waves they create (a combination of the intensity, size, and translation/forward speed of the cyclone); the presence or absence of geomorphological features that attenuate the wave energy; and the reef orientation, exposure, and community composition. The capacity of the system to recover after the impact is then affected by several factors, including the level of press disturbances, the fish community, and the residual benthic community (McClanahan et al. 2012). For example, overharvesting of herbivorous fish can impede recovery as rates of various herbivory functions are key in preventing algal overgrowth and maintaining substrates that are favourable to coral recruits for settlement (Hughes et al. 2007b; Webster et al. 2015). However, the relationship between herbivorous fish and resilience is complex and mostly driven by work from the Caribbean and may be less relevant in Indo-Pacific reefs (e.g. Russ et al. 2015; Bruno et al. 2019). Comparing recovery dynamics on reefs with different levels of anthropogenic disturbances, or under different management regimes, offers an opportunity to investigate how press disturbances impact system resilience to pulse disturbances.

For reefs in areas where press disturbances are present, several management interventions exist that provide opportunities to reduce their impacts, primarily by controlling or restricting extractive pressure on reef-associated fisheries through, for example, locally managed marine areas, marine protected areas (including parks and reserves) and marine conservation agreements (Jupiter et al. 2014; Mumby et al. 2014; Mangubhai et al. 2020). For generations, communities throughout the Pacific Island Countries and Territories have established rules within customary marine tenure boundaries (Foale et al. 2011), and in recent decades these rules have increasingly been motivated by resource management objectives (Jupiter et al. 2014). Within managed areas, fishing of certain species, at certain times or with certain gears can be managed, and/or fishing can be restricted to the resource owners and not accessible to outsiders (Cinner et al. 2006; Govan and Jupiter 2013; Jupiter et al. 2014). These locally managed marine areas often contain no-take areas (referred to as *tabu* in Fiji), in which fishing is entirely prohibited for specified periods (Jupiter et al. 2014; Mangubhai et al. 2019).

As global temperatures rise and cyclones intensify, coral reefs face unprecedented challenges, making them emblematic indicators of the impacts of climate change on marine ecosystems worldwide. Reefs in the Pacific Island Countries and Territories offer an excellent opportunity for us to understand how high diversity systems under different resource management interventions respond to elements of global change. In this context, our study investigates the coral community dynamics following severe cyclone impacts, providing crucial insights into the broader implications of global environmental changes on marine biodiversity and resilience. Using unique data covering prior, directly after, and four years following the impact of Category 5 Tropical Cyclone Winston across two large barrier reef systems in Fiji, each with different levels of management, this study had three main objectives: (1) determine how storm wave energy can be linked to changes in hard coral cover; (2) quantify cyclone impacts and recovery of benthic communities (including reassembly potential of the hard coral community) on reefs with different management interventions; and (3) assess trajectories of fish communities and whether they can be linked to observed differences in benthic communities and/or management. Given the limited data available to date, studies that assess both the impact and recovery dynamics of reefs exposed to damaging cyclones are key to fill gaps in knowledge around the mechanisms of resilience and to support ecological projections. Such data also contribute to discussions around the validity of approaches that prioritise conserving and managing reefs based on disturbance and recovery regimes (e.g. Beyer et al. 2018; Darling et al. 2019; McClanahan et al. 2024). Furthermore, analyses into the resilience of natural systems under different management scenarios can help inform management decisions in the face of climate change.

Materials and methods

Study sites

There were two focal areas for this study located on opposing sides of Bligh Waters between Fiji's two largest islands of Viti Levu and Vanua Levu: Nakorotubu District fishing ground (NFG) in Ra Province and Kubulau District fishing ground (KFG) in Bua Province (Fig. 1). These areas are both *i qoliqoli*—customary fishing grounds with use and access rights ascribed by birthright to Indigenous (*iTaukei*) Fijian kinship groups—and they are considered locally managed marine areas due to the presence of local management interventions within their boundaries (Mangubhai et al. 2019). Within both fishing grounds lie Fiji's two largest no-take (*tabu*) areas: the Vatu-i-Ra Conservation Park (ViRCP; 110.5 km^2 established 2012—Mangubhai et al. 2020) within the NFG, and the Namena Marine Reserve (NMR; 88 km^2 established 1997—Clarke and Jupiter 2010) within the KFG. Both NMR and ViRCP were established as marine conservation agreements, a form of payment for ecosystem services, between Indigenous rights holders and local tourism operators (Mangubhai et al. 2020). While these are not formally gazetted, they have been designated as a traditional *tabu* by the rights holders. Importantly, ViRCP

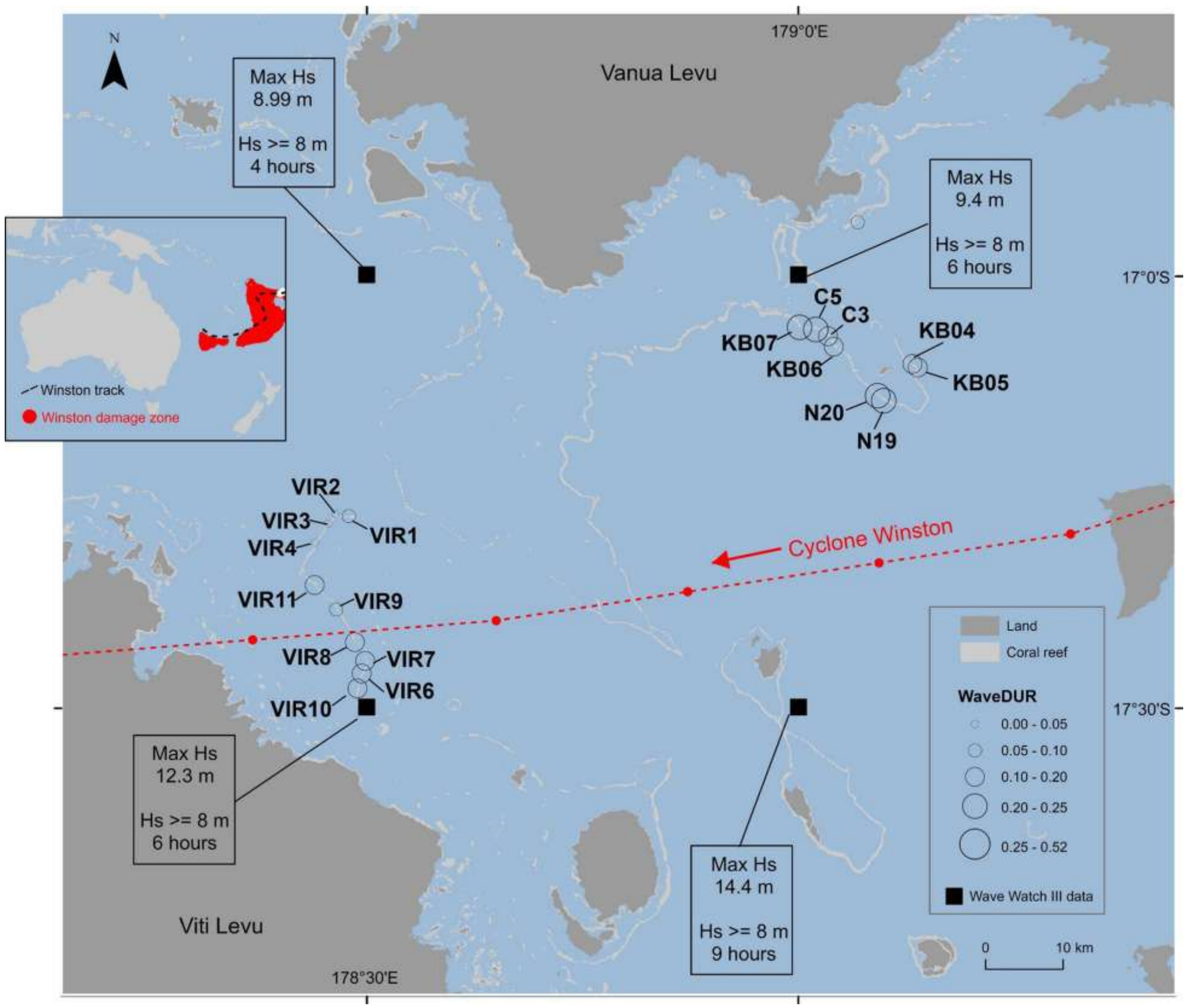


Fig. 1 Map of study sites: ViRCP_old (VIR1–4, VIR11; protected since 2012), ViRCP_new (VIR8–9; protected since 2016), NFG (VIR6–7, VIR10), NMR (N19–20, KB04–05) and KFG (C3, C5, KB06–07). Circles represent relative wave exposure during cyclone Winston multiplied by the duration of significant wave heights (Hs) greater than or equal to 4 m (metric 'WaveDUR'). Larger circles indicate higher and longer lasting wave exposure during the cyclone. Maximum Hs and the duration of extreme Hs (>= 8 m) recorded at each WAVEWATCH III data point are labelled. The spatial footprint of cyclone Winston is shown in red in the inset map, with this study area highlighted in white. The damage zone covers the entire area (and beyond) that is depicted in the main map, and the cyclone was at category 5 intensity for the entire time it traversed the main map

was expanded in 2016 to encompass a larger area, and thus ViRCP is broken down to ViRCP_old (sites VIR1, VIR2, VIR3, VIR4, VIR11; protected since 2012) and ViRCP_new (sites VIR8, VIR9; protected since 2016) for this study. Both no-take areas cover a range of different coral reef habitats. This study focuses on the following number of sites within each area which had survey points from 2013/2014, 2016 and 2020; NFG ($n = 3$), ViRCP_old ($n = 5$), ViRCP_new ($n = 2$), KFG (n = 4), NMR ($n = 4$) (Table 1).

Field surveys

Fish and benthic data were collected along 50 m transects (n = 3–6 per site) in 2013/2014 (pre-cyclone), 2016 (2–3 months post-cyclone), 2018 (ViRCP and NFG only; two years post-cyclone), and 2020 (four years post-cyclone). All transects were conducted at 4–12 m depth (8.1 ± 1.5 m; mean ± SD), with the exception of three deeper transects at 13–20 m at VIR6 in 2018 (but data from 2018 are not included in models, see below). Benthic data were collected

Table 1 Management characteristics of different areas and sites included in the study

Area	Code	Sites	Management type	Notes
Kubulau Fishing Ground[1]	KFG	C3, C5, KB06, KB07	Within Kubulau District's customary fishing ground—open to fishing	Open to traditional resource owners from Kubulau District for subsistence fishing. Any person fishing for 'trade or business' requires a fishing licence, granted by the Ministry of Fisheries.
Nakorotubu Fishing Ground[2]	NFG	VIR6, VIR7, VIR10	Within Nakorotubu District's customary fishing ground—open to fishing	Open to traditional resource owners from Nakorotubu District for subsistence fishing. Any person fishing for 'trade or business' requires a fishing licence, granted by the Ministry of Fisheries.
Namena Marine Reserve[3]	NMR	KB04, KB05, N19, N20	*Tabu*[a] area	Designated as a *tabu* area since 1997. Formally endorsed in Kubulau Ecosystem Based Management (EBM) Plan 2009 covering 60 km^2). Boundary adapted in Kubulau EBM Plan 2012 to additionally include a 500 m buffer, extending the area to 88 km^2. The only time the area can be opened up for short periods of time is when a high chief passes away.
Vatu-i-Ra Conservation Park[2]	ViRCP-new	VIR8, VIR9	*Tabu* area	Designated as a permanent *tabu* area in 2016 as part of establishing the Vatu-i-Ra Conservation Park. The management plan was launched in 2017.
	ViRCP-old	VIR1, VIR2, VIR3, VIR4, VIR11	*Tabu* area	Designated as a *tabu* area in 2012, but could be opened by communities if agreed to by the *Bose Vanua* (district chief meeting). It was included in the Vatu-i-Ra Conservation Park in 2016, and made a permanent *tabu* area. The management plan was launched in 2017.

[1] WCS (2009); [2] WCS (2018); [3] Clarke and Jupiter (2010). [a] Historically *tabus* are customary closures for specific periods of times and then opened for controlled harvest. However, they can be closed for long periods of time (e.g. NMR) or permanently (e.g. ViRCP), if the customary resource owners agree

using point-intercept transects by recording the benthos directly below the measuring tape every 50 cm, with hard corals recorded to genus level as well as the colony's growth form. Fish counts were collected using underwater visual census surveys within a 5 m belt along a 50 m transect (250 m^2 area) to species level and lengths were estimated (in 5 cm bins up to 40 cm and to the nearest cm $>$ 40 cm), allowing later conversion to biomass using established length–weight relationships from the mid-point of each size bin (Pauly and Froese 2006). All field surveys were conducted by professionals trained using the Wildlife Conservation Society Fiji Biological Monitoring Handbook (WCS 2010), which incorporates methodologies adapted from Hill and Wilkinson (2004) and other established practices in coral reef monitoring and surveys. To ensure consistency in data collection methods and species identification, the survey team participated in regular refresher training sessions.

Wave exposure models

Significant wave height (Hs; average of the top one-third of wave heights) and duration (Dur; hours reefs were exposed to waves $>$ 4 m in height) were taken from the National Oceanic and Atmospheric Administration WAVEWATCH III global hindcast dataset (Tolman 2009; http://polar.ncep.noaa.gov/waves/index2.shtml) during cyclone Winston and over a 10 year time series ending with cyclone Winston. Data were used from the WAVEWATCH III grid location closest to each survey site. As the spatial resolution of WAVEWATCH III is 50 km, three WAVEWATCH III grid locations were relevant. The spatial extent within which waves modelled by WAVEWATCH III can reasonably be attributed to cyclone Winston was defined based on a parametric cyclone wind/wave model (Puotinen et al. 2016). Based on these data, wave exposure and magnitude were estimated by calculating the per cent frequency that waves approached each site every 1 degree around the site (from 360 compass directions) combined with estimates of fetch (incorporating bathymetric data for potential obstacles), using a customised software (Puotinen 2005). Note that a 1 degree interval was necessary here for accurate results given the dense array of obstacles near the sites and their relative placement with respect to the sites given the dominant incoming wave directions during cyclone Winston. We first tried the 7.5 degree interval that is commonly used for this type of modelling and found upon close examination that the placement of the fetch lines missed key obstacles. We used the results of this to calculate a dimensionless index for wave exposure where a value of 0 means no exposure and a value of 1 means 100% exposure in all directions (e.g. Price et al. 2021; Gilmour et al. 2022). These were calculated separately for each individual site under: (i) routine wave conditions based on a 10 year time series, and (ii) during cyclone Winston. Multiple metrics were calculated that combined relative wave exposure, damaging wave duration, and maximum wave height during the cyclone versus routine conditions. The culminating metric selected to predict reef damage was a metric we term 'WaveDUR'; calculated by multiplying relative wave exposure during the cyclone by the number of hours for which waves met a threshold ($Hs > = 4$ m) generally assumed sufficiently energetic to severely damage vulnerable coral colonies (Puotinen et al. 2016). This captures both the level of exposure of each site to extreme waves, but also the duration of that exposure which is important because longer exposure gives more chances for severe physical damage to reefs from waves to occur.

Statistics

All statistical analyses were performed in R version 4.4.2 (R Core Team 2023). To test the ability to predict hard coral loss based on the wave exposure models, we used linear mixed-effects (LME) models using the *lmer* function from the 'lme4' package (Wood and Scheipl 2020) with both absolute and relative change in hard coral cover (pre- vs. post-cyclone; pre-cyclone being 2013 or 2014 surveys, with a preference given to 2014 as the closest time point to the cyclone, i.e. if a site was sampled in 2013 and 2014, only the 2014 data were used; post-cyclone being the 2016 surveys) averaged to site level as the response variable(s), 'WaveDUR' as the fixed effect (see Wave Exposure Models section), and 'Area' (5 levels; Table 1) as a random effect. For the model on relative hard coral loss, the response variable was square-root transformed with a constant shift ([min(x) + 1]; where x represented the original response values) added to each observation to address negative values and residual heteroscedasticity. To verify the significance of the fixed effect, we compared the full models to their respective null model by comparing the Akaike Information Criterion value and likelihood ratio tests, which required the models to be refitted using maximum likelihood rather than restricted maximum likelihood. Marginal and conditional R^2 values were calculated from models using the *r.squaredGLMM* function in the 'MuMIn' package (Bartoń 2023). Some sites (VIR4, VIR10, VIR11) were excluded from this analysis due to not having data from either 2013/2014 or 2016. Residuals from all models were examined for heteroscedasticity, and no issues were detected (Supplementary Figure 1).

Pairwise tests revealed overall consistency in cover of individual benthic categories (hard coral, rubble, turf algae, fleshy algae, soft coral, benthic cyanobacterial mats [BCMs] and bare substrate) between 2013 and 2014, aside from small fluctuations in the algal groups at some sites. Thus for the benthic statistical models, surveys were grouped into three time periods (hereafter Period): pre-cyclone (2013 or 2014 surveys, with a preference given to 2014 as the closest time point to the cyclone, as specified above), post-cyclone (2016 surveys), and recovery-2020 (2020 surveys). Changes in individual benthic categories over the study period were analysed using linear mixed-effects models. Hard coral cover (normally distributed) was modelled using the *lmer* function from the 'lme4' package (Bates et al. 2015). For all other benthic categories, which were right-skewed, we used GLMMs via the 'glmmTMB' package (Brooks et al. 2017), applying negative binomial distributions (*nbinom1* or *nbinom2*), with the optimal distribution selected based on the Akaike Information Criterion when both met model assumptions. Turf algae required a *tweedie* distribution to satisfy model assumptions. The predictors Period (3 levels: pre-cyclone, post-cyclone, recovery-2020) and Area (5 levels: NFG, ViRCP_new, ViRCP_old, NMR, KFG) were included as interactive fixed effects, and Site ($n = 18$, Table 1) was included as a random effect. Due to data from 2018 not being available for all management areas, we excluded this from the models and focused on observations from graphs for this time point. Depth was disregarded from models based on the relative consistency and due to initial exploratory models finding no effect. All model residuals were checked for heteroscedasticity using the 'DHARMa' package for glmmTMB models (Hartig 2024; Supplementary Figure 2). For rubble and turf algae, due to strongly heteroscedastic data, the terms '*dispformula* = ~*Area*" and '*dispformula* = ~*Period*Area*', respectively, were included. We retained all sites in the general models to increase replication within levels even though some lacked data from specific periods (see Supplementary Table 1).

The extent of the hard coral community reassembly was determined by visual interpretations of stacked bar plots showing relative proportion of coral genera and growth forms over time and correlation-based principal components analysis over time at the coral growth form level. Analyses of coral genera focused on the most common groups, with all genera consistently displaying $<5\%$ cover across sites being classified as 'Other'. The principal components analysis was conducted using the base *pca* function in R, with data standardised to account for variables measured at different scales, and plotted using the *ggbiplot* function of the 'ggbiplot' package (Vu 2011).

The sum of fish biomass, abundance, and mean length estimates were calculated by trophic feeding group per transect, before calculating site-level means. Mean lengths were weighted by the biomass of each 5 cm size class per trophic group. We focussed on seven trophic groups of reef fish: browser/cropper/grazer (by combining browsing, cropping, and grazing herbivores), corallivore, detritivore, excavator/scraper (by combining excavating and scraping parrotfish), invertivore (by combining micro-invertivores, macro-invertivores, and spongivores), piscivore (including pisci-invertivores), and planktivore. Dietary information used to classify reef fish into trophic groups was obtained from Fishbase (Froese and Pauly 2023).

In order to assess the effects of reef benthos on fish biomass, we ran a GLMM for each trophic group using the 'glmmTMB' package (Brooks et al. 2017). The log of fish biomass + 1 was used as the response in all models and the per cent cover of benthic categories were scaled (x—mean(x) / sd(x)) and included as covariates to allow the relative effects of different benthos types to be compared. Fishing was included as a categorical variable ('fishing' or 'marine conservation agreement'; representing *tabu* areas under marine conservation agreements), and Year ($n=5$, 2013–2020) and Site ($n=18$, Table 1) were included as random effects, to account for variance between years and between sites sampled in multiple years, respectively. Observer was included as a fixed effect in each model to account for variance between observers during surveys, and only data from observers trained to carry out fish surveys to Wildlife Conservation Society standards were included in analyses ($n=6$). All models were run with a Gaussian distribution, with zero-inflated models required for all trophic groups except the browser/cropper/grazer and invertivore groups, as datasets contained excess zeros. Variance inflation factors of all predictors were <3 in all models, indicating low levels of multicollinearity. Normality and heterogeneity of variance of residuals were checked for all models, showing reasonable model performance (Supplementary Figure 3).

Results

Cyclone-induced wave exposure differed across the sites (Fig. 2). Routine wave exposure was marginally higher at reefs in KFG/NMR (mean Hs = 0.76 m) than those in NFG/ViRCP (mean Hs = 0.65 m). On average, cyclone Winston generated waves with a significant wave height (Hs) that was 11 standard deviations above the long-term average, reaching an estimated maximum Hs of 9.43 and 12.31 m in KFG/NMR and NFG/ViRCP, respectively. Wave heights >4 m were encountered for 15 and 11 h at KFG/NMR and NFG/ViRCP, respectively, and all sites experienced maximum Hs >8 m for 6 h.

The most exposed site during cyclone Winston was C5, which lost 91% relative coverage of hard coral (37% absolute coverage; Fig. 2ab). Nearby site C3 also lost similar relative coral cover (88%; 49% absolute cover; Fig. 2ab). Both sites experienced very strong wave energy generated by the cyclone, but also were sites modelled to have high routine wave exposure. Sites VIR6–7 were less exposed than C3 and C5 but were much more exposed during the cyclone than during normal conditions (by a factor of 12.7 and 11.6, respectively), resulting in them losing similar high levels of cover (around 75% relative hard coral cover; Fig. 2). Some sites that had equal wave exposure during the cyclone exhibited very different responses (e.g. KB04 and KB05). Wave exposure was estimated to be much higher at sites within KFG, and some in NMR, and hard coral loss was correspondingly much generally higher than in ViRCP. Sites VIR1–3 (ViRCP_old) lost minimal hard coral coverage, in line with their projected low levels of exposure.

The calculated level of WaveDUR was significantly related to both relative (LME: SE = 8.285, DF = 12.8, t = −2.4, p = 0.031) and absolute hard coral loss (Fig. 2) (LME: SE = 46.567, DF = 12.5, t = −2.2, $p=0.047$). The model for relative cover change explained 26 and 74% variation based on marginal and conditional R^2 values, respectively, while the model for absolute cover change explained 21 and 76% of the variation, highlighting the distinctly different responses among areas. Comparisons of the Akaike Information Criterion and a likelihood ratio test comparing the full and null models for both relative and absolute coral cover validated this finding ($p<0.03$) (see Supplementary Table 2).

Benthic communities experienced distinct alterations over the study period (Fig. 3). Overall hard coral cover was significantly lower (Figs. 3a, 4a) in all areas apart from ViRCP-old in 2016 (Supplementary Table 3) compared to before the cyclone, with an average loss of 24 ± 4% (mean ± SE) (absolute loss; 54 ± 8% relative loss). The magnitude of change of hard coral was greatest in KFG which decreased by 41 ± 5% (absolute loss; 82 ± 5% relative loss) (Fig. 3a). Similarly, hard coral cover improved across all damaged

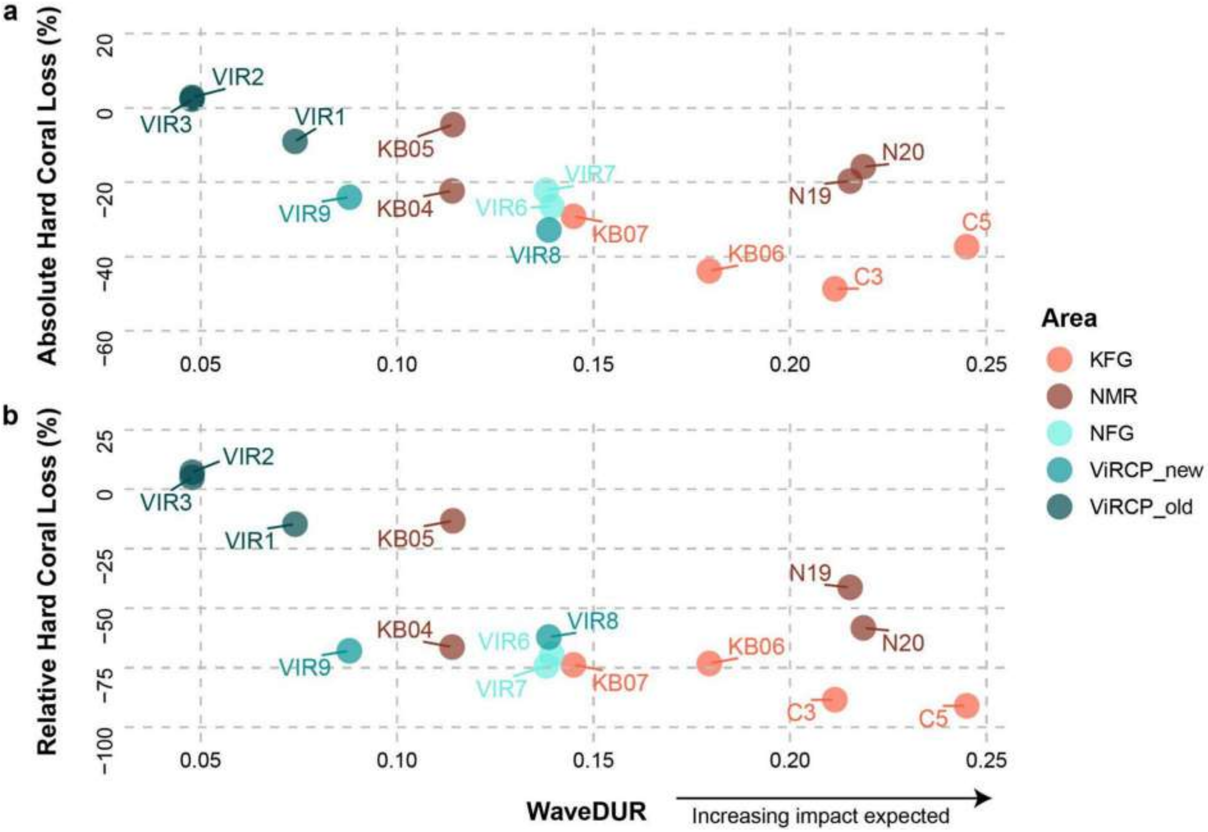


Fig. 2 Correlation between relative wave exposure during the cyclone multiplied by the duration of damaging wave conditions (WaveDUR—x-axis) and **a** absolute hard coral cover loss, and **b** relative hard coral loss (y-axis), with points representing sites (coloured by Area). Figure does not include sites VIR4, VIR10 or VIR11 due to no surveys being conducted either pre- or post-cyclone

areas (i.e. apart from ViRCP-old) by 2020. There was a corresponding significant increase in rubble (Fig. 3b) in 2016 compared to previous pre-cyclone levels in all areas other than the ViRCP areas (Supplementary Table 3). There was a significant increase in turf algae at KFG, NFG and ViRCP-new (Figs. 3c, 4b; Supplementary Table 3). Notably, NMR had significantly lower turf coverage after the cyclone and had in fact shifted towards bare substrate rather than turf algae in 2016 (Figs. 3ch, 4b). Turf algal cover was reduced by 2020 but overall remained higher than reference levels pre-cyclone (Fig. 4b). Other benthic categories remained relatively stable over time with some disparate differences across areas (Fig. 3d–h; Supplementary Table 3).

All benthic components affected by the cyclone were approaching (or on a trajectory towards) their pre-cyclone levels by 2020 (Fig. 3), including hard coral. Between 2016 and 2020 there was a rapid increase in hard coral observed across all sites (mean 2–6.5% absolute increase annually by area), though cover in 2020 remained significantly less than pre-cyclone levels (Fig. 4a). The highest recovery rate was observed in KFG (which had suffered the greatest loss following the cyclone), with one site (C5; which lost 37% absolute hard coral cover following the cyclone) regaining 38% coverage to match pre-cyclone levels by 2020. The 2018 data from ViRCP and NFG indicate that increases in hard coral cover were measured only after 2018 (Fig. 3a).

The composition of the coral community showed distinct changes following the cyclone (Fig. 5ab). The first (PC1: 53.2% variance explained) and second (PC2: 20.4% variance explained) components of the principal components analysis combined explained almost 75% of the variation in the coral composition (in terms of morphologies) (Fig. 5a). PC1 covers a gradient from complex fast-growing (positive values) to flatter slow-growing (negative values) coral morphologies (also foliose but the average cover was negligible, i.e. 2%). The distribution of areas by time over this axis indicates that the relative composition of the hard coral community experienced a loss of plating and branching *Acropora* and *Pocillopora* corals towards relatively higher cover of massive and encrusting morphologies, comprised by corals within genera such as *Porites*, *Montipora,* and *Pavona* (site-dependent for the latter two) (Fig. 5ab) after the cyclone (2016) compared with pre-cyclone composition (2013/2014). By 2020 the relative composition had returned to being very similar to the pre-cyclone composition, particularly so at NMR and NFG. Encrusting colonies were the dominant growth form after the

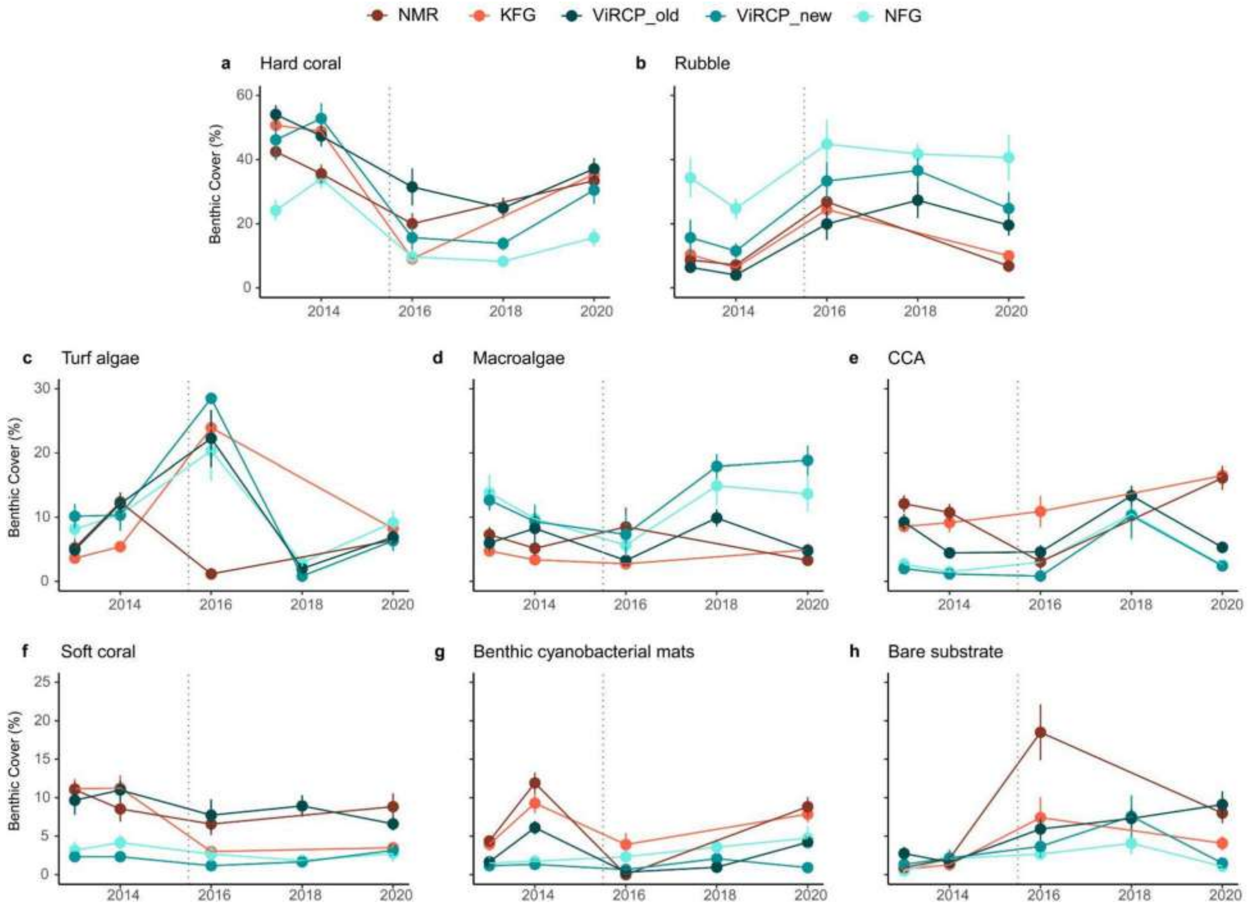


Fig. 3 Trajectories of change in proportional cover of major benthic classes (hard coral, rubble, turf algae, macroalgae, crustose coralline algae [CCA], soft coral, benthic cyanobacterial mats, bare substrate) from surveys 2013–2020. Points and error bars represent mean ± SE for each area. Note the different scales of the y-axes. Surveys in 2018 are limited to NFG, ViRCP_new and ViRCP_old. Vertical dashed lines indicate when cyclone Winston occurred (prior to reef surveys in 2016)

cyclone (Supplementary Figure 4). The loss of more fragile growth forms was particularly evident at KFG where wave exposure was highest (Fig. 5c), but the *Acropora* cover had recovered by 2020, even exceeding pre-cyclone levels.

Overall fish biomass remained relatively consistent over time (Fig. 6a), but the biomass of some trophic groups fluctuated over the years (Fig. 6b–h). The 2016 data indicated cyclone Winston had the most negative and consistent impact on corallivore biomass across all management areas, with the largest decrease of 95% observed in the new ViRCP sites (from 40.7 to 2.2 kg ha^{-1}) (Fig. 6c). Following cyclone Winston, biomass declines were also observed in most areas for browser/cropper/grazer, invertivore, and planktivore groups (from 2014 to 2016, by an average of 51, 53, and 60%, respectively; Fig. 6bfh). Prior to cyclone Winston, the biomass of most trophic groups increased from 2013 to 2014 across management areas, particularly corallivores in terms of proportional increase (3.5-fold increase on average), however corallivores contributed the least of all groups to the total biomass of reef fish assemblages (Fig. 6c). The largest absolute biomass increase from 2013 to 2014 was for invertivores in the NMR (by fourfold, from 279.6 to 1128.4 kg ha^{-1}); however, biomass in 2014 was highly variable (SE = 729.4 kg ha^{-1}) (Fig. 6f). During the 2016–2020 recovery period, the biomass of most trophic groups increased from 2016 to 2018 in the NFG and ViRCP areas (Nakorotubu District) before decreasing again in 2020 (with the exception of excavator/scrapers and piscivores). Detritivore biomass was generally higher in the KFG and NMR areas (Kubulau District) compared to the NFG and ViRCP, especially in 2020 after four years of post-cyclone coral recovery (KFG: 116.4 ± 33.0 kg ha^{-1}; NMR: 199.1 ± 99.7 kg ha^{-1}) (Fig. 6d). By 2020, excavator/scraper biomass was slightly higher than in 2013 in NFG and ViRCP and was similar to 2013 in KFG and NMR (Fig. 6e). Piscivore biomass differed between areas over time, however biomass in NFG and ViRCP converged at a similar level in 2020 (~ 105 kg ha^{-1}) following declines in the NFG and old ViRCP areas, while in

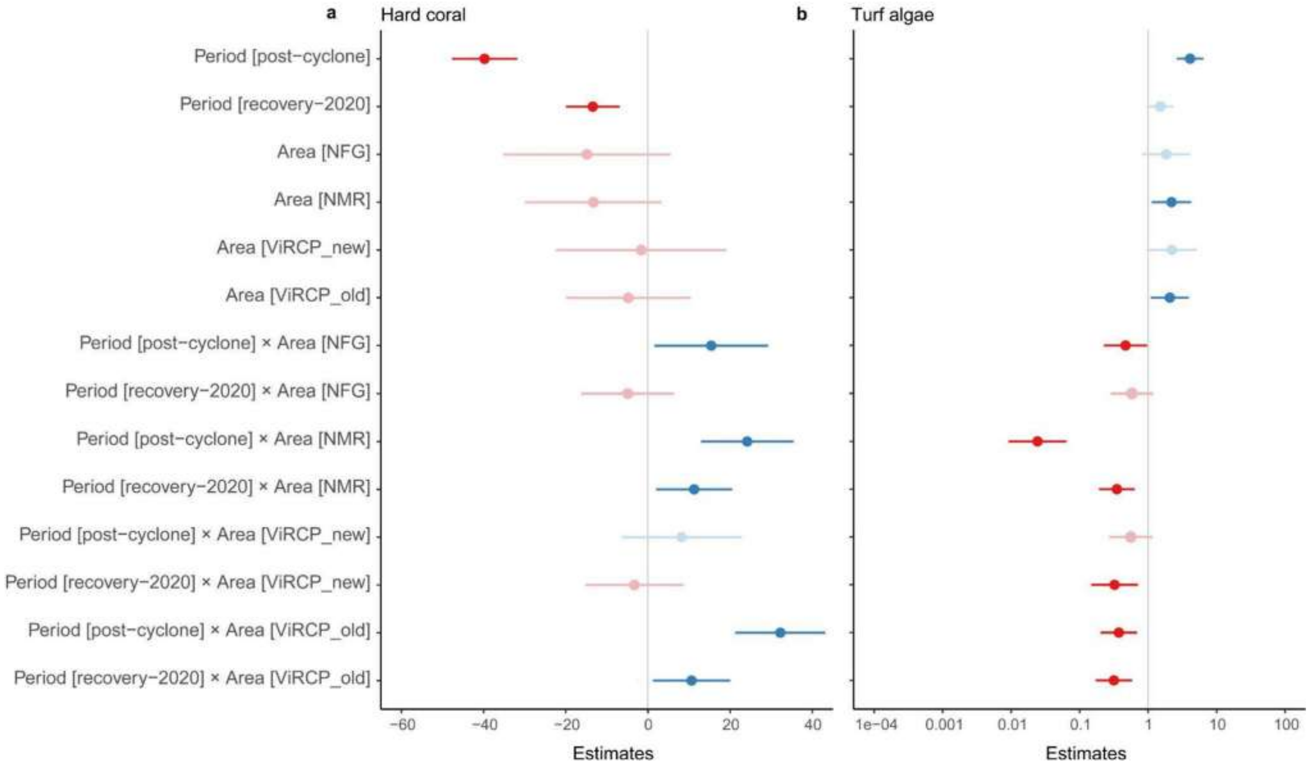


Fig. 4 Model estimates from GLMMs for **a** hard coral and **b** turf algae. Predictors where model estimates ± standard error do not overlap 0 are shown in bright colour, other terms are faded. All data from 2018 were excluded from this model. Model estimates visualised here were made using the plot_model function from the 'sjPlot' package (Lüdecke 2018). X-axes differ due to the *lmer* and *glmmTMB* models utilised for 'a' and 'b', respectively (with the latter given on the log scale). Note that while the full model for turf algae included a 'dispformula' term to account for heteroscedasticity, this term causes issues with visualisation functions and thus these results reflect the simplified model (i.e. without 'dispformula')

the Kubulau District, biomass in NMR increased above that of KFG by 2020 (NMR: 213.3 ± 86.5 kg ha^{-1}; KFG: 46.0 ± 12.6 kg ha^{-1}) (Fig. 6g).

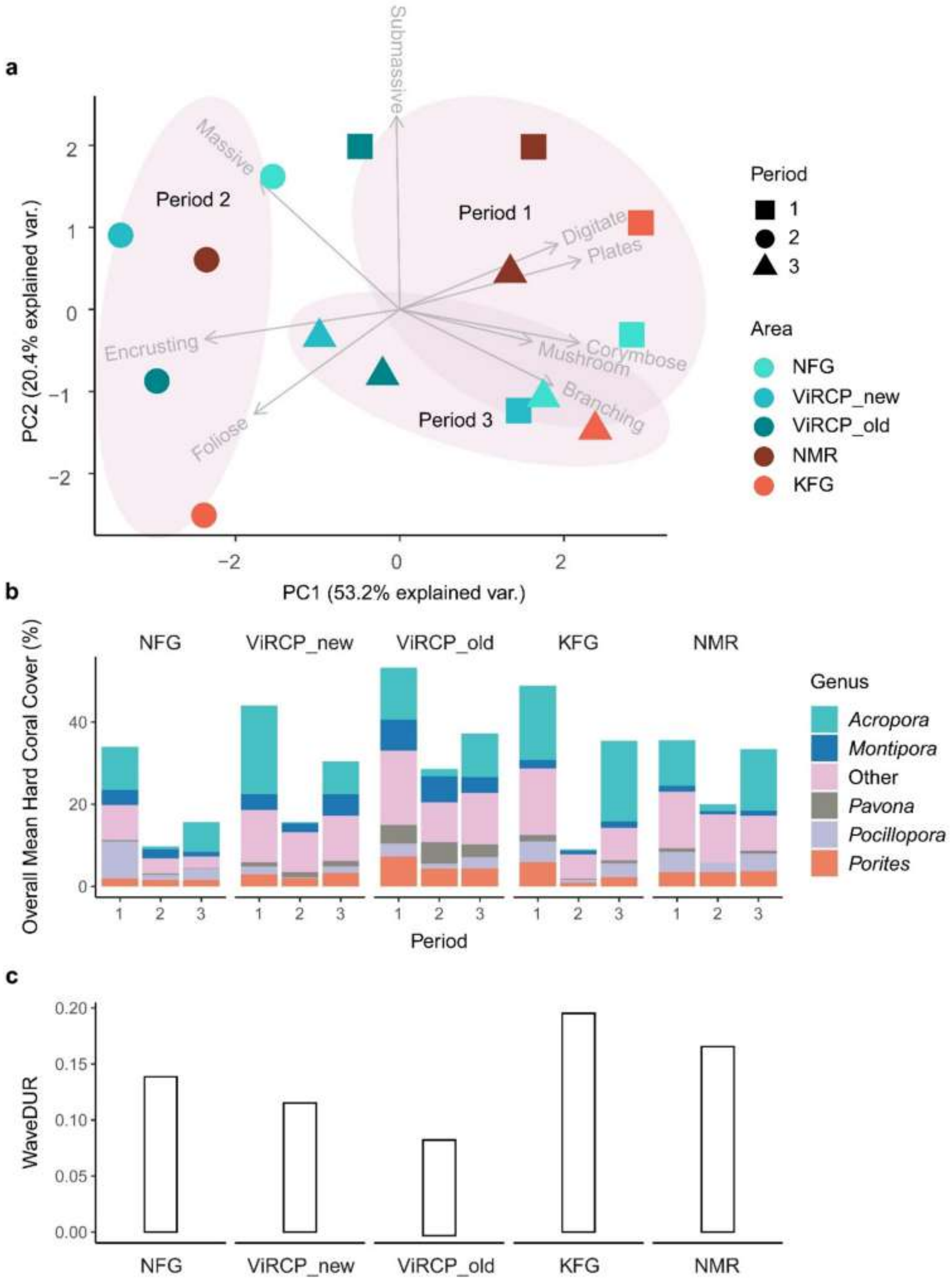
Post-cyclone detritivore, invertivore and planktivore biomass trends were mostly aligned with changes in fish abundance, while browser/cropper/grazer and corallivore biomass were more aligned with mean fish length (Supplementary Figure 5). The variation in excavator/scraper and piscivore biomass between management areas was reflected in both abundance and mean length trends.

GLMMs revealed effects of benthic components and protection from fisheries (marine conservation agreements) on fish functional groups (Fig. 7). On reefs with greater hard coral cover, fish biomass was lower for detritivores (standardised effect size = -0.3 ± 0.1 SE, z = -2.8, $p < 0.01$) and planktivores (-0.5 ± 0.2, z = -3.1, $p < 0.01$) but marginally higher for corallivores (0.2 ± 0.1, z = 1.9, $p = 0.06$). Detritivore biomass was lower on reefs with greater macroalgae cover (-0.2 ± 0.1, z = -2.6, $p < 0.01$). On reefs with greater turf algae cover, biomass was lower for excavator/scrapers (-0.2 ± 0.1, z = -2.5, $p = 0.01$) and planktivores (-0.3 ± 0.1, z = -3.0, $p < 0.01$), and marginally lower for piscivores (-0.2 ± 0.1, z = -1.8, $p = 0.08$). Benthic cyanobacterial/microbial mat coverage had a small positive association with the biomass of the browser/cropper/grazer group (0.2 ± 0.1, z = 2.3, $p = 0.02$) and a marginally positive effect for excavators/scrapers (0.1 ± 0.1, z = 1.8, $p = 0.07$). Rubble was associated with lower biomass of piscivores (-0.4 ± 0.2, z = -2.1, $p = 0.04$) and detritivores (-0.4 ± 0.1, z = -2.8, $p < 0.01$). The protective influence of marine conservation agreements had mixed and highly variable effects on fish biomass across trophic groups, with a clear positive impact observed for only excavators/scrapers (0.6 ± 0.2, z = 3.3, $p < 0.001$) (Fig. 7).

Discussion

Wave estimation models predicted that the two study areas experienced waves > 4 m in height for 11–15 h, and > 8 m for 6 h as a result of Category 5 Tropical Cyclone Winston. Hs of this magnitude were estimated recently in a global modelling study to occur about once every 50 years near Fiji, with about a 0.02 probability of occurring in

Fig. 5 Coral community composition of different areas represented by **a** principal components analysis at the coral morphology level and **b** stacked bar plots showing absolute coverage of coral genera at the coral genus level in each area, over three time points: 1 (pre-cyclone; 2013/2014); 2 (post-cyclone; 2016), 3 (2020), and **c** average wave exposure per area during the cyclone. Coral genus data are restricted to those that exhibit at least 5% cover overall in at least one area; other genera are grouped together as ‘Other’



any given year (Neary and Ahn 2023). Most of the surveyed reefs were generally severely impacted by these waves, averaging a 63% relative loss of hard coral cover compared to pre-disturbance levels. The only exceptions were coral reefs at the northern tip of the Vatu-i-Ra reef system (VIR1–3) where wave models had estimated the lowest wave exposure when accounting for orientation and obstacles. These sites lost no hard coral after the cyclone compared to pre-cyclone levels. The coral loss at other sites was primarily driven by reductions in branching and tabulate/plating *Acropora* corals and branching *Pocillopora*. All impacted study areas exhibited rapid recovery of coral communities by 2020, both in terms of absolute cover as well as composition, with monitoring data suggesting shallow communities (data from this study were collected from 8.1 ± 1.5 m depth) had mostly re-assembled to pre-cyclone levels by 2020. Although the responses of reef fish varied between trophic functional groups and areas, total fish biomass prior to cyclone Winston was well above the threshold indicating healthy ecosystem functioning and high recovery potential (~ 1000 kg ha^{-1}; MacNeil et al. 2015) which may explain the high biomass levels post-cyclone, even in fished areas. These results indicate an exceptional recovery capacity of these reef systems.

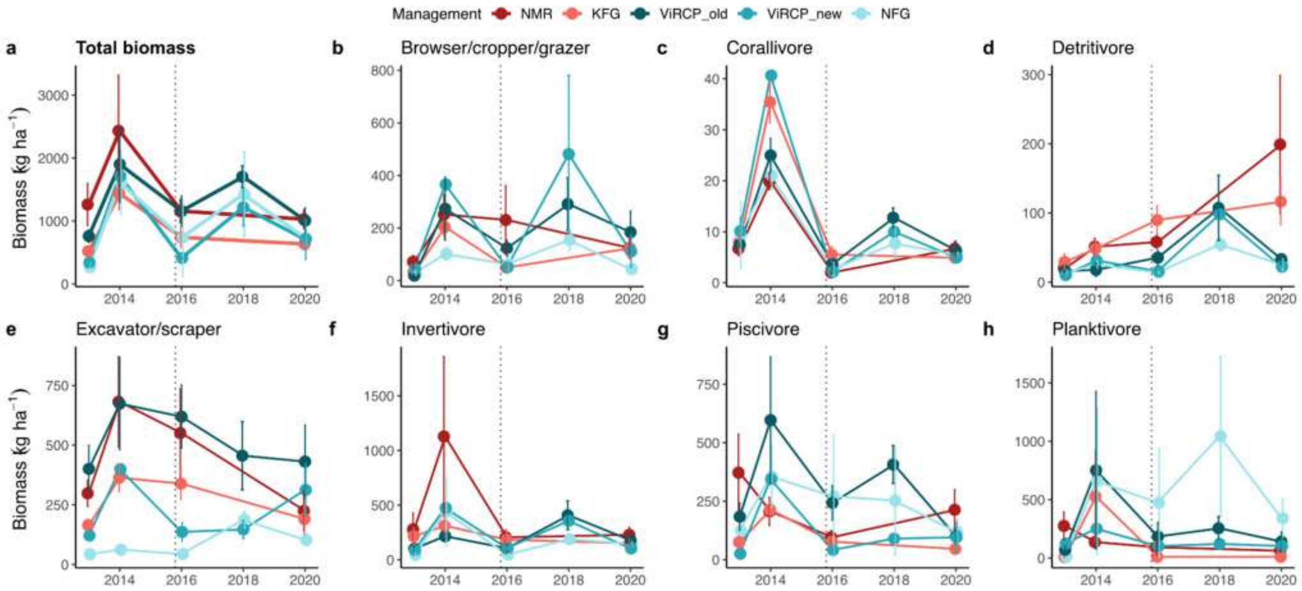


Fig. 6 Fish biomass over time in each management area for **a** the entire fish assemblage and **b-h** per functional feeding group. Points are means across sites in each management area (±SE, shown as error bars). Note y-axes differ between functional groups and no sites in KFG or NMR were surveyed in 2018. Vertical dotted lines indicate when cyclone Winston occurred (prior to reef surveys in 2016)

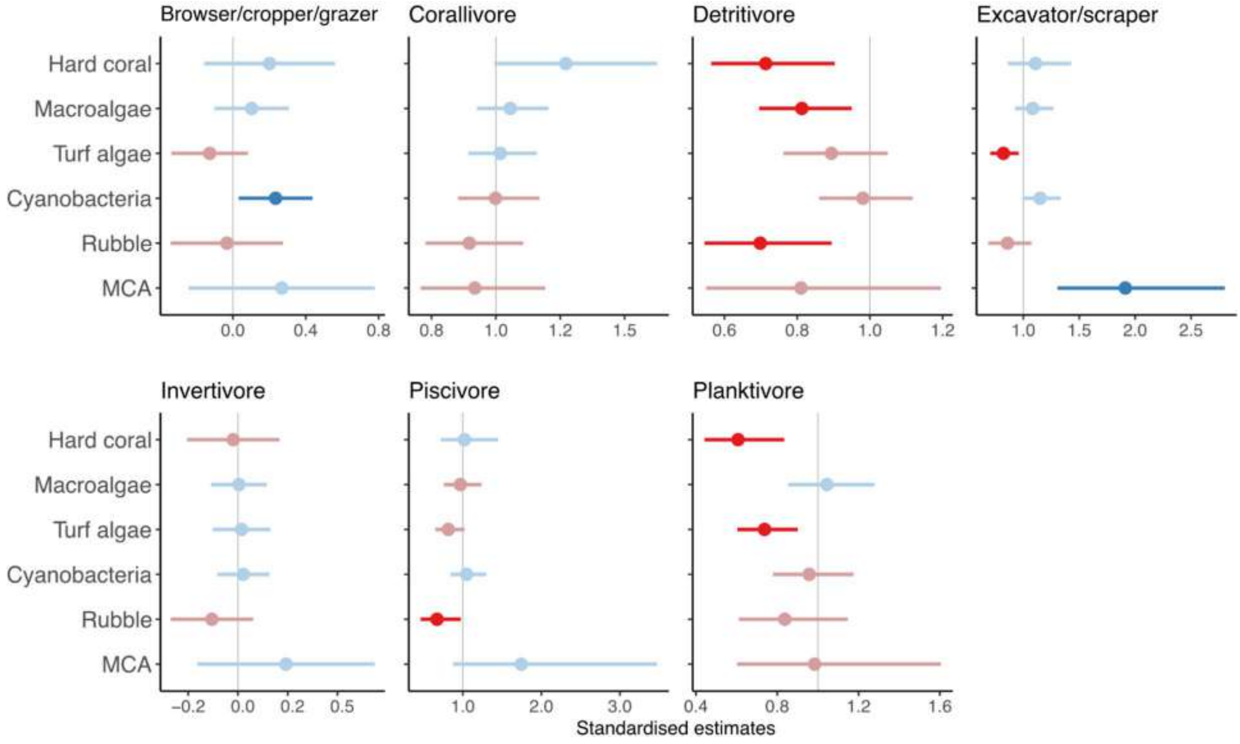


Fig. 7 Effect sizes from generalised linear mixed models investigating the effects of reef benthic characteristics and protection from fisheries (MCA = marine conservation agreement) on the biomass of trophic groups of reef fish. Separate models were used for each trophic group. Predictors where model estimates ± standard error do not overlap 0 are shown in bright colour, other terms are faded. Effect sizes for random effects are found in Supplementary Figure 6

Annual coral cover increases between 2016–2020 was high (2–6.5%), matching or exceeding most other reported recovery rates following similar-scale disturbances (i.e. 4% annual increase on the GBR at similar shallow depths to this study following Cyclone Yasi—Beeden et al. 2015; also see supplementary Table S6 in Koester et al. 2020 for annual recovery rates from 13 studies following bleaching events). The 2018 survey points from NMR and ViRCP suggest that the recovery was only detectable after 2018, indicating that annual recovery rates in 2019–2020 in fact well exceeded the calculated four-yearly average. This finding is unsurprising as despite the fast rate that *Acropora* corals in particular grow (up to 10 cm/year—Stimson 1985); and that their growth rate increases with colony size (Doropoulos et al. 2015); it would take time for new recruits to grow into measurable colonies. Alternative methodologies (e.g. photographs, quadrats) may have allowed their detection in 2018, with the potential that they were not well-captured by point-intercept transects. The rapid recovery is likely in part due to the position of the reefs in the path of the north-west Bligh Water Current which passes over several coral-rich reefs prior to reaching the studied reef systems (Drew and Barber 2012) thus providing new larvae for replenishment, the high and persistent levels of fish biomass (see also Mangubhai et al. 2019), as well as the regrowth and (a)sexual reproduction of remaining corals on the studied reefs. All reefs started with healthy levels of fish biomass, exceeding recognised thresholds for ecosystem stability (McClanahan et al. 2011), thus would have been expected to exhibit rapid recovery. Furthermore, a positive link between seabird guano and reef recovery following disturbances (Benkwitt et al. 2019) could be supported by research from Namena (Savage 2019) where guano from Namena Island has been found to enhance coral growth rates. ViRCP also has a central island supporting large breeding seabird populations (Tarburton 1978; WCS 2018), potentially driving similar productivity dynamics and rapid recovery on this reef system. A global meta-analysis recently found reefs that had been regularly exposed to disturbances exhibit fast recovery rates (Walker et al. 2024), likely due to morphological changes caused by cyclones that lead to similar community morphologies to those found in these reefs (but see contrasting findings on the Great Barrier Reef—Emslie et al. 2024).

The reassembly of the hard coral community to pre-cyclone composition by 2020 was striking. Community reassembly (returning to initial community structure) indicates high resilience of the coral community and ensures pre-disturbance ecosystem functions are restored (Nyström et al. 2008). Notably, the reassembly observed is likely driven by the most impacted coral taxa (based on vulnerable growth forms) also being the fastest-growing (i.e. the ‘competitive’ types identified by Darling et al. 2012). Following the cyclone, the faster-growing more complex genera (primarily *Acropora*) were dislodged, and families with more slower-growing, robust morphologies (e.g. *Porites* [predominantly massive, encrusting] and *Montipora* [predominantly encrusting]) remained, thus accounting for their higher relative cover. We could also hypothesise that the broken fragments of *Acropora* may have remained and survived at these sites which usually have low wave energy, thus facilitating rapid recovery (e.g. Linares et al. 2011).

While the no-take areas had an overall positive effect on the biomass of key herbivorous fish groups, the fished areas still had high biomass compared to global literature and exceeded identified critical thresholds (Robinson et al. 2018). The level of protection did not appear to have a strong influence on the post-cyclone trajectories of the system, with all reefs exhibiting similar recovery dynamics. Notably, even reef areas covered by the marine conservation agreements are subject to poaching, which may explain the lack of difference compared to customary fishing grounds; surveillance and enforcement in VIRCP did not commence until 2021 when a boat was secured, and stopped in NMR due to cyclone Winston destroying the resort that was leading efforts (S. Mangubhai, pers. comm.). However, previous studies (e.g. Jupiter & Egli 2011; Goetze & Fullwood 2013) have shown positive associations of protection in NMR, suggesting that the scale of the disturbance itself was so large that it may have obscured the impacts of protection within this specific analysis. All reefs aside from those in NMR shifted towards rubble (from broken corals and reef structure) and turf algae following the cyclone. Due to the low routine wave exposure at the sites, rubble likely remained in place as opposed to remaining mobilised as can occur at more routinely exposed sites following cyclones (Kenyon et al. 2023). While turf algae has been linked to reinforcing degraded reef states due to its ability to compete with corals for space (Swierts and Vermeij 2016) and impede coral recruitment (Speare et al. 2019), there is strong evidence that short turfs (<5 mm) controlled by high levels of herbivory can actually promote settlement of coral planulae (Mumby et al. 2013; Ford et al. 2018). The high biomass of herbivorous fish, even following the cyclone, would conceivably have been able to keep the turf algal canopy below this threshold (i.e. maintaining short productive algal turfs; Goatley et al. 2016), preventing the establishment of reinforcing feedbacks (sediment trapping, reduction in herbivory, impact on corals) that promote degradation. NMR reefs had bare substrate rather than turf algae recorded in 2016, which could be explained by these reefs having the highest biomass of herbivores and thus likely the highest level of herbivory functions. Importantly, fleshy macroalgae played an insignificant role on these reefs (even following the disturbance), which appears to be common for outer reefs in the Pacific (e.g. Smith et al. 2016; Ford et al. 2020). However, reefs with higher initial macroalgae coverage revealed reduced coral recovery and ended the sampling period with more algae, consistent with findings in Walker et al. (2024).

Despite the distinct impact of the cyclone on benthic communities, fish communities remained relatively stable following the cyclone (consistent with Price et al. 2021) and over the recovery period. Fishes that feed on benthic algal and microbial resources may benefit from increased primary productivity following a severe cyclone disturbance due to higher nutrient inputs from land (Russ and McCook 1999), which may explain the relatively high biomass of the excavator/scraper and detritivore groups we observed following the cyclone. The positive relationship between cyanobacteria and browser/cropper/grazer biomass may be an indication of this group benefiting from enhanced primary productivity on reefs more generally, as these fishes do not appear to feed on cyanobacteria directly (Ford et al. 2021). Additionally, the notable increases in detritivore biomass could be expected following coral loss as they generally feed on dead substrate (Russ et al. 2018). Invertivores could be expected to be positively affected by cyclone-induced reef degradation as they take advantage of novel feeding opportunities, such as rubble beds (Russ et al. 2015; Brandl et al. 2016); however, there was no indication of this from our fish biomass estimates. Notably detritivores also surprisingly showed a negative relationship with rubble, which may be a result of extensive unconsolidated rubble not retaining detritus and lacking structural complexity required for shelter. The particularly sharp decline in corallivore biomass immediately after the cyclone could be expected, due to the corals they feed on being damaged (Cheal et al. 2017). Indeed we found evidence of corallivore biomass showing a positive association with hard coral cover and a negative association with rubble (i.e. recently destroyed hard coral), albeit insignificant. The low biomass of planktivores following the cyclone could be due to a loss of shelter provided by branching corals (Brandl et al. 2016), though biomass levels remained low as coral recovered, with the exception of the NFG area where planktivore biomass appeared to recover to relatively high levels. It is unclear why hard coral cover was associated with lower planktivore biomass in our results and may require further investigation on these reefs. Both piscivores and planktivores have been found to show particularly large decreases in abundance with reductions in reef structure (Hall and Kingsford 2021), which may explain the negative influence of low-complexity rubble habitats on piscivore biomass in our results. Our results highlight nuances in the dynamic responses of reef fish communities to benthic disturbances, making general interpretations about temporal changes and links between fish and benthic communities challenging even at the scale of this study (e.g. Ceccarelli et al. 2025).

While these reefs are offshore they are within customary fishing grounds making them representative of other coral reefs in Fiji (Mills et al. 2011; Mangubhai et al. 2019) and the broader Pacific. Similar to other parts of the Pacific, the more distant fishing grounds likely experience lower subsistence fishing pressure, so setting aside part of these areas as no-take areas can be achieved without significantly impacting customary fishing activities. The challenge of this approach is that protected sites that are not visible from shore can also experience regular poaching and are challenging to enforce. The fishing grounds included in this study likely experience low levels of fishing pressure (due to distance from major markets), are exposed to high currents, and have strong connectivity across Fiji's extensive and diverse reef types (Drew and Barber 2012; Mangubhai et al. 2019), which may contribute to the resilience of these reefs. Furthermore, long-term and large no-take areas have been shown to support resilience through improvements in biomass and associated processes of key functional groups (Hughes et al. 2007a; Mumby et al. 2014; McClanahan 2021). In Fiji, both ViRCP and NMR are protected through marine conservation agreements, a type of payment for ecosystem services scheme from which the Indigenous customary owners and tourism operators mutually benefit (Mangubhai et al. 2020). The high recovery and reassembly potential observed at the reefs in the current study supports recommendations for protecting such less-accessible reefs within customary fishing grounds.

While future projections of wave damage to reefs from cyclone impacts remain uncertain (Dixon et al. 2022), there is general agreement that the relative proportion of severe cyclones will increase (Cheal et al. 2017; IPCC 2019). This is cause for serious concern in areas that are regularly exposed to tropical cyclones (Chand and Walsh 2009), especially if future cyclones move more slowly and are larger in size which would increase the magnitude and duration of waves they can generate (IPCC 2019). While these results are certainly optimistic and suggest that some remote reefs with high fish biomass are able to recover from extreme cyclone-generated waves within a short timeframe, the results must be interpreted with caution. Firstly, the regularity of such events, combined with the escalating severity of bleaching events, coral predator outbreaks and diseases, means the future remains highly concerning. Furthermore, the reefs involved in this study are exposed to strong currents supporting naturally higher fish biomass, and so extrapolations to other areas should be done with caution. Nevertheless, our findings provide rare and encouraging evidence that some Pacific reefs, particularly those that are remote, well-connected, and embedded within customary governance, can demonstrate rapid recovery and reassembly following severe disturbances. These results highlight the importance of regular reef monitoring to provide clearer information on the impact and recovery from disturbances, and the implementation of conservation strategies (including the protection of less-accessible offshore reefs), to maintain ecological resilience in the face of accelerating global change.

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Author's contribution A.F., Y.N., S.J., S.D., W.N. and S.M. collected monitoring data used within the manuscript. Y.N. checked and prepared the monitoring data. A.F. and S.M. developed the idea for the manuscript. M.P. calculated the wave exposure metrics. A.F. and M.H. led the data analysis. A.F., M.P. and M.H. prepared the figures. A.F. wrote the main manuscript text. All authors reviewed and contributed to the manuscript.

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Data availability All data have been uploaded to Data Mermaid (https://www.datamermaid.org) where aggregated site-level benthic data are available, and fish biomass data are available on request. Analysis scripts are available on Github here: https://github.com/Mark-H-22/cyclone-winston.

Declarations

Conflict of interest The authors declare no competing interests.

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