Coral Reefs (2015) 34:715–725
DOI 10.1007/s00338-015-1305-z

REPORT

Exposure-driven macroalgal phase shift following catastrophic disturbance on coral reefs

George Roff[1] · **Iliana Chollett**[1,2] · **Christopher Doropoulos**[1] · **Yimnang Golbuu**[3] · **Robert S. Steneck**[4] · **Adelle L. Isechal**[3] · **Robert van Woesik**[5] · **Peter J. Mumby**[1,2]

Received: 20 November 2014 / Accepted: 28 April 2015 / Published online: 15 May 2015

Abstract Environmental conditions play an important role in post-disturbance dynamics of ecosystems by modulating recovery of surviving communities and influencing patterns of succession. Here, we document the effects of wave exposure following a catastrophic disturbance on coral reefs in driving a phase shift to macroalgal dominance. In December 2012, a Category 5 super typhoon ('Typhoon Bopha') passed 50 km to the south of Palau (Micronesia), causing a major loss of reef corals. Immediately post-disturbance, a rapid and extensive phase shift of the macroalgae *Liagora* sp. (Rhodophyta) was observed at sites exposed to chronic wave exposure. To quantify the influence of biotic and abiotic drivers in modulating the extent of post-disturbance *Liagora* blooms, we compared benthic substrates and herbivore assemblages at sites surveyed pre- and post-disturbance across a gradient of wave exposure. Relative changes in herbivore biomass and coral cover before and after disturbance did not significantly predict the extent of *Liagora* cover, indicating that changes in herbivore biomass or reductions in grazing pressure were not directly responsible for driving the *Liagora* blooms. By contrast, the degree of wave exposure experienced at sites post-disturbance explained >90 % of model variance ($p < 0.001$, $R^2 = 0.69$), in that *Liagora* was absent at low exposure sites, while most extensive blooms were observed at highly exposed sites. At regional scales, spatial maps of wave exposure accurately predicted the presence of *Liagora* at impacted sites throughout the Palau archipelago (>150 km distance), highlighting the predictive capacity of wave exposure as an explanatory variable and the deterministic nature of post-disturbance macroalgal blooms. Understanding how physical conditions modulate recovery of ecosystems after disturbance allows insight into post-disturbance dynamics and succession of communities, ultimately allowing management strategies to prioritise restoration efforts in regions that are most effective.

Keywords Wave exposure · *Liagora* · Herbivory · Typhoon · Palau · Micronesia

Introduction

The impact of environmental disturbance on the structure and function of ecosystems is well documented, resulting in losses of diversity, regime shifts, and altered ecosystem function (Scheffer et al. 2001; Folke et al. 2004). Following disturbance, environmental conditions can also influence the recovery of ecosystems by affecting primary and secondary community succession. For example, rainfall mediates the recovery of the salt marsh plant *Spartina*

Communicated by Biology Editor Dr. Mark Vermeij

Electronic supplementary material The online version of this article (doi:10.1007/s00338-015-1305-z) contains supplementary material, which is available to authorized users.

✉ George Roff
g.roff@uq.edu.au

[1] Marine Spatial Ecology Lab, School of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia

[2] Marine Spatial Ecology Lab, College of Life Sciences, University of Exeter, Exeter, Devon EX4 4PS, UK

[3] Palau International Coral Reef Center, Koror, Palau

[4] Darling Marine Center, School of Marine Sciences, University of Maine, Walpole, ME 04573, USA

[5] Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL, USA

alterniflora following drought-induced die-offs (Angelini and Silliman 2012), and the cold, nutrient-rich waters associated with La Niña conditions facilitated the recovery of the giant kelp *Macrocystis pyrifera* following an El Niño-related mortality event (Edwards 2004). Understanding how physical conditions can modulate ecosystem recovery after disturbance allows insight into post-disturbance dynamics and succession of communities, ultimately allowing management strategies to prioritise restoration efforts in regions that are most effective (Levin and Lubchenco 2008; Holl and Aide 2011).

In the past few decades, increases in the frequency and intensity of disturbance have led to significant declines in function and diversity in coral reef ecosystems (Bruno and Selig 2007; De'ath et al. 2012), resulting in widespread transitions from coral to macroalgal dominance (e.g., Hughes 1994; Gardner et al. 2003), termed 'phase shifts' (sensu Done 1992). Once established, macroalgae can outcompete corals for space (McCook 1999), compromising ecosystem function and impacting the ability of reefs to return to a coral-dominated state (Mumby 2009). Following disturbance and loss of coral, macroalgal blooms can result from either top-down changes (depletion of herbivores or a reduction in grazing intensity; Mumby and Steneck 2008) or bottom-up environmental changes (increased productivity through changes in nutrient availability, and further rendering corals more susceptible to catastrophic disturbances; D'Angelo and Wiedenmann 2014). While patterns of increasing disturbance are relatively well understood (Mumby et al. 2013), little is known about deterministic factors that might predispose a reef to phase shifts following disturbance.

In shallow marine environments, wave exposure is critical in driving ecosystem productivity, primarily by increasing the capacity of macroalgae to acquire nutrients (Leigh et al. 1987). In temperate rocky shore ecosystems, wave exposure drives photosynthesis in intertidal macroalgae (e.g., Hepburn et al. 2007), influences macroalgal morphology (e.g., Wernberg and Thomsen 2005), and ultimately regulates trophic structure and ecological dominance among rocky intertidal algal communities (e.g., Dayton 1975; Mcquaid and Branch 1985). In tropical coral ecosystems, productivity is generally higher on windward than leeward reefs (Marsh 1970), enhancing coral growth rates (Barnes 1983), and influencing macroalgal patch dynamics (Renken et al. 2010). Despite such strong ecological regulation, surprisingly, little is known about the influence of wave exposure on the short-term dynamics of macroalgal phase shifts following disturbance.

On 2 December 2012, a Category 5 super typhoon ('Typhoon Bopha') with a central pressure of 922 hPa tracked westward and passed 50 km to the south of Palau (Micronesia; Electronic Supplementary Materials, ESM, Fig. S1), with maximum sustained wind speeds of >250 km h^{-1} at the centre and wind speeds of >90 km h^{-1} experienced throughout the Palau archipelago. Typhoon-driven waves exceeded heights of 10 m, resulting in widespread damage and loss of corals on the eastern reefs of Palau. In the wake of the typhoon, previously coral-dominated reefs underwent a phase shift to macroalgal dominance, with blooms of *Liagora* sp. (a Rhodophyte macroalga) observed across the impacted eastern reefs of Palau. Although blooms of *Liagora* have frequently been observed immediately following hurricane disturbance throughout the Caribbean (e.g., Woodley et al. 1981; Edmunds and Witman 1991; Fenner 1991; Hughes 1994), such rapid macroalgal blooms are less common in the Indo-Pacific, due to lower macroalgal growth rates, higher rates of herbivory, and greater diversity of herbivores (Roff and Mumby 2012). Such blooms of *Liagora* are an example of triggered ecosystem shifts (Scheffer et al. 2008), in that they result from a major disturbance and are highly ephemeral, lasting several months following disturbance (Fenner 1991; Hughes 1994). While *Liagora* blooms are thought to be triggered by a temporary relaxation of herbivory immediately after hurricane disturbance and/or nutrient pulses resulting from sediment recycling on the benthos (Hughes 1994; Scheffer et al. 2008), the drivers modulating the spatial distribution and extent of *Liagora* blooms are unknown, largely due to their ephemeral nature. Here, we investigate how chronic levels of wave exposure modulate ecosystem recovery following disturbance by driving macroalgal phase shifts. First, we map wave exposure throughout the Palau archipelago in the wake of Typhoon Bopha based upon wind speeds and coastline morphology. Second, taking advantage of eight sites surveyed across a gradient of exposure before and after the typhoon, we quantified the relative contributions of wave exposure and changes in herbivory in driving *Liagora* blooms at local scales. Finally, we relate the effects of wave exposure to the distribution of *Liagora* at sites throughout the entire Palauan archipelago (150 km north–south) following Typhoon Bopha to determine whether wave exposure would accurately predict *Liagora* blooms at a regional scale (i.e., 10–150 km scale). Despite significant losses of coral cover, reduced structural complexity, changes in herbivore biomass, and decreases in grazing intensity of herbivores following Typhoon Bopha, our results indicate that *Liagora* blooms are primarily influenced by the degree of chronic wave exposure across sites. At a regional scale, sites impacted by Typhoon Bopha with high wave exposure also exhibited *Liagora* blooms, further highlighting the deterministic nature of post-disturbance macroalgal blooms.

Materials and methods

Study sites

Located in the western Pacific Ocean, Palau experiences a predominantly eastern wind pattern from December to April, consistent with the Asian monsoon (Heron et al. 2006). We conducted detailed surveys at six sites on the eastern coast along a gradient of wave exposure and two sheltered sites on the western coast (Fig. 1) at a depth of 5–7 m. Surveys were conducted prior to the Typhoon Bopha in early March 2012, and in the aftermath of Typhoon Bopha in late February 2013.

Wave exposure

To quantify the degree of chronic wave exposure (i.e., the degree of wave action on an open shore) at our study sites following Typhoon Bopha, we used a wave-theory GIS approach that integrates information on the configuration of the coastline and reef crests and the wind patterns of the area (Chollett and Mumby 2012). Following this simple approach, exposure is only governed by the distance of open sea that the wind has blown over to generate waves (fetch), and the strength and direction of the winds. Therefore, exposure values depict wind-generated waves and exclude the effects of tides or swell that can only be captured using computationally intensive third generation wave models. First, fetch was calculated in 32 compass directions by tracing a line from each marine location (pixel) across the sea until either land or a reef crest was encountered. Then, the average wind speed and probability of occurrence were calculated for each of these 32 main directions. Finally, we used the values of fetch, wind speed, and probability of occurrence in each direction to calculate wave exposure (in Joules m^{-3}) using equations 1–8 in Ekebom et al. (2003). In situ hourly wind speed and direction for Koror Airport (~10 km from eastern study sites) were obtained from Weather Underground (www.wunderground.com/weather-forecast/KA/Koror.html). The location of the coastline and reef crests in Palau was obtained from a habitat map produced by Battista et al. (2007). The wave exposure model at 50 m spatial resolution was parameterised using wind data from immediately after Typhoon Bopha (6 December 2012) until the date of surveys (28 February 2013).

Benthic cover and structural complexity

To quantify benthic cover, twenty-five 1 m^2 quadrats were distributed at each site by using a randomly generated list of swimming directions (compass points) and a list of numbers for distance. The quadrats were photographed using a Canon Powershot G10 camera, and percentage cover of coral and *Liagora* within sites was determined from 20 points randomly placed in quadrat photos using the

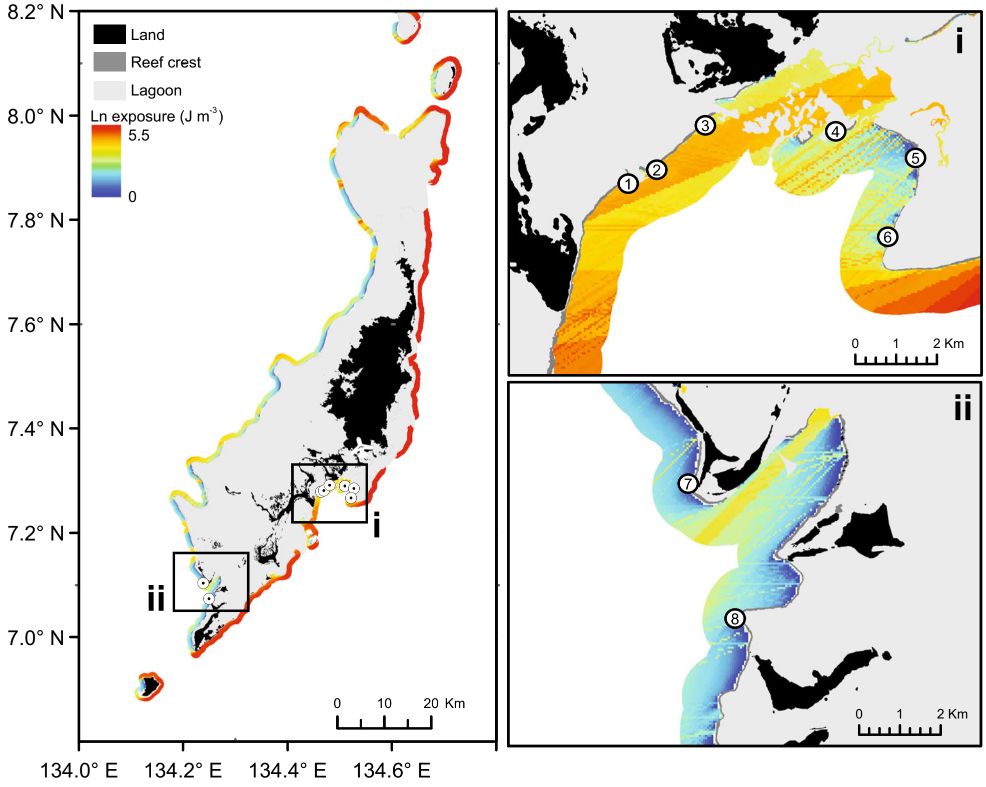

Fig. 1 Exposure map of Palau with inset study sites: i) eastern sites *1* Lighthouse Reef, *2* Ngederrak South, *3* Ngederrak North, *4* Beluu Lukes, *5* East Sheltered, *6* Short Drop Off, and ii) western sites *7* New Drop Off, *8* Ngercheu

image analysis software Coral Point Count (Kohler and Gill 2006). Estimates of structural complexity were obtained by using a measuring stick and calculating the distance between the lowest and highest points within each quadrat (Harborne et al. 2012).

Herbivore biomass

Roving herbivorous fish assemblages (including Acanthuridae, Scaridae, and Siganidae) were surveyed in March 2012 and February 2013 using ten replicate 30 m × 4 m transects per site. All surveys were conducted by the same observer (PJM). The identity, life phase (terminal, intermediate, and juvenile phases), and body length (i.e., total length to the nearest cm) were recorded for each individual. The lengths of individual fish were converted to biomass based on allometric scaling relationships.

Statistical analysis

Two-tailed *t* tests were used to compare differences in coral cover, *Liagora* cover, structural complexity, and herbivore biomass within sites before (March 2012) and after the typhoon using the 'stats' package in R (R Development Core Team 2014). Sites were categorised as 'impacted' where a significant decline in coral cover was observed between 2012 and 2013 surveys.

A generalised linear model (GLM) was used to test for the significance of the intensity of typhoon disturbance (i.e., change in coral cover before and after the typhoon), changes in absolute herbivory (i.e., changes in herbivore biomass before and after the typhoon), grazing intensity (i.e., herbivore biomass following the typhoon standardised to per cent grazeable area of substrate), and changes in productivity (i.e., wave exposure following the typhoon) on the extent of *Liagora* blooms (per cent cover) in R using the 'nlme' package (Pinheiro et al. 2014). Multicollinearity between predictors was tested using variance inflation factors. Where the variance inflation factor exceeded 10, predictors were examined and removed from the model (Kutner et al. 2004). Given the spatial distribution of our sites, we tested for spatial autocorrelation (Moran 1950) with Moran's *I* tests in R using the 'ape' package (Paradis et al. 2004) following an 'as the fish swims' approach (Little et al. 1997) by calculating the shortest in-water path between two sites. Spatial structure was confirmed using variograms and incorporated into the model using a gaussian correlation structure in R using the 'nlme' package (Pinheiro et al. 2014). Wave exposure was transformed using a power function to ensure normality of the residuals prior to the analyses. Model selection was conducted by selecting the lowest Akaike's Information Criterion results, and the degree of multicollinearity tested using variance inflation factor for each predictor. For each model, R^2 was calculated and adjusted for the number of fixed effects and correlation structure parameters in R using the 'lmmfit' package (Maj 2011). To provide estimates of effect sizes, the overall variation in the best-fit model was partitioned among predictors of *Liagora* cover and expressed as a proportion of the total variance.

Regional dynamics of *Liagora* blooms

To explore the potential effect of wave exposure in driving *Liagora* blooms at a regional scale, we took advantage of data collected during long-term monitoring surveys by the Palau International Coral Reef Center (PICRC) at existing exposed 'outer-reef' monitoring sites (Golbuu et al. 2012) during (January–March 2013; ESM Fig. S2) and prior (October 2012) to the *Liagora* bloom. Benthic cover at 3 m depth was assessed using 0.25 m^2 photoquadrats taken with a digital camera (Sea & Sea 2G, DX-2G) at each metre of a 50 m transect (totalling 50 photos per transect), with five replicate transects per site. Per cent cover of coral and *Liagora* within sites was determined from five points randomly placed in every quadrat photo (i.e., 250 points $transect^{-1}$) using the image analysis software Coral Point Count (Kohler and Gill 2006).

To quantify the impact of Typhoon Bopha at a regional scale, monitoring sites were categorised into either impacted sites (i.e., loss of coral cover and structural complexity resulting from Typhoon Bopha), or unimpacted sites (i.e., no visible loss of coral cover or structural complexity resulting from Typhoon Bopha) based upon post-typhoon surveys. The cover of *Liagora* estimated in regional surveys was not directly comparable to local surveys due to (1) differences in depth (3 vs. 5 m), (2) differences in sampling methods (transects vs. random quadrats), and (3) differences in the timing of surveys. Therefore, we used a presence/absence approach for regional surveys, where *Liagora* was considered either absent or in bloom among sites (ESM Fig. S2). A binomial GLM using a bias-reduction method in R using the 'brglm' package (Kosmidis 2013) was used to determine whether wave exposure would predict the presence of *Liagora* blooms, using wave exposure as the fixed predictor and *Liagora* presence as the response variable.

Results

Pre-disturbance patterns of benthic structure and herbivore biomass (2012)

Surveys in 2012, prior to the Typhoon Bopha, revealed high coral cover across all eight sites ranging from 21.9 ± 3 %

(average ± SE) at 'New Drop Off' on the western coast to a maximum of 79 ± 4 % coral cover at 'Lighthouse Reef' on the eastern coast (Table 1). Coral cover was dominated by branching and tabular acroporids at Sites 1–5 (Fig. 2a, c) with *Pocillopora* and small *Porites* colonies dominating Sites 6–8. Structural complexity ranged from 20.6 to 45.4 cm (Table 1) and was positively related to increasing coral cover ($R^2 = 0.88$, $F_6 = 44.68$, $p < 0.001$).

Levels of macroalgal cover were generally low across all sites (<2 %) and comprised mainly of *Halimeda* spp. underneath branching acroporid canopies. *Liagora* was entirely absent in 2012 surveys at all sites. Herbivore biomass ranged from 687 ± 91 g 120 m^{-2} at 'Ngederrak North' on the eastern reefs of Palau to a maximum of 7965 ± 1952 g 120 m^{-2} at 'New Drop Off' on the western reefs.

Post-disturbance patterns of benthic structure and herbivore biomass (2013)

Repeat surveys in 2013 following Typhoon Bopha revealed substantial losses in coral cover among the eastern sites (Fig. 2b, d, e). Impacted sites were characterised by significant losses of coral, ranging between −8.9 and −78.9 % absolute change in coral cover between 2012 and 2013 (Table 1; Fig. 3a). Per cent change in structural complexity between 2012 and 2013 was significantly and linearly related to absolute change in coral cover between 2012 and 2013 ($R^2 = 0.89$, $F_6 = 45.31$, $p < 0.001$), in that sites with the highest loss of coral cover suffered the greatest loss of structural complexity. Declines in structural complexity were highest at the most impacted sites, ranging between −58 and −72 %, while a non-significant increase in structural complexity was recorded at the least impacted site (Fig. 3).

Liagora blooms were observed at some, but not all impacted sites (Fig. 2f) and ranged from 0.14 ± 0.15 to 43.6 ± 5.1 % (Table 1; Fig. 3a). Repeat surveys of herbivores in 2013 demonstrated no significant differences in herbivore biomass compared to 2012 (Fig. 3c), with the exception of 'Beluu Lukes' where herbivore biomass declined 2.3-fold between 2012 and 2013 ($t = 5.53$, $df = 14$, $p < 0.001$; Fig. 3c).

Wave exposure

Analysis of the wind patterns and wave exposure following Typhoon Bopha indicated strong winds from the northeast, resulting in a high degree of exposure for eastern reefs, while the western reefs were relatively sheltered from wave action (Fig. 1). Eastern sites, however, experience heterogeneity in wave exposure patterns due to the complexity of the coastline in the area, with westernmost sites (Sites 1–4) showing the highest exposure (Fig. 1).

Environmental drivers of *Liagora* abundance following disturbance

Wave exposure significantly predicted *Liagora* cover ($p < 0.001$, $R^2 = 0.61$), which followed a power function ($y = ax^b$) such that impacted and non-impacted sites with exposure of <3 J m^{-3} did not experience *Liagora* blooms; impacted sites with exposure >3 J m^{-3} experienced blooms of *Liagora* ranging from 10.4 to 43.6 % (Fig. 4). Results from model simplification (Table 2) indicate that, while the best-fit model based on AIC also included herbivore biomass and change in coral cover ($R^2 = 0.69$), neither of these were significant predictors of *Liagora* cover ($p > 0.1$; Table 3). Variance inflation factors indicated that none of the predictors were highly correlated (Table 2). Partitioning the variance of the best-fit model among predictors indicated that wave exposure explained nearly all of the variance within the final model, whereas herbivore biomass (2.0 %) and change in coral cover (6.6 %) explained substantially less variance in the final model.

Regional dynamics of post-disturbance *Liagora* blooms

No *Liagora* was recorded at any sites throughout the region prior to the Typhoon Bopha. Consistent with our local-scale

Table 1 Percent coral cover, *Liagora* cover, and structural complexity (Δ height in cm) for sites in 2012 and 2013 (average ± SE)

Side	Reef	Coral cover		*Liagora* cover		Structural complexity	
		2012	2013	2012	2013	2012	2013
East	(1) Lighthouse Reef	79.0 ± 3.7	0	0	43.6 ± 5.1	45.4 ± 3	18.9 ± 2
East	(2) Ngederrak South	77.2 ± 4.7	2.5 ± 2.1	0	36.7 ± 4.7	40.4 ± 2	9.9 ± 1
East	(3) Ngederrak North	74.5 ± 3.6	1.1 ± 0.5	0	10.4 ± 3.2	44.5 ± 2	12.6 ± 2
East	(4) Beluu Lukes	57.5	4.1	0	0	34.6 ± 2	9.9 ± 1
East	(5) East Sheltered	70 ± 4.7	73.6 ± 4.1	0	0	39.5 ± 2	47.7 ± 3
East	(6) Short Drop Off	23.9 ± 4.6	15.1 ± 2.1	0	0.14 ± 0.15	20.6 ± 2	26.0 ± 2
West	(7) New Drop Off	21.9 ± 2.8	20.5 ± 3	0	0	22.1 ± 2	25.6 ± 1
West	(8) Ngercheu Reef	45.4 ± 4.3	42.3 ± 3.2	0	0	38.4 ± 3	36.4 ± 3

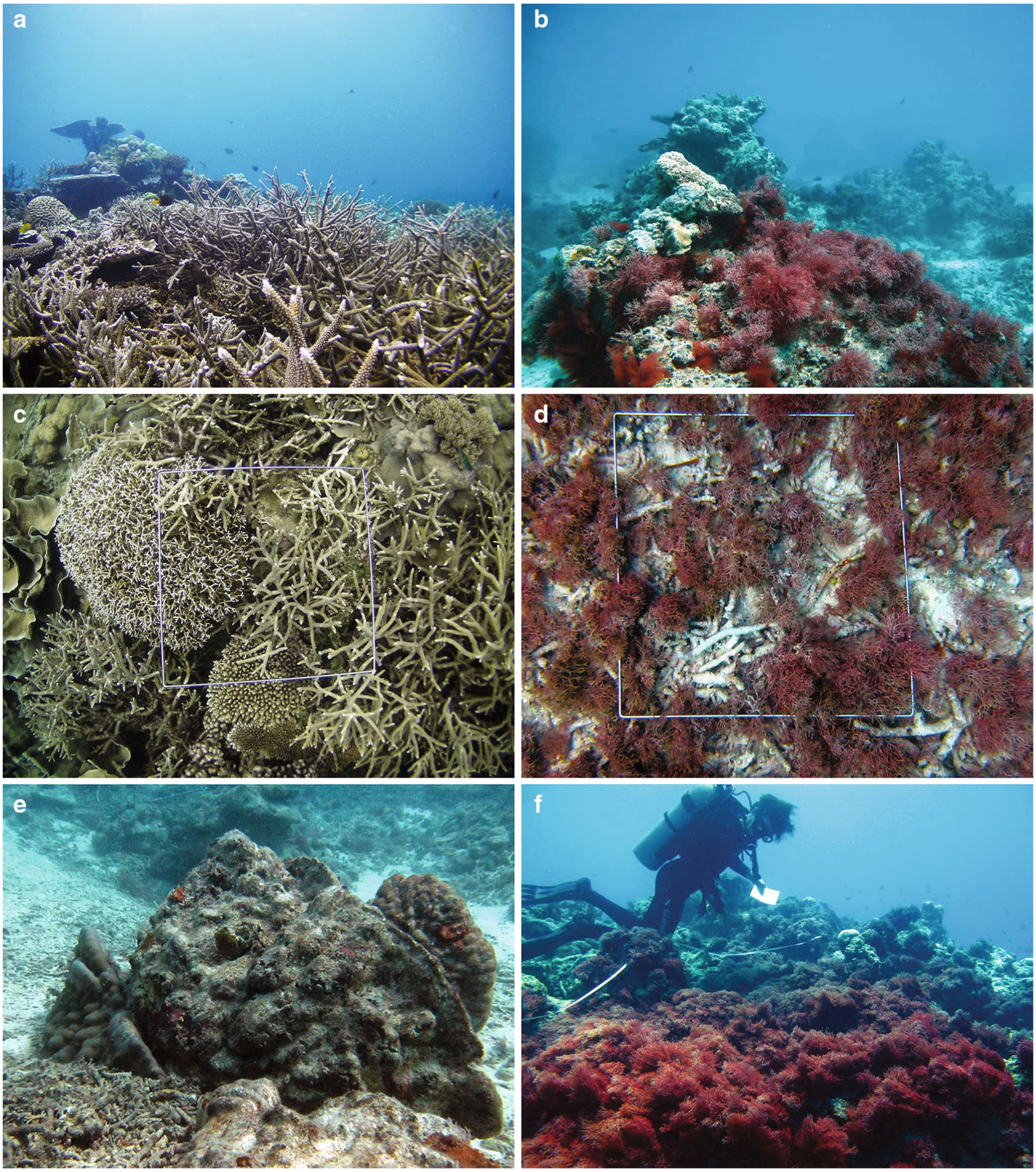

Fig. 2 **a** High coral cover at Lighthouse Reef in March 2012, **b** post-typhoon at Lighthouse Reef in February 2013, **c** near 100 % cover of coral pre-typhoon at Lighthouse Reef in March 2012, **d** ~40 % cover of *Liagora* and acroporid rubble at Lighthouse Reef in February 2013, **e** partially buried massive *Porites* colonies (1–2 m height) overturned by typhoon waves, **f** extensive *Liagora* blooms at Ngederrak South in February 2013

surveys, significant damage was observed across the eastern reefs following the typhoon. Survey sites that were unaffected by Typhoon Bopha with low wave exposure (<3 J m^{-3}, $n = 7$) showed no *Liagora* blooms (Fig. 5). Impacted sites with high wave exposure (>3 J m^{-3}) throughout the Palau Archipelago ($n = 4$) exhibited blooms of *Liagora* (Fig. 5) of >10 % cover (ESM Fig. S2). The binomial model indicated that wave exposure (power transformed) was a significant predictor of *Liagora* blooms ($Z = 1.987$, $p < 0.05$).

Discussion

A broad range of factors can influence succession and recovery of terrestrial and marine ecosystems following disturbance, such as competition (Dayton 1971), herbivory (Chapman and Johnson 1990), recurrent disturbance events (Connell et al. 1997), and environmental stress (Menge and Sutherland 1987). Favourable environmental conditions can modulate patterns of recovery by increasing

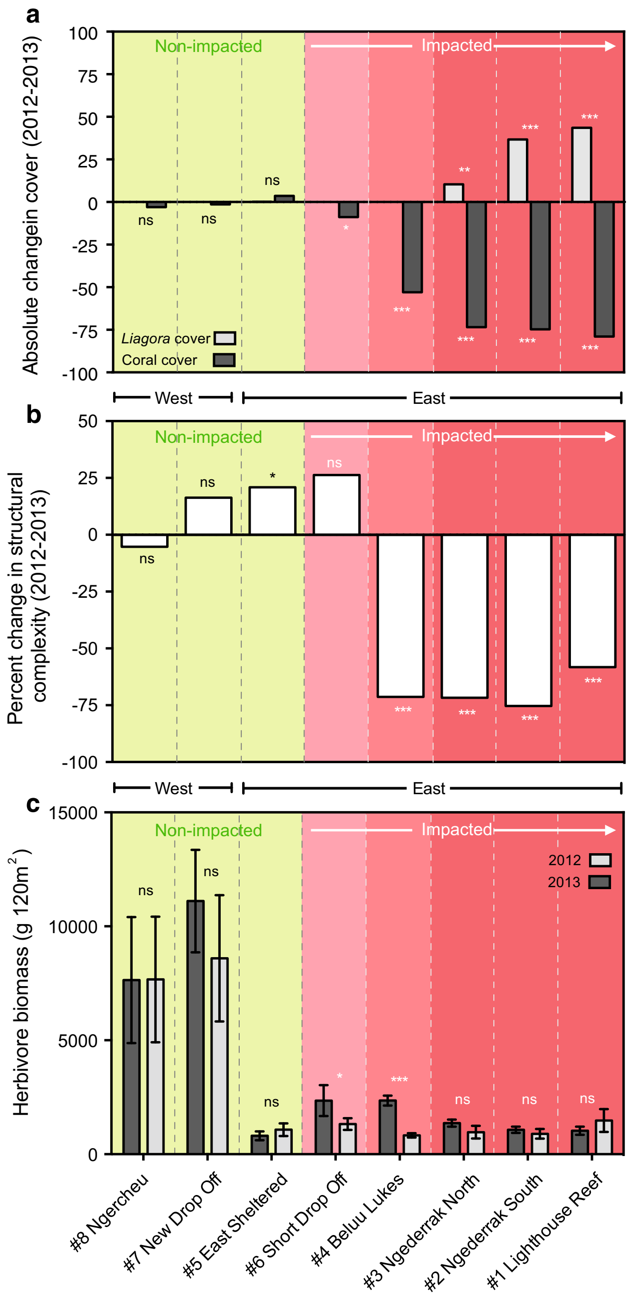

Fig. 3 **a** Absolute change in coral cover (*dark grey bars*) and *Liagora* (*light grey bars*) between 2012 and 2013, **b** per cent change in structural complexity between 2012 and 2013, and **c** total herbivore biomass among sites in 2012 surveys (*light grey bars*) and 2013 (*dark grey bars*). *Green shading* indicates sites unaffected by the typhoon and *red shading* indicates an increasing impact of typhoon disturbance among sites as measured by significant changes in coral cover. Annotations are the results of pairwise comparisons (*t* tests) between 2012 and 2013 (*ns* non-significant, $*p < 0.05$; $**p < 0.01$, $***p < 0.001$)

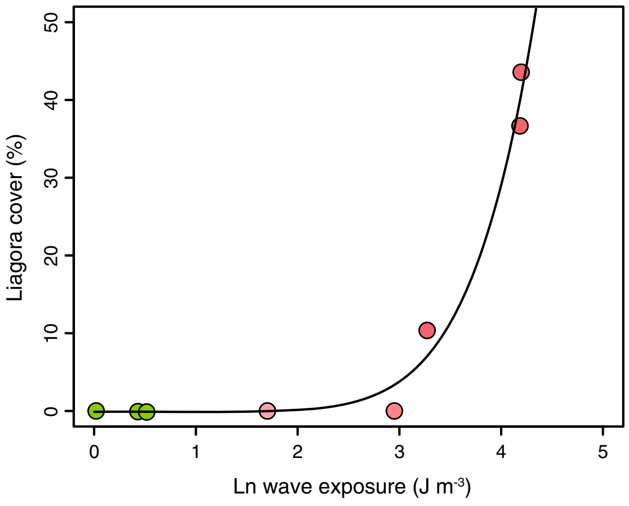

Fig. 4 Relationship between wave exposure and *Liagora* cover among sites ($y = ax^{b}$, $R^2 = 0.61$, $p < 0.001$). *Green shading* indicates sites unaffected by the typhoon and *red shading* indicates an increasing impact of typhoon disturbance among sites as measured by significant changes in coral cover

Table 2 Results from model simplification of linear mixed effects models, where ‘I(exposure^2)’ = power transformation of exposure, ‘biomass’ = absolute change in herbivore biomass, ‘δerbivor’ = herbivore biomass standardised to per cent grazeable area, and ‘Δcoral’ = per cent change in coral cover between 2012 and 2013 surveys, + is an additional term, the superscript number above the predictor variable is the variance inflation factor test result, and R^2 is the adjusted R^2

Model predictors	AIC	R^2
I(exposure^2)$^{2.6}$ + Δcoral$^{2.1}$ + δbiomass$^{1.5}$	62.4	0.67
I(exposure^2)$^{2.7}$ + Δcoral$^{2.7}$ + biomass$^{1.6}$	**59.4**	**0.69**
I(exposure^2)$^{1.5}$ + Δcoral$^{1.5}$	69.4	0.66
I(exposure^2)$^{1.5}$ + biomass$^{1.5}$	64.5	0.57
I(exposure^2)$^{1.5}$ + δbiomass$^{1.5}$	65.1	0.59
I(exposure^2)	64.3	0.61

Final model highlighted in bold

Table 3 Best-fit result from linear mixed effects models (see Table 2), where ‘I(exposure^2)’ = power transformation of exposure, ‘biomass’ = herbivore biomass, and ‘Δcoral’ = per cent change in coral cover between 2012 and 2013 surveys

Predictor	Value	SE	*t* value	*p* value
Intercept	−9.556	13.514	−0.71	>0.05
I(exposure^2)	2.640	0.279	9.47	<0.01
Biomass	0.057	0.185	0.31	>0.5
ΔCoral	0.191	0.086	2.22	>0.1

reproductive output (e.g., Nylehn and Totland 1999) and recruitment success (e.g., Edwards 2004), or by driving growth and expansion of existing patches of vegetation (e.g., Angelini and Silliman 2012). Conversely, adverse environmental conditions can be detrimental to post-disturbance recovery by impacting reproductive output (e.g.,

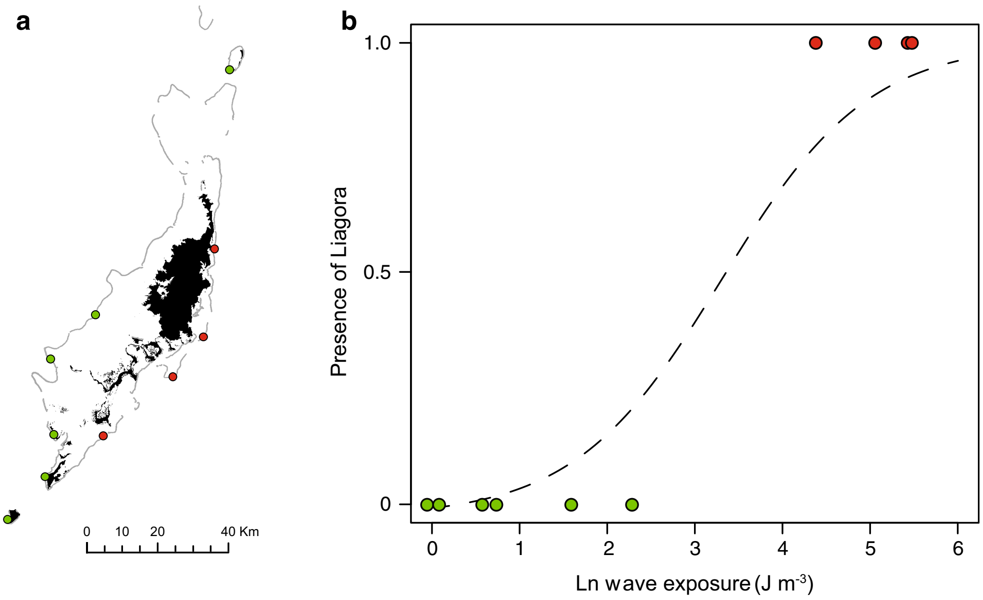

Fig. 5 **a** Map of long-term monitoring sites ($n = 10$) throughout the Palau archipelago (*green symbols* minimal typhoon impact, *red symbols* high typhoon impact), **b** binomial fit of wave exposure and presence of *Liagora*

Matson and Edwards 2007), altering patterns of competition and succession (e.g., Thompson and Naeem 1996), and affecting growth of surviving individuals (e.g., Larcher 2000). Here, we report a shift to a macroalgal dominance following catastrophic disturbance in a coral reef ecosystem, which was primarily correlated with wave exposure.

In the aftermath of the catastrophic disturbance upon the eastern reefs of Palau in the wake of Typhoon Bopha, we documented a transition from high coral cover to dominance of a monospecific macroalga, *Liagora*. Such blooms are thought to be triggered by a temporary relaxation of herbivory and/or nutrient pulses resulting from sediment recycling on the benthos (Hughes 1994; Scheffer et al. 2008). Yet, the drivers responsible for sustaining *Liagora* blooms are largely unknown. Several factors could be responsible for influencing the magnitude of *Liagora* blooms following Typhoon Bopha. Firstly, reductions in herbivore biomass following disturbance could have resulted in a reduction in grazing pressure (Mumby 2006), causing a proliferation of *Liagora*. Secondly, catastrophic losses of coral cover associated with Typhoon Bopha would have increased the amount of grazeable substrate available to herbivores (Mumby and Steneck 2008), causing a decrease in grazing pressure regardless of changes in herbivore biomass. Thirdly, wave exposure may have been directly responsible for driving *Liagora* blooms, in that *Liagora* cover would be greater in higher productivity sites. These hypotheses are discussed below.

Following Typhoon Bopha, wave damage resulted in extensive and significant coral losses at some, but not all eastern sites. Previous thickets of highly diverse, branching and tabular acroporids were reduced to rubble resulting in a rapid opening up of benthic space for algal colonisation. Within 3 months following extensive coral loss, *Liagora* cover was high at impacted sites, reaching upwards of >40 % cover at ‘Lighthouse Reef’ and >20 % at ‘Ngederrak South’. Such rapid macroalgal growth is surprising, considering that the levels of herbivore biomass in Palau are some of the highest in the Indo-Pacific (Mumby et al. 2013), two of our sites (North and South Ngederrak) were situated inside a no-entry/no-take marine reserve established in 2001, and that *Liagora* is readily consumed by herbivorous fish in feeding assays (Rasher and Hay 2010). Comparisons of surveys before and after the typhoon revealed no consistent differences in herbivore biomass, suggesting that herbivore assemblages did not decline as a result of the loss of coral cover or structural complexity, nor increase in response to increased macroalgal cover. Further, the results of our model also support the notion that changes in herbivore biomass did not significantly influence the extent of *Liagora* blooms, as herbivore biomass explained only a minor contribution to the overall variance (2.0 %), and was not significantly related to per cent cover of *Liagora* within sites.

While no significant changes in herbivore biomass were observed following the typhoon, as grazing intensity is inversely linked to the area of grazable substrate on reefs (Mumby and Steneck 2008), the rapid loss of coral cover at impacted sites most likely resulted in a near instantaneous relaxation of grazing intensity. Consequently, a successful recruitment pulse may saturate an area and escape grazing (Vadas et al. 1992; Doropoulos et al. 2013), enhancing the likelihood of establishment of macroalgal propagules. Yet, a reduction in grazing intensity brought about by a loss of coral cannot easily explain the magnitude of *Liagora* bloom at some of the typhoon-impacted sites. Despite a profound loss of coral at 'Beluu Lukes' (57–4 % cover) and a less severe, but still significant loss of coral at 'Short Drop Off' (24–15 % cover), *Liagora* failed to bloom (0 % cover), even though herbivore biomass declined 2.8-fold at 'Beluu Lukes' and 1.8-fold at 'Short Drop Off' following the typhoon. In contrast, near-complete loss of coral at 'Lighthouse Reef' and 'Ngderrak Reef' resulted in substantial blooms of *Liagora*. Further, herbivore biomass standardised to grazeable area was not a significant predictor of *Liagora* cover. Collectively, these results suggest that top-down controls (loss of herbivory or a change in available grazing area) were not directly responsible for the observed pattern of *Liagora* blooms following Typhoon Bopha.

By mapping the spatial patterns of wave exposure in the months following Typhoon Bopha, our results indicate that the extent of *Liagora* blooms (i.e., percentage cover) was strongly related to the degree of wave exposure at local scales, explaining >90 % of the variance in our model. While change in coral cover (2012–2013) explained a minor contribution to the overall variance (6.6 %), this was not significantly related to the cover of *Liagora* within sites, suggesting that the impact of the typhoon on loss of coral cover alone was not sufficient to trigger *Liagora* blooms. Indeed, despite a profound loss of coral at Beluu Lukes (from 57 to 4 %), wave exposure was insufficient to trigger a bloom of *Liagora*, while at impacted sites with high wave exposure (>3 J m^{-3}), substantial *Liagora* blooms were observed.

At regional scales, maps of wave exposure successfully predicted the presence of *Liagora* blooms at additional monitoring sites located throughout the entire Palauan archipelago (~ 150 km). Consistent with our local-scale studies, *Liagora* blooms were observed at sites with high wave exposure following the typhoon (>3 J m^{-3}). These results corroborate our local-scale results and further highlight the deterministic nature of *Liagora* blooms across broad spatial scales. The presence of blooms at remote sites throughout the Palau archipelago suggests that nutrients from terrestrial catchments cannot account for the observed pattern of *Liagora* blooms at a regional scale. Furthermore, as no *Liagora* was observed at any of our sites in Palau during extensive surveys in 2012, it is unlikely that post-disturbance blooms resulted from growth and expansion of remnant *Liagora* holdfasts. While these results demonstrate the importance of wave exposure in driving regional patterns of *Liagora* blooms following disturbance in the Indo-Pacific, future studies should be conducted in different biogeographic regions (e.g., Caribbean) and under varying wave exposure regimes for different macroalgal assemblages to test the generality of our results.

Water motion has long been recognised as a key factor influencing the growth of marine macroalgae (Leigh et al. 1987) through a range of direct and indirect responses (see Hurd 2000 for a concise review). Primarily, flow rates affect the boundary layer between the marine environment and the plant surface and influence the rates of mass transfer. High flow rates reduce the thickness of the boundary layer and increase rates of mass transfer (Carpenter et al. 1991). Mass transfer rates in turn enhance the metabolic functioning of algae (Munk and Riley 1952) through enhanced carbon exchange and fixation (Wheeler 1980), nitrogenase activity (Carpenter et al. 1991), and nitrate uptake (Gerard 1982). Experimental studies in giant kelp (*M. pyrifera*) indicate that the effect of flow on metabolism is substantial, with photosynthetic output increased by a factor of 300 % by increasing water speeds from 0 to 4 cm s^{-1} (Wheeler 1980). Field measurements indicate that growth of kelp blades is ~4 times higher in wave-exposed sites than in sheltered sites (Hepburn et al. 2007). Considering the significant relationship between wave exposure and *Liagora* cover in the present study and the absence of *Liagora* in sheltered sites, our results indicate that higher wave-driven productivity at exposed sites enhances the occurrence of *Liagora* blooms. These results are consistent with higher rates of productivity and calcification on windward than on leeward coral reefs (Marsh 1970; Barnes 1983). Further experimental studies are needed to determine the exact physiological mechanisms by which *Liagora* responds to increased wave exposure.

While our results imply that changes in herbivore biomass and grazing intensity were not directly linked to the proliferation of *Liagora* following disturbance, it seems plausible that wave action may have an interactive effect with herbivory in modulating algal dynamics. Increased wave exposure affects swimming performance in coral reef fish assemblages (Fulton et al. 2005), directly affecting grazing rates and foraging patterns in herbivores (Foster 1987) that may well have influenced the post-disturbance dynamics of *Liagora* blooms in our study. Similarly, resuspension of sediments at higher exposures may suppress herbivory following disturbance (Goatley and Bellwood 2013), providing an escape from herbivory and enabling proliferation of *Liagora* at exposed sites. While we hypothesise that wave exposure is the primary driver of *Liagora* dynamics post-disturbance, we suggest that further studies are needed to separate the potential interactive effects between herbivory and wave exposure in driving post-disturbance macroalgal dynamics.

As the frequency and intensity of disturbance on ecosystems increases (Scheffer et al. 2001; Folke et al. 2004), understanding factors that influence post-disturbance dynamics is of increasing importance. Our results highlight the relevance of environmental drivers in modulating the recovery of ecosystems following disturbance by driving phase shifts to macroalgal dominance. While ephemeral in nature, the post-disturbance *Liagora* blooms resulted in a range of direct and indirect effects, further impacting the recovery of coral assemblages following Typhoon Bopha. During our study, canopies of *Liagora* were observed to cause direct mortality of the few corals that survived the typhoon through direct contact and abrasion, reducing already fragmented surviving populations. Further surveys following Typhoon Bopha revealed that, while coral recruitment was recorded at low exposure sites where *Liagora* was absent, a near-complete recruitment failure was observed at high exposure sites dominated by *Liagora* blooms (Doropoulos et al. 2014), indicating indirect and lasting effects on coral recovery (Dixon et al. 2014). Unlike other parameters influencing macroalgal growth (e.g., herbivore biomass), wave exposure is consistent, predictable, and can be easily mapped requiring only information on the configuration of the coastline and the prevailing wind patterns (Ekebom et al. 2003; Chollett and Mumby 2012). The deterministic nature of blooms means that the vulnerability of reefs to phase shifts can be mapped at a scale that is useful for management allowing conservation strategies to prioritise restoration efforts at regional scales (Holl and Aide 2011). For example, if blooms of *Liagora* coincide with annual coral spawning events, targeting high exposure areas by removing *Liagora* could facilitate recruitment and recovery of reefs following catastrophic disturbance.

Acknowledgments We thank the topic Editor and two anonymous reviewers whose comments significantly improved the quality of the manuscript. This study was funded by a Laureate Fellowship from the Australian Research Council to P.J.M. Additional funding was provided by a Pew Fellowship in Marine Conservation and the EU FORCE project through the European Union 7th Framework programme (P7/2007–2013) under grant agreement No. 244161. C.D. was supported by an Australian Endeavour Award Postdoctoral Fellowship, during which time he was hosted by the Palau International Coral Reef Center.

References

Angelini C, Silliman BR (2012) Patch size-dependent community recovery after massive disturbance. Ecology 93:101–110

Barnes DJ (1983) Profiling coral reef productivity and calcification using pH and oxygen electrodes. J Exp Mar Bio Ecol 66:149–161

Battista TA, Costa BM, Anderson SM (2007) Shallow water benthic habitats of the Republic of Palau (DVD). NOAA Technical Memorandum NOS NCCOS 59, Biogeography Branch. Silver Spring, MD

Bruno J, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS One 2:e711

Carpenter RC, Hackney JM, Adey WH (1991) Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol Oceanogr 36:40–49

Chapman ARO, Johnson CR (1990) Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. Hydrobiologia 192:77–121

Chollett I, Mumby PJ (2012) Predicting the distribution of *Montastraea* reefs using wave exposure. Coral Reefs 31:493–503

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

D'Angelo C, Wiedenmann J (2014) Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Curr Opin Environ Sustain 7:82–93

Dayton PK (1971) Competition, disturbance, and community organization - provision and subsequent utilization of space in a rocky intertidal community. Ecolog Monogr 41:351–389

Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol Monogr 45:137–159

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A 109:17995–17999

Dixon DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery. Science 345:892–897

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132

Doropoulos C, Hyndes G, Abecasis D, Verges A (2013) Herbivores strongly influences algal recruitment in both coral and algal dominated coral reef habitats. Mar Ecol Prog Ser 486:153–164

Doropoulos C, Roff G, Zupan M, Nestor V, Isechal AL, Mumby PJ (2014) Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. Coral Reefs 33:613–623

Edmunds PJ, Witman JD (1991) Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St John, United States Virgin Islands. Mar Ecol Prog Ser 78:201–204

Edwards MS (2004) Estimating scale-dependency in disturbance impacts: El Ninos and giant kelp forests in the northeast Pacific. Oecologia 138:436–447

Ekebom J, Laihonen P, Suominen T (2003) A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. Estuar Coast Shelf Sci 57:887–898

Fenner DP (1991) Effects of Hurricane Gilbert on coral reefs, fishes and sponges at Cozumel, Mexico. Bull Mar Sci 48:719–730

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581

Foster SA (1987) The relative impacts of grazing by Caribbean coral reef fishes and *Diadema* - the effects of habitat and surge. J Exp Mar Bio Ecol 105:1–20

Fulton CJ, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance shape coral reef fish assemblages. Proc R Soc Lond B Biol Sci 272:827–832

Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gerard VA (1982) In situ water motion and nutrient-uptake by the giant-kelp *Macrocystis pyrifera*. Mar Biol 69:51–54

Goatley CHR, Bellwood DR (2013) Ecological consequences of sediment on high-energy coral reefs. PLoS One 8:e77737

Golbuu Y, Wolanski E, Idechong JW, Victor S, Isechal AL, Oldiais NW, Idip D, Richmond RH, van Woesik R (2012) Predicting coral recruitment in Palau's complex reef archipelago. PLoS One 7:e50998

Harborne AR, Mumby PJ, Ferrari R (2012) The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. Environ Biol Fishes 94:431–442

Hepburn CD, Holborow JD, Wing SR, Frew RD, Hurd CL (2007) Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. Mar Ecol Prog Ser 339:99–108

Heron SF, Metzger EJ, Skirving WJ (2006) Seasonal variations of the ocean surface circulation in the vicinity of Palau. J Oceanogr 62:413–426

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecol Manag 261:1558–1563

Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hurd CL (2000) Water motion, marine macroalgal physiology, and production. J Phycol 36:453–472

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259–1269

Kosmidis I (2013) brglm: Bias reduction in binomial-response Generalized Linear Models. R package version 0.5-9. http://www.ucl.ac.uk/~ucakiko/software.html

Kutner MH, Nachtsheim CJ, Neter J (2004) Applied linear regression models, 4th edn. McGraw-Hill/Irwin, Chicago

Larcher W (2000) Temperature stress and survival ability of Mediterranean sclerophyllous plants. Plant Biosyst 134:279–295

Leigh EG, Paine RT, Quinn JF, Suchanek TH (1987) Wave energy and intertidal productivity. Proc Natl Acad Sci U S A 84:1314–1318

Levin SA, Lubchenco J (2008) Resilience, robustness, and marine ecosystem-based management. Bioscience 58:27–32

Little LS, Edwards D, Porter DE (1997) Kriging in estuaries: as the crow flies, or as the fish swims? J Exp Mar Bio Ecol 213:1–11

Maj A (2011) lmmfit: Goodness-of-fit-measures for linear mixed models with one-level-grouping. R package version 1.0

Marsh JA (1970) Primary productivity of reef-building calcareous red algae. Ecology 51:255–263

Matson PG, Edwards MS (2007) Effects of ocean temperature on the southern range limits of two understory kelps, *Pterygophora californica* and *Eisenia arborea*, at multiple life-stages. Mar Biol 151:1941–1949

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367

Mcquaid CD, Branch GM (1985) Trophic structure of rocky intertidal communities - response to wave action and implications for energy-flow. Mar Ecol Prog Ser 22:153–161

Menge BA, Sutherland JP (1987) Community regulation - variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. Am Nat 130:730–757

Moran PAP (1950) Notes on continuous stochastic phenomena. Biometrika 37:17–23

Mumby PJ (2006) The impact of exploiting grazers (scaridae) on the dynamics of Caribbean coral reefs. Ecol App 16:747–769

Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs 28:761–773

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563

Mumby PJ, Bejarano S, Golbuu Y, Steneck RS, Arnold SN, van Woesik R, Friedlander AM (2013) Empirical relationships among resilience indicators on Micronesian coral reefs. Coral Reefs 32:213–226

Munk WH, Riley GA (1952) Absorption of nutrients by aquatic plants. J Mar Res 11:215–240

Nylehn J, Totland O (1999) Effects of temperature and natural disturbance on growth, reproduction, and population density in the alpine annual hemiparasite Euphrasia frigida. Arct Antarct Alp Res 31:259–263

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290

Pinheiro J, Bates D, DebRoy S, Sanker D (2014) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-117

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rasher DB, Hay ME (2010) Chemically rich seaweeds poison corals when not controlled by herbivores. Proc Natl Acad Sci U S A 107:9683–9688

Renken H, Mumby PJ, Matsikis I, Edwards HJ (2010) Effects of physical environmental conditions on the patch dynamics of *Dictyota pulchella* and *Lobophora variegata* on Caribbean coral reefs. Mar Ecol Prog Ser 403:63–74

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends Ecol Evol 27:404–413

Scheffer M, van Nes EH, Holmgren M, Hughes T (2008) Pulse-driven loss of top-down control: The critical-rate hypothesis. Ecosystems 11:226–237

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Thompson LJ, Naeem S (1996) The effects of soil warming on plant recruitment. Plant Soil 182:339–343

Vadas RL, Johnson S, Norton TA (1992) Recruitment and mortality of early post-settlement stages of benthic algae. Eur J Phycol 27:331–351

Wernberg T, Thomsen MS (2005) The effect of wave exposure on the morphology of Ecklonia radiata. Aquat Bot 83:61–70

Wheeler WN (1980) Effect of boundary-layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. Mar Biol 56:103–110

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755