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Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics

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ABSTRACT

With increasing stressors to coral reefs, defining tools that evaluate their dynamics and resilience is important to interpret system trajectories and direct conservation efforts. In this context, surveys must go beyond conventional monitoring approaches that focus on abundance and biomass of key groups and quantify metrics that better assess ecological processes and ecosystem trajectories. By measuring a variety of conventional (e.g. proportional cover of broad benthic groups, biomass of herbivorous fish) and complementary resilience-based metrics (e.g. algal turf height, coral recruitment rates, juvenile coral densities, herbivorous fish grazing rates), this study evaluated the ecosystem responses to community-based management in Fiji. The study was conducted across three paired *tabu* areas (periodically closed to fishing) and adjacent fished sites. Conventional metrics reflected no management effect on benthic or herbivorous fish assemblages. In contrast, the complementary metrics generally indicated positive effects of management, particularly within the benthos. Significant differences were observed for turf height (33% lower), coral recruitment rate (159% higher) and juvenile coral density (42% higher) within areas closed to fishing compared to adjacent open reefs. In addition, turf height was inversely related to coral recruitment and juvenile coral density, and longer turfs (≥ 5 mm) were more competitive in interaction with corals. These results emphasise that conventional metrics may overlook benefits of local management to inshore reefs, and that incorporating complementary resilience-based metrics such as turf height into reef survey protocols will strengthen their capacity to predict the plausible future condition of reefs and their responses to disturbances.

1. Introduction

The status of ecosystems over space and time has long been used as criterion for prioritisation and decision-making in conservation planning. Historically, ecosystem assessments have typically focused on quantifying common status metrics such as biomass and abundance of target groups, as well as species diversity (e.g. Yoccoz et al., 2001). Although such assessments offer the advantage of relying on generally fast and relatively simple estimation methods, their capacity to convey quantitative information on ecosystem function is limited (Wright et al.,

2006). It is thus important to identify indicators of dynamic processes to capture a further facet that may help to anticipate the likely trajectory of ecosystems over time and in response to disturbances (Glaser et al., 2012). If such indicators can be practically and cost-effectively integrated into ecosystem assessments, there is scope for (i) evaluating the effectiveness of conservation tools (e.g. marine reserves) more thoroughly, (ii) better understanding the impact of disturbances, and (iii) supporting managers in decision-making (high vs. low-risk conservation investments).

Anticipating trajectories of complex and diverse ecosystems such as

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coral reefs is particularly challenging due to the large number of species fulfilling various functions and responding differently to a changing environment (Pandolfi, 2015). Conventional coral reef monitoring protocols focus on measuring cover of broad benthic groups, as well as fish biomass along replicate transects. Percent cover of benthic organisms fails to provide information on important ecosystem functions for a variety of reasons. First, high live coral cover is generally interpreted as a sign of ecosystem health, and the contrary is assumed of high algal cover. Healthy reefs may however display variable levels of hard coral and fleshy algal cover depending on their location (Johannes et al., 1983; Kleypas et al., 1999; Couce et al., 2012). Just as low coral cover does not necessarily reflect unhealthy reefs, reefs dominated by live corals must not be unequivocally considered healthy and/or resilient (Mumby et al., 2014; Anthony et al., 2015). Second, the resolution at which benthic groups are defined differs strongly among studies. While a coarse resolution may suffice for an immediate broad diagnosis of benthic status and ecosystem service provision, it may impair the detection of relationships between particular benthic attributes and fish communities or behaviours (Mumby et al., 2013). Conventional assessments cannot, for instance, provide information on the colonisation processes of newly opened space. This space is usually recorded ambiguously as dead coral, bare rock, pavement or rubble (Harris, 2015), yet the settlement dynamics of coral larvae or algal propagules (among others) on available substrate determine the success of critical reef recovery processes. There are also limitations to how informative fish abundances are of the ecosystem functions that fishes sustain. Tidal changes, time of day, turbidity and variability among surveyors can lead to variations in the perceived fish abundance (Thompson and Mapstone, 2002; McClanahan et al., 2007), and some important species can be wary of divers and thus not encountered in fish censuses (Kulbicki, 1998). Stationary video cameras have consequently illuminated the previously unknown, yet crucial functional roles of species that tend to be rare in visual surveys (Hoey and Bellwood, 2009; Plass-Johnson et al., 2015). Conventional reef status assessments thus risk providing a superficial level of information that does not convey functionality and ecosystem robustness, and hence may not provide enough support for adaptive management decisions. Essentially, although conventional measures of abundance can provide an idea of the system's current state, they do not consider whether the system is most likely to improve or deteriorate over time and overlook important components of system resilience.

The likelihood of coral reefs changing over time and in response to disturbances is a product of many factors. In an attempt to improve predictions of these complex systems, several important ecological processes have been identified and alternative monitoring tools proposed (e.g. McClanahan et al., 2012). Benthic assessments are increasingly encouraged to consider more dynamic indicators that respond quickly to changes and drive system resilience, such as coral recruitment success, turf height and coral-algal interactions (Anthony et al., 2015; Flower et al., 2017). Furthermore, conventional benthic monitoring often applies broad categories such as 'dead coral' or 'rock' to describe seemingly 'free space' in the reef available for colonisation, while in reality very little space is actually free of benthic organisms. Rather, such substrate tends to be overgrown by a diverse assortment of early colonisers such as turf algae, benthic cyanobacteria or crustose coralline algae, which differ in their suitability for stony coral larvae to settle and survive, but are often not adequately captured in monitoring. To evaluate settlement dynamics on free space, hereon referred to as biotic substrate colonisation, surveys would benefit from refining the level of detail in which different benthic categories (e.g. algal turfs, crustose coralline algae, cyanobacterial mats) are recorded. One of the fastest colonisers of available substrates are algal turfs (Diaz-Pulido and McCook, 2002), yet their cover and intrinsic properties are often neglected in surveys (Harris, 2015; Flower et al., 2017). While algal turf cover itself may not be very informative, it can be a strong predictor of coral recruitment and subsequent development when combined with

turf height (Birrell et al., 2005; Mumby et al., 2013). For coral reef fish communities, efforts are increasingly invested towards monitoring key functional groups separately (Green and Bellwood, 2009) and quantifying herbivory (Fox and Bellwood, 2008; Rasher et al., 2013). Spatial, temporal and surveyor-related discrepancies, as well as differential species wariness (Kulbicki, 1998), imply that visual fish biomass surveys should be supported by: (i) remote video surveys, and (ii) parameters that reflect longer-term fish functions. The latter can include algal traits and prey behaviours in response to predatory fish (e.g. Vermeij et al., 2015).

Here we evaluate the effectiveness of local management using conventional reef status metrics in combination with a set of complementary metrics that have implications for system resilience. Conventional (e.g. percent cover of benthic groups, herbivorous fish biomass) and complementary resilience-based (e.g. algal turf height, coral recruitment, juvenile coral density, herbivorous fish grazing rates) metrics were quantified in paired inshore reefs open and closed to fishing within three locally managed marine areas (LMMAs) in Fiji. We hypothesised that a substantial discrepancy would be found when interpreting the level of effectiveness from these two different types of metrics, driven primarily by the limited resolution of conventional metrics. By quantifying the nature and magnitude of this discrepancy, we provide a more nuanced approach to evaluate the success of management. We also evaluate the informative value of measuring turf height in an inshore Pacific island reef setting by investigating its relationship with ecological processes that are critical for system resilience.

2. Material and methods

2.1. Study area

This study focused on three inshore reef sites within traditional fishing grounds (*qoliqoli*), namely Dakuibeqa (Beqa, Rewa Province), Nasinu (Ovalau, Lomaiviti Province) and Navakavu (Suva, Rewa Province; Fig. 1). Each *qoliqoli* contained a locally managed *tabu* area (periodically closed to fishing) that had been established for at least eight years. These locations were selected based on the premise that Fijian LMMAs represent a good example of effective community-based management (Techera, 2010; Weeks and Jupiter, 2013). All sites displayed similar characteristics regarding reef orientation (i.e. south-east facing) and topography. At paired reefs within and adjacent to each *tabu* area, surveys took place on both reef platforms (1–2 m depth) and lagoonal slopes (4–6 m depth), covering both inshore reef habitat types encompassed within all *tabu* areas. Surveys were carried out between September 2015 and February 2016.

2.2. Field surveys

2.2.1. Conventional reef status metrics

Conventional metrics of benthic and fish communities were quantified along transects at all survey sites (Table 1). Benthic surveys were carried out along three 30 m transects within each of the *tabu* and open areas, and in both reef habitats, at all sites. Benthic community structure was assessed using the line-point-transect method (English et al., 1997), with benthic cover recorded at 50 cm intervals, yielding a total of 60 points per transect. Fine-scale rugosity was quantified using the chain-and-tape method (Risk, 1972) with a small link chain (5 mm). Three replicate rugosity measurements were made along each transect (averaged per transect), with each measurement covering 5 m linear distance. Herbivorous fish biomass was quantified at all sites using underwater visual censuses (UVC) carried out along eight 30 × 5 m belt transects by a single surveyor (Dickens et al., 2011). The surveyor recorded the largest and wariest species during a first pass of the transect, and more site-attached territorial species (e.g. *Stegastes* spp.) in the second pass. Individual fishes were identified to the species level

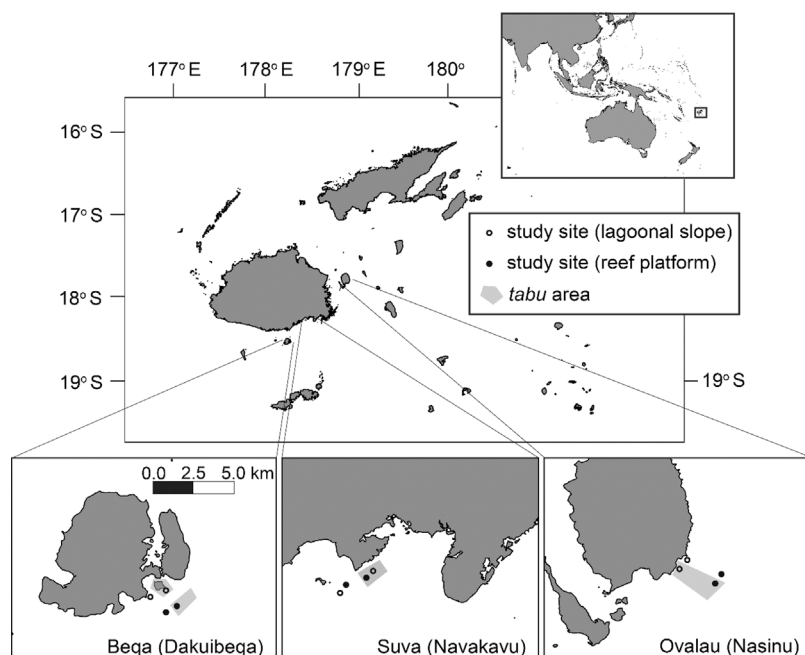


Fig. 1. Map of study sites in Fiji. Scaling is consistent across maps of each study site.

and assigned to fork length size classes (i.e. 5 cm intervals) to compute taxonomic richness and biomass, respectively. Biomass values were obtained using the midpoint of the size class from established length-weight relationships (Kulbicki et al., 2005; Green and Bellwood, 2009). Taxonomic richness and biomass were also calculated per functional feeding group (i.e. browsers, grazers/detritivores, scrapers/small excavators, large excavators/bioeroders – Green and Bellwood, 2009).

2.2.2. Complementary indicators of ecosystem resilience

Complementary resilience-based metrics were quantified in all survey sites along transects used for conventional metrics (Table 1). As proxies of the biotic substrate colonisation dynamics, turf height and juvenile coral density were quantified (Birrell et al., 2005; Flower et al., 2017). Turf height was measured to the nearest mm using a plastic ruler placed perpendicular to the substrate at 30 points under each transect where algal turfs were observed. We computed the turf index per site as the product of mean percent turf cover from line-point-transect data

and mean turf height (Steneck and Dethier, 1994; Mumby et al., 2013). To quantify juvenile coral density, individual juvenile corals (< 3 cm in diameter) were counted within ten 0.25 m² quadrats per transect, using a GOBE Nightsea UV lamp to aid the detection of coral tissue fluorescence (Piniak et al., 2005; Baird et al., 2006). Quadrats for juvenile corals were systematically placed on substrata other than live coral tissue or sand which would typically be avoided by coral recruits. Additionally, along the first 10 m of each transect, each coral colony found (with at least 50% of its area) within a 1 m belt of the transect line was assessed for coral-algal interactions. Any type of algae in contact with the coral was identified to the functional group level, height was measured for turf algae, and the status of the interaction (i.e. alga winning, coral winning or neutral) was determined by any visible mortality, bleaching or overgrowth of either the coral or the algae, according to Barott et al. (2012).

In the most accessible area, the Navakavu *qoliqoli* (Suva), 15 recruitment tiles were installed in each reef habitat within the *tabu* and

Table 1
Summary of the *in situ* conventional and complementary metrics selected for site comparisons in the current study.

Metric	Interpretations	References
Conventional metrics		
proportional cover of key benthic groups	state of benthic reef community according to dominance of different groups	Hughes (1994); Norström et al. (2009)
herbivorous fish biomass along visual transects	high herbivorous fish biomass implies top-down control of algae; (no-take) management should increase biomass	Mumby et al. (2006); Hughes et al. (2007)
herbivorous fish taxonomic richness along visual transects	high taxonomic richness reflects ecological insurance; within functional groups reflects functional redundancy, and more species to replace functions if species are removed	Elmqvist et al. (2003); Nyström (2006)
rugosity	a complex reef structure implies a healthier reef and a better habitat for fish; ecosystem service provision linked to rugosity	Alvarez-Filip et al. (2009); Graham and Nash (2013)
Complementary metrics		
turf height and index	ability of coral recruits to settle; herbivorous grazing function; sediment input	Birrell et al. (2005); Goatley et al. (2013); Mumby et al. (2013); Flower et al. (2017)
juvenile coral density	ability of coral larvae to settle and of settlers to grow/survive; high abundance contributes to reef recovery	McClanahan et al. (2012)
coral/algal interactions	which key benthic group has a competitive advantage and to what extent; frequency and severity indicates reef trajectory	Barott et al. (2012); Anthony et al. (2015)
coral recruitment	ability of coral larvae to settle and settlers to grow/survive; colonisation of open bare substrate from coral mortality or predation (e.g. bite scars); high abundance contributes to reef recovery	McClanahan et al. (2012)
bite (herbivory) rates from video observations	function and redundancy of herbivorous fish (species); top-down control of algae	Fox and Bellwood (2008); Hoey and Bellwood (2009); Plass-Johnson et al. (2015)

open areas. Untreated sandstone tiles (15 × 15 cm) were fixed onto dead coral using 15 cm stainless steel screws. As coral recruits preferentially settle on the undersides of surfaces, and small variations in tile angle do not affect coral recruitment patterns (Mundy, 2000), an angled 8 cm PVC pipe between the underside of the tile and the substrate ensured that tiles were suspended at an angle ($\sim 45 \pm 20^\circ$). Consequently, sedimentation was limited and recruits were able to access both tile surfaces. Tiles were installed in mid-October 2015 and collected in mid-January 2016, thus covering the main spawning times for broadcast spawning corals in Fiji (Quinn and Kojis, 2008). Upon collection, both tile surfaces were photographed, and tiles were immersed in 10% household bleach for 48 h, rinsed with fresh water and dried. Individual recruits on both surfaces were counted and photographed under a stereo microscope incorporating a digital camera, followed by identification into major families (Acroporidae, Pocilloporidae and other) (Babcock et al., 2003; Ferse et al., 2013). Analyses of coral recruitment rates focused on the underside of the tiles where 97% of the recruits settled.

Bite rates of herbivorous fish were quantified through *in situ* GoPro video recordings. Video cameras were fixed overlooking reef substratum for ca. 60 min ($n = 4\text{--}5 \text{ site}^{-1}$). A 1 m² quadrat was briefly placed on the benthos in front of the camera and photographed for subsequent quantification of grazable substrate (i.e. substrate other than live corals, sponges and sand). Video analysis excluded the initial 15 min to minimise any diver interference with usual fish behaviour. For the following 30 min, all nominally herbivorous fish detected within the frame were recorded to species level in order to assess taxonomic richness from video recordings. To quantify bite rates, all herbivorous fish observed feeding within the 1 m² quadrat frame were identified to species and the number of bites taken on the substratum was recorded. Bite rates were scaled to the amount of grazable surface available from the corresponding quadrat (bites m⁻² grazable surface h⁻¹).

2.2.3. Informative value of turf height measurements

To further evaluate the value of incorporating turf height into reef monitoring, we investigated its relationship with critical ecosystem processes that determine the continuity and renewal of coral populations after physical disturbances. To investigate the effect of turf height on coral recruitment rate, turf height was measured to the nearest mm at 3 points on each tile surface at collection. The relationship between juvenile coral density and both turf height and turf index were quantified from transect data. Effects of turf height on coral-algal interactions were evaluated by comparing the outcomes of interactions between corals and algal turfs < 5 mm and > 5 mm, which has previously been identified as a threshold by which turfs hinder important ecosystem processes (e.g. Birrell et al., 2005).

2.2.4. Water quality assessments

Although the close proximity of paired sites assured similar environmental conditions, water samples were additionally collected for subsequent analyses of inorganic nutrient concentrations to provide further support that observed differences between paired sites were not driven by water quality. Three water samples of 40 ml were collected from each site using syringes ca. 10 cm over the seabed without disturbing the sediment. Samples were immediately filtered over 0.45 µm membrane filters and transported on ice to a dry lab where they were frozen and maintained at -20°C until nutrient analysis was conducted. Inorganic nutrient (nitrate, nitrite and phosphate) concentrations were measured at the Leibniz Centre for Tropical Marine Research (ZMT), using a SKALAR Automated Wet Chemistry Analyzer (San + +).

2.3. Statistical analyses

The effect of local management and reef habitat on coral recruitment data (Suva only) were investigated using two-way ANOVA models

(*aov* function – R base package; R Development Core Team, 2013) investigating single and interactive effects of both factors. Arcsine transformed percentage benthic cover of live hard coral, fleshy algae and algal turfs, square root transformed herbivorous fish biomass and grazing rates, as well as turf height, turf index, juvenile coral counts, rugosity, and log ratios (percentage winning + 1/percentage neutral + 1) of coral-fleshy algae and coral-algal turf interaction outcomes were each individually tested for their responses to local management, reef habitat and any interactions between the two factors. Two-way ANOVA models accounted for the paired design of the study by including an error term for location to analyse within-subject (location) differences, and incorporated both management status and reef habitat as fixed interactive terms. Taxonomic richness of herbivorous fish species in total and within key functional groups was calculated per site both for data from UVC and video footage. Paired *t*-tests compared differences in taxonomic richness between *tabu* and open reefs, and also between the two data collection methods (i.e. UVC vs. videos). Differences in biomass across all herbivorous fish functional groups between *tabu* and adjacent open sites were tested by PERMANOVA (Anderson et al., 2008) using the PERMANOVA+ add-on in Primer v.6 (Primer-E, Plymouth, UK). PERMANOVA tests used the Bray-Curtis similarity coefficient, with type 3 sums of squares and unrestricted permutation of raw data, and incorporated the same statistical design as described for the within-subject (location) ANOVA models. Effect sizes (Cohen's f^2 value) for each predictor in multiple regressions were calculated according to Selya et al. (2012), using the formula: Cohen's $f^2 = (R^2\text{AB} - R^2\text{A}) / (1 - R^2\text{AB})$. Within this formula, $R^2\text{AB}$ refers to the eta-squared for a model comprising all predictors, and $R^2\text{A}$ refers to the eta-squared for a model comprising all factors minus the predictor of interest (B). Effect sizes for paired *t*-tests (Cohen's d) were quantified using the *CohensD* function within the *lsr* package (Navarro, 2015). According to Cohen (1988), small, medium, and large effect sizes are defined as $f^2 \geq 0.02$, $f^2 \geq 0.15$, and $f^2 \geq 0.35$ (for Cohen's f^2), and $d \geq 0.2$, $d \geq 0.5$, and $d \geq 0.8$ (for Cohen's d), respectively. Results are provided in effect size values with significance test outcomes (i.e. *p* values). Using the *pwr* package (Champely, 2017), we additionally calculated what effect sizes for each response variable would theoretically be detectable with 80% power. This package was also used to calculate the power to detect the effect sizes that we measured (i.e. how much power did our sampling and model design have to detect an effect of the predictors; Appendix C). To test overall differences among sites according to both conventional and complementary metrics, we used principal components analyses (PCA; *prcomp* function R) based on Euclidean distances after removing any collinear terms ($R^2 > 0.6$). To discard that differences between paired sites were attributable to differences in water quality, inorganic nutrient concentrations were compared between paired sites using two-way ANOVA models incorporating location as an error term. A generalised linear regression model (*glm* function – R base package), incorporating a quasi-poisson distribution, evaluated the relationship between turf height and coral recruitment rate across all tiles from all sites. A changepoint analysis was run to identify any potential thresholds in mean coral recruitment rate with different turf heights (*changepoint* R package; Killick and Eckley, 2013). The effects of turf height and turf index on juvenile coral density were analysed using generalised linear regression models (*glm* function – R base package) on transect data. Finally, one-way ANOVA models investigated the effect of turf height (< 5 mm, ≥ 5 mm) on the log ratio (percentage winning + 1/percentage neutral + 1) of coral-algal turf interaction outcomes. Model residuals for all models were extracted and checked visually to confirm that model assumptions were not violated.

3. Results

Conventional reef status metrics revealed no differences in benthic or fish communities between *tabu* and adjacent open areas (Table 2; Fig. 2a). Benthic cover of hard coral, fleshy algae and algal turfs, as well

Table 2

Statistical comparisons of the differences in individual metrics for management (*tabu*, T vs. open, O), reef habitat (platform, P vs. lagoonal slope, S), and the interaction between the predictors. Results provided in terms of effect size (Cohen's f^2 or Cohen's d ; large effect = blue, medium effect = light blue, small effect = grey) and significance tests ($< 0.001 = ***$, $< 0.01 = **$, $< 0.05 = *$). Superscripts refer to statistical designs used: ¹within-subject ANOVA, ²paired t -tests, ³two-way ANOVA, and whether the effect size is presented as ^fCohen's f^2 (for multiple regressions) or ^dCohen's d (for paired t -tests). (For interpretation of the references to colour in this table legend, the reader is referred to the web version of this article.)

		Management		Reef habitat		Interaction	
Metric	Cohen's f^2/d with 80% power	Cohen's f^2/d	effect	Cohen's f^2/d	effect	Cohen's f^2	effect
Conventional metrics							
live coral cover ^{1,f}	0.37	0.14	-----	0.32***	P < S	<0.01	-----
turf algal cover ^{1,f}	0.37	0.09	-----	0.09	-----	0.08	-----
fleshy algal cover ^{1,f}	0.37	0.06	-----	0.41**	P > S	0.05	-----
rugosity ^{1,f}	0.37	0.04	-----	0.60***	P < S	0.01	-----
herbivorous fish biomass UVC ^{1,f}	0.13	0.03	-----	0.02	-----	<0.01	-----
herbivorous fish taxonomic richness UVC ^{2,d}	1.68	0.30	-----	0.21	-----		
Complementary metrics							
turf height ^{1,f}	0.37	1.19***	O > T	0.14	-----	0.09	-----
turf index ^{1,f}	0.37	0.29**	O > T	0.02	-----	<0.01	-----
juvenile coral density ^{1,f}	0.37	0.41**	O < T	0.07	-----	0.06	-----
coral recruitment ^{3,f}	0.14	0.42***	O < T	0.03	-----	0.03	-----
outcome coral-algal turf interactions ^{1,f}	0.16	0.09*	O < T	0.02	-----	<0.01	-----
outcome coral-fleshy algae interactions ^{1,f}	0.16	0.14*	O > T	0.36***	P < S	0.03	-----
herbivorous fish grazing rates ^{1,f}	0.25	0.04	-----	0.05	-----	0.02	-----
herbivorous fish taxonomic richness video ^{2,d}	1.68	1.20**	O < T	0.26	-----		

as rugosity, were consistent across *tabu* and adjacent open reefs regardless of habitat type. The small effect sizes indicate that replication would have to be increased *ca.* four-fold to have strong power (i.e. 0.8) to detect significant differences in these metrics. Furthermore, neither biomass nor taxonomic richness of herbivorous fishes were affected by management according to UVC data (Fig. 2a; Fig. 3a; Table 2). Habitat type itself did however drive large differences according to conventional metrics, with lagoonal slopes exhibiting significantly higher rugosity, benthic cover of hard coral and herbivorous fish biomass, and lower cover of fleshy algae, in comparison to reef platforms.

The complementary resilience-based metrics indicated that local management was driving profound differences in biotic substrate colonisation (Fig. 2b; Table 2). The presence of local management had a large and significant effect on mean turf height ($33 \pm 8\%$ lower), juvenile coral density ($42 \pm 22\%$ higher), and to a slightly lesser extent turf index ($33 \pm 16\%$ lower). Management also had a very strong effect on coral recruitment rate at Suva, with significantly more recruits settling within the *tabu* area (736 ± 89 recruits m^{-2}) than in the adjacent open reef (284 ± 35 recruits m^{-2} ; Table 2; Fig. 4). The positive effect of local management was consistent across the two reef habitats, and the most common families of recruits (ANOVA, Acroporidae $p = 0.016$; Pocilloporidae $p < 0.001$; Fig. 4). In terms of coral-algal interactions, fleshy algae were more competitive against coral colonies in adjacent open areas, but in contrast algal turfs were more competitive against corals within *tabu* areas (Table 2; Appendix A).

In contrast to the UVC results, data extracted from video footage indicated that taxonomic richness of grazers/detritivores (paired t -test, $p = 0.007$) and of all functional groups combined (Table 2) were higher inside *tabu* areas compared with adjacent open areas (Fig. 3b). Videos

captured a higher taxonomic richness of herbivorous fish within the browser functional group than UVC (paired t -test, $p = 0.04$), but UVC found higher richness of grazers/detritivores (paired t -test $p < 0.001$) and scrapers/small excavators (paired t -test $p = 0.003$) than video footage. Bite rates of herbivorous fish showed large variation and did not differ significantly between *tabu* and adjacent open reefs within either reef habitat (PERMANOVA, $p = 0.752$; Fig. 3c). Grazers/detritivores were responsible for most bites among sites, and bite rates on the reef platform at Ovalau were significantly higher than elsewhere (PERMANOVA, $p < 0.01$; Fig. 3c). At Ovalau, turf height was also lower than at other sites (*tabu*: 1.6 ± 0.3 mm, open: 2.3 ± 0.1 mm; Fig. 2b).

A PCA based on conventional metrics revealed similarities of open sites across the second principal component (24.9% variance explained), whereas *tabu* sites were heterogeneously dispersed around the plot (Fig. 5a). In contrast, when the PCA incorporated more resilience-based metrics, a clear differentiation of local management was revealed across the first principal component (43.7% variance explained; Fig. 5b). The PCA revealed that open reefs were associated with higher turf height and diversity of excavators as extracted from video footage. *Tabu* reefs in contrast exhibited strong positive associations with juvenile coral density, bite rates and taxonomic richness of grazers/detritivores and scrapers/small excavators as determined from video footage. Two sites behaved as anomalies and fitted into the opposing cluster: the open platform at Ovalau driven by the exceptionally high bite rates, and the *tabu* slope at Suva driven by the high taxonomic richness of large excavators/bioeroders observed within video footage. The proximity of paired sites and insignificant differences between inorganic nutrient concentrations (Appendix B) suggested that differences

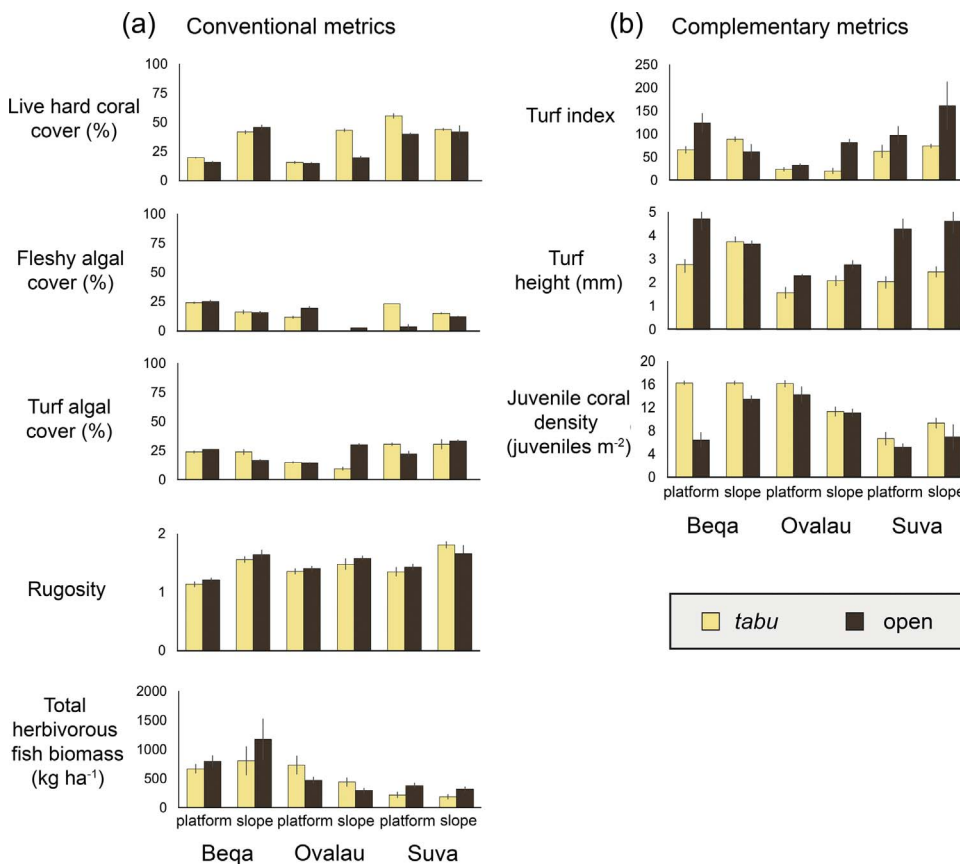


Fig. 2. Benthic and fish community responses (mean $\pm$ SE) to local management as determined by (a) conventional and (b) complementary metrics.

between paired *tabu* and open reefs were not driven by water quality.

As well as exhibiting significant responses to management, turf height was also itself strongly associated to other benthic processes. Turf height was inversely related to coral recruitment rate (GLM, $p = 0.028$), with a threshold height of 5.7 mm identified after which mean coral recruitment rate dropped from 578 to 133 recruits m^{-2} (Fig. 6a). Both turf height and turf index were also negatively correlated with juvenile coral density (GLM, $p = 0.03$; Fig. 6b and c). In addition to being detrimental to coral recruitment and succession, algal turfs with canopy heights ≥ 5 mm were also significantly more successful in competition with neighbouring corals compared to those < 5 mm in height (ANOVA, $F_{(1,70)} = 16.02$, $p < 0.001$; Fig. 7).

4. Discussion

By measuring a variety of metrics in paired *tabu* (periodically closed to fishing) and adjacent open reefs, this study allowed us to explore the ability of different approaches to detect changes within benthic and fish communities under local management in Fiji. The results demonstrate that contrasting interpretations of management effectiveness can be made depending on the metrics measured in surveys. According to conventional metrics, local management failed to induce positive ecological effects in either benthic or herbivorous fish communities. Conversely, a complementary set of resilience-based metrics that measured more dynamic ecosystem functions and processes indicated that local management was promoting ecosystem attributes of importance for securing the continuity and renewal of coral populations. Particularly, the scope to capture differences in biotic substrate colonisation allowed the detection of changes that have important implications for system resilience that would otherwise have been overlooked.

As coral recruitment and subsequent growth are key components of reef recovery (McClanahan et al., 2012), increased recruitment and

juvenile coral densities within *tabu* areas indicate that local management has effectively improved the system's resilience to perturbations. Laboratory choice experiments and field observations have shown that both fish and coral larvae preferentially settle on reefs dominated by coral rather than algal communities (Lecchini et al., 2013), for example on reefs that have exhibited a positive response to local management (Dixon et al., 2014). Although the *tabu* areas in this study did not exhibit differences in broad benthic groups such as hard coral or fleshy algae, turf height and turf index were significantly reduced when compared with adjacent open reefs. Coral recruitment rate indeed strongly declined with increasing turf height, with a threshold identified at 5.7 mm turf height above which recruitment rates exhibited a five-fold decrease, corroborating other studies (Birrell et al., 2005). Interestingly, turf height and turf index were also significantly negatively related to juvenile coral density despite turf heights on transects consistently averaging < 5 mm, showing the opposite trend to equivalent short-cropped turfs in Micronesia (Mumby et al., 2013). Algal turfs ≥ 5 mm in height were also significantly more competitive against neighbouring corals. Under conditions where algae gain a competitive advantage against corals (as also indicated for fleshy algae outside of *tabu* areas), the ability of coral communities to sustain dominance into the future can be compromised.

In addition to providing information on the effect of local management on coral recruitment processes, this study provides useful information on recruitment rates during warmer months on inshore Fijian reefs, for which data is sparse. Consistent with many previous coral recruitment studies, the significant majority of recruits settled on the underside of the tiles (Harriott and Fisk, 1987; Babcock and Mundy, 1996; Doropoulos et al., 2014). Coral recruitment rates at Suva were relatively high, particularly within the *tabu* area (mean > 700 recruits m^{-2}), compared with other studies in the region (Gleason, 1996; Quinn and Kojis, 2008) and elsewhere (e.g. Smith, 1992; Glassom et al., 2004). Abundances of acroporid and pocilloporid recruits consistently

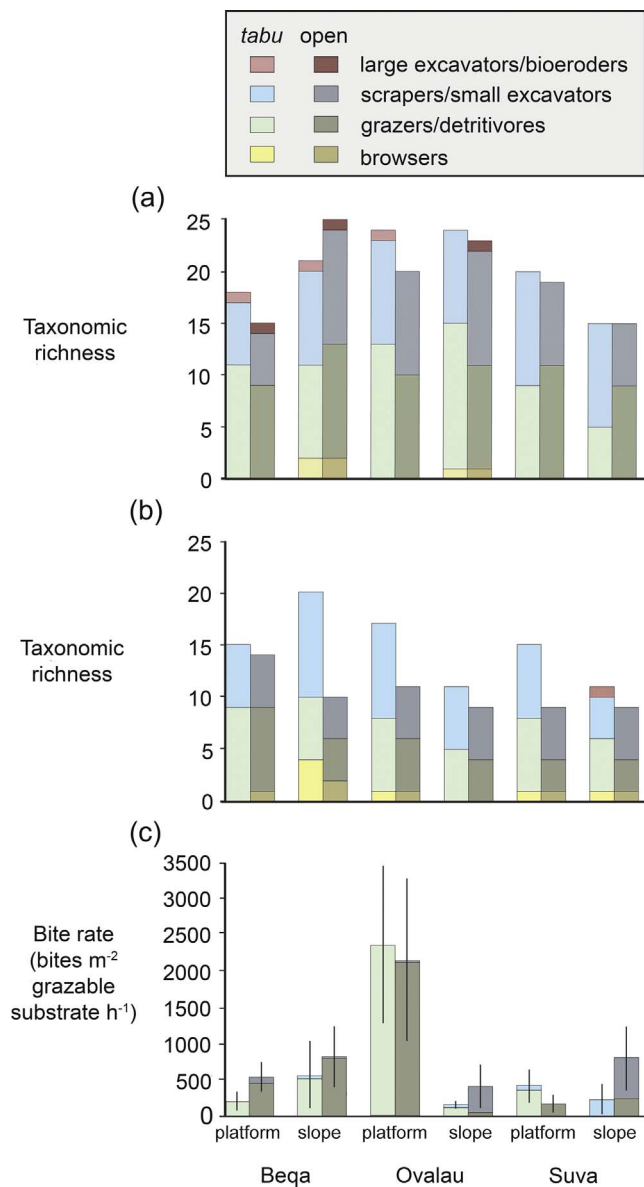


Fig. 3. Taxonomic richness of herbivorous fish at each reef, separated by functional group as determined from (a) UVC, and (b) video footage, and (c) herbivorous fish bite rates (mean $\pm$ SE) for each reef, separated by functional group.

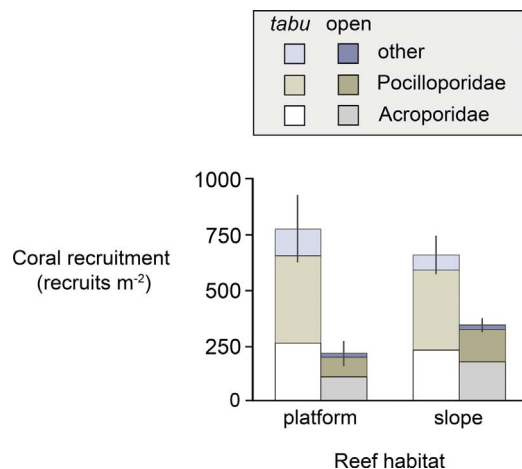


Fig. 4. Coral recruitment (mean $\pm$ SE) at each study reef in Suva, with relative contributions of major families (Acroporidae, Pocilloporidae, other).

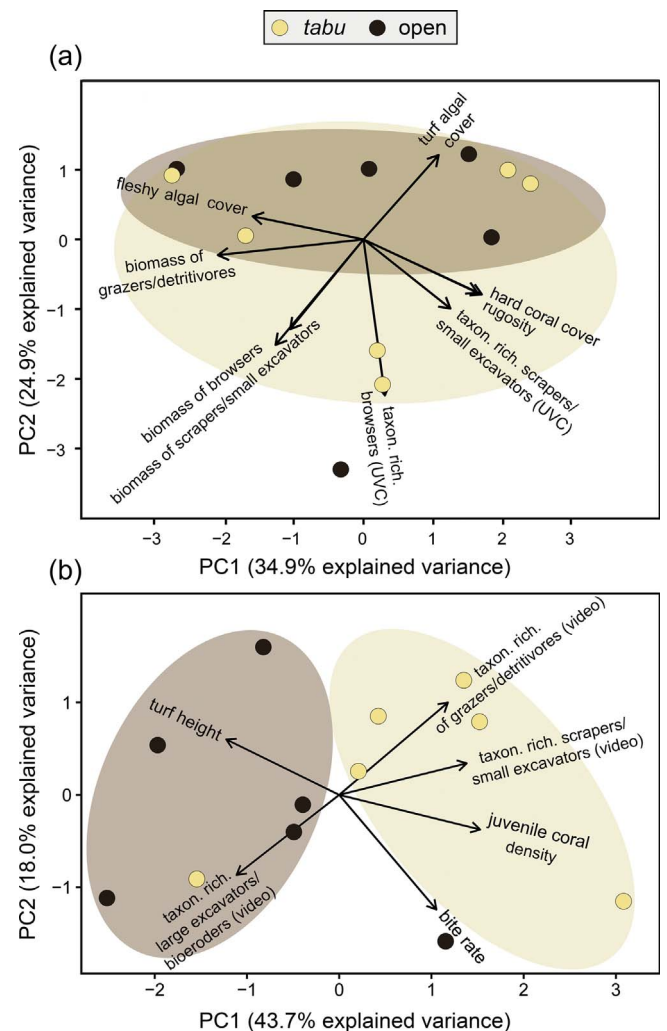


Fig. 5. Principal components analysis based on Euclidean distances of study reefs, according to (a) conventional and (b) complementary metrics. Shaded areas represent the extent of similarities between reefs of the same management status. Taxonomic richness is referred to as taxon rich.

comprised over 80% of the total coral recruit community, but the adult coral communities at these inshore sites were dominated by poritids and acroporids (Appendix D). This trend reflects a higher mortality of juvenile brooders such as pocilloporids compared with spawners such as acroporids (Doropoulos et al., 2015).

In terms of herbivorous fish communities, conventional surveys into biomass and taxonomic richness, and complementary measures of grazing rates, did not indicate any obvious benefits under local management. Nonetheless, video observations found higher overall taxonomic richness of herbivorous fishes inside *tabu* areas, and algal turf characteristics indicate that long-term grazing of herbivorous fish is greater inside protected areas. Provisional analyses into the functional space of herbivorous fishes also differed strongly depending on the method by which fish communities are measured (i.e. present in UVC, present in video footage or recorded grazing in video footage – Appendix E). Evidently conflicting interpretations of herbivorous fish communities can be made depending on the metrics used to measure them. There are also benefits from incorporating additional video footage into surveys. Browsers such as *Naso* (Acanthuridae) fulfil critical ecological roles in terms of maintaining system resilience (Hoey and Bellwood, 2009; Ford et al., 2016) but are particularly wary of divers and can consequently be overlooked during standard UVC (Kulbicki, 1998). Correspondingly, more browsers were encountered in video observations than during UVC. Although they were only responsible for

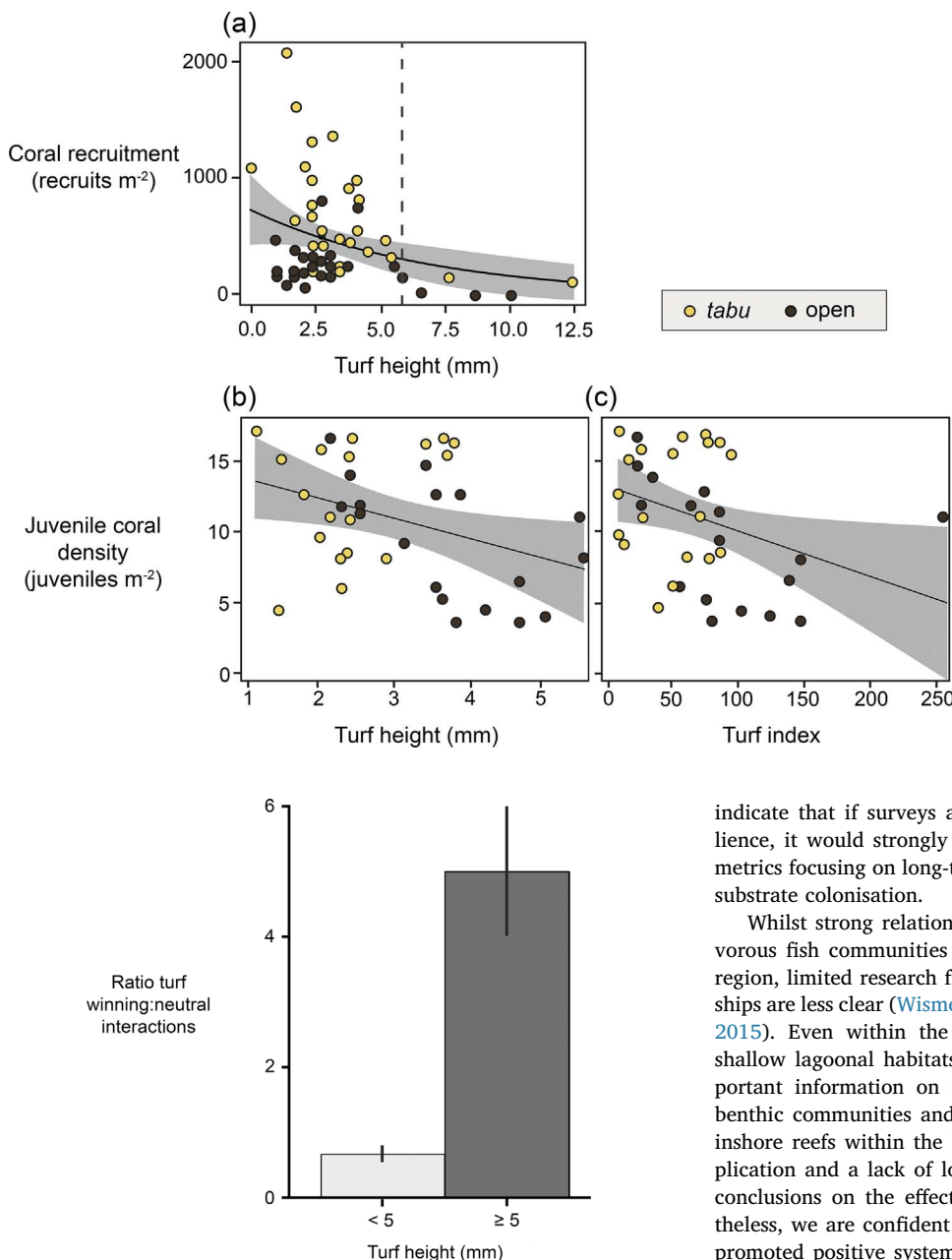


Fig. 7. Ratio (mean $\pm$ SE) of winning vs. neutral interactions (algal perspective) between short (< 5 mm) and long ($\geq$ 5 mm) algal turfs in interaction with neighbouring coral colonies. Larger ratios represent higher competitiveness of algal turfs.

a negligible proportion of bites, their browsing behaviour was probably limited by the minimal presence of fleshy algal types other than encrusting *Lobophora*. Video recordings of bioassays offering alternative fleshy algal varieties may reveal further insights into the potential function of browsing fishes at these sites, indicating their ability to consume fleshy algae which can bloom following disturbances (Hoey and Bellwood, 2009; Rasher et al., 2013). Poaching within *tabu* areas is a problem in the region, and may explain why there are no conspicuous benefits of protection in terms of herbivorous fish biomass in baseline surveys. Poaching may primarily be focused on night-time spearfishing that removes larger individuals, whilst fishers may still avoid net fishing within *tabu* areas thus facilitating survival of smaller individuals. There are thus many challenges associated with fish surveys, including temporal- and surveyor-related discrepancies, wariness of some key species and the potential dilution of conspicuous management effects on larger individuals caused by poaching. These challenges

Fig. 6. Generalized linear model output with confidence intervals shown in grey for (a) coral recruitment rate as a function of turf height on tiles (dashed line indicates threshold after which average recruitment significantly declines), and juvenile coral density as function of *in situ* (b) turf height and (c) turf index.

indicate that if surveys aim to measure system trajectories and resilience, it would strongly benefit them to incorporate complementary metrics focusing on long-term responses to fish function, such as biotic substrate colonisation.

Whilst strong relationships between coral reef benthos and herbivorous fish communities have been established across the Caribbean region, limited research from the Pacific region suggests that relationships are less clear (Wismer et al., 2009; Mumby et al., 2013; Russ et al., 2015). Even within the Caribbean region, studies tend to neglect shallow lagoonal habitats. Thus, this study additionally provides important information on relationships between coral reef herbivory, benthic communities and coral recruitment success in the context of inshore reefs within the Pacific Island region. Due to limited site replication and a lack of long-term data, we are hesitant to draw firm conclusions on the effectiveness of local management in Fiji. Nonetheless, we are confident from our results that local management has promoted positive system trajectories and resilience dynamics within the inshore reef ecosystems. Interestingly, a recent analysis of similar small protected areas nearby in Fiji contrastingly found that management significantly affected a variety of conventional metrics (Bonaldo et al., 2017). For example, the authors observed significantly higher coral cover, herbivorous fish biomass and species richness, and significantly less fleshy algae cover compared to neighbouring fished reefs. However, there may be a variety of reasons that these results are in contrast to ours: (i) replication was three-fold higher within each study area, allowing smaller effect sizes to be detected as significant, (ii) the reefs were generally closer to shore with the presence of some large hotels, potentially allowing better enforcement of, and incentives for, management, with the hotels likely providing alternative livelihoods to villagers, and (iii) the reefs seem to be in a more degraded state than in the present study, with for example lower coral cover, implying that the environment may be more stressful and thus that management may have more conspicuous and quick effects. However, the results from our study align well with Mumby (2017), who emphasised that surveys need to be better prepared to deal with ‘shades of grey’ in reef health as reefs become increasingly homogeneous in appearance. To achieve this, the author states that better tools are needed to measure and interpret

modest changes in reef state, for which the findings of this research are highly relevant. While confronted with increasing global change, we may fail to dramatically increase hard coral cover, and boosting resilience of the ecosystem and promoting positive trajectories will become increasingly important.

Most of the resilience-based metrics that were strongly affected by management and indicate system resilience (turf height, turf index and juvenile coral density) represent very quick and cost-effective tools to include in future monitoring. The effect sizes of these metrics were also large enough for them to be detected with a high power in relatively small-scale surveys. Furthermore, whilst reef habitat often had a large effect on conventional metrics, the resilience-based metrics generally remained consistent, indicating their suitability across different inshore environments. Remote videos can facilitate observations of wary or heavily targeted fish which are important for system resilience (e.g. browsers) but can be overlooked by conventional UVC. However, whilst using such videos to quantify grazing rates is important to understand herbivorous fish functions, the presence of large variability in data necessitates high replication with associated intensive and time-consuming post-hoc analyses. Coral recruitment can provide interesting information but also requires a relatively large time and cost investment, and in terms of resilience the same information can be obtained from juvenile coral counts or turf height which represent much easier measurements obtained from single time-points. Turf height exhibits particularly strong potential as an indicator for reef trajectories and resilience, as it was significantly related to coral recruitment success, juvenile coral abundances and the outcome of coral-algal interactions. As well as suppression of herbivory by external factors such as overfishing (Mumby et al., 2013; Clausing et al., 2014), increased canopy height can reflect higher sediment loading and accumulation within the benthos with associated reductions of grazing (Bellwood and Fulton, 2008; Goatley et al., 2013). Different characteristics of algal turfs can therefore reflect destabilised and thus degrading reef systems, or recovering reefs exhibiting healthy ecological processes. These results thus emphasise the informative value of incorporating this very simple measurement into future baseline surveys.

If local communities are not seeing any benefit of management, they may become disheartened and abandon their measures. Thus, incorporating resilience-based metrics, and particularly biotic substrate colonisation measurements, into monitoring increases the likelihood of conveying positive effects of management efforts back to communities. Few monitoring programmes currently include metrics that indicate aspects of biotic substrate colonisation (Appendix F), demonstrating the need to re-evaluate key indicators to diagnose coral reef health and resilience (McClanahan et al., 2012; Anthony et al., 2015; Flower et al., 2017). Our results do not undermine the importance of including conventional metrics into surveys, and indeed these measurements are particularly important over time to understand ecosystem service provision and confirm long-term trends. Furthermore, this long-term picture can clarify if processes and functions linked to reef resilience do eventually translate into higher coral cover.

5. Conclusions

Even under a scenario whereby climate agreements are implemented internationally, > 75% of reefs will experience annual severe bleaching by 2070 (van Hooidonk et al., 2016) and only 10% are projected to persist by 2100 (Frieler et al., 2012). It is thus important that managers are provided with the most effective tools to measure how well management is promoting ecological resilience, as well as to prioritise resilient areas in which to invest and focus future efforts. In data-poor regions such as many Pacific island countries and territories, long-term monitoring data from which to evaluate ecosystem trajectories may not be available. The additional inclusion of relatively simple, quick and cost-effective indicators that measure aspects associated with ecological resilience can overcome this limitation in future

surveys. Measurements that focus on biotic substrate colonisation in particular can be very easily incorporated and have the resolution to capture subtle but important differences between increasingly homogeneous reefs that provide a strong indication of ecosystem trajectories and resilience. Monitoring should thus focus on measurements that respond rapidly to changing conditions and that may indicate whether the system is likely to exhibit a stable temporal trajectory or to shift to alternative dominance states in response to future perturbations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.10.002>.

References

- Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B Biol. Sci.* 276, 3019–3025. <http://dx.doi.org/10.1098/rspb.2009.0339>.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.
- Anthony, K.R.N., Marshall, P.A., Abdulla, A., Beeden, R., Bergh, C., Black, R., Eakin, C.M., Game, E.T., Gooch, M., Graham, N.A.J., Green, A., Heron, S.F., van Hooidonk, R., Knowland, C., Mangubhai, S., Marshall, N., Maynard, J.A., McGinnity, P., McLeod, E., Mumby, P.J., Nyström, M., Obura, D., Oliver, J., Possingham, H.P., Pressey, R.L., Rowlands, G.P., Tamelander, J., Wachenfeld, D., Wear, S., 2015. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob. Chang. Biol.* 21, 48–61. <http://dx.doi.org/10.1111/gcb.12700>.
- Babcock, R., Mundy, C., 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *J. Exp. Mar. Biol. Ecol.* 206, 179–201. [http://dx.doi.org/10.1016/S0022-0981\(96\)02622-6](http://dx.doi.org/10.1016/S0022-0981(96)02622-6).
- Babcock, R.C., Baird, A.H., Piromvaragorn, S., Thomson, D.P., Willis, B.L., 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zool. Stud.* 42, 211–226.
- Baird, A.H., Salih, A., Trevor-Jones, A., 2006. Fluorescence census techniques for the early detection of coral recruits. *Coral Reefs* 25, 73–76. <http://dx.doi.org/10.1007/s00338-005-0072-7>.
- Barott, K.L., Williams, G.J., Vermeij, M.J.A., Harris, J., Smith, J.E., Rohwer, F.L., Sandin, S.A., 2012. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Mar. Ecol. Prog. Ser.* 460, 1–12. <http://dx.doi.org/10.3354/meps09874>.
- Bellwood, D.R., Fulton, C.J., 2008. Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea-levels and climate change? *Limnol. Oceanogr.* 53, 2695–2701. <http://dx.doi.org/10.4319/lo.2008.53.6.2695>.
- Birrell, C.L., McCook, L.J., Willis, B.L., 2005. Effects of algal turfs and sediment on coral settlement. *Mar. Pollut. Bull.* 51, 408–414. <http://dx.doi.org/10.1016/j.marpolbul.2004.10.022>.
- Bonaldo, R.M., Pires, M.M., Guimarães Junior, P.R., Hoey, A.S., Hay, M.E., 2017. Small marine protected areas in Fiji provide refuge for reef fish assemblages, feeding groups, and corals. *PLoS One* 12, e0170638. <http://dx.doi.org/10.1371/journal.pone.0170638>.
- Champely, S., 2017. Pwr: Basic Functions for Power Analysis. R Package Version 1. 2-1. <https://CRAN.R-project.org/package=pwr>.
- Clausing, R., Annunziata, C., Baker, G., Lee, C., Bittick, S., Fong, P., 2014. Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. *Mar. Ecol. Prog. Ser.* 517, 121–129. <http://dx.doi.org/10.3354/meps11029>.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd edition. Lawrence Erlbaum Associates, Hillsdale, N.J., pp. 579.
- Couce, E., Ridgwell, A., Hendy, E.J., 2012. Environmental controls on the global distribution of shallow-water coral reefs. *J. Biogeogr.* 39, 1508–1523. <http://dx.doi.org/>

- 10.1111/j.1365-2699.2012.02706.x.
- Diaz-Pulido, G., McCook, L., 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar. Ecol. Prog. Ser.* 232, 115–128. <http://dx.doi.org/10.3354/meps232115>.
- Dickens, L.C., Goatley, C.H.R., Tanner, J.K., Bellwood, D.R., Gascuel, D., 2011. Quantifying relative diver effects in underwater visual censuses. *PLoS One* 6, e18965. <http://dx.doi.org/10.1371/journal.pone.0018965>.
- Dixon, D.L., Abrego, D., Hay, M.E., 2014. Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. *Science* 345, 892–897. <http://dx.doi.org/10.1126/science.1255057>.
- Doropoulos, C., Roff, G., Zupan, M., Nestor, V., Isechal, A.L., Mumby, P.J., 2014. Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. *Coral Reefs* 33, 613–623. <http://dx.doi.org/10.1007/s00338-014-1149-y>.
- Doropoulos, C., Ward, S., Roff, G., González-Rivero, M., Mumby, P.J., Rubens, J., 2015. Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. *PLoS One* 10, e0128535. <http://dx.doi.org/10.1371/journal.pone.0128535>.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* [http://dx.doi.org/10.1890/1540-9295\(2003\)001\[0488:rdecar\]2.0.co;2](http://dx.doi.org/10.1890/1540-9295(2003)001[0488:rdecar]2.0.co;2).
- English, S., Wilkinson, C., Baker, V., 1997. Survey Manual for Tropical Marine Resources, 2nd edition. Australian Institute of Marine Science, Townsville, Australia. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- Ferre, S.C.A., Nugues, M.M., Romatzki, S.B.C., Kunzmann, A., 2013. Examining the use of mass transplantation of brooding and spawning corals to support natural coral recruitment in Sulawesi/Indonesia. *Restor. Ecol.* 21, 745–754. <http://dx.doi.org/10.1111/rec.12004>.
- Flower, J., Ortiz, J.C., Chollett, I., Abdullah, S., Castro-Sanguino, C., Hock, K., Lam, V., Mumby, P.J., 2017. Interpreting coral reef monitoring data: a guide for improved management decisions. *Ecol. Indic.* 72, 848–869. <http://dx.doi.org/10.1016/j.ecolind.2016.09.003>.
- Ford, A.K., Bejarano, S., Marshall, A., Mumby, P.J., 2016. Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 26, 790–805. <http://dx.doi.org/10.1002/aqc.2623>.
- Fox, R.J., Bellwood, D.R., 2008. Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (l. siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* 27, 605–615. <http://dx.doi.org/10.1007/s00338-008-0359-6>.
- Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S.D., Hoegh-Guldberg, O., 2012. Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat. Clim. Chang.* 3, 165–170. <http://dx.doi.org/10.1038/nclimate1674>.
- Glaser, M., Christie, P., Diele, K., Diskowitzky, L., Ferse, S., Nordhaus, I., Schlüter, A., Schwerdtner Mañez, K., Wild, C., 2012. Measuring and understanding sustainability-enhancing processes in tropical coastal and marine social-ecological systems. *Curr. Opin. Environ. Sustain.* 4, 300–308. <http://dx.doi.org/10.1016/j.cosust.2012.05.004>.
- Glassom, D., Zakai, D., Chadwick-Furman, N.E., 2004. Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar. Biol.* 144, 641–651. <http://dx.doi.org/10.1007/s00227-003-1243-0>.
- Gleason, M.G., 1996. Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. *J. Exp. Mar. Bio. Ecol.* 207, 79–101. [http://dx.doi.org/10.1016/S0022-0981\(96\)02647-0](http://dx.doi.org/10.1016/S0022-0981(96)02647-0).
- Goatley, C.H.R., Bellwood, D.R., Maher, W., Hendy, E., Lough, J., 2013. Ecological consequences of sediment on high-energy coral reefs. *PLoS One* 8, e77737. <http://dx.doi.org/10.1371/journal.pone.0077737>.
- Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32, 315–326. <http://dx.doi.org/10.1007/s00338-012-0984-y>.
- Green, A.L., Bellwood, D.R., 2009. Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators of Coral Reef Resilience. A Practical Guide for Coral Reef Managers in the Asia Pacific Region. IUCN Working Group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland.
- Harriott, V.J., Fisk, D.A., 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Mar. Ecol. Prog. Ser.* 37, 201–208.
- Harris, J.L., 2015. The Ecology of Turf Algae on Coral Reefs Ph.D. Thesis. University of California.
- Hoey, A.S., Bellwood, D.R., 2009. Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12, 1316–1328. <http://dx.doi.org/10.1007/s10021-009-9291-z>.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365. <http://dx.doi.org/10.1016/j.cub.2006.12.049>.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551. <http://dx.doi.org/10.1126/science.265.5178.1547>.
- Johannes, R.E., Wiebe, W.J., Crossland, C.J., Rimmer, D.W., Smith, S.V., 1983. Latitudinal limits of coral reef growth. *Mar. Ecol. Prog. Ser.* 11, 105–111.
- Killick, R., Eckley, I., 2013. changepoint: an R Package for changepoint analysis. *J. Stat. Softw.* 58, 1–15. <http://dx.doi.org/10.1359/JBMR.0301229>.
- Kleypas, J.A., McManus, J.W., Meñez, L.A.B., Menez, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39, 146–159.
- Kulbicki, M., Guillemot, N., Amand, M., 2005. A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybum* 29, 235–252.
- Kulbicki, M., 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J. Exp. Mar. Bio. Ecol.* 222, 11–30. [http://dx.doi.org/10.1016/S0022-0981\(97\)00133-0](http://dx.doi.org/10.1016/S0022-0981(97)00133-0).
- Lecchini, D., Waqalevu, V., Parmentier, E., Radford, C., Banaigs, B., 2013. Fish larvae prefer coral over algal water cues: implications of coral reef degradation. *Mar. Ecol. Prog. Ser.* 475, 303–307. <http://dx.doi.org/10.3354/meps10094>.
- McClanahan, T., Graham, N., Maina, J., Chabanet, P., Bruggemann, J., Polunin, N., 2007. Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Mar. Ecol. Prog. Ser.* 340, 221–234. <http://dx.doi.org/10.3354/meps340221>.
- McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu, I.J.B., Begor, M., Campbell, S.J., Darling, E.S., Eakin, C.M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddock, M.J., Selig, E.R., van Woessik, R., 2012. Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS One* 7, e42884. <http://dx.doi.org/10.1371/journal.pone.0042884>.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311, 98–101. <http://dx.doi.org/10.1126/science.1121129>.
- Mumby, P.J., Bejarano, S., Golbuu, Y., Steneck, R.S., Arnold, S.N., Van Woessik, R., Friedlander, A.M., 2013. Empirical relationships among resilience indicators on Indonesian reefs. *Coral Reefs* 32, 213–226. <http://dx.doi.org/10.1007/s00338-012-0966-0>.
- Mumby, P.J., Wolff, N.H., Bozec, Y.-M., Chollett, I., Halloran, P., 2014. Operationalizing the resilience of coral reefs in an era of climate change. *Conserv. Lett.* 7, 176–187. <http://dx.doi.org/10.1111/cons.12047>.
- Mumby, P.J., 2017. Embracing a world of subtlety and nuance on coral reefs. *Coral Reefs* 36, 1003–1011.
- Mundy, C.N., 2000. An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19, 124–131. <http://dx.doi.org/10.1007/s003380000081>.
- Navarro, D.J., 2015. Learning Statistics with R: A Tutorial for Psychology Students and Other Beginners (version 0.5). University of Adelaide, Adelaide, Australia.
- Norström, M., Nyström, M., Lokrantz, J., Folke, C., 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Mar. Ecol. Prog. Ser.* 376, 295–306. <http://dx.doi.org/10.3354/meps07815>.
- Nyström, M., 2006. Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* 35, 30–35. <http://dx.doi.org/10.1579/0044-7447-35.1.30>.
- Pandolfi, J.M., 2015. Incorporating uncertainty in predicting the future response of coral reefs to climate change. *Ann. Rev. Ecol. Syst.* 46, 281–303.
- Piniak, G.A., Fogarty, N.D., Addison, C.M., Kenworthy, W.J., 2005. Fluorescence census techniques for coral recruits. *Coral Reefs* 24, 496–500. <http://dx.doi.org/10.1007/s00338-005-0495-1>.
- Plass-Johnson, J.G., Ferse, S.C.A., Jompa, J., Wild, C., Teichberg, M., 2015. Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnol. Oceanogr.* 60, 1382–1391. <http://dx.doi.org/10.1002/lno.10105>.
- Quinn, N.J., Kojis, B.L., 2008. Variation in coral recruitment on Fijian reefs. *Proc. 11th Int. Coral Reef Symp.* 459–463.
- R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Rasher, D.B., Hoey, A.S., Hay, M.E., 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94, 1347–1358. <http://dx.doi.org/10.1890/12-0389.1>.
- Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153, 1–6.
- Russ, G.R., Questel, S.-L.A., Rizzari, J.R., Alcala, A.C., 2015. The parrotfish-coral relationship: refuting the ubiquity of a prevailing paradigm. *Mar. Biol.* 162, 2029–2045.
- Selya, A.S., Rose, J.S., Dierker, L.C., Hedeker, D., Mermelstein, R.J., 2012. A practical guide to calculating Cohen's f^2 , a measure of local effect size, from PROC MIXED. *Front. Psychol.* 3, 111. <http://dx.doi.org/10.3389/fpsyg.2012.00111>.
- Smith, S.R., 1992. Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. *Am. Zool.* 32, 663–673. <http://dx.doi.org/10.1093/icb/32.6.663>.
- Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69, 476–498. <http://dx.doi.org/10.2307/3545860>.
- Techera, E., 2010. Customary Law and Community Based Conservation of Marine Areas in Fiji. In: *The Interface/Probing the Boundaries*, vol. 62. pp. 143–164.
- Thompson, A., Mapstone, B., 2002. Intra- versus inter-annual variation in counts of reef fishes and interpretations of long-term monitoring studies. *Mar. Ecol. Prog. Ser.* 232, 247–257. <http://dx.doi.org/10.3354/meps232247>.
- Vermeij, M., DeBey, H., Grimsditch, G., Brown, J., Obura, D., DeLeon, R., Sandin, S., 2015. Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Mar. Ecol. Prog. Ser.* 528, 289–296. <http://dx.doi.org/10.3354/meps11243>.
- Weeks, R., Jupiter, S.D., 2013. Adaptive comanagement of a marine protected area network in Fiji. *Conserv. Biol.* 27, 1234–1244. <http://dx.doi.org/10.1111/cobi.12153>.
- Wismer, S., Hoey, A., Bellwood, D., 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Mar. Ecol. Prog. Ser.* 376, 45–54. <http://dx.doi.org/10.3354/meps07790>.
- Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B., Tilman, D., 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecol. Lett.* 9, 111–120. <http://dx.doi.org/10.1111/j.1461-0248.2005.00850.x>.
- Yoccoz, N.G., Nichols, J.D., Boulenger, T., 2001. Monitoring of biological diversity in space and time. *Trends Ecol. Evol.* 16, 446–453. [http://dx.doi.org/10.1016/S0169-5347\(01\)02205-4](http://dx.doi.org/10.1016/S0169-5347(01)02205-4).
- van Hooidonk, R., Maynard, J., Tamelander, J., Gove, J., Ahmadi, G., Raymundo, L., Williams, G., Heron, S.F., Planes, S., 2016. Local-scale projections of coral reef futures and implications of the Paris Agreement. *Sci. Rep.* 6 (10), ep39666. <http://dx.doi.org/10.1038/srep39666>.