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QUANTIFYING RESILIENCE

Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience

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Summary

1. Functional redundancy contributes to resilience if different species in the same functional group respond to disturbance in different ways (response diversity). If species in a functional group perform their functional role at different spatial scales (cross-scale redundancy), they are expected to respond differently to scale-specific disturbance. Consequently, variance in the spatial scales over which species perform their functional role may provide a proxy for resilience.

2. Coral reefs are diverse systems that provide key ecosystem services and are subject to increasing anthropogenic disturbances. Algal grazing by herbivorous fish contributes to the maintenance of coral-dominated reefs. To date, there has been little evaluation of the traits driving response diversity among herbivorous fish and how this relates to coral recovery following acute disturbances.

3. Using body size as a proxy for the spatial scale at which fish function, we tested whether cross-scale redundancy in herbivores was an effective indicator of response diversity and coral recovery on 21 reefs monitored through a climate-induced disturbance that caused coral bleaching and widespread coral mortality.

4. When herbivorous fish assemblages that operated over a broader range of spatial scales were present on reefs prior to disturbance, the reefs were more likely to recover to coral-dominated states after the disturbance. After the temperature-induced disturbance, the loss of small herbivores was compensated for through increases in large herbivores. This was indicative of high response diversity and drove the overall increase in herbivore biomass at recovering sites. These compensatory mechanisms were not found at sites where herbivores operated over a narrower range of spatial scales.

5. *Synthesis and applications*. Cross-scale redundancy provides managers with an indicator of coral reef resilience, although the contribution of cross-scale redundancy to resilience will vary among sites. Maintaining high cross-scale redundancy at a given site requires that no size classes of reef herbivores are disproportionately depleted by fishing. Balanced harvesting, where species are all fished in proportion to their potential production, would help achieve this.

Key-words: body size, coral reef management, ecosystem processes, fisheries, functional diversity, herbivory, trait

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Introduction

The resilience of an ecosystem can be defined as its capacity to absorb disturbances while maintaining structure and function (Holling 1973). It has proved challenging to predict ecosystem resilience because its loss may only be apparent when thresholds are reached and the system moves to an alternate state (Bellwood *et al.* 2004). Reversing or mitigating unwanted ecosystem shifts may also be expensive or unfeasible, so it is critical for managers to seek out methods to anticipate and, if possible, prevent unwanted shifts (Scheffer *et al.* 2001). One set of methods seeks indicators of ecosystem state or function as proxies of resilience, but there have been few empirical tests of indicator performance (Thrush *et al.* 2009).

Species provide a variety of functions that drive key ecosystem processes, and thus, functional diversity within a community supports a range of processes underpinning ecosystem performance (Walker, Kinzig & Langridge 1999). However, ecosystems are dynamic, experiencing a range of natural and anthropogenic impacts; to allow system recovery, ecosystem processes need to be buffered to ensure their maintenance in the face of disturbance. Multiple species performing a similar functional role should give a degree of redundancy because the decline of one species, and hence its function in response to a disturbance, may be compensated for by increased contributions of other species (Mori, Furukawa & Sasaki 2012). However, functional redundancy only helps sustain ecosystem function if different species respond to a disturbance in distinct ways (response diversity; Elmqvist *et al.* 2003). This response diversity may help promote recovery of a habitat post-disturbance (Mori, Furukawa & Sasaki 2012).

Peterson, Allen & Holling (1998) proposed the cross-scale resilience model. They argued that members of a functional group operating at different spatial scales (termed cross-scale redundancy) would likely respond to scale-specific disturbances in different ways. Consequently, variance in the range of spatial scales over which species perform a particular function should reflect ecosystem resilience and the potential for a site to recover after a perturbation (Fig. 1; Peterson, Allen & Holling 1998). To date, the cross-scale resilience model has undergone little testing (but see Fischer *et al.* 2007; Sundstrom, Allen & Barichievy 2012; Angeler, Allen & Johnson 2013), and we seek to empirically assess whether cross-scale redundancy within important functional groups supports the recovery of a system through a major disturbance event.

Coral reefs are high-diversity systems that provide key ecosystem services such as fisheries and coastal protection (Duffy 2002). Human impacts are causing significant and ongoing reef degradation, with some reefs shifting from coral to algal-dominated reefs in response to pressures such as abnormally warm water and overfishing (e.g. Gardner *et al.* 2003). Herbivorous fishes mediate competition between corals and macroalgae and are thus expected to affect the response of reefs to disturbance (Mumby *et al.* 2006), generating an extensive literature examining functional diversity and functional impact within these species (e.g. Bellwood *et al.* 2004; Burkepile & Hay 2008; Cheal *et al.* 2010). Herbivorous fishes exhibit a range of responses following coral loss (Wilson *et al.* 2006), indicative of considerable response diversity within this group (Pratchett *et al.* 2011; Thibaut, Connolly & Sweatman 2011). However, exploration of the traits that support a range of responses to acute environmental impacts and their consequences for ecosystem function is lacking. The cross-scale resilience model provides a means of evaluating the importance of the spatial scales over which reef herbivores provide their functions as a driver of response diversity. Furthermore, given the functional role of herbivorous fishes in controlling algae, the cross-scale resilience model predicts that variance in the range of spatial scales over which herbivores perform their function would influence resilience, here defined as the capacity of a reef to retain the same structure and function across a disturbance event.

Seychelles' reefs were substantially disturbed in 1998 when the interaction of an El Niño and the Indian Ocean

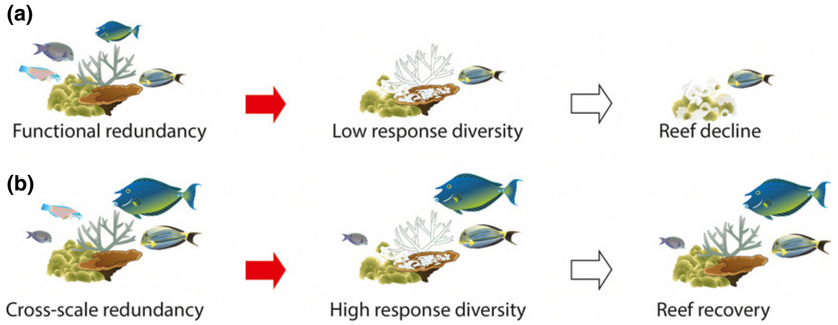

Fig. 1. Responses to a disturbance event predicted by the cross-scale resilience model, showing the proposed influence of (a) high herbivore functional redundancy (multiple species providing the same role) and (b) high herbivore functional and cross-scale redundancy (multiple species providing the same role but at different spatial scales as indicated by variable body sizes) on community response diversity, leading to either reef recovery or decline. Both communities have the same total herbivore biomass and functional diversity prior to disturbance. Filled arrows indicate a disturbance event (e.g. coral bleaching), and white arrows indicate reef trajectories post-disturbance.

dipole led to elevated water temperatures, coral bleaching and a resultant loss of >90% live coral cover (Wilkinson 2000). Benthic community composition and the size and species composition of herbivorous fishes have been monitored over 17 years from 1994, spanning the 1998 disturbance, through to 2011. Following the climate-induced disturbance event, some reefs have shown signs of recovery, whereas other areas shifted to an algal-dominated state (Chong-Seng *et al.* 2012). These divergent post-disturbance benthic trajectories are influenced by various site-level attributes, such as the initial structural complexity of the reef, water depth and herbivorous fish biomass (Graham *et al.* 2015). Fishes are the dominant herbivores on Seychelles reefs, with relatively little grazing pressure provided by other herbivores such as urchins. However, the specific facets of the herbivorous fish community that contribute to reef recovery in Seychelles have yet to be determined. Here, we use these long-term data to (i) compare the performance of cross-scale and functional redundancy in herbivorous fishes as indicators of recovery and thus resilience; (ii) evaluate the relationship between response diversity across the disturbance event (indicated by the best performing redundancy metrics) and herbivore function over time; and (iii) determine how redundancy and the potential for response diversity within sites changes across the disturbance event. The analyses are intended to guide the selection of resilience indicators and to identify whether there are any options for reef management that would increase resilience to temperature-induced disturbances.

Materials and methods

FIELD METHODS

Fish and benthic communities were surveyed at 21 reef sites in the inner Seychelles in 1994, 2005 and 2011. Fish abundance and individual body length (to the nearest cm) of diurnally active non-cryptic herbivorous species (37 species from four families) were estimated in 8–16 replicate survey areas (7 m radius measured with a pre-cut length of rope) at each site using instantaneous underwater visual census (UVC). Larger, mobile species were recorded before smaller, more site attached species to minimize bias caused by diver effects. The accuracy of fish body length estimations were assessed daily using sections of PVC pipe prior to the start of data collection, and length estimates were consistently within 5% of actual lengths. On completion of each UVC replicate, the per cent cover of different benthic components (macroalgae, hard coral, soft coral and non-living substrata) and the structural complexity of the reef (six point visual scale) were estimated. This method provided rapid estimates of percentage cover and complexity in the replicate survey areas and gives comparable results to methods such as line intercept transects and the linear vs. contour rugosity measure (Wilson, Graham & Polunin 2007). In 1994 and 2005, 16 replicate areas were surveyed at each site, whereas in 2011, eight replicates were surveyed as statistical power analyses indicated that surveying 16 replicates did not significantly alter the percentage change detectable among years in either coral cover or fish biomass (Table S1, Supporting Information). Individual body mass was estimated from body length using published length–mass relationships (Froese & Pauly 2012). Further details of survey methods and data processing are provided by Jennings, Grandcourt & Polunin (1995), Graham *et al.* (2006) and Wilson *et al.* (2012).

DATA ANALYSIS

Benthic condition

Variation in the benthic composition among sites and time periods was assessed using principal component analysis (PCA) in the statistical software PRIMER (Clarke 1993). Data were log $(x + 1)$-transformed, and Euclidean distances were used to develop the distance matrix. PCA axis 1 values (hereafter PCA1), which separated sites with high coral cover and complexity (positive values) from those with high macroalgal cover (negative values), were extracted for each site as an index of benthic condition.

Redundancy metrics

Herbivorous fishes were assigned to one of three functional groups: grazers/detritivores, scrapers/excavators and browsers (Bellwood *et al.* 2004). Grazers/detritivores and scrapers/excavators reduce the colonization rates of macroalgae and potentially promote coral recruitment (Hughes *et al.* 2007), with the latter group also contributing to bioerosion (Bellwood, Hoey & Hughes 2012). In contrast, browsers feed on mature macroalgae and can help reverse shifts from coral to macroalgal dominance (Green & Bellwood 2009).

Two approaches were used to calculate redundancy within each site and year: (i) redundancy across functional groups and (ii) redundancy across functional groups and size classes, with each approach consisting of two complementary ordination-based metrics (dispersion and evenness). The first approach (hereafter termed 'functional group redundancy') solely incorporated the categorical trait 'functional group' (browser, grazer/detritivore, scraper/excavator) and consisted of the metrics, '*functional dispersion*' and '*functional evenness*', to indicate the distribution of biomass across functional groups (Villéger, Mason & Mouillot 2008; Laliberté & Legendre 2010). Functional dispersion is the mean distance of each species to the mean functional group value weighted by biomass. Higher values indicate biomass is more dispersed among the functional groups (Table S2Ai). Functional evenness describes the distribution of biomass among functional groups. Higher values indicate biomass is more evenly distributed among functional groups (Table S2Aii). In combination, these indices indicate the functional group diversity and redundancy within groups (Fig. S1). To calculate the indices, two matrices were developed: sites × species, populated with biomass data, and species × trait, populated with trait attributes (Table S3). Functional dispersion and evenness were calculated using the FD package in R (Laliberté & Legendre 2010).

The second approach for calculating redundancy (hereafter termed 'cross-scale redundancy') incorporated both the categorical trait 'functional group' and the continuous trait 'size' and consisted of the metrics '*function & size dispersion*' and '*function & size evenness*', to indicate the distribution of biomass among functional groups and size classes. Body size was incorporated into this second set of metrics as the cross-scale resilience model is based on the assumption that size is positively correlated with the scale at which a species operates and provides its function (Calder 1984). Recent work exploring the relationship between body length and the scale of functional movements made by herbivorous reef fishes supports this assumption, with larger herbivores exhibiting longer foraging movements than their smaller-bodied counterparts (Nash, Graham & Bellwood 2013). Intraspecific variability in body length also affects interactions between reef fishes and their habitat (Welsh, Goatley & Bellwood 2013), and thus, to incorporate intraspecific size variability into the indices, each species was split into 5 cm size classes (hereafter referred to as species–size categories). We developed two matrices based on these species–size categories: sites × species–size categories, populated with biomass data, and species–size categories*traits, populated with trait attributes (Table S4). In this second approach for calculating redundancy, higher values of functional dispersion indicate biomass is more dispersed among functional groups and size classes (Table S2Bi), while higher values of functional evenness indicate biomass is more evenly distributed among functional groups and size classes (Table S2Bii). In combination, the complementary metrics indicate the degree of functional group diversity and cross-scale redundancy for any group of fishes (Fig. S1).

Herbivorous reef fish are targets of small-scale artisanal fisheries in Seychelles. Some of our study sites were located in no-take marine reserves ($n = 9$), and others in fished areas ($n = 12$). Fishing often targets large individuals (Jennings, Reynolds & Polunin 1999); therefore, there was a need to assess whether fishing affected redundancy within the herbivore community and thus needed to be accounted for in subsequent analyses. We modelled the effect of fishing (fished vs. no-take) on the different redundancy metrics: '*functional dispersion*', '*functional evenness*', '*function & size dispersion*', and '*function & size evenness*'. None of these relationships were significant, and therefore, we did not incorporate fishing into subsequent analyses (Table S5).

Redundancy as an indicator of reef resilience

To evaluate whether redundancy predicts resilience, we assessed whether the metrics calculated for the fish communities in 1994 predicted post-disturbance benthic trajectories. To achieve this, change in benthic condition (position on the PCA1) post-disturbance (2005–2011) was modelled as a function of the two different approaches for calculating redundancy: functional dispersion 1994 + functional evenness 1994 and function & size dispersion 1994 + function & size evenness 1994 and a null model incorporating herbivore biomass 1994. This null model was to ensure any differences in performance among the redundancy models were not purely due to variation in overall herbivore biomass among sites. Models were compared with the Akaike Information Criteria adjusted for small sample sizes (AICc, AICCMODAVG package in R; Mazerolle 2013). To understand the relative importance of the two explanatory variables in the optimal model, a second model selection step evaluated the relative performance of all possible models within the optimal global model (function & size dispersion 1994 + function & size evenness 1994). Prior to model fitting, the explanatory variables were checked for collinearity. The residuals were checked to ensure they met the assumptions of the models. The explanatory variables in the optimal model were used in subsequent analyses.

Response diversity within the herbivore community

Herbivore biomass is a useful proxy for overall rates of herbivory within a community (Bellwood *et al.* 2004). Thus, temporal changes in herbivore biomass were assumed to reflect changes in the delivery of herbivory (before and following the disturbance event). To understand how redundancy was related to the ongoing delivery of herbivory, for those metrics that successfully predicted benthic trajectories, we evaluated their relationship with herbivore biomass through time. Herbivore biomass (square root transformed to meet model assumptions) in 1994, 2005 and 2011 was modelled as a function of '*function & size dispersion*' and '*function & size evenness'* in 1994.

For those indices related to the maintenance of herbivore function, we investigated patterns of response diversity among size classes. Sites were ranked ordered according to their values of '*function & size dispersion*' in 1994 and then were grouped according to low, mid and high values (equal groupings with seven sites in each category). We calculated mean change in herbivore biomass within size classes, through the disturbance event (1994–2005) and post-disturbance (2005–2011) for each of the three categories. Bootstrapped 95% confidence intervals were calculated for each mean biomass change.

Redundancy over time

For those redundancy metrics that successfully predicted benthic trajectories, we evaluated the stability of the metrics, and hence redundancy, through the disturbance event. This would allow us to understand whether redundancy within the herbivore community remained constant over time and thus sites exhibiting highly redundant communities before the disturbance retained this high redundancy, or whether communities exhibited fluctuations in redundancy over time. To achieve this, values of the '*function & size'* metrics in each sampling year were compared with their values in other years (2005 vs. 1994, 2011 vs. 2005, 2011 vs. 1994).

Results

BENTHIC COMMUNITY CHANGE

The sites showed differential resilience to the bleaching event as reflected in the different trajectories of benthic community change (Fig. 2). The first principle component axis (PCA1) explained 35·9% of the variation among sites and time periods and differentiated between high coral cover and complexity at positive PCA1 scores and high macroalgal cover at negative PCA1 scores. The second axis (PCA2) explained 24·4% of the variation among sites and time periods and differentiated between high rubble and sand at negative PCA2 scores and high rock cover at positive PCA2 scores. In 1994, sites were located at positive values on PCA1 (high coral cover and complexity and low algal cover, mean of 0·35 ± 0·14 SE). In 2005, following bleaching in 1998, sites had moved varying distances in a negative direction along PCA1 (mean of −0·43 ± 0·31 SE). By 2011, sites were even more dispersed along PCA1, with some returning to locations on PCA1 that were close to those in 1994, whereas other sites

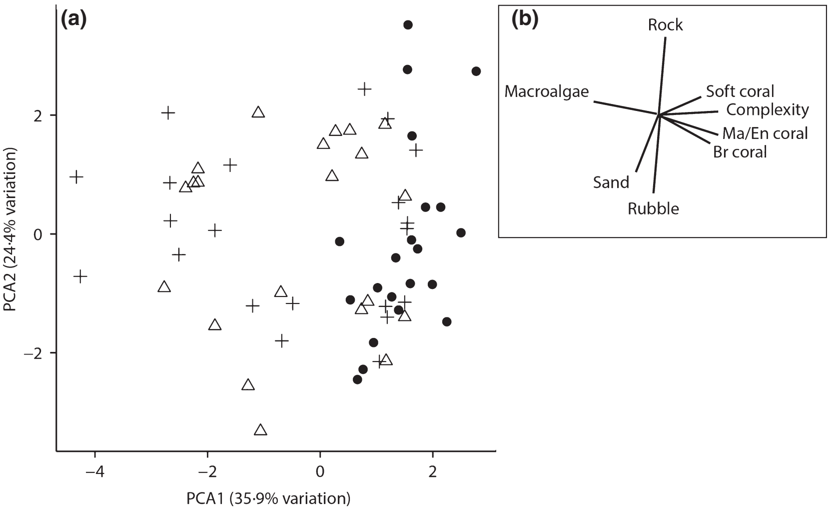

Fig. 2. Principal component analysis (PCA) of benthic habitat variables in 1994 (circles), 2005 (triangles) and 2011 (crosses). (a) Variation in the benthic habitat among sites shown for the first two axes of a PCA. (b) Relative contribution of the benthic variables to the variation in benthic condition. Ma/En are massive and encrusting hard corals; Br is branching coral.

moved further towards the negative end of PCA1 with high macroalgal cover and low coral cover and complexity (mean of −0·57 ± 0·45 SE).

REDUNDANCY AS AN INDICATOR OF REEF RESILIENCE

Change in benthic condition post-disturbance was best explained by a model incorporating the '*function & size'* metrics (Table 1a), variables that reflected levels of cross-scale redundancy. Furthermore, there was more support for the *'function & size'* model incorporating both dispersion and evenness than for one solely including dispersion (Table 1b). The optimal model explained 26% of the variation in changing benthic condition, with sites with greater dispersion and evenness in 1994 showing greater recovery post-disturbance (larger positive change on benthic PCA1 between 2005 and 2011; Fig. 3).

RESPONSE DIVERSITY WITHIN THE HERBIVORE COMMUNITY

Evaluation of the maintenance of herbivore function over time showed a positive relationship between *'function & size dispersion*' in 1994 and herbivore biomass in 1994, 2005 and 2011 (Table 2a; Fig. 4). Sites with low dispersion in 1994 exhibited some variation in biomass over time, whereas sites with high dispersion in 1994 exhibited a more consistent increase in biomass from 1994 to 2011. This suggests ecosystem function was enhanced at these latter sites, although there was no significant increase in the slopes among years (Fig. 4). In contrast, there was no relationship between '*function & size evenness'* in 1994 and herbivore biomass in 1994, 2005 and 2011 (Table 2b).

Patterns of response diversity among size classes indicated a decline in biomass of the smallest size classes following the disturbance, for sites with low, mid and high '*function & size dispersion'* in 1994 (Fig. 5). There were concurrent increases in biomass of mid–large size classes for those sites with mid and high dispersion in 1994. This increase was only replicated in some of the mid-size classes at sites with low '*function & size dispersion*' in 1994. Post-disturbance (2005–2011), there was considerable variability in biomass trends among sites; however, there were some consistent increases in biomass at small- to mid-size classes across all sites.

Table 1. Model selection comparing the performance of the different redundancy metrics in 1994 as predictors of reef benthic trajectories from 2005 to 2011. (a) Step 1 evaluated the performance of the indices from the functional group and the functional and size approaches, and (b) Step 2 evaluated the performance of models combining different indices arising from the functional and size approach

Model	*K*	Akaike Information Criteria (AICc)	Δ AICc	AICc Wt
(a)				
Functional group and size dispersion + Functional group and size evenness	4	62·2	0·00	0·86
Herbivore biomass	3	66·9	4·70	0·08
Functional group dispersion + Functional group evenness	4	67·7	5·42	0·05
(b)				
Functional group and size dispersion + Functional group and size evenness	4	62·2	0·00	0·66
Functional group and size dispersion	3	65·2	2·96	0·15
Functional group and size evenness	3	65·6	3·42	0·12
Herbivore biomass	3	66·9	4·70	0·06

REDUNDANCY OVER TIME

There was no evidence of consistent relationships between the redundancy metrics over time. Specifically, there was no relationship between '*function & size dispersion*' in 1994 and 2005, 2005 and 2011 or 1994 and 2011 (Table S6A). Similarly, no relationships were found for '*function*

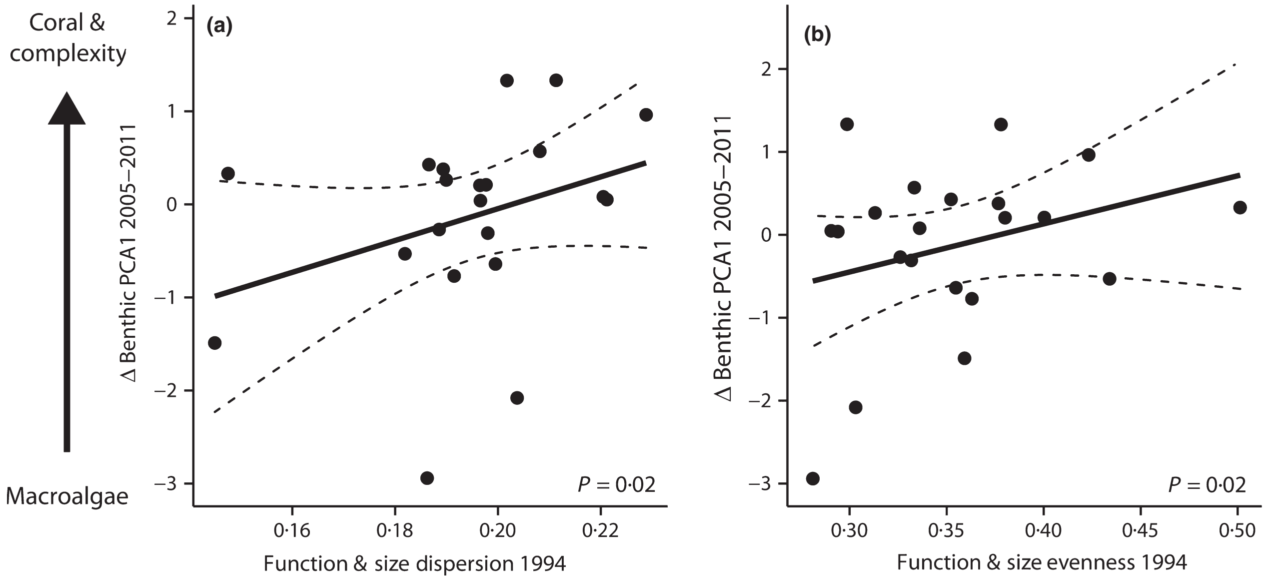

Fig. 3. The relationship (±SE) between change in benthic condition (position on PCA1) from 2005 to 2011 and the cross-scale redundancy metrics (a) function and size dispersion and (b) function and size evenness. $F_{2,18} = 4{\cdot}51$; $P = 0{\cdot}03$; Adj. $R^2 = 0{\cdot}26$. PCA, principal component analysis; PCA1, PCA axis 1.

Table 2. Models of relationships between herbivore biomass in different years and (a) functional and size dispersion and (b) functional and size evenness. Significant relationships are shown in bold. Herbivore biomass was square-root-transformed to meet model assumptions

Model	*F*	*P* value	Adj R_2
(a) Functional group and size dispersion 1994			
Herbivore Biomass 1994	12·06	<0·01	0·36
Herbivore Biomass 2005	8·83	<0·01	0·28
Herbivore Biomass 2011	7·96	0·01	0·26
(b) Functional group and size evenness 1994			
Herbivore Biomass 1994	3·89	0·06	0·17
Herbivore Biomass 2005	2·48	0·13	0·07
Herbivore Biomass 2011	1·44	0·24	0·02

& size evenness' between the same year combinations (Table S6B). This suggests that cross-scale redundancy varies through time.

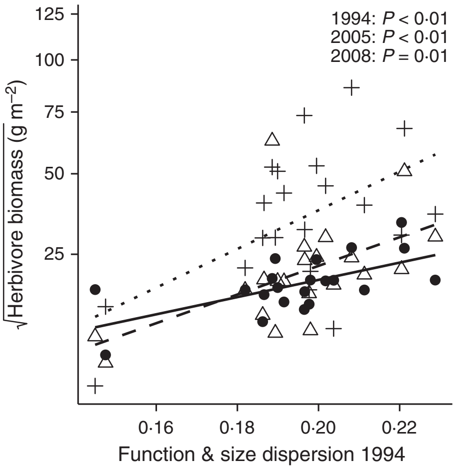

Fig. 4. Relationships between log herbivore biomass in 1994 (circles, solid line), 2005 (triangles, dashed line) and 2011 (crosses, dotted line) and function and size dispersion in 1994.

Discussion

Consistent with the predictions of the cross-scale resilience model, redundancy metrics incorporating the distribution of herbivore biomass across functional groups and size classes (and therefore spatial scales; Nash, Graham & Bellwood 2013) were better indicators of reef recovery than those solely describing the distribution of species' biomass across functional groups, or than total herbivore biomass. The distribution of herbivores across size classes reflected response diversity, with small individuals more negatively impacted by the bleaching event. Loss of the function provided by small individuals appears to have been compensated for through increases in the biomass of large individuals. Patterns of cross-scale redundancy were not retained through the disturbance event and had not recovered to pre-disturbance levels by 2011, suggesting fish community regeneration is leading to new community configurations.

CROSS-SCALE REDUNDANCY AS AN INDICATOR OF REEF RESILIENCE

Cross-scale redundancy provides a useful indicator of reef resilience to bleaching events. Specifically, greater dispersion and evenness of herbivores across size classes (and therefore spatial scales) and functional groups appear to have contributed to coral recovery after disturbance. Sites with low dispersion and evenness across both functional

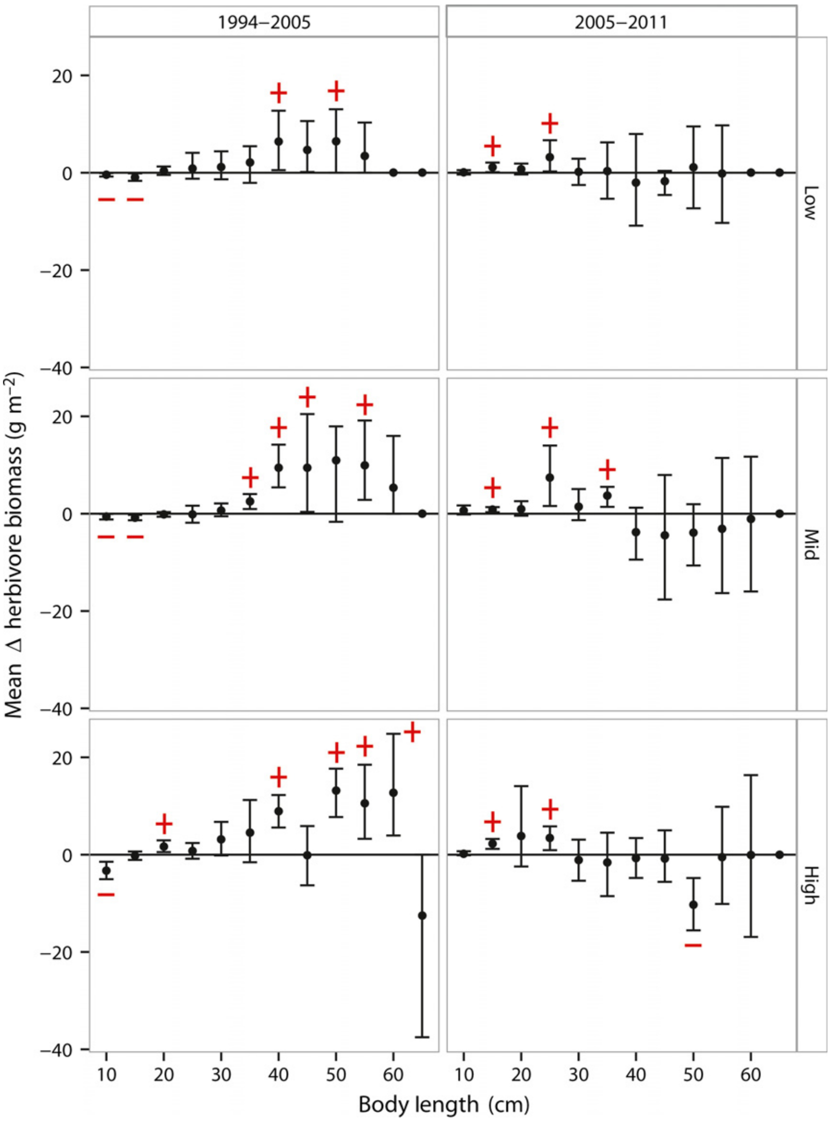

Fig. 5. Mean change (±95% CI) in herbivore biomass within size classes between 1994 and 2005, and 2005 and 2011 for sites with low, mid or high function and size dispersion in 1994. Sites were classified as low, mid or high according to their rank-ordered dispersion values, with seven sites in each category. Symbols represent confidence intervals that are significantly different from zero. Change in biomass for large size classes may be driven by few individuals due to their large mass; for example, non-significant decline of individuals >65 cm between 1994 and 2005 at sites with high function and size dispersion is driven by loss of one individual.

groups and size classes before the bleaching were more likely to shift to a macroalgal-dominated state.

Conservation of the herbivore function through time was a consequence of the breadth of responses by different-sized individuals to coral bleaching and mortality. The proximate driver of decline in small individuals is likely to be habitat loss, in particular the collapse of coral skeletons following coral mortality (Graham *et al.* 2006). An increase in large-bodied herbivores may result from the subsequent proliferation of algae, leading to more feeding opportunities and reduced competition (Pratchett *et al.* 2008). Similar declines in small herbivores, coincident with stable or increased abundance of large herbivore following coral bleaching, were recorded at Scott Reef in the eastern Indian Ocean (Halford & Caley 2009) and in Fiji (Wilson *et al.* 2010). Such coherence suggests this is a general response of herbivore communities following extensive coral mortality. Critically, reorganization of the benthos and coral recovery were reliant on the presence of large herbivores. In contrast, on reefs where recovery was not seen, there was no increase in the biomass of large individual, presumably due to the scarcity of large herbivores pre-disturbance.

Our study indicates that body size of reef fish affects the way individuals respond to a disturbance. Prior work has highlighted that body size may also affect functional impact, with large herbivores providing greater functional impact. For example, larger individuals remove disproportionately more algae per unit body mass (Lokrantz *et al.* 2008) and have greater functional breadth (Green & Bellwood 2009) than small-bodied counterparts. As a consequence, body size of herbivorous fishes appears to influence the function of an individual both by affecting its functional impact and through the maintenance of that function in the face of external disturbances.

We tested cross-scale response diversity in relation to a single type of disturbance (elevated water temperatures). Testing could usefully be extended to a wider range of acute natural and anthropogenic disturbances such as cyclones or sediment laden flood plumes, to assess the extent to which responses of large and small individuals are consistent. Cyclones, in particular, might be expected to drive different changes in the fish community, as unlike bleaching events, cyclones directly impact the structure of the reef, which provides critical refuge for fish (Wilson *et al.* 2006). Results from a broader range of studies would indicate whether cross-scale redundancy was also an effective indicator of resilience in instances where large rather than small individuals respond negatively to disturbance. Resilience may be observed in these instances if high densities of small herbivores control algal growth, opening space for coral recruitment and recovery (e.g. Adam *et al.* 2011).

REDUNDANCY OVER TIME

We found no relationship either between the function and size index of dispersion over time or the index of evenness over time; therefore, sites with high redundancy within their herbivore communities prior to the disturbance did not necessarily retain this redundancy across the disturbance. This temporal variability in dispersion and evenness was disguised at recovering sites by the compensatory increases in herbivore biomass in large size classes maintaining the functional impact of this group. However, further disturbances that occur either before cross-scale patterns of function return to pre-disturbance levels or where patterns of cross-scale function reorganize to a new configuration may have different effects compared to those seen after the 1998 bleaching event because (i) the predominance of large individuals in the community at recovering sites suggests lower levels of size-based response diversity at these sites into the future; (ii) small individuals from large species were depleted, and thus, the mortality of existing large individuals is unlikely to be fully compensated for by recruits, compromising the long-term viability of populations (Graham *et al.* 2007); and (iii) other types of disturbance occurring in the future, for example cyclones, may result in different response capabilities among fish size classes (Graham, Nash & Kool 2011).

Work on other isolated Indian Ocean reefs showed recovery of coral cover after 12 years (e.g. Scott Reef; Gilmour *et al.* 2013) following the 1998 bleaching event, but community composition differed from starting conditions with fewer mature acroporids providing three-dimensional. A study on the Great Barrier Reef found that fish communities have not returned to a pre-bleaching composition more than 16 years after the 1998 bleaching event (Bellwood *et al.* 2012). Thus, it is perhaps not surprising that while some Seychelles reefs were showing signs of coral recovery 11 years after the 1998 bleaching event (Wilson *et al.* 2012), neither coral nor fish communities were approaching pre-disturbance composition or cross-scale redundancy at individual sites, with different long-term configurations emerging. Thus, those reefs that were resilient to past disturbances due to cross-scale redundancy may not exhibit the same degree of resilience to future disturbances and warrant increased management attention.

MANAGEMENT IMPLICATIONS

Our findings indicate that maintaining or rebuilding cross-scale redundancy provides one means of ensuring reef resilience and reducing the risk of shifts to macro-algal-dominated states following disturbance. Non-random loss of herbivores following bleaching suggests it is not enough for managers to seek to maintain species in some important functional groups; their actions must also conserve the response diversity that underpins redundancy. In practical terms, this means maintaining many sizes of species and individuals in the community.

In our study, we found no evidence of fishing effects on redundancy. However, our indicator of fishing pressure, based on whether a site is in a fished area or a no-take marine reserve, may not reflect large differences in fishing effort because compliance with no-take marine reserve rules is mixed in the Seychelles (Daw *et al.* 2011). Importantly, maintaining the abundance of large individuals may be difficult when fishing efforts are typically directed at larger bodied individuals and species, and these are more vulnerable to a given rate of fishing mortality (Jennings, Reynolds & Polunin 1999). However, if maintaining resilience as well as fish yields is a management priority, our results suggest it is preferable to distribute fishing mortality more widely among size classes. This strategy has been dubbed 'balanced harvesting' and aims to distribute fishing mortality among size classes and species in proportion to their relative productivity (Garcia *et al.* 2012). Balanced harvesting has already been proposed as one way of improving trade-offs between biodiversity conservation and fishery yields in other contexts (Garcia *et al.* 2012). Although it can be a significant technical challenge to allocate mortality in this way, some subsistence reef fishers already make use of a much wider range of species and size classes than commercial and recreational fisheries (Dalzell 1996). Nonetheless, the extent to which fishery management actions alone will bolster resilience at individual sites will depend on the relative contribution of other factors such as reef structural complexity, coral recruitment, water depth, nutrient regimes and coral community composition that have contributed to the resilience of coral-dominated reefs in the Seychelles and elsewhere in the region (McClanahan *et al.* 2012; Graham *et al.* 2015).

Although cross-scale redundancy provides a useful indicator of reef resilience and more redundancy is expected to confer greater resilience at a given site, the results do not allow us to define ubiquitous targets for '*function & size dispersion*' that could be linked to defined levels of resilience. This is for three reasons: (i) we focus on a single disturbance type; (ii) we recognize the variable role of cross-scale redundancy in contributing to resilience among sites; and (iii) we appreciate that different levels of cross-scale redundancy in functional groups may be linked to the evolutionary history of a region (Walker, Kinzig & Langridge 1999). Nevertheless, our results provide clear evidence that a wide distribution of herbivore biomass among functional groups and size classes increases the resilience of reefs to disturbance, and the cross-scale resilience model provides a promising avenue for managers developing frameworks for predicting reef resilience.

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Data accessibility

Data are available through the James Cook University data repository Tropical Data Hub (https://eresearch.jcu.edu.au/tdh/data/d2605d62-da63-4d3a-892c-3e3b68c06911).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Conceptual figure of species-size groupings in trait space.

Table S1. Power analysis for surveys.

Table S2. Description of redundancy metrics.

Table S3. Matrices for the metrics incorporating functional group.

Table S4. Matrices for the metrics incorporating functional group and size.

Table S5. Relationships between redundancy metrics and fishing.

Table S6. Relationships between function & size metrics.