

Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs

ALISTAIR J. CHEAL,¹ MICHAEL EMSLIE, M. AARON MACNEIL, IAN MILLER, AND HUGH SWEATMAN

Australian Institute of Marine Science, PMB No. 3, Townsville, Queensland 4810 Australia

Abstract. Many ecosystems face degradation unless factors that underpin their resilience can be effectively managed. In tropical reef ecosystems, grazing by herbivorous fishes can prevent coral–macroalgal phase shifts that commonly signal loss of resilience. However, knowledge of grazing characteristics that most promote resilience is typically experimental, localized, and sparse, which limits broad management applications. Applying sound ecological theory to broad-scale data may provide an alternative basis for ecosystem management. We explore the idea that resilience is positively related to the diversity within and among functional groups of organisms. Specifically, we infer the relative vulnerability of different subregions of the Great Barrier Reef (GBR) to phase shifts based on functional characteristics of the local herbivorous fish communities. Reef slopes on 92 reefs set in three zones of the continental shelf in eight latitudinal sectors of the GBR were surveyed on multiple occasions between 1995 and 2009. Spatial variation in fish community structure was high and driven primarily by shelf position. Measures of functional diversity, functional redundancy, and abundance were generally higher offshore and lower inshore. Two turbid inshore subregions were considered most vulnerable based on very low measures of herbivore function, and this was supported by the occurrence of phase shifts within one of three subregions. Eleven reefs that resisted phase shifts after major coral mortality included some with very low measures of herbivore function. The fact that phase shifts did not necessarily occur when large herbivores were scarce indicates that other environmental factors compensated to preserve resilience. Estimates of vulnerability based solely on herbivore function may thus prove conservative, but caution is appropriate, since compensatory factors are largely unknown and could be eroded unwittingly by anthropogenic stresses. Our data suggest that managing the threat of phase shifts in coral reef ecosystems successfully will require spatially explicit strategies that consider both the functional characteristics of local herbivore communities and environmental factors that may raise or lower resilience thresholds. A strong positive correlation between water clarity and the species richness and abundance of herbivorous fishes suggests that management of water quality is of generic importance to ensure the ecosystem services of this important group of herbivores.

Key words: coral reefs; ecosystem resilience; functional diversity; functional group; functional redundancy; herbivory; macroalgae; management; phase shift; reef fishes; resilience threshold; turbidity.

INTRODUCTION

Ecosystems around the world are under increasing stress from human activities, highlighting the need to better understand and manage the factors that promote ecosystem resilience (Folke et al. 2004). Conservation of biodiversity is fundamental to modern natural resource management but it is not species richness per se that confers resilience, but the functional contribution of species to important ecological processes (Worm et al. 2006). Management strategies that take into account the functional implications of species' distributions and abundances may help conserve vulnerable ecosystems but examples are rare, in part because of uncertainty

about how specific functional roles contribute to ecosystem resilience. It is often impractical to investigate these relationships experimentally at ecologically meaningful scales. Given the urgent need to preserve many ecosystems and the limitations of manipulative approaches, assessment of the *relative* resilience of natural communities using theoretically important measures of functional potential (i.e., functional diversity and functional redundancy) that are based on field data may provide a practical scientific foundation for effective ecosystem management (Allen et al. 2005, Fischer et al. 2007). Here we apply this approach to a large coral reef ecosystem, Australia's Great Barrier Reef. While the concept of resilience has many facets, we focus specifically on the capacity of coral reefs to resist shifts to a macroalgal-dominated state of lesser ecological and socioeconomic value following coral mortality, which is a concern for reef managers worldwide (Hughes

Manuscript received 15 December 2011; revised 25 May 2012; accepted 4 June 2012; final version received 23 July 2012.
Corresponding Editor: P. K. Dayton.

¹ E-mail: a.cheal@aims.gov.au

et al. 2010). We assessed the relative vulnerability of reefs in different environmental settings to such phase shifts based on the functional characteristics of their communities of herbivorous fishes, a group considered to be critically important for the prevention of macroalgal blooms (Hughes et al. 2007). As threats to the existence of coral reef ecosystems are increasing (Hoegh-Guldberg et al. 2007, Hughes et al. 2010) we highlight the general applicability of our findings to coral reef conservation.

Darwin (1859) first suggested that ecological stability is positively related to species richness. Others followed his lead (MacArthur 1955, Tilman et al. 1996, Kiessling 2005) and the concept is now widely accepted and routinely applied in modern conservation strategies through efforts to preserve biodiversity. However, decades ago Holling (1973) recognized that management strategies based on theories of ecological stability were not preventing species declines or environmental degradation. Acknowledging that natural systems can persist while fluctuating in an unstable fashion, Holling advocated a management approach based on the concept of resilience in ecological systems. A definition of resilience was subsequently refined as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks” (Walker et al. 2004). Resilience concepts incorporate the idea that the capacity of a system to cope with ecological disruptions without stabilizing in a fundamentally different state depends on maintenance of important ecosystem processes. Because these processes are often driven by the functional roles of constituent species, resilience is likely to be highest when both functional diversity and functional redundancy are high within and across scales (Walker 1992, Tilman et al. 1996, Peterson et al. 1998, Hooper et al. 2005, Folke 2006). The realization that human actions continue to erode the capacity of ecosystems to sustain natural resources and to provide desired services (Folke 2006) has motivated searches for more effective approaches to management. Resilience concepts have received increased attention and the application of these concepts to identify vulnerable ecosystems and to inform management decisions is now a high priority (Folke et al. 2004, Allen et al. 2005, Nyström et al. 2008, Hughes et al. 2010).

Concerns for the resilience of coral reef ecosystems have centered on the capacity of reefs to resist shifts from dominance of space by hard corals to dominance by fleshy macroalgae following coral mortality (Bellwood et al. 2004, Hughes et al. 2010). Such phase shifts have been most common in the Caribbean (Bruno et al. 2009), but many other reef systems appear poised to follow, based on predictions that the frequency and intensity of disturbance events will increase with global warming (Hughes et al. 2003, Hoegh-Guldberg et al. 2007, MacNeil et al. 2010), and because large herbivores

have been widely over-exploited (Jackson et al. 2001). Fishes and urchins are the most numerous large herbivores on coral reefs and are primarily responsible for keeping the reef surface free of macroalgae that may inhibit coral growth and for maintaining a surface suitable for settlement by coral recruits (Green and Bellwood 2009). Four strands of evidence support the importance of herbivorous fishes in maintaining reef resilience: (1) the association of phase shifts with overfishing (Hughes 1994); (2) field experiments (Lewis 1986, Hughes et al. 2007, Mantyka and Bellwood 2007, Burkepile and Hay 2008, 2010); (3) theoretical modeling (Mumby 2006, Mumby et al. 2007); and (4) long-term observations of reef community dynamics (Cheal et al. 2010). Together, these suggest that phase shifts are unlikely to occur when the diversity and abundance of a range of functional groups of herbivorous fishes is high.

The diversity and abundance of herbivorous fish communities on coral reefs may be depleted by overfishing, but other factors that limit these fishes are not well understood. Disturbances to the benthos negatively affect many reef fishes but appear to have little effect on large herbivorous fishes (Ledlie et al. 2007, Cheal et al. 2008) unless associated with extreme loss of habitat complexity (Halford et al. 2004, Graham et al. 2007). It is likely, however, that the distribution of herbivorous reef fishes is fundamentally linked to the productivity of their algal diet and associated detritus (Russ and McCook 1999, Russ 2003), which is related in part to water clarity and its effect on the penetration of sunlight through the water column (Klumpp and McKinnon 1989). Water clarity has been positively associated with the abundance and diversity of herbivorous reef fishes (Williams and Hatcher 1983, Russ 2003, Mallela et al. 2007, Nemeth and Appeldoorn 2009) and may be a useful indicator of coral reef health in general (De'ath and Fabricius 2010). While low water clarity may occur naturally in some situations, it commonly signals detrimental anthropogenic influences such as sediment runoff from cleared land and excessive nutrient inputs that enhance algal growth. Sedimentation and eutrophication are often associated and increase the likelihood of coral-macroalgal phase shifts (Fabricius et al. 2005, De'ath and Fabricius 2010), particularly if the resultant lower water clarity enhances negative feedbacks with herbivory. At present, data on the strength of association between water clarity and the distribution of herbivorous fishes on coral reefs and the consequences for phase shift vulnerability are sparse.

The prediction that phase shifts will become more frequent on coral reefs with changing climate has increased calls to manage for resilience (Bellwood et al. 2004, Nyström et al. 2008, Hughes et al. 2010), but it is not always clear how this can be achieved. One obvious strategy is to protect all herbivorous fishes, but this is unrealistic in many regions where these fishes are a staple food for coastal populations. Strategies that allow fishing but regulate fishing pressure so as to maintain critical

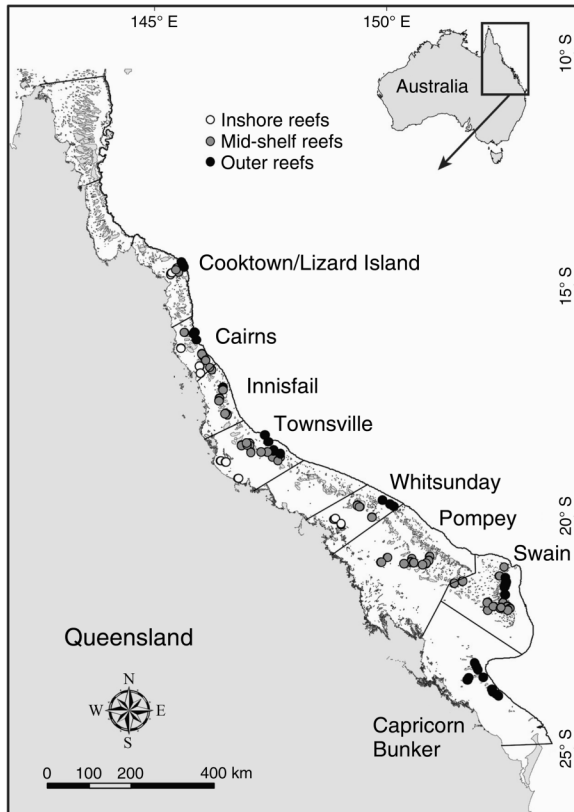


FIG. 1. Map of the Great Barrier Reef, Australia, showing locations of the 92 survey reefs within eight sectors.

herbivore functions are beginning to appear (McClanahan et al. 2011), but remain difficult to implement. This is partly because of considerable spatial variation in the structure of herbivorous fish communities within and between reefs (Russ 1984, Cheal et al. 2012), with associated spatial variation in their functional characteristics. Strong spatial patterns in herbivorous reef fish communities can result from differing habitat preferences and competitive interactions but may also be influenced by regional evolutionary histories. For instance, similar functional groups of herbivorous fishes occur on Caribbean and Indo-West Pacific reefs, but species richness and taxonomic richness is less in the Caribbean (Green and Bellwood 2009), in theory making Caribbean reefs more vulnerable to phase shifts through lower functional redundancy. In fact, the assumption that coral reefs will flip to a macroalgal-dominated state if large herbivores are removed has almost reached paradigm status, driven largely by patterns in the Caribbean and particularly by the well-known Jamaican case study, where loss of herbivorous fishes, and then urchins, allowed macroalgae to flourish and persist (Hughes 1994). The threat of such phase shifts within different coral reef ecosystems cannot effectively be managed without a clear understanding of spatial patterns in herbivore communities and their functional capacity to prevent macroalgal blooms.

Most information on the spatial patterns of herbivory in coral reef ecosystems has come from disparate local studies that use a variety of methods, so broad-scale patterns are often unclear. Most reef ecosystems have also been subject to anthropogenic influences for many years, and estimating “natural” levels of herbivory from present-day communities raises the issue of shifting baselines (Jackson et al. 2001). Australia’s vast Great Barrier Reef (GBR) is possibly an exception. It covers >350 000 km², extends >2300 km from north to south, and is one of the world’s least degraded reef ecosystems (Pandolfi et al. 2003), due in part to comprehensive management regimes, but also because human coastal populations are small and their impacts are localized and relatively light (Lawrence et al. 2002). Reef fishes appear to be the principal large herbivores on the GBR. Even though the contribution of urchins to phase shift prevention has not been considered as fully as that of herbivorous fishes, they are not abundant on the GBR in comparison with the Caribbean in former times (Hutchings et al. 2007, Green and Bellwood 2009). Populations of herbivorous fishes on the GBR are probably relatively intact, since they are not commonly targeted or caught by professional, artisanal, or recreational fishers. Thus, the GBR provides an ideal system to assess spatial differences among unmodified communities of functionally important herbivorous reef fishes and the ramifications for reef resilience.

Since the mid 1990s, communities of fishes and benthic organisms on reefs in a wide variety of environmental settings across the GBR have been systematically surveyed by the Australian Institute of Marine Science (AIMS) (Sweetman et al. 2008). Here, we use these data to investigate links between the functional characteristics of herbivorous fish communities, the occurrence of coral–macroalgal phase shifts, and water clarity. Specifically:

- 1) We map spatial variability in three theoretically important measures of herbivore function: functional diversity, functional redundancy, and abundances within functional groups.
- 2) We relate these patterns to occurrences of phase shifts and of resilience (resistance to phase shifts).
- 3) We examine the association between spatial patterns of herbivorous fishes and water clarity.

We use this information to assess the relative vulnerability of different GBR environments to coral–macroalgal phase shifts and highlight the implications for management of coral reef resilience in general.

METHODS

Study sites and sampling procedures

Reef fish communities and benthic cover were surveyed annually on 47 “core” GBR reefs between 14° S and 24° S, and between 1995 and 2005 (Fig. 1; see also Sweetman et al. 2008). These reefs were all surveyed

again in 2007 and in 2009. In 2006 and 2008 another 45 “noncore” reefs between 16° S and 24° S were surveyed. Reefs were situated in three positions on the continental shelf. Inshore reefs were relatively close to the coast (5–30 km from land). Mid-shelf reefs were located on the continental shelf within the bulk of the GBR matrix. Outer reefs had few reefs to seaward, and so were exposed to oceanic influences from the Coral Sea. Reefs were haphazardly selected within eight sectors that represent different latitudes of the GBR (Fig. 1). The sectors differed in some or all of the following: temperature range, cross-shelf width, mean reef size and spacing (influencing permeability to oceanic intrusions as well as connectivity), and terrestrial influences. Each shelf position within a sector is hereafter referred to as a subregion. Data were not gathered in some subregions, either because suitable reefs were not available or for logistical reasons; only mid-shelf reefs were surveyed in the Pompey sector, only outer reefs in the Capricorn Bunker sector, and only mid-shelf and outer reefs in the Innisfail and Swain sectors. All but 3 of the 18 subregions incorporated at least three reefs; only two inshore reefs in the Cooktown–Lizard Island and in the Townsville sectors and a single outer reef in the Innisfail sector were surveyed (Fig. 1). Three sites were established on or near the northeast flank of each survey reef, each consisting of five permanently marked 50-m transects at depths between 6 and 9 m. The abundances of 210 noncryptic, diurnal fish species from 10 families were recorded along each transect using underwater visual census (Halford and Thompson 1996). Benthic organisms were surveyed concurrently along the same transects on a strip ~0.75 m wide using video (to 2006) or still cameras (after 2006), and cover of different benthic components was later estimated from images of each transect (Jonker et al. 2008). Identical methods were used to analyze camera and still video images, and the type of image (camera or video) did not alter the ability to distinguish the benthic components. The benthos was analyzed to genus for hard coral species and broad groupings for algae (i.e., macroalgae and turf algae). Mean values of total percentage cover of hard corals and macroalgae based on the 15 transects at each reef were used in analyses. Note that the term macroalgae here refers to larger frondose forms, not filamentous, turfing, blue-green and crustose algae. Water clarity was estimated at each site at each visit by recording the distance (in meters) along the transect tape measure at which objects became indistinct. These estimates were regularly checked by a second observer.

Target fish taxa and functional groups

This study concerned large, roving herbivorous fishes, including the majority of surgeonfishes (Acanthuridae), and all parrotfishes (Labridae) and rabbitfishes (Siganidae). Some large herbivorous fish taxa were not included in the target list (i.e., Kyphosidae, Ephippidae, and some Pomacanthidae species) because they were rarely

encountered. Our visual observations along with other visual census and video data on similar GBR reef slope habitats (Fox and Bellwood 2007, 2008) suggest that the species in our target list constitute most of the large reef fish grazing capacity on the GBR. Damselfishes (Pomacentridae) were counted during surveys, but none were included in this study, because their broad diets make it difficult to assign them to functional groups, and species that are clearly herbivorous tend to farm algae for their own consumption, making their contribution to reef resilience unclear (Green and Bellwood 2009). Other small herbivorous fishes such as blennies (Blennidae) and gobies (Gobiidae) were not surveyed because of their cryptic habits, but they are unlikely to have the capacity to prevent phase shifts.

Fish species were placed into one of four functional groups based on their method of feeding and their impact on the benthos (from published information, e.g., Bellwood and Choat 1990, Froese and Pauly 2006, Green and Bellwood 2009; and field observations). The groups were: (1) scrapers; parrotfishes that scrape the substrate, ingesting the epilithic algal matrix (EAM) and often leaving some organisms in the feeding scrapes; (2) excavators; parrotfishes that gouge the substrate deeply, ingesting the EAM and considerable amounts of substrate, leaving few organisms in the feeding scar; (3) Grazer/detritivores; surgeonfishes that feed in the EAM, leaving few distinctive feeding marks. Grazer/detritivores ingest a range of items including sediment, detritus, algal turf, and microalgae, and may also remove macroalgae before it becomes established; and (4) algal browsers; rabbitfishes and surgeonfishes that specifically crop turf and/or macroalgae, ingesting little of the EAM. The strictly detritivorous *Ctenochaetus* spp. were included with grazer/detritivores. A few nominally herbivorous species were not strict herbivores, and so were excluded from analyses. These included some surgeonfishes (*Naso* spp.) that are predominantly planktivores and one parrotfish species (*Bolbometopon muricatum*) that often feeds on live corals. All were rarely encountered during surveys.

Data analyses

Spatial patterns in community structure.—Initially we used nonparametric multivariate analysis of variance (MANOVA) to understand the extent of spatial and temporal differences in the structure of herbivorous fish communities on the GBR. This was important to broadly substantiate our subsequent approach to assessing the relative resilience of different subregions; if spatial differences were minimal or temporal differences were large, then using the functional characteristics of current herbivore communities to infer relative resilience may not have been useful or appropriate. We used the 47 core reefs that had been regularly surveyed for well over a decade, and included time in the model. Statistical significance was based on restricted permutation of observations (Anderson and ter Braak 2002).

Because we sampled fixed transects (i.e., repeated measures), among-reef variability was used as the error term for the spatial effects of shelf, sector, and their interaction. Models were fitted using the DISTLM program (Anderson 2001, McArdle and Anderson 2001). Data for herbivorous fishes was row centered and fourth-root transformed in order to reduce the influence of occasional encounters with large spawning aggregations and to adjust for the large numbers of zeros commonly encountered in this type of community data.

Functional measures.—We employed three measures of herbivore function to assess the relative vulnerability of different GBR subregions to phase shifts. These were derived from data from all 92 core and noncore reefs surveyed by AIMS between 2006 and 2009. This approach, using a subset of the entire data range, maximized spatial coverage by using data from all survey locations, reduced analytical problems due to uneven sample sizes, as each reef was sampled twice within the same time period, and provided the most up-to-date characterization of GBR herbivorous fish communities applicable to management. The definition and derivation of each functional measure follows;

- 1) *Functional diversity*: the number of functional groups observed at a site within a reef. Higher functional diversity should enhance the capacity of a system to cope with a range of different perturbations. For spatial comparisons, functional diversity was averaged, rather than modeled, over all sites within a subregion because values were maximal at the majority of sites.
- 2) *Functional redundancy*: the average probability of occurrence for species in each functional group at each site. Higher functional redundancy provides greater ecological insurance that a particular function will be maintained even if some contributing species are lost from the local community. Functional redundancy was quantified for each subregion and estimated using diversity-based occupancy models that estimate both the probability of occurrence (i.e., occupancy) and probability of detection for species within a given community based on a series of capture or observation occasions (Dorazio et al. 2006, MacKenzie et al. 2006). This partitioning of occurrence and detectability is important because imperfect detection in underwater visual surveys generates consistent downward bias in species richness that varies directly with abundance. (That is, species may not be recorded at a given reef either because they were not present or because they were not observed [MacNeil et al. 2008].) By marginalizing the effect of abundance on diversity, occupancy models better reflect functional redundancy than do conventional species richness values that implicitly, and unrealistically, assume that the probability of observing each species present on a transect is equal

to one. Specific details of the Bayesian hierarchical occupancy models are presented in the Appendix.

- 3) *Abundance*: the total number of individuals in each functional group at each site. Higher abundance means a greater capacity to fulfill a function and increases the spatial scale of influence. Abundance was quantified for each subregion and modeled using a negative binomial, Bayesian hierarchical model (see the Appendix for more details).

Herbivore function and occurrences of phase shifts and of reef resilience.—In order to test the usefulness of our functional measures of herbivory as indicators of phase shift vulnerability, we related known occurrences of phase shifts and resilience (resistance to phase shifts) on reefs to the functional characteristics of their local herbivore communities. The first criterion for a reef to be included in this comparison was that large areas of substrate suitable for algal colonization had been exposed following disturbances so conditions were favorable for phase shifts. Thus we only considered reefs where live hard coral cover had fallen from >30% cover (the average GBR wide coral cover [Osborne et al. 2011]) to <15%. We tracked cover of macroalgae and coral cover at each reef for a 5-year period after the disturbances (the maximum extent of data for some reefs). A phase shift was deemed to have occurred if cover of macroalgae increased after the disturbances and exceeded coral cover. As short-term increases in macroalgal cover may merely indicate a transient growth spurt, and not a prolonged phase shift, we also recorded the years in which macroalgae were dominant over corals. At reefs where phase shifts occurred we examined the species richness and abundance of local herbivorous fish functional groups at the survey when coral cover was low, just prior to the survey when macroalgal cover first exceeded coral cover. Presumably the fish community at this time was unable to prevent the phase shift. A reef was considered resilient if macroalgal cover was unchanged and/or did not exceed coral cover following disturbances. For each resilient reef we noted the community of herbivorous fishes that were present at the time of lowest measured cover of hard coral when surface area for algal growth was highest and the activity of herbivorous fishes was likely to be most important for the prevention of phase shifts.

Water clarity and herbivore abundance and species richness.—Average water quality values were calculated from site level data from all surveys conducted between 1995 and 2009 so that variability in day-to-day processes (i.e., tide, winds, and other factors) and seasonality were temporally integrated. Some subregions were sampled less intensively and so had smaller sample sizes; this did not appear to bias results, as means calculated from the entire data set in other subregions were comparable with those calculated from equivalent subsets. We applied a basic linear model to data from all subregions of the GBR to quantify the overall relationship between water

TABLE 1. Results of MANOVA using 47 reefs on Australia's Great Barrier Reef surveyed for more than a decade.

Parameter	<i>F</i>	df	<i>P</i>	Partial eta squared
Sector	18.557	305, 7560	<0.001	0.428
Shelf	54.713	122, 3018	<0.001	0.689
Time	1.471	732, 18 228	<0.001	0.056
Sector × shelf	12.932	427, 10 598	<0.001	0.343
Sector × time	1.176	3660, 94 020	<0.001	0.044
Shelf × time	1.186	1464, 36 744	<0.001	0.045
Sector × shelf × time	1.083	5124, 95 648	<0.001	0.055

Notes: Pillai's trace was used as the test of significance (*P*). The partial eta squared is an estimate of the effect size.

clarity and both herbivore abundances and species richness. We also focused the analysis to reef level data in inshore subregions, where turbidity is often highest and spatially variable, to assess finer-scale influences of water clarity on herbivorous fishes.

RESULTS

A total of 59 species from the three herbivore families were recorded on the 92 survey reefs over the 15-year study period: 46 species were recorded on inshore reefs, 54 species on mid-shelf reefs, and 56 species on outer reefs.

Community level patterns

Examination of the structure of herbivorous fish communities revealed significant interaction effects for all combinations of sector, shelf position, and time (MANOVA), but these interactions were mostly the result of sector × shelf position effects (Table 1) that were partially caused by unbalanced sampling. Shelf position effects accounted for the greatest amount of spatial variation in herbivorous fish community structure ($F_{122,3018} = 54.71$) and the effect size was large (partial eta squared of 0.69). Sector effects accounted for a lesser but still significant proportion of variation in community structure ($F_{305,7560} = 18.56$, partial eta squared of 0.43). Temporal effects alone or within interaction terms were minimal compared with spatial factors, and although significant, the effect sizes involving any temporal components were always very low (partial eta squared <0.06) compared with effect sizes for any spatial components alone (>0.34). In summary, there were strong spatial patterns in the community structure of herbivorous fishes, and these changed little over time.

Spatial patterns of herbivore function

Three of the four inshore subregions (Cairns, Townsville, and Whitsunday) had relatively low measures of herbivore function (Fig. 2). The magnitude of functional measures in inshore subregions also varied with latitude; values generally decreased from north to south, and lowest mean values of all functional measures across the GBR were recorded in either the Whitsunday or Townsville inshore subregions (Fig. 2). Functional

diversity was particularly low on Whitsunday inshore reefs (Fig. 2), indicating that functional groups of herbivores were regularly absent from survey sites. Functional measures for fish communities in the more northern Cairns inshore subregion were mostly higher than those of the inshore fish communities farther south. Farther north in the Cooktown/Lizard Island inshore subregion, functional measures were generally highest among inshore subregions aside from relatively low functional redundancy and abundance of excavators.

Among fish communities in offshore (mid-shelf and outer) environments, only those in two subregions, Swain outer and Pompey mid-shelf, stood out as having relatively low measures of function (Fig. 2). While values of individual functional measures for herbivorous fish communities in the Swain outer shelf subregion were consistently low compared with those in other offshore subregions, these difference were often negligible (95% confidence intervals often overlapped; Fig. 2). In contrast, fish communities in the Pompey mid-shelf subregion had very low abundances of both grazer/detritivores and algal browsers compared with those in other offshore subregions, and grazer/detritivore abundances were comparable to those recorded in the two inshore subregions that ranked lowest in herbivore function (Fig. 2). Furthermore, the low mean functional diversity of 3.58 in the Pompey mid-shelf subregion (Fig. 2) reflects the absence of grazer/detritivores from many sites. Values for measures of herbivore function in other offshore subregions of the GBR were more homogeneous, although there was a tendency for higher values in outer shelf subregions (Fig. 2). The Cooktown/Lizard Island sector had strong sector-wide measures of function, with maximal functional diversity across the entire shelf. The abundances of three of the four functional groups were particularly high on the outer shelf in this sector (Fig. 2).

Patterns of herbivore function on phase-shifted and resilient reefs

Twelve reefs suffered coral declines that were great enough to favor phase shifts (Table 2). These declines followed storms, cyclones, coral disease, bleaching, outbreaks of crown-of-thorns starfish, or a combination of these. The mean area of hard substrate suitable for

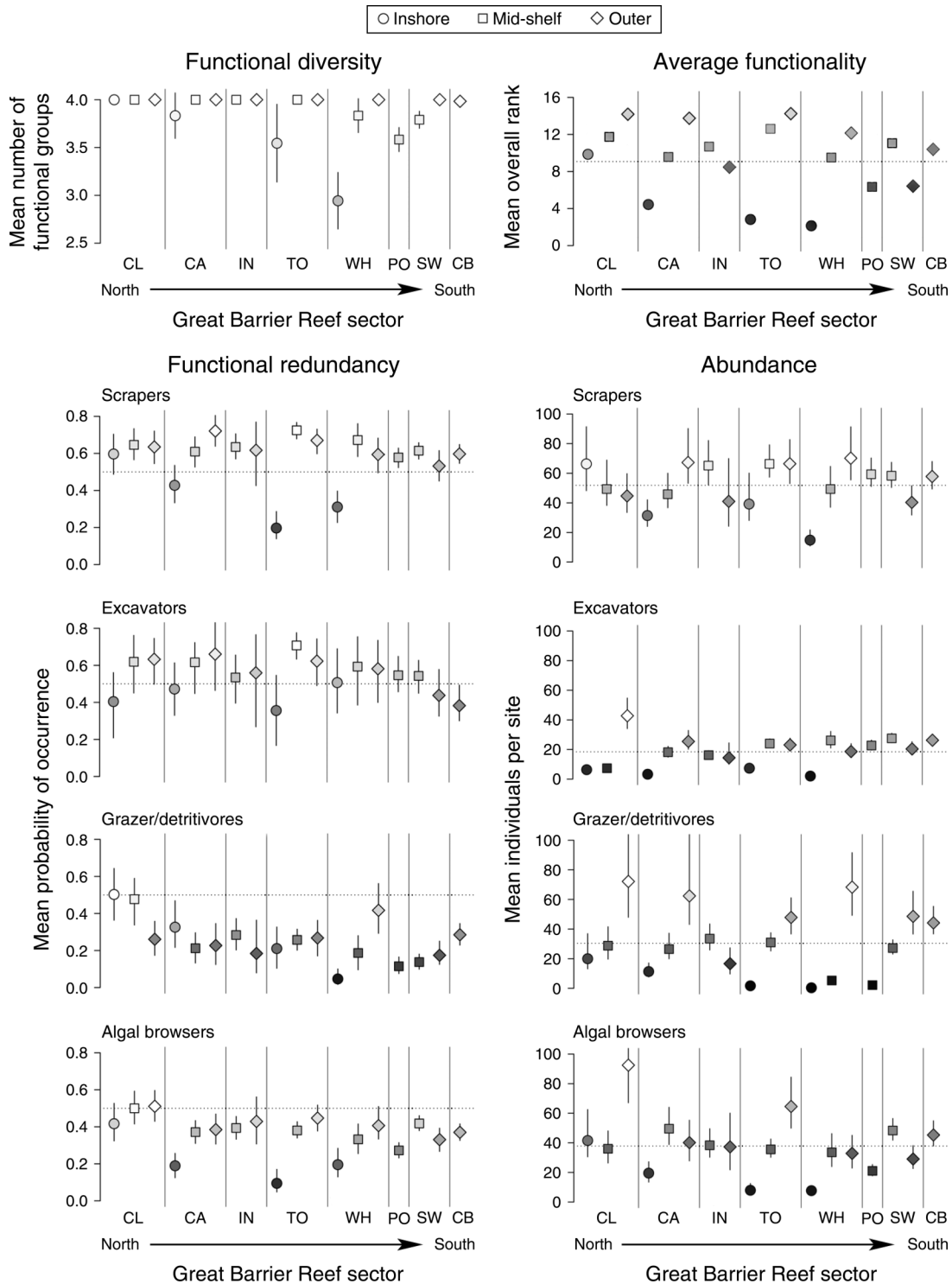


FIG. 2. Functional diversity and measures of functional redundancy and abundance for each functional group of herbivorous fishes in each Great Barrier Reef (GBR) subregion. The top right panel is a summary of functional patterns from each of the nine other panels. Data from each subregion were ranked against the data from the other 17 subregions, and these nine ranks were averaged to get a measure of overall functionality (a rank of 1 indicates the value was lowest among all 18 subregions, and a value of 18 indicates values were highest). Shelf positions are defined by symbols (see key) and abbreviated sector names (full names are in Fig. 1) are shown from north to south (left to right). Error bars show 95% confidence intervals. The dotted lines for functional redundancy are at 0.5, representing the dividing line between occupied on average and not occupied on average: those above the line are locations where most of the species in the functional group are likely to be present, and those below are locations where most are unlikely to be present. The dotted lines for abundance represent the model-estimated median value across all sites. For ease of viewing, relative values in each panel are depicted by gray scales, with white being highest and black being zero.

TABLE 2. Mean percentage cover of hard coral and macroalgae at 12 reefs before major coral mortality (Pre), when the lowest coral cover was recorded (Post-initial), and five years later.

Reef type and shelf	Sector	Reef	Coral cover (%)			Macroalgal cover (%)				Disturbance period and type (C, S, B)†
			Pre	Post-initial	5 yr later	Pre	Post-initial	5 yr later	Max	
Resilient reefs (no phase shift)										
Inshore	Cairns	Fitzroy Island	31.9	6.3	16.6	0.2	0.1	0.2	2.1	1999–2001: B, C
		Low Isles	35.4	8.9	16.0	0.1	3.9	0.0	8.0	1997–2000: C, S
Mid-	Cairns	Thetford	36.1	3.9	23.4	1.3	0.5	1.9	3.2	1999–2003: C, S, B
		John Brewer	28.9	0.7	3.5	1.6	0.0	1.4	1.4	1999–2004: S, B, C
	Townsville	Rib	44.4	3.2	11.0	1.0	0.3	1.2	1.3	1999–2003: C, B
		Gannett Cay	44.4	3.7	16.7	0.1	0.1	0.3	0.3	1996–2002: C
	Swain	Horseshoe	52.0	10.7	30.6	0.1	0.1	0.4	0.4	1997–2003: C
		Chicken	37.0	12.9	15.6	1.3	0.1	3.1	6.2	2002–2004: C
Outer	Swain	Turner Cay	31.0	12.9	19.1	0.1	0.1	0.6	0.8	2001–2004: C
		Lady Musgrave	95.7‡	8.6	65.4	?	0.3	0.0	0.5	1989: S
	Capricorn Bunker	One Tree	92.9‡	8.1	64.3	?	1.5	0.1	3.0	1989: S
		Mean	48.2	7.3	25.7	0.6	0.6	0.8	2.5	
Degraded reefs (phase shift)										
Inshore	Townsville	Havannah Island	42.8	5.9	6.9	0.5	46.6	42.1	60.4	1997–2002: B, S, C

Notes: Reefs were designated as resilient or degraded depending on whether macroalgal cover exceeded coral cover after disturbances (i.e., a phase shift occurred). “Max” is the maximum cover of macroalgae recorded in the five-year period following disturbances. Question marks (?) show that no data were collected. Benthic data were obtained from surveys conducted on the same sites between 1995 and 2009, except for two cases, as noted. Disturbances were deemed to have started in the year when annual declines in absolute coral cover exceeded 5% and then continued on a downward trajectory.

† The types of disturbances included crown-of-thorns starfish outbreaks (C), large storms or cyclones (S), and bleaching (B).

‡ Data collected in 1987.

algal growth (total area less the combined cover of sand and benthic organisms other than algae) on each reef more than doubled to >80% following disturbance. Despite this, only Havannah Island underwent a phase shift; mean coral cover declined from 42.8% to 5.9%, while macroalgal cover increased from 0.5% to >40% and remained high for five years after disturbances with little sign of coral recovery (Table 2). There was nothing unique about either the nature of the disturbances (Cheal et al. 2010) or the benthic community at Havannah Island compared with the 11 resilient reefs. Havannah Island is in the Townsville inshore subregion, one of those with lowest measures of herbivore function (Fig. 2). On average, hard coral cover on the other 11 resilient reefs dropped from 48.2% to 7.3% following disturbances, but macroalgae did not proliferate. Five years later, mean cover of hard coral had increased to 25.7%, while mean cover of macroalgae remained very low at 0.8% (Table 2). No phase shifts occurred on the other 80 survey reefs that had lesser or no hard coral declines, and average cover of macroalgae (2006–2009) was very low ($1.04\% \pm 0.14\%$; mean \pm SE).

At Havannah Island, where the phase shift occurred, the species richness and abundance of each of the four herbivore functional groups were among the lowest recorded on any of the 12 reefs (Fig. 3). Grazer/detritivores were absent on Havannah Island, but abundances of this group were often very low and highly variable on the resilient reefs. There was no consistent pattern in species richness or abundance of the four functional groups of herbivores on the 11 “resilient” reefs (Fig. 3). In fact, there were often

significant differences (no overlap in 95% confidence intervals) in the species richness and/or abundance values from resilient reefs in the same position on the continental shelf (Fig. 3). For example, One Tree Reef on the outer shelf had extremely low species richness and abundances of fish functional groups compared with virtually all the other resilient reefs. In addition, one functional group (excavators) was absent, and values for the other functional groups were generally comparable with those from Havannah Island where the phase shift occurred. Two inshore reefs in the Cairns inshore subregion (Fitzroy Island and Low Isles) were resilient despite having significantly lower species richness of scrapers and algal browsers, and very low abundances of nearly all functional groups compared with the majority of offshore reefs (Fig. 3).

Water clarity

Mean water clarity increased across the shelf from 7 m on inshore reefs to 15.9 m on mid-shelf reefs and 20.7 m on outer reefs. There were strong positive relationships between water clarity and both total abundance and total species richness of herbivorous fishes (Fig. 4). These relationships were particularly strong on inshore reefs where lowest water clarity on the GBR was recorded (Fig. 4). Water clarity in inshore subregions generally decreased from north to south, a pattern that was not related to distance from the coast; Cooktown/Lizard Island inshore reefs in the far north were located closer to the coast than all southernmost inshore reefs in the Whitsunday sector (Fig. 4). Differences in communities of herbivores differed with water clarity even

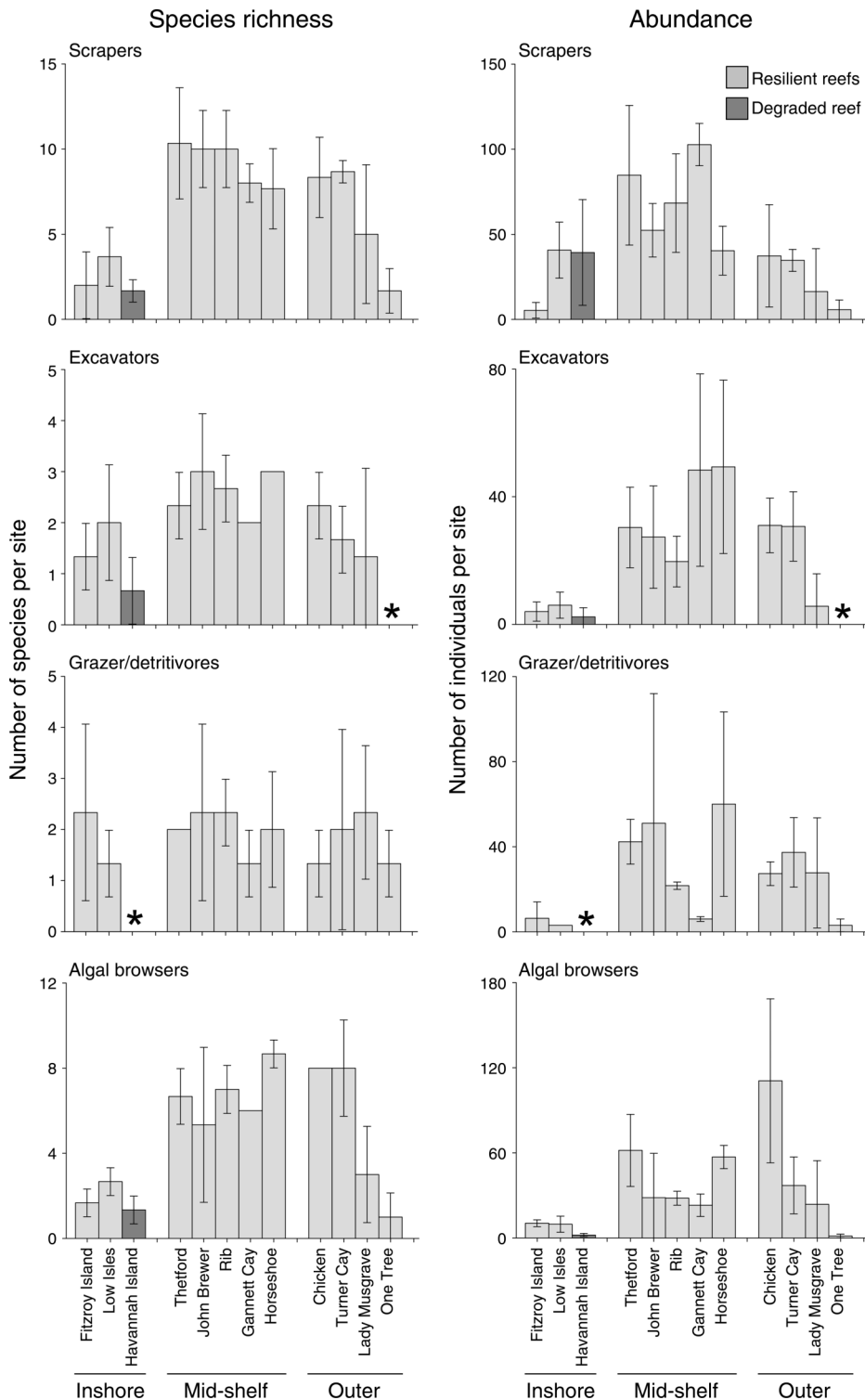


FIG. 3. Mean species richness and abundance of the four functional groups of herbivorous fishes at 11 (resilient) reefs that did not undergo phase shifts and at one (degraded) reef that did. Reefs are grouped by shelf position. Stars (*) indicate that no individuals were recorded. Error bars show 95% confidence intervals.

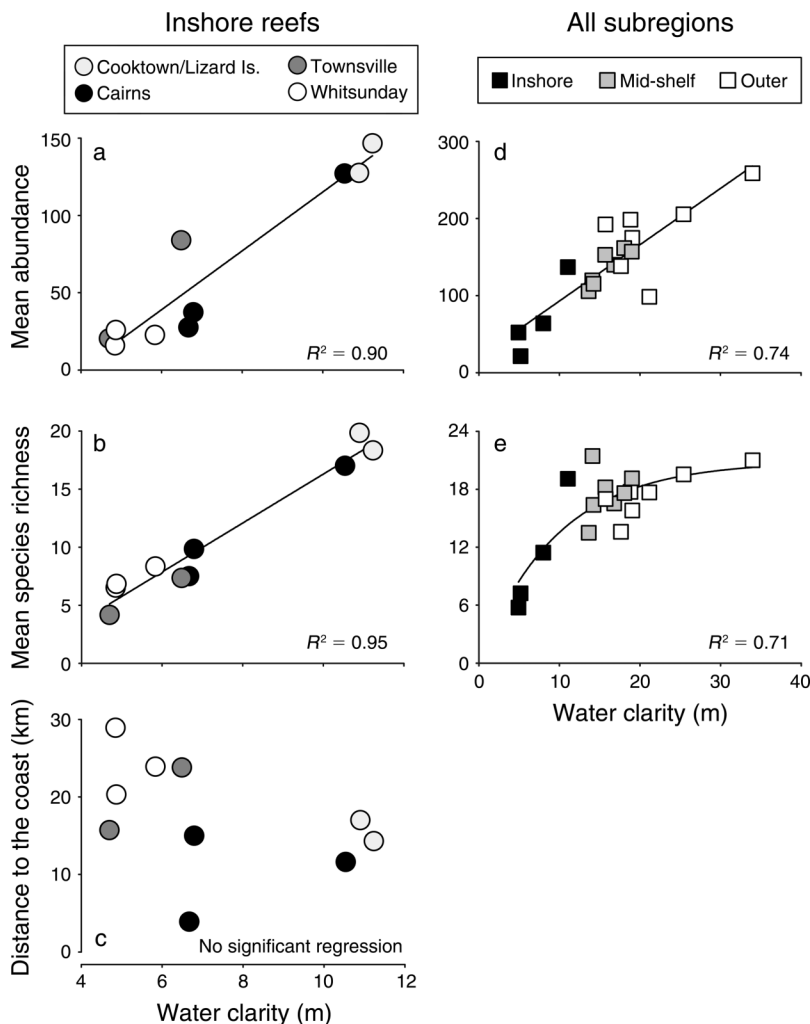


FIG. 4. Relationships between water clarity, and total herbivore abundance and species richness on the GBR. Panels (a) and (b) focus on inshore subregions; symbols representing reefs (circles) are coded (white, light gray, dark gray, black) by sector. Panels (d) and (e) focus on the entire GBR; symbols representing subregions (squares) are coded (white, gray, black) by shelf position. Panel (c) shows the relationship between inshore reef water clarity and distance to the coast. Linear (a, b, d) or asymptotic (e) regressions best fitted the data; there was no significant fit in panel (c). Fitted regressions were highly significant ($P < 0.0001$).

among inshore reefs; one Cairns inshore reef with relatively high water clarity had far greater herbivore abundances and species richness than two more turbid reefs in the same subregion (Fig. 4).

DISCUSSION

Few studies have used contemporary resilience theory to assess the relative vulnerability of locations within large ecosystems. In this study we used broad-scale data to show that the functional characteristics of herbivorous fish communities can differ markedly among similar habitat types within a large, relatively unmodified coral reef ecosystem. Assuming that the theories linking herbivory and resilience are sound, these results suggest that certain reef environments are naturally more vulnerable to coral-macroalgal phase shifts than

others. The notion that phase shifts will follow major coral mortality if the grazing capacity of large herbivores is very low was supported by long-term data in one subregion, but contradicted in others. This indicates that different environmental settings have intrinsically different capacities to buffer low levels of herbivory and so preserve resilience. The high spatial variation recorded in this study suggests that broad-brush approaches to management of herbivorous reef fishes will not widely ensure maintenance of herbivore functions or minimization of phase shift vulnerability throughout coral reef ecosystems. Rather, management strategies that explicitly consider geographic differences in both the functional characteristics of local herbivorous fish communities and the environmental setting

should result in the most effective allocation of resources to enhance ecosystem resilience.

Spatial patterns of herbivore function

The structure of herbivorous fish communities and their functional characteristics showed marked spatial variation, particularly across the continental shelf. These patterns are likely to have arisen naturally, as herbivorous fishes are not exploited on the GBR, and there was no evidence of anthropogenic degradation on survey reefs. Furthermore, there was little temporal variation in these broad spatial patterns over the 15-year study period despite numerous disturbances (Osborne et al. 2011), and similar cross-shelf patterns were recorded almost 30 years ago in the Townsville sector (Williams 1982, Williams and Hatcher 1983, Russ 1984). Such long-term stability suggests that the current distribution and abundance of herbivorous fishes on the GBR reflect their relative abilities to inhabit the different physical and biological environments that broadly characterize each shelf position (Done 1982, Williams 1982). Inshore subregions generally appeared least habitable.

Inshore reefs supported fewest herbivorous fish species, and the lowest overall measures of function were recorded in three of four inshore subregions. Reefs in the turbid Whitsunday and Townsville inshore subregions were theoretically most vulnerable to phase shifts, because the lowest values of all functional measures were recorded in one or other of those subregions. This vulnerability assessment was supported in the Townsville inshore subregion by the occurrence of a phase shift at Havannah Island (see also Cheal et al. 2010), and by evidence of a phase shift on a neighboring reef (Done et al. 2007). The importance of grazing in this particular subregion was further demonstrated by a field experiment showing that macroalgae will proliferate if herbivorous fishes are artificially excluded (Hughes et al. 2007). Both Whitsunday and Townsville inshore reefs were ranked as similarly vulnerable to phase shifts, but the capacity of the Whitsunday herbivorous fish communities to prevent them was not tested by major disturbances during this study. Benthic communities of corals and other sessile organisms in the Whitsunday inshore subregion remained stable for over a decade (Sweetman et al. 2008), with very low cover of macroalgae and little suitable space for algal colonization. Whether or not the small sizes of the herbivore populations on these reefs were influenced by long-term patterns of food availability, their numbers were probably sufficient to control macroalgal growth under the observed conditions. We suggest that this ability will be challenged if disturbances open up sufficient free space so that algal growth exceeds the currently low grazing capacity (see Williams et al. 2001, Cheal et al. 2010).

In mid- and outer shelf subregions the functional diversity of herbivorous fish communities was generally maximal, and values for a range of the other functional

measures were often high. Accordingly, most of these subregions (and the Cooktown/Lizard Island inshore subregion) supported herbivorous fish communities with functional characteristics most likely to enhance resilience. In support of this, no phase shifts were recorded in these subregions, and three reefs in the Cooktown/Lizard Island outer shelf subregion, which had particularly high measures of herbivore function, recovered relatively rapidly from major coral mortality without phase shifts (Emslie et al. 2008). The Pompey mid-shelf subregion was unusual among offshore (mid- and outer shelf) environments in having relatively low measures of herbivore function, mainly due to a lack of surgeonfishes (Cheal et al. 2012), but there is no clear explanation for this anomaly. A distinguishing environmental feature of the Pompey subregion is the extreme tidal ranges that are among the highest recorded on the GBR and often cause very strong currents (>2.6 m/s [5 knots]) on survey sites, though there is no obvious reason why such currents should particularly affect surgeonfishes.

Average rankings of herbivore function were mostly higher in outer shelf subregions than in mid-shelf subregions, but this pattern was not consistent among the individual functional measures. Herbivorous fishes also tend to be larger on mid-shelf reefs than on outer reefs of the GBR (Gust et al. 2002), so our use of abundance rather than biomass may have underestimated the functional significance of herbivorous fishes on mid-shelf reefs, because larger individuals are likely to play a greater role in resilience than smaller ones (Bonaldo and Bellwood 2008). Biomass may be a more useful functional measure than abundance as it encapsulates a broader range of ecological influences, but given that fish lengths were not estimated during surveys and maximum sizes can vary across the GBR shelf (Gust et al. 2002), any attempts to estimate biomass a posteriori would be very prone to error. Cross-shelf patterns in biomass of parrotfishes in the northern GBR were reflected in their patterns of abundance (Gust et al. 2001), which suggests that the strong spatial patterns in abundance we recorded are likely to be reasonable approximations of patterns in biomass.

Patterns of herbivore function and the occurrence of phase shifts

There was little consistency in the functional characteristics of herbivorous fish communities on the 11 reefs that did not undergo phase shifts following extensive coral mortality; some reefs supported communities with strong and diverse functional characteristics while others had communities that appeared to be functionally depauperate. This variability is not surprising in an ecosystem where herbivorous fishes are not exploited; many reefs on the GBR are likely to support more than enough herbivorous fishes to prevent phase shifts. More interesting is why phase shifts did not occur on a number of highly disturbed reefs that all had relatively low measures of herbivore function. Experimental reduc-

tions in biomass of herbivorous fishes (>85%) have shown that very low levels of grazing can lead to phase shifts on inshore reefs of the GBR (Hughes et al. 2007), as occurred in the archetypical Caribbean case study (Hughes 1994). However, the critical levels of grazing at which such phase shifts occur are not known. These thresholds may be very low on the GBR; though herbivore communities on two inshore reefs in the Cairns sector had relatively very low measures of herbivore function, phase shifts did not occur after major coral mortality, unlike the case on Havannah Island where herbivore communities were even more functionally depauperate and a phase shift did occur (Cheal et al. 2010). A complementary and more pragmatic alternative is that the minimum levels of grazing required to prevent phase shifts will vary between locations and will depend on a range of environmental factors that affect the local phase shift threshold.

Relative vulnerability to phase shifts must vary spatially depending not only on the functional makeup of the local herbivore communities, but also on a wide range of other biological, physical, and hydrodynamic factors that interact to raise or lower phase shift thresholds (Mumby et al. 2007, Cheal et al. 2010). In effect, different locations within a reef system may have equally low measures of herbivore function, but one may be less likely to undergo a phase shift due to stronger influences of positive compensatory factors. Patterns on one resilient reef in particular highlight how such factors may operate, and the potentially complicated nature of resilience dynamics. Following major coral mortality at One Tree Reef on the outer GBR, measures of herbivore function were the lowest out of the 11 resilient reefs and were mostly of equal or lower magnitude to those on the inshore Havannah Island that underwent a phase shift. So why was there no phase shift on One Tree Reef? Red macroalgae can grow profusely on the exposed reef slopes of this reef (A. J. Cheal, *personal observation*), but brown macroalgae that drive inshore phase shifts on the GBR are less common in all reef zones on outer reefs (McCook and Price 1997). Based on underwater observations, we suspect that heavy wave action more regularly dislodges macroalgae from offshore reefs than from relatively protected inshore reefs. This would frequently provide space for growth of coral recruits, and crustose coralline algae that are most abundant on outer reefs of the GBR (Fabricius and De'ath 2001). Other factors may also favor coral recovery over macroalgal growth on such outer reefs. Crustose coralline algae provide settlement cues for coral recruits (Fabricius and De'ath 2001) and can suppress growth and recruitment of macroalgae (Vermeij et al. 2011). In addition, nutrients from terrestrial runoff that may enhance macroalgal growth only reach outer reefs of the GBR infrequently in the very largest floods. It is noteworthy that an experimental study at One Tree Reef also concluded that variation in

benthic algal standing crop was largely controlled by factors other than grazing intensity, including nitrogen availability and seasonal senescence of macroalgae (Hatcher and Larkum 1983).

Water clarity and herbivorous fishes

We found a strong positive relationship between water clarity and both the diversity and abundance of herbivorous fishes on reefs of the GBR that broadly related to functional patterns. Distance to the coast and proximity to a more turbid reef did not influence these patterns; clearer waters always supported more robust herbivore communities irrespective of their physical location (i.e., the Cooktown/Lizard Island inshore subregion). This relationship may be universal on coral reefs, as turbid reefs also support more depauperate herbivore communities in the Caribbean (Mallela et al. 2007, Nemeth and Appeldoorn 2009). The low productivity of algae on turbid reefs (Russ and McCook 1999) could have led to the selection of mechanisms that favor the movement of larval herbivorous fishes away from sediment-enriched waters (Russ 1984), particularly given that turbidity can disrupt settlement cues of larval reef fishes (Wenger et al. 2011). Selective movement of larvae to clearer waters is especially feasible for herbivorous fishes, as many have long planktonic durations, swim strongly, and have well-developed sensory capabilities (reviewed in Leis and McCormick 2002). While the mechanisms linking herbivore distributions and water clarity are uncertain, our results suggest that chronic increases in turbidity will have detrimental effects on populations of herbivorous fishes and their functional roles on coral reefs.

The GBR, though relatively pristine, is not immune to such pressures. In fact land use practices adjacent to the GBR have been extensively regulated in recent years in an attempt to reduce sedimentation and turbidity in reef environments. The value of such initiatives is supported by our finding that herbivorous fishes were more diverse and abundant in less turbid waters, although it is unclear whether turbidity levels on inshore reefs of the GBR still represent a near "natural" state (see Larcombe and Wolfe 1999 and McCulloch et al. 2003 for opposing viewpoints). Whether or not coastal anthropogenic influences have increased inshore turbidity and affected herbivore populations, there is little room for complacency, because the grazing capacity on those inshore reefs where herbivore populations are small may naturally be close to phase shift thresholds, as has been suggested for Caribbean reefs (Mumby et al. 2007).

Implications for coral reef management

Applying resilience theory to a long-term and broad-scale data set on the GBR has revealed facets of coral reef resilience that may have broad applicability to reef conservation. While our data were gathered exclusively from the reef slope zone, this is unlikely to affect generalizations about broad spatial patterns. Although

other zones within reefs of the GBR (crest, flat, lagoon, and back reef) may support different herbivore communities, they all display strong cross-shelf structure (Russ 1984). Furthermore, the reef slope zone is particularly important in a management context, as it generally supports a high diversity of organisms and is often targeted for recreational and commercial purposes (i.e., for tourism and fishing).

We have shown that, even within a large, relatively pristine reef ecosystem, there can be great variability in the relative vulnerability of different reef environments to phase shifts based on the functional characteristics of herbivorous fishes. Relatively low functional measures of herbivory suggest closer proximity to phase shift thresholds and signify enhanced vulnerability. Whether that vulnerability leads to a phase shift following major coral declines seems to depend on the relative influence of local environmental factors that alter phase shift thresholds. Such interactions are likely to be complex, making it difficult for coral reef managers to know how these thresholds vary among different reef environments and how they are altered by human actions. Given these difficulties and the parlous state of many reef ecosystems, it seems prudent to adopt a precautionary management approach using spatial patterns in herbivore function as one tool to indicate the relative vulnerability of different reef environments to phase shifts, while aiming to broadly preserve herbivore functions.

The large differences in herbivorous fish communities between subregions and sometimes even between adjacent reefs on the GBR indicates that spatially targeted management strategies will best ensure that the capacity of herbivorous fishes to prevent phase shifts is maintained throughout large reef ecosystems. Broad, sweeping regulations may aid resilience in one location but not necessarily in another; both subregional and local-scale regulatory approaches will be necessary. For example, generic fishing bag limits throughout an entire reef ecosystem could result in critical losses of function in locations where functional groups have low redundancy or are in low numbers. It seems inevitable that fishers will eventually target herbivorous fishes on the GBR, so protection strategies that are underpinned by knowledge of fish distributions and spatial patterns of function should be considered before fisheries develop.

The strong positive association of water clarity with diverse and abundant herbivore communities and the occurrence of a phase shift in one subregion with low water clarity suggest that turbid inshore reefs on the GBR and coastal reefs elsewhere are particularly vulnerable to phase shifts. Such turbid environments will require special attention from managers to ensure that herbivorous fish stocks are not overfished, so as to maximize resilience. Furthermore, if our results and arguments are broadly applicable, chronic increases in turbidity on nearshore reefs around the world due to coastal developments (Fabricius 2005) could cause decreases in herbivore diversity and abundance as

ecological tolerances of fish species are exceeded and larvae die or select other habitats. Decreased grazing pressure may then favor macroalgal dominance over coral recovery following major disturbances. Management practices that reduce the exposure of coral reefs to anthropogenic sediment loads have been implemented in some places, particularly through catchment management strategies and more effective controls of marine dredging. This has mainly been to prevent negative impacts on corals, but our data suggest an even greater imperative; populations of functionally important herbivorous fishes could decline with increases in turbidity, even in the absence of fishing pressure.

ACKNOWLEDGMENTS

We thank all colleagues, past and present, who have contributed to gathering the data used in this study. The insightful comments of Faye Christidis and two anonymous reviewers are also appreciated. The study was supported by AIMS, the CRC Reef Research Centre, and the Australian Government's Marine and Tropical Sciences Research Facility.

LITERATURE CITED

- Allen, C. R., L. Gunderson, and A. R. Johnson. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8:958–966.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Australian Journal of Ecology* 26:32–46.
- Anderson, M. J., and C. J. F. ter Braak. 2002. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73:85–113.
- Bellwood, D. R., and J. H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* 28:189–214.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bonaldo, R. M., and D. R. Bellwood. 2008. Size dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 360:237–244.
- Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.
- Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences USA* 105:16201–16206.
- Burkepile, D. E., and M. E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* 5(1):e8963.
- Cheal, A. J., M. Emslie, I. Miller, and H. Sweatman. 2012. The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology* 159:1143–1154.
- Cheal, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29:1005–1015.
- Cheal, A. J., S. K. Wilson, M. J. Emslie, A. M. Dolman, and H. Sweatman. 2008. Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series* 372:211–223.
- Darwin, C. 1859. *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. First edition. John Murray, London, UK.

- De'ath, G., and K. Fabricius. 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications* 20:840–850.
- Done, T. J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95–107.
- Done, T. J., E. Turak, M. Wakeford, L. DeVantier, A. McDonald, and D. Fisk. 2007. Decadal changes in turbid water coral communities at Pandora Reef: loss of resilience or too soon to tell? *Coral Reefs* 26:789–805.
- Dorazio, R., J. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854.
- Emslie, M. J., A. J. Cheal, H. S. Sweatman, and S. Delean. 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 371:177–190.
- Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125–146.
- Fabricius, K., and G. De'ath. 2001. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303–309.
- Fabricius, K., G. De'ath, L. McCook, E. Turak, and D. McB. Williams. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* 51:384–398.
- Fischer, J., D. B. Lindenmayer, S. P. Blomberg, R. Montague-Drake, A. Felton, and J. A. Stein. 2007. Functional richness and relative resilience of bird communities in regions with different land use intensities. *Ecosystems* 10:964–974.
- Folke, C. 2006. Resilience: the emergence of a perspective for social-ecological systems analyses. *Global Environmental Change* 16:253–267.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Fox, R. J., and D. R. Bellwood. 2007. Quantifying herbivory across a coral reef depth gradient. *Marine Ecology Progress Series* 339:49–59.
- Fox, R. J., and D. R. Bellwood. 2008. Direct versus indirect methods of quantifying herbivore grazing impact on a coral reef. *Marine Biology* 154:325–334.
- Froese, R., and D. Pauly. 2006. FishBase. <http://www.fishbase.org>
- Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. Robinson, J. P. Bijoux, and T. M. Daw. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries and ecosystems. *Conservation Biology* 21:1291–1300.
- Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous 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.
- Gust, N., J. H. Choat, and J. L. Ackerman. 2002. Demographic plasticity in tropical reef fishes. *Marine Biology* 140:1039–1051.
- Gust, N., J. H. Choat, and M. I. McCormick. 2001. Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Marine Ecology Progress Series* 214:237–251.
- Halford, A., A. J. Cheal, D. Ryan, and D. McB. Williams. 2004. Resilience to large-scale disturbance in coral and reef assemblages on the Great Barrier Reef. *Ecology* 85:1892–1905.
- Halford, A., and A. Thompson. 1996. Visual census surveys of reef fish. Australian Institute of Marine Science, Townsville, Australia.
- Hatcher, B. G., and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Journal of Experimental Marine Biology and Ecology* 69:61–84.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hughes, T. P. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes, T. P., et al. 2003. Climate change, human impacts and the resilience of coral reefs. *Science* 301:929–933.
- Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* 25:633–642.
- Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltischniyskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase shifts, herbivory and the resilience of coral reefs to climate change. *Current Biology* 17:360–365.
- Hutchings, P., S. Ahyong, M. Byrne, R. Przeslawski, and G. Worheide. 2007. Vulnerability of benthic invertebrates of the Great Barrier Reef to climate change. Pages 309–356 in J. E. Johnson and P. A. Marshall, editors. *Climate change on the Great Barrier Reef: a vulnerability assessment*. Great Barrier Reef Marine Park Authority and Greenhouse Office, Townsville, Australia.
- Jackson, J. B., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Jonker, M., K. Johns, and K. Osborne. 2008. Surveys of benthic reef communities using underwater digital photography and juvenile coral counts. Australian Institute of Marine Science, Townsville, Australia.
- Kiessling, W. 2005. Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs. *Nature* 433:410–413.
- Klumpp, D. W., and A. D. McKinnon. 1989. Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. *Journal of Experimental Marine Biology and Ecology* 131:1–22.
- Larcombe, P., and K. J. Wolfe. 1999. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* 18:163–169.
- Lawrence, D., R. Kenchington, and S. Woodley. 2002. *The Great Barrier Reef: finding the right balance*. Melbourne University Press, Melbourne, Australia.
- Ledlie, M. H., N. A. J. Graham, J. C. Bythell, S. K. Wilson, S. Jennings, N. V. C. Polunin, and J. Hardcastle. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26:641–653.
- Leis, J. M., and M. I. McCormick. 2002. The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes. Pages 171–200 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183–200.
- MacArthur, R. H. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–536.
- MacKenzie, D., J. Nichols, J. Royle, K. Pollock, J. Hines, and L. Bailey. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, San Diego, California, USA.

- MacNeil, M. A., N. A. J. Graham, J. E. Cinner, N. K. Dulvy, P. A. Loring, S. Jennings, N. V. C. Polunin, A. T. Fisk, and T. R. McClanahan. 2010. Transitional states in marine fisheries: adapting to predicted global change. *Philosophical Transactions of the Royal Society B* 365:3753–3763.
- MacNeil, M. A., E. Tyler, C. Fonnesbeck, S. P. Rushton, and M. J. Conroy. 2008. Accounting for detectability in reef fish biodiversity estimates. *Marine Ecology Progress Series* 367:249–260.
- Mallela, J., C. Roberts, C. Harrod, and C. R. Goldspink. 2007. Distributional patterns and community structure of Caribbean coral reef fishes within a river impacted bay. *Journal of Fish Biology* 70:523–537.
- Mantyka, C. S., and D. R. Bellwood. 2007. Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs* 26:435–442.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance based redundancy analysis. *Ecology* 82:290–297.
- McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem based management of coral reef fisheries. *Proceedings of the National Academy of Sciences USA* 108:17230–17233.
- McCook, L. J., and I. R. Price. 1997. Macroalgal distributions on the Great Barrier Reef: a review of patterns and causes. Pages 37–46 in *The Great Barrier Reef: science, use and management: a national conference, Proceedings*. Volume 2. Great Barrier Reef Marine Park Authority, Townsville, Australia.
- McCulloch, M., S. Fallon, T. Wyndham, E. Hendy, J. Lough, and D. Barnes. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* 421:727–730.
- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747–769.
- Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
- Nemeth, M., and R. Appeldoorn. 2009. The distribution of herbivorous coral reef fishes within fore-reef habitats: the role of depth, light and rugosity. *Caribbean Journal of Science* 45:247–253.
- Nyström, M., N. A. J. Graham, J. Lokrantz, and A. V. Norström. 2008. Capturing the cornerstones of coral resilience: linking theory to practice. *Coral Reefs* 27:795–809.
- Osborne, K., A. M. Dolman, S. C. Burgess, and K. A. Johns. 2011. Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). *PLoS ONE* 6(3):e17516.
- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenahan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Russ, G. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series* 20:23–24.
- Russ, G. R. 2003. Grazer biomass correlates more strongly with production than biomass of algal turfs on coral reefs. *Coral Reefs* 22:63–67.
- Russ, G. R., and L. J. McCook. 1999. Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 235:237–254.
- Sweatman, H., A. J. Cheal, G. J. Coleman, M. J. Emslie, K. Johns, M. Jonker, I. R. Miller, and K. Osborne. 2008. Long term monitoring of the Great Barrier Reef. Status Report No. 8. Australian Institute of Marine Science, Townsville, Australia.
- Tilman, D., D. Wedin, and J. Knopps. 1996. Productivity and sustainability influenced by biodiversity in grasslands ecosystems. *Nature* 379:718–720.
- Vermeij, M. J. A., M. L. Dailer, and C. M. Smith. 2011. Crustose coralline algae can suppress growth and recruitment of macroalgae on Hawaiian coral reefs. *Marine Ecology Progress Series* 422:1–7.
- Walker, B. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18–23.
- Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* 9(2):5. <http://www.ecologyandsociety.org/vol9/iss2/art5>
- Wenger, A. S., J. L. Johansen, and G. P. Jones. 2011. Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs* 30:879–887.
- Williams, D. McB. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1:35–43.
- Williams, D. McB., and A. I. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* 10:239–250.
- Williams, I. D., N. V. C. Polunin, and V. J. Hendrick. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187–196.
- Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790.

SUPPLEMENTAL MATERIAL

Appendix

Additional information on the statistical analysis of functional redundancy and abundance of functional groups of herbivorous fishes (*Ecological Archives* A023-012-A1).