

Drivers of herbivory on coral reefs: species, habitat and management effects

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ABSTRACT: Ecosystems are under increasing pressure from external disturbances. Understanding how species that drive important functional processes respond to benthic and community change will have implications for predicting ecosystem recovery. Herbivorous fishes support reefs in coral-dominated states by mediating competition between coral and macroalgae. Spatiotemporal variability in herbivore populations and behaviour have direct effects on the removal of algae, but knowledge of how different drivers impact on herbivore populations and their foraging is currently lacking. Such knowledge is important to understand whether herbivory is likely to compensate for changing resource availability, and thus, the potential for reefs to recover from disturbance. The relative importance of these drivers has implications for the suitability of specific management actions put in place to support herbivory. Variability in density, body size, foraging movements and grazing rate of 2 parrotfish species was investigated across reefs exhibiting a range of benthic and fish community compositions. Foraging movements were influenced by the benthos, with foraging distances greatest on degraded reefs. In contrast, parrotfish densities were driven by the management status of the reef; parrotfish size was primarily linked to species identity, whereas grazing rate was influenced by both management status and species. These findings suggest that the distribution of foraging effort will vary over time in response to reef condition, such that feeding becomes more dispersed as reefs degrade. Gear restrictions that protect large, high-grazing-rate species, or designation of no-take areas, are likely to maximise algal removal, regardless of reef condition.

KEY WORDS: Coral reef · Foraging · Functional role · Inter-foray distance · Resilience · Spatial ecology

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INTRODUCTION

Ecosystems are subject to an increasing array of natural and anthropogenic disturbances (Halpern et al. 2008). The functional roles played by species

underpin key ecosystem processes, supporting ecosystem resilience and the potential for ecosystems to absorb impacts and to recover following disturbance (Lundberg & Moberg 2003, Folke 2006, Fischer et al. 2007). Thus, the influence of disturbance on ecosys-

tem structure and function will depend, in part, on the temporal and spatial consistency with which species perform their functions (Best et al. 2015). Effective mitigation of the effects of human-driven impacts will be reliant on a sound understanding of the degree of functional plasticity exhibited by species (Best et al. 2015), the interplay between behaviour and other variables affecting functional impact such as species' abundance (Gaston & Fuller 2008) and knowledge of the drivers that impact on functional behaviour and community composition.

Coral reefs are high-diversity systems that provide key ecosystem services, for example, fisheries and coastal protection (Moberg & Folke 1999). However, there is evidence of large-scale, widespread coral decline, loss of structural complexity and reef degradation due to multiple stressors (Alvarez-Filip et al. 2009, De'ath et al. 2012). Herbivorous fishes mediate competition between corals and macroalgae and are thus expected to influence the response of reefs to disturbance, helping to maintain reefs in a coral-dominated state (Mumby et al. 2006). The capacity of the herbivore assemblage to control algae will be driven by resource availability; foraging effort is spread over a larger area on algal-dominated reefs than at coral-dominated sites, such that herbivorous fishes can become overwhelmed by resource availability if more substrate opens up to algal growth (Williams et al. 2001). However, the relative impact of resource availability on the capacity of the herbivore assemblage to control algae will be mediated by: (1) the foraging behaviour of fishes and (2) the density and size composition of the herbivore community.

Foraging behaviour affects the delivery of the herbivore function in a variety of ways, for example, grazing rate underpins the speed at which algae is removed, whereas, foraging movements will influence the distribution of foraging effort over the reef. A range of factors drives variation in foraging behaviour in time and space. The composition of the fish community may affect foraging, due to social facilitation, leading to increased feeding rates (Michael et al. 2013), competition affecting patterns of habitat use (Robertson & Gaines 1986) and increased predation risk reducing the size of foraging movements (Madin et al. 2010b) (but see Nash et al. 2012). Similarly, heterogeneity in environmental conditions may influence foraging. For example, foraging movements vary among reefs with different benthic compositions (Nash et al. 2012, Tootell & Steele 2016), and fish may exhibit substantial spatio-temporal variability in grazing rates in response to temperature changes (Smith 2008) and algal quality (Polunin

& Klumpp 1989). Importantly, there is evidence that this behavioural flexibility in herbivorous fishes has functional consequences, altering the distribution of algae on reefs (Madin et al. 2010a). Nonetheless, an understanding of how different aspects of foraging behaviour interact to drive control of algae is currently lacking.

Characteristics of the herbivorous fish assemblage will affect algal removal because the density of fish directly relates to the number of foraging mouths, and larger fish forage over larger areas and detach a greater volume of algae with each bite than smaller individuals (Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Nash et al. 2013, Welsh et al. 2013). The density and size composition of herbivores may be impacted by the benthic environment and fish community composition (e.g. Williams & Polunin 2001, Adam et al. 2011, Bozec et al. 2012). However, it may be difficult to tease apart the relative influence of drivers, such as fishing pressure and predation risk (Mumby et al. 2006), and the influence of specific drivers varies among and within studies. For example, evidence exists of significant increases in herbivore density following large disturbances that impact benthic conditions, such as crown of thorns starfish outbreaks or elevated sea-surface temperatures, with associated benefits for the control of algal growth (Adam et al. 2011, Gilmour et al. 2013). However, these increases do not appear to be consistent among sites, even in response to a single disturbance (Russ et al. 2015b). Similarly, changes in the size composition of herbivore communities have been observed following benthic disturbance and habitat change, driving both increases and decreases in size (Graham et al. 2007, Adam et al. 2011).

Despite this expanding literature on drivers of the herbivore community and behaviour, few studies have simultaneously explored the relationships between multiple fish community and habitat-level drivers, and different aspects of foraging behaviour and herbivore community composition. As a result, the relative importance of these relationships with respect to the capacity of herbivorous fishes to control algae, and thus effectively support reef recovery following disturbance, is poorly understood. This type of inclusive research is needed to inform the suitability of management actions aimed at maximising herbivory on coral reefs, by highlighting which characteristics of foraging behaviour or the herbivore community may be influenced by management. In addition, such work may indicate which management actions are appropriate with respect to specific objectives, for example, what strategies would pro-

mote the grazing rate of herbivores versus those that may drive increases in herbivore densities. Herein, for 2 species of parrotfishes, we investigate the following. (1) How does foraging behaviour (grazing rate and size of foraging movements) respond to different fish community and habitat-level drivers? (2) How do characteristics of parrotfish populations (density and mean size) vary with different fish community and habitat characteristics? We explore these questions across reefs exhibiting a wide range of community and habitat characteristics (as assessed using benthic composition). We discuss the findings in light of the appropriateness of management actions that might be implemented to support the herbivore function.

MATERIALS AND METHODS

Study sites

The coral reefs of the Central Visayas region of the Philippines have been subject to a variety of disturbances driving large, site-specific differences in the benthic habitat (Russ et al. 2015a). Typhoons in 2011 and 2012 substantially impacted reefs on the windward, eastern side of some islands, reducing coral cover to <5% (Russ et al. 2015a), and a number of reefs have experienced crown-of-thorns starfish outbreaks causing extensive coral mortality (Magdaong et al. 2014). Concurrently, there have been shifts in the density of herbivores inhabiting some impacted

reefs, which has been linked to the availability of suitable habitat (Russ et al. 2015b). Thus, the reefs display variability in their herbivore communities and a range of benthic conditions. To explore herbivore function at sites along a gradient of benthic and fish community parameters, surveys and behavioural observations were carried out at 9 reef sites at 2 small offshore islands (Apo and Sumilon) and 2 larger islands (Negros and Siquijor) (Fig. 1). Three of the sites were in no-take areas, whereas the remainder were in fished areas (Table 1). All surveys were carried out concurrently in April and May 2015 to avoid potential effects of season on foraging behaviour (Lefevre & Bellwood 2011).

Study species

The initial phases of 2 parrotfish species (*Scarus niger* and *Chlorurus bleekeri*) were selected for study. These species are abundant members of the herbivore assemblage in the study region (Russ et al. 2015b). Both species are diurnal herbivores that graze predominantly on the epilithic algal matrix (EAM). However, *S. niger* is a 'scraper', removing algal material, whereas *C. bleekeri* is an 'excavator', removing substrate as well as algae when it feeds (Bellwood & Choat 1990). Scrapers and excavators reduce the colonisation rates of macroalgae and potentially promote coral recruitment, although coral recruits may be removed by these fish as they feed (Hughes et al. 2007, Mumby 2009). Excavators also contribute to bio-

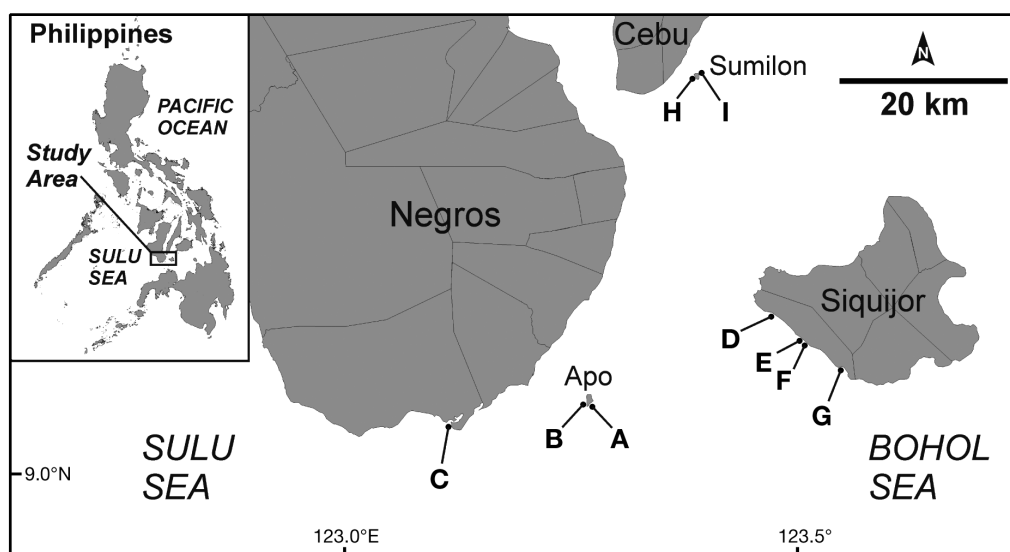


Fig. 1. Study sites. A: Apo Reserve; B: Apo Fished; C: Kookoos; D: Solangon; E: Tubod Fished; F: Tubod Reserve; G: Cangmunag; H: Sumilon Reserve; I: Sumilon Fished

Table 1. Study sites with details of management status and disturbance history. COTs: crown-of-thorns starfish. Empty cells represent sites where no major disturbances have occurred

Island Site	Status	Latitude (N)	Longitude (E)	Recent disturbance
Apo				
Apo Reserve	No-take	09°04'17.3	123°16'09.0	Typhoon 2011, 2012
Apo Fished	Fished	09°04'17.2	123°16'01.9	
Negros				
Kookoos	Fished	09°02'50.2	123°07'09.2	COTs outbreak 2010
Siquijor				
Cangmunag	Fished	09°06'44.2	123°33'04.6	COTs observed
Solangon	Fished	09°10'14.0	123°27'54.3	
Tubod Reserve	No-take	09°08'29.3	123°30'29.5	
Tubod Fished	Fished	09°08'39.3	123°30'19.0	COTs observed
Sumilon				
Sumilon Reserve	No-take	09°25'48.9	123°23'14.8	Typhoon 2011, 2012
Sumilon Fished	Fished	09°26'02.8	123°23'32.4	

erosion (Bellwood et al. 2012). Only initial phase (female) individuals of these 2 species were targeted due to their high relative abundance at the sites, and to remove the potentially confounding effect of the reproductive behaviour of mature terminal phase males protecting a harem of females, from interacting with foraging behaviour. *S. niger* individuals from 15 to 25 cm and *C. bleekeri* individuals from 15 to 28 cm were selected due to the prevalence of these size classes, with efforts made to collect data from individuals evenly across these size ranges at each site.

Behavioural studies

Fish make foraging decisions within a hierarchy of spatial and temporal scales, for example, at larger scales in relation to home range and at smaller scales in relation to the selection of food from within and among patches (Holling 1992). We quantified 2 fine-scale aspects of fish foraging behaviour: (1) foraging mobility, as this affects how bites are distributed across the reef surface, and (2) grazing rate, which drives the rate of algal removal. We explored fine-scale foraging mobility of target individuals using inter-foray distance, where a foray was defined as a cluster of feeding bites separated from the previous cluster of bites by elevation of the fish's head >45° from the substratum and a period of active swimming (following Nash et al. 2012). Larger distances among forays suggest a greater dispersion of bites across the reef surface, for example, driving more elongate foraging ranges (Nash et al. 2012). A focal individual

was identified and followed until it commenced feeding. To estimate inter-foray distance, markers were dropped at the last bite of the first foray taken by the fish and the first bite of the next foray. The distance between markers was measured. Inter-foray distance is therefore the linear distance between successive forays. The grazing rate of target individuals was estimated by counting the number of bites taken by an individual over a 3–5 min period. For all behavioural observations, the zone of each foray (crest or slope) and the size of the fish (estimated visually) were also noted.

A single observation of either inter-foray distance or grazing rate was recorded for each individual, and these observations were repeated for at least 30 individuals of each species at every site (see Table S1 in the Supplement). Two strategies were used to minimise the chance of sampling the same individual more than once: (1) parrotfish have relatively small home ranges (Welsh et al. 2013); thus, the observer moved linearly along the reef after each observation, away from the area used by individuals that had already been sampled; and (2) where members of the same species were targeted sequentially, fish of different body sizes were chosen. Fish behaviour may be affected by the presence of observers. The distance at which a fish will flee from an approaching diver (flight initiation distance or FID) may be influenced by the protective status of a reef and the distance to available refuge (Gotanda et al. 2009, Januchowski-Hartley et al. 2012). To account for among-site differences affecting diver–fish interactions and thus potentially influencing foraging range estimations, FID was estimated at each site (Supplementary Text 1 & Table S1 in the Supplement at www.int-res.com/articles/suppl/m554p129_supp.pdf). When performing the behavioural observations, a distance of at least 2.5 m was maintained from all fish, although this distance was increased to 5 m at some sites due to increased FIDs. Data were discarded where fish showed signs of disturbance by the observer or where a constant visual fix on the individual could not be maintained. Accuracy of observer estimations of fish body length were tested daily, prior to the start of data collection, using lengths of PVC pipe. Estimates were consistently within 6% of actual lengths. All behavioural data

were collected by SCUBA between 09:30 and 15:00 h, distributed approximately evenly to minimise the effect of time of day on feeding (Bonaldo & Bellwood 2008). All observations were performed on the reef slope or crest, unless the fish moved to the reef flat over the course of the observation, in which case the fish was followed on to the flat. Those observations set partially on the reef flat accounted for <1% of bites observed and 1.5% of foraging movements.

Fish and benthic censuses

The abundance and size of diurnally active, non-cryptic herbivorous and piscivorous fish species were estimated at each site using instantaneous underwater visual census (UVC) along 50 m transects. There were 3 or 4 replicate transects located on the reef slope and 3 or 4 on the reef crest; the number of replicates depended on the linear extent of the site. All individuals (≥ 5 cm) were recorded in a 5 m swath as the transect was laid. Replicates were haphazardly arranged along the reef, with a minimum of 15 m separating neighbouring transects. The percent cover of different hard corals, EAM and other benthic organisms were recorded along each transect using the point intercept method (every 50 cm). Structural complexity was estimated for each transect using a 6-point visual scale (Wilson et al. 2007).

Data analysis

To estimate the biomass of potential competitors and predators, individual body mass was estimated from body lengths recorded in the UVC using published length–mass relationships (Froese & Pauly 2012). Competitors were defined as the combined biomass of all herbivores, including the 2 focal species. Predation risk was estimated using the biomass of all piscivorous fishes that had a gape size larger than the body depth of the smallest size classes studied, hereafter termed ‘large piscivores’ (following Madin et al. 2010b, Nash et al. 2012). Principle component analysis (PCA) was used to condense the benthic variables (cover of hard coral, EAM, macroalgae and structural complexity) into a single PCA axis for use as a benthic variable in the site-level analysis. PC1, which explained 64% of the variation among combinations of site and zone, represented a gradient from high EAM cover (negative values) to high coral cover and structural complexity (positive values; Fig. S1 in the Supplement).

Generalised additive mixed models (GAMMs) with Gaussian distributions were used to model the relative influence of benthic condition, competition, predation risk and management status (fished or reserve) on foraging behaviour, and focal species density and mean size (mgcv package in R; Wood 2011). We included the size of focal individuals as a covariate for the behavioural dependent variables to account for any difference in the distribution of sizes of individuals observed at the different sites and zones. Herbivore biomass was excluded from the model of focal species density as these species had been chosen for study specifically because they were dominant herbivores across the sites.

The data were aggregated to the site-level: median values were used for inter-foray distance and the densities of the focal species due to positively skewed distributions within sites. Grazing rate and size were normally distributed within sites; therefore, mean values were used. Large piscivore biomass was square root transformed to meet model assumptions. Collinearity between the explanatory variables was assessed by calculating the variance inflation factor (VIF; following Zuur et al. 2007); none of the explanatory variables were collinear ($VIF < 3$). For each dependent variable, site and reef zone were modelled as random effects, and we evaluated models with every combination of variables (up to 3 variables per model). These models were then compared using Akaike’s information criterion adjusted for small sample sizes (AICc; MuMIn package in R; Barton 2013). The number of knots for each smoother was set at 3 to allow for non-linear relationships but prevent overfitting (Zuur et al. 2009). Model averaging was used to estimate coefficients for each explanatory variable, and to explore their relative importance, AICc weights were summed across all models incorporating each explanatory variable to understand the relative importance of each variable. Those models with substantial support (< 2 AICc units of the best model; Burnham & Anderson 2002) and variables contributing > 0.5 of the summed AICc weights are highlighted.

RESULTS

Benthic and fish assemblage

Site level coral cover varied from 2 to 65% on the crest and 7 to 61% on the slope (Table S2 in the Supplement at www.int-res.com/articles/suppl/m554p129_supp.pdf). Those sites with high coral cover tended to have high levels of structural complexity

(>3.5), and sites with low coral cover had the lowest complexity (<1.7). Cover of EAM varied from 13 to 58% on the crest and 14 to 52% on the slope. In general, those sites with high cover of EAM had low coral cover (Fig. S1 in the Supplement), but there were some exceptions, e.g. Sumilon Reserve had relatively high EAM cover (32–35%) and coral cover (29–46%).

The biomass of herbivores ranged from 9 to 60 g m⁻² on the crest and from 9 to 63 g m⁻² on the slope (Table S2 in the Supplement). The highest biomasses were recorded in Apo Reserve (60–63 g m⁻²) and Apo Fished crest (40 g m⁻²), whereas the lowest biomasses were observed at Cangmunag, a fished site. The biomass of large predators (large enough gape to consume focal individuals) ranged from 0 to 44 g m⁻² (Table S2). The highest biomasses were observed at Sumilon Reserve (23–44 g m⁻²), whereas the lowest biomasses were observed at Cangmunag (0–1 g m⁻²).

Drivers of foraging behaviour, fish density and size

Inter-foray distance. PC1 (benthic cover) and species were in the best model for inter-foray distance (Table 2A). The best model explained 40% of the variation in inter-foray distance. Summed across all models, benthic composition was the most important explanatory variable (summed AICc weights >0.5;

Table 2. Model selection comparing the relative influence of competitor biomass (Herbivores), predator biomass (Large piscivores), the benthic community (PC1, see Fig. S1 in the Supplement), management status (Status), species and size of focal individuals on: (A) inter-foray distance, (B) grazing rate, (C) focal species density and (D) focal species' mean size. Note size of focal individuals was only included in the behavioural models where specific individuals were observed. A maximum of 3 variables were included in each model. Site and Zone were added as random effects to all models. Only those models within 2 AICc units of the best model are shown. AICc: corrected Akaike's information criterion; Wt: weight

Model	Adj. R ²	df	AICc	ΔAICc	AICc Wt
(A) Inter-foray distance					
1 PC1 + Species	0.40	7	490.34	0.00	0.32
2 PC1	0.35	6	409.43	0.01	0.31
(B) Grazing rate					
1 Status + Species	0.54	6	222.26	0.00	0.49
2 Species	0.48	5	224.02	1.77	0.20
3 Status + Herbivores + Species	0.59	8	224.25	2.00	0.18
(C) Density					
1 Status	0.22	5	167.30	0.00	0.41
2 Status + Large piscivores	0.32	7	168.01	0.71	0.29
(D) Mean size					
1 Species	0.53	4	190.53	0.00	0.68

Fig. 2). The distance moved among forays was greatest on reefs with high algal cover (negative PC1 values), decreased on reefs with moderate algal cover and increased slightly on reefs with high coral cover (Fig. 3A). The median inter-foray distances of *Scarus niger* were greater than those of *Chlorurus bleekeri*.

Grazing rate. Management status of the reef and species was in the best model for grazing rate (Table 2B). The best model explained 54% of the variation in grazing rate. Summed across all models, management status and species were the most important (summed AICc weights >0.5; Fig. 2). *S. niger* had a greater mean grazing rate than did *C. bleekeri* (Fig. 3Bi). The mean grazing rate was higher in the no-take areas than in fished areas (Fig. 3Bii).

Focal species density. Management status was the only term in the best model for focal species density (Table 2C). The best model explained 22% of the variation in focal species density. Summed across all models, management status was the most important variable (summed AICc weights >0.5; Fig. 2). Focal species density was greater in the no-take areas than in the fished areas (Fig. 3C).

Focal species mean size. Species was the only term in the best model for mean size (Table 2D), and the best model was the only model with substantial support (models within AICc values of best model). Summed across all models, species was the most important variable (summed AICc weights >0.5; Fig. 2). *C. bleekeri* had a larger mean size than did *S. niger* (Fig. 3D). This model explained 53% of the variation in mean size.

DISCUSSION

A robust understanding of the contribution of herbivorous fishes to ecosystem structure and function is reliant on knowledge of how fish density, body size and foraging behaviour vary in response to a changing environment and how they interact to affect algal removal by herbivores. Variability in the inter-foray distances exhibited by parrotfishes appear to be driven primarily by benthic condition, with the greatest distances moved on low-complexity, high-algal-cover reefs; moderate distances moved at high complexity and coral cover reefs; and the shortest distances

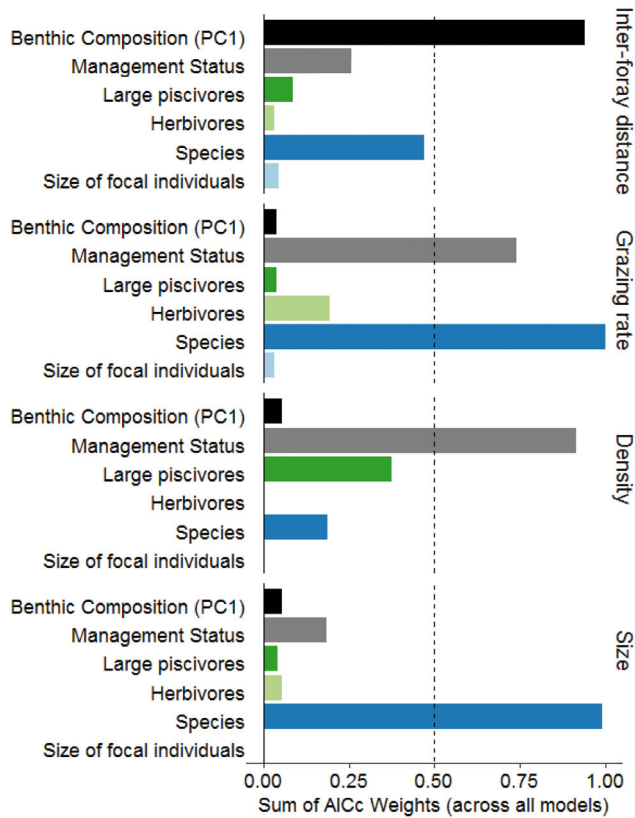


Fig. 2. Relative importance of explanatory variables for foraging behaviour, density and mean size of focal species (*Scarus niger*, *Chlorurus bleekeri*), based on the sum of AICc weights across all models incorporating each explanatory variable. Dashed lines represent summed AICc weights of 0.5. Note size of focal individuals was only included in the behavioural models where specific individuals were observed, and herbivore biomass was not included in the models of focal species density, as these species were specifically chosen because of their high relative abundance across the sites

moved on reefs with an intermediate benthic composition. In contrast, variation in grazing rate was predominantly linked to species identity and management status, with greater rates exhibited by *Scarus niger* and in no-take areas. Similarly, variations in fish density were influenced by management status, with greater densities found inside reserves. Species identity was the predominant driver of size differences. These findings have important implications regarding the potential for herbivores to support reef recovery and the suitability of management actions aimed at maximising herbivory.

Inter-foray distance

Moving between resource patches represents a potential energetic cost to foragers, and as such, these

movements are a trade-off between acquisition of food and factors such as predation risk (MacArthur & Pianka 1966, Webster & Laland 2012, Nunes et al. 2013). Benthic condition was an important driver of inter-foray distance. At sites with high coral cover and complexity, inter-foray distances were moderate in size, with some variation around the fitted relationship. Small movements likely provide benefits linked to focusing on limited food resources, but larger movements will be required to move among patches when resources become depleted (Senft et al. 1987, Haskell et al. 2002). At reefs of intermediate benthic condition, inter-foray distances were shortest, with forays concentrated on localised, patchy algal turfs. These small movements have positive implications for the localised control of algal growth (Williams et al. 2001). On reefs with high cover of EAM, fish moved further among forays, with negative implications for the localised control of algal growth (Williams et al. 2001) and potential costs associated with travelling these larger distances. Even though we found no evidence of our proxy of predation risk influencing inter-foray distance, moving large distances on low-complexity reefs is expected to result in an increased exposure to predators (Madin et al. 2010b, 2011, Graham & Nash 2013). Thus, making large movements when resources are plentiful and refuges are few and far between is potentially a risky strategy. Indeed, this finding conflicts with optimal foraging theory, which predicts smaller, concentrated foraging areas in locations with more resources (Ford 1983, Börger et al. 2008). It may be that the 'restless' foraging behaviour observed at sites characterised by high EAM cover was reflective of more choosy foraging when resources are plentiful; more open, degraded habitat, lacking the complexity of healthy living coral, may allow individuals a broader field of view over which to select feeding locations (Rilov et al. 2007, Catano et al. 2016). Further work is now needed to test such hypotheses. Nonetheless, our results correspond to work by Nash et al. (2012), who found large inter-foray distances on low complexity, high EAM cover reefs (Nash et al. 2012). Importantly, the larger movements at sites with high EAM cover are likely to result in shifts in how grazing effort is dispersed across the reef as it degrades, potentially diluting grazing effort at specific locations. As algal cover increases, there will be a dilution in the grazing effort per unit area of reef, where fish density size and grazing rate remain constant (Williams et al. 2001). But this dilution may be compounded across specific reef areas that have previously been subjected to a high concentration of foraging effort, due

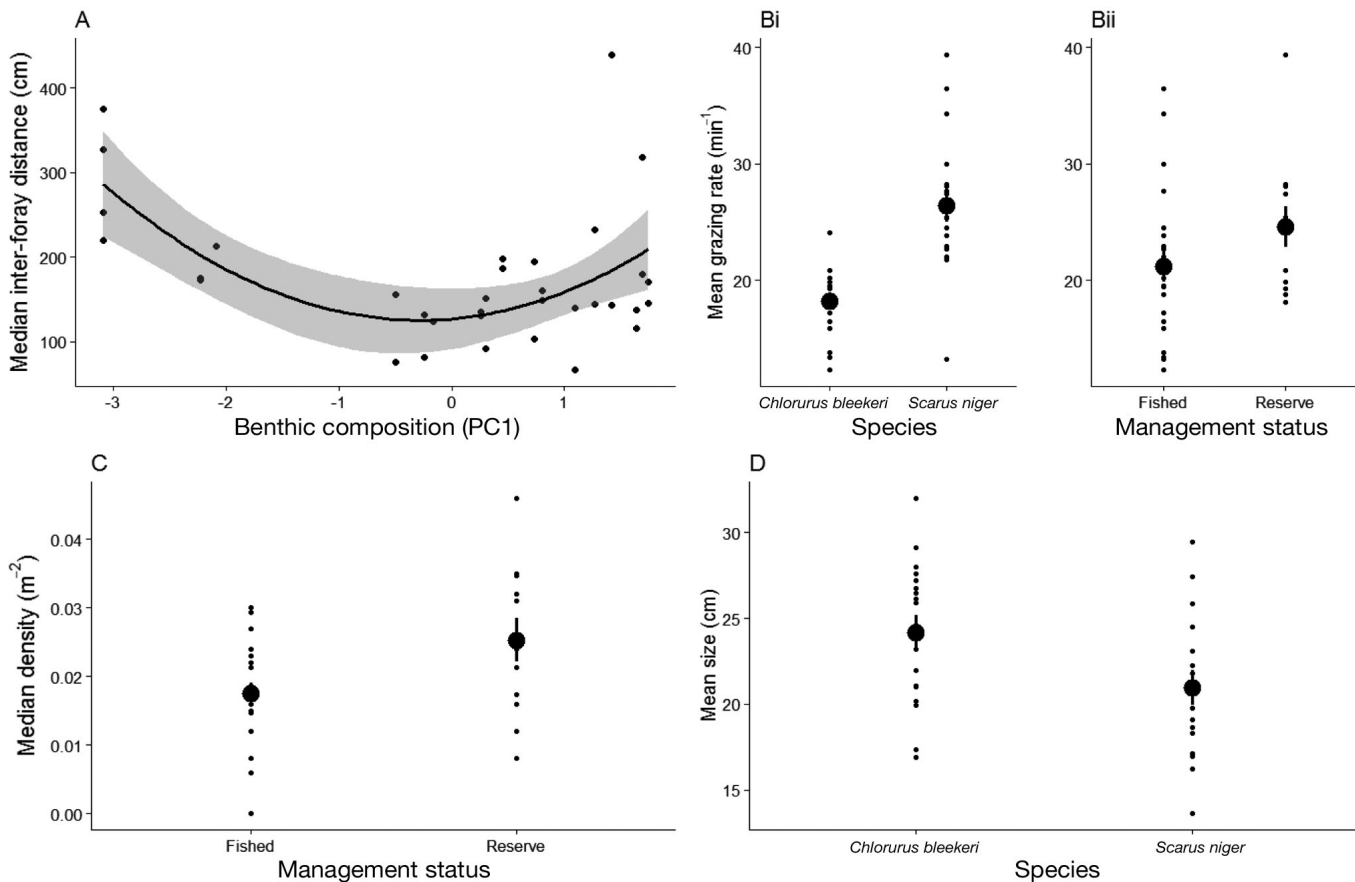


Fig. 3. Relationships between important drivers (summed AICc weight of >0.5 across all models) in generalised additive mixed models for: (A) inter-foray distance, (B) grazing rate, (C) density of focal species and (D) mean size of focal species. Plot shows fitted values (\pm SE) and raw data

to the increasing dispersion of bites. This has implications for the spatial distribution of algae.

Grazing rate

The effect of species on grazing rate (*Scarus niger* > *Chlorurus bleekeri*) suggests that, although biomass of herbivores may provide an indicator of reef condition and recovery potential (e.g. Graham et al. 2015), further distinctions in function among species are important (Mouillot et al. 2014). The differences in grazing rate among species may reflect: (1) variation in the energetic demands of individual species (Morris & North 1984, Brown et al. 2004), (2) differences in the time taken to collect and process food between those species removing EAM (*S. niger*) and those species removing EAM and the underlying substrate (*C. bleekeri*) (Laca et al. 1994), or (3) the nutritional value of particular components of the EAM targeted by different species (Burkepile & Hay 2009).

The management status of the reef was an important driver of grazing rate. Recent work by Mellin et al. (2016) indicated greater resilience of reefs found in marine protected areas, with greater community stability and faster recovery following disturbance. Greater grazing rates by herbivores in no-take areas may be one factor supporting this increased resilience in protected areas compared to on fished reefs. The pathway by which reserves support greater grazing rates is unclear. The fished reefs in the Philippines are subject to spear fishing, a practice that has been shown to affect fish flight behaviour (Januchowski-Hartley et al. 2013). Research is now needed to explore whether this wariness of fish exposed to spear fishing is a contributor to the reduced grazing rates of herbivores in fished areas. Variability in bite rate may be linked to among-site variation in the nutritional value of the EAM (Purcell & Bellwood 2001, Russ 2003). Work examining differences in the algal composition among no-take and fished zones would build understanding of the importance

of the nutritional value of EAM on grazing rates in this context.

The lack of any impact of predators on either grazing rate or foraging movements, as found in other studies (e.g. Madin et al. 2010b, Catano et al. 2016), may be due to the comparatively narrow range of predator biomass we observed across sites (1–44 g m⁻²) compared with that found in other studies (e.g. ~50–120 g m⁻² in Madin et al. 2010b). As a result, there may have been insufficient predation pressure to drive changes in the foraging behaviour of parrotfishes in our study.

Focal species density

Focal species density was greater at the reserve sites than on fished reefs. This is not surprising considering the local fishery for herbivorous species (Alcala & Russ 2002). Benthic composition did not influence density of the focal species, a finding that contrasts with those of a temporal study that found strong bottom-up impacts of the benthos on herbivore densities on Philippine reefs (Russ et al. 2015b). It may be that interactions between site-specific disturbance regimes and fisheries exploitation masked the spatial influence of habitat condition on fish density (Abesamis et al. 2014) or that there is a lagged effect of habitat on density which is mediated by the availability of settling larvae from source populations. Nonetheless, our results suggest that, although fish density has been observed to increase post-disturbance in some areas (e.g. Adam et al. 2011), the designation of no-take areas is important in order to build robust herbivore communities that may support reef recovery following a disturbance.

Focal species mean size

The lack of any impact of management status or benthic condition on herbivore size was unexpected. Mean size of fish has been shown to decline with fishing pressure in a number of studies (Nash & Graham 2016), and spear fishers have the ability to specifically target and remove large individuals (Januchowski-Hartley et al. 2011). Similarly, benthic differences have been linked to variations in herbivore size (Graham et al. 2007). The species-specific differences in mean size, and the link between body size and volume of algae removed per bite (Bonaldo & Bellwood 2008, Lokrantz et al. 2008), highlight the importance of moving beyond estimates of fish den-

ties when quantifying herbivory on reefs; the composition of the herbivore community is critical, as different species will remove algae at different rates.

Implications for herbivory in a changing environment

Our results suggest that simple allocation of fish to broad functional groups such as ‘scraping herbivores’ is unlikely to reflect herbivory in space and time, other than at a coarse level (Simberloff & Dayan 1991, Petchey & Gaston 2006, Villéger et al. 2008). Instead, we need to incorporate knowledge on behavioural flexibility into our characterisation of herbivores and to invest effort in understanding species-specific differences (Lefevre & Bellwood 2011, Brandl & Bellwood 2013).

Low grazing pressure by herbivorous fishes has been linked to observed increases in macroalgal cover on coral reefs (Williams et al. 2001, Steneck et al. 2014), and the spatial dispersion of grazing pressure has been implicated as a driver of the spatial distribution of algae (Hoey & Bellwood 2010). Fish density, body size and foraging behaviour influence grazing pressure and its spatial distribution. As a consequence, our understanding of the contribution of herbivorous fishes to the removal of algae in time and space is reliant on knowledge of the important drivers of fish density, body size and foraging behaviour. Our study outcomes suggest that reef degradation and an increase in EAM are unlikely to be compensated for by increases in herbivore grazing rate, density, or size, but reef degradation will have consequences for the distribution of foraging across the reef. These findings have implications for the effect of different management actions aimed at supporting herbivory on coral reefs.

The larger foraging movements we observed on degraded reefs, combined with consistent grazing rates, fish densities and body sizes among reefs of different benthic composition, suggest the potential for a more dispersed distribution of grazing effort as reefs degrade. As foraging effort becomes more dispersed, this may lead to dilution of grazing effort in areas that have previously experienced high grazing pressure. It is now important to understand how consecutive foraging movements and forays are dispersed across the reef over time, driving patterns in the spatial distribution of algae (Owen-Smith et al. 2010, Fox & Bellwood 2013). Nevertheless, our findings suggest that managers cannot rely on a static allocation of foraging effort across the reef as it

degrades. Instead, foraging may become more dispersed following disturbance, with the potential for positive feedbacks among algal cover and fish behaviour further constraining algal removal (Hoey & Bellwood 2011).

Managers interested in increasing the rate of algal removal must consider the species composition of the herbivore community, as this will have direct implications for grazing rates and the volume of algae removed (driven by the mean size of fish: Lokrantz et al. 2008). Management actions focused on protecting specific species, e.g. through gear restrictions (Hicks & McClanahan 2012, Graham et al. 2013), may be particularly important in this context. Finally, the importance of management status combined with the lack of any impact of benthic composition on focal species density and grazing rate suggest that establishment of no-take areas may, in the long term, support higher levels of algal removal on both degraded and healthy reefs (MacNeil et al. 2015, Abelson et al. 2016); greater herbivore densities and higher grazing rates in no-take areas may support the resistance of healthy reefs to disturbance or promote the recovery of already degraded reefs.

Further work is now needed in 3 key directions: first, here, we focus on site-averaged herbivore community characteristics and behaviour. An important next step will be to explore how individual traits interact with site-level variables to drive patterns in herbivory in time and space, for example, the effect of size on different aspects of foraging behaviour (Welsh et al. 2013). Second, due to logistical constraints, we were only able to quantify foraging behaviour at 9 sites, as such our analytical models focused on the main effects of our drivers. Further work, collecting data over a wide range of sites, is now needed to explore how drivers such as benthic composition and management status interact to drive foraging behaviour or mean herbivore size. Third, we explored herbivory in the initial phases of 2 parrotfish species; coral reefs are diverse ecosystems, with a range of herbivorous species exhibiting different foraging behaviours (e.g. Fox et al. 2009). Our study now needs to be extended to explore drivers of herbivory in other fish species and across different life stages (e.g. terminal phase parrotfishes).

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