Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales

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Abstract. The function of species has been recognized as critical for the maintenance of ecosystems within desired states. However, there are still considerable gaps in our knowledge of interspecific differences in the functional roles of organisms, particularly with regard to the spatial scales over which functional impact is exerted. This has implications for the delivery of function and the maintenance of ecosystem processes. In this study we assessed the allometric relationship between foraging movements and fish body length at three sites, for 20 species of herbivorous reef fishes within four different functional groups: browsers, farmers, grazer/detritivores, and scraper/excavators. The relationship between vulnerability of species to fishing and their scale of foraging was also examined. We present empirical evidence of the strong, positive, log-linear relationship between the scale of foraging movement and fish body length. This relationship was consistent among sites and between the two different movement metrics used. Phylogeny did not affect these results. Functional groups foraged over contrasting ranges of spatial scales; for example, scraper/excavators performed their role over a wide range of scales, whereas browsers were represented by few species and operated over a narrow range of scales. Overfishing is likely not only to remove species operating at large scales, but also to remove the browser group as a whole. Large fishes typically have a significant role in removing algae on reefs, and browsers are key to controlling macroalgae and reversing shifts to macroalgal-dominated states. This vulnerability to exploitation has serious consequences for the ability of fish assemblages to deliver their functional role in the face of anthropogenic impacts. However, identification of the scales at which herbivorous fish assemblages are susceptible to fishing provides managers with critical knowledge to design management strategies to support coral-dominated reefs by maintaining function at the spatial scales at which vulnerable species operate.

Key words: allometry; coral reef; ecosystem processes; fisheries; functional group; Great Barrier Reef, Australia; herbivore; redundancy; resilience.

INTRODUCTION

Species of different body sizes perceive and interact with their environment over different spatial and temporal scales (Holling 1992). These relationships have been explored thoroughly in many terrestrial systems, particularly for birds and mammals, with respect to length of stride (Calder 1984), home range area (Peters 1983, Harestad and Bunnel 1979), and aggregation of resources (Laca et al. 2010). In contrast, such relationships have not been adequately investigated in aquatic systems, with many studies of movement limited to one or a few species (e.g., Nanami and Yamada 2008, Freiwald 2012), and few reviews aimed at consolidating this information with respect to body size (but see Kramer and Chapman 1999). Aquatic organisms are subject to different processes and constraints than

terrestrial species (White et al. 2007), and as such may show contrasting allometric patterns, driving a need for further studies in this area.

The role or function organisms play within a particular environment, such as pollination, grazing, and nitrogen fixation has attracted considerable attention in recent years (Folke et al. 2004). There is an increasing awareness that management may support a system within a desired state by maintaining the core ecosystem processes provided by different functional groups (e.g., Christensen et al. 1996, Bellwood et al. 2004, Pikitch et al. 2004). In response, there have been calls for new ways to evaluate the delivery of function to provide the knowledge needed by managers to effectively implement appropriate mitigation strategies to support important ecosystem processes (Hughes et al. 2010). One avenue of research has examined the significance of multiple species performing a similar role within an ecosystem, providing redundancy or a degree of "insurance" in the face of anthropogenic pressures that drive species declines and, in turn, may reduce

functional impact (Walker et al. 1999, Elmqvist et al. 2003, Cheal et al. 2010). The benefits of this redundancy are reliant on the members of a functional group responding to a disturbance differently, with some species maintaining or increasing their functional impact to compensate for the loss or decline of other members of their functional group (Walker et al. 1999, Elmqvist et al. 2003). Species performing similar functions at different spatial and/or temporal scales are likely to exhibit a range of responses to disturbances impacting at specific scales, thus providing effective redundancy (Peterson et al. 1998, Elmqvist et al. 2003). As a result, characterizing the scales at which species within a functional group operate and provide their role is fundamental knowledge needed to inform management actions aimed at supporting: (1) redundancy of function across scales (termed cross-scale redundancy), and (2) delivery of function at specific scales.

The temporal and spatial characteristics of movement may be assessed at a number of levels, from the large scales of dispersal, through mid-scales of home range use, down to small scales of patch and food selection (Holling 1992). Movements at these various scales have a range of implications for the ecology of communities and populations, and a species' impact on the ecosystems they inhabit. For example, dispersal will influence community assembly (Chase 2003), whereas more localized movements may affect the function of a species within a system (e.g., Vaughn and Hakenkamp 2008). Movement is often investigated at the scale of home range (Börger et al. 2008). However, these types of studies may not effectively describe the spatial dimensions of a species' functional impact. Home range encompasses the area occupied by an organism while performing a range of activities such as feeding, sleeping and breeding (Samuel et al. 1985, Börger et al. 2008). The location of these activities may not overlap (Lazenby-Cohen and Cockburn 1991); as a result, the home range will incorporate areas in which an individual is exerting critical functional impact, and areas where this impact may not be as significant (Welsh and Bellwood 2012). Furthermore, differences in home range size among species may not correlate with differences in functional range size among species, as distinct drivers influence decision-making and movements at different scales (Senft et al. 1987). For example, decisions regarding reproductive opportunities within the broader home range will be driven by different factors than those regarding movements in relation to food choice (Senft et al. 1987). As a result, although there is evidence from a range of systems that species' body size is positively related to home range (e.g., Harestad and Bunnel 1979), it cannot be assumed that the relationship between body size and movement at the home range scale is representative of movements at other scales. To gain a comprehensive understanding of the functional impact of a species, there is a need to examine the allometry of movement at a scale relevant to the use of space while individuals are actively performing their functional role.

Herbivorous reef fishes drive a key ecosystem process on coral reefs by mediating competition between coral and algae, removing algae, and creating space for coral recruits (Hughes et al. 2007). However, there is growing evidence that herbivorous fish functions on reefs are more complex than simple classifications such as "herbivore" suggest, with important differences both within and among species. For example, ontogenetic changes and growth within species may influence diet (e.g., Buckle and Booth 2009), grazing rate, and bite size, with larger individuals providing greater functional impact through higher rates of grazing and larger bite areas (Ferreira et al. 1998, Paddack et al. 2006, Lokrantz et al. 2008). Similarly, interspecific differences in foraging behavior have been shown to influence finer scale functional classifications within broad diet groups. Herbivorous fish species may be split into farmers, grazer/detritivores, scraper/excavators, and browsers (Green and Bellwood 2009). Farmers are site-attached species that actively tend and defend algal resources within their territory (Ceccarelli et al. 2001). Grazer/detritivores feed on the epilithic algal matrix (EAM), which is composed of algal turf, detritus, microbes, sediment, and invertebrates (Wilson and Bellwood 1997), and scraper/excavators remove both components of the EAM and underlying substrate, and therefore, are also important for the process of bioerosion (Green and Bellwood 2009). These groups help reduce colonization by macroalgae and so assist in maintaining reefs within a coral-dominated state. In contrast, browsers feed on mature macroalgae and as such are critical for reversing shifts from coral to macroalgal dominance (Bellwood et al. 2006). Despite this growing literature on the role of herbivores on reefs, very little work has examined the scale of foraging by fish species.

One of the greatest potential threats to herbivore redundancy on coral reefs is fishing. Fishing is exerting significant pressure on marine systems worldwide (Jackson et al. 2001), influencing the delivery of ecosystem processes (Hughes 1994). For example, in areas subject to heavy fishing pressure, 95% of parrotfish may be <25 cm in length, with significant consequences for sediment removal and bioerosion (Bellwood et al. 2012). Currently, however, we have no understanding of how fishing is likely to impact the scale at which ecosystem functions are delivered. In light of the degree of overfishing in certain areas, there is potential for significant modifications to cross-scale patterns of redundancy within functional groups, with serious implications for the stability of ecosystem processes. For managers to be able to address these pressures effectively, detailed knowledge of the spatial scales of functional impact is needed.

In examining the scales over which herbivorous reef fishes forage, this study evaluated interspecific patterns in functionally important space use by herbivorous
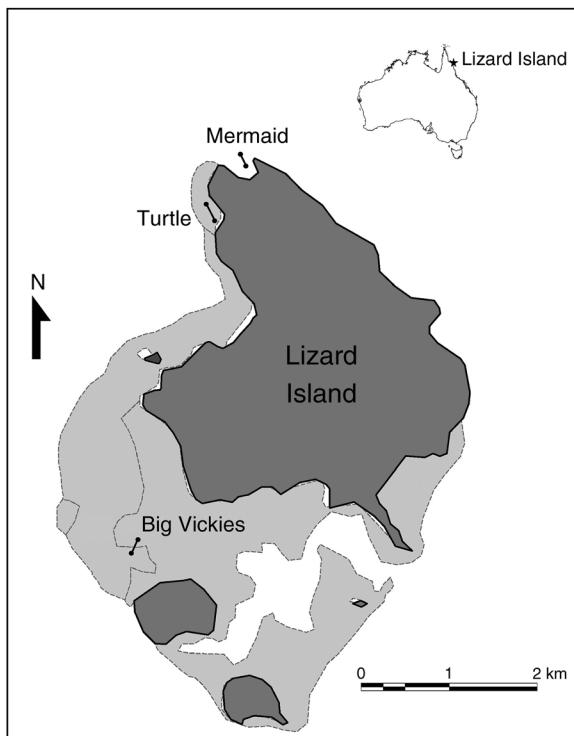
FIG. 1. Map of study sites at Lizard Island on the Great Barrier Reef, Australia. Light gray areas represent reef and lagoon. Prevailing winds are from the southeast.

species. The outcomes indicate the potential for cross-scale redundancy within reef ecosystems, and reveal the influence of fishing pressure on these patterns, neither of which has been assessed to date. The aims of this study, therefore, were to use assessments of foraging movements to: (1) determine the interspecific relationship between body size and space use at scales pertinent to functional impact, (2) examine if the scales of operation of species within herbivorous functional groups are distributed across spatial scales (i.e., assess the potential for functional redundancy), and (3) determine the relationship between vulnerability to fishing and foraging scale. This will provide fundamental knowledge needed to understand patterns of cross-scale redundancy of function on reefs. Furthermore, it will indicate how fishing impacts may modify the delivery of ecosystem processes, and thus highlight the scales at which targeted mitigation measures are needed to support reefs within a coral-dominated state.

METHODS

Study sites and species

This study was undertaken in July and August 2012 on the sheltered, western side of Lizard Island (14°40′ S, 145°28′ E; Fig. 1) on the Great Barrier Reef, Australia. Observations of foraging behavior were made at three sites (Mermaid, Turtle Beach, and Big Vickies; Fig. 1) to

determine whether foraging behavior varied consistently with body size across sites. Mermaid and Turtle Beach are southwest-facing fringing reefs with a narrow reef flat and shallow slope down to a maximum depth of ~10 m. Big Vickies is a large patch reef and observations were made on the southeast side, where the reef structure meets the sand at a depth of 5–7 m. All three sites are in a marine park, designated as a no-take area since 2003, and subject to fishing restrictions since 1983.

Fish and benthic censuses

Fish abundance of diurnally active non-cryptic herbivorous species were estimated at each site using instantaneous underwater visual census (UVC) along eight 50-m transects; four transects were located on the reef slope and four on the reef crest. All species (≥5 cm) were recorded in a 5-m swath as the transect was laid, with the exception of Pomacentrids, which were recorded on the return swim along the transect in a 2-m swath. Replicates were haphazardly arranged along the reef, with a minimum of 15 m separating neighboring transects. The percent cover of different benthic types, such as coral genera and life-form, algae, sponges, and so on, were calculated from observations taken every 50 cm along each transect using the point intercept method. Structural complexity was estimated for each transect, using a six-point visual scale (Wilson et al. 2007).

Study species

Herbivorous species were chosen as the focus for this study for two reasons: (1) they drive a critical ecosystem function on reefs (Bellwood et al. 2004), and (2) by feeding on the substrate, it is possible to clearly delineate and mark where feeding occurs and to observe multiple feeding events, thus ensuring high levels of replication. Twenty nominally herbivorous reef fish species (Appendix A) were selected for study at each site, including representatives from browser, farmer, grazer/detritivore, and scraper/excavator functional groups (Green and Bellwood 2009). The exact composition of species differed between sites due to localized relative abundance. The species ranged in length from 6 cm to 55 cm total length (TL), and at least a 36-cm body size range was maintained at all sites. The focus of the study was interspecific differences in foraging and space use by adult herbivorous reef fishes. Fish species may exhibit ontogenetic shifts in diet (e.g., from herbivore as a juvenile to planktivore as an adult; Green and Bellwood 2009), and foraging behavior (Lokrantz et al. 2008). Therefore, to remove the influence of ontogenetic changes within species (Bonaldo and Bellwood 2008), and allow comparability among species of different adult body sizes, a single 5–6 cm size class was selected for each species up to 35 cm, and a 5–10 cm size class for the larger species (Appendix A). These size classes were based on the most abundant adult body lengths.

Behavioral studies

All behavioral data were collected between 09:30 hours and 14:30 hours, and distributed approximately evenly to minimize the effect of time of day on feeding (Zemke-White et al. 2002). Fine-scale foraging mobility of target individuals was estimated using two metrics: (1) intra-foray distance and (2) 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 greater than 45 degrees from the substratum and a period of active swimming (following 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. To estimate intra-foray distance, markers were placed at the location of the two most distant bites within the second foray. The distance between markers was measured. Inter-foray distance is therefore an integration of all movements between successive forays, whereas intra-foray distance is the maximum linear dimension covered by all movements within a foray. The benthos on which the fish fed (e.g., EAM, macroalgae, soft coral) identified by each marker, was recorded. A single observation of intra- and inter-foray distance was recorded for each individual, and where possible, these observations were repeated for 30 individuals of each species at each site (Appendix A). Two strategies were used to minimize the chance of sampling the same individual more than once: (1) after each observation, observers moved linearly along the reef 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. Where the population size of a species was too small to allow the desired degree of replication without resampling individuals, smaller sample sizes were used (Appendix A).

When estimating the foraging range metrics, a distance of at least 2.5 m was maintained from all fish, although this distance was increased to 5 m for some of the larger, more mobile species due to increased flight initiation distances for larger individuals (Januchowski-Hartley et al. 2011). 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 using lengths of polyvinyl chloride (PVC) pipe, prior to the start of data collection, with estimates consistently within 10% of actual lengths.

Data analysis

The relationship between body size and the two foraging metrics (intra- and inter-foray distance) were analyzed using ordinary least squares regression as this approach is more suitable when: (1) there is a clear predictor and dependent variable in the relationship, and (2) residuals will be used for further analysis

(Warton et al. 2006, Smith 2009). The error structure of the data was determined using the guidelines provided by Xiao et al. (2011); likelihood analysis indicated that the data showed log-normal error and was therefore suitable for analysis using regression on log-transformed data (Xiao et al. 2011). Analysis of covariance (ANCOVA) and log-likelihood ratio tests were used to compare the slopes and elevations of relationships among sites (Warton et al. 2012). Data were back-transformed to allow presentation of the relationship between foraging metrics and body size on the arithmetic scale. Residuals were calculated for each species. To assess the influence of functional-group membership on the relationship between body size and the foraging metrics, the analysis was repeated with function as a categorical variable for those groups which had sufficient species (farmers, grazer/detritivores, and scraper/excavators). Phylogenetic relationships may confound interspecific relationships due to nonindependence of data points; therefore, the analysis was repeated at the family level (Martin et al. 2005), and the results compared to the species-level analysis.

To evaluate the potential effects of fishing on scales of functional impact provided by herbivorous fishes, the relationship between scales of foraging movements and vulnerability to fishing were analyzed using correlations. Data on the vulnerability of each species to fishing pressure were extracted from FishBase (*available online*),[4] and are based on an index developed by Cheung et al. (2005) using a fuzzy logic expert system. This index combines information on eight life-history traits of fish species that affect susceptibility to fishing. It has been shown to provide sound predictions for species from a range of marine systems (Reynolds et al. 2005). Spearman rank correlations between both intra- and inter-foray distance, and fishing vulnerability were calculated.

RESULTS

Benthic cover and herbivore abundance

Benthic cover was primarily composed of live hard coral and epilithic algal matrix (EAM) at all of the three sites. However, the structural complexity and coral cover were slightly higher, and the EAM cover lower at the lagoonal Big Vickies (complexity 3.7 ± 0.2 [all values shown are mean ± SE]; coral 36.2% ± 4.9%; EAM 34.3% ± 2.5%) compared to the fringing reefs at Mermaid (complexity 2.9 ± 0.1; coral 24.6% ± 3.0%; EAM 52.9% ± 5.3%) and Turtle (complexity 2.8 ± 0.2; coral 26.6% ± 6.9; EAM 46.0% ± 5.3%). Macroalgal cover was <1% at each of the three sites. The density of herbivorous fishes varied between 21.1 fish/100 m² at Turtle, to 33.5 fish/100 m² at Mermaid, but at all sites, grazer/detritivores were the most common herbivores (over 10 fish/100 m²), and browsers the least common

TABLE 1.   Density of fish (mean ± SE) within the four herbivorous functional groups and the proportion of functional group abundance represented by species assessed for foraging metrics and included in Fig. 2, at each site at Lizard Island on the Great Barrier Reef, Australia.

Functional group	Density (fish/100 m²)			Proportion of functional group		
	Big Vickies	Mermaid	Turtle	Big Vickies	Mermaid	Turtle
Browser	0.4 ± 0.1	1.6 ± 0.4	1.2 ± 0.4	42.9	46.4	69.6
Farmer	5.9 ± 1.1	7.3 ± 1.5	4.5 ± 1.1	63.6	73.4	65.2
Grazer/detritivore	12.6 ± 1.4	16.2 ± 2.7	10.6 ± 2.1	86.1	96.1	94.3
Scraper/excavator	10.2 ± 1.6	8.4 ± 1.0	4.9 ± 0.5	79.3	84.4	84.7
Total herbivores	29.0 ± 3.2	33.5 ± 2.9	21.1 ± 2.7	78.6	85.8	84.6

Note: Data are based on underwater visual census (UVC) counts, pooled to site level, and incorporating all size classes.

(under 2.0 fish/100 m²; Table 1A). The species studied in the behavioral observations accounted for over 75% of all herbivore individuals at each site, although this proportion was lower for browsers (over 40% of individuals) than for the other three herbivorous functional groups (Table 1B).

Behavioral metrics

Both log(intra-foray distance) and log(inter-foray distance) were positively, linearly related to log(fish body length) at all three sites (Fig. 2A, B; Table 2); therefore, as body size increases among species, the fine-scale movements made by foraging fish increase exponentially in length (Fig. 2C, D). The slope and elevation of the linear relationship between log(foraging metric) and log(body size) was not significantly different between sites (Table 2), giving common parameters of α = 0.03 and β = 2.19 for intra-foray distance, and α = 0.34 and β = 2.12 for inter-foray distance, where parameters represent $y = \alpha x^\beta$ in the back-transformed data (Fig. 2ii). The four herbivorous functional groups were not evenly spread across the scales of movement for either metric (Fig. 2C, D); farming species had small intra- and inter-foray distances, grazer/detritivores species exhibited mid-size foraging movements, while scraper/excavators and browsers showed mid- to large-size foraging movements.

The residuals for these relationships varied among functional groups (Fig. 3). Residuals were predominantly negative for farmers with respect to both intra- and inter-foray distance (mean of −0.28 and −0.14, respectively), and for scraper/excavators with respect to intra-foray distance (−0.05), indicating these groups were generally moving shorter distances than predicted by the regressions. In contrast, predominantly positive residuals were recorded for both foraging metrics for grazer/detritivores (mean of 0.12 and 0.06, respectively), and for browsers with respect to intra-foray distance (0.08), indicating generally larger movements than predicted. Members of all the four herbivorous functional groups fed primarily on EAM (over 85% of bites; Appendix B). No browsers were observed feeding on macroalgae; those species that did feed on macroalgae were primarily farmers or scraper/excavators.

When analyzed at the functional-group level, the relationship between body size and the two foraging metrics was nonsignificant for farmers, but was strongly positive for both the grazer/detritivores and the scraper/excavators (Appendix C). However, the intercepts varied among groups for intra-foray distance, and the slopes varied for inter-foray distance (Appendix C). There was insufficient data on browsing species to incorporate this group into the analysis. The results produced from the family-level analysis were both qualitatively and quantitatively similar to those at the species level, for both α and β (Appendices D and E), therefore, the species-level data were used for the remaining analyses.

There was a strong positive correlation between vulnerability to fishing and both intra- and inter-foray distance (Spearman rho = 0.69, $P < 0.001$ and rho = 0.62, $P < 0.001$, respectively); therefore, those species that moved further while foraging were also more vulnerable to fishing (Fig. 4). Members of grazer/detritivores and scraper/excavator functional groups showed a range of vulnerabilities to fishing, and foraged over a range of spatial scales. Farmers showed low vulnerability to fishing and low-movement distances, in contrast the browser species targeted in the foraging observations were highly vulnerable to fishing, and travelled mid-range distances while foraging.

DISCUSSION

This study empirically tests the allometric relationships between foraging movements and the body length of herbivorous reef fishes, indicating that body size is a good proxy for scale of functional impact in these species. Large species operate and deliver their functional role over larger areas than small herbivorous fish species. This finding has important ramifications for the redundancy of function in reef fishes. Analysis of different herbivorous functional groups suggests that although there is cross-scale redundancy for herbivorous fishes as a whole, there is the lack of redundancy in some of the more narrowly defined functional groups within the herbivore classification such as macroalgae browsers. Furthermore, vulnerability of certain species to fishing indicates that fish assemblages may lose function at certain scales in the face of overfishing, and this loss is
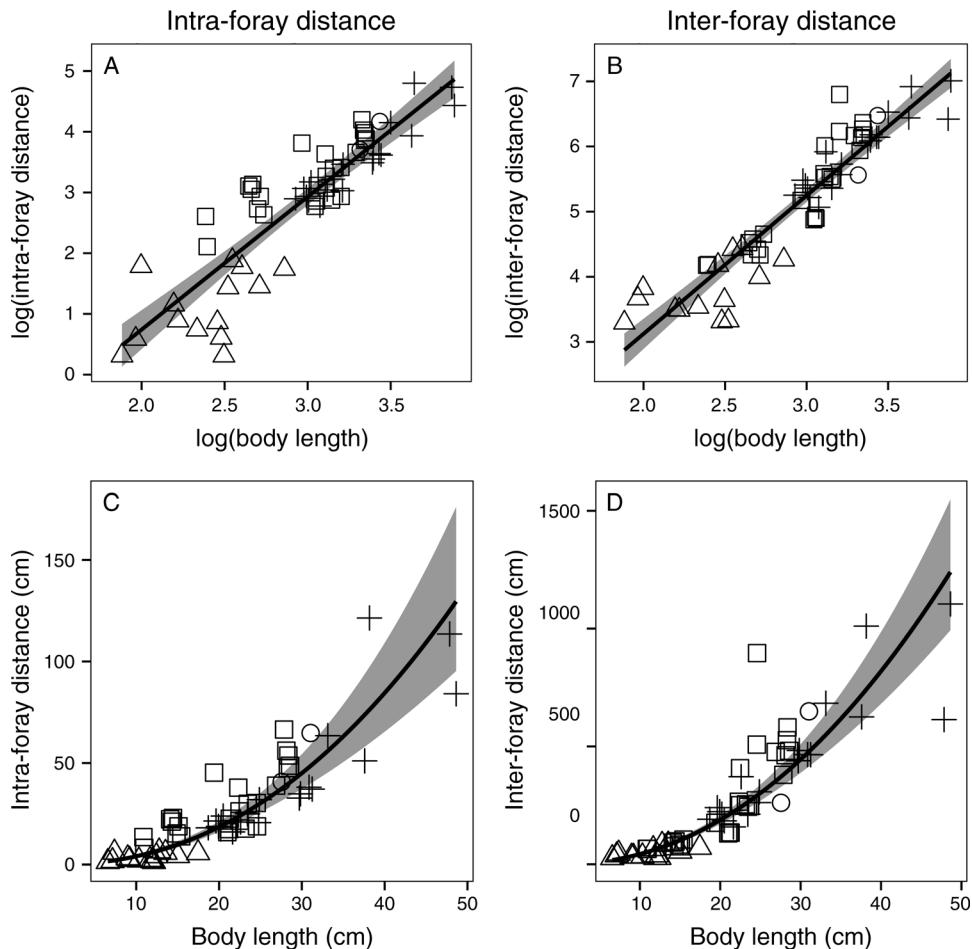
FIG. 2. Relationship between body length and (A, C) intra-foray distance or (B, D) inter-foray distance for herbivorous reef fish, presented in (A, B) log–log scales (intra- and inter-foray distances, and body length originally measured in centimeters) and (C, D) back-transformed to arithmetic scales. Lines represent significant relationships (with 95% CI) based on ordinary least-squares (OLS) regression, showing common slope and intercept among sites for both variables. Symbols indicate the functional group: triangles for farmers; squares for grazers/detritivores; circles for browses; and crosses for scrapers/excavators. See *Methods: Behavioral studies* for clarification of intra- and inter-foray distance.

not limited to the function provided by large species. This highlights the need for management actions that support functions at scales used by relatively few, or vulnerable, herbivore species.

Allometric relationships

The positive relationships between body size and both metrics of foraging movement indicate that small species forage over smaller scales than large species. This pattern may be expected as swimming speed and cost of transport decreases with increasing body size in fish (McMahon and Bonner 1983), suggesting that large fish are more able to exploit resources at larger scales. In addition, large individuals require more resources and therefore are likely to forage over greater distances to meet energy requirements (Harestad and Bunnel 1979).

The allometric relationships were exponential in form, indicating that larger species not only feed at larger scales than smaller species, but they are also feeding over

a wider range of scales, suggesting that they have broader functional roles than smaller species with regards to space use. The importance of large herbivorous fish species for delivering function is mirrored by terrestrial herbivore species, where grazing by large species has been shown to drive habitat structure and functioning (Gordon et al. 2004). Species experience ontogenetic changes in function, and there is evidence that larger individuals may exhibit exponentially higher grazing rates (Lokrantz et al. 2008) and remove greater volumes of algae (Bonaldo and Bellwood 2008) than small individuals. Our study specifically focused on interspecific allometric patterns of space use while foraging. Further work is needed to look at intraspecific patterns of function and space use to understand if these mirror the positive relationships found between body size and grazing rates or bite volume within herbivorous species (Bonaldo and Bellwood 2008, Lokrantz et al. 2008).

TABLE 2. Summary of scaling parameters for the relationship between body length and (A) intra-foray distance and (B) inter-foray distance, where parameters represent $y = \alpha x^{\beta}$ in the back-transformed data.

Site	α (95% CI)	β (95% CI)	R^2	P
A) Intra-foray distance				
Big Vickies	0.01 (0.00–0.06)	2.35 (1.89–2.83)	0.86	<0.001
Mermaid	0.01 (0.00–0.08)	2.48 (1.81–3.14)	0.77	<0.001
Turtle	0.10 (0.03–0.34)	1.81 (1.40–2.21)	0.83	<0.001
Common parameters	0.03 (0.01–0.06)	2.19 (1.89–2.49)	0.79	<0.001
B) Inter-foray distance				
Big Vickies	0.44 (0.15–1.31)	1.99 (1.63–2.35)	0.88	<0.001
Mermaid	0.18 (0.05–0.70)	2.35 (1.89–2.80)	0.87	<0.001
Turtle	0.36 (0.12–1.10)	2.09 (1.72–2.46)	0.89	<0.001
Common parameters	0.34 (0.17–0.62)	2.12 (1.91–2.34)	0.87	<0.001

Notes: For panel A, the common-slope likelihood-ratio statistic was 4.54, df = 2, $P = 0.10$; and the common-elevation Wald statistic was 5.75, df = 2, $P = 0.06$. For panel B, the common-slope likelihood-ratio statistic was 2.53, df = 2, $P = 0.37$; and the common-elevation, Wald statistic was 2.41, df = 2, $P = 0.30$.
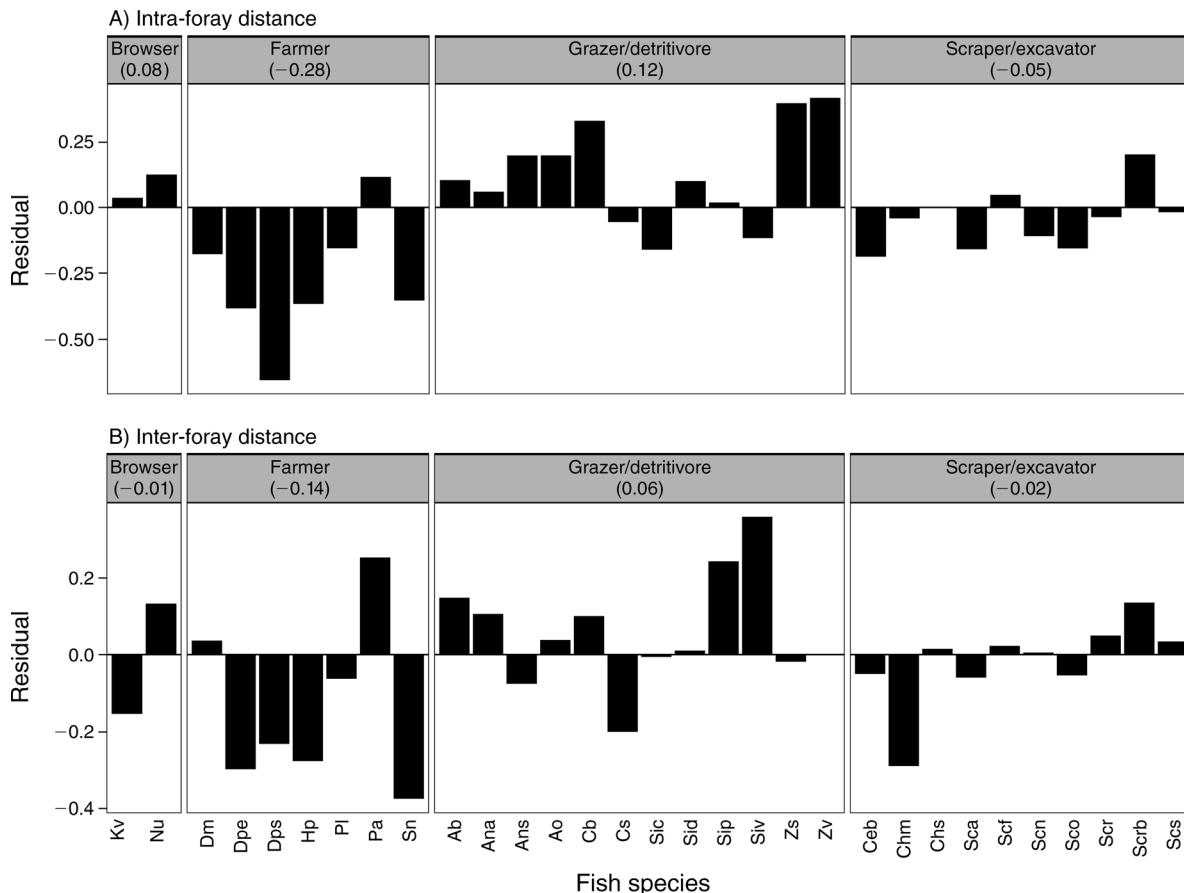

FIG. 3. Residuals for the relationship between body length and (A) intra-foray distance or (B) inter-foray distance for species of herbivorous reef fish. Bars represent the mean value across sites where a species was observed at multiple sites. Numbers in parentheses provide the mean residual for that functional group. Species abbreviations are as follows: Kv, *Kyphosus vaigiensis*; Nu, *Naso unicornis*; Dm, *Dischistodus melanotus*; Dpe, *Dischistodus perspicillatus*; Dps, *Dischistodus psuedochrysopecilus*; Hp, *Hemiglyphidodon plagiometopon*; Pl, *Plectroglyphidodon lacrymatus*; Pa, *Pomacentrus adelus*; Sn, *Stegastes nigricans*; Ab, *Acanthurus blochii*; Ana, *Acanthurus nigricauda*; Ans, *Acanthurus nigrofuscus*; Ao, *Acanthurus olivaceus*; Cb, *Centropyge bicolor*; Cs, *Ctenochaetus striatus*; Sic, *Siganus corallinus*; Sid, *Siganus doliatus*; Sip, *Siganus punctatus*; Siv, *Siganus vulpinus*; Zs, *Zebrasoma scopas*; Zv, *Zebrasoma veliferum*; Ceb, *Cetoscarus bicolor*; Chm, *Chlorurus microrhinus*; Chs, *Chlorurus sordidus*; Sca, *Scarus altipinnis*; Scf, *Scarus flavipectoralis*; Scn, *Scarus niger*; Sco, *Scarus oviceps*; Scr, *Scarus rivulatus*; Scrb, *Scarus rubroviolaceus*; and Scs, *Scarus schlegeli*.
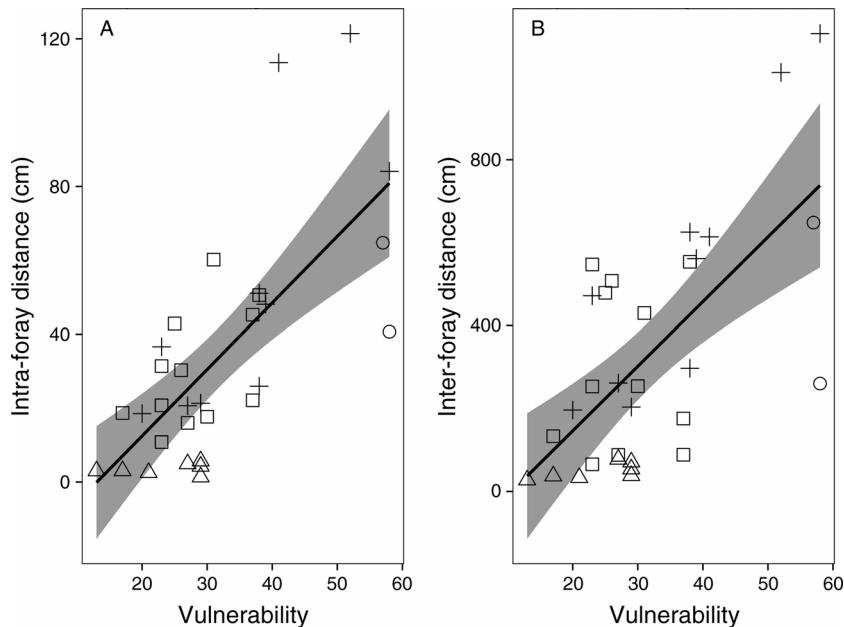
FIG. 4. Correlation between vulnerability to fishing pressure (based on an index by Cheung et al. [2005], where increasing numbers indicate increasing vulnerability) and (A) intra-foray distance (Spearman rho = 0.69, $P < 0.001$) or (B) inter-foray distance (Spearman rho = 0.62, $P < 0.001$). Intra-foray and inter-foray data for each species were pooled across sites. Symbols indicate the functional group: triangles for farmers; squares for grazers/detritivores; circles for browses; and crosses for scrapers/excavators.

The slopes of the relationships between body size and both intra- and inter-foray distance were similar, indicating that interspecific patterns may be comparable at different levels of the foraging decision hierarchy; for example, for within- or between-patch movements. Furthermore, the results mirror those found for the relationship between body size and home range (Kramer and Chapman 1999), suggesting that these comparisons may be made among levels of movement relating to foraging and other activities. The slopes and intercepts of the allometric relationships were not significantly different among sites, although the intercept was only slightly nonsignificant among sites for intra-foray distance. The three sites were chosen due to their similar benthic composition and geographic location. Changing habitat condition, and therefore resource availability and distribution, is likely to result in changes to both the intercept and slope of these relationships; Nash et al. (2012) reported reduced inter-foray distances of parrot-fishes in response to increasing coral cover, but the shape of this decrease differed among species. Further work is needed to analyze whether these variations among species result in stronger or weaker allometric foraging relationships in the face of habitat degradation. Additionally, the effect of school size on foraging range was not assessed. Group size has been shown to be positively related to home range in mammal species (e.g., Dias and Strier 2003). Research is needed to analyze the effect of school size on the allometry of function and space use in herbivorous reef fishes.

Foraging decisions, at the scale relating to choice of specific EAM components, were not explicitly studied. However, consistency in the positive or negative nature of residuals within functional groups suggests that, although all species fed primarily on the EAM, different components of the algal matrix may have been selected for by species within the four functional groups (Cross-man et al. 2005, Nash et al. 2012). The quality and composition of EAM varies over space (Purcell and Bellwood 2001), therefore differences in the distribution of constituents has the potential to influence the variation around the predicted allometric relationships for members of each functional group (Holling 1992). Farming species exhibited large, primarily negative residuals, signifying that these species cover smaller distances than expected based on body size. This is likely due to their ability to manipulate resource availability, concentrating food resources into a small patch through farming activities (Ceccarelli 2007); therefore, they are less reliant on existing resource distributions. This supposition is further supported by the pattern of large negative residuals recorded for farming species that are known to have a greater influence on benthic composition (intensive/extensive farmers; detailed in Appendix A), compared with the positive residuals of *Pomacentrus adelus* which exerts less influence on the benthos (an indeterminate farmer; Emslie et al. 2012).

The relationships between body size and the foraging metrics estimated for all species were qualitatively similar to those calculated for the separate functional groups, although these relationships were not significant

for farming species, suggesting body size is less critical within this group. Farmers are territorial and as such, space use may be limited by the costs arising from defending a territory (Brown 1964). The relationships between body size and the foraging metrics were quantitatively similar between species-level, and family-level analyses suggesting these patterns hold at a number of taxonomic levels, and is not an artifact of phylogenetic relationships. Therefore, the scale of functional impact of herbivorous reef fishes is positively and exponentially related to body size, although the rate of increase in spatial scale across body sizes depends on functional-group membership.

Cross-scale patterns

Foraging movements of herbivores, and scraper/excavators in particular, cover a wide range of scales, suggesting the potential for redundancy in the face of disturbances occurring at a given scale (Peterson et al. 1998, Elmqvist et al. 2003), i.e., impacts deriving from the disturbance may be ameliorated by herbivores that are foraging at scales that do not coincide with the scale of the disturbance. The scraper/excavator group is composed of parrotfish species, therefore, this finding supports the well-described importance of parrotfishes for providing herbivory on coral reefs (Choat et al. 2004, Mumby 2006, Adam et al. 2011). Grazer/detritivores and farmers were somewhat more constrained in the scales of their movements, being restricted to mid and small scales, respectively. Siganids appear to extend the range of grazer/detritivores somewhat, as indicated by the large positive residual of *Siganus vulpinus*, a pattern that appears to be widespread in siganids (Fox and Bellwood 2012). In contrast, the range of scales over which farmers move is likely constrained by the costs associated with defending territories at larger scales (Brown 1964). Most surprisingly, browsers were limited to mid-scale movements. This finding may be a function of the low numbers of browsers studied (two species); however, individuals of these two species represented between 42% and 70% of browser abundance at the three sites. A maximum of five browsing species were observed at any one site, and mean density was <1.6 fish/100 m^2 at all sites; therefore, both cross-scale redundancy and abundance of this functional group appears to be low. This suggests that in the face of disturbances, which affect species operating at mid scales, there may be ecologically significant declines in the delivery of the browsing function. Demarcation of the scales across which the four functional groups operate highlight the relative potential for redundancy in each group. Similar multi-scale foraging patterns have been modeled in terrestrial herbivore communities, driven by interspecific body size variation (Illius and Gordon 1987, Ritchie and Olff 1999, Cumming and Cumming 2003), suggesting corresponding potential for cross-scale redundancy in certain taxa (Peterson et al. 1998, Cromsigt and Olff 2006, Laca et al. 2010).

Eighty-five percent of forays by members of each functional group were observed targeting the EAM, including 100% of forays by browsers. Browsers are defined as species which primarily target macroalgae and are therefore important for reversing shifts to a macro-algal-dominated state (Bellwood et al. 2006a). Browsers targeting EAM, rather than macroalgae, is likely a consequence of the limited cover of macroalgae at the study sites (<1%), and supports the contention that herbivores exhibit feeding versatility in response to changing availability of resources (Bellwood et al. 2006b). This has positive implications for control of EAM cover, but doesn't necessarily infer the same positive consequences for control of macroalgae, unless members of other functional groups switch to feeding on macroalgae when it is abundant, e.g., *Platax pinnatus* (Bellwood et al. 2006a).

Although certain functional groups appear to show low levels of redundancy across scales, this is not necessarily due to past disturbances, or impacts such as overfishing, occurring over ecological time scales. The study sites at Lizard Island have been closed to all fishing for eight years, prior to which there were restrictions on fishing for over 25 years. The presence of low redundancy and a high number of specialized functions within the herbivores is likely driven by relatively low variation in abiotic factors over evolutionary timescales (Walker et al. 1999), rather than due to recent impacts reducing cross-scale redundancy. If this is the case, then the distributions of functional groups observed in this study may be representative of relatively unexploited reefs, and therefore present a best case scenario for managers of reef systems. Reefs subject to high fishing pressure are likely to have experienced erosion of redundancy within functional groups and thus be characterized by a more depauperate cross-scale herbivore assemblage.

A number of caveats apply to the interpretation of cross-scale patterns of foraging movements by functional groups: (1) Assignment of functional groups necessarily results in relatively coarse classifications. As a result, feeding behaviors specific to individual species (e.g., Fox and Bellwood 2012) are not accounted for, potentially overestimating redundancy across scales. (2) The predominant role a species plays may change over time. This may have both negative consequences (e.g., herbivorous urchins driving significant bioerosion with increasing population abundance [McClanahan and Shafir 1990]), or positive impacts (e.g., the invertivore *Platax pinnatus* removing macroalgae in experimental phase-shifts [Bellwood et al. 2006a]). Nevertheless, the future delivery of a particular function is not guaranteed (Nyström 2006).

The spatial patterns of foraging by herbivores suggest that the four functional groups exhibit different degrees of cross-scale redundancy. The next step is to assess how foraging areas overlap among members of a functional group operating at different scales to provide this

redundancy. In boreal forests, birds foraging over a wide range of scales help control spruce budworm outbreak. Different sized species of bird forage for budworm at different scales during an outbreak, with larger species switching to this prey item as budworm becomes more aggregated over larger scales (Peterson et al. 1998). Similar research, examining the effect of broad vs. narrow ranges of foraging scales provided by members of herbivorous functional groups is needed to understand the importance of redundancy mechanisms on coral reefs and how this redundancy interacts with environmental factors (Cheal et al. 2013).

Vulnerability of cross-scale patterns to fishing

The positive relationship between vulnerability to fishing and the scale of foraging movements indicates that overfishing has the potential to reduce the range of scales over which herbivores are providing function by removing species operating at larger spatial scales. Although there is a strong correlation between species size and vulnerability to fishing (Jackson et al. 2001, Friedlander and DeMartini 2002), some species were more vulnerable than their body size alone would suggest, e.g., browsers. This is perhaps not surprising considering that the vulnerability metric used incorporates size as just one of eight traits (Cheung et al. 2005). Characteristics of a species, other than size, contribute to their relative susceptibility to being caught and the likelihood of populations rebounding from a given fishing pressure, both of which contribute to fishing vulnerability. Variability in the influence of different traits on hunting risk has been explored in terrestrial systems; large body size has been shown to be positively correlated with hunting risk in Australian mammal species (e.g., Cardillo and Bromham 2001), whereas work on African bushmeat exploitation has emphasized the importance of large population sizes and species' behavior (Fa et al. 2005). Indeed, behavioral changes in response to predation pressure add considerable complexity to assessments of species' vulnerability to exploitation. Predation risk may affect foraging behavior in communities subject to natural predators (e.g., in baboons [Cowlishaw 1997] and coral reef fishes [Randall 1965, Madin et al. 2011]), but there is also potential for behavioral modifications in response to hunting, which may affect vulnerability to being caught (Thiel et al. 2007). For example, recent work on coral reefs has demonstrated that herbivorous fishes flee from spearfishers earlier when they are in locations that experience greater fishing pressure (Januchowski-Hartley et al. 2011). An increased understanding of the vulnerability of herbivorous fishes to fishing, and how this is likely to vary under different fishing pressures and management contexts, should improve our understanding of how the delivery of herbivorous functions across spatial scales are likely to change over time.

Loss of function at specific scales may proceed unnoticed if metrics of function, such as herbivore abundance, are used to monitor essential ecosystem processes (Bellwood et al. 2004). Where species are large and vulnerable to fishing, there are the compound issues of losing species operating over large scales and losing species that contribute most to functional impact via higher grazing rates and volumes (Bonaldo and Bellwood 2008, Lokrantz et al. 2008). These large species are primarily scraper/excavators and there is, therefore, the potential for losing a critical component of the herbivore assemblage responsible for algal control and bioerosion, even in areas subject to moderate fishing pressure (Bellwood et al. 2012). Where fishing reaches greater levels, we may see a subsequent reduction in grazer/detritivores, which are foraging at mid-scales. Cross-scale redundancy has the potential to counteract some of the impact of losing species operating at certain scales. For example, the positive effects of small individuals have been seen in Moorea, where large numbers of small parrotfishes controlled algal growth (Adam et al. 2011). However, there is evidence that species operating over small scales may be less effective at compensating for loss at larger scales than vice versa, particularly in the face of large scale disturbances. For example, assemblages of small-scale mammalian seed dispersers are unable to provide dispersal at scales sufficient to maintain tree populations when faced by large-scale disturbances, a problem that does not occur in assemblages with both large- and small-scale dispersers (Peterson et al. 1998). These contrasting findings suggest that caution needs to be taken when predicting the consequences of cross-scale redundancy for the continuation of ecosystem processes in the face of different disturbance regimes. There is a need to assess cross-scale patterns of function in concert with future levels of overfishing and the scale of disturbance regimes to make predictions about the usefulness of current cross-scale redundancy patterns for the ongoing maintenance of coral-dominated reefs.

Vulnerability to fishing is not limited to large species; the browsers exhibited significant susceptibility. When this vulnerability is considered in conjunction with (1) the low number of browsing species found at the three sites, (2) the low abundance of these species, and (3) the narrow range of spatial scales over which they operate, there is a clear need for concern regarding the redundancy of function within this group, and thus, the ongoing delivery of browsing function in the face of future change. However, in highlighting the susceptibilities of certain functional groups and spatial scales of function, this study provides managers with the fundamental knowledge needed to plan mitigation measures to counteract fishing pressure that undermines ecosystem processes at critical scales. There is an emerging body of work describing targeted mitigation strategies, such as gear-based management, which may minimize catches of important or susceptible species, including herbivores (Cinner et al. 2009, Johnson 2010). Our study provides the first step to enable managers to select from

these mitigation strategies appropriate tools to maintain function across scales. Due to the local to regional nature of fisheries management, there is the potential to implement such actions in a timely manner, resulting in relatively quick responses within the fish community (Graham et al., *in press*).

Conclusions

The small-scale movement metrics used in our study revealed the tight relationship between fish body size and space use at scales appropriate to the functional impact of herbivorous reef species. The results indicate that body size is a useful proxy for scale of foraging and functional impact among species, and that functional groups are not evenly distributed across scales. The influence of fishing pressure on cross-scale distributions of function is of significant concern for two key reasons: (1) Fishes operating over large scales (primarily scraper/excavators), and which likely exhibit greater grazing impacts, are particularly susceptible to exploitation; and (2) the few species that act as browsers, targeting mature macroalgae, provide their role over a narrow range of spatial scales and are extremely vulnerable to fishing. This study identifies the scales at which herbivorous function is at risk, and therefore provides critical information needed to inform management actions to support function at specific scales and the provision of the key ecosystem process of herbivory.

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SUPPLEMENTARY MATERIAL

Appendix A

Table summarizing fish species and sizes used in behavioral observations (*Ecological Archives* A023-084-A1).

Appendix B

Table summarizing benthos targeted during forays by each functional group (*Ecological Archives* A023-084-A2).

Appendix C

Table summarizing relationships between foraging metrics and body size for each functional group (*Ecological Archives* A023-084-A3).

Appendix D

Table summarizing relationships between foraging metrics and body size at the family level (*Ecological Archives* A023-084-A4).

Appendix E

Figure showing relationships between foraging metrics and body size at the family level (*Ecological Archives* A023-084-A5).