

Research

Species differences drive spatial scaling of foraging patterns in herbivorous reef fishes

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Herbivory is a core ecosystem function that is delivered heterogeneously across space. Disentangling the drivers of foraging patterns is key to understanding the functional impact of herbivores. Because intrinsic drivers of foraging like metabolism, nutritional requirements and movement costs scale allometrically, foraging movement patterns in terrestrial herbivores have been shown to also scale positively with body size. However, spatial patterns of herbivory can also be explained by orthogonal factors such as trophic position, competition and functional groupings. Here, we investigate body size and species traits as drivers of the spatial scaling of foraging patterns in herbivorous coral reef fishes. We quantified foraging patterns of 119 individuals from nine common herbivorous species using focal individual surveys. Body size, species identity, feeding substrata, social grouping and functional group were tested as predictors of three foraging metrics: foraging area, inter-foray distance and tortuosity. Our resulting model revealed that species identity overshadowed body size as a predictor in models for all foraging metrics. While foraging area was explained best by species only, the resulting tortuosity and mean inter-foray distance models included a small effect of body size that explained within-species variation. We do not find strong support for size-scaling of foraging patterns in our study species. These findings indicate that foraging allometry based on Optimal foraging theory cannot be generally applied to reef fish assemblages due to a diversity of foraging strategies, such as spatial partitioning and territoriality. Our work reveals the importance of behavioural ecology and taxonomic diversity in understanding herbivory, especially given the functional differences across species. With coral reefs under threat across the world, this is an important step to disentangling the spatial delivery of a core ecosystem function.

Keywords: allometry, coral reef fish, foraging ecology, function delivery, functional impact, herbivory

Introduction

Ecosystem functions are processes of energy storage or transfer within an ecosystem which can be classified in two broad categories of production and consumption

(Reichle et al. 1975). Many functions relating to consumption are mediated by foraging, such as herbivory, pollination, bioturbation and predation (Schmitz et al. 2008). Hence, the spatial distribution of foraging has important consequences for ecosystem functions. Foragers that are wide-ranging often result in greater functional impacts due to their delivery across a larger spatial scale (Lundberg and Moberg 2003). Predator assemblages have often been the focus for studies on foraging scale and impacts as they tend to be highly mobile (Laundré et al. 2010, Lyly et al. 2015, Catano et al. 2016). However, recent findings on the role of herbivores in ecosystem functioning and resilience highlight the need to understand scales of herbivory (Kaarlejärvi et al. 2015, Eynaud et al. 2016, Vergés et al. 2016, Chung et al. 2019). Here we investigate body size and species-specific traits as drivers of the spatial scale of foraging in roving herbivores.

The way a herbivore utilises space in its environment for energy acquisition is influenced by intrinsic and extrinsic factors, many of which link with body size. Individual intrinsic factors include metabolic requirements, body condition and hunger states. These are highly plastic and vary widely, even within individuals and species. Seminal theories like Optimal Foraging Theory and Charnov's Marginal Value Theorem (Charnov 1976, Schoener 1983, Belovsky 1986, 1997, Senft et al. 1987) have established the relationship between some of these factors in the balance of costs (energy expenditure and predation risk) and benefits (acquisition of energy and nutrients) of foraging (Pyke 2019). Studies stemming from these theories have established that because drivers like metabolic needs, movement costs and patch search scale positively with body size, foraging ranges also scale similarly with body size (Senft et al. 1987, Swihart et al. 1988, Laca et al. 2010, Ofstad et al. 2016). The vast majority of these studies, however, have focused on predation dynamics which are governed by sparsely distributed but energy-dense prey, whereas spatial dynamics of herbivory are driven less by resource availability and more so by habitat structure and nutritional quality. Indeed, the effect of body size is not uniform across assemblages and taxa and is influenced by trophic position (Hendriks et al. 2009) and habitat quality (Nash et al. 2016a). These findings highlight the need to integrate traits specific to species and functional groups for a more accurate picture of size-dependent foraging ranges.

Using herbivorous coral reef fishes as our model taxa, we investigate the relationship between size and foraging spatial scales, as well as the effect of different species traits on this relationship. Herbivorous coral reef fishes are a diverse guild that exhibit a large degree of niche differentiation and functional complementarity (Burkepile and Hay 2008, Rasher et al. 2013). There has been considerable work on linking foraging impacts with traits in feeding substrata, jaw morphology, dentition, biting behaviour and food selectivity (Bellwood and Choat 1990, Green and Bellwood 2009, Streit et al. 2015, Adam et al. 2018). Broadly, five functional groups emerge from characterising foraging strategies using these traits: excavators, scrapers, algal croppers, detritivores and macroalgal browsers (Hoey and Bellwood 2011). While

macroalgal browsers typically feed on large fleshy macroalgae, the remaining four groups typically bite on substrata covered by epilithic algal matrix (EAM; sensu Wilson et al. 2003) but differ in the amount of material and/or underlying substrata that is removed when feeding (Green and Bellwood 2009). Excavators and scrapers refer to parrotfishes exclusively. Due to their beak-like dentition, these two groups remove parts of the underlying substratum together with the EAM when feeding, leaving areas of bare substrata, with excavators taking deeper bites and removing greater volumes of substrata than scrapers (Bellwood and Choat 1990). In contrast, algal croppers remove the upper portions of algal material when feeding, leaving the underlying substrata largely undisturbed (Russ 1984, Streit et al. 2015) while detritivores, such as *Ctenochaetus* spp., possess specialised comb-like teeth that enable them to selectively remove detritus from the EAM (Purcell and Bellwood 1993, Tebbett et al. 2017).

Herbivory functions provided by reef fish are critical for the stability and resilience of reef ecosystems. Herbivorous reef fish are capable of reducing algal cover by 50% within hours (Lewis 1986), and removing up to 65% of net primary productivity on a reef seasonally (Polunin and Klumpp 1992). Moreover, excluding herbivorous reef fishes from small areas of reef has been shown to trigger rapid increases in algal biomass (Lewis 1986, Hughes et al. 2007). Further studies have shown that herbivore assemblages are a key predictor of whether reefs recover to coral-dominated states or shift to algae-dominated states following severe disturbances such as massive bleaching and/or cyclones (Bellwood et al. 2006, Ledlie et al. 2007, Adjeroud et al. 2009, Adam et al. 2015, Graham et al. 2015, Holbrook et al. 2016, Chung et al. 2019). For these reasons, herbivorous reef fish perform a core process for coral reef ecosystems (Plass-Johnson et al. 2015, Brandl et al. 2019). While differences in herbivory impacts between different species and functional groups have received considerable attention (Burkepile and Hay 2008, 2010, Hoey and Bellwood 2009, Cheal et al. 2010, Brandl and Bellwood 2014), relatively little is known regarding the spatial variation in the delivery of herbivory.

Body size is an important factor to understanding the foraging impacts of herbivorous reef fish and has been shown to influence rates of macroalgal browsing (Hoey and Bellwood 2009), bioerosion and grazing (Bonaldo and Bellwood 2008, Hoey and Bellwood 2008, Lokrantz et al. 2008) and ontogenetic shifts in diet (Green and Bellwood 2009, Pereira et al. 2016). Moreover, recent studies have shown that home-range size and distances travelled during successive foraging bouts (inter-foray distance henceforth; Fig. 1b) scale with body size among herbivorous coral reef fishes (Nash et al. 2013, 2015). This allometric scaling of inter-foray distance suggest that the total area covered by active foraging movement (i.e. foraging area; Fig. 1b) may also scale allometrically, however this remains largely unknown. Therefore, our study addresses this need to investigate the potential effects of body size and a range of species traits (feeding substrata, feeding social grouping, functional grouping) on spatial foraging patterns both within and among species of herbivorous reef fish.

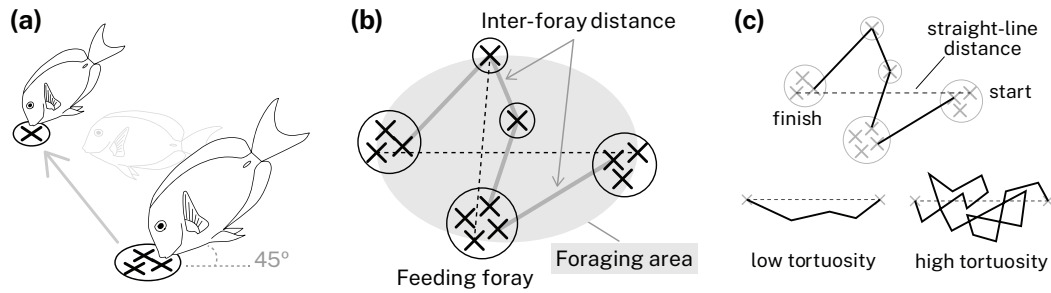


Figure 1. A conceptual illustration of foraging pattern metrics quantified during focal individual surveys: inter-foray distance (a,b), foraging area (b), and tortuosity (c). Feeding forays are defined as consecutive bites where a fish individual does not lift the head $> 45^\circ$ (a), represented with grouped circles of bites indicated with cross marks (a, b). Solid lines in panels (b) and (c) connecting forays show the foraging paths of the fish between forays (i.e. inter-foray distance). The dashed lines in panel (b) show the estimation of foraging area (shaded light grey) as an ellipse based on the four farthest perpendicular bites observed. Tortuosity is quantified as the ratio between the sum of inter-foray distances to the straight-line distance between the first and final bites (c). Panel (c) compares the tortuosity of two possible foraging movements with identical straight line distances. Os et velenectur as et dolore eveles molorer spedit eatas di ducius as dis dollab is et et quam,

Specifically, our study aims to 1) identify the strongest predictors of foraging space use in herbivorous reef fish and 2) develop a model that captures drivers of spatial foraging patterns.

Methods

Study system

This study was conducted on Lizard Island ($14^\circ 40' S$, $145^\circ 28' E$) on the mid-shelf of the northern Great Barrier Reef in October 2014. Lizard Island is a high continental island located approximately 30 km from the Queensland coast and has extensive reef formation around its margins. We conducted our surveys on the reef crest (2–5 m depth) to the south of the island, an area that is obliquely exposed to the prevailing southeasterly swell. The reef crest was used as it supports abundant and species rich assemblages of herbivorous fishes (Fox and Bellwood 2007). Our focal species are nine locally abundant herbivorous fish species that encompass a range of taxonomic and functional groups: surgeonfishes (Family: Acanthuridae) *Acanthurus nigricauda*, *Ctenochaetus striatus*, *Naso unicornis* and *Zebrosoma scopas*; parrotfishes (Family Labridae; Tribe: Scarini) *Chlorurus spilurus*, *Scarus frenatus* and *Scarus rivulatus*; and rabbitfishes (Family: Siganidae) *Siganus doliatus* and *Siganus vulpinus*.

Benthos and fish assemblage surveys

Because foraging patterns of reef fish can be influenced by resource availability and social behaviour with conspecifics, we established eight 50 m transects ($n = 8$) placed at random at our study site to survey the benthos and fish assemblage first. For benthos composition, we used the point-intercept transect method with 81 random sampling points per transect. Possible benthos classification categories were hard coral, soft coral, EAM/pavement, rubble, macroalgae and cyanobacteria. To survey the fish assemblage, we conducted an underwater visual census along the transects. We counted and estimated the length of fish individuals throughout the water column within a 5 m belt along the transects. Fish were

classified into total length size classes of 5 cm inclusive (e.g. 0–5, 5–10 cm). To minimize sampling bias, fish surveying was done in a unidirectional swim. For each size class, we estimated biomass for the median class length using published length–weight relationships in FishBase and other literature (Pauly and Froese 2019).

Foraging patterns

We quantified foraging patterns using focal individual observations conducted between 9:00 and 16:00 h. For each observation, we haphazardly selected an individual of a focal species and followed for a short period (~30–60 s) to allow the fish to acclimate to the presence of the observer. During the acclimation period we estimated the total length (TL) of the focal fish to the nearest centimetre and recorded their social grouping (alone, conspecific pair, conspecific school or heterospecific school). We also noted the phase (i.e. initial or terminal phase) for parrotfish individuals. Following the acclimation period, an observation period lasting 5 min began following the first observed bite on the substratum. We maintained an observation distance between 5 and 12 m to minimise potential observer effects. In cases where the focal fish showed any altered behaviour due to observer presence, we abandoned the observation. During the 5-min observation period, we quantified the foraging pattern by marking the location of sequential feeding forays with sequentially numbered small lead weights. A foray was defined as a single bite or a series of bites where the focal individual did not lift the head ($> 45^\circ$) between consecutive bites (Fig. 1a). This shares a similar definition with Nash et al. (2012, 2013) but differs in that we do not use a bout of active swimming to delineate between forays. We did so to remove any influence of body size that would potentially bias our metrics. For closely clustered forays, we noted the position of the forays and delayed marker placement until after the focal individual swam away from the area to minimize disturbance to the natural foraging behaviour of the focal individuals. To avoid resampling individuals, we noted unique body markings of observed individuals, always moved along the reef in the same direction between

observations, and did not conduct consecutive observations on conspecifics of a similar body size (following Keith et al. 2018). We aimed to survey 15 individuals that encompassed the available body size range for each species at the study site.

After the observation period, we measured the distance between each consecutive foray marker (i.e. inter-foray distance), the straight-line distance between the first and last foray markers, the distance between the two farthest markers and the two farthest apart markers on a line perpendicular to the first (Fig. 1b–c). Functional groupings and diet/feeding substrata were assigned to each species based on literature (Choat et al. 2004, Green and Bellwood 2009, Hoey et al. 2013), acknowledging that many species that feed on EAM-covered surfaces are targeting specific microscopic components (e.g. parrotfishes: Clements et al. 2017, Nicholson and Clements 2020). Ontogenetic diet changes occur for many herbivorous reef fish species (Bellwood 1988, Chen 2002, Green and Bellwood 2009), and we ascertained that our sampled individuals did not fall within the body size range that this was documented to occur in our trait assignment. The resulting trait data are provided in the Supporting information.

Data analysis

We calculated three metrics to assess foraging patterns: foraging area, tortuosity and mean inter-foray distance. Foraging area captures the spatial extent of herbivory while mean inter-foray distance captures movement between consecutive

Table 1. Ranking results of foraging area candidate models according to ascending AIC values and residual deviance (res. dev.). This is also shown with AICc differences (Δ AICc) relative to the top-ranking model and AICc degrees of freedom. The selected model is indicated in bold. Candidates are of every possible combination of predictors with and without interaction terms: individual size in total length (Size), species, social grouping trait (SG), feeding substrata and functional group (Func). More complex candidates with additional interaction terms that did not converge were omitted.

Foraging area candidate models	df	AICc	Res. dev.	Δ AICc
Size + Species	11	1150.944	130.981	
Species	10	1151.602	90.499	0.658
Size + SG + Species	12	1153.199	122.657	2.255
SG + Species	11	1153.896	121.748	2.952
Size \times Species	19	1155.356	125.284	4.412
Size + Substrata	4	1178.99	124.27	28.046
Size + SG + Substrata	5	1179.396	125.614	28.452
Size \times Substrata	5	1180.145	121.088	29.201
Size	3	1180.716	88.369	29.772
Size + Func	4	1181.915	123.339	30.971
Size \times SG	5	1181.935	88.516	30.991
Size + SG	4	1182.279	77.961	31.335
Size \times Func	5	1182.973	133.562	32.029
Size + SG + Func	5	1183.738	90.592	32.794
SG + Substrata	4	1188.079	134.393	37.135
Substrata	3	1188.22	133.148	37.276
SG	3	1188.652	133.354	37.708
Func	3	1189.516	124.961	38.572
SG + Func	4	1190.576	126.141	39.632

forays within the foraging area. Tortuosity provides a measure of foraging density. All three metrics together provide a more holistic picture of foraging behaviour across space. We estimated foraging area as the ellipse defined by the distance between the two farthest markers and the two farthest apart markers on a line perpendicular to the first (Fig. 1b). Tortuosity was measured as a ratio between the sum of inter-foray distances to the straight-line distance between the first and final bites of the observation period (Fig. 1c; adapted from Batschelet 1981, Secor 1994). We assessed the utility of inter-foray distance as a metric of habitat use as a predictor of foraging area in a quantile regression (quantreg R package; Koenker 2021).

To determine these metrics as a function of fish traits, we constructed a set of generalised linear models (GLM) with gamma error distribution and a log-link function for each foraging pattern metric with every possible combination of explanatory variables (species, individual size, social grouping, feeding substrata and functional group), with and without interactions. All candidate models for the respective metrics are listed in Table 1–3. Candidate models for variance in inter-foray distances as response variables are provided in the supplementary materials (Supporting information). We determined the best predictor structure for foraging area, tortuosity and mean inter-foray distance by ranking candidate models according to the lowest Akaike information criterion corrected for small sample sizes (AICc) with at least a difference of 2 AICc (Δ AICc) with the next best candidate. If candidates were $< 2 \Delta$ AICc, model selection would be by

Table 2. Ranking results of tortuosity candidate models according to ascending AIC values and residual deviance (res. dev.). This is also shown with AICc differences (Δ AICc) relative to the top-ranking model and AICc degrees of freedom. The selected model is indicated in bold on the first row. Candidates are of every possible combination of predictors with and without interaction terms: individual size in total length (Size), species, social grouping trait (SG), feeding substrata and functional group (Func). More complex candidates with additional interaction terms that did not converge were omitted.

Tortuosity candidate models	df	AICc	Res. dev.	Δ AICc
Size + Substrata	7	603.998	72.601	
Size + Species	11	605.278	68.187	1.28
Substrata	6	605.958	74.98	1.96
Size + SG + Substrata	10	607.298	70.558	3.3
SG + Substrata	9	608.265	72.393	4.267
Size + SG + Species	14	608.45	65.916	4.452
Species	10	609.072	71.524	5.074
SG + Species	13	610.306	68.202	6.308
Size \times Substrata	11	612.91	72.299	8.912
Size \times Species	19	620.923	65.326	16.925
Size	3	633.026	96.609	29.028
Func	5	636.376	95.911	32.378
SG	5	637.185	96.491	33.187
Size \times Func	9	637.278	90.194	33.28
Size + Func	6	638.415	95.783	34.417
Size + SG	6	639.327	96.435	35.329
SG + Func	8	642.624	95.533	38.626
Size + SG + Func	9	644.891	95.479	40.893

Table 3. Ranking results of mean inter-foray distance candidate models according to ascending AIC values and residual deviance (res. dev). This is also shown with AICc differences (Δ AICc) relative to the top-ranking model and AICc degrees of freedom. The selected model is indicated in bold on the first row. Candidates are of every possible combination of predictors with and without interaction terms: Individual size in total length (Size), species, social grouping trait (SG), feeding substrata and functional group (Func). More complex candidates with additional interaction terms that did not converge were omitted.

Mean inter-foray distance candidate models	df	AICc	Res. dev.	Δ AICc
Size + Species	11	380.815	17.704	
Size + Substrata	7	381.613	19.256	0.798
Size \times Substrata	11	386.76	18.588	5.945
Size + SG + Species	14	387.132	17.523	6.317
Size + SG + Substrata	10	387.492	19.076	6.677
Size \times Species	19	388.812	15.884	7.997
Species	10	388.878	19.293	8.063
Substrata	6	390.503	21.093	9.688
SG + Species	13	394.385	18.992	13.57
SG + Substrata	9	394.865	20.66	14.05
Size \times SG	9	397.439	21.099	16.624
Size + SG	6	403.601	23.469	22.786
Size + SG + Func	9	404.742	22.394	23.927
Size \times Func	9	405.579	22.547	24.764
Size	3	408.798	25.818	27.983
Size + Func	6	409.769	24.676	28.954
SG	5	416.199	26.47	35.384
SG + Func	8	417.696	25.361	36.881

lowest residual deviance. We also compared univariate model rankings with each other to analyse the effect of each predictor in isolation. The two criteria ensure that the resulting model is the most parsimonious (lowest AICc) and has the greatest predictive capacity (lowest residual deviance). We also checked for influential outliers in sensitivity analyses by comparing model fit results without these outliers. Analysis was conducted in R ver. 4.0.3 (<www.r-project.org>).

Results

We quantified foraging patterns for a total of 119 individuals from our nine focal species. Sample size for each species ranged from 12 to 15 individuals with a mean of 13.2. The study site benthos consisted primarily of epilithic algal matrix/pavement ($67.7\% \pm 6.7\%$ SD) and hard coral ($32.4\% \pm 13.0\%$ SD; Supporting information). We observed a total of 503 herbivorous fish individuals during our belt transect surveys, 223 of which belonged to eight of our nine focal species. Our focal species occurred in relatively low abundances ranging a total count of 4–31 individuals except for *C. striatus* (total = 98 individuals; Supporting information). *A. nigricauda* was not observed in any of our transects.

Model selection using AICc and residual deviance showed that foraging area was best predicted by species identity alone (Table 1). Tortuosity and mean inter-foray distance were both best predicted by species and body length independently (Table 2, 3). Two other candidate models including feeding

substrata were similarly high-ranking for tortuosity and mean inter-foray distance (Table 2, 3). We also note that candidate tortuosity and mean inter-foray distance models with an interaction between species and body size had the lowest residual deviance (Table 2, 3). Not all predictor combinations resulted in models that were possible to fit, because multi-collinearity of the predictor variables resulted in many categories having no representatives in our data. For example, there were no scraping or excavating fishes that also fed on macroalgae.

We inferred through multi-model selection that species was the strongest predictor for all foraging metrics (Table 1–3) with the largest effect size (Table 4). The univariate species model best explained observed variation in foraging area (Fig. 2b) while for tortuosity and mean inter-foray distance, body size (i.e. total length) had an orthogonal but weaker positive effect (Table 4). This combined effect of species and body size had similar support for foraging area as one of the highest-ranked model candidates (Δ AICc = -0.658), but ranked second due to greater residual deviance (Δ residual deviance = 40.482; Table 1). Comparing among species, *Zebbrasoma scopas* ($2.974 \text{ m}^2 \pm 0.337 \text{ SE}$) and *Ctenochaetus striatus* ($2.676 \text{ m}^2 \pm 0.343 \text{ SE}$) tended to have smaller foraging areas, whereas *Scarus rivulatus* ($4.503 \text{ m}^2 \pm 0.343 \text{ SE}$) and *Siganus vulpinus* ($4.748 \text{ m}^2 \pm 0.331 \text{ SE}$) had larger foraging areas (Fig. 2b, Table 4). Partial predictions at the overall mean body size (total length of 20.2 cm) for mean inter-foray distance showed similar trends to foraging area in these four species (Fig. 3). Three of these four species (except for *C. striatus*) exhibited inverse extremes in tortuosity. Partial predictions showed highly tortuous foraging patterns for *Z. scopas*, while foraging patterns for *S. vulpinus* and *Sc. rivulatus* were straighter (Fig. 4). Of the three parrotfish species (*Ch. spilurus*, *Sc. frenatus*, *Sc. rivulatus*) only *Ch. spilurus* showed a grouping pattern in mean inter-foray distance scaling, but this species also seemed to have a clearer size threshold from initial to terminal phases (Fig. 3). We did not see distinct patterns due to ontogenetic phases in foraging metrics for the other species (Fig. 2–4).

Comparisons among foraging social grouping show that isolated individuals generally had smaller foraging areas than those that foraged in conspecific pairs or schools (Fig. 2c) but had no effect on tortuosity (Fig. 2h). Foraging areas were largest for the cyanobacteria feeder (i.e. *S. vulpinus*) and smallest for the detritus feeder (*C. striatus*, Fig. 2d). Conversely, tortuosity was the lowest in the cyanobacteria feeder (Fig. 2i). Feeding substrata was the best univariate predictor of tortuosity, but the combined effects of body size and species exhibited greater predictive capacity (Table 2). Interestingly, we detected no effect of functional group on foraging area (Fig. 2e) or tortuosity (Fig. 2j).

For ease of interpreting effects of size and species in our selected tortuosity and mean inter-foray distance models, we show adjusted parameter estimates for each species from our model results (Table 4). The deriving achieves an equivalent to Eq. 1 and 2, where foraging tortuosity (Eq. 1) and mean inter-foray distance (Eq. 2) is a function of total length as size for species *i*.

Table 4. Derived coefficient estimates of the selected foraging area, tortuosity and mean inter-foray distance GLM models. Foraging area has a structure of $\beta_0 + \text{Species} + \epsilon$ and both tortuosity and mean inter-foray distance $\beta_0 + \text{Species} + \epsilon$. β_0 estimates are reported by species for clarity and shown with their standard error.

Parameter	Foraging area		Tortuosity		Mean inter-foray distance	
	Estimate	SE	Estimate	SE	Estimate	SE
Size	–	–	0.026	0.013	0.020	0.006
<i>A. nigricauda</i>	3.639	0.350	1.111	0.369	0.621	0.167
<i>C. striatus</i>	2.676	0.343	1.303	0.355	0.376	0.160
<i>N. unicornis</i>	3.909	0.343	0.666	0.393	0.502	0.177
<i>Z. scopas</i>	2.974	0.337	1.961	0.351	0.478	0.159
<i>Ch. spilurus</i>	3.925	0.337	1.089	0.349	0.730	0.158
<i>Sc. frenatus</i>	3.604	0.350	1.171	0.375	0.493	0.169
<i>Sc. rivulatus</i>	4.503	0.343	0.825	0.367	0.861	0.166
<i>S. doliatus</i>	3.937	0.243	1.213	0.332	0.785	0.150
<i>S. vulpinus</i>	4.748	0.331	–0.175	0.353	1.225	0.159

$$E(\text{Tortuosity}_i) = \exp(\beta_{0i} + \beta_{1i} \text{Total length}_i) + \epsilon_i \quad (1)$$

$$E(\text{Mean inter – foray distance}_i) = \exp(\beta_{0i} + \beta_{1i} \text{Total length}_i) + \epsilon_i \quad (2)$$

Surprisingly, our model selection revealed that the variation in foraging area was most parsimoniously explained by species identity alone (Table 1). There were marked contrasts in tortuosity among species but differences in mean inter-foray distance were on a much smaller scale (Fig. 3, 4). Body size explained within-species variation in these two metrics, but the similar positive effects (tortuosity: 0.026 ± 0.013 SE; mean inter-foray distance: $0.020 \text{ m} \pm 0.006$ SE) were relatively small given the range of body size spanning 7–55 cm (Table 4, Fig. 3, 4). Our sensitivity analyses showed that these effects of body size and species were robust to outliers in response and predictor variables (Supporting information). In combination these results show that the overall relationship between all foraging metrics is best predicted by species identity.

Inter-foray distance as proxy for foraging extent

In this study we used both inter-foray distance and foraging area as metrics of foraging patterns. Our data shows that although the two variables are correlated, which is reflected in the similarity of species-specific trends (Fig. 2b, 3), there is a great deal of scatter. The differences in slope among median, bottom and top 0.05 centile regressions indicate that this is a triangular rather than linear relationship (Fig. 5). Resulting model selection rankings and effect sizes for variance in inter-foray distance were largely consistent with those for mean inter-foray distance and tortuosity (Supporting information).

Discussion

Body size has often been described as an important predictor of the foraging movement patterns of mobile organisms (Belovsky 1997, Hendriks et al. 2009, Laca et al. 2010). Using

herbivorous coral reef fish as our model taxa, we investigated the potential importance of body size, species identity, feeding substrata, functional grouping and social grouping in shaping foraging patterns. In contrast to previous studies on foraging area allometry (Greenleaf et al. 2007, Laca et al. 2010, Nash et al. 2013), our multi-model inference showed that the best model for foraging area was strongly predicted by species identity alone with no size-scaling relationship. Species identity was similarly a strong predictor of tortuosity with a positive but smaller orthogonal effect from body size as well. We interpret this variation of size-scaling in foraging patterns of our reef fish species as indicators of more complex factors driving the spatial distribution of herbivory, such as area-restricted search, habitat complexity and niche differentiation.

Species-specific differences overshadow body size

The effect of body size in model selection for both mean inter-foray distance and tortuosity was overshadowed by the strength of species as a predictor and was absent in the foraging area model (Table 4). Some of the largest individuals observed in our study (*N. unicornis* and *Sc. rivulatus*) foraged in areas less than 100 m², comparable with considerably smaller-bodied *S. doliatus*, *S. vulpinus* and *A. nigricauda*. Due to the strong relationship between body size and a range of physiological and behavioural traits (Kleiber 1947, Ritchie 1998, de Knegt et al. 2007, Dial et al. 2008), mechanistic links between body size and foraging patterns have been identified in several large-bodied terrestrial herbivores (Hendriks et al. 2009, Laca et al. 2010). One argument for allometric scaling of foraging patterns is that there are physical constraints to the minimum distance an animal can travel while foraging due to appendage size and power (Nash et al. 2013). We see this potential limitation in the overall increase of mean inter-foray distances and tortuosity with increasing body size in our focal species (Fig. 3, 4), but further evidence is needed from incorporating comparative physiology with reef herbivory studies. Instead of detecting larger foraging areas with increasing body size, we find increased tortuosity that may be driven by more intense foraging in resource abundant areas (Carlson et al. 2017) as a result of allometric scaling of nutritional and metabolic needs (Barneche et al. 2014). Tortuosity may also be driven

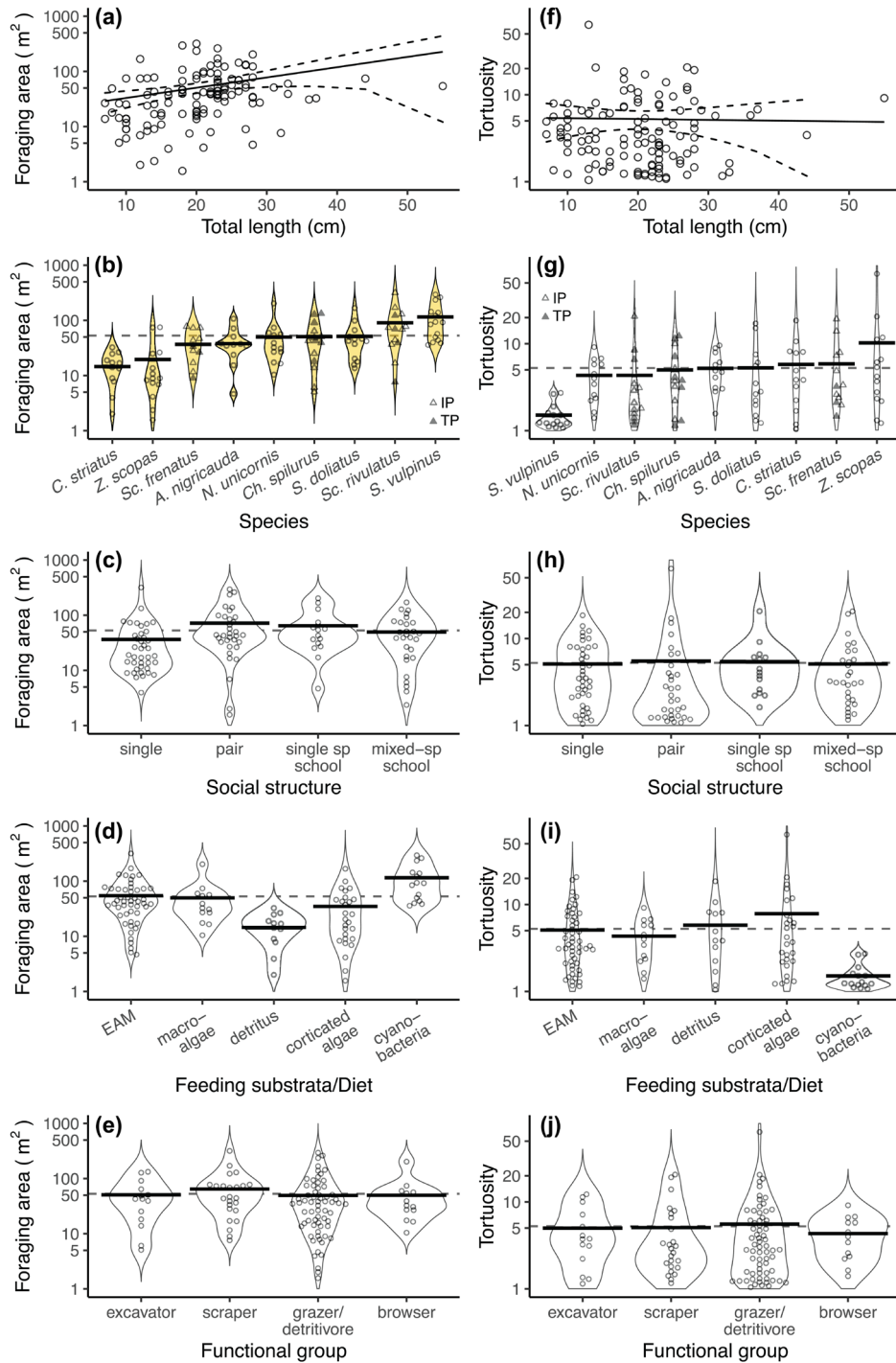


Figure 2. Univariate model estimates for foraging area (m^2) and tortuosity (a ratio of sum of inter-foray distances:straight-line distance between start and end of foraging) in herbivorous reef fish individuals ($n = 119$). Foraging area (left) and tortuosity (right) are shown on a log scale. These predictors are body size in total length (cm) (a, f), species in ascending order of model estimates (b, g), social grouping (c, h), feeding substrata/diet (d, i) and functional group (e, j). The univariate species model (b) is shaded for emphasis as the final selected model for foraging area. Tortuosity was best predicted by species and body length (Table 2). All panels except for (a) and (f) show the distribution of foraging area and tortuosity for each discrete category in violin plots. Black circles indicate individual fish. In panel b, initial phase (IP) individuals are shown with black circles and terminal phase (TP) individuals with white triangles where applicable for parrotfish species. Bold black horizontal lines indicate the predicted mean for each group with the overall mean indicated with the dashed line. The model predictions in panels (a) and (f) are shown as a black line with 95% confidence interval in dotted lines. Social grouping describes the observed foraging social grouping patterns. The epilithic algal matrix feeding substrata is abbreviated as EAM in panel (d) and (i). Functional categories of excavator, scraper, grazer/detritivore and browser are assigned according to definitions from Choat et al. (2004), Green and Bellwood (2009) and Hoey et al. (2013).

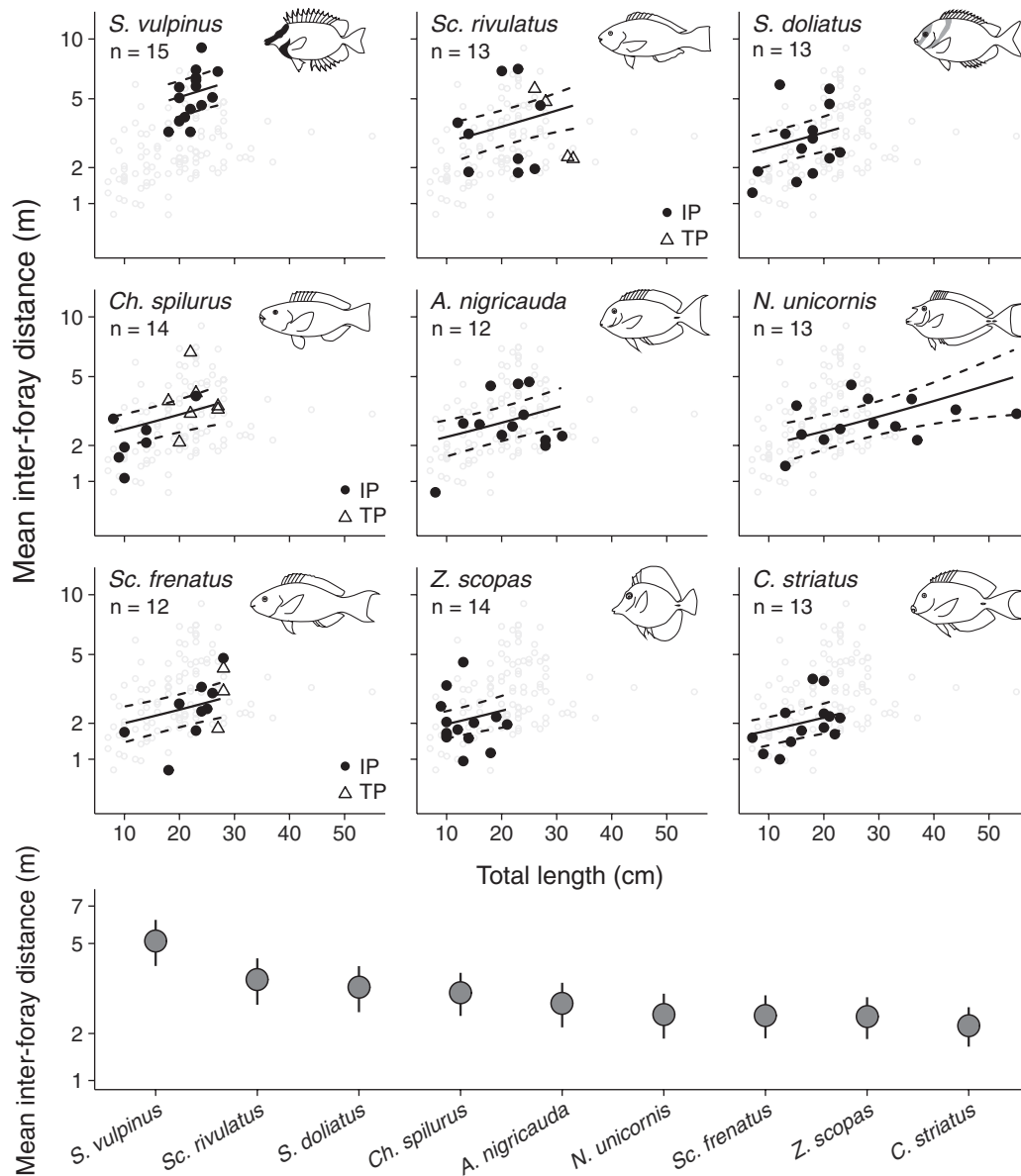


Figure 3. Model predictions of the relationship between mean inter-foray distance, body size in total length (cm) and species identity of nine herbivorous reef fish. The generalized linear model is structured as $E(\text{Mean inter-foray distance}) \sim \exp(\text{Species} + \text{Body size} + \epsilon)$. Mean inter-foray distance is shown in log scales. The panel grid shows predictions in black lines with 95% confidence intervals in dashed lines for each species. Black circles in each panel represent observed individuals for the corresponding species while small grey circles represent all other observed individuals. For parrotfish species, initial phase (IP) individuals are shown with black circles and terminal phase (TP) individuals with white triangles. Partial predictions for each species (shaded circles) at the mean total length of 20.2 cm are shown at the bottom with error bars representing the 95% confidence intervals. Arrangement of species in the panel grid and corresponds to the descending order of partial predictions.

by emerging territorial behaviours with increasing body size, which we discuss below. However, comparing observations with model predictions shows that our data does not reflect positive scaling with body size unilaterally among species. For example, mean inter-foray distances for *A. nigricauda* (Fig. 3) and tortuosity patterns for *Z. scopas* and *Sc. frenatus* (Fig. 4) show clear departures from the model estimates. It is possible that our sample size was not large enough to detect these species-specific scaling relationships (i.e. a model including

interaction between species and body size) to overcome AICc penalties in model selection. A positive relationship between body size and foraging patterns within herbivorous reef fishes is therefore not as clear and universal as previously thought.

Diversity in foraging strategies

We find more evidence for species-specific scaling of foraging patterns rather than body size-driven scaling. By eliminating

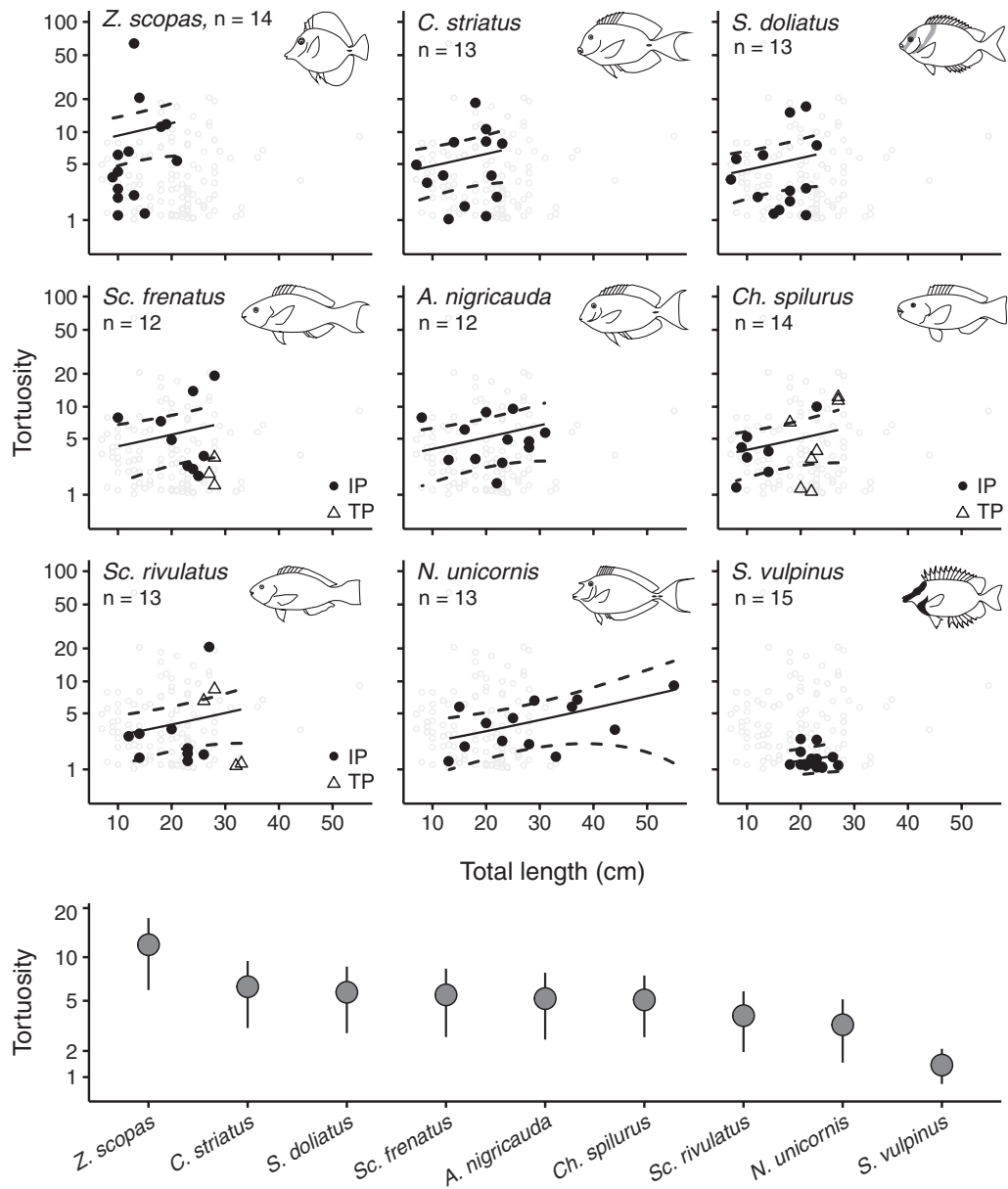


Figure 4. Model predictions of the relationship between foraging tortuosity (a ratio of sum of inter-foray distances:foraging straight-line distance; this ratio is further detailed in Methods), body size in total length (cm) and species identity of nine herbivorous reef fish. The generalized linear model is structured as $E(\text{Tortuosity}) = \exp(\text{Species} + \text{Body size} + \epsilon)$. Tortuosity is shown in log scales. The panel grid shows predictions in black lines with 95% confidence intervals in dashed lines for each species. Black circles in each panel represent observed individuals for the corresponding species while small grey circles represent all other observed individuals. For parrotfish species, initial phase (IP) individuals are shown with black circles and terminal phase (TP) individuals with white triangles. Partial predictions for each species (shaded circles) at the mean total length of 20.2 cm are shown at the bottom with error bars representing the 95% confidence intervals. Arrangement of species in the panel grid and corresponds to the descending order of partial predictions.

body size, the predictive accuracy of the foraging area model increased (as seen by residual deviance), but for tortuosity and mean inter-foray distance, size was important to explain variation within species (Table 1–4). While foraging across a larger area is a common strategy to increase resource availability (Wilmschurst et al. 2000), this may not be the case in a highly complex and heterogeneous habitat like coral reefs. The consensus across our models on the strong effect

of species identity shows that physiological and behavioural are not primary drivers of foraging patterns in reef fishes. While many herbivorous reef fishes share similar feeding substrata (e.g. EAM), recent studies have shown that even closely related species have distinct dietary targets (Clements et al. 2017, Clements and Choat 2018, Nicholson and Clements 2020) and collectively feed in a non-overlapping manner (Davis et al. 2017a, Streit et al. 2019). Studies in terrestrial

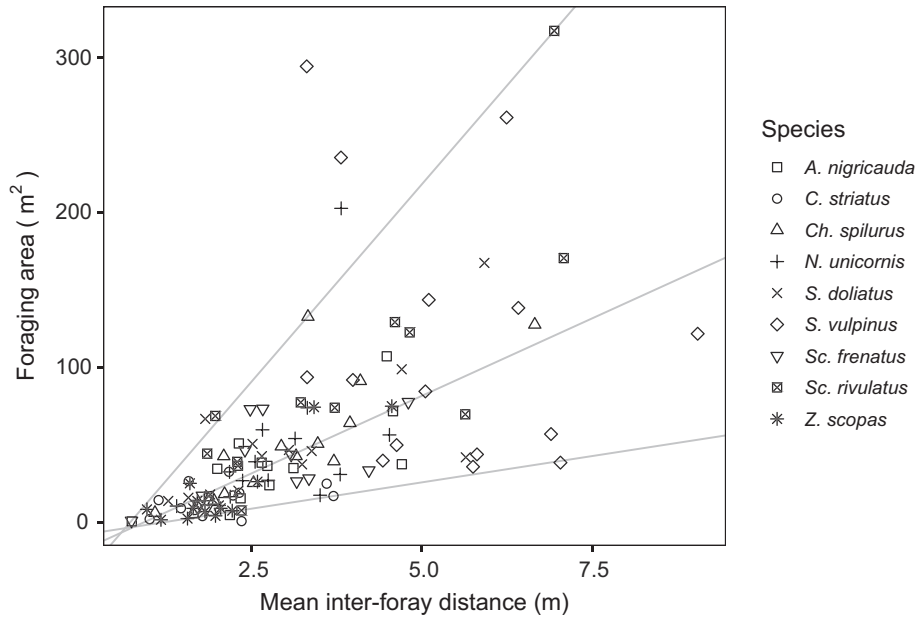


Figure 5. Quantile regression analysis assessing mean inter-foray distance as a proxy of foraging area. Points represent individual fish with shapes according to the nine focal species. Grey lines indicate quantile regression results of the top, median and bottom 0.05 centile.

herbivory suggest that cognitive foraging mechanisms like spatial memory help animals reduce patch search costs and possibly competition (Bailey and Provenza 2008). Given the scope of our study, we cannot ascertain the decision processes underpinning the foraging movement of our focal species and whether pre-selection of resource patches by spatial memory or other sensory processes shaped their foraging patterns.

One extreme example of spatial partitioning of resource patches can be seen in territorial behaviours. For example, our foraging area model estimated far smaller areas for *Z. scopas* and *C. striatus* compared to the overall mean (Fig. 2b), both of which have previously been observed to display territorial behaviours (Robertson et al. 1979, Robertson and Gaines 1986). Thus, studies further assessing differences in behavioural traits both among and within herbivorous reef fish species are needed to understand the potential role of territoriality and other behaviours in shaping foraging patterns.

Our tortuosity and foraging area models also highlight the stark difference of movement observed in *S. vulpinus* compared to other species. *S. vulpinus* foraging patterns covered the largest areas (Fig. 2b, Table 3) with consistently low tortuosity across all body sizes, and mean inter-foray distances show a steep positive size-scaling relationship (Fig. 3). *S. vulpinus* is the sole representative of macroscopic cyanobacteria feeders in our focal species (compared to the epilithic microscopic cyanobacteria that is targeted by many parrotfishes; Nicholson and Clements 2020), and likely drove the predictive power in similarly high-ranking tortuosity models that included feeding substrata (Table 2). Fox and Bellwood (2013) and Semmler et al. (2021) also investigated foraging movement patterns of this species at Lizard Island and found similar characteristics of large inter-foray distances. Observed low tortuosity here could indicate higher patch selectivity

with *S. vulpinus* and/or more sparsely distributed cyanobacteria mats. While foraging intensity by this siganid may not be concentrated, foraging impact is delivered across areas almost two-fold greater than that of other species. This has interesting implications to the importance of fish foraging impacts on reef recovery following disturbances, as dominance of cyanobacterial mats can significantly impede coral recruitment (Ford et al. 2018). While this regulatory function via feeding is well understood for macroalgae-feeding herbivores (Ledlie et al. 2007, Hoey and Bellwood 2009), further studies on these dynamics should not exclude cyanobacteria feeders like *S. vulpinus* given the spatial extent of their foraging.

Generality of foraging metrics

We also compared mean inter-foray distance against foraging area as a metric of spatial foraging patterns. Measurement of inter-foray distance is faster and logistically easier to quantify during in situ observations of fish behaviour, especially in regard to fine-scale movements. In contrast with our findings on foraging area, Nash et al. (2013) used inter-foray distance as a proxy for spatial scale and revealed a positive allometric scaling in foraging range. A possible explanation for this disagreement with our results in foraging area emerges from our quantile regression (Fig. 5). Despite a positive correlation between foraging area and mean inter-foray distances, their relationship is triangular with greater variance in inter-foray distance as foraging area increases (i.e. heteroscedastic; Fig. 5). Alternatively, slight differences in the definition of what constituted a distinct foray, and hence the inter-foray distance, may have contributed to the differences between studies. While both studies distinguished between sequential forays based on the focal fish lifting its head ($> 45^\circ$) between consecutive bites, Nash et al. (2013) also

required the focal fish to actively swim between bites. A bout of active swimming in a large individual is likely to cover a larger distance than in a small individual. While we do see this in the scaling of tortuosity (Table 3, Fig. 4) and mean inter-foray distances (Fig. 3) with body size, this relationship breaks down for foraging area (Table 1). Hence, inter-foray distances remains an important metric of foraging patterns, but it does not directly explain spatial scales of foraging in isolation.

While inter-foray distance maxima directly relate to the size of the foraging area, tortuosity describes search and foraging density rather than the extent of space use. Studies in foraging movement do show that many taxa employ specific area-restricted search patterns, where animals employ a more tortuous movement mode when searching within a resource patch (de Knecht et al. 2007, Fryxell et al. 2008, Paiva et al. 2010, Bailey et al. 2019). Evidence from a case study on parrotfish confirms this pattern of intense but spatially restricted foraging (Davis et al. 2017b). Although we used foraging area as a primary metric for our aim, inter-foray distance remains an important metric of foraging patterns. Future studies on herbivorous reef fish would benefit from employing multiple metrics to disentangle foraging intensity and search efficiency from observed movements.

We also recognise that both this current study and that by Nash et al. (2013) on herbivorous reef fishes investigates short-term foraging patterns, while terrestrial herbivore studies conducted with animal-borne tags often span seasons (Pita et al. 2011, Owen-Smith and Martin 2015). Because our methodology restricts individual observations to 5-min intervals, we may not have captured foraging at larger spatiotemporal scales to show patch search from the landscape level to the smallest food item patch (Senft et al. 1987, Fryxell et al. 2008, Owen-Smith et al. 2010). Although there is evidence of reef fish interacting with patch selection at the reefscape level, their roving foraging is more site-attached and constrained by diel movements from central refuges in comparison to migratory terrestrial herbivores (Nash et al. 2015, Davis et al. 2017b). Furthermore, reef herbivory patterns are often confined to small areas and sometimes microhabitats, even for more large-bodied parrotfishes (Fox and Bellwood 2013, Brandl et al. 2015, Carlson et al. 2017, Davis et al. 2017b, Canterle et al. 2020, Puk et al. 2020). For these reasons, our observation methods are proportional with previously observed spatiotemporal scales of reef fish herbivory, but, as most things in ecology, observed short-term foraging patterns here are dependent on both spatial and temporal scale. Hence, we caution against generalizing the species identity and body size effects seen here on a larger spatial scale such as diel home range movements.

Link with functional impact

Herbivory plays a critical role in regulating algal turf and macroalgae cover, which in turn affects the replenishment and recovery of coral assemblages (Bellwood et al. 2006, Hughes et al. 2007, Ledlie et al. 2007, Burkepille and Hay 2010, Suchley and Alvarez-Filip 2017). Functional traits have provided a way to identify generalities across species on how

they bite, like removal of entire algae stands by surgeonfish or the substrate clearing by parrotfish for coral juveniles (Green and Bellwood 2009, Hoey and Bellwood 2009, Cheal et al. 2010, Streit et al. 2015). While functional groupings have provided a useful metric and tool in summarising these differences, our findings highlight that species within the same functional group do still vary considerably from each other.

Although body size has been shown to influence grazing and browsing rates by herbivorous fishes and is important to consider for management of fish assemblage size structure (Wilson et al. 2010, Lange et al. 2020, Robinson et al. 2020), we caution against the generalisation of size to the spatial scaling of functional impacts. From an individual-based perspective, we reveal that the spatial extent and density of foraging are largely driven by species-specific behaviours with size scaling in feeding intensity across space. Area-based studies show that patchy herbivory is driven by several bottom-up forces in algal density (Hoey and Bellwood 2011, Carlson et al. 2017, Gil et al. 2017), nutritional quality of resource patches (Duffy and Paul 1992, Catano et al. 2015, Shantz et al. 2017), primary production rates (Russ 2003), sediment load (Tebbett et al. 2020), topographic complexity (Vergés et al. 2011) and niche partitioning (Streit et al. 2019). The spatial delivery of herbivory impacts reflects diversity as well as the size structure of a fish assemblage. Herbivory intensity as driven by species diversity, size structure, bite impact and spatial scaling can potentially address the mechanisms giving rise to heterogeneous patterns of reef recovery on local and regional scales (Houk et al. 2010, Eynaud et al. 2016, Nash et al. 2016b).

Conclusion

Our work demonstrates different scaling relationships of foraging area and tortuosity with fish species and body size. In the aggregate there was evidence of scaling of foraging area with body size, however this was largely driven by differences among species. We did detect body size scaling in tortuosity, but its effect was also small compared to that of species. This absence of allometric relationships suggests that the diversification of foraging strategies, especially in spatial partitioning, can result in a departure from typical patterns of roving patch search. We show that understanding the behaviour and taxonomic composition of the guild in the study site is therefore integral for understanding the spatial distribution of the herbivory function, especially when different species perform functionally different types of herbivory. Reef ecosystems are rich in complexity and patterns in species composition, resource distribution and disturbance can vary widely across space. Our study takes steps towards understanding and potentially predicting how patterns of herbivory can be distributed across highly heterogeneous and complex spaces. With coral reefs across the world under threat, the importance of understanding key ecosystem functions such as herbivory becomes ever increasing.

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Author contributions

Cher F. Y. Chow: Formal analysis (lead); Methodology (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Emmy Wassénius:** Conceptualization (equal); Formal analysis (lead); Investigation (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Maria Dornelas:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Supervision (lead); Writing – review and editing (equal). **Andrew S. Hoey:** Conceptualization (equal); Funding acquisition (equal); Investigation (lead); Methodology (supporting); Resources (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from Github <<https://github.com/bio-TIMEHub/HerbivoreForageScaling/>> and Zenodo <<https://doi.org/10.5281/zenodo.5517171>> (Chow et al. 2021).

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