**Habitat and fishing control grazing potential on coral reefs**

**Authors**

James PW Robinson1, Jamie M McDevitt-Irwin2, Jan-Claas Dajka1, Jeneen Hadj-Hammou1, Samantha Howlett1, Alexia Graba-Landry3, Andrew S Hoey3, Kirsty L. Nash4,5, Shaun K Wilson6,7, Nicholas AJ Graham1.

**Affiliations**

1. Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK
2. Stanford University, Hopkins Marine Station, Pacific Grove, CA 93950, USA
3. ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia
4. Centre for Marine Socioecology, University of Tasmania, Hobart, TAS 7001, Australia
5. Institute for Marine & Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia
6. Department of Biodiversity, Conservation and Attractions: Marine Science Program, Kensington, WA 6151, Australia
7. Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia

**Target Journals**

* Global Ecology and Biogeography
* Functional Ecology
* Ecological Applications
* Coral Reefs

**Keywords**

functional ecology, herbivory, fishing, bottom-up, top-down, grazing, benthic

**Abstract**

**Introduction**

Herbivory is crucial to ecosystem function and community structure across terrestrial and aquatic ecosystems, playing a key role in cycling nutrients (Metcalfe et al. 2014), regulating species diversity and productivity (Royo et al. 2010, Prieditis et al. 2017), and controlling habitat regime shifts (Zimov et al. 1995, Hughes et al. 2007, Keesing and Young 2014, Verges et al. 2014). Herbivory processes are generally measured at local scales relevant to individual behaviours and population sizes, which restricts our understanding of how ecosystem functions operate across larger spatial scales. Furthermore, anthropogenic pressures typically impact ecosystem processes, including herbivory, across much larger areas (ref, Wather et al. 2010?). Therefore, developing our understanding of both natural and anthropogenic drivers on herbivory at large scales requires the integration of fine-scale herbivory observations with macroecological datasets. Such analyses are particularly relevant for coral reef ecosystems, which are facing multiple damaging human pressures and where herbivory is a key ecosystem function (Hughes et al. 2007, Cheal et al. 2010, Hughes et al. 2017).

On tropical coral reefs, the removal of algae by herbivorous fishes is a critical process which clears space for coral settlement and growth (Bellwood et al. 2004). Herbivorous fishes can be categorized into browsers, which remove established macroalgae, and a diverse guild of grazers (Green & Bellwood 2009). Within the grazers, observations of feeding morphology and behaviour have identified two distinct grazing functions: cropping and scraping (Bellwood and Choat 1990, Polunin et al. 1995, Green and Bellwood 2009). Cropping species in the *Acanthuridae* and *Siganidae* families target filamentous turf algae and detritus, which maintains algae in cropped states, promoting coral settlement and preventing transitions to fleshy macroalgae (Arnold et al. 2010). Scraping species in the tribe *Scarinae* graze dead coral substrate to consume microscopic epiphytes and epilithic and endolithic phototrophs (Choat and Clements 2018). By removing detritus and epilithic algal matrix (EAM), scrapers promote coral recruitment by clearing settlement space (Bonaldo & Hoey 2014). Combined, cropping and scraping are considered essential functions which help sustain coral-dominated states (Bellwood et al. 2004, Hughes et al. 2007) and potentially reverse algal regime shifts (Graham et al. 2013).

Mature algae can proliferate in the absence of sufficient grazing pressure (Mumby et al. 2006, Burkepile and Hay 2008), and correlative analyses of fished reef ecosystems have provided evidence of grazing biomass thresholds below which reefs become algae dominated (Graham et al. 2015, Jouffray et al. 2015, Robinson et al. 2018). Herbivorous fish populations are overexploited across much of the tropics (Edwards et al. 2014), which has compromised grazing functions on reefs which fail to maintain herbivore biomass thresholds (Bellwood et al. 2012, Graham et al. 2015, Robinson et al. 2018). However, fishing effects can be confounded by bottom-up productivity influences on herbivore assemblages (Russ et al. 2003, 2015), while species-specific habitat associations can also structure herbivore assemblages across a range of spatial scales (Hoey & Belwood 2008, Doropoulos et al. 2013) and benthic compositions (Hoey & Bellwood 2011, Heenan et al. 2016). Such bottom-up influences on fish populations may be particularly strong when fish rely on habitat for both structure and food, such as algal cropping fishes which are generally small and particularly dependent on the reef matrix for shelter (Wilson et al. 2008). Thus, herbivore assemblage structure is mediated by both habitat composition and fishing intensity but links between these drivers and grazing functions are not well resolved, particularly at macroecological scales.   
 Patterns in herbivore biomass are widely used to imply changes in herbivore functioning on coral reefs (e.g., Nash et al. 2016, Robinson et al. 2018). However, biomass data overlooks size- and species-specific differences in feeding rates and functional roles and so measures of grazing impacts have been developed by integrating information on XTZ of croppers and feeding behaviours of scrapers (Bellwood and Choat 1990, Bellwood et al. 2003) to estimate grazing rates. Furthermore, though allometric grazing ~ body size relationships (Lokrantz et al. 2008, Nash et al. 2013) indicate that the functional role provided by larger species is disproportionately greater (Bonaldo and Bellwood 2008), grazing potential may also depend on community size structure (Bellwood et al. 2012). Abundance decreases logarithmically with increasing body size, meaning that an assemblage of many small-bodied fish may be functionally equivalent to an assemblage of several large-bodied individuals (Munday and Jones 1998, Lokrantz et al. 2008). Indeed, size-selective fishing which removes larger individuals (Robinson et al. 2017) and species (Taylor et al. 2014) has produced fish communities dominated by small-bodied fishes, but size distribution and grazing rate are unexplored.

Here, we assess the drivers of herbivore functioning on coral reefs across four regions in the Indo-Pacific (Fig. S1). Our macroecological-scale analysis spans a benthic gradient from coral to macroalgal dominance and a fishing gradient from open-access fisheries to no-take fishing zones and near-pristine wilderness areas. By integrating feeding observations with underwater visual census (UVC) data on grazing fish abundance, we measured potential grazing rates at the scale of reef sites, which is highly relevant for understanding how benthic and fishing influences may alter ecosystem functioning (Nash et al. 2016). We examine 1) how fishing pressure and benthic composition influences the functioning of two major feeding groups (croppers and scrapers), and 2) how grazing rates are controlled by both the biomass and size structure of grazing assemblages.

**Methods**

*Survey methods*

We surveyed 72 reefs in Seychelles (n = 21), Maldives (11), the Chagos archipelago (25), and the Great Barrier Reef (GBR, 15) (Supplementary Methods). Grazing fish assemblages were surveyed using point counts of 7 m radius (Seychelles) or belt transects of 50 m length (Maldives, Chagos, GBR) conducted on hard-bottom reef slope habitat at 3-8 m depth. Surveys were designed to minimise diver avoidance or attracting fish, and conducted by a single observer (NAJG). In point counts, large mobile species were censused before smaller territorial species. In belt transects, large mobile fish (> xxcm total length, TL) were surveyed in a 5-m wide belt while simultaneously deploying the transect tape, and small site-attached species (< xxcm TL) within a 2-m wide belt were recorded in the opposite direction. For both survey types, all diurnal, non-cryptic (>8 cm TL) reef-associated fish were counted and their TL estimated to the nearest centimetre. Length measurements were calibrated by estimating the length of sections of PVC pipe and comparing it to their known length prior to data collection each day. Fish lengths were then converted to body mass (grams) using published length-weight relationships (Froese and Pauly 2018), and standardised by survey area to give species-level biomass estimates that were comparable across datasets (kg ha-1). The UVC dataset included 101 herbivore species, with 11 species common to all four regions (Table S1). Although we combined two UVC methods to estimate fish biomass, point counts and belt transects give comparable biomass estimates (Samoilys and Carlos 2000).

Following fish surveys, benthic habitat composition was surveyed with eight 10-m line intercept transects (Seychelles by SKW), or eight 50-m point intercept (benthos recorded every 50 cm) transects (Maldives and Chagos by data contributors, GBR by KLN). We recorded the cover of hard corals, macroalgae and turf algae, as well as non-living substrate (rock, bare substrate, rubble and sand). The structural complexity of the reef was visually estimated on a six-point scale, ranging from 0 (no vertical relief) to 5 (complex habitat with caves and overhangs) (Polunin and Roberts 1993), which correlates strongly with a range of other methods for capturing the structural complexity of coral reefs (Wilson et al. 2007). Survey methods and site descriptions for each region are described in the Supplementary Material.

*Herbivore feeding observations*

Feeding observations of Indo-Pacific grazing fishes provided species-level estimates on bite rates of croppers and scrapers. Surveys were conducted in the Red Sea (AH), Indonesia (AH), and GBR (AH and AGL). We analysed feeding observations for species observed in the UVC dataset (n = 39). Briefly, an individual fish of a target species was haphazardly selected and its body length (total length in cm) estimated. After a ~30 second acclimation period, each individual was followed for a minimum of 3 minutes during which the number of bites and the feeding substratum was recorded (minimum n=xx individuals per species, per site, per location).

We estimated the average feeding rate (bites per minute) for each observed fish. For scrapers, we also estimated the bite scar size of each individual.

*Ecological variable processing*

Grazing species were categorised as croppers or scrapers according to their morphology and feeding behaviour (Green and Bellwood 2009). While both groups of grazing fishes feed primarily on the epilithial algal matrix (EAM) covered substrata, they differ in the amount of material/substratum that is removed during the feeding action. Croppers remove the upper portions of the algae and associated detritus and microbes leaving the basal portions of the algae intact on the substratum, while scraping parrotfishes remove shallow pieces of the substratum together with the EAM, leaving distinct bite scars (Choat et al. 2002, Wilson et al. 2003, Hoey and Bellwood 2008) (Table S1).

We used feeding observations to convert UVC biomass estimates into the total grazing potential of croppers and scrapers. We defined grazing functions separately for each functional group whereby cropping function was measured as feeding intensity (bite rate data) and scraping function was measured as area grazed (bite rate and bite area data). We used a Bayesian hierarchical modelling framework that estimates species- and genera-level functional rates. This method allowed us to estimate grazing rates for UVC species which were not observed in feeding surveys (n = 63). Cropper function was quantified in terms of potential feeding intensity, the total number of bites per minute, and derived from a predictive model which accounted for species- and genera-specific bite rates (Eqs. 1,2). In our cropper feeding data, bite rates were weakly correlated with TL (Pearson’s r = -0.18), and so we assumed bite rates were unrelated to body size.

 Eq. 1

[](https://www.codecogs.com/eqnedit.php?latex=log(%5Cmu)%20%3D%20X%20%2B%20species_i%20%2B%20genus_j%20%2B%20dataset_k%250) Eq. 2

From this model, we generated species- and genera- level posterior predictions of grazing rates and assigned to each individual cropping fish observed in UVCs. We then used allometric relationships to convert bite rates into grams of carbon removed through EAM consumption (Marshell and Mumby 2015). Following Van Rooij et al. (1998), daily carbon intake was linked to body mass as

 Eq. 3

which we then divided by the predicted number of bites per day to produce an estimate of grams carbon consumed per minute by each individual cropping fish. We summed estimates within UVC replicates (i.e. point count or transect) and averaged across replicates to give site-level estimates of potential cropping function.

For scrapers, we defined the potential scraping function in terms of area of substrata cleared per minute. Feeding observations provided estimates of bite rates, which we modelled as a function of body size (TL, cm) according to species- and genera-specific grazing rates, for gamma distributed errors (Eqs. 4, 5).

 Eq. 4

[](https://www.codecogs.com/eqnedit.php?latex=log(%5Cmu)%20%3D%20A%20%2B%20B.TL%20%2B%20species_i%20%2B%20genus_j%20%2B%20dataset_k%250) Eq. 5

To account for potential differences in scraping action among species and across body sizes, we used a second underwater feeding observation dataset of scraper bite areas. Bite scar area (cm2) was modelled as a function of body size (TL, cm), for Gamma distributed errors (Eqs. 6,7).

 Eq. 6

[https://lh5.googleusercontent.com/E1F_wGQdoWdWog6V9FD9yISCZEdDh1sTdhEaf73rcXr_Krw7rOCi_aotYv5KAI4c1LknEq66J-o1EazXrdznDbyG_yH1MByFzzM1sf66-Nzgj977EVph56cPAeuoVgeILWMV8ooF](https://www.codecogs.com/eqnedit.php?latex=log(%5Cmu)%20%3D%20A%20%2B%20B.TL%250) Eq. 7

By including size (TL) as an explanatory covariate, our model accounted for scar area increasing with body size (Fig. S2A) and bite rates decreasing with body size (Fig. S2B). For each observed scraper in the UVC dataset, we generated posterior predictions for bite rate and scar size according to its species identity and body size. Species which were not observed in feeding observations were assigned genera-level bite rates. These predictions were converted to area scraped per minute (bite rate \* scar size = area scraped) (m2 minute-1 hectare-1), summed within surveys and averaged to give site-level estimates of potential scraping function.

All models fitted to feeding data were fitted with weakly informative priors (Table S2) using Markov Chain Monte Carlo sampling implemented in Stan. We sampled three chains of 3,000 iterations (warmup = 1,500) each for model checks, and one long chain of 5,000 iterations (warmup =1,500) for generating grazing predictions. Model convergence was assessed by inspecting posterior predictions, Gelman-Rubin diagnostic (), and the number of effective samples (Table S2).

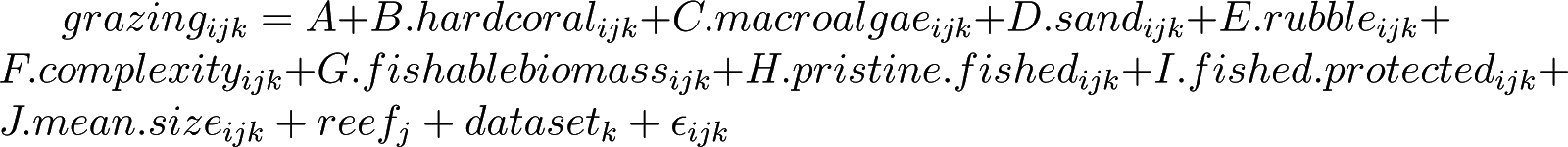
*Statistical modelling*

We modelled variation in herbivore functioning according to 1) gradients in benthic habitat composition and exploitation pressure and 2) grazer biomass and assemblage size structure. Explanatory covariates were derived from fish and benthic surveys. First, to account for fishing effects ranging from the remote and protected Chagos archipelago to heavily-exploited reefs in Seychelles, we estimated total fish community biomass as a proxy for exploitation pressure. This proxy, hereafter fishable biomass, is highly sensitive to exploitation pressure and, in the Indian Ocean, is predicted by human population size, access to markets, and fisheries management (McClanahan et al. 2016). Reefs were also assigned a categorical fishing pressure covariate to distinguish between protected (i.e. no-take areas), exploited, and remote reefs (Supplementary Methods).

Second, benthic surveys provided site-level estimates of benthic composition. We estimated the site-level cover for four major habitat-forming groups (live hard coral, macroalgae, available substrate, and rubble) and structural complexity by averaging across replicates at each site. Available substrate was the total cover of rock, bare substrate, and turf algae, and represents the area of substrate available for EAM growth. To understand the range of benthic habitat types across the dataset, we categorised reefs according to their benthic regime, using a correlation-based PCA and K-means clustering (Jouffray et al. 2015). The optimal number of clusters was found using an elbow method with k=2-15 range, and then applied to the K-means clustering. For reefs in Seychelles which were surveyed in multiple years, we estimated regimes at each site by averaging cover values over time.

Third, we estimated the biomass of each functional group (kg ha-1) and a large fish indicator (LFI) as a measure of size structure. We defined large fish separately for each group as the length at the 75% quantile of the size distribution in the full dataset, where the LFI was the relative abundance of fish greater than 15 cm for croppers and 30 cm for scrapers. Biomass and the LFI were estimated for each replicate and averaged at each reef.

Prior to statistical modelling, we scaled and centered all continuous covariates to a mean of zero and standard deviation of one, and converted the categorical fishing status covariate into two dummy variables (fished - protected, fished - pristine) (Schielzeth 2010). We used multimodel inference to assess parameter effect sizes. For each function, we fitted a global linear mixed effects model with five benthic fixed effects (hard coral, macroalgae, sand, rubble and structural complexity) and four exploitation fixed effects (fishable biomass, pristine reef, protected reef and mean size), for gamma distributed errors (). Potential covariance among reefs in the same dataset and year was modelled using nested random intercept terms where, for each observation *i* at each reef *j* in dataset *k*:

[](https://www.codecogs.com/eqnedit.php?latex=grazing_%7Bijk%7D%20%3D%20A%20%2B%20B.hardcoral_%7Bijk%7D%20%2B%20C.macroalgae_%7Bijk%7D%20%2B%20D.sand_%7Bijk%7D%20%2B%20E.rubble_%7Bijk%7D%20%2B%20F.complexity_%7Bijk%7D%20%2B%20G.fishablebiomass_%7Bijk%7D%20%2B%20H.pristine.fished_%7Bijk%7D%20%2B%20I.fished.protected_%7Bijk%7D%20%2B%20J.mean.size_%7Bijk%7D%20%2B%20reef_j%20%2B%20dataset_k%20%2B%20%5Cepsilon_%7Bijk%7D%250) Eq. 8

From the global model, we fitted all possible subset models (Bartoń 2013) and assessed their support using Akaike’s Information Criterion (AIC), where the top-ranked model had the lowest AIC score (Burnham and Anderson 2003). Initial modelling indicated support for multiple competing models (i.e. ∆AIC < 2), so we visualised relative covariate effect sizes by extracting standardised t-values for all models within 7 AIC units of the top-ranked model and, for each model, rescaling t-values so that 1 is the strongest predictor in a given model, and weighing that value by the models’ AIC weight (Cade 2015). These scaled t-values represent the relative effect size of each covariate between 0 (unimportant) and 1 (important). Next we generated model predictions to visualise the effect of each covariate with scaled t-value > 0.4, excluding remaining fixed effects and random effects and correcting predictions by each models’ AIC weight, with prediction uncertainty represented by the AIC-weighted sample variance (Robinson et al. 2017). Our multi-model approach accounts for uncertainty in the ‘best’ fitted model when AIC scores indicate several models are equally valid (Burnham and Anderson 2003). We avoid potential biases in model-averaged coefficient sizes by presenting effect sizes as standardised t-values, which are more informative measures of covariate importance than sums of AIC weights (Cade 2015).

Next, we harness the range of grazing rates controlled by benthic and fishing influences to examine links between grazing potential, grazer biomass, and assemblage size composition. As grazing estimates were derived from feeding data combined with UVC biomass data, we expect grazer biomass to correlate strongly with grazing rates, and therefore also with the modelled benthic and fishing drivers. Assemblages of equal biomass may, however, differ in their size composition, leading to variation in grazing rates. For each function, we fitted a generalized linear mixed effects model for each observation *i* at each reef *j* in dataset *k*, for Gamma distributed errors:

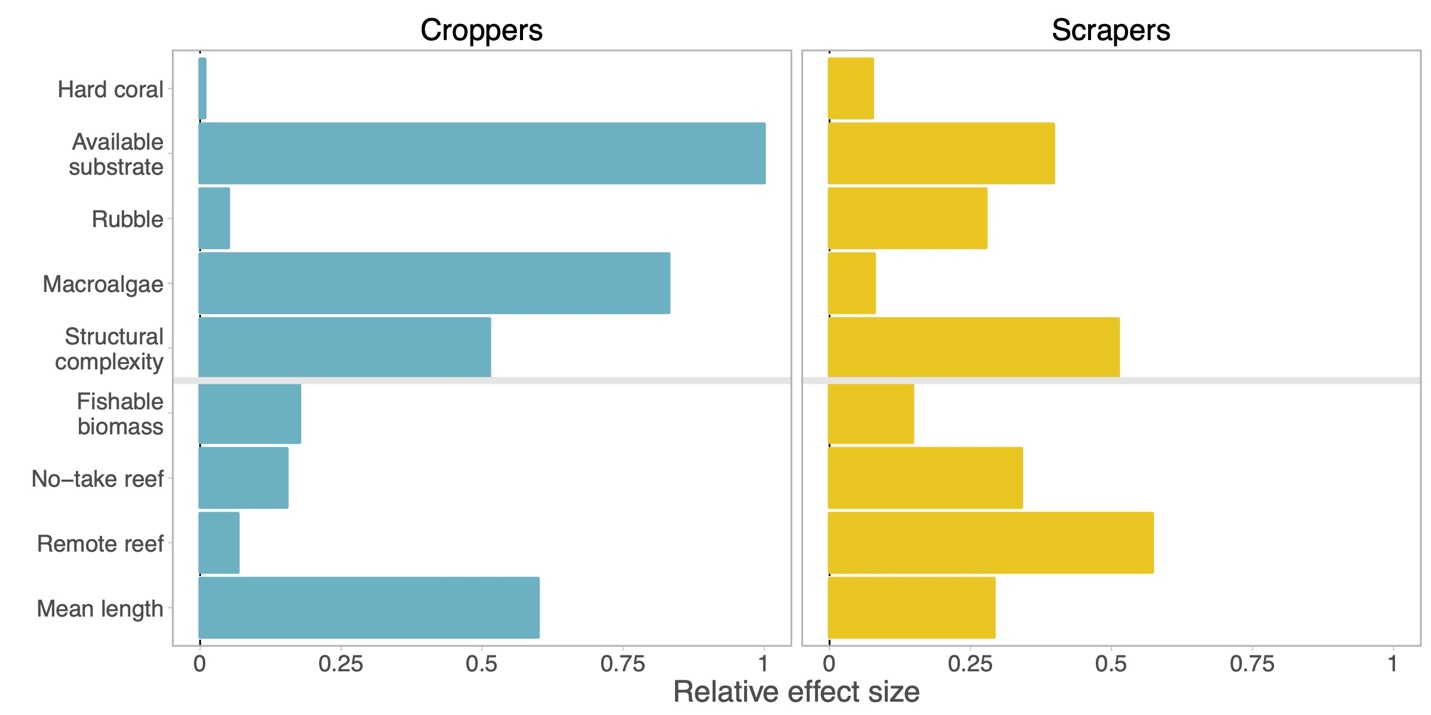
[https://lh3.googleusercontent.com/-0Ts4IBzul54U0s48in2cWQSRGq1OXYFK4t7DWZ9UMxF7HcWg4-Qy4_VyObJdlDfPqzds_CE5js6E-Mgw29hZ7AUMKvOKmFfX3lWtd63gO50URWA3BUvSHk7Fwj9gDRK-YssfCKl](https://www.codecogs.com/eqnedit.php?latex=grazing_%7Bijk%7D%20%3D%20A%20%2B%20B.biomass_%7Bijk%7D%20*%20C.LFI%7Bijk%7D%20%2B%20reef_j%20%2B%20dataset_k%20%2B%20%5Cepsilon_%7Bijk%7D%250) Eq. 9

We weighed model support for each covariate and the interaction between biomass and the LFI with AIC (Burnham and Anderson 2003), selecting the top-ranked model for interpretation and visualization.

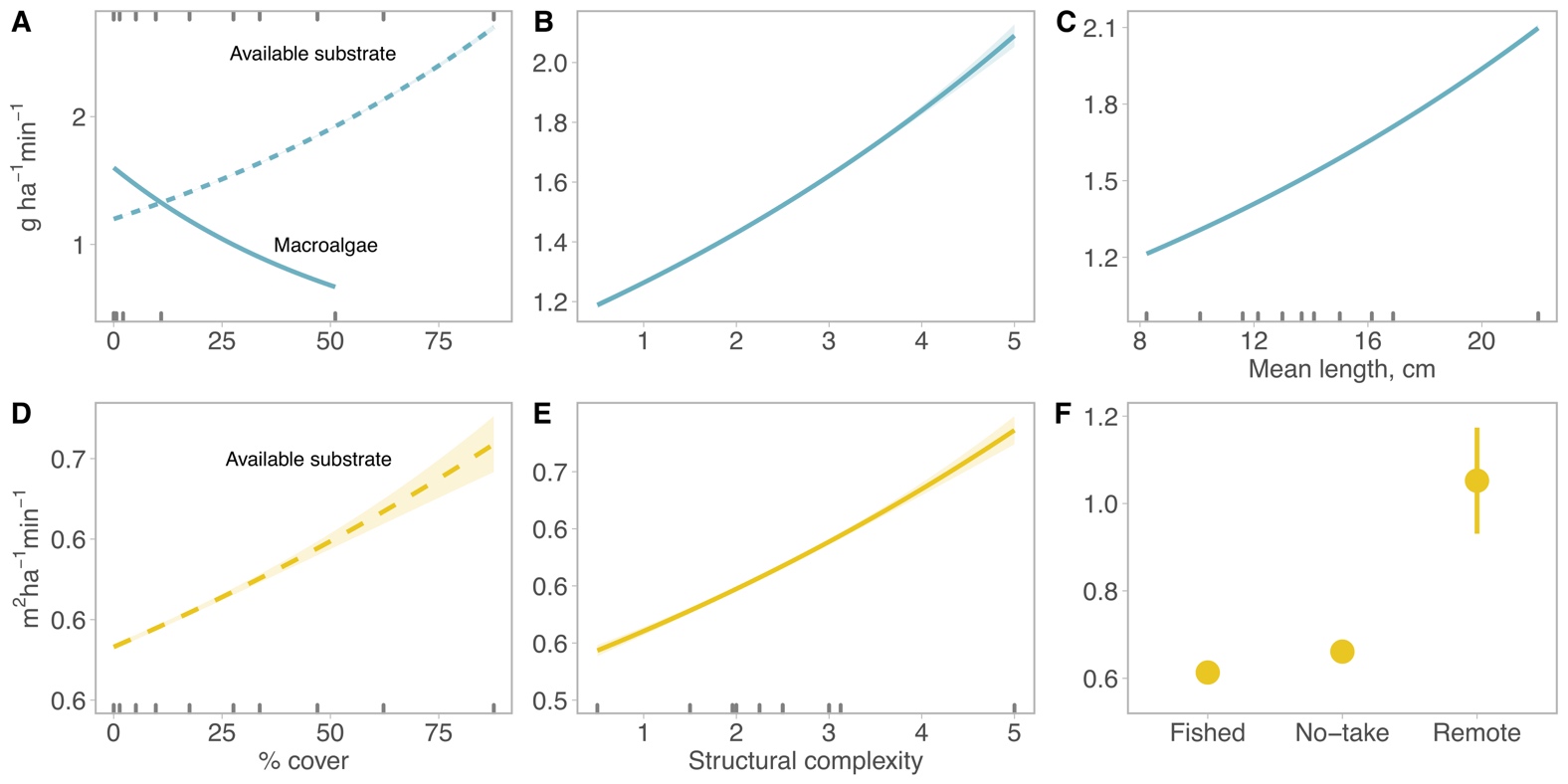
All data were analysed in R (R Core Team 2018), using packages *lme4* (linear mixed effect models, Bates et al. 2015), *MuMIn* (multimodel inference, Bartoń 2013), *rethinking* (Bayesian models, McElreath 2017), and *vegan* (diversity estimates, Oksanen et al. 2017).

**Results**

Visual census data were integrated with *in situ* feeding observations for 131 reefs in four Indo-Pacific archipelagos. For cropping fishes, 9 species were assigned individual bite rates (32.9% of UVC biomass), and remaining species were assigned genera-specific (54.4%) or an average cropper bite rate (12.6%). Combined with herbivore biomass, bite rates corresponded with modelled assemblage-level cropping rates ranging from 0.04 to 5.52 g ha-1 min-1, with grazing highest on GBR and Chagos reefs (Fig. S3A). Irrespective of region, cropping was maximised in complex habitats with high substrate availability and low macroalgal densities, while hard coral or rubble cover were weak influences (Fig. 1, 2A). Cropping rates were unaffected by fishing intensity, and were similar across remote, protected and fished reefs (Fig. 1). Cropping rates did increase with average cropper size, indicating that reefs with cropping assemblages dominated by larger fishes had a higher grazing potential (Fig. 2B).



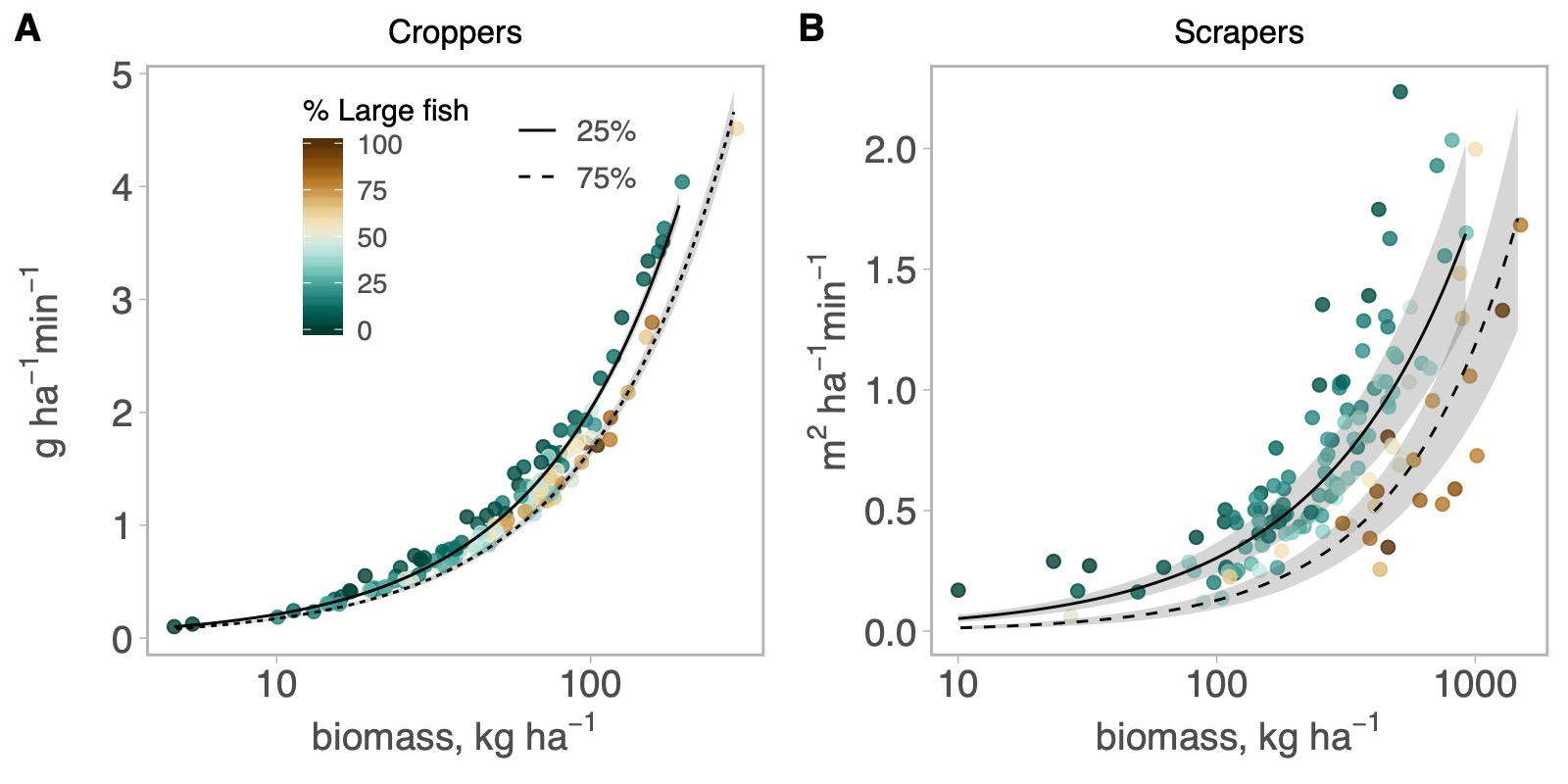
**Figure 1. Relative effect of benthic composition and fishing pressure on potential grazing rates for croppers (left) and scrapers (right).** Bars are relative effect size ratios of each covariate for top-ranking model sets (models ≤ 7 AIC units of top-ranked model), scaled to indicate very weak (0) or very important (1).



**Figure 2. Predicted effects of benthic and fishing drivers on potential cropping (A-C) and scraping (D-F) rates.** Benthic effects are macroalgae (A) for croppers, and available substrate (A, D) and structural complexity (B, E) for both grazing groups. Fishing effects are mean length for croppers (C) and management status for scrapers (F). Lines and points are grazing rates as predicted by top model sets (≤ 7 AIC units from top-ranking model) holding other covariates to their means, with each model prediction weighted by its AIC weight and error represented as sample variance. All visualized covariates had relative effect size ratios > 0.4 (Fig. 1). Decile rugs indicate the spread of observed data (in A, top rug is available substrate and bottom rug is macroalgae).

Feeding data were more highly resolved for scraping herbivores, with all fishes assigned size-based bite areas, and either species- (27 of 35 species, 80.9% of UVC) or genera-specific bite rates (19.1%). Potential scraping rates were greatest on GBR reefs (> 1 m2 min-1 ha-1) and lowest on Maldives reefs (< 0.3 m2 min-1 ha-1) (Figure S4B). Scraping rates increased with structural complexity (Fig. 2C) but, in contrast to croppers, were relatively invariant across benthic cover covariates (Fig. 1). Remote reefs had the greatest scraping rates, which were considerably lower on fished reefs than protected ones (Figs. 1, 2D). After accounting for these coarse protection effects, scraping was only weakly associated with total fishable biomass and mean fish length (Fig. 1).

Fish biomass is often used as a proxy for the magnitude of their function, but the relationship between biomass and function is rarely tested. Here, cropping rates were strongly and positively correlated with cropper biomass (R2 = 0.99, Fig. 3A), indicating that the drivers of biomass variation would match tightly to the modelled drivers of cropper function. Scraping rates also increased with scraper biomass, but with greater levels of unexplained variation in area scraped (m2 min-1 ha-1) (R2 = 0.81) which occurred across biomass gradient (Fig. 3B). Size structure (LFI, the proportion of large-bodied individuals in each assemblage) modified function ~ biomass relationships, with potential grazing function increasing as assemblages became dominated by smaller-bodied individuals (Fig. 3, Table 1). Size structure effects were moderately stronger for scrapers (parameter coefficient = -0.317 ± 0.03 standard error) than croppers (-0.087 ± 0.0007). For example, at average grazer biomass levels (croppers = 65 kg ha-1, scrapers = 370 kg ha-1), grazing rates were 15% (croppers) and 21% (scrapers) greater in small-bodied assemblages (LFI = 25%) than in large-bodied assemblages (LFI = 75%).



**Figure 3. Association between grazing function, grazer biomass, and assemblage size structure.** Reef-level estimates of cropper algal consumption (A) and scraper area grazed (B) plotted against UVC biomass (log10 scale), coloured by the LFI. Lines are model fits of grazing ~ biomass relationships for small-bodied assemblages (solid line: 25% large fish) and large-bodied assemblages (dashed line: 75% large fish), shaded with two standard errors. Large fishes are defined as ≥ 15 cm for croppers and ≥ 30 cm for scrapers.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Intercept** | **Biomass** | **LFI** | **LFI\*biomass** | **AICc** | **∆AIC** | **AIC weight** |
| *Croppers* |  |  |  |  |  |  |
| **0.024** | **0.728** | **-0.087** | **-** | **-296.935** | **0** | **0.748** |
| 0.025 | 0.727 | -0.086 | -0.002 | -294.759 | 2.176 | 0.252 |
| 0.077 | 0.681 | - | - | -208.064 | 88.871 | 0 |
| 0.414 | - | 0.183 | - | 226.190 | 523.125 | 0 |
| 0.362 | - | - | - | 4.000 | 239.595 | 0 |
| *Scrapers* |  |  |  |  |  |  |
| **-0.581** | **0.693** | **-0.317** | **0.084** | **-117.791** | **0** | **1** |
| -0.542 | 0.654 | -0.306 | - | -100.337 | 17.454 | 0 |
| -0.526 | 0.522 | - | - | -45.345 | 72.446 | 0 |
| -0.445 | - | - | - | 97.598 | 215.389 | 0 |
| -0.446 | - | 0.074 | - | 98.559 | 216.350 | 0 |

**Table 1. AIC selection for grazing function ~ grazer biomass + LFI models.** Parameter coefficients, AICc and AIC weights are shown for all competing models, ranked by AICc and with the top-ranked model in bold.

**Discussion**

By focusing on a wide range of benthic composition and fishing pressures, macroecological approaches to measuring reef-level processes such as herbivory provide insights into the functioning of protected, heat-stressed, and exploited coral reefs. We found that herbivore grazing rates varied substantially across the Indo-Pacific, and in accordance with top-down (i.e. fishing pressure) and bottom-up (i.e. benthic habitat) drivers which were specific to each functional group. Cropping rates were primarily controlled by bottom-up influences, with function maximised in complex habitats with high substrate availability and low macroalgae cover. Conversely, for parrotfishes, scraping rates were maximised on remote reefs in the Chagos archipelago which is isolated from fishing pressures, and increased with available substrate and structural complexity. Benthic and fishing influences were underpinned by the strong dependence of grazing rates on fish biomass, although we also demonstrate that reefs dominated by small-bodied fishes exert moderately greater grazing rates.

Cropping rates were primarily mediated by benthic habitat type, in particular structural complexity, macroalgae cover, and substrate availability. Our results emphasize the strong dependence of small-bodied reef fishes on benthic composition (Munday and Jones 1998, Wilson et al. 2010), and demonstrate that potential cropping is not affected by top-down fishing effects, likely because cropping assemblages are dominated by small-bodied fishes which are not targeted in many reef-associated fisheries (Hicks & McClanahan 2012). Strong relationships between benthic composition and the grazing function of small-bodied reef fish may reflect the importance of resource availability, which has been shown to have stronger control on cropping surgeonfishes than fishing pressure (Russ et al. 2018). For example, the decrease in cropping rates with increasing macroalgae is likely due to feeding avoidance in macroalgal-dominated areas (Hoey & Bellwood 2011), as well as lower accessibility of turf algae under macroalgal canopies (Roff et al. 2015). In contrast, reefs with high EAM (i.e. substrate availability) support expansive and easily accessible turf mats which are targeted by large grazer populations (Williams & Polunin 2001), which in turn limit the development of larger macroalgae. Strong benthic effects imply that cropper functioning will respond more strongly to habitat disturbances, such as coral bleaching, habitat destruction or enrichment of algal communities, than to fishing. Indeed, disturbances which increase substrate availability for turf algal growth, such as coral mortality from heat stress, typically stimulate an increase in grazer abundances (Wilson et al. 2006, Adam et al. 2011, Gilmour et al. 2013, Russ et al. 2019). However, since structural complexity was also shown to be a strong driver, any positive rebound of cropping function may be negated if disturbances also erode structural complexity (Graham et al. 2006).

Scraping was strongly influenced by fishing pressure at inhabited reefs. Across the Indo-Pacific, local extirpation of one parrotfish species (*Bolbometopon muricatum*) has diminished bioerosion and coral predation functions (Bellwood et al. 2012) and here we show that exploitation has also suppressed scraping rates far below those supported at remote, unfished reefs. This effect superseded influences of benthic cover and small-scale fishing protection, suggesting that bottom-up control of scraping assemblages on reefs leads to minimal variation in their function, and that small-scale fishing protection does not conserve wilderness levels of scraping function. Movement of fish across reserve boundaries, particularly larger-bodied parrotfish which have bigger home ranges (Green et al. 2014), and poor compliance with fishing regulations (Bergseth et al. 2018) likely limited the effectiveness of these small MPAs, many of which are adjacent to fishing grounds. Scraping rates also increased moderately with structural complexity, further underlining the importance of coral reef structure in supporting herbivory (Nash et al. 2016). As for croppers, the positive effect of available substrate on scraping rates is consistent with evidence that many scraping species respond positively to disturbances that clear substrate area (e.g. coral declines, Wilson et al. 2006), with increases in scraping function likely to promote coral recovery (Gilmour et al. 2013).

By modelling observed data and omitting benthic and fishing covariates, we demonstrated how grazing rates can vary simply as a function of biomass and size structure. As expected, grazing rates were highly dependent on grazer biomass, suggesting that benthic and fishing drivers are proximate drivers of grazing function through their effect on biomass. However, for a given level of biomass, assemblages dominated by small-bodied fishes had a higher grazing potential than those dominated by large-bodied fishes. Given that fishing is a key driver of reef fish size distributions (Robinson et al. 2017), these findings are consistent with evidence that grazing functions on exploited reefs are maintained by high densities of small-bodied parrotfish (Bellwood et al. 2012). Indeed, smaller fish have higher mass-specific metabolic rates and thus may feed more intensively per unit of fish biomass than large fish, which may explain why the LFI relationship was strongest for scraping rates which were modelled using size-specific feeding data. In contrast, large-bodied fishes comprised a greater fraction of assemblage biomass on high-biomass reefs (e.g. > 500 kg ha-1, Fig. 3), which suggests that reefs where grazing functions are maintained by few large individuals may be particularly vulnerable to fishing effects.

To integrate UVC data across the Indo-Pacific we were required to generalize across cropper species which are known to perform distinct feeding roles. For example, croppers have well-documented differences in morphology, diet (e.g. detritivores or turf), and feeding behaviours (Choat et al. 2002, Wilson et al. 2003, Brandl et al. 2015, Tebbett et al. 2017), though large-scale studies such as ours typically aggregate all cropping species into a single functional group (e.g. Heenan et al. 2016). We defined cropping function using species- or genera-specific bite rates, with a high proportion of individuals assigned average grazing rates. As such, current practices for estimating cropping function at the scale of assemblages are largely reflective of biomass levels rather than species-specific differences in feeding rate. In contrast, sscraping functions are more consistent among species (Bellwood and Choat 1990, Bellwood et al. 2003, Bonaldo & Hoey 2014) and our feeding data were more highly resolved with species-, genera- and size-specific bite rates). By modelling genera- and species-specific bite rates from observations collected in several regions, our approach did enable us to leverage observational data in a hierarchical framework which predicts grazing rates of new, related species, given uncertainties in species, genera and body sizes. For example, we were able to assign bite rates to species observed in UVC but not observed in feeding surveys, with estimates that were informed by the feeding behaviour of closely related congeners. Such models could be further improved with additional feeding data on other herbivore species in different regions, and could even be developed to account for temperature effects on grazing rates (Bruno et al. 2015) and examine how herbivory might respond to ocean warming.

Random intercepts in the predictive models indicated that regional similarities in grazing rates were unexplained by benthic and fishing covariates, which is likely due to unmeasured processes that control feeding rates and herbivore biomass. For example, herbivore biomass variation (and thus grazing function) has been linked to differences in benthic (Russ et al. 2003) and oceanic productivity (Heenan et al. 2016). Similarly, behavioural observations indicate that grazing intensity is constrained by wave exposure (Bejarano et al. 2017), while scraping rates can be higher in no-take fishing areas (Nash et al. 2016) which may have led us to underestimate grazing function on protected reefs. More broadly, our space-for-time approach precludes detection of non-linear changes in grazing rates that may arise when herbivore assemblages reorganize in response to acute disturbances (Han et al. 2016). Temporal analyses which link habitat suitability, primary productivity, and herbivory would greatly develop our understanding of how grazing functions influence long-term changes in reef state.

By integrating feeding rates with UVC data across a gradient of grazing biomass, we generated reef-level estimates of potential grazing pressure at four Indo-Pacific coral reefs. Our study demonstrates how benthic habitat and fishing pressure influence the functional potential of herbivore assemblages, at scales which are relevant for understanding ecosystem-level responses to disturbances such as bleaching (Nash et al. 2016). Cropping pressure is likely to increase in response to stressors which clear substrate space for turf growth, though post-disturbance grazing activity may be performed by more generalist cropping species (REF). Intact reef structure will be critical for maintenance of scraping functions, though reefs in close proximity to human populations are unlikely to return to wilderness levels of grazing pressure, even with protection from fishing (MacNeil et al. 2015). For a given level of biomass, dominance by smaller-bodied fishes will enhance grazing, though we stress that biomass was by far the most important predictor of grazing functions and recovery or protection of fish biomass will help ensure herbivory processes are functionally intact on degraded coral reefs (Williams et al. 2016).

**Acknowledgements**

We thank Morgan Pratchett (Chagos) and Fraser Januchowski-Hartley (GBR) for collecting and sharing UVC data. We acknowledge funding from the Australian Research Council (ASH) (DE130100688), Lizard Island Reef Research Foundation Doctoral Fellowship (AGL), Nick??

[**Supplementary Material**](https://github.com/jpwrobinson/grazing-gradients/blob/master/writing/ms/supp-material.pdf)

**References**

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. PLoS One 6:e23717

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Bartoń K (2013) MuMIn: multi-model inference. R package version 1:18

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bejarano, S., Jouffray, J.-B., Chollett, I., Allen, R., Roff, G., Marshell, A., … Mumby, P. J. (2017). The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. *Functional Ecology*, *31*(6), 1312–1324.

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fishes 28:189–214

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc Biol Sci 279:1621–1629

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bergseth, B. J., Gurney, G. G., Barnes, M. L., Arias, A., & Cinner, J. E. (2018). Addressing poaching in marine protected areas through voluntary surveillance and enforcement. *Nature Sustainability*, *1*(8), 421–426.

Best RJ, Chaudoin AL, Bracken MES, Graham MH, Stachowicz JJ (2014) Plant–animal diversity relationships in a rocky intertidal system depend on invertebrate body size and algal cover. Ecology 95:1308–1322

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bonaldo, R. M., & Hoey, A. S. (2014). The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review*, *52*, 81–132.

Brandl, S. J., Robbins, W. D., & Bellwood, D. R. (2015). Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. *Proceedings. Biological Sciences / The Royal Society*, *282*(1815), 20151147.

Bruno JF, Carr LA, O’Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc Natl Acad Sci U S A 105:16201–16206

Burkepile DE, Hay ME (2011) Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. Coral Reefs 30:351–362

Burnham KP, Anderson DR (2003) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media, New York

Cade BS (2015) Model averaging and muddled multimodel inference. Ecology 96:2370–2382

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547

Cheal AJ, MacNeil MA, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (2010) Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs 29:1005–1015

Choat JH, Clements KD (2018). Nutritional ecology of parrotfishes (Scarinae, Labridae). In *Biology of parrotfishes* (pp. 42-68). CRC Press.

Choat J, Clements K, Robbins W (2002) The trophic status of herbivorous fishes on coral reefs. Mar Biol 140:613–623

Choat JH, Robbins WD, Clements KD (2004) The trophic status of herbivorous fishes on coral reefs. Mar Biol 145:445–454

Doropoulos C, Hyndes GA, Abecasis D, Vergés A (2013) Herbivores strongly influence algal recruitment in both coral- and algal-dominated coral reef habitats. Mar Ecol Prog Ser 486:153–164

Doropoulos C, Ward S, Marshell A, Diaz-Pulido G, Mumby PJ (2012) Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. Ecology 93:2131–2138

Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. Proc Natl Acad Sci U S A 113:6230–6235

Edwards CB, Friedlander AM, Green AG, Hardt MJ, Sala E, Sweatman HP, Williams ID, Zgliczynski B, Sandin SA, Smith JE (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. Proc Biol Sci 281:20131835

Froese R, Pauly D (2018) FishBase.

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Graham NAJ, Bellwood DR, Cinner JE, Hughes TP, Norström AV, Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11:541–548

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Graham NAJ, McClanahan TR (2013) The Last Call for Marine Wilderness? Bioscience 63:397–402

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(22), 8425–8429.

Graham NAJ, Chong-Seng KM, Huchery C, Januchowski-Hartley FA, Nash KL (2014) Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. PLoS One 9:e101204

Green AL, Bellwood DR (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience - A practical guide for coral reef managers in the Asia Pacific region.

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., … White, A. T. (2014). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews of the Cambridge Philosophical Society*, *90*(4), 1215–1247.

Han, X., Adam, T. C., Schmitt, R. J., Brooks, A. J., & Holbrook, S. J. (2016). Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* , *35*(3), 999–1009.

Heenan A, Hoey AS, Williams GJ, Williams ID (2016) Natural bounds on herbivorous coral reef fishes. Proc Biol Sci 283:20161716

Hicks, C. C., & McClanahan, T. R. (2012). Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, seagrass and coral reef fishery. *PloS One*, *7*(5), e36022.

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37–47

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. Nature 546:82–90

Jouffray J-B, Nyström M, Norström AV, Williams ID, Wedding LM, Kittinger JN, Williams GJ (2015) Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. Philos Trans R Soc Lond B Biol Sci 370:20130268

Keesing F, Young TP (2014) Cascading Consequences of the Loss of Large Mammals in an African Savanna. Bioscience 64:487–495

Lokrantz J, Nyström M, Thyresson M, Johansson C (2008) The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27:967–974

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NVC, McClanahan TR (2015) Recovery potential of the world’s coral reef fishes. Nature 520:341–344

Marshell A, Mumby PJ (2015) The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. J Exp Mar Bio Ecol 473:152–160

McClanahan TR, Maina JM, Graham NAJ, Jones KR (2016) Modeling Reef Fish Biomass, Recovery Potential, and Management Priorities in the Western Indian Ocean. PLoS One 11:e0154585

McElreath R (2017) Rethinking: statistical Rethinking book package. R package version 1:

Metcalfe DB, Asner GP, Martin RE, Silva Espejo JE, Huasco WH, Farfán Amézquita FF, Carranza-Jimenez L, Galiano Cabrera DF, Baca LD, Sinca F, Huaraca Quispe LP, Taype IA, Mora LE, Dávila AR, Solórzano MM, Puma Vilca BL, Laupa Román JM, Guerra Bustios PC, Revilla NS, Tupayachi R, Girardin CAJ, Doughty CE, Malhi Y (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecol Lett 17:324–332

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101

Munday PL, Jones GP (1998) The Ecological Implications of Small Body Size Among Coral-Reef Fishes. Ocean Coast Manag 36:373–411

Nash KL, Graham NAJ, Bellwood DR (2013) Fish foraging patterns, vulnerability to fishing, and implications for the management of ecosystem function across scales. Ecol Appl 23:1632–1644

Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR (2016) Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. J Appl Ecol 53:646–655

Nash, K. L., Abesamis, R. A., Graham, N. A. J., McClure, E. C., & Moland, E. (2016). Drivers of herbivory on coral reefs: species, habitat and management effects. *Marine Ecology Progress Series*, *554*, 129–140.

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) vegan: Community Ecology Package. R package ersion 2.4-4:

Polunin NVC, Harmelin-Vivien M, Galzin R (1995) Contrasts in algal food processing among five herbivorous coral-reef fishes. J Fish Biol 47:455–465

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology-Progress Series 100:167–167

Robinson JPW, Williams ID, Edwards AM, McPherson J, Yeager L, Vigliola L, Brainard RE, Baum JK (2017) Fishing degrades size structure of coral reef fish communities. Glob Chang Biol 23:1009–1022

Robinson JPW, Williams ID, Yeager LA, McPherson JM, Clark J, Oliver TA, Baum JK (2018) Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines. Coral Reefs

Rooij JM, Videler JJ, Bruggemann JH (1998) High biomass and production but low energy transfer efficiency of Caribbean parrotfish: implications for trophic models of coral reefs. J Fish Biol 53:154–178

Royo AA, Collins R, Adams MB, Kirschbaum C, Carson WP (2010) Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91:93–105

Prieditis, A., Howlett, S.J., Baumanis, J., Bagrade, G., Done, G., Jansons, A., Neimane, U., Ornicans, A., Stepanova, A., Smits, A. and Zunna, A., 2017. Quantification of Deer Browsing in Summer and Its Importance for Game Management in Latvia. *Baltic Forestry*, *23*(2), pp.423-431.

Russ GR, Questel S-LA, Rizzari JR, Alcala AC (2015) The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar Biol 162:2029–2045

Samoilys MA, Carlos G (2000) Determining Methods of Underwater Visual Census for Estimating the Abundance of Coral Reef Fishes. Environ Biol Fishes 57:289–304

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients: Interpretation of regression coefficients. Methods Ecol Evol 1:103–113

Tebbett SB, Goatley CHR, Bellwood DR (2017). Clarifying functional roles: algal removal by the surgeonfishes Ctenochaetus striatus and Acanthurus nigrofuscus. Coral Reefs, 36(3), 803–813.

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KL Jr, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, van Sebille E, Gupta AS, Smale DA, Tomas F, Wernberg T, Wilson SK (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc Biol Sci, 281(20140846).

Williams, I., & Polunin, N (2001). Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs, 19(4), 358–366.

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41:279–310

Wilson, S. K., Fisher, R., Pratchett, M. S., Graham, N. A. J., Dulvy, N. K., Turner, R. A., … Rushton, S. P. (2008). Exploitation and habitat degradation as agents of change within coral reef fish communities. Global Change Biology, 14(12), 2796–2809.

Wilson SK, Fisher R, Pratchett MS, Graham NAJ, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecol Appl 20:442–451

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar Biol 151:1069–1076

Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. Mar Ecol Prog Ser 590:155–169

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC (1995) Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. Am Nat 146:765–794