Ecological surveys

Survey methods

Fish surveys were point counts of 7 m radius (Seychelles) or belt transects of 50 m length (Maldives, Chagos, GBR) conducted on hard-bottom reef habitat at 8-10 m depth. Surveys were designed to to minimize diver avoidance or attraction. In point counts, large mobile species were censused before smaller reef-dwelling species. In belt transects, large mobile fishes were surveyed in one direction for a 5 m transect width, and small site-attached species were recorded in the opposite direction for a 2 m transect width. For both survey types, all diurnal, non-crypic (>8cm) reef-associated fish were counted and sized to the nearest centimetre (total length, TL). TL 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. All fish sizes (total length, cm) were then converted to body mass (grams) using published length ~ weight relationships (Froese & Pauly 2017), and standardized by survey area to give species-level biomass estimates that were comparable across datasets (kg hectare⁻¹).

Following fish surveys, benthic habitat composition was surveyed with 50 m line transects. Benthos composition was recorded by noting the benthic taxa directly under the transect line at 50 cm intervals (line intercept method, REF). Taxa were grouped into broad functional groups (e.g. CCA, macroalgae, turf algae) and, if they were hard corals, identified to genus level. 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 & Roberts 1993).

Observation error and bias were minimized because one observer (NAJG) performed all surveys, except for benthic surveys in Seychelles (SW). Point counts and belt transects give comparable biomass estimates (REF).

Region details

In Seychelles, 21 reefs were surveyed in 2008, 2014, and 2017. Sites were located on two inhabited islands (Mahe, Praslin) and were stratified to include carbonate fringing reefs, granitic rocky reefs with coral growth, and patch reef habitats on a sand, rubble, or rock base (Fig MAP). Counts were replicated at each site, with 16 surveys conducted in 2008 and 8 surveys in 2011, 2014 and 2017. Power analysis indicated that only 8 replicates were needed (REF), and thus we only considered surveys from 8 replicates per site per survey year. Replicate survey points were haphazardly located on the reef slope at least 15m away from each other. Overall, the surveys covered up to 0.5km of reef front and 2,500m² of reef habitat.

In the GBR, surveys were conducted between November 2010 and January 2011. Five mid-shelf reefs near the city of Townsville were surveyed by splitting them into 3 wave exposed and 3 wave sheltered sites. Each of these 6 sites were split up again along a zonal gradient into 3 zones - crest (2-3m depth), slope (7-9m depth), and flat (100m distance from crest). Each zone was surveyed with four transects, thus giving 72 transects per reef (four replicates for three wave zones nested in 6 sites per reef) and 360 total transects.

In Chagos, surveys were conducted in 2010 at 25 sites on 4 atolls (Fig MAP). Belt transects were placed at yadda yadda yadda. Four replicates transects conducted at each site.

In Maldives, surveys were conducted in 2013 at 11 sites on 1 atoll (Fig MAP).

Herbivore feeding observations

Feeding observations of Indo-Pacific herbivores provided species-level estimates on bite rates and, for scrapers, bite volumes. Surveys were conducted in the Red Sea (AH), Indonesia (AH), and GBR (AH and AGL). We only analysed feeding observations for species observed in the UVC dataset (39). For each observed fish, we

estimated the average feeding rate (bites per minute). For scrapers, we also estimated the average bite scar size.

Ecological variable processing

Herbivore species were categorised as grazers, scrapers or browsers according to published diet observations (REF). Fish biomass estimates were averaged across replicates at each site to give the total biomass (kg ha⁻¹) of each functional feeding group (grazers, scrapers, browsers), and these estimates formed the basis of all subsequent analyses.

Explanatory covariates were derived from fish and benthic surveys. First, to account for fishing effects ranging from pristine Chagos reefs to heavily-exploited Seychelles reefs, we estimated total community biomass as a proxy for exploitation pressure. Fishable biomass JUSTIFICATION (REF). 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, sand, and rubblerubble), and structural complexity, by averaging across replicates at each site. To understand the range of benthic habitat types across the dataset, we conducted a PCA to identify common habitat groupings (i.e. benthic regimes) (Jouffray et al. 2015). 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 protection covariate to two dummy variables (fished - protected, fished - pristine) (Schielzeth 2010).

Statistical	analyses			

Biomass analysis

We used linear mixed effects to model to examine variation in herbivore biomass along gradients in benthic habitat composition and fishing intensity. Benthic fixed effects were hard coral, macroalgae, sand, rubble and structural complexity, and fishing fixed effects were fishable biomass and fishing protection. Models were fitted separately for each functional feeding group for normally distributed errors, and biomass was log_10_transformed. Parameter estimates were extracted to compare effect sizes of each explanatory covariate, and fitted relationships were visualized with model predictions that excluded random effects.

Grazing function analysis

Fish functions were defined separately for each functional feeding group, and feeding observations used to convert UVC observations to one of three grazing functions. We used a Bayesian hierarchical modelling framework that estimate species- and genera-level functional rates, which allowed us to estimate grazing for UVC species which were not observed in feeding surveys (63). For grazers, which feed on turf and other filamentous algal material, herbivory maintains turf in cropped states that are expected to be benign states for coral recruitment. Grazing function was quantified in terms of potential feeding intensity, measured as the total number of bites per hour. Feeding observations were modelled with species- and genera-specific bite rates:

 $bite_rate = Gamma(\mu, \theta) \ log(\mu) = X + species_i + genus_i$

Grazing bite rates were unrelated to body size (Fig. SX), and thus we did not consider potential size differences in functional rates.

For scrapers and excavators, 'scraping' of endolithic and detrital material exposes substrate and promotes coral recruitment. Scraping function was quantified in terms of area of substrate removed per hour. Feeding observations provided estimates of bite rates and average scar sizes (scar_area), which we modelled with species- and genera-specific grazing rates.

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\begin{aligned} bite &= Gamma(\mu, \theta) \ log(\mu) = X + B * TL + species_i + genus_j \\ scar_area &= Gamma(\mu, \theta) \ log(\mu) = X + B * TL + species_i + genus_j \\ area_removed &= Normal(\mu, \sigma) \ \mu = X + ?? \end{aligned}
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By including size (TL) as an explanatory covariate, our model accounted for body size effects, as scar sizes increased with body size (Fig. SX) and bite rates decreased with body size (Fig. SX).

For browsers, consumption of established macroalgae acts to suppress macroalgal growth (REF), though grazing can be inhibited at hig macroalgal densities (Hoey & Bellwood 2011). Browsing function was quantified in terms of algal material removed per hour. Feeding observations provided estimates of bite rates and ?????. Browsing feeding observations were limited to two species from two genera, so we only fitted genera-specific random effects:

$$bite = Normal(\mu, \sigma)$$

$$\mu = X + genus_j$$