REVIEWERS' COMMENTS TO THE AUTHORS

**Reviewer: 1**  
This paper looks at the relationship between benthic variables, estimates of fishing pressure and UVC-based fish abundances from which ecosystem functions are estimated. The extensive author list includes many of the world’s leading coral reef researchers. I therefore anticipated a conceptual or analytical breakthrough. Unfortunately, there are major problems with this paper. At a conceptual level the manuscript largely repeats earlier work. It represents yet another paper where fish numbers are multiplied by bites to estimate rates of presumed functions. This was extensively applied 10 years ago. The main conclusions from the paper have been previously reported, especially for parrotfishes, by Russ and Hoey. In this respect the paper is at best confirmatory.

* Published coral reef grazing studies which have integrated visual census data with feeding observations described 1) spatial patterns in scraping and bioerosion at one reef (Hoey & Bellwood 2008. *Coral Reefs*) and 2) influences of human population density on scraping rates at 18 Indo-Pacific reefs (Bellwood et al. 2003 *Ecol. Lett.*, Bellwood et al. 2012, *Proc R. Soc.* *B.*). None of these studies considered influences of bottom-up processes (benthic composition) and fish community size structure on functional rates, or measured grazing by algal-cropping fishes.

However, the main problems are methodological. Most of the data collection methods are fundamentally flawed.  
1.      The paper considers benthic correlates. Unless all surveys were in the same reef habitat the results are simply demonstrating the effects of habitat variability not the role of specific benthic components.

* All surveys are from the same reef habitat (reef slope) (L139).

2.      The claim that point censuses yield the same data as belt transects is incredulous. The authors have themselves published work on the extent of diver effects. This misleading statement sweeps aside a vast literature that effectively and conclusively demonstrates the extent of diver effects when counting fishes. The UVC counting methods are a mixture of barely adequate (belt) and fundamentally flawed (point).

* There is substantial precedent in the literature for combining point counts and belt transects (McClanahan et al. 2011 *PNAS*, MacNeil et al. 2015 *Nature*, Cinner et al. 2016 *Nature*)
* These survey methods have been shown to produce comparable fish density estimates (Samoilys and Carlos 2000 *Environ. Biol. Fish.*)
* Our statistical models include a random effect term which estimates grazing rate mean and variance separately for each dataset (i.e. separating point counts from belt transects)
* The datasets we analyse have been combined before (Cinner et al. 2016 *Nature*, Graham et al. 2017 *Curr Biol*, Darling et al. 2017 *Coral Reefs*)
* A single observer (N Graham) surveyed fish communities at all of the 4 locations
* For feeding data, visual surveys have been shown to provide comparable estimates of cropping and scraping rates (Fox & Bellwood 2008, *Mar. Biol.*), and so diver effects are minimal.

3.      To claim that the size of a fish can be estimated to the nearest centimetre from 7m distance underwater is likewise incredulous. I do not accept that this is possible with any degree of accuracy.

* Size estimations were validated daily during surveys at each location and were accurate within 2-3%. This has also been shown previously (Graham et al. 2007, *Cons. Biol.*), and we now note this in the methods (L150).

4.      An 8cm size cut-off is bizarre. Especially for this paper as I suspect that most scrapers are croppers at this size.

* All the methods used are established and widely used reef survey techniques, including the small size cut-off (8 cm here) to avoid poor sampling of smaller cryptic fish. We add a caveat that we may underestimate grazing contributions from small-bodied croppers (L440-442).

5.      The different methods for counting fishes and quantifying the benthos are put into the analyses under the assumption that they are effectively the same type of data. I do not accept this as a valid assumption.

* Benthic and fish data are collected at the same spatial scale within each location, though using different techniques. This is a well-established practice for studies exploring the influence of habitat on fish. It is incorrect to claim that statistical models must use the same 'type' of data. If the reviewer is referring to the differences within fish or within benthic datasets, we used random effects to account for regional dataset effects, as detailed in response to point 2 above.

6.      For feeding behaviour fishes are allowed to acclimatise for 30s before following them for 3 minutes. This is not a credible means of quantifying fish feeding behaviour. Fishes either need no acclimation time (they are not scared) or no amount of time will suffice (they simply swim off). This is not rigorous best practice but an ad-hoc method with no quantifiable justification.

* For behavioural studies, a short acclimation period (generally up to 30s) is widely accepted (e.g., Choat and Clements 1993, *Mar. Biol.*; Bruggemann et al. 1994, *Mar. Ecol. Prog. Ser.;* Pratchett 2005, *Mar. Biol.*; Feary et al. 2018, *Mar. Ecol. Prog. Ser.)* ensuring that any potential effects of diver presence on feeding are minimised. Further, less than 5 % of fishes followed in the present study showed any negative response to the presence of a diver.

7.      A Bayesian modelling approach was used to estimate grazing values for the 63 species not included in feeding observations (=39). This means that the bite rates of almost two thirds of the species in the analyses were based on observations from the remaining third. This is not acceptable.  
Given the fundamental problems with the basic data collection methods other problems with the analyses and subsequent interpretations do not need to be addressed. The results and subsequent interpretations are irrelevant.

* Using Bayesian models enables us to borrow information from a well understood element of a problem to inform the likely distribution for a less well understood element. That is not controversial. Here, we use this approach to generate posterior predictions for cropping species without bite rate data, based on posterior distributions for closely-related species with bite rate data. We do now acknowledge that data scarcity for croppers is a limitation of our study, and that future research will require more complete databases of grazing behaviours (L432-442).

**Reviewer: 2**This is an interesting and well written manuscript. Here, Robinson et al. explore the top-down and bottom-up drivers of herbivory on coral reefs using “snapshot” data from numerous coral reefs throughout the Indo-Pacific region. Employing elegant models, they tease apart the relative importance of habitat and fishing effects on this key process. By doing so using a macroecological approach (at large spatial scales), this work notably advances a rich body of literature on this topic. I commend the authors for their creativity and execution. Well done.

Thank you for your positive comments about the importance of our study, and the appropriateness of our datasets and statistical analyses.  
  
That being said, I take issue with certain elements of the study, which I think should be dealt with before the manuscript is considered further for publication:  
(1) The feeding data for croppers are poorly resolved (i.e., were only collected for a few species), thereby requiring extensive inference when calculating cropping rates. I appreciate the challenges of collecting data for all observed species, and would not advocate for more data collection here – however, I’d like to see a direct acknowledgement of this study limitation (i.e., some text on the issue, citing the relevant supp. table to point out the limitation, etc.).  After all, it speaks to the trade-off between conducting small-scale studies of herbivory (where such data are finely resolved but limited in spatial scope) and large-scale studies of herbivory (where such data are inferred for many species, but are much greater in spatial scope). I think this inherent trade-off should be addressed in the Discussion, thus giving the study greater context.

Thank you for the suggestion to better caveat the results for croppers. To clarify these issues, we add the following to the Discussion:

## identify a trade-off between small- and large-scale studies

## acknowledge that data scarcity for cropping feeding behaviours is a limitation of our study, and emphasize that we use data for 9/46 cropping species (with link to Table S1 and Fig. S3)

## identify the unification of small- and large-scale studies as an important avenue for further research on grazing functions on coral reefs

## L432-438: *We inferred feeding rates of 46 unobserved species from nine well-studied species, which limited our understanding of assemblage-level cropping function. Although small-scale studies of feeding behaviours (e.g. Marshell & Mumby 2015, Tebbett et al. 2017) inevitably provide greater taxonomic resolution than large-scale studies which infer feeding behaviours for high numbers of species (here), uniting behavioural data with community-level ecological surveys is a key frontier for functional ecology research on coral reefs.*

## (2) Common to the field of “macroecology” is the study of local and regional species richness and community composition. While the authors argue for taking a macroecological approach to studying reef herbivory, they ignore differences among sites and regions with respect to herbivore community richness and composition (alpha and beta diversity). Fishing likely impacts both metrics by way of selectively removing large bodied species (which will in turn influence biomass and thus impact bite rate). See Lefcheck et al. 2019 (Science Advances) as an example where herbivore community biomass, richness, and composition collectively account for much of the observed variance in turf grazing rates on Caribbean coral reefs (that is, after statistically controlling for bottom-up habitat influences on herbivore bite rate). At a minimum, I think the potential role of herbivore community richness/composition should be briefly addressed in the Discussion (a sentence or two) as another potential source of unexplained variance in grazing rate in this study (see technical comment below).

Thank you for bringing the Lefcheck study to our attention. We agree that our approach overlooks potential biodiversity influences, which are likely to influence macroecological patterns which operate across biogeographic regions. To acknowledge these limitations, we now include a section in the Discussion which considers how richness and community composition may contribute to the unexplained variation in grazing rates in our statistical models.

L464-470: *Grazing rates may also increase with biodiversity, whereby grazing is maximised when numerous common species are abundant (i.e. high species richness) and when the identity of dominant grazing species varies among neighbouring reefs (i.e. high β-diversity) (Lefcheck et al. 2019), or simply because biodiversity promotes fish biomass (Duffy et al. 2016). Because such biodiversity effects operate at regional scales, compositional differences may further contribute to the unexplained variation in our modelled grazing rates.*  
  
(3) The authors mention ecosystem “thresholds” of herbivory in the Introduction, but do not touch on this concept again in the manuscript. It seems they possess one of the better datasets for identifying/proposing such thresholds, so I came away wanting more in this area.

Analyses of grazing thresholds typically test the hypothesis that benthic cover is predicted by herbivore biomass (i.e focused on top-down grazing of benthos), and are best suited to time-series datasets where temporal changes in benthic cover can be ascribed to temporal changes in grazing biomass (e.g. Graham et al. 2015, Nature). However in our study, we focus on the drivers of herbivore function, including both bottom-up benthic and top-down fishing influences. To clarify these distinctions, we now note that temporal analyses might be used to identify grazing function thresholds (L475), and emphasize that our analysis is focused on relative roles of bottom-up and top-down drivers of grazing functions (L471).  
  
(4) Lastly, the statistics need clarification (see below). I feel confident in the authors execution, but some additional information is needed to ensure that correct decisions were made.

Thank you for your suggestions to improve communication of the statistical models. We now demonstrate that model covariates were not collinear (L247-249), and justify the use of fishable biomass as a metric of exploitation pressure that is not strongly dependent on herbivore biomass (L208-213). Please see our more detailed responses below.  
  
Overall, I am very supportive of this manuscript – I think it’s important.  After some modest revision, I would advocate for its publication in Functional Ecology.  
  
Technical comments:  
line 65: Perhaps replace “restricts” with “limits”.

Corrected  
  
line 114: I think this statement is a bit misleading – it’s probably true with respect to cropping bite rate, but not true regarding the depth to which the fish community can scrape the reef. Due to morphometrics, it’s hard to imagine a case in which many small fish can scrape/excavate the reef to the same depth as a few large fish. In other words, gouging the reef is important to coral recruitment, and I just don't see how small fish would be physically capable of carrying out this function with the same capacity. Please clarify.

Thanks for this insightful comment, in this section we considered metabolic effects on grazing (i.e. size structuring) rather than behavioural differences among size classes. We have clarified that size structure may influence the potential bite rates, rather than being functionally equivalent (L114).

line 173: By whom? Unclear.

Added detail that A Hoey and A Graba-Landry conducted feeding surveys (L175).  
  
line 174: reference Table S1, as it indicates which fish you did (and did not) survey with regard to feeding rate/behaviour.

Table S1 now referenced (L176).  
  
line 233-234: I suspect that some of these predictors are highly collinear (e.g., coral cover and available substrate; fishable biomass and protection status). Have you tested for multicollinearity? How have you dealt with this issue?

We tested for collinearity by estimating the variance inflation factor (VIF) of each covariate in the global models. All covariates had low VIF (< 2), meeting the recommended guideline of including only covariates with VIF below 3 (Zuur et al. 2010, *Methods Ecol. Evol.*). We have added these details to the Methods.

L247-249: *We inspected variance inflation factors (VIF) for each covariate, which indicated that global models were not biased by collinearity (VIF < 2 for all covariates in both cropper and scraper models) (Zuur et al. 2010).*  
  
line 260: I’m concerned about the circularity of using herbivore biomass as both a proxy for fishing intensity (a predictor) and also a component of grazing computation (the response). Please briefly explain why this is OK.

Fishable biomass is primarily comprised of large-bodied predatory fishes which are typically targeted by reef fisheries, and thus represents a more finely-resolved metric of fishing pressure than our categorical covariate ‘fished – protected – remote’. Fishable biomass has been widely used to measure exploitation pressure in the Indian Ocean, and is predicted by other fishing metrics such as population size and access to markets (L208). Although herbivores are targeted at some of these reefs and this could potentially bias our analysis, fishable biomass was also only weakly correlated with cropper (Pearson’s *r* = 0.50) and scraper biomass (r = 0.48), and so indicates that fishable biomass estimates capture additional information on the exploitation pressure at each reef. We have clarified these details in the Methods.

L208-213: *This proxy, based on total fish community biomass, is highly sensitive to exploitation pressure and predicted by human population size, access to markets, and fisheries management (Cinner et al. 2016), and has been used to represent large-scale fishing gradients in numerous studies (e.g. McClanahan et al. 2011, Graham et al. 2017). Here, fishable biomass was only moderately correlated with grazing biomass (Pearson’s r: croppers = 0.50, scrapers = 0.48) and thus captures information on exploitation pressure for the full reef fish assemblage.*  
  
line 290: Figure 2 is cited in the manuscript before Figure 1. Please revise the text, or the order of the Figures, to as to comply with the general rule of citing in the order of presentation.

Thank you for noticing this mistake. Figures 1 and 2 have been switched.   
  
line 321: One would expect this if biomass is being used both as a predictor and to compute the response variable. See comment above.

Fishable biomass captures information on exploitation pressure for the entire reef fish community, is predicted by other market-based metrics, and has been used in other Indian Ocean coral reef studies. We now note these points - please see response above.

line 326: change “grazing” to “cropping/scraping”, for the uninformed reader.

Corrected.  
  
line 404: And also species identity/richness (which places bounds on biomass, in turn placing bounds on grazing potential).

Added comment in the Discussion that species richness influences grazing rates through its effect on biomass (L468)  
  
line 437-449: Differences in the richness and composition of the herbivore assemblage may also account for some of your unexplained variance. See note above and example from Lefcheck et al. 2019.

Added comment in the Discussion on how biodiversity influences grazing rates, and might contribute to unexplained variation in models (L465-470).