Natural bounds on herbivorous coral reef fishes

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Humans are an increasingly dominant driver of Earth’s biological communities, but differentiating human impacts from natural drivers of ecosystem state is crucial. Herbivorous fish play a key role in maintaining coral dominance on coral reefs, and are widely affected by human activities, principally fishing. We assess the relative importance of human and biophysical (habitat and oceanographic) drivers on the biomass of five herbivorous functional groups among 33 islands in the central and western Pacific Ocean. Human impacts were clear for some, but not all, herbivore groups. Biomass of browsers, large excavators, and of all herbivores combined declined rapidly with increasing human population density, whereas grazers, scrapers, and detritivores displayed no relationship. Sea-surface temperature had significant but opposing effects on the biomass of detritivores (positive) and browsers (negative). Similarly, the biomass of scrapers, grazers, and detritivores correlated with habitat structural complexity; however, relationships were group specific. Finally, the biomass of browsers and large excavators was related to island geomorphology, both peaking on low-lying islands and atolls. The substantial variability in herbivore populations explained by natural biophysical drivers highlights the need for locally appropriate management targets on coral reefs.

1. Introduction

Humans are increasingly a dominant global force influencing the structure and function of ecosystems through the removal of key species and functional groups, habitat modification, and the effects of pollution and climate change [1–3]. Coral reef ecosystems are especially vulnerable to such human-forcing [4], and whereas anthropogenic impacts are globally pervasive, they occur against a backdrop of high natural variability in reef systems caused by differences in the environment and biogeographic context. Oceanic productivity, water temperature, habitat area, reef geomorphology, and larval connectivity can have substantial impacts on coral reef fish assemblages [5–10]. For example, the natural fish carrying capacity of a coral reef has been shown to double along a gradient of increasing oceanic productivity [11]. Understanding the relative influence of human versus natural drivers is key to assessing the current status of these ecosystems.

Here, we focus on one component of coral reef systems, namely herbivorous fishes in the Pacific Ocean. Despite some uncertainty, particularly in the Indo-Pacific, about the relative importance of herbivory in mediating coral–algal dynamics [12–16], herbivorous fishes are widely recognized to play an important role in maintaining the competitive dominance of reef calcifiers (e.g. hard corals and crustose coralline algae), over other benthic components (e.g. fleshy macroalgae) [17–20]. For example, following climate-induced coral bleaching, fished reefs with reduced herbivore populations have a greater propensity to become dominated by macroalgae [21]. For that reason, some coral reef management
strategies now focus specifically on protecting or restoring her- 
vivorous fish populations [22,23]. There is a need, therefore, to 
to better understand the role of the natural environment in deter-
mining distribution patterns of herbivorous fishes [8,24–26] 
independent of local human impacts on coral reefs. Indeed, 
the upper bounds of herbivore biomass will be determined 
by a reef’s local biophysical setting, and once identified, 
will allow for realistic fisheries management strategies to 
address the widespread effect of fishing on this trophic group 
[7,8,11,27–30].

Herbivorous reef fish assemblages vary with local envi-
rmental factors. For instance, parrotfish tend to be more 
abundant and species rich on barrier reefs compared with 
atoll, and fringing or low coral cover reefs [31]. Intra-island 
variation in herbivore species composition and behaviour is 
also evident among different reef habitats. Typically, the abun-
dance and feeding activity of grazing surgeonfishes and large 
parrotfishes is lower on nearshore coastal reefs compared with 
wave-exposed offshore reefs [32,33]. Conversely, browsing 
herbivores are often more abundant on wave-protected back 
reef habitats, when compared with the exposed fore-reef 
areas [32,34,35]. Furthermore, herbivore biomass and rates of 
herbivory tend to be the greatest on the reef crest, and both 
decrease across the reef flat and down the reef slope [35–38]. 
These patterns in herbivorous fishes are variously attributed 
to the availability and quality of food and shelter, in addition 
to the wave energy and sedimentation regimes experienced 
[34,38–40]. The implication of this localized among- 
and within-habitat variation is that the need for, and potential 
effectiveness of, fishery management interventions are highly 
dependent on natural bounds set by the location’s biophysical 
setting [41].

Here, we make use of a consistent monitoring dataset from 
33 islands and atolls across the central and western Pacific to 
better understand the relative role of anthropogenic impacts 
and biophysical drivers (habitat and physical environmental 
conditions) in structuring herbivore populations on coral 
reefs. These islands span large gradients of human population 
density (0–27 people per hectare of reef) [11,42] and biophysi-
cal condition [43], allowing us to separate the relative effect of 
those in driving variation in herbivore biomass.

2. Methods

(a) Fish assemblage and reef habitat surveys

We used coral reef monitoring data collected between 2010 and 
2015 across 33 Pacific islands and atolls (electronic supplementary 
material, table S1). The surveys were performed for the National 
Oceanic and Atmospheric Administration (NOAA) Pacific Reef 
Assessment and Monitoring Programme (Pacific RAMP), a long-
term ecosystem monitoring effort focused on United States and 
United States-affiliated coral reefs [44]. Data from two underwater 
visual census techniques were used, the stationary point count 
(SPC) and the towed-diver (tow) survey method (Coral Reef 
Ecosystem Program; Pacific Islands Fisheries Science Center 
random surveys (StRS) of reef fish, including benthic estimate 
data of the U.S. Pacific Reefs since 2007. NOAA National Centers 
for Environmental Information. Unpublished Dataset. [15 
Coral Reef Ecosystem Program; Pacific Islands Fisheries Science 
Center (2016). Towed-diver surveys of large-bodied fishes of the 
U.S. Pacific Reefs since 2000. NOAA National Centers for
site-level metrics were calculated, first by averaging values within each depth stratum per island, and then weighting the mean estimates by the total area of each stratum per island \([54,55]\). Island-level tow estimates of piscivore biomass were calculated as equally weighted means of each tow per island across years. Species richness per functional group was estimated by generating species accumulation curves for each island, using the rarefaction method in the R package vegan \([56]\).

(c) Quantifying human and biophysical predictors

We used the published estimates of the following human and biophysical covariates, derived at the island level: human population density, chlorophyll \(a\) (mg m\(^{-3}\)) as a proxy for phytoplankton biomass and oceanic productivity, total area of reef habitat, sea-surface temperature (SST °C), wave energy (kW m\(^{-1}\)), and island type (electronic supplementary material, table S3.2). Island types were based on geomorphology, and classed as either high (e.g. basalt island) or low lying (e.g. carbonate island or atoll). Islands were also grouped by region (Hawaii, Central Polynesia, Gilbert, Ellis, and Marshall Islands, and Tropical Northwest Pacific \([57]\)).

To determine anthropogenic impacts on herbivorous fishes, we used human population density (the number of people resident per island (from the 2010 US census) divided by the area of fore-reef habitat per island from Geographic Information System (GIS) habitat layers maintained by Pacific RAMP (electronic supplementary material, table S3.2). Island types were based on geomorphology, and classed as either high (e.g. basalt island) or low lying (e.g. carbonate island or atoll). Islands were also grouped by region (Hawaii, Central Polynesia, Gilbert, Ellis, and Marshall Islands, and Tropical Northwest Pacific \([57]\)).

To test for influential data points and to check for model stability, we calculated Akaike’s information criterion, corrected for small sample size (AICc) and the AICc-based relative importance weights \((wi)\) to assess the conditional probability of each model. We report the model-average estimates for each predictor term based on the top-ranked models for each fish metric, top-ranked models being those with more than 0.05 Akaike weight. To test for influential data points and to check for model stability, we performed a jack-knife sensitivity test, calculating the percentage of times sequentially deleting single response variable data points produced the same top-ranking model structure \(\text{sensu} \ [61]\).

Finally, to visualize the effect of predictor terms on the herbivorous fish responses, we used the coefficients from the top-ranked models for each response variable separately to generate a predicted dataset. We set all other predictor terms to their median value then generated smoother terms for the predictor of interest and plotted these against the untransformed, unscaled fish metrics \([11]\).

3. Results

Across the western central Pacific, a large degree of variability exists in the biomass and composition of herbivorous fish assemblages, including the species richness within functional groups. Generally, there is greater biomass and richness of detritivores in Central Polynesia, and a greater biomass of browsers in the unpopulated northerly latitudes \(\text{figure 1 and electronic supplementary material, S4.1}\). Functional group biomass and richness was positively related in large excavators/bioeroders, scrapers/small excavators, and detritivores \(\text{electronic supplementary material, figure S4.2 and table S4.2}\).

Major drivers of this spatial variation in total herbivorous fish biomass were identified as reef complexity, hard coral cover, and human population density \(\text{electronic supplementary material, table S5}\). The original smooths fitted to the functional group and total herbivore biomass values are in the electronic supplementary material, \text{figure S5}. Total herbivore biomass plateaued at intermediate complexity, decreased at highest coral cover, and continually decreased with human population density \(\text{electronic supplementary material, figure S5}\). The best-fit model that contained these three biological variables had high explanatory power and stability \(\text{approx. 69% variability explained in total herbivore biomass, 94% jack-knife stability; electronic supplementary material, table S5}\). When functional groups were modelled individually, the top candidate models showed similar stability. Specifically, the dominant predictors identified from the variable importance \(\text{vi}\) estimates from the top candidate model of the entire dataset matched those identified from the jack-knifing method \(\text{electronic supplementary material, table S5}\). The amount of variance explained by the top-ranking models of herbivore biomass for each functional group \(\text{figure 2}\) was as follows: browsers \(\text{84%}\); detritivores \(\text{84%}\); grazers \(\text{73%}\); scrapers/small excavators \(\text{36%}\); and large excavators/bioeroders \(\text{59%}\); electronic supplementary material, \text{figure S5}\).

The relationship between the top predictor terms and herbivore biomass was distinct for different functional groups. Biomass of large excavators/bioeroders \(\text{all parrotfishes more than 35 cm in total length and browsers was significantly greater at low islands/atolls when compared with high islands (figure 3 and electronic supplementary material, table S5)}\). These were also the only functional groups for which human population density was a strong predictor of biomass \(\text{figure 3 and electronic supplementary material, table S5}\), with both groups declining rapidly from low-to-mid human population density.

The dominant drivers of variability in browsers, detritivores, grazers, and scrapers/small excavators were biophysical. These data showed that reefs in warmer waters have lower browser biomass and greater detritivore biomass and species richness \(\text{figure 3 and electronic supplementary material, table S5}\). Increased detritivore, grazer and scraper/small excavator biomass was evident from low-to-mid habitat complexity. The biomass of grazers continued to increase at high complexity locations, whereas for detritivores and scrapers, large excavators the biomass either plateaued or was reduced at high complexity \(\text{figure 3}\). Locations with a larger amount of fore-reef habitat had greater biomass of detritivores, whereas areas with intermediate wave energy and high chlorophyll a had increased grazer biomass \(\text{figure 3 and electronic supplementary material, table S5}\).
4. Discussion

Our results are consistent with the growing understanding that regional variability in the biophysical attributes of coral reef ecosystems acts to determine ecological state independent of local human impacts [11,61,62]. Specifically, our findings confirm clear anthropogenic impacts to herbivorous fishes across the Pacific, but importantly also show that (i) effects are functional-group-specific, and (ii) the biophysical attributes of reefs, especially SST and large-scale geomorphological habitat complexity also drive herbivorous coral reef fish assemblage states. Prior to this study, quantitative evidence for anthropogenic impacts on herbivorous fishes, while simultaneously accounting for large-scale natural variability in fish assemblages, has been sparse [8,30,31]. To the best of our knowledge, this is the first ocean basin-scale study quantifying the relative effects of human versus natural biophysical drivers of herbivorous fish functional group biomass.

In the absence of fisheries-dependent data on subsistence, recreational and commercial take, human density, and distance to market have proven to be useful proxies for the influence of humans on coral reef fishes [11,63,64]. Our results show a steep and rapid decline in the biomass of large excavators and browsers with increasing human population density. This pattern is consistent with other global and regional assessments documenting the negative effect of fishing on herbivores [27,28]. Herbivorous fishes, in particular large excavating parrotfishes, and browsing surgeonfishes, are highly desired fisheries targets in the Pacific [65–68]. Our results demonstrate the sensitivity of populations of these large herbivores to fishing mortality, presumably owing to their large maximum body size and for some species, late age at maturity and the disproportionate contribution of large old females to population replenishment [65,69–72]. The vulnerability of these two functional groups to human impacts is particularly important as they contribute disproportionately to reef processes [50,73,74].

Herbivores vary in richness, abundance, and biomass by island geomorphology [8,31]. Our results show approximately 24–45% greater biomass of large-excavating and browsing...
The increased biomass of grazers in the areas of moderate wave exposure and increased oceanic productivity could also be related to food availability. Both algal and detrital mass tends to decrease with increasing wave energy and the highest edible algal mass occurs at moderately exposed reefs [85]. The positive association between chlorophyll a and grazer biomass could be owing to greater food availability for grazing fishes, specifically nutrients and sinking detrital particles such as phytodetritus, faeces, or dead planktonic material [77]. If this were the case, then one might expect to see a similar effect on detritivore biomass, however, we did not. Instead, the dominant biophysical driver of variability in detritivore biomass was SST.

Notably, detritivores and browsers showed opposing responses to SST, with browser biomass being negatively and detritivore biomass positively related to SST. Similar decreases in the biomass of browsing fishes with decreasing latitude, and hence SST, are evident in both the Atlantic [25] and southern Pacific Ocean [86]. Temperature fundamentally constrains the metabolic processes of ectotherms, and various hypotheses have been proposed to explain how temperature might impact the performance and fitness of individuals [87]. For instance, the temperature–size rule predicts ectotherms to be smaller in warmer waters, owing to reduced mean body size, earlier maturation, and increased initial growth rates [88–90]. While the temperature-constraint hypothesis relates to the interacting effects of temperature and food quality on fish physiology [25,91]. Here, we found increased browser biomass in cooler waters and increased detritivore biomass in warmer waters. Whether these trends in the standing stock of these functional groups relate to larger individuals and/or intraspecific variability in life-history characteristics across the temperature gradients surveyed would require location-specific, age-based studies on individual species.

The different effect of temperature on these functional groups could also be a response to the very different dietary strategies of these fishes. Browsing acanthurids, such as *Naso unicornis* and kyphosids, are the only functional group that hindgut ferment, which allows these fish to gain energy from refractory fleshy macroalgal carbohydrates, including mannitol [92–95]. Macroalgae, the preferred food of browsers, is more abundant on reefs in cooler climes in the Pacific [61] and thus browser biomass may be tracking the availability of their target resource. It is difficult to ascertain the primary nutrient sources of detritivores that feed on the epilithic algal matrix (EAM) [96]. The EAM contains a mixture of filamentous algal turfs, cyanobacteria, macroalgal spores, microalgae (diatoms and dinoflagellates), heterotrophic bacteria, sediment, and organic detritus [97]. Stomach content analyses of the detritivore *Ctenochaetus striatus* reveal large amounts of loose plant
cells, sediment, and algal filaments while the composition of short-chain fatty acids in Ctenochaetus striatus and Ctenochaetus strigosus guts are indicative of a diet of diatoms and bacteria [51,98]. Whether detritivorous fish biomass tracks spatial variability in the abundance and production of their target resource remains to be established.

5. Conclusion

Our findings highlight that coral reefs’ biophysical setting strongly determine their carrying capacity and community composition of herbivorous reef fishes. Human impacts are superimposed over the backdrop of these naturally occurring drivers. Herbivore-focused management interventions are likely to become more widely implemented owing to the perception that greater herbivore biomass promotes reef resilience. Our results show large natural differences in the capacity of individual reefs to support herbivore populations and therefore, it is unlikely that all reefs will respond similarly to particular interventions, such as prohibition of fishing. Moreover, our results show that herbivore functional groups respond in different ways along gradients of those natural biophysical drivers. Locally appropriate management targets for herbivore functional group biomass must therefore factor in the natural bounds set by the reef’s biophysical setting.

Data accessibility. All raw data collected for the Pacific Reef Assessment and Monitoring Programme are available upon request (email: nmts.pic.credinfo@noaa.gov). All data used within the paper are available at https://github.com/adelheenan/ProcB_herbivores.

Authors’ contributions. A.H., I.D.W., and A.S.H. conceived and designed the analysis; A.H. and G.J.W. performed the analysis; all authors wrote the paper.

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References


