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Herbivory through the lens of ecological processes across Pacific coral reefs

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Abstract

Coral reefs are in global decline primarily due to climate change. Herbivory is often viewed as key to maintaining coral-dominated reefs, and herbivore management is gaining traction as a possible strategy for promoting reef resilience. The functional impact of herbivorous fishes has typically been inferred from total biomass, but robust estimates of ecological processes are needed to better inform management targets. Here, we provide a framework to calculate rates of herbivory across Pacific reefs. We synthesized available observations of foraging metrics in relation to fish body size and found considerable variation, even among closely related species. We then applied these allometric functions to survey data and calculated rates of herbivory for acanthurids and scarines, which make up the vast majority of herbivorous fish biomass in the Pacific. Estimated rates of algal consumption, area scraped, and bioerosion varied across islands, with noticeable differences that may align with the relative influence of human population density among underlying herbivore functional groups. We found no evidence of compensatory relationships among herbivore processes whereby decreasing rates in one type of herbivory is offset by increasing rates in another. We observed nonlinear, positive relationships between fish biomass and rates of herbivory. Yet, for a given biomass, the corresponding rates of herbivory varied among regions, and we observed instances where islands with the greatest biomass did not also have the highest rates of herbivory. Islands with the largest size classes of herbivores did not consistently exhibit greater rates of herbivory, and we did not find a clear, consistent pattern between the number of fish species and corresponding rates of herbivore processes. Cropping *Acanthurus* spp. provided the greatest proportion of algal consumption at every island, yet no single species accounted for the majority of this process, whereas we identified parrotfish species that provided >75% of scraping or bioerosion at certain islands. Our results emphasize the importance of considering the species and size composition of herbivore assemblages when estimating processes, rather than relying on total biomass alone. Lastly, we highlight gaps in foraging observations and

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additional work needed to further broaden our ability to quantify the ecological processes of herbivores.

KEYWORDS
bioerosion, coral reef fishes, ecological process, ecosystem function, grazing, herbivory, tropical Pacific

INTRODUCTION

Marine ecosystems continue to be threatened by global change (Doney et al., 2012; Harley et al., 2006; Poloczanska et al., 2013) in conjunction with local human impacts (Gissi et al., 2021; He & Silliman, 2019; Todd et al., 2019). Together, these stressors are leading to biodiversity loss, the reorganization of communities, and ultimately altering ecosystem functioning and the goods and services they provide (Bannar-Martin et al., 2018; Gamfeldt et al., 2015; Hobbs et al., 2009; Pecl et al., 2017; Worm et al., 2006). Coral reefs are in serious decline worldwide (Gardner et al., 2003; Hoegh-Guldberg et al., 2007; Hughes, Kerry, et al., 2018), primarily due to climate change with extreme thermal events predicted to increase in both frequency and severity (Hughes, Anderson, et al., 2018; van Hooidonk et al., 2016). Such thermal anomalies have resulted in global-scale coral bleaching events (Eakin et al., 2019; Hughes, Anderson, et al., 2018; Skirving et al., 2019) with subsequent shifts in the composition of coral assemblages (Burgess et al., 2021; Graham et al., 2015; Hughes, Kerry, et al., 2018; Moore et al., 2012; Pratchett et al., 2021; Smith et al., 2014), even on remote reefs that are removed from local human pressures (Baum et al., 2023; Baumann et al., 2022).

Herbivory is widely considered to be a core ecological process for maintaining coral-dominated reefs (Bellwood et al., 2004; Brandl et al., 2019) by mediating competition between corals and algae (Hughes et al., 2007). Herbivore management has been proposed as a key management intervention to promote resistance and recovery of reefs—and thereby persistence—in a changing climate (Bellwood et al., 2004; Chung et al., 2019; Cinner et al., 2009; Graham et al., 2013; McClanahan et al., 2012; Mumby & Steneck, 2008; Russ et al., 2015; Williams et al., 2019). Herbivorous fishes vary in their feeding modes and thus functional impact on the benthos (Hoey, 2018). Broad functional groupings are based on feeding substrata, whereby browsers feed predominately on fleshy macroalgae and associated epibiota and grazers feed on substrata colonized by the epilithic algal matrix (EAM; Bellwood et al., 2006). Grazers may be further subdivided into scrapers, excavators, croppers, and detritivores based on the amount of the underlying substrata removed when feeding (Hoey & Bellwood, 2008, 2011; Robinson et al., 2019). Body size can further influence the amount of material removed by individuals, with larger fish removing disproportionately greater amounts of benthic material (Lange et al., 2020; Lokrantz et al., 2008; Nash et al., 2013). Thus, in the face of disturbance, diverse feeding modes and size structures of herbivores can be important for maintaining reefs in a coral-dominant state (Burkepile & Hay, 2008; Lefcheck et al., 2019; Rasher et al., 2013).

Total herbivore biomass has often been used to infer the provision of ecological processes from local fish assemblages on coral reefs; however, this metric does not incorporate variation in the functional role of individual fish both within and among species. To account for this variation, recent studies have developed methods that integrate species- and size-specific data on fish abundance, feeding behavior, and resource intake to estimate rates of herbivory on coral reefs (Kelly et al., 2017; Lange et al., 2020; Perry et al., 2012, 2022; Robinson et al., 2019; Ruttenberg et al., 2019). These methods, however, hinge on in situ foraging observations that are both time-intensive and costly. Efforts to leverage existing observations through data compilation and synthesis can reduce (or eliminate) the additional field effort needed to assess local herbivore communities, thereby broadening the utility of reef-monitoring data to inform management. For example, foraging observations that have been compiled and summarized allow users to calculate parrotfish bioerosion as an input of reef erosion in carbonate budgets (Perry et al., 2012, 2018, 2022).

To understand how herbivory varies in space, we provide a framework to estimate ecological processes across Pacific coral reefs. We first synthesize available data on fish foraging metrics, considering all herbivorous fishes, and examine species- and genus-specific relationships with body size (and temperature for bite rate) within each functional group (i.e., browser, detritivore, cropper, scraper, and excavator). We then apply the resulting allometric equations to fish surveys recently conducted by the National Coral Reef Monitoring Program (NCRMP; funded by the United States National Oceanic and Atmospheric Administration [NOAA] Coral Reef Conservation Program [CRCP]) to calculate rates of ecological processes by acanthurids and scarines (surgeonfish and parrotfish, respectively), which make up the vast majority of herbivore biomass across the Pacific (Heenan et al., 2016). Our results reveal the ecological processes of herbivorous fishes differ across islands and regions due to variance in the combination of fish biomass, species composition, and size structure.

METHODS

Synthesis of foraging metrics

We compiled data sourced from scientific publications, technical reports, and unpublished datasets (Appendix S1: Table S1, Section S1) that were collected in tropical waters, excluding locations in the Atlantic Ocean (Appendix S1: Figure S1). We synthesized foraging metrics of herbivorous fishes that occur across the U.S. Pacific Islands, examining relationships between individual body size and bite rate (in bites per minute), bite area (in square centimeters), bite volume (in cubic centimeters), and proportion of bites that leave grazing scars on the substrate. See Appendix S1: Section S1 for detailed descriptions of data selection, extraction, and preparation.

We expected bite rates to differ with water temperature (Bellwood, 1995; Hoey, 2018; Smith, 2008), yet temperatures at the time of foraging observations were almost never reported. Thus, we estimated the mean monthly sea-surface temperature (SST) from satellite data for every observation (Appendix S1: Section S1) to at least account for broader scale regional variance in temperature. Given that bite rates can further vary across time of day (Bellwood, 1995; Bonaldo & Bellwood, 2008; Khait et al., 2013; Polunin et al., 1995) and depth (Brokovich et al., 2010; Fox & Bellwood, 2007), we also compiled these metadata when reported by studies (Appendix S1: Section S1); however, only about a third of studies provided such information, preventing direct assessment of these variables as covariates. We did, however, review the reported times of day and excluded any observations that were conducted outside of the overall range of the majority of studies (06:00–18:30; Appendix S1: Figure S2), such as observations conducted at night. In contrast to bite rate, we expected bite area, bite volume, and the proportion of bites that result in grazing scars to be mostly dependent on the morphology and body size of fish.

We excluded observations of zero total bites and any bite areas or volumes of zero (i.e., bites that did not result in a measurable mark). Only among proportions of bites that left grazing scars did we maintain zeros since all studies reported them in a consistent manner. The resulting datasets per species consisted of individual observations (raw data) and mean responses and errors from pooled observations (aggregate data), or a combination of both. We analyzed responses that encompassed an overall range in fish size of at least 10 cm total length (TL), and a minimum sample size of five raw or three aggregate values. In instances where we did not have enough observations to assess the bite area of a parrotfish but could assess the bite volume for that species (or vice versa), we converted between area and volume using bite depths of 0.01 cm for scrapers and 0.15 cm for bioeroders (Bellwood, 1995).

We modeled foraging metrics per species and per genus within functional group (hereafter "function–genus") as a function of body size as follows: negative binomial generalized linear models (GLMs) with a log link function for over-dispersed bite-rate data, power regressions of bite area and volume, and logarithmic regressions via binomial GLMs with a logit link function for proportion of scars. Among bite rates, we further assessed the additive effect of SST since we did not expect temperature to alter the functional relationship between bite rate and body size. We used meta-analytical models or GLMs as appropriate to analyze datasets with aggregate data (Stijnen et al., 2010). We incorporated *study* as a random effect for models of all raw or all aggregate data from multiple studies and *replicate* nested within *study* to account for the hierarchical data structure for models of a combination of raw and aggregate data. In models with aggregate data, weights consisted of the inverse SE (bite rate, area, and volume) and sample size (proportion of scars), capped between the overall 5th and 95th percentiles to prevent any single weight from greatly overpowering all other observations.

Ecological processes from survey data

To calculate herbivory across the jurisdictional regions of the U.S. Pacific Islands, we applied the synthesized relationships between foraging metrics and body size to recent surveys conducted by the NCRMP. All of the synthesized equations and summaries of data that informed each model are available in a public repository (https://doi.org/10.6084/m9.figshare.23672010.v1). NCRMP surveys occurred in Guam and the Commonwealth of the Northern Mariana Islands (2017), American Samoa (2018), the Pacific Remote Islands Area (2018), and Hawaii (2019) and the Northwestern Hawaiian Islands (2017). Survey effort was allocated around each island or atoll in accordance with the area of forereef stratified by depth bin: shallow (>0–6 m), mid (6–18 m), and deep (18–30 m). Adhering to this proportional allocation, sites were then randomly distributed within each stratum. Fish surveys at each site consisted of stationary point counts (SPC) conducted by a pair of divers conducting simultaneous surveys in adjacent cylindrical plots, each 15 m in diameter. Divers visually estimated the number and size of fish to the nearest centimeter TL within each of their respective cylinders (see Ayotte et al., 2015; Heenan et al., 2017, for more details). SPC surveys can under-represent herbivore biomass (Williams et al., 2010) and the density of less mobile (sedentary) acanthurids (Samoilys & Carlos, 2000) relative to the more widely used belt transect method (Caldwell et al., 2016); thus, our estimates of herbivory and biomass may be conservative.

We focused on the processes of the main herbivores in the Pacific, acanthurids and scarines (Heenan et al., 2016), which were also the fish with an ample amount of synthesized foraging functions. Individuals were further defined by their functional groups (browser, detritivore, cropper, scraper, and excavator) based on the observed species and size; this further accounted for known shifts in function with size for several species (Green & Bellwood, 2009; Heenan et al., 2016). We calculated foraging metrics for each observed fish, using higher level equations of function–genus when species-specific equations were unavailable. The resulting values were then used as inputs to calculate individual rates of algal consumption for acanthurids (browsers, detritivores, and croppers) and browsing scarines (*Calotomus* spp.), and area scraped and bioerosion for scraper and excavator parrotfishes:

$$\begin{aligned}&\text{Algal consumption}\ \left(\text{kg ind.}^{-1}\,\text{year}^{-1}\right)\\&\quad=\text{bites}\ \left(\text{min}^{-1}\right)\times\text{biomass per bite}\ \left(\text{g dry mass}/10^{3}\right)\\&\qquad\times 60\ (\text{min})\times\text{hours of daylight}\times 365\ \text{days},\end{aligned}$$

$$\begin{aligned}&\text{Area scraped}\ \left(\text{m}^{2}\,\text{ind.}^{-1}\,\text{year}^{-1}\right)\\&\quad=\text{bites}\ \left(\text{min}^{-1}\right)\times\text{bite area}\ \left(\text{cm}^{2}\right)/10^{4}\times P(\text{scar})\\&\qquad\times 60\ (\text{min})\times\text{hours of daylight}\\&\qquad\times\text{proportion of daytime feeding}\times 365\ \text{days},\end{aligned}$$

$$\begin{aligned}&\text{Bioerosion}\ \left(\text{kg ind.}^{-1}\,\text{year}^{-1}\right)\\&\quad=\text{bites}\ \left(\text{min}^{-1}\right)\times\text{bite vol}\ \left(\text{cm}^{3}\right)\times P(\text{scar})\\&\qquad\times\text{carb density}\ \left(\text{g cm}^{-3}\right)/10^{3}\times 60\ (\text{min})\\&\qquad\times\text{hours of daylight}\times\text{proportion of daytime feeding}\\&\qquad\times 365\ \text{days}.\end{aligned}$$

Algal biomass removed per bite (in grams of dry mass/10^3) was calculated as $4\times10^{-8}\times(\text{TL})^{3.3307}$ for acanthurids and $5\times10^{-10}\times(\text{TL})^{4.3744}$ for browser scarines as defined by Kelly et al. (2017). We used 12 h of daylight for the islands closest to the equator (Howland, Baker, Kingman, Palmyra, and Jarvis of the Pacific Remote Islands Areas) and 10 h for all other islands. We used 0.833 for excavators and 0.877 for scrapers as the proportions of daytime feeding (adapted from Bellwood, 1995). Diurnal feeding patterns of acanthurids have not been well documented; thus, we did not include proportional feeding as a component of algal consumption in order to remain consistent between estimates of acanthurids and browser scarines. Using values reported in the Western, Central, and South Pacific regions from Perry et al. (2018), we calculated $1.45\pm0.20\ \text{g cm}^{-3}$ as the mean density of reef carbonate ("carb density"). This value was similar to the lower end of the range reported in Hawaii (1.46–2.08 g cm^{-3}; Ong & Holland, 2010), as well as mean values in the Chagos Archipelago (1.52 g cm^{-3}; Lange et al., 2020) and Maldives (1.44 g cm^{-3}; Morgan & Kench, 2016) in the Indian Ocean.

Individual rates were combined with density data (number of individuals per square meter) consisting of species-size counts divided by the area of the survey cylinder ($\pi\times7.5^2$) to calculate community-level annual rates of each process per unit area (in square meters). We also calculated fish biomass using length-to-weight conversion parameters from FishBase (Froese & Pauly, 2021; summarized in Heenan et al., 2017). Herbivore biomass and rates of processes were averaged between each pair of adjacent survey cylinders to generate site-level estimates. Similar to previous efforts (Heenan et al., 2016), we inspected site-level estimates and defined outlier values as those greater than the 99% interquartile range. These observations tended to consist of encounters with extremely large schools of individual species that introduce large variability in the data. We therefore capped outliers at the respective 99% quantiles. We calculated summary statistics by averaging across sites within each depth stratum, which we then weighted by the area of each stratum when pooling up to the spatial unit of island or atoll. We used Gamma GLMs with a log link function to test whether herbivore processes correlate with fish biomass and regressions to test for correlations between processes. For all models, we first tested interactions with *region* and conducted post hoc Tukey's tests as needed for pairwise comparisons between regions.

All data manipulation, analysis, and visualization were conducted in R (version 3.6.2; R Core Team, 2021) with the packages metafor (version 2.4.0; Viechtbauer, 2010), lme4 (version 1.1.26; Bates et al., 2015), and glmmTMB (version 1.1.4; Brooks et al., 2017).

RESULTS

Synthesis of foraging metrics

We synthesized relationships between body size and parameters that inform algal and reef-substrate removal for a total of 47 fish species from 11 genera (Appendix S1: Table S2). Information about bite rate was the most abundant in regards to the variety of species and genera observed and the geographical spread of studies (Appendix S1: Figure S1). Bite rate relationships varied among species (Appendix S1: Table S3) and function–genus groups (Appendix S1: Table S4). Bite rates significantly decreased with body size (except among *Scarus flavipectoralis*, *Acanthurus blochii*, and *A. nigricans*) and significantly increased with SST for all but *A. blochii* (Appendix S1: Figures S3 and S4). Across bite rate observations, SST values ranged from 22 to 30°C yet were skewed in frequency toward the warmer end of the range (Appendix S1: Figure S2). Of the 39 studies reporting bite rates, only about a third provided information about the water depth ($n = 12$ studies) or time of day ($n = 13$ studies) of the observations. Among those studies, only three conducted observations in depths greater than 10 m (0.067% of observations), and the majority occurred at depths less than 5 m (Appendix S1: Figure S2).

We detected positive relationships in both bite area and volume with body size across almost all parrotfish species and function–genera with a sufficient amount of data (Appendix S1: Tables S3 and S4, Figures S5 and S6). Almost half of the parrotfish species and all of the parrotfish function–genera we could assess significantly increased in the proportion of bites that left grazing scars with increasing body length (Appendix S1: Tables S3 and S4, Figure S7). Across all three of these foraging metrics, excavators tended to have larger values than scrapers (Appendix S1: Figures S5–S7).

Ecological processes across the Pacific

Across the Pacific, we observed variability in herbivore processes across regions, as well as among islands within regions (Figure 1). Estimated algal consumption of browsers, detritivores, and croppers ranged by about an order of magnitude, from the lowest mean value at Guam (S. Marian) of 0.051 ± 0.006 kg m^{-2} year^{-1} to the greatest at Kahoolawe (MHI) of 0.527 ± 0.085 kg m^{-2} year^{-1}. Kingman Reef (PRIA) had the highest mean levels of both area scraped (1.346 ± 0.559 m^{2} m^{-2} year^{-1}) and bioerosion (2.680 ± 0.997 kg m^{-2} year^{-1}) by scraper and excavator parrotfishes, whereas Kauai (MHI) had the lowest values which were respectively about two and three orders of magnitude lower (area scraped: 0.013 ± 0.009 m^{2} m^{-2} year^{-1}; bioerosion: 0.002 ± 0.002 kg m^{-2} year^{-1}). Herbivore processes increased nonlinearly with fish biomass and further varied among regions (Appendix S1: Table S5; Figure 2). Algal consumption was the highest in the Main Hawaiian Islands and lowest in the Southern Marianas, whereas area scraped and bioerosion tended to be lower in the Northwestern Hawaiian Islands and Main Hawaiian Islands, respectively (Appendix S1: Table S6).

Although there were overall positive trends between biomass and herbivory, we also observed several islands with the greatest biomass that did not also have the highest rates of a given process (Figure 2). For example, among estimates of parrotfish-only processes (scrapers and excavators), Jarvis Island (PRIA) was an outlier; despite having the greatest biomass in the Pacific, area scraped and bioerosion did not scale accordingly and were lower than expected (Figure 2b,c). Removal of these values from Jarvis Island resulted in the interaction between fish biomass and region no longer being significant in best-fit models (Appendix S1: Table S5). In contrast, islands with the lowest biomass tended to align with the lowest rates of processes (Figure 2). For example, both biomass and herbivory in the Southern Marianas region tended to be lower in magnitude relative to the other regions (Figure 2); in particular, algal consumption there was the lowest of all the Pacific regions (Appendix S1: Table S6). Furthermore, the ranges in these values were greatly limited in the Southern Marianas and had yet to reach levels in biomass that corresponded with a disproportionate increase in herbivory (Figure 2).

Among island assemblages, we did not find a clear, consistent pattern between the number of fish species and corresponding rates of herbivory (Appendix S1: Figure S8). Similarly, islands with the largest size classes of herbivores did not always correspond with the highest levels of processes (Appendix S1: Figure S9), although islands with the lowest biomass (e.g., Southern Marianas region) or rates of processes tended to lack larger sized herbivores (Appendix S1: Figure S9). The degree of accordance in proportional provision of herbivores to ecological processes versus biomass also varied across islands and regions (Appendix S1: Figures S10 and S11). Cropping *Acanthurus* spp. consistently provided the greatest proportion of algal consumption at every island (Figure 3a), and proportional consumption by some of these species exceeded their proportional biomass within certain islands (Appendix S1: Figure S10), yet no single species within any function–genus accounted for ≥75% of this process (Appendix S1: Figure S8a). Relatively larger proportions of feeding by excavator parrotfishes, particularly *Chlorurus* spp., tended to occur among islands with higher rates of scraping and especially bioerosion (Figure 3b,c). This explains why the high fish biomass at Jarvis Island, likely driven by the large

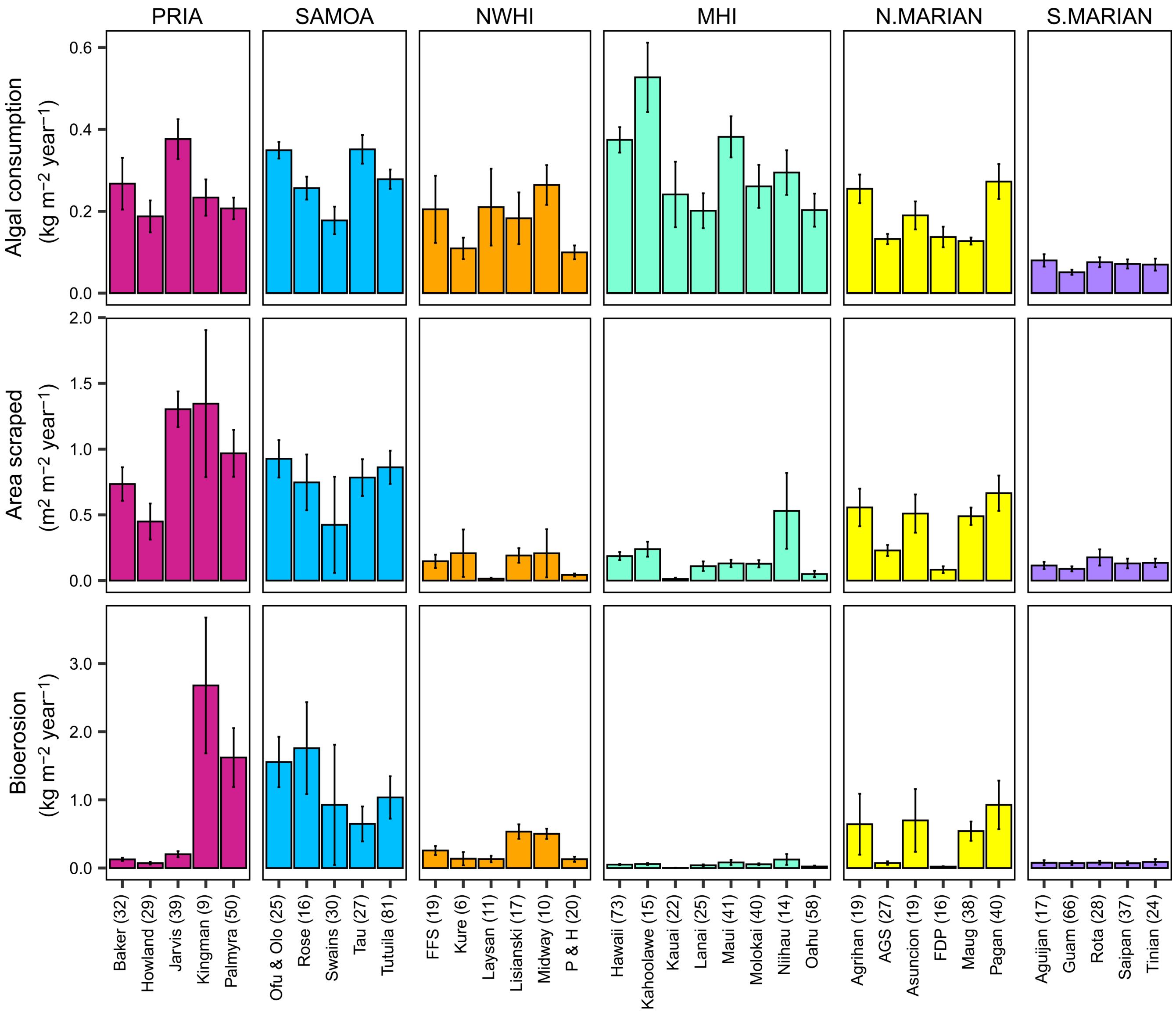

FIGURE 1 Herbivore processes across Pacific coral reefs. Error bars are SE of the mean. Algal consumers are acanthurids (browsers, detritivores, and croppers) and browsing scarines (*Calotomus* spp.), and the remaining parrotfishes are scrapers and bioeroders. Numbers in parentheses indicate the number of sites surveyed per island. Islands are abbreviated as follows: AGS, Aguijan, Guguan, and Sarigan combined; FDP, Farallon de Pajaros; FFS, French Frigate Shoals; Ofu & Olo, Ofu and Olosega; P & H, Pearl and Hermes.

size classes present (Appendix S1: Figure S9b,c), did not reach predicted rates of scraping and bioerosion for its region (Figure 2b,c); scraper and excavator *Scarus* spp. provided the majority of these processes rather than *Chlorurus* spp. (Figure 3b,c).

Per island, excavator parrotfishes tended to provide larger proportions of bioerosion than scraping, and scraper parrotfishes typically contributed larger proportions of scraping than bioerosion (Figure 3b,c). The excavating parrotfish *Chlorurus microrhinos* (CHMC) provided 84.7% of area scraped and 97.7% of bioerosion at Kingman Reef (Appendix S1: Figure S8b,c), as well as >80% of bioerosion at three other islands with relatively high rates (Palmyra Atoll = 82.7%, Asuncion Island = 90.9%, Swains Island = 95.6%; Appendix S1: Figure S8c). Across several Northwestern Hawaiian Islands, scraping parrotfish contributed the majority of area scraped (*Chlorurus spilurus* [CHSL]: 77.2% at Lisianski Island; *Scarus dubius* [SCDU]: 86.7% at Kure Atoll and 89.2% at Midway Atoll) and bioerosion (*Chlorurus perspicillatus* [CHPE]: 81.7% at Laysan Island and 76.3% at Lisianski Island). Bioerosion was relatively low at Farallon de Pajaros and Lanai, and was provided mostly by scrapers *Scarus forsteni* (SCFO; 76.0%) and smaller sized *C. spilurus* (CHSL; 77.8%), respectively (Appendix S1: Figure S8c). Where identified, proportional area scraped and bioerosion by these parrotfishes also tended to outpace their proportional biomass (Appendix S1: Figure S11).

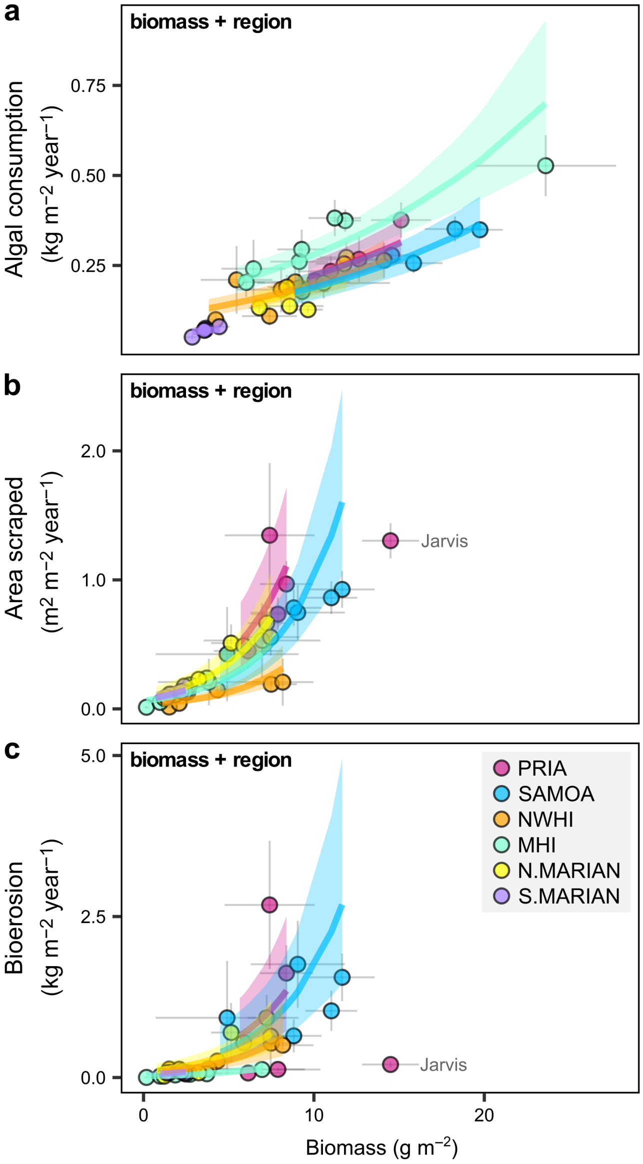

FIGURE 2 Relationships between herbivore processes in relation to fish biomass and region across Pacific coral reefs. Algal consumers are acanthurids (browsers, detritivores, and croppers) and browsing scarines (*Calotomus* spp.), and the remaining parrotfishes are scrapers and bioeroders. Error bars are SE of the mean. Trend lines and 95% CIs are from best-fit models, with significant variables in bold inside each plot. Where labeled, Jarvis Island was excluded from final models as an outlier.

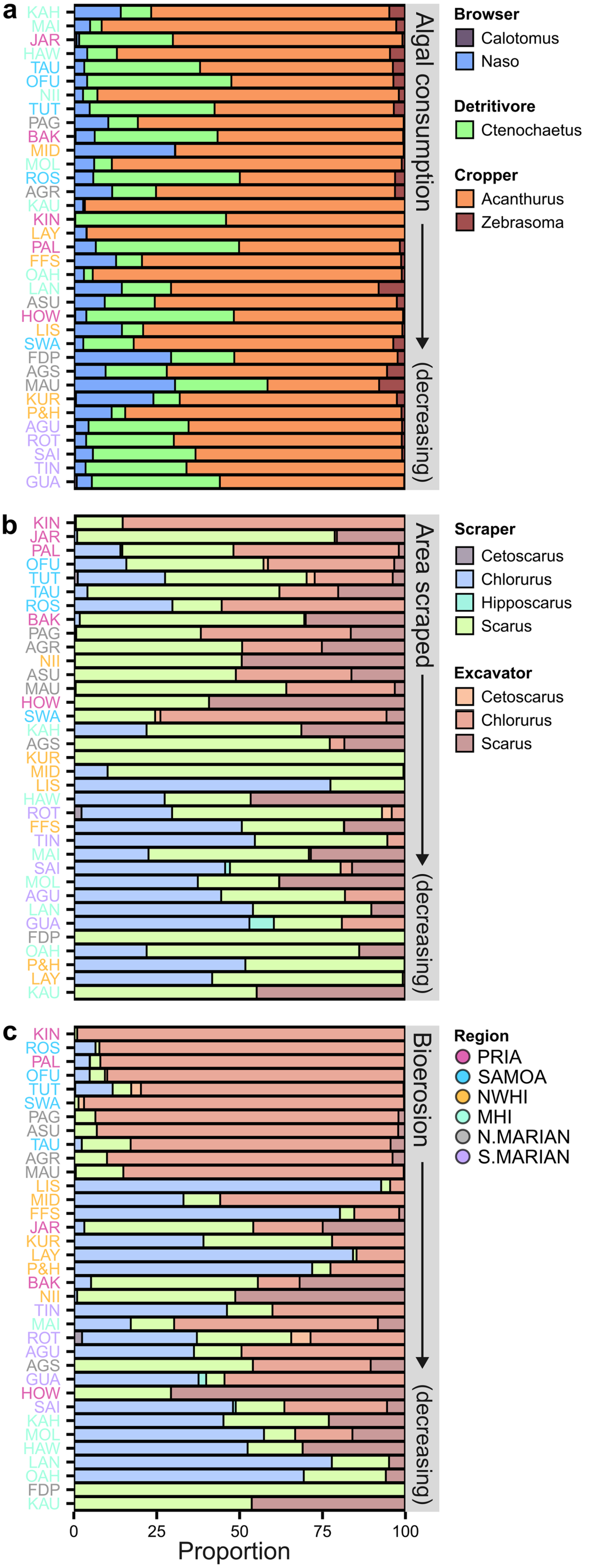

FIGURE 3 Proportional herbivore processes per fish genus within functional group ("function–genus") per island. Islands are ordered from top to bottom in decreasing rates of process. Island labels are color-coded by region.

Although in the Main Hawaiian Islands we found a contrast consisting of the highest rates of algal consumption and lowest rates of bioerosion in the Pacific (Appendix S1: Table S6; Figure 2), we did not detect an overall relationship between these processes (Appendix S1: Table S7; Figure 4b). Area scraped, however, increased with algal consumption (Appendix S1: Table S7; Figure 4a). Among models testing for correlations between herbivore processes, regional variance was consistently significant

(Appendix S1: Tables S7 and S8; Figure 4). Exclusion of Jarvis Island had no influence on the final variables in best-fit models of correlations with algal consumption (Appendix S1: Table S7); we used the full dataset when assessing those correlations. We did, however, remove Jarvis Island when examining the relationship between parrotfish-only processes (Figure 4c), which resulted in a significant interaction between area scraped and region (Appendix S1: Table S7).

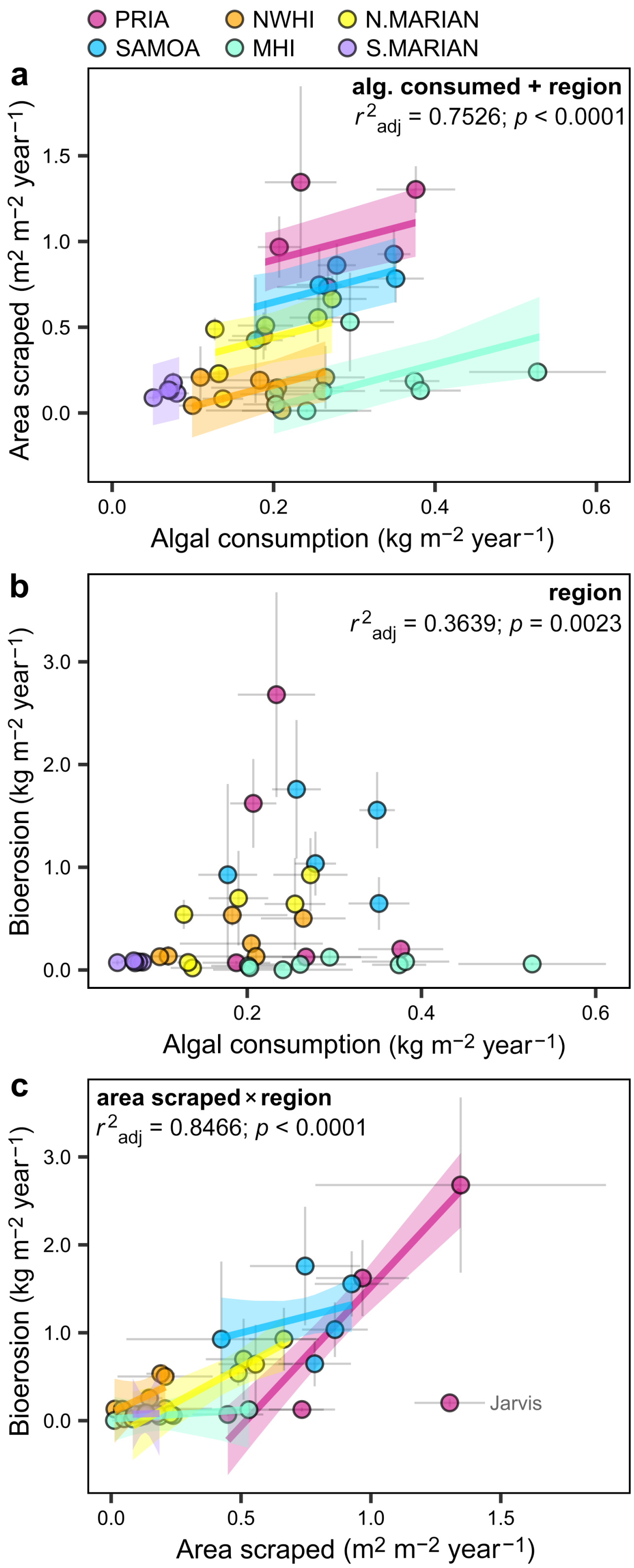

FIGURE 4 Relationships between herbivore processes and region. Algal consumers are acanthurids (browsers, detritivores, and croppers) and browsing scarines (*Calotomus* spp.), and the remaining parrotfishes are scrapers and bioeroders. Error bars are SE of the mean. Trend lines and 95% CIs are from best-fit models, with significant variables in bold inside each plot. Where labeled, Jarvis Island was excluded from final models as an outlier.

DISCUSSION

Across the Pacific, we detected regional variance in the ecological processes of herbivorous fishes. Overall, we observed nonlinear, positive relationships between fish biomass and rates of herbivory, consistent with parrotfish scraping and erosion in the Maldives and Chagos Archipelago (Lange et al., 2020; Taylor et al., 2022). For a given level of biomass, the corresponding rates of herbivory varied among regions, and we observed instances where islands with the greatest biomass did not also have the highest rates of herbivory. This was especially apparent at Jarvis Island, where despite having the greatest parrotfish biomass in the Pacific, the area scraped and bioerosion rates were lower than predicted. This is likely attributed to *Scarus* spp. providing most of the scraping and bioerosion at Jarvis Island, whereas islands with the highest rates predominantly feature large contributions from excavator *Chlorurus* spp. Indeed, our synthesis of foraging metrics revealed *Chlorurus* spp. reach larger bite areas and volumes than *Scarus* spp., thus having a larger functional impact (Hoey, 2018). We conclude that total biomass of herbivorous fishes per se is an imperfect predictor of ecological processes, and we emphasize the importance of fish identity underlying herbivory, which was similarly concluded in the Florida Keys (Ruttenberg et al., 2019) and Indo-Pacific regions (e.g., Bellwood et al., 2012; Lange et al., 2020; Robinson et al., 2019; Yarlett et al., 2018).

Rates of algal consumption in the Main Hawaiian Islands were among the highest in the Pacific, which may complement the region's low rates of parrotfish herbivory. We did not, however, find evidence of compensatory relationships among herbivore processes whereby decreasing rates in one type of herbivory is offset by increasing rates in another (i.e., negative correlations). In fact, we found algal consumption is decoupled from bioerosion across the Pacific, and correlations between remaining combinations of processes were generally positive. Parrotfish processes in the Florida Keys are also positively correlated in certain reef zones (Ruttenberg et al., 2019), whereas others have shown these processes are decoupled in the Indo-Pacific (e.g., Bellwood et al., 2012; Hoey & Bellwood, 2008). The discrepancy in algal consumption correlating with parrotfish scraping but not bioerosion across the Pacific may be linked to human population density (Bellwood et al., 2012; Edwards et al., 2014; Heenan et al., 2016) and fishing (Bejarano Chavarro et al., 2014; Houk et al., 2012; Mccauley et al., 2014; Sabater & Carroll, 2009), which heavily influence large excavating parrotfishes and browsers, and less so scrapers, croppers, or detritivores. We found browsers contributed relatively low proportions of algal consumption, especially browsing parrotfishes that tend to be rare and have a limited impact on algae removal in the Indo-Pacific (Hoey & Bellwood, 2008, 2009; Michael et al., 2013). Thus, we might expect a weaker signal of human drivers underlying algal consumption and area scraped than bioerosion in the Pacific. Indeed, this hypothesis may further explain the noticeable differences in herbivory we observed among regions, including the highest algal consumption and lowest bioerosion in a more heavily populated region, the Main Hawaiian Islands.

Islands with the lowest herbivore biomass typically also had the lowest rates of herbivory, and contributions from larger herbivores tended to be lower or the largest size classes were missing altogether. This was particularly apparent in the Southern Marianas region where levels of biomass and herbivore processes were greatly limited in range at the lower end of Pacific-wide values. Yet overall, any patterns in the number of size classes (or species) that appeared to align with the variance in rates of herbivory were not consistently upheld by all islands in the Pacific. Importantly, formal assessments of the role of biodiversity in enhancing herbivory should consider multiple spatial scales (i.e., site and region) when relating diversity metrics to biomass-standardized herbivory rates (Lefcheck et al., 2019).

Similar to parrotfish herbivory in the Atlantic (Ruttenberg et al., 2019) and locations within the Great Barrier Reef and Indo-Pacific (Bellwood et al., 2012; Hoey & Bellwood, 2008; Loffler et al., 2015), we were able to identify key parrotfishes that accounted for the majority of scraping or bioerosion at certain islands, yet algal consumption was typically conducted by a greater mix of species. Locations where herbivore processes were dominated by one or two species may warrant further consideration for targeted management, but these results may also suggest increased vulnerability of ecosystem function to species loss than islands with more diverse assemblages (Hooper et al., 2005; Lefcheck et al., 2015, 2019). Nonetheless, islands with speciose communities could still have limited functional redundancy if there is little overlap in functional roles (Bellwood et al., 2003, 2004). For example, the loss of large excavators can reduce bioerosion, whereas other processes that are supported by less-targeted species may be maintained through compensatory feeding by smaller fish (Bellwood et al., 2012).

Our synthesis of foraging metrics revealed variance among species that emphasizes the importance of defining species-specific relationships (Ruttenberg et al., 2019). For example, the elevated bite areas, volumes, and proportions of scars of *Chlorurus microrhinos* drove the overall model estimates for excavator *Chlorurus* spp. as a function–genus group. Although these higher-level models were useful when we lacked species-specific models for particular excavating species (e.g., *C. frontalis*), we may have overestimated the functional impact of those species. Similarly, individual rates of algal consumption would be improved with species-specific estimates of algal biomass removed per bite, rather than applying general equations for acanthurids and browser scarines (Kelly et al., 2017).

Lastly, we highlight the need for consistent reporting of metadata to accompany observations of foraging behavior in order to better account for known sources of variance when synthesizing multiple datasets, and to understand important caveats when applying outputs to local surveys. We detected variance in bite rate with SST among only seven species, although the lack of a relationship with SST may reflect a limited range in SST values across observations of a given species. Reporting in situ water temperature when observing foraging behavior of herbivores would enhance our understanding of finer scale variance in bite rates, as has been demonstrated with seasonal variance in temperature (Afeworki et al., 2013; Bellwood, 1995; Ong & Holland, 2010; Smith, 2008). In addition, herbivores exhibit diel feeding patterns (Bellwood, 1995; Bonaldo & Bellwood, 2008; Khait et al., 2013; Polunin et al., 1995) and bite rates can further vary with depth (Brokovich et al., 2010; Fox & Bellwood, 2007). Only about a third of the studies we incorporated in our synthesis provided information about either of these variables, and those that did consisted of observations of bite rates that were skewed toward shallower depths of <5–10 m. The Pacific-wide surveys we assessed span a broader depth range of >0–30 m; thus, we might expect the herbivory we estimated to further vary at deeper depths. We also recommend capturing the benthic composition of reef areas where fish are observed (e.g., Bejarano, 2009; Kelly et al., 2016) to include resource availability (e.g., percent cover of macroalgae or turf) as a covariate in syntheses of foraging metrics.

To enhance the accuracy of estimates of herbivory on coral reefs, a relative metric of diet composition (i.e., selectivity, or the amount of resource consumed relative to the amount of resource available) could be incorporated into estimates. There is also a clear need to broaden the types of organisms we can assess. Efforts to date have focused almost entirely on foraging by acanthurids and scarines, yet other taxa such as siganids and kyphosids are common and abundant herbivores in the Indo-Pacific (Choat et al., 2002; Fox & Bellwood, 2008; Hoey et al., 2013; Hoey & Bellwood, 2009; Loffler et al., 2015; Michael et al., 2013; Vergés et al., 2012). An even more inclusive approach would consider any fish known to ingest algae during any life stage. For example, we accounted for shifts in feeding mode with size among excavating species that function as scrapers prior to transitioning to excavators (Bonaldo et al., 2014; Ong & Holland, 2010) and included individuals of *Naso* spp. only when their size corresponded with algal browsing (Green & Bellwood, 2009). This flexibility supports the call for adaptive functional groups (Bellwood et al., 2018) and demonstrates the advantage of using relationships that allow for size-related shifts in relevant foraging metrics. Furthermore, interference competition between herbivorous fishes and urchins can impact levels of algal consumption (Hay & Taylor, 1985) and urchins can be as effective as parrotfish in preventing algal-turf dominance on some reefs (Humphries et al., 2020). By considering any organisms with herbivory as a component of their niche, we can better determine the degree of functional redundancy in an ecosystem as well as the extent to which ecosystem function is maintained on reefs subjected to local disturbances or human impacts.

CONCLUSION

We have provided the framework to estimate herbivory in the Pacific, expanding on previous efforts (e.g., Lange et al., 2020; Perry et al., 2022; Ruttenberg et al., 2019) to assess functional impact beyond parrotfishes. As in other locations (Lange et al., 2020; Perry et al., 2022; Ruttenberg et al., 2019), we found herbivory in the Pacific is determined by a combination of fish biomass, species composition (including key herbivores), and population size structure. We therefore conclude that although nonlinear increases in rates of herbivory with total biomass suggests the potential for threshold values, we too advise against defining management targets based on thresholds of total biomass alone (Ruttenberg et al., 2019). Future work should relate rates of herbivory to reef condition and benthic composition, and incorporate temporal assessments to elucidate when and where ecological processes are enhanced (e.g., positive feedback following disturbance; Mumby & Steneck, 2008; Taylor et al., 2020; van de Leemput et al., 2016) versus impeded (e.g., grazing refuges; Bozec et al., 2019). Ultimately, this information should help managers quantify location-specific targets needed to maintain sufficient levels of ecological processes. Estimating herbivory should also help with assessments of candidate sites for reef restoration actions such as coral outplanting (Ladd et al., 2018; Seraphim et al., 2020). Lastly, synthesis and meta-analysis will continue to serve as a critical tool to ascertain general patterns in the functional impact of organisms. We have highlighted gaps in foraging observations of herbivores so that future research can be strategically leveraged to minimize the effort required to enhance our overall understanding of ecological processes and ecosystem function.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Two sets of data were analyzed: (1) a database of fish foraging observations compiled by the authors, and (2) fish survey data collected in the Pacific by the National Coral Reef Monitoring Program (NCRMP). Data are available from the NOAA National Centers for Environmental Information (NCEI) as follows:

Database of foraging observations:

1. Appendix S1: Table S1 provides an overview of all the data sources compiled and analyzed, and an indicator ("Public data") of data that we have made publicly available.
2. These public data are available from NCEI: https://accession.nodc.noaa.gov/0259399.
3. Remaining data supporting this research are sensitive and not available publicly. Appendix S1: Table S1 indicates which data are not public and were provided to us directly from each cited source who owns the rights to these data. The citation for each source is provided, and data can be requested by contacting the corresponding author using the contact information provided therein. Restrictions may apply at the discretion of the respective parties who own the rights to the data.

NCRMP surveys: all fish data analyzed and species-specific length–weight parameters are publicly available from NCEI.

1. American Samoa: https://accession.nodc.noaa.gov/0183543.
2. Main Hawaiian Islands: https://accession.nodc.noaa.gov/0210958.
3. Northwestern Hawaiian Islands: https://accession.nodc.noaa.gov/0181483.
4. Guam and the Commonwealth of the Northern Mariana Islands: https://accession.nodc.noaa.gov/0166381.
5. Pacific Remote Islands Area: https://accession.nodc.noaa.gov/0183544.

All R code and associated datasets (Kindinger et al., 2024) are available from Figshare: https://doi.org/10.6084/m9.figshare.23672010.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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