

Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales

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Abstract. Overexploitation of key species can negatively impact ecosystem processes, so understanding the ecological roles of individual species is critical for improving ecosystem management. Here, we use coral reefs and the process of herbivory as a model to examine how species identity of consumers influence ecosystem processes to inform management of these consumers. Herbivorous fishes can facilitate the recruitment, growth, and recovery of corals by controlling the fast-growing algae that can outcompete corals for space. However, herbivorous fish guilds are species rich with important differences among species in diet, movement, and habitat preferences. Yet, we lack a general understanding of (1) how these species-specific differences in feeding and behavior scale up to reef-wide rates of ecosystem processes and (2) how species identity and diversity impact these processes. To address these knowledge gaps, we used field observations to derive key species- and size-specific foraging parameters for nine herbivorous parrotfish species on coral reefs in the Florida Keys, USA. We then combined these foraging parameters with fish survey data spanning multiple spatial scales to estimate the rates of three ecosystem processes: area of reef grazed, amount of macroalgae removed, and rate of bioerosion. We found that predicted rates of ecological processes varied dramatically among habitats and among reef zones within habitats, driven primarily by variation in abundance among species with different foraging behaviors. In some cases, assemblages with similar levels of total biomass had different rates of ecological processes, and in others, assemblages with different biomass had similar rates of ecological processes. Importantly, our models of herbivory using species-specific parameters differed from those using genus-level parameters by up to 300% in rates of ecological processes, highlighting the importance of herbivore identity in this system. Our results indicate that there may be little overlap in the roles species play, suggesting that some systems may be vulnerable to loss of ecological function with the reduction or loss of just a few species. This work provides a framework that can be applied across the region to predict how changes in management may affect the ecological impact of these important herbivores.

Key words: bioerosion; coral reef; ecological impacts; facilitation; Florida Keys; grazing; herbivory; macroalgae; parrotfish.

INTRODUCTION

The defaunation of ecosystems continues unabated with larger animals at the highest risk of overexploitation and, ultimately, extinction (Dirzo et al. 2014, McCauley et al. 2015). This loss of consumer diversity clearly impacts the function of many ecosystems (Hooper et al. 2012, Lefcheck et al. 2015). Declining herbivore diversity can impact primary production, plant diversity, consumption of producer biomass, and

links to upper trophic levels (Duffy et al. 2007, Burkepile and Parker 2017). While the loss of important herbivore species and declines in diversity clearly impact a variety of ecosystem functions, it is not clear whether these changes in ecosystem processes are due to complementarity among herbivore species or the idiosyncratic importance of individual species (Cardinale et al. 2006).

Coral reefs are an excellent model system in which to examine how identity and functional diversity of herbivores can impact ecosystem processes, processes that are increasingly important for managing these systems (Bellwood et al. 2004). Herbivores are important in coral reef ecosystems since they can facilitate the settlement, growth and resilience of corals by controlling the fast-growing algae that compete with corals for space

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(Hughes 1994, Hughes et al. 2007, Adam et al. 2015a). Over the last several decades, coral cover on Caribbean reefs has declined precipitously (Gardner et al. 2003, Schutte et al. 2010, Jackson et al. 2014), likely driven by a combination of global factors such as climate change, regional factors such as disease, and local factors including fishing and land-based sources of pollution (Hughes 1994, Bellwood et al. 2004, Hoegh-Guldberg et al. 2007). All of these factors have played a role in the loss of live coral in the Caribbean, but the loss of key herbivores is likely a key contributor to an increase in algae and loss of resilience of corals across the region (Hughes 1994, Jackson et al. 2014, Adam et al. 2015a, Zaneveld et al. 2016).

The Caribbean-wide die-off of the herbivorous sea urchin *Diadema antillarum* in the mid 1980s left parrotfishes as the dominant herbivorous group on many Caribbean reefs (Williams and Polunin 2001, Hughes et al. 2010, Schutte et al. 2010, Jackson et al. 2014). As herbivores, parrotfishes play several key roles in coral reef ecosystems. Some species remove turf algae by scraping and excavating the carbonate reef framework. This action can provision space and create microhabitats that are suitable for coral recruitment (McCook et al. 2001, Hughes et al. 2007). Other species target macroalgae that may directly compete with existing corals for space. These macroalgal browsers can be important for controlling macroalgae that would otherwise harm reef-building corals (Bellwood et al. 2006, Burkepile and Hay 2008, 2010, Rasher et al. 2011, but see Suchley et al. 2016). Finally, species that excavate the carbonate framework to target crustose and endolithic algae can act as significant bioeroders and can be key sources of sediment production on reefs (Hubbard et al. 1990, Bruggemann et al. 1996, Bellwood et al. 2012, Perry et al. 2014). Collectively, these processes help shape reef ecosystems.

In recognition of the importance of the ecological roles parrotfish play in coral reef resilience, previous work has sought to better understand the net ecological impacts of parrotfish herbivory on reef ecosystems (Mumby 2006, Perry et al. 2013, Bozec et al. 2016). These studies have generally assumed that foraging behavior and diets of parrotfishes are strongly conserved phylogenetically. Therefore, to predict the impacts of herbivory of a parrotfish assemblage, researchers have often applied field-derived behavioral data from one species in a genus to other congeners. These models have been extremely influential for both basic and applied research on how herbivory impacts coral reef ecosystems. However, parrotfishes display species- and size-specific foraging behaviors; different species of parrotfish, even within a genus, vary in their diet preference, target certain reef substrates, and have different habitat preferences (Bruggemann et al. 1994, Burkepile and Hay 2011, Adam et al. 2015b, 2018). Furthermore, species may also vary ontogenetically in their diet and habitat preferences; size-specific differences in foraging

suggest that the per unit biomass impact of a given species will vary with changes in size structure (Bonaldo and Bellwood 2008, Lokrantz et al. 2008, Adam et al. 2018). Thus, making broad assumptions about the equivalence of species within genera and individuals within species may poorly represent how species diversity contributes to herbivory.

The impact of parrotfish species identity and diversity likely also differs across space since many species have specific habitat preferences. For example, in the Caribbean, species such as *Sparisoma viride* and *Scarus vetula* are more abundant in high relief habitats, others such as *Sp. chrysopterus* are more abundant in low-relief habitats, while still others, such as *Sp. aurofrenatum*, are habitat generalists (Adam et al. 2015b). Since different species prefer different habitats, some species may be disproportionately important in maintaining certain ecological processes in particular habitats or locations. For example, work on Indo-Pacific coral reefs found that different species of parrotfishes drove differences in herbivory and bioerosion both across and within regions of the Great Barrier Reef (Hoey and Bellwood 2008) and between forereef and backreef areas within a small remote Pacific atoll (Hamilton et al. 2014). Collectively, these studies strongly suggest that the net ecological impacts of parrotfishes may vary greatly in space. Therefore, species will differ in their relative contributions to different ecological processes (e.g., turf grazing, macroalgal browsing, bioerosion) across the reefscape.

Importantly, parrotfishes are often the targets of fisheries throughout the Caribbean (Hawkins and Roberts 2004a, SERO-LAPP 2012, Vallès and Oxenford 2014, Bozec et al. 2016). While these fisheries can be locally important both culturally and economically, fishery extraction may reduce the ecological impacts of targeted species by suppressing overall biomass and altering the species composition and size-structure of the parrotfish assemblage (Hawkins and Roberts 2004a). Therefore, understanding how these processes of herbivory vary in space and which species are responsible for them is critical to allowing managers to prioritize conservation efforts on those species and at those locations that are prime habitat for corals (Mumby 2014, Steneck et al. 2014, Adam et al. 2015b).

In this paper, we explore how the species identity of herbivorous parrotfishes controls ecological processes among habitats and across multiple spatial scales. We use data from a long-term, spatially explicit reef fish monitoring program from the Florida Keys, USA to examine variation in parrotfish assemblages across major habitat types, such as patch reefs, high-relief spur-and-groove reef, and lower relief forereefs, in a large reef system. We combine these data with size- and species-specific estimates of parameters of herbivory to predict the ecological impacts of parrotfish assemblages in different habitats. We focus on the Florida Keys because extensive monitoring data and behaviorally derived parameters of herbivory exist for the entire assemblage

of larger-bodied, reef-associated parrotfishes. We then use finer scale survey data to examine how the ecological impacts of parrotfish vary across reef zones within the broader high-relief habitat type. Our results show that the ecological impact of parrotfishes varies greatly across multiple spatial scales due to differences in species identity within parrotfish assemblages.

METHODS

Study area

We conducted field research in the Florida Keys, a bank-barrier reef system along the southeastern corner of Florida that runs 250 km from Miami to Key West, USA. The reef system extends 8 km seaward from the islands of the Florida Keys and includes a variety of reef/hard-bottom habitats, as well as soft-bottom habitats such as sand, seagrass, and mangroves (Keller and Causey 2005). Because we were interested in patterns of herbivory by parrotfishes in habitats that were suitable for corals, we included only hard-bottom habitats in this study. Following previous work in the Florida Keys (Smith et al. 2011a,b), we divided habitats into the following seven habitat categories, from landward to seaward: inshore patch reef, mid-channel patch reef, and offshore patch reef (all found landward of the reef crest, generally >6 m depth), high-relief spur and groove reef around the reef crest, and three forereef categories, shallow (<6 m), mid-depth (6–18 m), and deep (>18 m). To examine variation in processes at smaller spatial scales, we also examined reef zones within the high-relief habitat category. These reef zones follow the work of Adam et al. (2015b) and include high-relief spurs, low-relief reef, and nearby boulder-rubble areas.

Parrotfish surveys

We used two separate methods to quantify abundance and size structure of parrotfish. First, to assess heterogeneity in parrotfish abundance across the landscape, we used existing data from the Florida Keys Reef Visual Census (RVC) monitoring program (Smith et al. 2011a), an ongoing fishery-independent monitoring program that uses professionally trained divers to record the size and abundance of reef fishes within 7.5 m radius circular plots (data *available online*).⁶ The program uses a random-stratified design to select sample locations annually in hard-bottom habitats across the Florida Keys coral reef ecosystem, providing robust estimates of habitat-specific abundance at a given size (in 1 cm bins) for most species of diurnally active, non-cryptic reef fish, including parrotfish (see Bohnsack and Bannerot [1986] and Smith et al. [2011a] for more details of sampling protocols and survey design). We used data from 2003–2012, which include the last 10 yr that this program collected

data across the entire Florida Keys on an annual basis. See Appendix S1: Table S1 for details on sampling effort for this program.

Second, to assess the impact of smaller-scale habitat heterogeneity on parrotfish abundance and estimated ecological processes within reefs, we conducted separate timed-swim surveys in 2013 within the high-relief spur and groove habitat category as defined by the RVC monitoring program ($n = 4$ reefs). The spur and groove habitat is generally the most structurally complex habitat and historically harbored the highest levels of coral cover, greatest biomass of reef fish, and the highest biodiversity for many groups of organisms (Keller and Causey 2005, Smith et al. 2011a,b). However, the high-relief reef habitat class is not homogeneous; it includes several different reef zones that are not captured at the scale of the RVC classification across the Florida Keys. These zones include high-relief spurs, low-relief areas seaward of the spurs, and boulder-rubble areas, generally landward of the spurs as well as in the grooves. These surveys allowed us to partition the abundances of different parrotfish species and size classes and their contributions to estimated ecological processes within the broader high-relief habitat class.

For the timed swims, divers swam in a consistent direction, along isobaths, or along a specific habitat feature (e.g., along a spur) and counted and estimated the size of all individual parrotfish ≥ 15 cm fork length (FL) in a 5 m-wide swath (2.5 m on either side of the diver), following the methodology of Adam et al. (2015b). Because swims covered multiple reef zones, divers towed a GPS receiver and recorded the zone they were in every minute with a watch that was synchronized with the GPS. Using the time stamps from the GPS receiver, we calculated the total distance covered during each swim, as well as distance covered in each reef zone. We multiplied linear distance by the 5 m wide swath to calculate area sampled in each zone and for the entire swim. Together, the fish abundance data and area covered data allowed us to estimate zone-specific density of all species across all size classes (Adam et al. 2015b). We calculated biomass of each individual fish from both types of surveys using published length-weight relationships for Caribbean reef fishes (Bohnsack and Harper 1988, Froese and Pauly 2017). See Appendix S1: Table S2 for details on sampling effort from these surveys.

Parrotfish behavioral data

To estimate feeding impacts of the different parrotfish species, we used estimates of bite rate, bite area, bite volume, total algal consumption and proportion of diet comprised of macroalgae for each of 10 species that account for >99% of the parrotfish biomass on reefs in the Florida Keys. Species included *Scarus coelestinus*, *Sc. coeruleus*, *Sc. guacamaia*, *Sc. iseri*, *Sc. taeniopterus*, *Sc. vetula*, *Sparisoma aurofrenatum*, *Sp. chrysopterus*, *Sp. rubripinne*, and *Sp. viride*. We used published

⁶ https://grunt.sefsc.noaa.gov/rvc_analysis20/?action=index

relationships to estimate size-specific bite area and bite volume (Bruggemann et al. 1996, Adam et al. 2018; Table 1). To estimate total algal consumption for an individual fish, we used an empirically derived allometric relationship between fish mass and carbon consumption for coral reef herbivores (van Rooij et al. 1998):

$$AC = 0.0342 \times M^{0.816} \times 365 \quad (1)$$

where M is the biomass of a given species in a given size class. This equation estimates algal consumption per year in grams of carbon for a parrotfish of a given mass.

We estimated bite rate and proportion of macroalgae in the diet of different sized fishes from behavioral observations (Adam et al. 2015b, 2018). Some species are more likely to scrape or excavate the substrate, thereby completely removing algae and its point of attachment from the substrate as opposed to merely cropping some algal tissue. For these species, we analyzed photographs of haphazardly selected bites to examine the probability of leaving a grazing scar and the size of scars that were made (Adam et al. 2018). From these data, we derived parameters describing how grazing scar size, bite rate, and the proportion of the diet comprised of different food items varied with fish size (Adam et al. 2015b, 2018; Table 1).

We used these parameters to calculate estimates of key ecological processes of herbivory for each species of parrotfish, including the biomass of macroalgae removed, the proportion of reef area scraped by species (referred to as “area grazed”), and bioerosion. Because previous work has shown that the bite rate, bite area, bite volume, and diet of different parrotfish species are dependent on size, all parameters were size-specific (Bruggemann et al. 1996, Lokrantz et al. 2008, Adam et al. 2018). To estimate the amount of macroalgae removed, we multiplied size-specific mass of organic carbon required per day (Eq. 1) by the proportion of the diet comprised of macroalgae by density of fish in each size class:

$$MC = AC \times pm \quad (2a)$$

where MC is macroalgae consumed per day in g, AC is algal consumption (Eq. 1), and pm is the species-specific proportion of macroalgae consumed for species that showed no change in macroalgal consumption with size. For species that varied in macroalgal consumption with size, we modified 2a

$$MC = AC \times \frac{e^{(pm_inter + pm_size \times FL)}}{1 + e^{(pm_inter + pm_size \times FL)}} \quad (2b)$$

where pm is replaced by the logistic regression evaluating the probability of a given species consuming macroalgae at a given size, FL is fork length of the fish, and pm_inter and pm_size are the intercept and slope terms from the logistic regression (Adam et al. 2018).

We converted MC to consumption per year per unit area by multiplying MC by density of a given species and size class.

To estimate areal grazing and bioerosion rates we determined species- and size-specific bite rates and the proportion of bites that resulted in a distinct grazing scar where some carbonate substrate was removed. To determine bite rate, we used species-specific regressions of bite rate and size:

$$BR = (\text{biterate_m} \times FL + \text{biterate_b}) \times 600 \quad (3)$$

where BR is bite rate per day, FL is fork length, biterate_m and biterate_b are the slope and intercept of the linear regression equation of bite rate as a function of size, and 600 is the estimated number of effective foraging minutes per day (assuming 10 h of foraging per day; Adam et al. 2015b).

To estimate the probability of leaving a bite scar, we calculated separately for each species

$$P_{bs} = \frac{e^{(\text{bsp_inter} + \text{bsp_size} \times TL)}}{1 + e^{(\text{bsp_inter} + \text{bsp_size} \times TL)}} \quad (4a)$$

where P_{bs} is the probability of leaving a bite scar, FL is fork length, and bsp_inter and bsp_size are the intercept and slope terms from the logistic regression evaluating the probability of leaving a scar as a function of size. We then calculated the area of reef scraped per bite for a given species in a given size class:

$$AS = (\text{bs_q} \times FL^2) \times P_{bs} \quad (4b)$$

where AS is area scraped per bite (in cm^2), bs_q is the parameter derived from the relationship between bite scar size and size of the fish (Adam et al. 2018), FL is fork length, and P_{bs} is the probability of leaving a scar (Eq. 4a). The reef area scraped per year is

$$RA = BR \times AS \times \text{density} \times 365 \quad (5)$$

where RA is reef area scraped (in $\text{cm}^2 \cdot \text{yr}^{-1} \cdot \text{m}^{-2}$), BR is bite rate (Eq. 3), AS is area scraped (Eq. 4), density is number of fish of a given species in a given size class per unit area surveyed, and 365 is days per year. To convert this value to percent area scraped per year, we divided by 10,000 (to convert to $\text{m}^2 \cdot \text{yr}^{-1} \cdot \text{m}^{-2}$) and multiplied by 100.

To estimate bioerosion, we multiplied bite volume by bite rate by the probability of leaving a scar by the fish density in each size class by bulk density of reef carbonate (Bruggemann et al. 1996, Mallela and Perry 2007):

$$BE = (\text{bioeros_v} \times FL^3) \times BR \times P_{bs} \times \text{density} \times 1.7 \times 365/1000 \quad (6)$$

where BE is bioerosion in $\text{kg} \cdot \text{yr}^{-1} \cdot \text{m}^{-2}$, bioeros_v is the species-specific bioerosion coefficient, FL is fork length, BR is bite rate (Eq. 3), P_{bs} is the probability of leaving a

TABLE 1. Herbivory parameter estimates, with variable names in parenthesis

Species	Proportion macroalgae			Bite scar			Bite rate		Length-mass		Bioerosion coefficient, bioeros_v
	Estimate,pm	Size intercept, pm_inter	Size slope, pm_size	Coefficient, bs_q	Probability intercept, bsp_inter	Probability slope, bsp_size	Slope, biterate_m	Intercept, biterate_b	Coefficient, lw_a	Exponent, lw_b	
<i>Scarus coelestinus</i>	0.016 ± 0.00091†			$5.79 \times 10^{-4} \pm 1.93 \times 10^{-4} \ddagger$	-1.99 ± 0.83‡	0.059 ± 0.020‡	-0.091 ± 0.045#	14.76 ± 1.98#	0.020	3.02	$2.78 \times 10^{-7} \pm 2.88 \times 10^{-8} \ddagger$
<i>Scarus coeruleus</i>	0.0035 ± 0.00023†			$5.79 \times 10^{-4} \pm 1.93 \times 10^{-4} \ddagger$	-3.50 ± 1.0‡	0.11 ± 0.026‡	-0.091 ± 0.045#	14.76 ± 1.98#	0.012	3.11	$2.78 \times 10^{-7} \pm 2.88 \times 10^{-8} \ddagger$
<i>Scarus guacamaia</i>	0.014 ± 0.00057†			$4.01 \times 10^{-4} \pm 1.34 \times 10^{-4} \P$	-2.21 ± 0.84‡	0.035 ± 0.028‡	0#	23.89 ± 3.02#	0.016	3.06	$1.93 \times 10^{-7} \pm 2.00 \times 10^{-8} \ddagger \P$
<i>Scarus iseri</i>	0.022 ± 0.0012†			$4.01 \times 10^{-4} \pm 1.34 \times 10^{-4} \P$	-2.21 ± 0.84‡	0.035 ± 0.028‡	0#	23.89 ± 3.02#	0.017	3.02	$1.93 \times 10^{-7} \pm 2.00 \times 10^{-8} \ddagger \P$
<i>Scarus taeniopterus</i>	0.022 ± 0.00096†			$4.01 \times 10^{-4} \pm 1.34 \times 10^{-4} \P$	-2.21 ± 0.84‡	0.035 ± 0.028‡	0#	23.89 ± 3.02#	0.018	3.0	$1.93 \times 10^{-7} \pm 2.00 \times 10^{-8} \ddagger \P$
<i>Scarus vetula</i>	0.0055 ± 0.00017†			$4.01 \times 10^{-4} \pm 1.34 \times 10^{-4} \S$	-1.31 ± 0.76‡	0.035 ± 0.023‡	0#	23.89 ± 3.02#	0.019	3.04§	$1.93 \times 10^{-7} \pm 2.00 \times 10^{-8} \ddagger \P$
<i>Sparisoma aurofrenatum</i>		-1.18 ± 0.42‡	0.059 ± 0.020‡						0.0047	3.43	
<i>Sparisoma chrysopteron</i>		-2.56 ± 0.78‡	0.075 ± 0.029‡						0.0099	3.17	
<i>Sparisoma rubripinne</i>		-1.39 ± 0.77‡	0.074 ± 0.26‡						0.019	3.0	
<i>Sparisoma viride</i>	0.090 ± 0.0058†			$5.26 \times 10^{-4} \pm 1.75 \times 10^{-4} \S$	-1.19 ± 0.49‡	0.071 ± 0.017‡	-0.11 ± 0.034#	11.39 ± 0.95#	0.025	2.92	$1.30 \times 10^{-6} \pm 6.60 \times 10^{-8} \ddagger \P$

Notes: In all cases, size of fish is total length (TL) in cm. Blank cells indicate that a given parameter does not apply. Parameters that include a size slope and intercept were not included for those species for which there was no relationship between size of the fish and that aspect of foraging. Error is reported SD. See Table 2 for calculations using these values.

† Adam et al. (2015b).

‡ Adam et al. (2018).

§ Bruggemann et al. (1994).

¶ Values applied from *Scarus vetula*.

This study, calculated from previously collected but unpublished data collected by the authors.

|| Bruggemann et al. (1994); estimates of error were not published.

†† Bruggemann et al. (1996).

‡‡ Values applied from *Sc. vetula*.

bite scar (Eq. 4a), density is number of fish of a given species in a given size class per unit area surveyed, 1.7 g cm^{-2} is the estimated bulk density of reef carbonate (Mallela and Perry 2007), 365 d yr^{-1} , and $1000 \text{ is g kg}^{-1}$.

Unfortunately, there are no bite-volume data available for *Sc. coelestinus*, *Sc. guacamaia*, *Sc. iseri*, or *Sc. taeniopterus*; since bite-volume potential is likely constrained phylogenetically and by size, whereas behavioral foraging is not (Streelman et al. 2002, Bonaldo et al. 2014, Adam et al. 2015b, 2018), we apply size–bite-volume relationships for *Sc. vetula* to *Sc. iseri* and *Sc. taeniopterus*. For *Sc. coelestinus* and *Sc. guacamaia*, we scale bite volume estimates to bite area estimates based on our observations of bite area for these larger species. See Table 1 for estimates of input parameters and their associated errors, and Table 2 for formulas for all calculations.

Finally, we summed the individual species- and size-specific estimates of ecological processes for each species in each habitat. We accounted for measurement error associated with each parameter by propagating error at each stage in the above-referenced calculations. To do this, we estimated each parameter value from a random draw based on the mean and standard deviation of that parameter using the `rnorm` function in R (R Core Team 2016). We repeated each calculation at each step 1,000

times, recording the mean, standard deviation, and variance of the resulting calculation. We then used the calculated means and standard deviations for a given process in each subsequent calculation that used the estimate of that process as an input value (e.g., reef area scraped [Eq. 5] depends on bite rate [Eq. 3] and area scraped per bite [Eq. 4b], each of which was estimated from several other parameters; Tables 1, 2). When response values (e.g., percent area grazed per year) were summed across groups (e.g., fish from a given species in a given year in a given habitat across all size classes), we also summed the variance, and when values were averaged across groups (e.g., a given species in a given habitat across years), we calculated the mean of the variance. In this way, we tracked the mean value of each estimate as well as the propagated error associated with it.

To examine the importance of species identity, we examined how species-specific estimates of ecological processes compared to the commonly used estimates based on genus-level process rates. Therefore, we calculated rates of ecological processes at the genus level for all *Scarus* and *Sparisoma* species using parameters from either *Sc. vetula* or *Sp. viride*, the two species that previously had the most available foraging parameters. We then compared these estimates of ecological processes using genus-level parameters to those using species-level parameters.

TABLE 2. Formulas used to predict metrics of herbivore ecological impact.

Metric	Formula	Notes
Algal consumption, AC (g C/yr)	$AC = 0.0342 \times M^{0.816} \times 365$	applies to all species; include mass (M) of a given species at a given size and 365 d/yr ; van Rooij et al. (1998)
Macroalgae consumption, MC (g C/yr)	$MC = AC \times pm$	applies to species with whose macroalgal consumption is size independent (e.g., <i>Scarus</i> spp. and <i>Sparisoma viride</i>)
Macroalgae consumption (g C/yr)	$MC = AC \times \frac{e^{(pm_inter + pm_size \times FL)}}{1 + e^{(pm_inter + pm_size \times FL)}}$	applies to species whose macroalgal consumption is size dependent (<i>Sparisoma</i> spp. aside from <i>Sp. viride</i>); includes the algal consumption multiplied by the size-based probability of a fish consuming macroalgae
Bite rate, BR (bites/d)	$BR = (\text{biterate_m} \times FL + \text{biterate_b}) \times 600$	used only for areal grazing rates and bioerosion, so applies only to species that frequently leave scars; 600 min/d for mean 10 h feeding/d
Probability of leaving a bite scar, P_{bs}	$P_{bs} = \frac{e^{(bsp_inter + bsp_size \times TL)}}{1 + e^{(bsp_inter + bsp_size \times TL)}}$	applies to species that frequently leave grazing scars
Area of reef scraped, AS (cm^2/bite)	$AS = (bs_q \times FL^2) \times P_{bs}$	applies only to species that frequently leave scars; includes the scar area as a function of fish size multiplied by the size-based probability of that fish leaving a scar
Reef area scraped, RA ($\text{cm}^2 \cdot \text{yr}^{-1} \cdot \text{m}^{-2}$)	$RA = BR \times AS \times \text{density} \times 365$	applies only to species that frequently leave scars; includes the density of fish in a given size class and 365 d/yr
Bioerosion, BE ($\text{kg} \cdot \text{yr}^{-1} \cdot \text{m}^{-2}$)	$BE = (\text{bioeros_v} \times FL^3) \times BR \times P_{bs} \times \text{density} \times 1.7 \times 365/1000$	only measured for <i>Sp. viride</i> and <i>Sc. vetula</i> ; includes the size-based bite volume multiplied by density of reef CaCO_3 (1.7 g/cm^3 ; Mallela and Perry 2007) multiplied by 365 d/yr , multiplied by the size-based probability of that fish leaving a scar

Note: See Table 1 for abbreviations of parameter values.

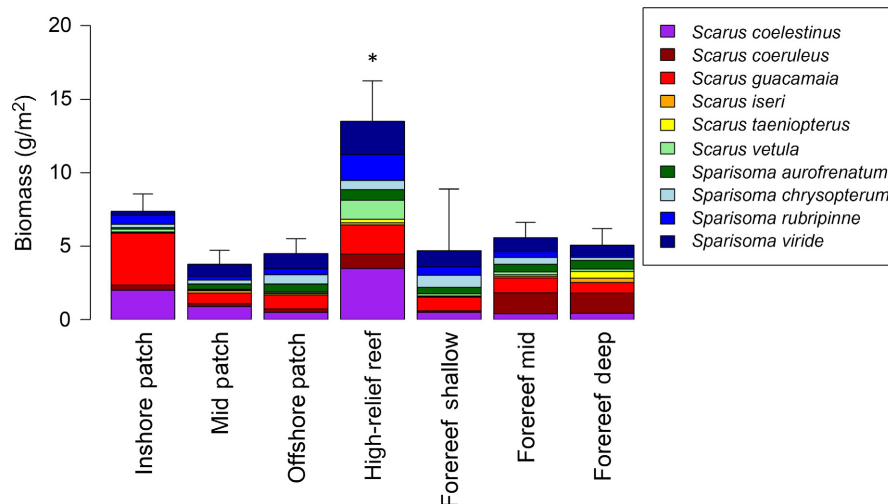


FIG. 1. Mean biomass (and 95% CI) of 10 species of parrotfishes across seven main habitat classes in the Florida Keys. See *Methods* for detailed descriptions of habitat classes. An asterisk indicates biomass was significantly different from all other habitats ($P \leq 0.05$).

Statistical analysis

We used the R Programming Environment for all analysis (R Core Team 2016). We used permutation tests to examine differences in parrotfish biomass and ecological processes (i.e., area grazed, macroalgae consumed, and bioerosion) across different habitats and reef zones. We used the `aovp` function in the `lmPerm` package (Wheeler and Torchiano 2016) to determine if differences existed among habitats and reef zones, and used the function `pairwisePermutationMatrix` with a Bonferroni method for multiple comparisons in the `companion` package (Mangiafico 2018) to examine pairwise differences among habitats or reef zones. We used PERMANOVA to examine differences in species composition across different habitats as well as across reef zones within the high-relief reef habitat. To visualize differences in parrotfish assemblage structure in different habitats and reef zones, we used canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) in the `vegan` package (Oksanen et al. 2016) using Bray-Curtis distance matrices from species-specific biomass estimates in each habitat and each zone within the high-relief reef habitat. CAP is a constrained ordination technique that identifies combinations of variables that best discriminate among a priori groups (e.g., habitats or reef zones). Like other ordination techniques, CAP provides site scores that can be used to visualize multivariate patterns, and species scores to evaluate the relative contributions of individual species. We created separate plots for each fish abundance dataset. Finally, we used linear regression to examine the extent to which different ecological processes covaried and whether total parrotfish biomass and species diversity were associated with changes in rates of these key processes.

RESULTS

Patterns of parrotfish biomass and ecological processes across reef habitats

Parrotfish biomass varied significantly across all habitats across the Florida Keys reef tract (permutation test, $P < 0.001$; Fig. 1). Notably, the high-relief reef had two- to threefold more biomass than all other habitats. The remaining habitats had relatively similar biomass, but differed significantly in species composition (PERMANOVA, pseudo- $F_{6,63} = 8.56$, $P < 0.001$; Fig. 2). Biomass of most species was higher in high-relief reefs than any other habitat, but other habitats were dominated by other species (e.g., *Sc. guacamaia* on inshore patch reefs and *Sc. coeruleus* on mid- and deep forereefs). These patterns are clear in multivariate space (Fig. 2), where the high-relief reef, inshore patch reef, and deep forereef habitats were well-differentiated in multivariate space and the remaining habitats showed a great deal of overlap. Across all years, all species were present in all habitats, and Shannon diversity (H') of mean biomass was remarkably similar across all habitats (range 1.94–2.06) except on inshore patch reefs (1.41), where *Sc. guacamaia* dominated (Fig. 1). Estimates of all three ecological processes (proportion of reef area grazed, biomass of macroalgae removed, and bioerosion) were significantly higher in the high-relief reef habitat, where parrotfish biomass was highest (permutation test, $P < 0.001$ for all three ecological processes), but different species dominated the different processes across habitats (Fig. 3). Interestingly, there was no relationship between Shannon diversity and any ecological process ($P > 0.10$ in all cases).

Multiple species contributed to the proportion of reef area grazed in most habitats; no species contributed

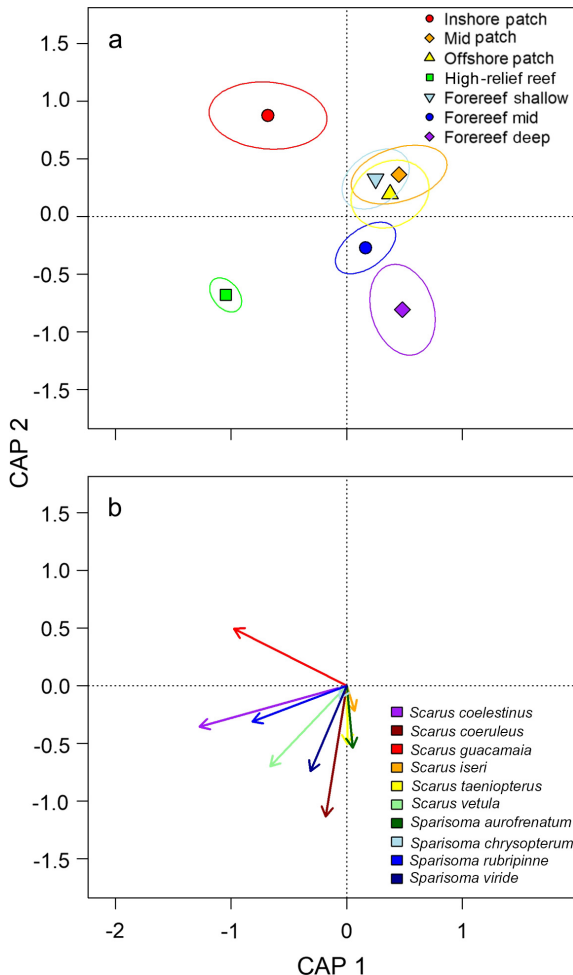


FIG. 2. Canonical analysis of principal coordinates for the parrotfish community across seven main habitat classes in the Florida Keys over 10 yr. (a) Centroids and 95% confidence ellipses for each habitat. (b) Species vectors in multivariate space.

more than 50% of the total within a habitat except *Sc. guacamaia* in inshore patch reefs (62%). In contrast, *Sp. viride* was responsible for the majority of bioerosion (57–72%) in nearly all habitats, except inshore patch reefs where *Sc. guacamaia* dominated. Macroalgal consumption rates were dominated by *Sp. aurofrenatum* and *Sp. rubripinne*; these two species accounted for 57–74% of macroalgal consumption in all habitats, with *Sp. chrysopteron* responsible for most of the remaining browsing (Fig. 3).

When we examined the relationships among predicted ecological processes using individual year-habitat combinations as replicates for the RVC dataset that spans the entire Florida Keys, all were significantly positively correlated (Bonferroni-corrected $P < 0.0001$ in all cases; Fig. 4), as was total parrotfish biomass with all ecological processes (Appendix S1: Fig. S1). Shannon diversity was uncorrelated with biomass or any ecological process

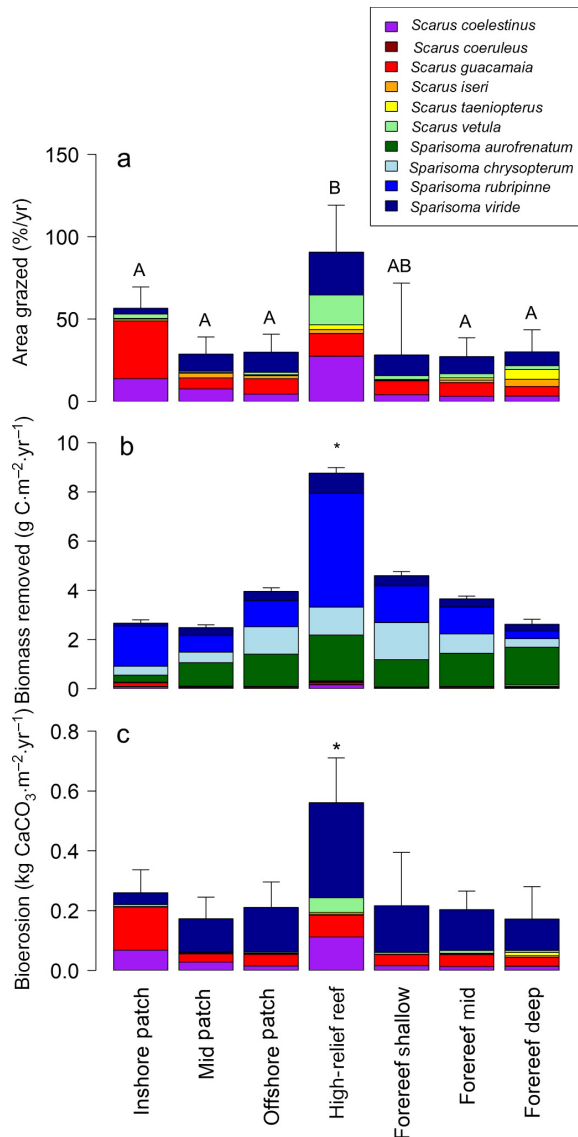


FIG. 3. Estimated ecological metrics among habitats across the Florida Keys, based on abundance and size structure of parrotfish assemblages (mean \pm SE). (a) Percent area grazed per year, (b) biomass of macroalgae removed, (c) bioerosion (kg of CaCO₃ removed per m² per year). Results of significant post hoc indicated by asterisks if only one group differs significantly ($P \leq 0.05$), or by letters over bars indicate to indicate different groups.

($P > 0.10$ in all cases; Appendix S1: Fig. S1). Not surprisingly, the high-relief reef habitat had high levels of all predicted ecological processes since biomass of most species is highest in this habitat. When we removed the high-relief reef from the regression, the relationships between area grazed and bioerosion and bioerosion and macroalgae remained significant ($P < 0.05$), but the relationship between macroalgae and area grazed became nonsignificant ($P > 0.10$), and the r^2 value for this relationship decreased from 0.32 to 0.04 (Fig. 4,

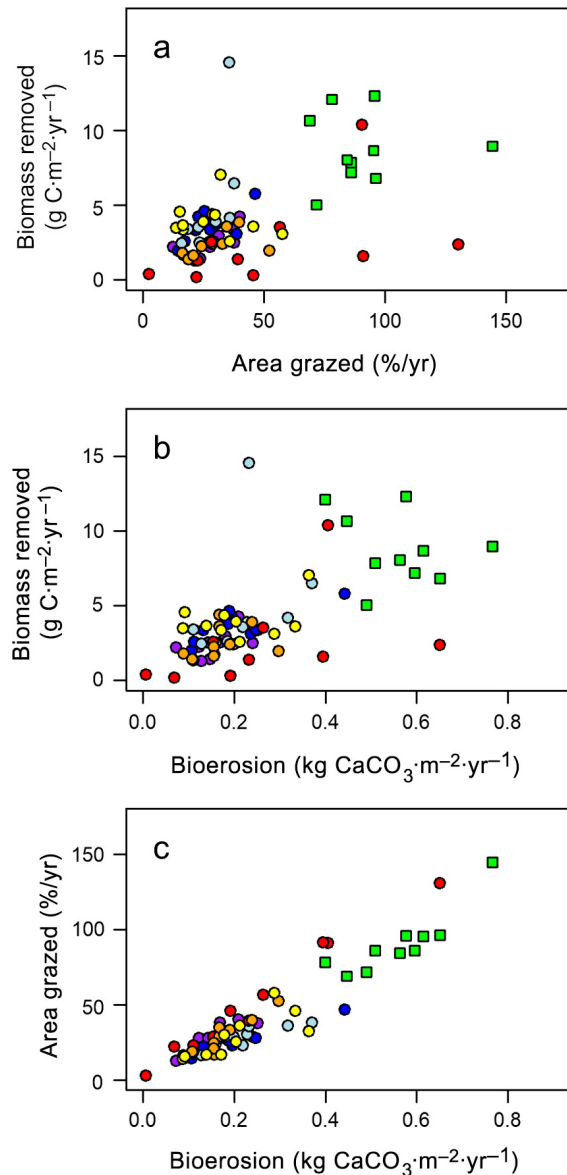


FIG. 4. Pairwise relationships between estimated ecological process rates. Colors for habitats follow Fig. 2a. Note that high-relief reef habitat is indicated with green squares; reported r^2 values and Bonferroni-corrected P values for each relationship are for all habitats and all habitats excluding high-relief reef, respectively. (a) Macroalgal consumption vs. percent reef area grazed ($r^2 = 0.32$ and $P < 0.0001$; $r^2 = 0.04$ and $P > 0.10$ excluding high-relief reef). (b) Macroalgal consumption vs. bioerosion ($r^2 = 0.41$ and $P < 0.0001$; $r^2 = 0.14$ and $P = 0.02$ excluding high-relief reef). (c) Percent reef area grazed vs. bioerosion ($r^2 = 0.88$ and $P < 0.0001$; $r^2 = 0.75$ and $P < 0.0001$ excluding high-relief reef).

Appendix S1: Fig. S2). Relationships between macroalgae consumed and all other factors were non-significant when examining the high-relief reef habitat only (Appendix S1: Fig. S3). Collectively, these patterns highlight that predicted ecological processes may be decoupled from each other within and among habitats. This is particularly true for the key processes of area grazed and macroalgae removed, arguably the two most important ecological processes for corals that parrotfish facilitate, since they both remove algae that may

compete for corals for space on the reef (Adam et al. 2015a).

Patterns of parrotfish biomass and ecological processes within high-relief reefs

Reef zones within high-relief reefs did not differ in total biomass, in contrast to significant differences in biomass among habitats across the landscape scale (permutation test, $P > 0.10$; Fig. 5). However, reef zones

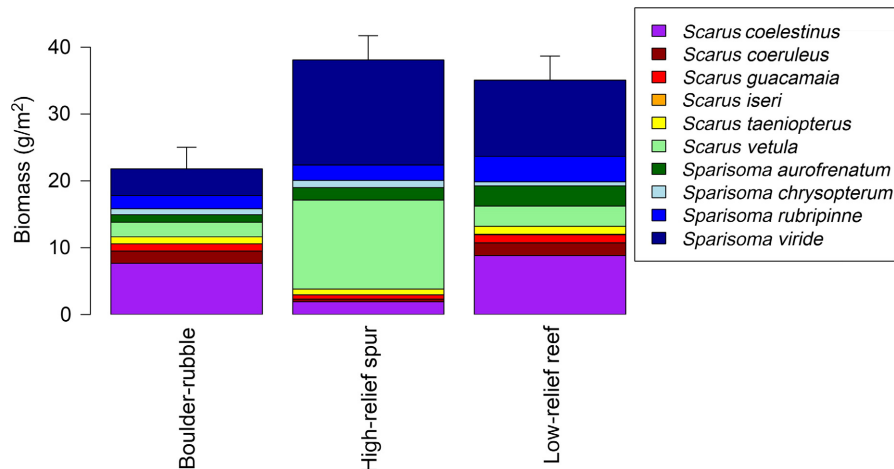


FIG. 5. Mean biomass (and 95% CI) by reef zone within the high-relief spur and groove habitat class across three sites in the Florida Keys using roving diver surveys.

differed markedly in species composition (PERMANOVA, pseudo- $F_{2,9} = 3.18$, $P < 0.01$; Fig. 6). The high-relief spur habitat was dominated by *Sc. vetula* and *Sp. viride*, while the low relief reef habitats were dominated by *Sc. coelestinus* and *Sp. viride*, with relatively higher abundances of *Sp. aurofrenatum* and *Sp. rubripinne* compared to the high-relief spurs. The boulder/rubble zones had relatively low abundances of most species except *Sc. coelestinus*, which we often observed in large aggregations.

As with habitats at the broader scale, the ecological processes we considered (i.e., area grazed, macroalgae consumed, and bioerosion) also varied across zones within high-relief reefs (Fig. 7). Using Bonferroni-corrected permutation tests, area grazed was marginally significantly higher ($P = 0.05$) in the high-relief spur compared to the boulder-rubble zone, and bioerosion was lower ($P = 0.01$) in the boulder-rubble zone compared to the other two zones. Macroalgae consumed was marginally significantly higher in the low relief reef than boulder-rubble ($P = 0.05$). However, like habitats at broader scales, area grazed was dominated by *Sp. viride*, *Sc. vetula*, and *Sc. coelestinus*. As in broader habitats, macroalgal browsing was dominated by *Sp. aurofrenatum* and *Sp. rubripinne*. Relationships between ecological processes across reef zones at the smaller scale were qualitatively similar to those relationships across habitats at the larger scale; relationships between predicted macroalgal consumption and the other process rates and biomass were non-significant, as were all relationships with diversity, but relationships between all other pairs were significant (Appendix S1: Fig. S4). Estimated levels of all ecological processes were generally much higher in all zones within the high-relief reef using data from roving surveys than estimates of the same metrics in the high-relief reef at the coarser scale.

The importance of species identity for estimating ecological processes

To estimate the impact of species identity on ecosystem processes, we compared our estimates using species-specific parameters (i.e., the results presented above) to those generated when applying a single set of grazing parameters to all species in a given genus. Since species-specific parameters of herbivory were not available until recently (Adam et al. 2015b, 2018), many previous studies used one species in the genus (usually *Sc. vetula* and *Sp. viride*, the two species for which the most data had previously been available) to estimate parameters for the other species in the genus (Mumby 2006, Perry et al. 2013). Therefore, our genus-level estimates of ecological processes applied all grazing parameters of *Sc. vetula* to the other *Scarus* species, and those of *Sp. viride* to all other *Sparisoma* species. Estimates of ecological processes using genus-level parameters were much different than those generated using our more precise species-specific parameters. Comparing habitats across the Florida Keys, reef area grazed was 64–157% lower using species-level estimates, macroalgal consumed was 230–339% higher using species-level estimates, and bioerosion was 87–152% lower using species-level estimates (Fig. 8).

DISCUSSION

Our analyses revealed significant differences in both parrotfish assemblages and the important ecological processes they perform among habitats over multiple spatial scales on coral reefs. Since different species are responsible for different ecological processes (Hoey and Bellwood 2008, Adam et al. 2015b, 2018), differences in fish assemblage structure translated into marked differences in predicted rates of ecological processes. However, in some habitats, species assemblages differed but overall

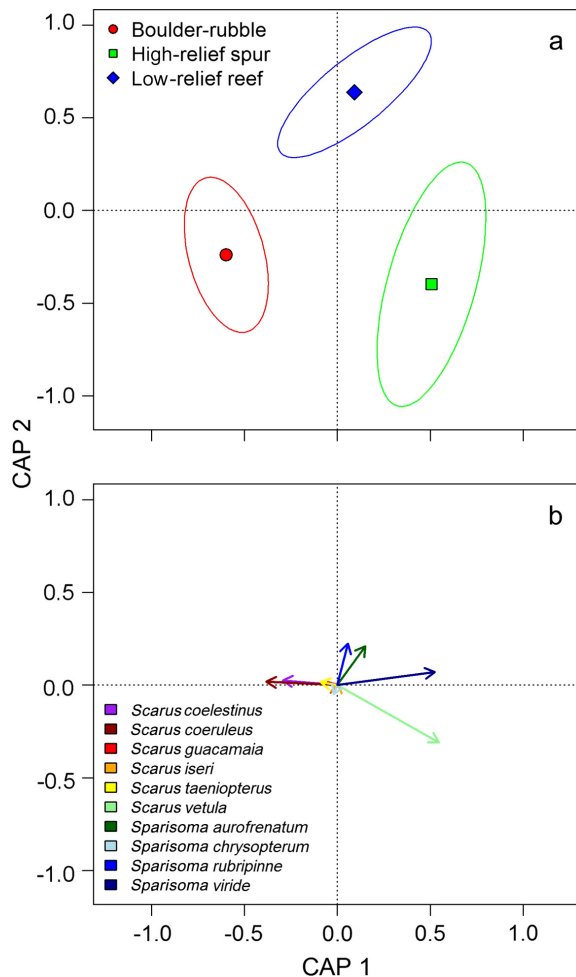


FIG. 6. Canonical analysis of principal coordinates for the parrotfish community across three reef zones in the high-relief spur and groove habitat class in the Florida Keys. (a) Centroids and 95% confidence ellipses for each zone; (b) species vectors in multivariate space.

rates of predicted ecological processes were similar, suggesting that functional redundancy in parrotfish assemblages may be important for maintaining relatively consistent rates of ecological processes. These findings across multiple spatial scales suggest that differences in community composition, in addition to simple changes in overall biomass, may drive differences in predicted rates of key ecological processes among habitats. One important finding is that total biomass of parrotfishes, which is often emphasized as a dominant controller of benthic community composition, was not necessarily a good predictor of ecosystem processes. In several instances, biomass was similar between habitats while predicted process rates were different or process rates were similar despite different biomass among habitats. In addition, predicted rates of ecological processes, especially the important processes of area grazed and macroalgae removed, were weakly correlated or

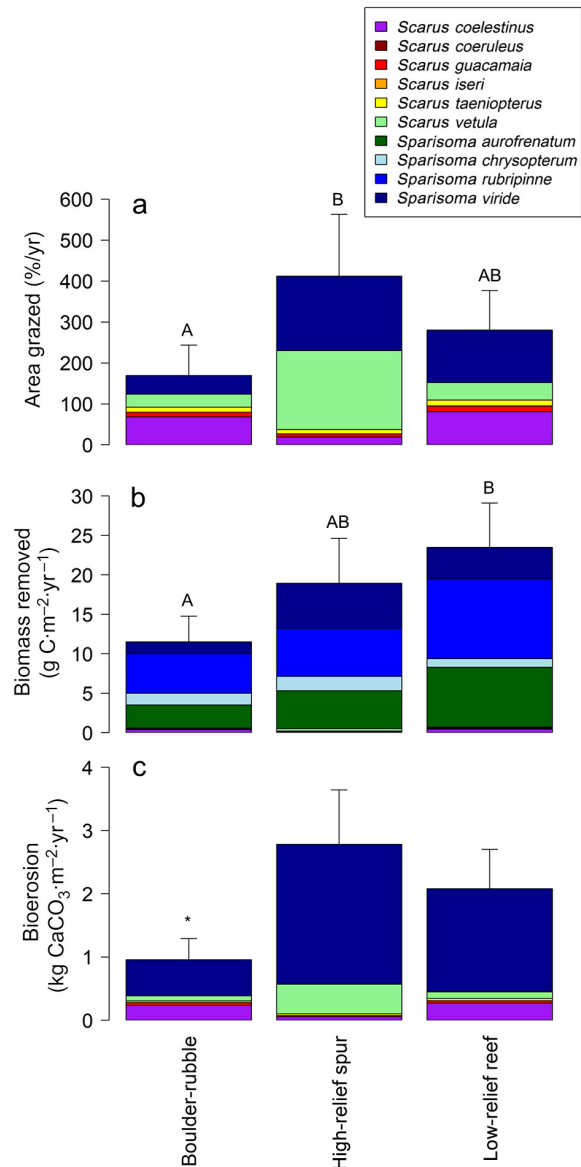


FIG. 7. Estimated metrics of ecological impact (mean and 95% CI) among reef zones within the high-relief spur and groove habitat class in the Florida Keys: (a) percent area grazed per year, (b) biomass of macroalgae removed, (c) bioerosion. Results of significant post hoc test ($P \leq 0.05$) are indicated by an asterisk if only one group differs, or by letters over bars to indicate different groups.

uncorrelated. Furthermore, we also found that estimates of ecological processes using species-specific parameters differed greatly from estimates using parameters at the genus level. Combined, these results highlight that species identity and the ecological roles different species play may strongly affect the overall ecological impacts of a given species assemblage.

High relief reefs, where we focused much of our analyses, often harbor the highest diversity and abundance of

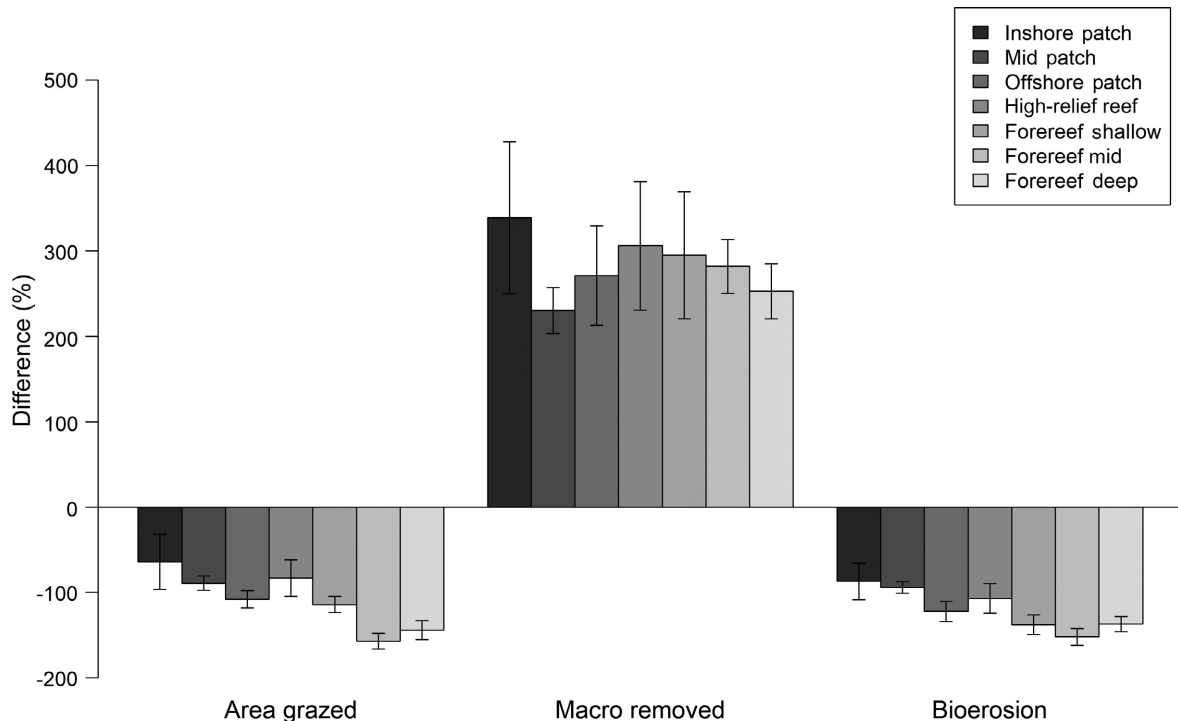


FIG. 8. Difference between estimates of ecological impacts using species-specific parameters vs. estimates at the genus level (using *Scarus vetula* and *Sparisoma viride* for other congeners). Values are percentage differences, where positive values indicate that species-specific estimates are greater, negative numbers indicate that values for species-specific numbers are smaller (e.g., a value of 100% indicates that a value generated using species-specific estimates are two times higher than those generated using single values for all species a genus, a value of -100% indicates that values are two times lower, and 0 indicates that values are the same). Error bars are \pm SD.

corals and other reef organisms (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Porter and Meier 1992, Gratwicke and Speight 2005, Smith et al. 2011a,b). Biomass in the high relief reef habitat on the high relief spurs was dominated by *Sc. vetula* and *Sp. viride*, species that in turn dominated area grazed and bioerosion. In contrast, macroalgal consumption tended to be higher in the lower relief areas, where the abundance of macroalgae tends to be higher and macroalgal browsers were most abundant. While there are many examples of herbivore zonation in coral reef systems (Russ 1984a,b, Hoey and Bellwood 2008, Han et al. 2016), this is a key finding since reef zones likely differ in their suitability for coral recruitment and growth. On the high relief reefs in the Florida Keys, the high-relief spurs were formed by reef building corals, and likely once served as the best habitat for corals (Dustan 1985, Dustan and Halas 1987). Since area grazed is highest in these habitats, they may be some of the most suitable for corals and coral recruitment in the future if we are able to better understand and mitigate the factors that have led to coral decline in the Florida Keys. Still, increased recruitment may not lead to coral recovery, especially in the Florida Keys, where a number of other factors may be limiting coral recovery (van Woesik et al.

2014). In contrast, the boulder-rubble zones, where grazing pressure is lower, are likely unsuitable for most corals and extensive reef development (Dustan 1985, Porter and Meier 1992).

Similar to findings for many taxa across disparate ecosystems, our analyses suggest that different species are likely responsible for different processes, but there may be some overlap in function among different species (Tilman et al. 2014, Deraison et al. 2015). This functional redundancy can be important in maintaining ecosystem processes, since when certain species decline, other species may be able fill their role in the herbivore guild. Across all habitats in the Florida Keys, the level of functional redundancy for each of the ecological processes we estimated varied greatly. In most habitats, our estimates suggest that several species contributed to grazing rates, but only one or two species appeared to drive rates of macroalgal browsing and bioerosion. For example, estimated rates of macroalgal consumption were similar on inshore patch reefs and deep forereefs but were driven by entirely different species (*Sp. rubripinne* on inshore patch reefs and *Sp. aurofrenatum* on deep forereefs). In contrast, *Sp. viride* primarily drove predicted bioerosion rates in all habitats except inshore patch reefs, where *Sc. guacamaia* compensated for

reduced biomass of *Sp. viride*. These results are similar to more diverse locations on the Great Barrier Reef and elsewhere in the Indo-Pacific, where only a few species are responsible for bioerosion while a more diverse assemblage of fishes influence overall rates of herbivory with different species dominating in different habitats (Hoey and Bellwood 2008, Bellwood et al. 2012, Löffler et al. 2015). Ecological processes that are maintained by only one or a few species are likely to be more vulnerable to species losses than functions that are carried out by a diverse assemblage (Hooper et al. 2005, Lefcheck et al. 2015).

Some ecological processes may not represent a net benefit to coral and reef ecosystems more broadly. For example, bioerosion has received increasing attention as Caribbean reefs lose structural complexity (Alvarez-Filip et al. 2009, Kuffner and Toth 2016). Since net reef accretion is generally a balance between growth of major calcifiers (e.g., corals, calcareous algae, etc.) and bioerosion, the rate of reef accretion has declined as coral cover has declined (Perry et al. 2013, Kuffner and Toth 2016). The decline of reef accretion has resulted in a loss of topographic complexity (Alvarez-Filip et al. 2009), which often leads to declines in the biomass and diversity of fish and other reef organisms (Friedlander and Parrish 1998, Graham and Nash 2013). Our estimates of parrotfish bioerosion in the highest relief habitats and zones ($\sim 1\text{--}4\text{ kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) generally match those of other studies (Perry et al. 2014), despite the fact that bioerosion is a complex process involving more than just parrotfishes. Still, these results suggest that while parrotfishes have the potential to facilitate coral recovery, the strongest bioeroders (e.g., *Sp. viride*) may also contribute to loss of structural complexity and associated ecological services in areas where corals are slow to recover.

Vulnerability to ecological or biological extinction also varies with body size in many systems, with the largest species often being most vulnerable (Reynolds et al. 2005, McCauley et al. 2015). Across large swaths of the Caribbean, the largest species of *Scarus* parrotfishes are either absent or so rare as to be functionally absent (Hawkins and Roberts 2004b). While there is little ecological information available for any of these species from around the Caribbean (but see Mumby et al. 2004), they are still relatively common in the Florida Keys, likely in part a result of a ban on their harvest for several decades and the fact that there is no cultural preference for parrotfishes in Florida. One striking pattern in our analyses is the importance of two of these large parrotfish, *Sc. coelestinus* and *Sc. guacamaia*, in impacting estimates of ecosystem processes. These species combined represent 75% fish biomass on inshore patch reefs where *Sc. guacamaia* alone is estimated to be responsible for 62% of the areal grazing and 55% of bioerosion. On high relief reefs, *Sc. coelestinus* made up an estimated 26% of parrotfish biomass and contributed an estimated 30% of the total area grazed. In comparison, the other large parrotfish, *Sc. coeruleus*, minimally

influenced ecosystem processes even in habitats where they were abundant, such as the deeper forereef areas, because they crop rather than scrape turf algae and they spend much of their time foraging off of the reef itself in habitats that are more marginal for corals (Adam et al. 2015b). Overall, these patterns suggest that the absence of two large *Scarus* species from most of the Caribbean may result in lower rates of key ecological processes in habitats where corals are more likely to thrive. Yet, most work focusing on the role of herbivory on reefs across the Caribbean ignores the potential impact of the missing roles these largest species play (but see Mumby et al. 2004).

Previous models examining the impact of herbivory and fishing on Caribbean reefs has focused on parameterizing herbivores at the genus level (Mumby 2006, Bozec et al. 2016), since species-level behavioral parameters were lacking. As a result, models based on genera may have misestimated the levels of grazing, macroalgal consumption, and bioerosion compared to our models based on species- and process-specific foraging parameters. Thus, our updated estimates using species-specific parameters highlights the importance of species identity in this assemblage of species in maintaining key ecological functions across the seascape (Burkepile and Hay 2008, Rasher et al. 2013). More importantly, our analyses suggest that setting thresholds of parrotfish biomass needed to maintain adequate ecosystem processes without accounting for species-specific differences in foraging is potentially dangerous, especially if these estimates are used as management targets.

This research also has direct implications for management of coral reef systems. Parrotfishes support key local fisheries, and in some areas, parrotfishes are culturally important as food. Therefore, it is difficult and often undesirable to simply ban parrotfish harvest. Understanding which species are most important in maintaining certain processes can help managers prioritize species-specific fishery management and conservation efforts. In addition, information about where these species are most likely to have disproportionate impacts can help managers focus spatial management efforts on habitats that are most likely to benefit from the ecological processes that parrotfish facilitate. For example, a high-relief reef that requires additional grazing pressure might benefit from higher abundances of certain species such as *Sc. coelestinus*, *Sc. vetula*, or *Sp. viride*, while similar reefs with excessive macroalgae might require additional protections for *Sp. aurofrenatum* or *Sp. rubripinne*. Our results should help identify which species are most important in maintaining key ecological processes and the specific habitats and reef zones where they are most likely to benefit corals.

Future work should focus on providing accurate estimates about what levels of impacts of herbivory are needed to facilitate corals. In other parts of the Caribbean, recent studies have begun to generate field-based estimates of impacts of herbivory (Steneck et al. 2014,

Kuempel and Altieri 2017). While these estimates are preliminary, they find that very different fish assemblages appear able to maintain different levels of ecological processes that subsequently may allow recovery of corals. Managers will need more precise estimates of herbivore-mediated ecological processes required in their specific systems. This will enable managers to set location-specific, quantitative targets for parrotfish abundance by species, size, and habitat to maintain sufficient ecological impacts of these herbivores.

In summary, we apply behavioral parameters to generate quantitative estimates of the ecological impacts of parrotfish across multiple spatial scales. Our results indicate that different species of parrotfishes are responsible for different ecological processes and that differences in species' abundance in different habitats lead to different rates of these ecological processes in these habitats. Furthermore, we show that estimates are very different when using the same parameters for multiple species in a genus, demonstrating the importance of detailed, species-specific information. These findings underscore the importance of species complementarity in reducing potential algal competition and facilitating corals, and they create a framework for better understanding and predicting the ecological impacts of these key herbivores throughout the Caribbean. Ultimately, this information should help scientists and managers develop more quantitative and achievable management targets to preserve and recover coral reefs.

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LITERATURE CITED

- Adam, T. C., D. E. Burkepile, B. I. Ruttenberg, and M. J. Padack. 2015a. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Marine Ecology Progress Series* 520:1–20.
- Adam, T. C., M. Kelley, B. I. Ruttenberg, and D. E. Burkepile. 2015b. Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* 179:1173–1185.
- Adam, T. C., A. Duran, C. E. Fuchs, M. V. Roycroft, M. C. Rojas, B. I. Ruttenberg, and D. E. Burkepile. 2018. Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Marine Ecology Progress Series* 597:207–220.
- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* 276:3019–3025.
- Anderson, M. J., and T. J. Willis. 2003. Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology* 84:511–525.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral reef recovery. *Current Biology* 16:2434–2439.
- Bellwood, D. R., A. S. Hoey, and T. P. Hughes. 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B* 279:1621–1629.
- Bohnsack, J. A. and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41. NOAA, USA. <https://spo.nmfs.noaa.gov/sites/default/files/legacy-pdfs/tr41.pdf>
- Bohnsack, J. A. and D. E. Harper. 1988. Length-weight relationships of selected marine reef fishes from the Southeastern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-215. NOAA, USA. <https://www.st.nmfs.noaa.gov/tm/sefc/sefc215.pdf>
- Bonaldo, R. M., and D. R. Bellwood. 2008. Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 360:237–244.
- Bonaldo, R. M., A. S. Hoey, and D. R. Bellwood. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review* 52:81–132.
- Bozec, Y.-M., S. O'Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proceedings of the National Academy of Sciences USA* 113:4536–4541.
- Bruggemann, J. H., M. W. M. Kuyper, and A. M. Breeman. 1994. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* 112:51–66.
- Bruggemann, J. H., A. M. Van Kessel, J. M. Van Rooij, and A. M. Breeman. 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* 134:59–71.
- Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences USA* 105:16201–16206.
- Burkepile, D. E., and M. E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* 5:e8963.
- Burkepile, D. E., and M. E. Hay. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* 30:351–362.
- Burkepile, D. E. and J. D. Parker. 2017. Recent advances in plant-herbivore interactions. *F1000Research* 6:119.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Deraison, H., I. Badenhausser, N. Loeuille, C. Scherber, and N. Gross. 2015. Functional trait diversity across trophic levels determines herbivore impact on plant community biomass. *Ecology Letters* 18:1346–1355.

- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters* 10:522–538.
- Dustan, P. 1985. Community structure of reef-building corals in the Florida Keys: Carysfort Reef, Key Largo and Long Key Reef, Dry Tortugas. *Atoll Research Bulletin* 288:1–29.
- Dustan, P., and J. C. Halas. 1987. Changes in the reef-coral community of Carysfort reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs* 6:91–106.
- Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224:1–30.
- Froese, R., and D. Pauly. 2017. Fishbase. www.fishbase.org
- Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–960.
- Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326.
- Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66:650–667.
- Hamilton, S. L., J. E. Smith, N. N. Price, and S. A. Sandin. 2014. Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. *Marine Ecology Progress Series* 501:141–155.
- Han, X., T. C. Adam, R. J. Schmitt, A. J. Brooks, and S. J. Holbrook. 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* 35:999–1009.
- Hawkins, J. P., and C. M. Roberts. 2004a. Effects of fishing on sex-changing Caribbean parrotfishes. *Biological Conservation* 115:213–226.
- Hawkins, J. P., and C. M. Roberts. 2004b. Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology* 18:215–226.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Hoey, A. S., and D. R. Bellwood. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27:37–47.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
- Hubbard, D. K., A. I. Miller, and D. Scaturro. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* 60:335–360.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551.
- Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanowskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17:360–365.
- Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* 25:633–642.
- Jackson, J., M. Donovan, K. Cramer, and V. Lam. 2014. Status and trends of Caribbean coral reefs: 1970–2012. Page Global Coral Reef Monitoring Network, Gland, Switzerland.
- Keller, B. D., and B. D. Causey. 2005. Linkages between the Florida Keys National Marine Sanctuary and the South Florida Ecosystem Restoration Initiative. *Ocean & Coastal Management* 48:869–900.
- Kuempel, C. D., and A. H. Altieri. 2017. The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Scientific Reports* 7:39670.
- Kuffner, I. B., and L. T. Toth. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conservation Biology* 30:706–715.
- Lefcheck, J. S., J. E. K. Byrnes, F. Isbell, L. Gamfeldt, J. N. Griffin, N. Eisenhauer, M. J. S. Hensel, A. Hector, B. J. Cardinale, and J. E. Duffy. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications* 6:6936.
- Löffler, Z., D. R. Bellwood, and A. S. Hoey. 2015. Among-habitat algal selectivity by browsing herbivores on an inshore coral reef. *Coral Reefs* 34:597–605.
- Lokrantz, J., M. Nyström, M. Thyresson, and C. Johansson. 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* 27:967–974.
- Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49:317–323.
- Mallela, J., and C. T. Perry. 2007. Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs* 26:129–145.
- Mangiafico, S. 2018. rcompanion: Functions to Support Extension Education Program Evaluation. Version 2.0.3. <https://CRAN.R-project.org/package=rcompanion>
- McCauley, D. J., M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, and R. R. Warner. 2015. Marine defaunation: Animal loss in the global ocean. *Science* 347:1255641.
- McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs* 19:400–417.
- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747–769.
- Mumby, P. J. 2014. Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. *Fish and Fisheries* 17:266–278.
- Mumby, P. J., et al. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536.
- Oksanen, J., F. Blanchet, R. Kindt, P. Legendre and R. O'Hara. 2016. Vegan: community ecology package. <https://cran.r-project.org/web/packages/vegan/index.html>
- Perry, C. T., G. N. Murphy, P. S. Kench, S. G. Smithers, E. N. Edinger, R. S. Steneck, and P. J. Mumby. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications* 4:1402.
- Perry, C. T., G. N. Murphy, P. S. Kench, E. N. Edinger, S. G. Smithers, R. S. Steneck, and P. J. Mumby. 2014. Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. *Proceedings of the Royal Society B* 281:20142018–20142018.
- Porter, J. W., and O. W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. *American Zoologist* 32:625–640.

- R Core Team. 2016. R: a language and environment for statistical computing. R Core Team, Vienna, Austria. www.R-project.org
- Rasher, D. B., E. P. Stout, S. Engel, J. Kubanek, and M. E. Hay. 2011. Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences USA* 108:17726–17731.
- Rasher, D. B., A. S. Hoey, and M. E. Hay. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* 94:1347–1358.
- Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B* 272:2337–2344.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41:1–8.
- Russ, G. 1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series* 20:23–34.
- Russ, G. 1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Marine Ecology Progress Series* 20:35–44.
- Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* 402:115–122.
- SERO-LAPP. 2012. Analyses of commercial parrotfish landings in the U.S. Caribbean. National Marine Fisheries Services, Southeast Regional Office, St. Petersburg, Florida, USA.
- Smith, S. G., J. S. Ault, J. A. Bohnsack, D. E. Harper, J. Luo, and D. B. McClellan. 2011a. Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. *Fisheries Research* 109:25–41.
- Smith, S. G., D. W. Swanson, M. Chiappone, S. L. Miller, and J. S. Ault. 2011b. Probability sampling of stony coral populations in the Florida Keys. *Environmental Monitoring and Assessment* 183:121–138.
- Steneck, R. S., S. N. Arnold, and P. J. Mumby. 2014. Experiment mimics fishing on parrotfish: Insights on coral reef recovery and alternative attractors. *Marine Ecology Progress Series* 506:115–127.
- Streelman, J. T., M. Alfaro, M. W. Westneat, D. R. Bellwood, and S. A. Karl. 2002. Evolutionary history of the parrotfishes: Biogeography, ecomorphology, and comparative diversity. *Evolution* 56:961–971.
- Suchley, A., M. D. McField, and L. Alvarez-Filip. 2016. Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs. *PeerJ* 4:e2084.
- Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* 45:471–493.
- Vallès, H., and H. A. Oxenford. 2014. Parrotfish size: a simple yet useful alternative indicator of fishing effects on Caribbean reefs? *PLoS ONE* 9:e86291.
- van Rooij, J. M., J. J. Videler, and J. H. Bruggemann. 1998. High biomass and production but low energy transfer efficiency of Caribbean parrotfish: implications for trophic models of coral reefs. *Journal of Fish Biology* 53:154–178.
- van Woesik, R., W. J. Scott, and R. B. Aronson. 2014. Lost opportunities: Coral recruitment does not translate to reef recovery in the Florida Keys. *Marine Pollution Bulletin* 88:110–117.
- Wheeler, B. and M. Torchiano. 2016. lmpPerm: permutation tests for linear models. <https://CRAN.R-project.org/package=lmpPerm>
- Williams, I. D. and N. V. C. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358–366.
- Zaneveld, J. R., et al. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications* 7:11833.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1893/full>

DATA AVAILABILITY

Data are available from the NOAA National Centers for Environmental Information at <https://accession.nodc.noaa.gov/0185785>

Supporting Information. Benjamin I. Ruttenberg, Thomas C. Adam, Alain Duran, and Deron E. Burkepile. 2019. Identity of coral reef herbivores drives variation in ecological processes over multiple spatial scales. Ecological Applications.

Appendix S1

Table S1. Sampling effort from Florida Keys reef fish monitoring program. Habitats range from furthest inshore (inshore patch reef) to furthest offshore (forereef deep). Values are number of sites surveyed in a given habitat in a given year. See Methods and references therein for description of habitats and details about sample allocation.

Year	Inshore patch	Mid-channel patch	Offshore patch	High-relief reef	Forereef shallow	Forereef mid	Forereef deep
2003	15	32	15	59	31	71	13
2004	3	10	12	42	17	33	9
2005	7	33	19	46	32	77	23
2006	13	43	23	51	51	112	21
2007	9	52	18	48	37	124	24
2008	14	58	36	44	54	146	23
2009	23	73	54	57	60	201	47
2010	10	47	39	23	62	166	32
2011	13	40	34	32	62	145	73
2012	9	71	46	26	51	172	40
Total	116	459	296	428	457	1247	305

Table S2. Sampling effort for roving diver surveys; units are number of timed swims and total area covered per reef zone (in m²) at each site.

Reef name	Number of Surveys	Boulder-rubble (m ²)	High-relief spur (m ²)	Low-relief reef (m ²)
Carysfort	5	2545	3408	2138
Elbow	5	3730	2804	685
French	4	1968	245	2314
Molasses	6	3073	3177	2533

Figure S1. Scatterplot pairs for all three ecological process metrics plus biomass and diversity, including high-relief reef in green squares. Each point represents a given habitat in a given year. Colors for habitats follow Fig. 2. Note that diversity values for individual habitat-year combinations are generally lower than diversity of the mean values in each habitat across all years. Upper panels are data points, lower panels include r^2 and the Bonferroni-corrected p-value for each pair.

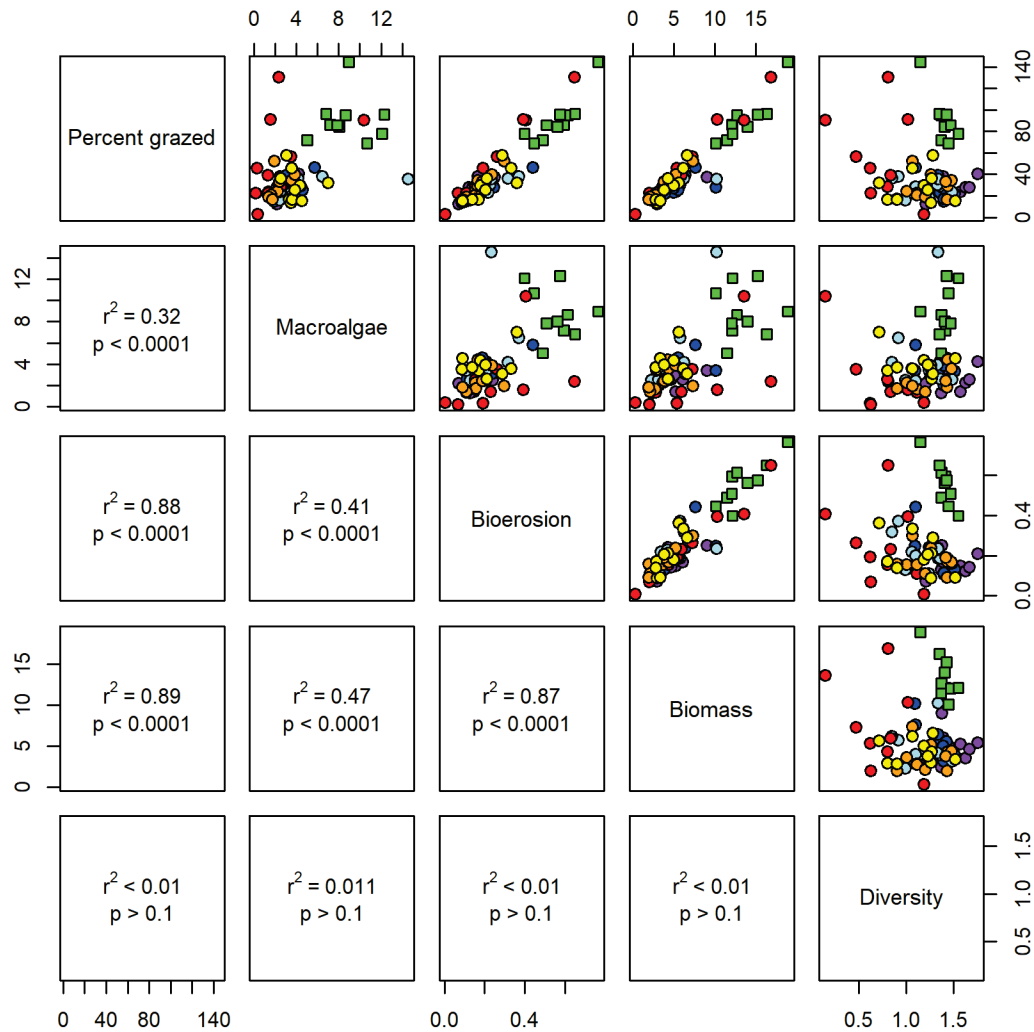


Figure S2. Scatterplot pairs for all three ecological process metrics plus biomass, excluding high-relief reef. Upper panels are data points, lower panels include r^2 and the Bonferroni-corrected p-value for each pair. Points and colors follow Appendix S1: Fig. S1.

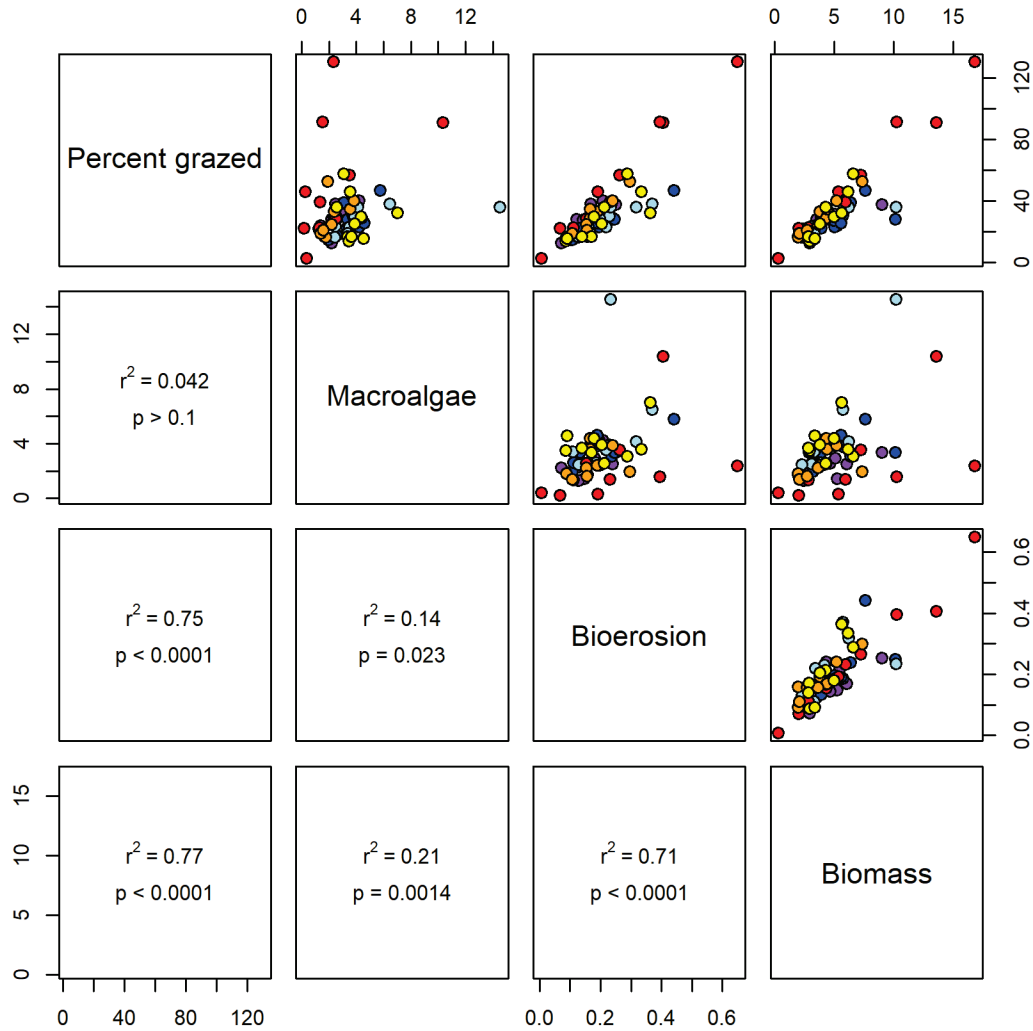


Figure S3. Scatterplot pairs for all three ecological process metrics plus biomass, including only high-relief reef. Upper panels are data points, lower panels include r^2 and the Bonferroni-corrected p-value for each pair. Points and colors follow Appendix S1: Fig. S1.

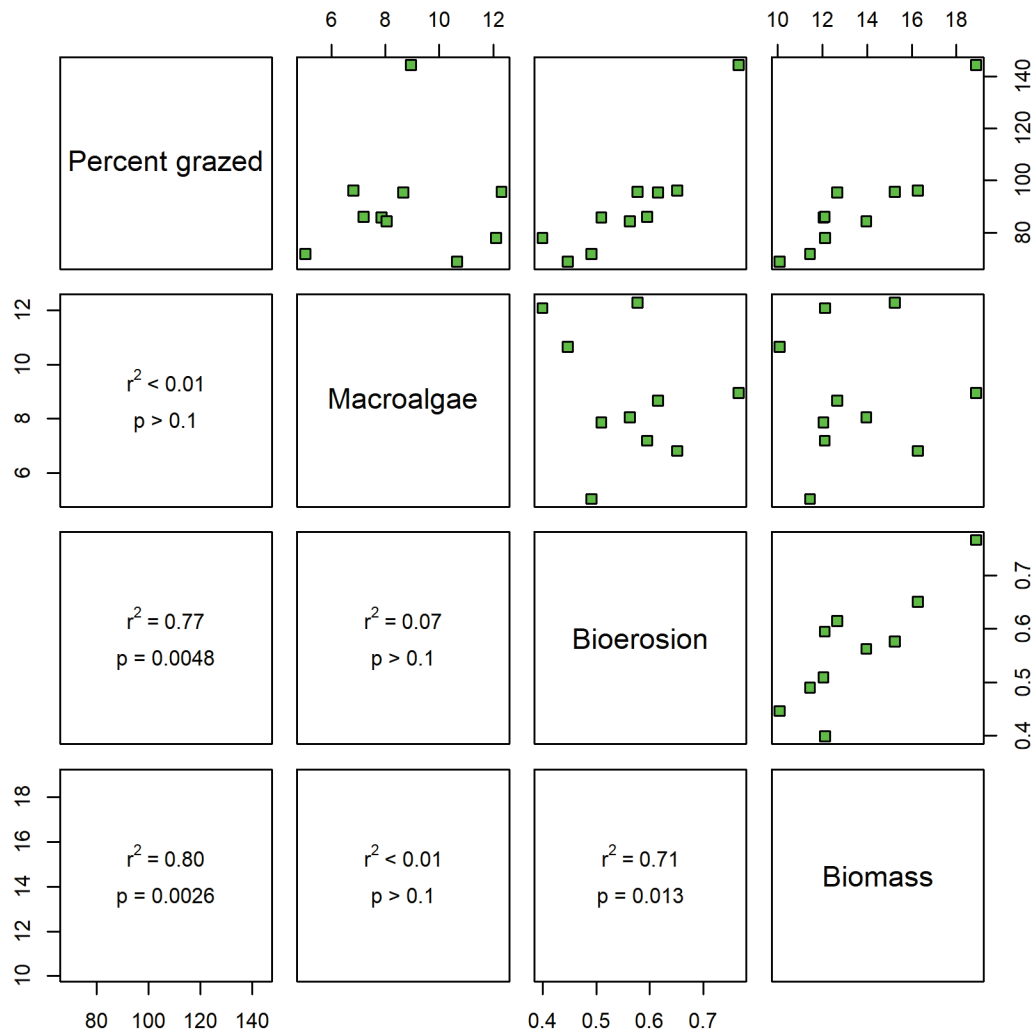


Figure S4. Scatterplot pairs for all three ecological process metrics plus biomass for zones within high-relief reefs. Upper panels are data points, lower panels include r^2 and the Bonferroni-corrected p-value for each pair. Each point represents a given habitat at a given reef location. Colors for habitats follow Fig. 6.

