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.
(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 *S. chrysopterus* are more abundant in low-relief habitats, while still others, such as *S. 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 reefscapes.

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 fore reef 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). 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 Bannert [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 swim 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. taeniopeterus, Sc. vetula, Sparisoma aurofrenatum, Sp. chrysopterum, Sp. rubripinne, and Sp. viride*. We used published

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6https://grnt.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):

\[ AC = 0.0342 \times M^{0.816} \times 365 \]  \hspace{1cm} (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:

\[ MC = AC \times pm \]  \hspace{1cm} (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 macroagal consumption with size. For species that varied in macroalgal consumption with size, we modified 2a

\[ MC = AC \times \frac{e^{(pm_{inter} + pm_{size} \times FL)}}{1 + e^{(pm_{inter} + pm_{size} \times FL)}} \]  \hspace{1cm} (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:

\[ BR = (\text{biterate}_m \times FL + \text{biterate}_b) \times 600 \]  \hspace{1cm} (3)

where \( BR \) is bite rate per day, \( FL \) is fork length, \( \text{biterate}_m \) and \( \text{biterate}_b \) 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

\[ P_{bs} = \frac{e^{(bsp_{inter} + bsp_{size} \times TL)}}{1 + e^{(bsp_{inter} + bsp_{size} \times TL)}} \]  \hspace{1cm} (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:

\[ AS = (bs_q \times FL^2) \times P_{bs} \]  \hspace{1cm} (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

\[ RA = BR \times AS \times \text{density} \times 365 \]  \hspace{1cm} (5)

where \( RA \) is reef area scraped (in \( cm^2 \cdot yr^{-1} \cdot m^{-2} \)), \( BR \) is bite rate (Eq. 3), \( AS \) is area scraped (Eq. 4), \( \text{density} \) 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 \( m^2 \cdot yr^{-1} \cdot m^{-2} \)) 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):

\[ BE = (\text{bioeros}_v \times FL^3) \times BR \times P_{bs} \times \text{density} \times 1.7 \times 365/1000 \]  \hspace{1cm} (6)

where \( BE \) is bioerosion in kg yr\(^{-1} \cdot m^{-2} \), \( \text{bioeros}_v \) 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

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion macroalgal mass</th>
<th>Bite scar</th>
<th>Bite rate</th>
<th>Length–mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate, pm</td>
<td>Size intercept, pm_inter</td>
<td>Size slope, pm_size</td>
<td>Coefficient, bs_q</td>
</tr>
<tr>
<td><em>Scarus coelestinus</em></td>
<td>0.016 ± 0.00091††</td>
<td>5.79 × 10⁻⁴ ± 1.93</td>
<td>-1.99 ± 0.83‡</td>
<td></td>
</tr>
<tr>
<td><em>Scarus coeruleus</em></td>
<td>0.0035 ± 0.00022†</td>
<td>5.79 × 10⁻⁴ ± 1.93</td>
<td>-3.50 ± 1.01‡</td>
<td></td>
</tr>
<tr>
<td><em>Scarus grccamae</em></td>
<td>0.014 ± 0.00057††</td>
<td>4.01 × 10⁻⁴ ± 1.34</td>
<td>-2.21 ± 0.84‡</td>
<td></td>
</tr>
<tr>
<td><em>Scarus iseri</em></td>
<td>0.022 ± 0.0012‡</td>
<td>4.01 × 10⁻⁴ ± 1.34</td>
<td>-1.31 ± 0.76‡</td>
<td></td>
</tr>
<tr>
<td><em>Scarus taeniopterus</em></td>
<td>0.0055 ± 0.00017††</td>
<td>4.01 × 10⁻⁴ ± 1.34</td>
<td>-1.31 ± 0.76‡</td>
<td></td>
</tr>
<tr>
<td><em>Sparisoma aurofrenatum</em></td>
<td>-1.18 ± 0.42‡ †</td>
<td>0.09 ± 0.20‡</td>
<td></td>
<td>0.047</td>
</tr>
<tr>
<td><em>Sparisoma chrysopterum</em></td>
<td>-2.56 ± 0.78‡ †</td>
<td>0.075 ± 0.29‡</td>
<td></td>
<td>0.009</td>
</tr>
<tr>
<td><em>Sparisoma rubripinne</em></td>
<td>-1.39 ± 0.77‡ †</td>
<td>0.074 ± 0.26‡</td>
<td></td>
<td>0.019</td>
</tr>
<tr>
<td><em>Sparisoma striate</em></td>
<td>0.090 ± 0.0058‡</td>
<td>5.26 × 10⁻⁴ ± 1.75</td>
<td>-1.19 ± 0.49‡</td>
<td></td>
</tr>
</tbody>
</table>

**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*. 

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**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.

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# 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*.
Owing to the wide variety of factors influencing fish feeding, 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 differed from 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.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Formula</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algal consumption, AC (g C/yr)</td>
<td>$AC = 0.0342 \times M^{0.816} \times 365$</td>
<td>applies to all species; includes mass (M) of a given size and 365 d/yr; van Rooij et al. (1998)</td>
</tr>
<tr>
<td>Macroalgae consumption, MC (g C/yr)</td>
<td>$MC = AC \times pm$</td>
<td>applies to species with whose macroalgal consumption is size independent (e.g., Sc. spp. and Sp. viride)</td>
</tr>
<tr>
<td>Macroalgae consumption (g C/yr)</td>
<td>$MC = AC \times \frac{\left(bite\ rate_m \times FL + bite\ rate_b\right)}{600}$</td>
<td>applies to species whose macroalgal consumption is size dependent (Sp. spp. aside from Sp. viride); includes the algal consumption multiplied by the size-based probability of a fish consuming macroalgae 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</td>
</tr>
<tr>
<td>Bite rate, BR (bites/d)</td>
<td>$BR = \left(bite\ rate_m \times FL + bite\ rate_b\right)$</td>
<td>applies to species that frequently leave grazing scars</td>
</tr>
<tr>
<td>Probability of leaving a bite scar, $P_{bs}$</td>
<td>$P_{bs} = \frac{\left(bite\ rate_m \times FL + bite\ rate_b\right)}{600}$</td>
<td>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</td>
</tr>
<tr>
<td>Area of reef scraped, AS (cm$^2$/bite)</td>
<td>$AS = \left(bite\ rate \times FL\right) \times P_{bs}$</td>
<td>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</td>
</tr>
<tr>
<td>Reef area scraped, RA (cm$^2$·yr$^{-1}$·m$^{-2}$)</td>
<td>$RA = BR \times AS \times density \times 365$</td>
<td>applies only to species that frequently leave scars; includes the density of fish in a given size class and 365 d/yr</td>
</tr>
<tr>
<td>Bioerosion, BE (kg·yr$^{-1}$·m$^{-2}$)</td>
<td>$BE = \left(bioerosion \times FL\right) \times BR \times P_{bs} \times density \times 1.7 \times 365/1000$</td>
<td>only measured for Sp. viride and Sc. vetula; 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</td>
</tr>
</tbody>
</table>

Note: See Table 1 for abbreviations of parameter values.
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 rcompanion 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. 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...
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. chrysopterum* 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

(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,
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
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
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 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

![Graphical representation of ecological processes](image)

**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.

**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.
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 macroalgae 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. guacamala* 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, Lohfner 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 (1–4 kg m⁻² 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 Mumbay 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. coelestius* 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. coelestius* 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 Mumbay et al. 2004).

Previous models examining the impact of herbivory and fishing on Caribbean reefs has focused on parameterizing herbivores at the genus level (Mumbay 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. coelestius*, *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,


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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.

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

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.

<table>
<thead>
<tr>
<th>Reef name</th>
<th>Number of Surveys</th>
<th>Boulder-rubble (m²)</th>
<th>High-relief spur (m²)</th>
<th>Low-relief reef (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carysfort</td>
<td>5</td>
<td>2545</td>
<td>3408</td>
<td>2138</td>
</tr>
<tr>
<td>Elbow</td>
<td>5</td>
<td>3730</td>
<td>2804</td>
<td>685</td>
</tr>
<tr>
<td>French</td>
<td>4</td>
<td>1968</td>
<td>245</td>
<td>2314</td>
</tr>
<tr>
<td>Molasses</td>
<td>6</td>
<td>3073</td>
<td>3177</td>
<td>2533</td>
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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.