



Ecological drivers of parrotfish coral predation vary across spatial scales

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ABSTRACT: Parrotfishes (Labridae: Scarini) are widely recognized for their important functional role in reducing coral–algae competition by grazing algae, yet some species are also coral predators (corallivores) and thereby have direct negative impacts on corals they prey upon. To better understand the ecological drivers of parrotfish corallivory intensity, we compared patterns of relative predation scar size and abundance across spatial scales from individual coral colonies (<1 to several meters in size), to reefs within islands (1 to 10s of km), to 4 regions across the Greater Caribbean (100s to 1000s of km) including Panamá, Florida, St. Croix, and Bonaire. Across reef sites, there was a positive correlation of both parrotfish density and biomass with the relative coral area preyed upon, but not predation scar abundance. While there was no apparent site-level effect of coral cover on corallivory intensity, we found that the abundance of colonies preyed upon was positively correlated with both coral diversity and the proportional cover of frequently targeted coral taxa within localized 30 m² reef areas. At the scale of individual coral colonies, we found that while numerous coral taxa were preyed upon, corallivory was concentrated on a few species across regions, such as *Orbicella* spp., *Porites* spp., and *Stephanocoenia intersepta*. Our findings suggest that while increased parrotfish densities may result in an increased coral area preyed upon across reefs, corallivory intensity within reefs may decrease in response to declines in the cover of frequently targeted coral taxa and overall coral diversity.

Spanish and Papiamentu versions of the abstract are provided in the Supplement at www.int-res.com/articles/suppl/m740p145_supp.pdf

KEY WORDS: Corallivory · Parrotfish · Coral reef · Predation · Spatial scales · Ecosystem interactions

1. INTRODUCTION

Understanding how the outcomes of species interactions vary across spatial scales and gradients of

human impact is integral to informing management strategies to facilitate the resilience and recovery of coral reefs (Rogers et al. 2018, Ruttenberg et al. 2019, Chow et al. 2021). Parrotfishes (Labridae: Scarini) are

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widely recognized to play key roles in facilitating coral recruitment, growth, and survival by grazing on the algae and cyanobacteria that compete with corals (Kuffner et al. 2006, Hughes et al. 2007, Cissell et al. 2019). Intensive fishing of parrotfishes can reduce their abundance and compromise their ability to maintain reef algae in a grazed state (Hawkins & Roberts 2004, Bozec et al. 2016). Therefore, protecting parrotfishes from overfishing is believed to be an important management practice to promote coral reef resilience and recovery at the local scale (Hughes et al. 2007, Bozec et al. 2016, Holbrook et al. 2016, Steneck et al. 2019). While parrotfishes predominantly graze algae and cyanobacteria-covered substrates, which can indirectly benefit corals (Kuffner et al. 2006, Chasqui-Velasco et al. 2007, Adam et al. 2015, Nicholson & Clements 2020), some species are also facultative coral predators (corallivores) and thereby have potential negative impacts on the corals they prey upon (Reyes-Nivia et al. 2004, Bonaldo et al. 2011, Burkepile et al. 2019). Therefore, the net impact of consumption by parrotfishes on changing coral communities remains under debate (Rotjan & Lewis 2008, Mumby 2009, Rice et al. 2019). Parrotfish corallivory has presumably been a stressor on corals for millennia; however, when combined with modern human impacts, there is concern that the chronic biotic stress of parrotfish corallivory could be increasingly detrimental to coral resilience (Bellwood et al. 2003, Rotjan & Lewis 2008, Zaneveld et al. 2016, Rice et al. 2019, Rotjan et al. 2022). Evaluating ecological processes that influence parrotfish corallivory intensity across spatial scales and broad gradients in parrotfish density, coral cover, and coral diversity will enable us to better understand how corallivory may change in response to stressors such as overfishing and reef degradation.

Parrotfishes predominantly graze a diverse assemblage of turf algae and associated detritus known as the epilithic algal matrix, as well as cyanobacteria, crustose coralline algae (CCA), and fleshy macroalgae (Adam et al. 2015, Cissell et al. 2019, Nicholson & Clements 2020, Homma et al. 2022). Since algae and cyanobacteria compete with corals (Kuffner et al. 2006, Arnold et al. 2010), parrotfish grazing is widely believed to play an important role in indirectly promoting coral recruitment, growth, and survival (Hughes et al. 2007, Holbrook et al. 2016, Steneck et al. 2019; but see Trapon et al. 2013). Parrotfishes are also major reef bioeroders that differ in their impacts on reef substrate based on feeding mode, preferences, and body size (Alwany et al. 2009, Ong & Holland 2010, Adam et al. 2018, Lange et al. 2020).

Browsers crop macroalgae and help control its overgrowth, while scraping and excavating species leave more frequent reef grazing scars (Adam et al. 2018), which may facilitate the settlement of CCA and corals (Arnold et al. 2010, Charendoff et al. 2023). Through these complementary feeding modes, parrotfishes are believed to play important roles in promoting coral reef resilience (Rasher et al. 2013, Bonaldo et al. 2014, Adam et al. 2018).

Some parrotfishes are also facultative coral predators, although corallivory rates are low for most species (Bonaldo & Bellwood 2009, Bonaldo et al. 2014, Burkepile et al. 2019), with the notable exceptions of *Bolbometopon muricatum* and *Chlorurus strongylocephalus* in the Indo-Pacific (Hoey & Bellwood 2008, Lokrantz et al. 2008, Alwany et al. 2009). However, since parrotfishes are highly abundant on many reefs, even infrequent corallivory could cumulatively have a negative impact on corals, particularly when co-occurring with other stressors (Zaneveld et al. 2016, Ezzat et al. 2020, Rotjan et al. 2022). While small scars often heal, intensive corallivory can cause partial colony mortality and, in extreme cases, total colony mortality (Bruckner & Bruckner 1998, Miller & Hay 1998, Sánchez et al. 2004, Welsh et al. 2015, Rempel et al. 2020). Corallivory may also have indirect consequences such as reducing coral growth and fecundity and potentially acting as a disease vector (Rotjan & Lewis 2009, Cameron & Edmunds 2014, Ezzat et al. 2020). However, it may also have indirect benefits for corals such as dispersing coral symbionts (Symbiodiniaceae) via fish feces and introducing beneficial bacteria to the coral microbiome (Ezzat et al. 2020, Grupstra et al. 2021). Therefore, the consequences of parrotfish corallivory for coral tissue loss likely vary in response to the magnitude of local stressors and across ecological gradients in coral reef condition.

Furthermore, the ecological drivers of parrotfish corallivory intensity likely differ across spatial scales, as consumers often operate at different scales than their prey (Wiens 1989). For example, parrotfishes forage over 10s to 100s of meters (Adam et al. 2015, Chow et al. 2021), while coral cover and community composition can vary at the scale of a few meters. Furthermore, fishing pressure, which can influence parrotfish density and body size (Vallès & Oxenford 2014, Nash et al. 2016), often varies on the scales of reefs to regions (10s to 100s of km). Additionally, local reef conditions can influence the spatial extent of parrotfish–benthos interactions, as parrotfish foraging distances may increase on more degraded reefs (Nash et al. 2016). To disentangle how parrotfish–coral interactions may change in response to reef degradation and increased

fishing pressure, we first need to understand how the drivers of parrotfish corallivory vary from the scale of individual coral colonies to regions.

Over the past decade, there has been increasing interest in the putative ecological drivers of parrotfish corallivory intensity across gradients in reef community composition (Burkepile 2011, Roff et al. 2011, Huertas et al. 2021). There are 3 main factors thought to influence corallivory intensity; however, findings have been inconsistent across studies. First, most parrotfishes appear to selectively target certain coral species. For example, in the Indo-Pacific, *Porites* spp. corals are intensively preyed upon (Bonaldo & Bellwood 2011), whereas in the Caribbean, *Orbicella* spp. and *Siderastrea siderea* corals are commonly targeted in addition to *Porites* spp. (Reyes-Nivia et al. 2004, Rotjan & Lewis 2006, Burkepile 2011, Roff et al. 2011). Second, coral cover is thought to influence corallivory rates. A study in Florida found that scar density increased as coral cover decreased on reefs spanning from <1 to nearly 8% coral cover (Burkepile 2011), whereas a study from the Bahamas found no relationship between parrotfish scar density and coral cover on reefs spanning from 2.5 to 22.5% (Roff et al. 2011). Another study from the Great Barrier Reef found that corallivory intensity declined after coral cover decreased from 22 to ~7% after a decade of disturbance events (Huertas et al. 2021). Third, there is conflicting evidence as to whether parrotfish density affects corallivory intensity. For example, a study from Belize found a positive relationship between predation scar density on *Orbicella faveolata* and the abundance of one parrotfish species (Rotjan & Lewis 2006), whereas other studies from the Bahamas, Florida, Columbia, and the Great Barrier Reef found no such relationship (Reyes-Nivia et al. 2004, Burkepile 2011, Roff et al. 2011, Huertas et al. 2021). Whether the balance between relative parrotfish abundance and coral abundance is tipped because of an increase in parrotfishes or a decrease in coral, there are concerns that if the intensity of parrotfish corallivory does not decrease as coral cover declines, it could create a positive feedback loop that further exacerbates coral loss (Burkepile 2011).

The apparent disagreement between prior studies as to the relationship between corallivory intensity and the ratio of parrotfish to coral abundance may be in part due to the response variable chosen by investigators—most previous studies have not accounted for scar size, only density. Previous studies have also focused on reef-scale or inter-reef patterns (Rotjan & Lewis 2006, Burkepile 2011, Roff et al. 2011), while characteristics of individual coral colonies or local-

ized reef cover and diversity may be important but previously understudied factors that influence corallivory intensity. Parrotfish predation scars can vary in size, and the majority are small scars from individual bites that often fully heal (Sánchez et al. 2004, Bonaldo et al. 2011, Welsh et al. 2015, Rempel et al. 2020). However, parrotfishes sometimes repeatedly bite large, contiguous areas of coral colonies, which can cause far larger predation scars (Welsh et al. 2015, Rempel et al. 2020). While infrequent, these large scars can cause disproportionate amounts of coral tissue loss (Bonaldo et al. 2011, Welsh et al. 2015, Rempel et al. 2020). This suggests that scar size may be a more important metric than scar abundance when considering the long-term impacts of corallivory. Additionally, most previous studies have not differentiated between recent and older predation scars. Given that coral species differ in their healing capacities (Henry & Hart 2005), this may lead to an overestimation of relative corallivory intensity for slower-healing coral species.

Our objectives were to compare patterns in the relative size and abundance of recent parrotfish predation scars across broad gradients in parrotfish density, coral cover, and coral community composition. As an understanding of how the drivers of consumer–resource interactions vary across spatial scales is critical to informing management under changing environmental conditions (Wiens 1989, Levin 1992), we compared patterns across scales ranging from individual coral colonies to reefs spanning 4 Caribbean regions. Our research questions asked (1) how patterns of corallivory intensity vary across regions and reef sites in response to parrotfish density, coral cover, and coral community composition; (2) how the relative predation intensity on target coral taxa varies in response to local coral diversity and taxaspecific coral cover within small areas of reefs; and (3) how the relative intensity of corallivory on individual colonies varies in response to coral size, taxa, and region.

2. MATERIALS AND METHODS

2.1. Study sites

We collected data across 10 sites in Bocas del Toro, Panamá, in 2013; 4 in the Florida Keys, USA, in 2013; 8 in St. Croix, US Virgin Islands, in 2018; and 4 in Bonaire, Dutch Caribbean, in 2019 (Fig. 1). We conducted surveys of all regions between June and August. These sites and regions spanned broad

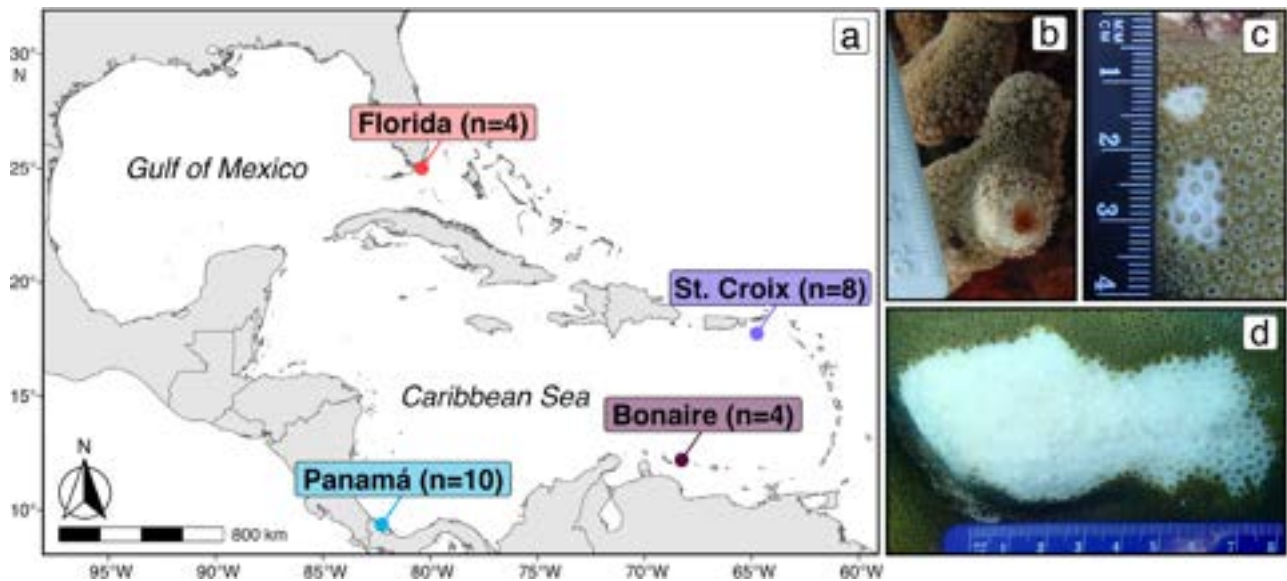


Fig. 1. (a) Study regions and the number of survey sites (for individual site coordinates, see Table S1). (b) An older parrotfish predation scar on a branching *Porites* spp. coral. (c) Recent scars on an *Orbicella annularis* colony left by the upper and lower jaws of a parrotfish. (d) A large, recent scar on an *O. annularis* colony caused by repetitive, focused predation

gradients in parrotfish density and biomass (see Fig. 2, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m740p145_supp.pdf) and also varied in parrotfish fishing intensity. Parrotfish populations in Bocas del Toro, Panamá, are dominated by small-bodied species (Kuempel & Altieri 2017). Although their harvest has been prohibited in Panamá since 1994 (Harms-Tuohy 2021), paleoecological evidence suggests local populations have undergone major declines, possibly in response to over 2 centuries of overfishing and land-use change (Cramer et al. 2017). Sites in Florida were within a no-take reserve (NOAA 1997) and illegal parrotfish fishing is rare (Harms-Tuohy 2021). In St. Croix, parrotfishes are a major commercial fishery with the highest landings in the US Caribbean (NOAA NMFS 2012, Harms-Tuohy 2021). Five of the 8 survey sites in St. Croix were in fished areas, while the other 3 were in a no-take marine reserve established in 2001 (DPNR 2005). In Bonaire, parrotfishes are not a traditional fishery and their harvest has been prohibited since 2010 (Island Council of the Bonaire Island Territory 2010, Harms-Tuohy 2021). Coral cover across these sites also spanned broad gradients, ranging from <1% at some sites in Florida to >30% at some sites in Bonaire and Panamá. Gradients in parrotfish density, coral cover, and coral community composition across these regions make them ideal for comparing ecological factors that may influence the relative intensity of parrotfish corallivory.

2.2. Coral demography and predation scar surveys

While direct observations of parrotfish corallivory are infrequent, several parrotfish genera (including *Scarus* and *Sparisoma*) have completely fused beak-like teeth (Bellwood & Choat 1990, Evans et al. 2023) that leave characteristic, often paired scars from their upper and lower jaws as they denude portions of the coral tissue (Fig. 1b–d). These distinctive scars are commonly used to quantify parrotfish corallivory intensity (Rotjan & Lewis 2006, Burkepile 2011, Huerstas et al. 2021). While a few Tetrodontiformes species in the region are occasional corallivores that also denude coral skeletons (e.g. *Cantherhines macrocerus* and *Melichthys niger*), it typically makes up <1% of their ingesta (Randall 1967), and parrotfishes are the predominant skeleton-denuding corallivorous fishes in the Caribbean (Cole et al. 2008). To facilitate consistent parrotfish scar identification across regions, a principal investigator in charge of data collection in each region met in the Florida Keys prior to the study to collectively train in parrotfish predation scar identification and develop common scar survey methods. Notably, in some regions, these methods were slightly adapted to fit local ecosystem conditions (e.g. surveying corals in size bins in all regions but the Florida Keys, as most other regions had much higher coral densities; see details below).

Across all regions, we surveyed the size and abundance of scleractinian coral species ≥ 3 cm in diame-

ter in 30×1 m transects parallel to the reef formation across a range of depths between 2.1 and 15.8 m ($n = 2\text{--}11$ transects site⁻¹; Table S1). We chose to sample this depth gradient because parrotfishes are mobile foragers known to feed across this range of depths (Bruggemann et al. 1994, Rempel et al. 2022) and they have territories that can span 100s to >1000 m² (Mumby & Wabnitz 2002, Manning & McCoy 2023). Whenever possible, we identified corals to the species level. However, we grouped branching *Porites* spp. due to the lack of consensus on genetic and morphological distinctions between these taxa across the Caribbean (Prada et al. 2014, Dimond et al. 2017). Additionally, due to similar appearances among some *Agaricia* spp., particularly for smaller colonies, we identified some to the genus level.

For coral colonies with predation scars, we recorded colony diameter and perpendicular width to the nearest cm, scar abundance, and the percentage of recent scars. We defined an individual scar as one contiguous lesion. We classified scars as recent if there were no signs of tissue healing at the scar perimeter or growth of algae or cyanobacteria within the scar (Fig. 1b), which typically appears within the first few days after a scar is inflicted (Rempel et al. 2020). For colonies with ≤ 3 scars, we recorded scar length and width (cm), then estimated scar surface area as the area of an oval. While most colonies had few scars, some had >100 and it was not practical to measure each scar. Therefore, for colonies with >3 scars, we measured the visually estimated minimum, median, and maximum scars to estimate approximate scar size distributions. We used these size estimates and scar abundance to interpolate scar size distributions based on a normal distribution centered on the median and bounded by the minimum and maximum scar size, as scar sizes distribute approximately normally overall in a region (Rempel et al. 2020). Similar methods have been used in prior studies to estimate size distributions of parrotfish bite scars (Rempel et al. 2020), as well as fish populations (Brandt et al. 2009, Smith et al. 2011). Given that coral species differ in healing rates (Henry & Hart 2005), including older scars in surveys may lead to inaccurate comparisons of the relative predation intensity between species. To estimate the coral area preyed upon per colony based on recent scars, we used bootstrapping with 10 000 iterations to randomly sample size estimates based on the percentage of recent scars and total scar abundance per colony (Rempel et al. 2020).

For coral colonies without predation scars, we recorded coral taxa and colony size. In Florida, coral abundance was low, so we directly measured each

colony *in situ* to the nearest cm. In other regions, the higher abundance of colonies made directly measuring each colony impractical. In Panamá, we recorded colony diameter in bins of 3 to <5 , 5 to <10 , 10 to <20 , 20 to <40 , 40 to <80 , and ≥ 80 cm. In St. Croix and Bonaire, some sites had a high abundance of small coral colonies. In these regions, we recorded colonies with a diameter <20 cm using the same size bins as in Panamá, but measured colonies ≥ 20 cm to the nearest cm. This allowed us to survey many small colonies within the time constraints of SCUBA surveys, while still obtaining precise measurements for larger colonies that varied more in size and shape. For colonies partially within the transect, we recorded the percent of the colony within the transect to the nearest 5% to correct coral cover estimates, and only recorded scars within the transect. For colonies with partial mortality, we estimated the percent living coral tissue. For all coral species for which we had direct measurements, we calculated colony surface area (SA) based on the area of an oval:

$$SA = \pi \left(\frac{\text{Max. diameter}}{2} \right) \left(\frac{\text{Perpendicular width}}{2} \right) \left(\frac{\% \text{ live tissue}}{100} \right) \left(\frac{\% \text{ colony in transect}}{100} \right) \quad (1)$$

For all analyses, we restricted estimates of coral cover to taxa for which we observed ≥ 3 colonies with recent predation scars ($n = 323$ total colonies), hereafter referred to as target coral taxa (Table S2). These taxa were as follows: *Agaricia agaricites*, *A. humilis*, *A. tenuifolia*, *Agaricia* spp., *Madracis auretenra*, *M. decactis*, *Orbicella annularis*, *O. faveolata*, branching *Porites* spp., *P. astreoides*, *Siderastrea siderea*, and *Stephanocoenia intersepta*. To estimate the surface area of corals within size bins, we calculated the mean surface area of each coral taxa and size class from colonies for which we had direct measurements. We calculated the percent of coral cover based on the total area of these coral taxa relative to the transect area.

2.3. Parrotfish density surveys

To quantify corallivorous parrotfish density, we surveyed their abundance within 80–100 m² transects at each site, a survey area comparable to that of a similar prior study in the region (Burkepile 2011). Behavioral research suggests that *Scarus taeniopterus*, *Sc. vetula*, and *Sparisoma viride* are the major Caribbean corallivores (Cardoso et al. 2009, Burkepile et al. 2019), while other parrotfish species typically take $<1\%$ of their average bites on live coral (Text S1, Table S3).

Additionally, parrotfish bioerosion and corallivory rates vary by ontogeny, where the onset of bioerosion capabilities is typically at ~15 cm and juveniles and small adults do not typically consume live coral (Bruggemann et al. 1994, 1996, Ong & Holland 2010, Bonaldo & Rotjan 2017). Therefore, we restricted our estimates of corallivore density to individuals of these 3 species that were ≥ 15 cm fork length (Fig. S2). In Panamá and Florida, we surveyed individuals within 25×4 m transects (100 m^2). In St. Croix and Bonaire, we conducted 20–25 min roving surveys while towing a Garmin GPS 72 on a taut line to measure distance traveled and recorded parrotfishes observed in a 5 m wide belt for each minute of the survey (Adam et al. 2015, Rempel et al. 2022). Using the 'distm' function from the 'geosphere' R package, we calculated the haversine distance traveled per minute (Hijmans et al. 2019). To integrate these surveys with 100 m^2 surveys from Panamá and Florida, we filtered the data to only include segments from consecutive minutes that spanned a 16 to 20 m length (i.e. 80 to 100 m^2). Additionally, for any back-to-back segments, we filtered the data to select every other segment, ensuring that there were at least 16 to 20 m between each. We acknowledge that differences in survey methods between regions may be a potential source of variation; however, these steps to integrate these surveys can facilitate reasonable comparisons across regions. We conducted 2 to 32 surveys per site stratified across depths ranging from 1.5 to 17.7 m (Table S1). While we focus on patterns of parrotfish density, we describe methods used to estimate corallivore biomass and related analyses in the Supplement (Text S2).

2.4. Statistical analysis

2.4.1. Variation in corallivory intensity among regions

We conducted statistical analyses using R v.4.3.0 (R Core Team 2023). We analyzed variation in site-level mean corallivorous parrotfish density (no. per 100 m^2), parrotfish biomass (g per 100 m^2), target coral cover (%), and coral area preyed upon (%) among regions using Kruskal-Wallis tests, as these data violated normality or homogeneity of variance assumptions. We conducted post hoc Dunn's tests using the 'rstatix' package (Kassambara 2023) with a Benjamini-Hochberg correction for multiple comparisons (Benjamini & Hochberg 1995). We conducted ANOVA to evaluate regional differences in the natural log-transformed scar density (no. m^{-2} target

coral), followed by a post hoc Tukey test. We tested ANOVA model assumptions via visual inspection of the residuals, as well as a Shapiro-Wilk test of normality, Levene test of homogeneity of variance, and interquartile range outlier test using the 'rstatix' package (Kassambara 2023).

2.4.2. Variation in corallivory intensity within and among reefs

To assess how relative scar density (no. m^{-2} target coral) and coral area preyed upon (%) varied in response to corallivorous parrotfish density (no. per 100 m^2), target coral cover (%), and the interaction of these variables, we used generalized and general linear mixed models (GLMMs), respectively, with a random intercept by region. We used a t -distribution for the model of scar density, as residual plots indicated it was a better fit than Gaussian, and used a Gaussian distribution for the model of coral area preyed upon. For both models, we included a natural log transformation of the response variable as they follow a conditional log-normal distribution and a square-root transformation of parrotfish density to address quantile deviations from normality.

Our observations suggest that *O. annularis*, branching *Porites* spp., *P. astreoides*, and *S. siderea* are the most frequently preyed upon Caribbean coral taxa. We used a negative binomial GLMM to evaluate how the abundance of coral colonies with predation scars of these taxa varied within 30 m^2 areas of reefs in response to local coral diversity, the natural log-transformed ratio of the cover of a given taxa to total target coral cover, transect depth (m), and region with a random intercept of transect nested within site. We calculated coral diversity (H') using the Shannon Diversity Index (Shannon 1948). We used a negative binomial GLMM because residual plots and diagnostic tests indicated it was a better fit than Poisson.

2.4.3. Variation in corallivory intensity among coral colonies

We used a negative binomial GLMM to assess how the abundance of recent predation scars on target coral colonies varied in response to coral taxa, colony surface area (cm^2), transect depth (m), and region with a random intercept of transect nested within site. We used a negative binomial GLMM because residual plots and a likelihood ratio test indicated that it was a significantly better fit than Poisson ($\chi^2_1 =$

3549.1, $p < 0.001$). For target coral colonies with predation scars, we used GLMMs with t -distributions to compare how the natural log of mean scar area and natural log of percent of coral area preyed upon varied in response to coral taxa, the natural log of colony surface area (cm^2), transect depth (m), and region with a random intercept of transect nested within site. For these 2 models, we used t -distributions because residual plots and diagnostic tests indicated it was a better fit than Gaussian.

2.4.4. Assessing GLMM fit

We analyzed all general and GLMMs using the 'glmmTMB' package, which estimates p-values using a Wald Z-statistic (Brooks et al. 2017). We assessed the fit of all mixed models using the 'DHARMA' package (Hartig 2022), using estimated residuals from 1000 simulations to visually inspect the model fit and test for overdispersion, outliers, and normality via Kolmogorov-Smirnov tests. Additionally, for GLMMs of count data, we tested for zero-inflation.

3. RESULTS

3.1. Variation in corallivory intensity among regions

There was significant variation in corallivorous parrotfish density (Kruskal-Wallis test, $H_3 = 17.66$, $p < 0.001$), parrotfish biomass ($H_3 = 14.92$, $p = 0.002$), and target coral cover ($H_3 = 13.65$, $p = 0.003$) across the 4 observed Caribbean regions (Table 1, Fig. 2 & Fig. S1). We observed significantly higher parrotfish densities in Florida and Bonaire than in Panamá (Dunn's tests, $p_{\text{adj}} = 0.042$ and < 0.001 , respectively), and a higher biomass of parrotfishes in Bonaire than in Panamá ($p_{\text{adj}} = 0.001$). Additionally, there was higher coral cover in Bonaire than in Florida and

St. Croix ($p_{\text{adj}} = 0.014$ and 0.035 , respectively) and in Panamá than in Florida ($p = 0.014$). There were significant regional differences in relative predation scar density (ANOVA, $F_{3,22} = 21.88$, $p < 0.001$) and percent of coral preyed upon (Kruskal-Wallis test, $H_3 = 15.72$, $p = 0.001$). There were significantly higher scar densities in Florida than in Panamá, St. Croix, and Bonaire (Tukey test, $p < 0.001$ for all), as well as a higher percent of coral area preyed upon in Florida than in Panamá (Dunn's test, $p_{\text{adj}} < 0.001$; see Figs. S3 & S4 for patterns of corallivory intensity by region and coral genera).

3.2. Variation in corallivory intensity within and among reefs

At the reef scale, we found no evidence of an effect of target coral cover on relative scar density or percent of coral preyed upon after accounting for random regional variation (Fig. 3, Table S4). We found a significant effect of square-root transformed corallivorous parrotfish density on the percent of coral preyed upon (GLMM, $\beta = 1.34$, $Z = 2.509$, $p = 0.012$) but not relative scar density (Fig. 3). Similarly, when we compared models using corallivorous parrotfish biomass instead of density, we also found a significant effect on percent of coral area preyed upon ($\beta = 0.064$, $Z = 2.207$, $p = 0.027$) but not relative scar density (Fig. S5, Table S4). For all models, we found no evidence of an interactive effect of parrotfish density (or biomass) and coral cover on corallivory intensity. Slight variation in survey methods across regions may have led to increases in sampling error, but the fact that the main findings are robust and consistent for both parrotfish abundance and biomass suggests that this is unlikely to have influenced the overall findings.

Within 30 m^2 areas of reefs, we found a significant positive effect of coral diversity on the abundance of *Orbicella annularis*, branching *Porites* spp.,

Table 1. Regional means \pm SE of the density (no. per 100 m^2) of major corallivorous parrotfish (*Scarus taeniopterus*, *Sc. vetula*, and *Sparisoma viride*) individuals of $\geq 15 \text{ cm}$ fork length, coral cover of taxa targeted by parrotfishes (%), parrotfish predation scar density (no. m^{-2} coral), mean scar area for coral colonies with predation scars (cm^2), and mean proportion of the coral colony area with preyed upon (%). Darker shades indicate larger values

Region	Parrotfish density	Coral cover	Scar density	Mean scar area	Colony area preyed upon
Panamá	0.8 \pm 0.4	18.0 \pm 3.7	0.9 \pm 0.2	0.333 \pm 0.044	0.003 \pm 0.001
Florida	3.9 \pm 1.0	2.8 \pm 1.9	121.7 \pm 38.9	0.630 \pm 0.091	0.553 \pm 0.147
St. Croix	2.4 \pm 0.5	7.2 \pm 1.3	1.4 \pm 0.7	1.170 \pm 0.446	0.010 \pm 0.002
Bonaire	7.6 \pm 0.5	23.3 \pm 4.1	2.0 \pm 0.8	1.993 \pm 0.791	0.014 \pm 0.004

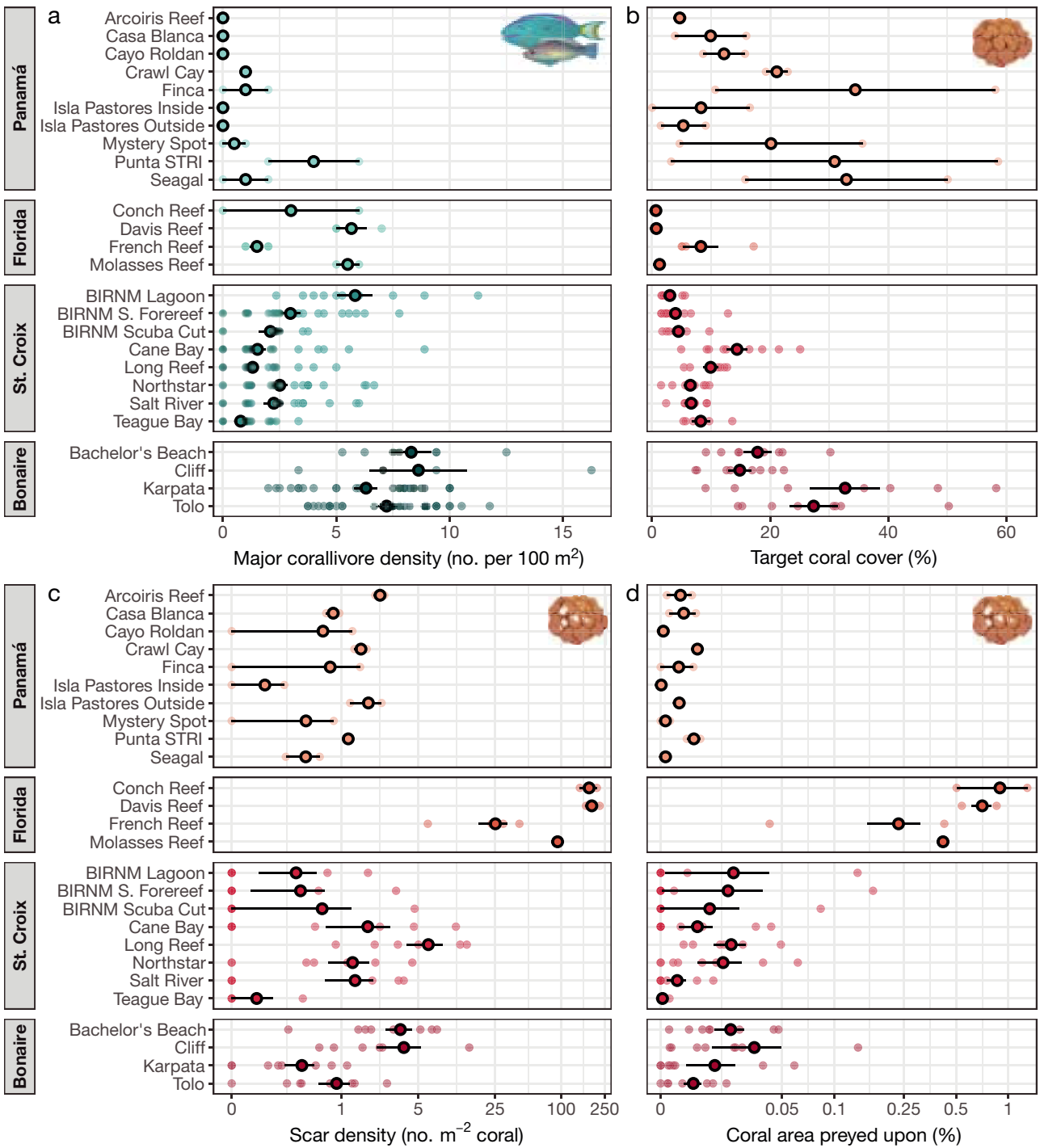


Fig. 2. Site-level means \pm SE of the (a) density of major corallivorous parrotfishes ≥ 15 cm, (b) cover of coral species targeted by parrotfishes, (c) density of parrotfish predation scars, and (d) coral area preyed upon. Raw data points are shown transparently in the background. Values of scar density and coral area preyed upon (c,d) are on a natural log-transformed scale, showing values $+0.1$ and $+0.01$, respectively, to account for 0 values in raw transect-level data points

P. astreoides, and *Siderastrea siderea* colonies with predation scars (GLMM, $Z = 2.950$, $p = 0.003$). For every 1-unit increase in coral diversity (H'), there were 4.3 times more coral colonies with predation scars on

average after accounting for other model parameters (Fig. S6). For all 4 coral taxa, there was a significant positive effect of the relative cover of a given coral taxa on the abundance of colonies of that taxa with

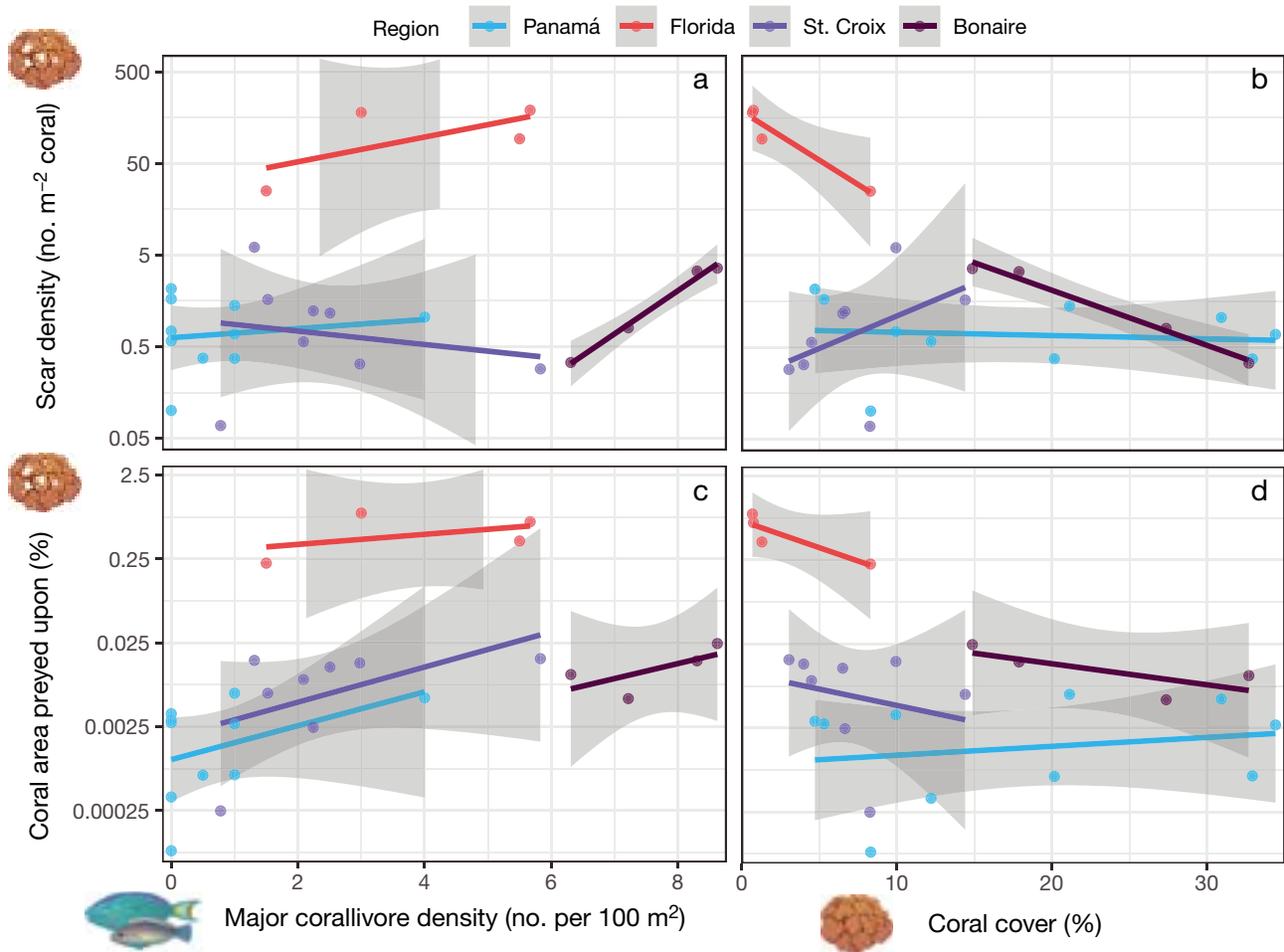


Fig. 3. (a,b) Site-level predation scar density and (c,d) percent of coral area preyed upon in response to (a,c) major corallivorous parrotfish density of individuals ≥ 15 cm and (b,d) the percent cover of target coral species, with the line of best fit by region and 95% confidence intervals. Relative scar density and percent coral area preyed upon are shown on a natural log-transformed scale

predation scars ($p < 0.001$ for all; Table S5). On average, for every 1% increase in the ratio of the cover of the respective coral taxa to total target coral cover, the abundance of coral colonies with predation scars increased by 4.5 times for *O. annularis*, 1.8 times for *P. astreoides*, 2.1 times for branching *Porites* spp., and 2.6 times for *S. siderea*. Compared to branching *Porites* spp. colonies, there were significantly fewer *P. astreoides* colonies with predation scars (est. 0.31 times fewer; $Z = 1.180$, $p = 0.032$) and *S. siderea* (est. 0.24 times fewer; $Z = 1.433$, $p = 0.004$) but not *O. annularis*. Among regions, there were significantly more coral colonies with predation scars in Florida than in Panamá (est. 9.2 times more; $Z = 5.493$, $p < 0.001$) and fewer in St. Croix than in Panamá (est. 0.34 times fewer; $Z = -2.771$, $p = 0.006$) after accounting for other model parameters. There was no significant effect of reef depth (ranging from 2.1 to 15.8 m) on the abundance of colonies with predation scars.

3.3. Variation in corallivory intensity among coral colonies

We evaluated how region, coral colony surface area, coral taxa, and reef depth influenced corallivory intensity as measured by the (1) scar abundance per colony, (2) mean size of scars for colonies with predation scars, and (3) percent of coral colony area preyed upon for colonies with predation scars. We observed significant differences in scar abundance per coral colony in response to region, colony surface area, and taxa, but not reef depth (Table S6). Compared to Panamá, there was a significantly higher scar abundance per colony in Florida (GLMM, est. 86.92 times more; $Z = 5.42$, $p < 0.001$) and a lower abundance in St. Croix (est. 0.04 times fewer; $Z = -4.95$, $p < 0.001$) but no significant difference in Bonaire. While we found a significant positive relationship between scar abundance and coral colony surface area ($Z = 6.61$,

$p < 0.001$), the effect size was small, with an estimated 1.001 times more scars per colony for every 1.0 cm² increase in colony area. Additionally, compared to *Agaricia agaricites*, there was a significantly higher abundance of scars on *Madracis decactis* (est. 16.3 times more; $Z = 3.37$, $p = 0.001$), *O. annularis* (est. 68.5 times more; $Z = 5.36$, $p < 0.001$), branching *Porites* spp. (est. 92.1 times more; $Z = 5.71$, $p < 0.001$), and *P. astreoides* (est. 65.0 times more; $Z = 5.42$, $p < 0.001$).

We observed significant differences in mean scar size in response to region, colony surface area, and taxa, but not reef depth (Table S7). After accounting for coral taxa and colony size, we observed that compared to Panamá, there were significantly larger mean scar sizes in Florida (est. 2.9 times larger; $Z = 4.82$, $p < 0.001$), St. Croix (est. 2.3 times larger; $Z = 3.18$, $p = 0.016$), and Bonaire (est. 2.9 times larger; $Z = 3.95$, $p < 0.001$). There was a significant effect of colony size on mean scar size ($Z = 2.17$, $p = 0.030$), where for every 1.0% increase in colony surface area the average scar area increased by 0.082%. Among taxa, there were significantly larger mean scar sizes on *A. tenuifolia* (est. 3.7 times larger; $Z = 3.06$, $p = 0.002$), branching *Porites* spp. (est. 2.2 times larger; $Z = 2.90$, $p = 0.004$), and *Stephanocoenia intersepta* (est. 3.6 times larger; $Z = 2.259$, $p = 0.024$) compared to *A. agaricites* after accounting for other model parameters (Fig. 4).

We observed significant differences in the percent of coral colony preyed upon in response to region, colony surface area, and taxa, but not reef depth (Fig. 4, Table S8). There was a smaller percent of colony area preyed upon in Panamá than in Florida,

St. Croix, and Bonaire ($Z = 6.49$, 4.29, and 5.71, respectively, $p < 0.001$ for all). Compared to Panamá, we estimate that there were 5.4, 3.7, and 6.0 times more coral areas preyed upon in Florida, St. Croix, and Bonaire, respectively. We found a negative relationship between colony surface area and the percent of colony area preyed upon (GLMM, $Z = -15.09$, $p < 0.001$), where for every 1.0% increase in colony size, the percent colony area preyed upon decreased by an average of 0.74%. Compared to *A. agaricites*, there was a higher colony area preyed upon for *A. tenuifolia* (est. 5.0 times more; $Z = 3.36$, $p = 0.001$), *Agaricia* spp. (est. 7.7 times more; $Z = 3.06$, $p = 0.002$), *O. annularis* (est. 2.2 times more; $Z = 2.05$, $p = 0.040$), branching *Porites* spp. (est. 3.1 times more; $Z = 3.45$, $p = 0.001$), and *P. astreoides* (est. 2.2 times more; $Z = 2.29$, $p = 0.022$).

4. DISCUSSION

While parrotfishes may indirectly facilitate coral resilience by grazing on the algae and cyanobacteria that compete with corals (Edwards et al. 2011, Ste-neck et al. 2019, Cissell et al. 2019), they also have negative impacts on coral colonies that they prey upon (Alwany et al. 2009, Welsh et al. 2015, Rempel et al. 2020, Huertas et al. 2021). Quantifying how coral-livory intensity may differ on reefs with lower coral cover and diversity as well as varying parrotfish densities is critical to understanding and managing the net impacts of parrotfishes under changing reef conditions (Rotjan & Lewis 2008, Mumby 2009). We eval-

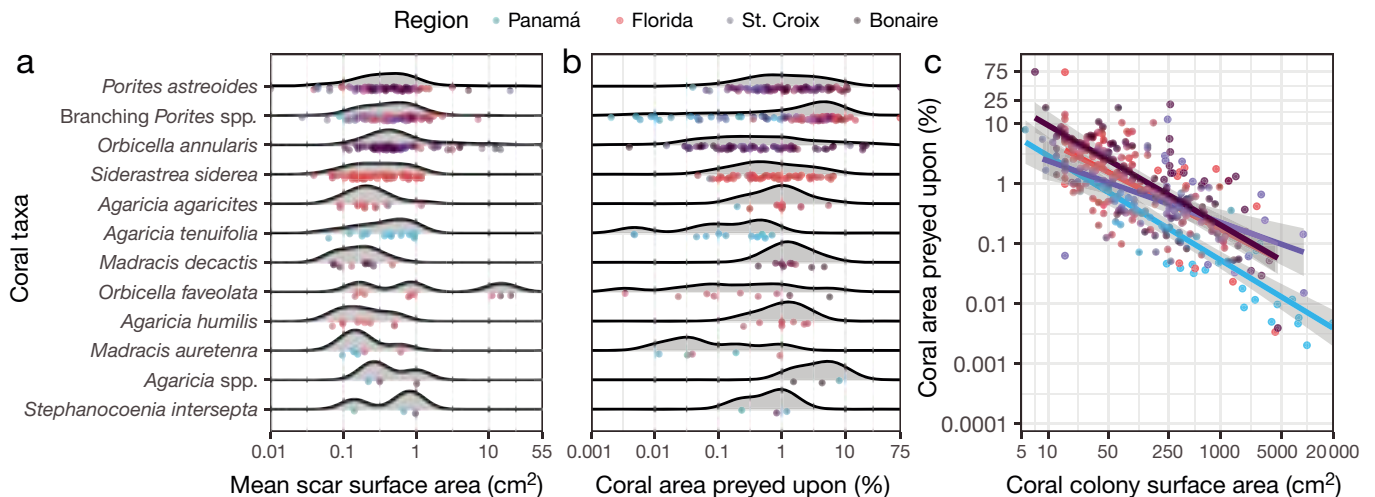


Fig. 4. Distributions of the natural log-transformed (a) mean predation scar surface area and (b) colony area preyed upon by parrotfishes for all target coral taxa. Coral taxa are arranged by the number of colonies with predation scars from highest to lowest. (c) Coral colony area preyed upon (%) in response to colony surface area on a natural log-transformed scale with the line of best fit by region and 95% confidence interval. Raw data points are shown transparently in the background

uated how corallivory intensity varied across spatial scales from coral colonies, to reefs, to 4 regions of the Greater Caribbean. These reefs spanned broad gradients in corallivorous parrotfish density and biomass (0–8.6 ind. per 100 m² and 0–2517 g per 100 m², respectively), as well as coral cover (<1 to >34%), allowing us to better assess how these factors may influence parrotfish predation scar density and coral area preyed upon. This study helps resolve previously inconclusive or contradictory findings on the purported ecological drivers of parrotfish corallivory intensity. Overall, our findings suggest that broad-scale patterns in corallivory intensity at the reef to regional scales are more strongly influenced by parrotfish density and biomass, while patterns within reefs and at the scale of individual coral colonies are more strongly driven by coral cover, coral species composition, and colony-level traits.

4.1. Effects of parrotfish density

While researchers have expressed concerns that management actions that increase the abundance of parrotfishes to promote herbivory could lead to an increase in corallivory intensity (Rotjan & Lewis 2008), relationships between parrotfish density and coral predation remain poorly understood (Mumby 2009). Several prior studies found no relationship between corallivorous parrotfish density and the relative abundance of predation scars (Reyes-Nivia et al. 2004, Burkepile 2011, Roff et al. 2011), while one study found a positive relationship between *Orbicella faveolata* scar density and *Sparisoma aurofrenatum* parrotfish density (Rotjan & Lewis 2006). Given that these studies were conducted in areas with relatively abundant parrotfishes, researchers suggested that the effects of corallivory may be more apparent when comparing sites where fishing pressure has created stronger gradients in parrotfish density (Roff et al. 2011). Our study spanned that gradient, including regions such as Panamá, where larger corallivorous parrotfish species are uncommon (Kuempel & Altieri 2017), possibly due to historical overfishing (Cramer et al. 2017); St. Croix, where parrotfishes are a major commercial fishery and their densities are lower; and the Florida Keys and Bonaire, where parrotfishes are protected and their densities are higher (Harms-Tuohy 2021). Additionally, while scar size may be a more important predictor of coral tissue loss from parrotfish predation than scar abundance (Rempel et al. 2020), this is one of the first studies in the region to assess how parrotfish densities may influence scar

area in addition to density. We found that as parrotfish density and biomass increased, the relative coral area preyed upon increased but the relative abundance of scars did not. These contrasting findings suggest that there may be larger scars in areas with more abundant and/or larger parrotfishes.

Larger-bodied parrotfishes create larger grazing scars, as scar area scales exponentially with fish length (Bruggemann et al. 1994, Adam et al. 2018, Lange et al. 2020). Furthermore, parrotfish species vary in their foraging targets and bite mechanics, and excavating parrotfishes like *Sp. viride* may denude larger coral areas than scraping species (Hoey & Bellwood 2008, Alwany et al. 2009, Adam et al. 2018, Burkepile et al. 2019). Reefs with higher parrotfish density and biomass may have also had more abundant large-bodied individuals and/or excavating species (Figs. S1 & S2), which typically leave larger grazing scars (Bellwood et al. 2012). This could help explain why parrotfish density influenced the relative coral area preyed upon but not scar density.

Intensive fishing of larger-bodied parrotfishes can reduce their mean size and alter their species composition (Hawkins & Roberts 2004, Bellwood et al. 2012, Kuempel & Altieri 2017, Shantz et al. 2020). In Bonaire and Florida, where parrotfish harvest is prohibited, there were higher average parrotfish densities and biomasses than in St. Croix and Panamá (Fig. S1). Similarly, Bonaire and Florida also had higher average densities of the excavating parrotfish *Sp. viride* (Fig. S2), which is the most frequent Caribbean corallivore (Table S3). Importantly, larger-bodied parrotfishes may also have disproportionately higher contributions to processes such as bioerosion and clearing reef substrate of algae (Adam et al. 2018, Lange et al. 2020). Research suggests that the loss of larger-bodied Caribbean parrotfishes can increase algal biomass by 10-fold (Shantz et al. 2020). Therefore, intensive fishing pressure may indirectly reduce the intensity of corallivory but could also compromise other key functional roles of parrotfishes.

4.2. Effects of coral cover and community composition

If parrotfish corallivory intensity remains constant as coral cover declines, the stress from chronic predation could exacerbate coral tissue loss in areas with declining coral cover (Rotjan & Lewis 2008, Burkepile 2011); however, previous findings have been inconclusive. Furthermore, it is unclear how corallivory intensity on targeted coral species may vary in response

to coral diversity (Mumby 2009). One study on low coral cover reefs in Florida found that relative scar density increased as coral cover declined (Burkepile 2011), another study from the Bahamas found no such effect (Roff et al. 2011), while a third study from the Great Barrier Reef found that scar density on massive *Porites* spp. declined following disturbances that caused a large decline in coral cover (Huertas et al. 2021). Across reef sites, we found that coral cover ranging from <1 to >30% had no observable effect on corallivory intensity. However, within localized 30 m² areas of reefs, the abundance of coral colonies preyed upon from frequently targeted coral species (*Orbicella annularis*, branching *Porites* spp., *P. astreoides*, and *Siderastrea siderea*) decreased as their relative cover and overall coral diversity decreased. Previous studies noted that corallivory intensity on *Porites* spp. appeared to intensify on reefs where preferred corals like *Orbicella* spp. were rare (Burkepile 2011). Additionally, research suggests that parrotfishes selectively graze certain coral taxa (Rotjan & Lewis 2006, Bonaldo & Bellwood 2011, Burkepile 2011, Roff et al. 2011) but these patterns vary by reef habitat type and season and may be influenced by colony traits such as coral skeletal density, reproductive state, and the presence of macroboring organisms (Bruggemann et al. 1996, Reyes-Nivia et al. 2004, Rotjan & Lewis 2006, 2009, Hoey & Bellwood 2008, Alwany et al. 2009, Rice et al. 2020). These findings suggest that parrotfishes may alter their predation preferences in response to coral community composition within reefs. However, these patterns may only be apparent for intensively grazed species, may be influenced by colony-specific traits, and/or influenced by the local 'coral neighborhood', and therefore may be attenuated at the reef scale.

While we observed that *Agaricia*, *Madracis*, *Orbicella*, *Porites*, *Siderastrea*, and *Stephanocoenia* spp. corals were targeted across regions, over 80% of colonies with predation scars were from 4 species alone (*O. annularis*, branching *Porites* spp., *P. astreoides*, and *S. siderea*). Similarly, previous studies have found that most coral taxa are not intensively preyed upon, with the exceptions of *Porites* spp., *Orbicella* spp., and *S. siderea* in some Caribbean regions (Rotjan & Lewis 2006, Burkepile 2011, Roff et al. 2011), and massive *Porites* spp. corals in the Indo-Pacific (Bonaldo & Bellwood 2011, Huertas et al. 2021).

4.3. Effects of coral colony-level variables

At the scale of individual coral colonies, researchers have questioned whether parrotfishes may focus their

predation on a few targeted colonies as neighboring coral cover declines, increasing partial to total colony mortality on these individuals, or whether predation will be dispersed across a larger number of colonies, increasing scar abundance per colony but not necessarily scar area (Mumby 2009). We found that there was a far higher abundance of scars per coral colony in Florida than in all other regions, although Florida had a similar coral colony area grazed and mean scar area compared to Bonaire. Previous studies have also found that Florida has notably high scar densities (Burkepile 2011), possibly driven by the combination of moderately high parrotfish densities but extremely low coral cover. Yet some reefs in a marine reserve in St. Croix that had comparable parrotfish densities and only slightly higher coral cover did not have similarly high levels of predation. Interestingly, one site in Florida that had somewhat higher coral cover (8.3% compared to 0.7 to 1.3%) had 3.7 to 7.6 times lower relative scar density and 1.8 to 4.0 times lower coral area preyed upon. There may be thresholds of extremely low coral cover at which these relationships become more apparent or there may be other unique factors of Floridian reefs influencing these patterns.

Research suggests that corallivory can be a significant source of tissue loss for small coral recruits and outplanted colonies (Miller & Hay 1998, Shantz et al. 2020, Koval et al. 2020), which has important implications for restoration efforts (Knoester et al. 2023). A study from the Great Barrier Reef found that smaller coral colonies had a lower absolute scar abundance but a higher density of scars relative to coral area (Huertas et al. 2021). Similarly, we found a slight increase in scar abundance per colony and mean scar size for larger colonies but a lower percent colony area preyed upon. Since scar area may be a more important predictor of long-term coral tissue loss from corallivory than scar abundance (Rempel et al. 2020), there may be greater impacts of parrotfish corallivory on smaller coral colonies. However, studies suggest that the loss of large-bodied parrotfishes can indirectly reduce overall coral growth and survivorship due to increases in algae and cyanobacteria (Kuffner et al. 2006, Hughes et al. 2007, Shantz et al. 2020). This suggests that the indirect benefits of parrotfish grazing on algae and cyanobacteria may outweigh the negative impacts of their corallivory for smaller coral colonies (Hughes et al. 2007, Knoester et al. 2019).

After accounting for coral colony size, we found more abundant scars on *Madracis decactis*, *O. annularis*, branching *Porites* spp., and *P. astreoides* colonies and a higher percent of coral area preyed upon

for *Agaricia tenuifolia*, *O. annularis*, branching *Porites* spp., and *P. astreoides*. Furthermore, we found that there were larger mean scar sizes on *A. tenuifolia*, branching *Porites* spp., and *Stephanocoenia intersepta*, though the average scar size—even for these species—was $<1\text{ cm}^2$. A study on *O. annularis* healing from parrotfish predation found that scars of $\leq 1.25\text{ cm}^2$ often fully heal and that scar size may be a more important predictor of long-term coral tissue loss from corallivory than scar abundance (Rempel et al. 2020). Furthermore, research from both the Caribbean and Indo-Pacific suggests that most scars from individual parrotfish bites are likely to fully heal (Sánchez et al. 2004, Welsh et al. 2015, Charendoff et al. 2023). However, large scars from repetitive, focused parrotfish predation may cause the vast majority of coral tissue loss (Welsh et al. 2015, Rempel et al. 2020). While infrequent, we observed particularly large predation scars ($>8\text{ cm}^2$) on a few coral taxa (*O. annularis*, *O. faveolata*, and *P. astreoides*), suggesting that there may be greater long-term consequences of corallivory for these species. Corallivory may also have indirect impacts such as reduced coral growth and fecundity (Rotjan & Lewis 2009, Bonaldo et al. 2012). Furthermore, when corallivory occurs in combination with stressors such as nutrient enrichment or coral bleaching events there may be greater coral tissue loss from interactive effects (Ezzat et al. 2020, Rotjan et al. 2022). Notably, corallivory can also have indirect benefits, such as dispersing viable coral symbionts in corallivore feces (Grupstra et al. 2021), which could be a mechanism for dispersing resilient Symbiodinaceae following coral bleaching events.

4.4. Conclusions

This study provides several important advances to our understanding of the ecological drivers of parrotfish corallivory across spatial scales. At the reef scale, the relative coral area preyed upon increased with increased corallivorous parrotfish density and biomass while scar density did not, highlighting how relative abundance versus area-based metrics can be decoupled, necessitating the use of area-based metrics of corallivory intensity. While coral cover was not a strong driver of corallivory intensity at the reef scale, the abundance of colonies with predation scars from frequently targeted taxa increased as coral diversity and the relative cover of targeted coral colonies increased within localized 30 m^2 areas on reefs. At the scale of individual colonies, the average size of scars across taxa was relatively small, suggesting that

most scars may result in minimal long-term coral tissue loss under normal reef conditions, although several taxa were more intensely preyed upon. Broadly, these findings suggest that while corallivory intensity may increase with increased parrotfish populations at the reef scale, at smaller spatial scales within reefs, corallivory intensity decreases in response to decreased coral cover and diversity. These findings underscore how the processes driving finer-scale consumer–prey dynamics such as coral ‘neighborhood’ effects may be attenuated at broader spatial scales such as the reefscape, emphasizing the need to consider ecological interactions across spatial scales.

Data archive. Data from this study are available through the NOAA National Centers for Environmental Information (Accession No. 0293333, <https://www.ncei.noaa.gov/archive/accession/0293333>). Data analysis code is available through a public GitHub repository (https://github.com/hannahrempele/ecological_drivers_corallivory).

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