Coral Reefs (2023) 42:967–975
https://doi.org/10.1007/s00338-023-02404-5

REPORT

Preferential consumption of benthic cyanobacterial mats by Caribbean parrotfishes

Joshua C. Manning[1] · **Sophie J. McCoy**[2]

Received: 16 November 2022 / Accepted: 2 July 2023 / Published online: 16 July 2023

Abstract Cyanobacteria are ubiquitous on coral reefs and perform many important ecosystem functions. Benthic cyanobacterial mats (BCMs) have become increasingly abundant on degraded reefs. Mat-forming benthic cyanobacteria have frequently been considered unpalatable to reef fishes. Regardless, recent studies have documented substantial grazing of BCMs by reef fishes, including parrotfishes. Here, we observed foraging in five Caribbean parrotfishes on the fringing coral reefs of Bonaire, Netherlands, to investigate BCM consumption relative to other benthic substrates. Three of our study species preferentially targeted conspicuous BCMs (i.e., macroscopic, cohesive colonies taxonomically composed primarily of Cyanobacteria and Proteobacteria), often taking several consecutive bites on them. Additionally, a high proportion of bites by all species targeted substrates characterized by filamentous turfs and crustose coralline algae. These substrates also contain diverse communities of epilithic and endolithic cyanobacteria and microalgae. Our work is, therefore, consistent with and provides direct evidence supporting the recently proposed trophic categorization of parrotfishes as microphages. Contrasting observations of reef fishes avoiding substrates dominated by BCMs on other reefs suggests variation in the palatability of BCMs to grazing reef fishes, or species-specific differences in preference for these potentially nutritional trophic resources.

Keywords Coral reef · Cyanobacteria · Electivity · Foraging · Parrotfish · Preference

Introduction

Cyanobacteria are a ubiquitous component of benthic coral reef communities and serve many important functional roles, including in nitrogen fixation, carbonate cycling, and primary productivity (Charpy et al. 2012). As coral reefs have become degraded by rising ocean temperatures and localized stressors (e.g., eutrophication), conspicuous benthic cyanobacterial mats (BCMs) have increased in abundance on many coral reefs (de Bakker et al. 2017; Reverter et al. 2020, 2022). These BCMs vary widely in morphotype and taxonomic composition (Brocke et al. 2018; Zubia et al. 2019; Stuij et al. 2023), but contain a structurally dominant cyanobacterial assemblage with associated non-oxygenic autotrophs, heterotrophic bacteria, archaea, and viruses (Cissell and McCoy 2021). BCMs overgrow and smother benthic organisms, including corals (Puyana and Prato 2013). Overgrowth of corals causes significant tissue damage and reduces growth rates (Titlyanov et al. 2007). BCMs may also act as reservoirs for potentially pathogenic bacteria (Cissell et al. 2022), and the increased cover of BCMs has been correlated with an increase in coral disease (Reverter et al. 2020). Additionally, some bloom-forming benthic cyanobacteria can inhibit larval recruitment and survival in some coral species (Kuffner et al. 2006; Ritson-Williams et al. 2020). As such, there is growing interest and urgency in understanding the dynamics of mat formation and persistence.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-023-02404-5.

✉ Joshua C. Manning
jmanning@bio.fsu.edu

[1] Department of Biological Sciences, Florida State University, 319 Stadium Drive, Tallahassee, FL 32306-4295, USA

[2] Department of Biology, University of North Carolina at Chapel Hill, 120 South Road, Chapel Hill, NC 27599-3280, USA

Many mat-forming benthic cyanobacteria (e.g., *Lyngbya* spp.) can produce secondary metabolites that have been demonstrated to deter grazing in some herbivores (Thacker et al. 1997; Nagle and Paul 1998, 1999). However, mat forming benthic cyanobacteria are also a potentially rich source of nutrients for herbivores due to lower C:N content than many other algal resources (Atkinson and Smith 1983; Capper et al. 2006), and experimental work confirms that fish will consume them in equal abundances to algal resources when secondary metabolites are undetectable (Capper et al. 2006). Production of secondary metabolites in mat-forming benthic cyanobacteria varies spatiotemporally (Nagle and Paul 1999; Paul et al. 2007), even at small scales (Capper et al. 2006). Thus, the composition of mat-forming bacterial communities and variation in the production of secondary metabolites by these communities may drive geographic differences in the prevalence and consumption of cyanobacterial mats (Cissell and McCoy 2022).

Microscopic photoautotrophs, including benthic cyanobacteria, are the primary nutritional target of parrotfishes (Clements et al. 2017; Nicholson and Clements 2020, 2021, 2022). A recent study on the fringing coral reefs of Bonaire, Netherlands, found that BCMs comprised a substantial proportion of bites taken by striped parrotfish (*Scarus iseri*), and were frequently consumed by other fishes, including blue parrotfish (*Scarus coeruleus*; Cissell et al. 2019). Frequent consumption of BCMs suggests that they may be an important and relatively novel nutritional resource for parrotfishes, particularly in Bonaire, where their cover has steadily increased in recent decades (de Bakker et al. 2017). However, BCMs have been found to disrupt natural grazing processes on other reefs where they are rarely consumed (Ford et al. 2021; Ribeiro et al. 2022). As such, additional research is needed to determine the importance of BCMs as a resource for parrotfishes.

Here, we observed foraging behavior in five Caribbean parrotfishes common to the fringing coral reefs of Bonaire: *Scarus vetula*, *Sc. taeniopterus*, *Sc. iseri*, *Sparisoma viride*, and *Sp. aurofrenatum*. We investigated the relative importance of BCMs to these five parrotfish species compared to other components of their diets, including both terminal phase (TP) and initial phase (IP) fish for three of those species (*Sc. vetula*, *Sc. taeniopterus*, and *Sp. viride*). We discuss our findings in light of recent studies on the nutritional ecology of parrotfishes.

Materials and methods

Study location and site characteristics

We collected data from five fringing coral reef sites along the leeward coast of Bonaire during May–July 2019: Bachelor's Beach, The Lake, Angel City, Aquarius, and Invisibles (Fig. 1). We estimated the cover of different foraging substrates at each site from 25 × 25 cm photoquadrats placed at 1 m intervals along 10 m transect lines (n = 4 per site) that were haphazardly placed within our foraging observation areas and run perpendicular to the reef slope at ~ 10 m depth. At Aquarius and Invisibles, we included a few additional photoquadrats as described in the Supplemental Information (SI: Table S1). Photoquadrats were not moved to

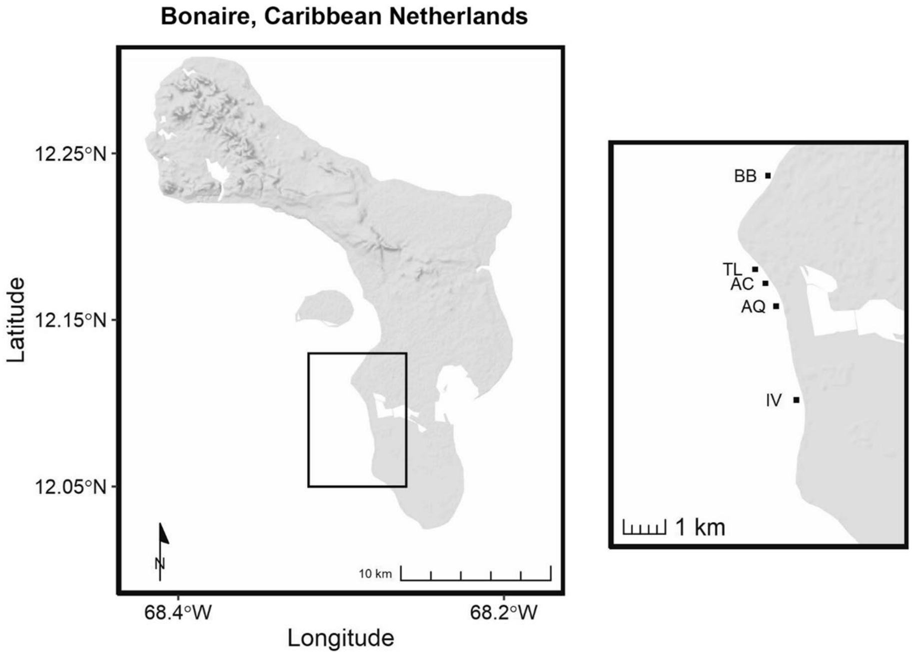


Fig. 1 A map of our field sites in Bonaire, Caribbean Netherlands Angel City (AC), Aquarius (AQ), Bachelor's Beach (BB), Invisibles (IV), and The Lake (TL)

artificially select for hard substrates and, therefore, did not excluded sediment and rubble habitat where BCMs are often observed. We randomly allocated 49 points to the image for each photoquadrat and identified the benthic substrate (i.e., macroalgae, coral, etc.) under each point using the software Coral Point Count with Excel Extensions (Kohler and Gill 2006).

We estimated the density of parrotfishes at ~ 10 m depth at each site by conducting visual censuses along eight 4 × 25 m belt transects (similar to Steneck et al. 2019). We swam each transect at a constant rate (~ 5 m min^{-1}) and counted all TP and IP parrotfishes greater than 5 cm fork length, placing them into size class bins (6–10, 11–20, 21–30, and 31–40 cm). We used the densities and the mean fork length (8, 15.5, 25.5, and 35.5 cm) of each bin to estimate biomass of each species using published length–weight relationships (Bohnsack and Harper 1988). Mean (± SE) parrotfish densities (counts 100 m^{-2}) and biomass (g 100 m^{-2}) are presented for each site in the SI (Table S2).

Foraging observations

We conducted video-recorded, behavioral observations of five Caribbean parrotfish species: *Sc. taeniopterus, Sc. vetula*, *Sp. viride*, *Sc. iseri*, and *Sp. aurofrenatum*. Behavioral observations were made during peak parrotfish foraging periods (1000–1600 h; Bruggemann et al. 1994a, b). We observed 128 territorial TP parrotfishes, including *Sc. taeniopterus, Sc. vetula*, and *Sp. viride* at all five study sites, and *Sc. iseri* and *Sp. aurofrenatum* at two study sites (Aquarius and Invisibles). Territorial TPs forage in fixed diurnal home ranges, from which intraspecific TPs are largely excluded (Pickholtz et al. 2022; Manning and McCoy 2023). In contrast, non-territorial (transient) TPs are often chased along the reef by territory holders, making consistent observation difficult and likely influencing foraging behavior. Thus, we excluded these transient fishes from our analyses. To explore the effect of ontogenetic phase on foraging behavior, we also observed 34 large IP *Sc. vetula*, *Sc. taeniopterus*, and *Sp. viride* at two sites (Aquarius and Invisibles). The total number of behavioral observations and the mean (± SE) duration of these observations are reported for each species and ontogenetic phase in the SI (Table S3).

Focal parrotfishes (TP or IP) were identified haphazardly at ~ 10 m depth on SCUBA at each site and allowed to acclimate to diver presence for ~ 1–2 min, during which time the observer estimated its standard length to the nearest cm (Table S3). We then followed the focal fish for 12.9 ± 0.2 min (mean ± SE observation time, n = 162) from ~ 2 m away and recorded foraging behavior with a GoPro Hero 4 Silver (GoPro, Inc; 4 k resolution) attached to a 'selfie-stick', to be analyzed later in the behavioral analysis software BORIS (v. 7.9.8; Friard and Gamba 2016). All bites were counted and the identity of the substrate targeted during each bite was recorded.

Substrates targeted were grouped as follows: BCM, filamentous turfs and crustose coralline algae, fleshy erect macroalgae (hereafter, macroalgae), live coral (Scleractinia and Milleporidae), sediment, soft coral (Gorgonia), sponge, and other (all other bites on benthic substrates). BCMs have been defined as macroscopic, cohesive colonies growing over sediment and hard reef substrates (including live benthic organisms), which are taxonomically composed primarily of Cyanobacteria and Proteobacteria (Cissell and McCoy 2021). We have observed several BCM morphotypes at our study sites, all of which are readily distinguishable from other benthic substrates, including filamentous turfs (Fig. S1). Some of the BCMs present at our study sites are morphotypically similar to the BCMs sequenced by Brocke et al. (2018) in Curaçao and Cissell and McCoy (2021) in Bonaire. The cyanobacterial order Nostocales dominated the metagenome of the BCM sampled by Cissell and McCoy (2021). However, taxonomic composition can vary widely, even among similar morphotypes (Stuij et al. 2023). As such, we do not attempt to differentiate among mat morphotypes in this study.

Filamentous turfs are heterogenous communities that include filamentous algae and cyanobacteria, small non-calcified crusts, macroalgal propagules, and associated detritus (Bruggemann et al. 1994c; Wilson and Bellwood 1997; Adey 1998; Fricke et al. 2011). Filamentous turfs often, though not always, contained sediments. In a few rare occurrences, fishes were observed cropping filamentous turf from the surface of sponges without any obvious removal of sponge tissue. These bites were scored as filamentous turf. Bites scored as sediment had no obvious epilithic algal/cyanobacterial filaments within or BCMs atop them. When identification of a bite target was impossible or questionable because the view of the bitten substrate was obscured by another structure or by the body of the focal fish, the substrate target was scored as "unknown". Parrotfishes frequently consumed the feces of planktivorous reef fishes (i.e., coprophagy). We include these bites in our analyses of bite rates and discussed their importance elsewhere (Manning and McCoy 2022).

Statistical analyses

We analyzed all foraging data in R (v. 4.0.2; R Core Team 2020). We investigated the effect of site, species, and ontogenetic phase on bite counts with an additive generalized linear model fit to a negative binomial distribution with the log of the observation time included as an offset (glmmTMB v. 1.0.2.1; Brooks et al. 2017). We also fit a reduced model including only the species for which we had observations of both ontogenetic phases. The reduced model included site, species, ontogenetic phase, and a species by ontogenetic phase interaction as fixed effects. We checked both models for overdispersion and zero-inflation (DHARMa v. 0.3.3.0; Hartig 2020) and for multicollinearity (performance v. 0.6.1; Lüdecke et al. 2020). We then tested for the significance of the fixed effects in each model using Type III Wald's χ^2 tests (car v. 3.0–10; Fox and Weisberg 2019). We chose not to include body size as a predictor in our models because we focused our sampling on larger individuals of the two ontogenetic phases rather than a representative range of body sizes (Fig. S2). However, we discuss the potential importance of body size in explaining foraging differences within and among species.

We calculated Chesson's α electivity index for each individual (dietr v. 1.0; Borstein 2019) to investigate foraging preferences based on the relative abundance of the different foraging targets at each site (Chesson 1983). Chesson's α electivity indices were calculated only for the eight benthic substrates targeted by parrotfishes during foraging observations (bites on unknown substrates and fecal matter in the water column were excluded from this analysis). A Chesson's α electivity index of 1/8 (i.e., 1/number of categories) represented no preference. Mean Chesson's α electivity indices (± 95% CI) were plotted by species and ontogenetic phase to visualize preference or avoidance for targeted substrates. Finally, we quantified the mean proportion of bites taken on BCMs for each species and the number of foraging bouts with five or more consecutive bites on BCMs to determine whether parrotfishes were sampling BCMs or selectively foraging upon them.

Results

Scarus. vetula, *Sc. taeniopterus*, *Sc. iseri*, *Sp. viride*, and *Sp. aurofrenatum* were the only five parrotfish species observed at all of our study sites during surveys of fish abundance and account for the majority (> 96%) of the parrotfish biomass at these sites (Table S2). Bite rates differed significantly by species and ontogenetic phase (full model: $\chi^2 = 803.79$, df = 4, $p < 0.001$ and $\chi^2 = 40.39$, df = 1, $p < 0.001$, respectively). Bite rates of *Scarus* spp. were higher than bite rates of *Sparisoma* spp. (Fig. 2) and there was a significant interactive effect of species and ontogenetic phase when bite rates were compared among *Sc. vetula*, *Sc. taeniopterus*, and *Sp. viride* (reduced model: $\chi^2 = 8.24$, df = 2, $p = 0.02$). Bite rates were higher for IPs than for TPs of *Sc. vetula* and *Sc. taeniopterus*, but there was no effect of ontogenetic phase on bite rates in *Sp. viride* (Fig. 2). There were no differences in total bite rates among sites.

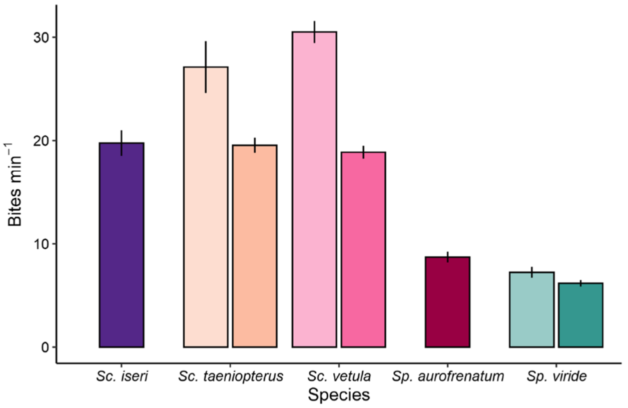


Fig. 2 Mean (±SE) bite rates (bites min^{-1}) for TP and IP (when observed) *Sc. taeniopterus*, *Sc. vetula*, *Sc. iseri*, *Sp. aurofrenatum*, and *Sp. viride*

We observed all five study species consuming BCMs, primarily from the sediment, but also from atop hard substrates (Fig. 3). BCMs were a preferred foraging substrate for TP and IP *Sc. iseri*, *Sc. taeniopterus*, and *Sc. vetula* (Fig. 4), despite their relatively low coverage on the reef (< 9%; Table S1). Bites on BCMs were between 7.1 ± 2.3 and 13.1 ± 1.4% (mean ± SE, *Sc. iseri* and *Sc. taeniopterus*, respectively) of the total bites taken on benthic substrates for these three species (Fig. 3). BCMs comprised only 1.5 ± 0.3 and 6.0 ± 1.6% of the bites taken by *Sp. viride* and *Sp. aurofrenatum*, respectively, and were not a preferred foraging substrate for either of these species (Figs. 3 and 4). *Scarus* spp., particularly *Sc. taeniopterus* and *Sc. vetula*, had many more feeding bouts with 5 or more consecutive bites on BCMs than either *Sparisoma* spp. (Fig. S3).

The majority of the bites taken by all five species targeted substrates characterized as filamentous turfs and crustose coralline algae (69.5 ± 7.7 to 91.1 ± 0.9%, mean ± SE; *Sc. iseri* and *Sc. vetula*, respectively). Filamentous turfs and crustose coralline algae were largely targeted in accordance with their high proportional abundance on the reef, though there was some evidence for preferential targeting by TP *Sc. taeniopterus* and TP *Sc. vetula* (Fig. 4). Both *Sp. viride* (TP and IP) and *Sp. aurofrenatum* preferentially targeted macroalgae (Fig. 4), which accounted for 7.9 ± 1.0 and 8.5 ± 2.1% of their bites, respectively. In contrast, *Sc. taeniopterus* (TP and IP) avoided macroalgae, while *Sc. vetula* (TP and IP) and *Sc. iseri* showed no preference or avoidance (Fig. 4). All species avoided live coral substrates (Fig. 4), though 3.3 ± 0.7% of the bites taken by *Sp. viride* were on live corals.

Discussion

The abundance of BCMs has increased globally on coral reefs, including in Bonaire (de Bakker et al. 2017; Ford et al. 2018; Reverter et al. 2022). Our findings support other

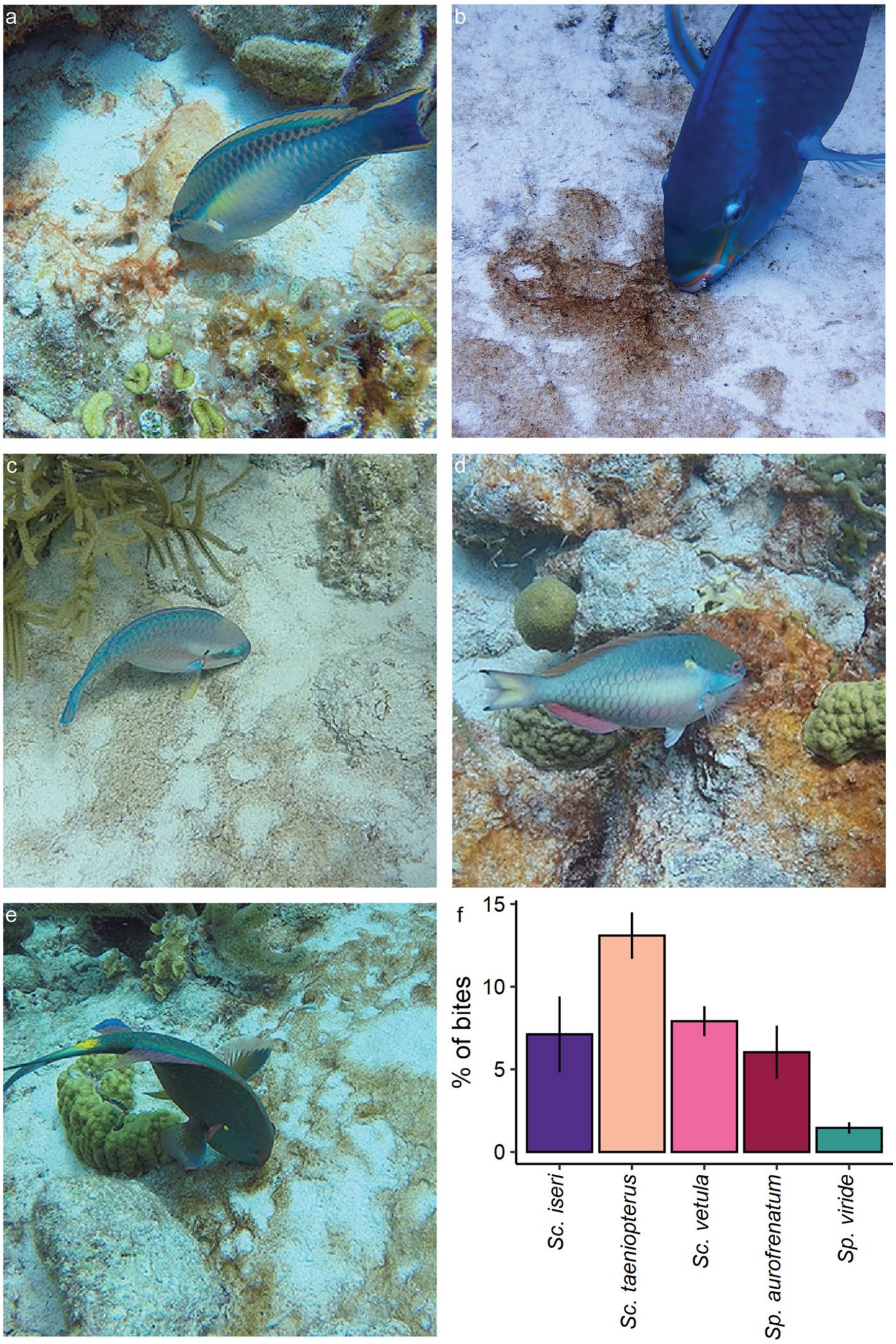
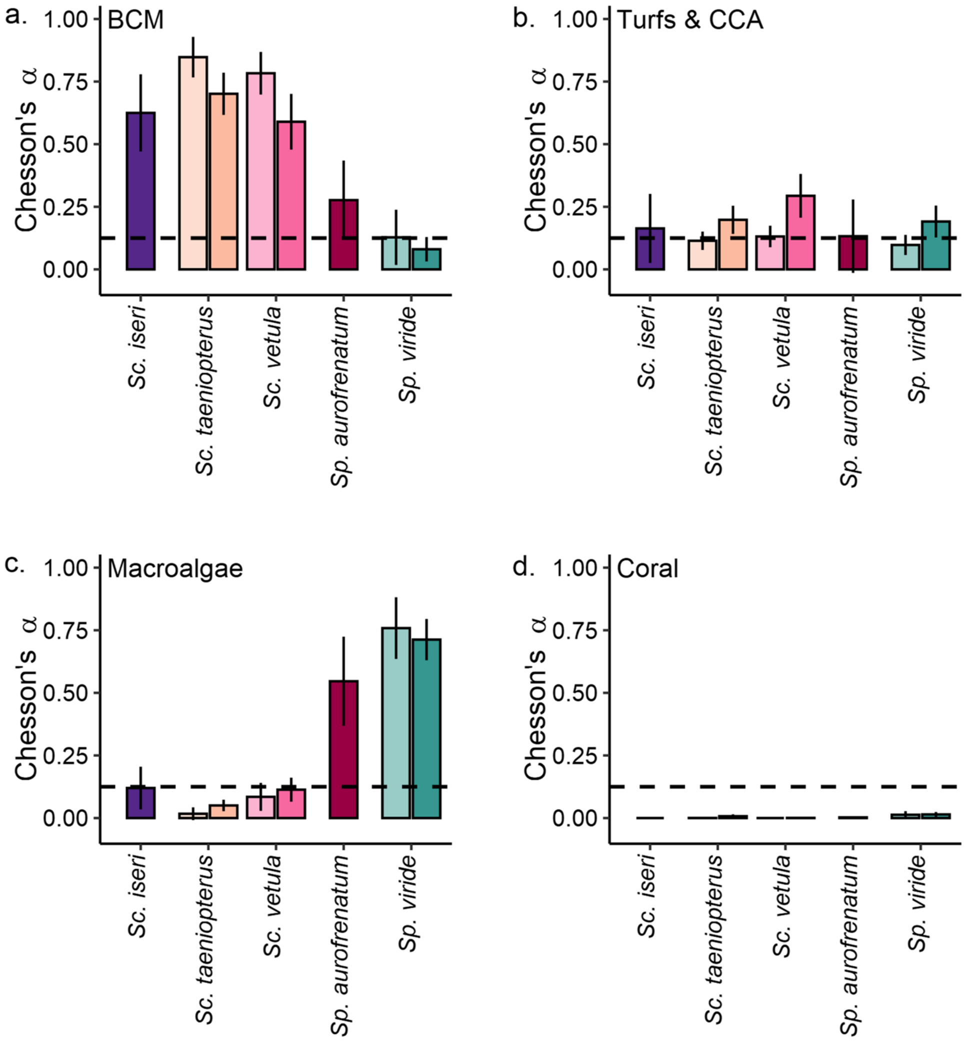


Fig. 3 Examples of TP *Sc. taeniopterus* **a**, *Sc. vetula* **b**, *Sc. iseri* **c**, *Sp. aurofrenatum* **d**, and *Sp. viride* **e** taking bites of BCMs on the fringing coral reefs of Bonaire, and **f** the mean (± SE) percentage of bites taken on benthic cyanobacterial mats by each species

recent work in contradicting the view that fish are deterred by mat-forming benthic cyanobacteria, some of which are known to produce secondary metabolites (Nagle and Paul 1998, 1999). Reef fishes have not been expected to play an important role in controlling mat proliferation, despite their importance in controlling reef macroalgal abundances. However, Cissell et al. (2019) recently documented extensive foraging on BCMs by multiple reef fishes in Bonaire, including parrotfishes. Consistent with Cissell et al. (2019), we have provided evidence that three common Caribbean parrotfishes in Bonaire preferentially consume BCMs growing over sediment and hard reef substrates. Our findings suggest that these parrotfishes may exert strong top-down control on these mat communities. In contrast, Ford et al. (2021) found that the presence of BCMs significantly reduced foraging by herbivorous reef fishes.

Conflicting evidence of BCM consumption may reflect geographic differences in the composition of these mat communities or the production of secondary metabolites within them. Few studies have investigated the taxonomic

Fig. 4 Mean (±95% CI) Chesson's α electivity index for terminal phase (TP) and initial phase (IP, when observed) *Sc. taeniopterus*, *Sc. vetula*, *Sc. iseri*, *Sp. aurofrenatum*, and *Sp. viride* and four major substrates **a** BCMs, **b** filamentous turfs and crustose coralline algae, **c** macroalgae, and **d** live coral. The dashed line represents no preference (1/n; n = 8 foraging substrates)



composition of BCMs (but see Biessy et al. 2021; Cissell and McCoy 2021; Stuij et al. 2023), and much of the research surrounding the chemical defenses of BCMs has focused on secondary metabolites isolated from a few mat-forming species (e.g., *Lyngbya* spp.; Thacker et al. 1997; Nagle and Paul 1999). The production of secondary metabolites can also vary, even at small spatiotemporal scales (Nagle and Paul 1999; Capper et al. 2006; Paul et al. 2007). Thacker et al. (1997) hypothesized that fishes may sample BCMs to effectively determine the concentrations of deterrent chemicals without over-ingesting toxins. When secondary metabolites are undetectable, some reef fishes consume BCMs in equal abundance to less defended food resources (Capper et al. 2006). In this study, we recorded multiple foraging bouts during which focal fishes, particularly the *Scarus* spp., took many consecutive bites (> 5) on BCMs in Bonaire. Therefore, it appears that these fishes are selectively targeting BCMs rather than sampling them, suggesting that BCMs at the sites studied here are not deterring foraging chemically or that the parrotfishes are not affected by the chemical defenses present. These findings provide direct evidence in support of the hypothesis that parrotfishes are microphages that target protein rich microscopic photoautotrophs, primarily cyanobacteria (Clements et al. 2017).

A proportionally high number of the bites taken by our five study species were on substrates categorized as filamentous turfs and crustose coralline algae. This is consistent with prior work in Bonaire. Specifically, Bruggemann et al. (1994a, b, c) found that both *Sc. vetula* and *Sp. viride* primarily targeted sparse epilithic (i.e., filamentous) turfs growing atop endolithic communities; and that *Sp. viride* had greater access to the substrate-bound endoliths as an excavating species. Benthic cyanobacteria are a major and sometimes dominant component of both epilithic and endolithic communities on the reef benthos (Adey 1998; Diaz-Pulido and McCook 2002; Tribollet et al. 2006; Fricke et al. 2011; Charpy et al. 2012), including in Bonaire (Bruggemann et al. 1994c). Recently, Nicholson and Clements (2020, 2021) found that high densities of filamentous cyanobacteria were the only consistent component of substrates targeted by several Indo-Pacific parrotfishes, though there was evidence of resource partitioning at fine spatial scales related to successional status of the targeted substrates. *Scarus spinus*, in particular, exclusively grazed upon crustose coralline algae that were associated with epiphytic, endophytic, and endolithic filamentous cyanobacteria (Nicholson and Clements 2020, 2022). Therefore, it is likely that our reported bites on filamentous turfs and crustose coralline algae contained substantial cyanobacterial biomass and that resource partitioning occurred at much finer spatial scales than we could differentiate from our video analyses. This contrasts the view that parrotfishes are generalist herbivores that target the whole, heterogenous, epilithic algal matrix (Steneck et al. 2017; Arjunwadkar et al. 2022).

In this study, we found that *Sp. viride* and *Sp. aurofrenatum* preferentially targeted macroalgae, with the majority of bites taken on *Dictyota* spp. (Fig. S4). In the Caribbean, *Sparisoma* spp. have often been described as macroalgal browsers (Adam et al. 2015), and *Sp. aurofrenatum* is known to preferentially target macroalgae, primarily *Dictyota* spp. (Dell et al. 2020). It is possible that *Dictyota* spp. are targeted for their unusually high lipid content compared with other macroalgae (McDermid and Stuercke 2003). Alternatively, parrotfishes could be attempting to remove epiphytic cyanobacteria that often grow upon fleshy macroalgae (Capone et al. 1977; Ballantine 1979; Gauna et al. 2015). This hypothesis is supported by observations of multiple parrotfish species (Lefévre and Bellwood 2011; Vergés et al. 2012; Nieder et al. 2022). For example, Lefévre and Bellwood (2011) found that grazing by *Scarus rivulatus* increased on *Sargassum* in the winter months when it was most heavily epiphytized. Nieder et al. (2022) observed juveniles of four parrotfish species scraping epiphytes, including cyanobacteria, from the surface of the alga *Galaxaura divaricata*. While parrotfishes in our study did occasionally ingest *Dictyota* spp. thalli, they also frequently spit thalli out after removing them from the substrate. This process is important for the fragmentation and proliferation of *Dictyota* spp. at small spatial scales (Herren et al. 2006), and is suggestive that the macroalgae are not the primary nutritional target for these parrotfishes. Thus, our findings and those of others challenge the assumptions underlying the narrative that parrotfishes, with the exception of maybe a few (e.g., *Sp. aurofrenatum*), are important controls on macroalgal abundances (e.g., Sheppard et al. 2023). Regardless, there is still a need for deeper investigation into the role of epibionts in the selection of macroalgae by parrotfishes.

Grazing by parrotfishes and other reef fishes acts as a disturbance that maintains reef substrates in cropped early successional states dominated by productive nitrogen-fixing cyanobacteria (Sammarco 1983; Wilkinson and Sammarco 1983; Grange et al. 2015; Clements et al. 2017). However, grazing intensities and substrates targeted differ within and among species. In three of our study species (*Sc. taeniopterus*, *Sc. vetula*, and *Sp. viride*), we explored the effect of ontogenetic phase on foraging. Ontogenetic phase and body size are known to affect bite rates in parrotfishes (Bruggemann et al. 1994a, b; Afeworki et al. 2013), and there is some evidence that electivity for foraging substrates may differ by ontogenetic phase (Smith et al. 2018). We found little evidence that terminal and initial phase parrotfishes target different substrates. However, we did find that bite rates for *Sc. vetula* and *Sc. taeniopterus* were greater in initial phase than in terminal phase individuals, and our data suggested an inverse relationship between body size and total bite rates, consistent with prior work (Bruggemann et al. 1994a, 1994b; Bonaldo et al. 2006; Afeworki et al. 2013). We also found species-specific differences in parrotfish bite rates. Specifically, *Scarus* spp. took bites more frequently than *Sparisoma* spp.

Excavating parrotfishes, including *Sp. viride*, are more likely to denude the substrate than non-excavating species (e.g., *Sc. vetula*), though the probability of leaving grazing scars and the size of grazing scars also scales positively with body size in some species (Bellwood and Choat 1990; Bruggemann et al. 1994b, 1994c; Bonaldo and Bellwood 2008; Adam et al. 2018). Thus, excavators are likely to have very different effects on the successional dynamics of epilithic and endolithic communities than non-excavating species (Clements et al. 2017). Additionally, food intake per bite can be much higher for excavators because of their ability to exploit energy rich substrate-bound endoliths. For example, food intake per bite in *Sp. viride* is about three times higher than in similarly sized *Sc. vetula* (Bruggemann et al. 1994b). This could, in part, explain why non-excavating species more frequently targeted BCMs than *Sp. viride* in our study. BCMs may represent an easily accessible nutrient-rich resource for parrotfishes that are unable to utilize endolithic resources.

As cyanobacterial abundances increase on reefs globally (Ford et al. 2018), a knowledge gap has grown around trophic interactions involving BCMs, which are critical to consumer ecology and BCM dynamics. Our study provides further evidence that BCMs could be an important and preferred resource for parrotfishes. Intense grazing on BCMs by parrotfishes and other fishes may act as an important control on BCM proliferation. Future work should investigate variation in mat consumption (e.g., due to composition and palatability) and the effect of consumption on the trophic dynamics of BCMs. More generally, our findings support recent evidence that cyanobacteria are the primary dietary resources for parrotfishes (Clements et al. 2017; Nicholson and Clements 2020, 2022).

Acknowledgements This research was supported by Florida State University (FSU) start-up funding and the Tatelbaum Ocean Research

Fund awarded to S.J.M, as well as a Mote Research Assistantship from the William R. and Lenore Mote Eminent Scholar in Marine Biology Endowment at FSU and a Lerner-Gray Memorial Fund for Marine Research grant from the American Museum of Natural History awarded to J.C.M. We would like to thank C. Eckrich and R. Francisca for providing assistance in obtaining permits to work in the Bonaire National Marine Park. We would also like to thank the undergraduate field and lab assistants that assisted in data collection and processing: I. Basden, M. Dziewit, B. Clark, J. Portillo, B. Koechle, and J. Henson. Finally, we would like to thank K. Clements for valuable discussions regarding parrotfish nutritional ecology, and E. Cissell and the rest of the McCoy lab for feedback on earlier drafts of this manuscript. Finally, we would like to thank our two anonymous reviewers for their helpful and insightful comments.

Declarations

Conflict of interest The authors have not conflict of interest.

References

Adam TC, Kelley M, Ruttenberg BI, Burkepile DE (2015) Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. Oecologia 179:1173–1185

Adam TC, Duran A, Fuchs CE, Roycroft MV, Rojas MC, Ruttenberg BI, Burkepile DE (2018) Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. Mar Ecol Prog Ser 597:207–220

Adey WH (1998) Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. J Phycol 34:393–406

Afeworki Y, Zekeria ZA, Videler JJ, Bruggemann JH (2013) Food intake by the parrotfish *Scarus ferrugineus* varies seasonally and is determined by temperature, size and territoriality. Mar Ecol Prog Ser 489:213–224

Arjunwadkar CV, Tebbett SB, Bellwood DR, Bourne DG, Smith HA (2022) Algal turf structure and composition vary with particulate loads on coral reefs. Mar Pollut Bull 181:113903

Atkinson MJ, Smith SV (1983) C:N:P ratios of benthic marine plants. Limnol Oceanogr 28:568–574

Ballantine DL (1979) The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. Bot Mar 22:107–110

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fishes 28:189–214

Biessy L, Wood SA, Chinain M, Roué M, Smith KF (2021) Exploring benthic cyanobacterial diversity and co-occurring potentially harmful dinoflagellates in six islands of the South Pacific. Hydrobiologia 848:2815–2829

Bohnsack JA, Harper DE (1988) Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. NOAA Tech Memo NMFS-SEFC-215 1-31

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bonaldo RM, Krajewski JP, Sazima C, Sazima I (2006) Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. Mar Biol 149:423–433

Borstein S (2019) dietr: diet estimated trophic levels. R package version 1.0. https://github.com/sborstein/dietr

Brocke HJ, Piltz B, Herz N, Abed RMM, Palinska KA, John U, den Haan J, de Beer D, Nugues MM (2018) Nitrogen fixation and diversity of benthic cyanobacterial mats on coral reefs in Curaçao. Coral Reefs 37:861–874

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Bruggemann JH, Begeman J, Bosma EM, Verburg P, Breeman AM (1994a) Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein and energy. Mar Ecol Prog Ser 106:57–72

Bruggemann JH, Kuyper MWM, Breeman AM (1994b) Comparative-analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Mar Ecol Prog Ser 112:51–66

Bruggemann JH, van Oppen MJH, Breeman AM (1994c) Foraging by the stoplight parrotfish Sparisoma viride. I. Food selection in different, socially determined habitats. Mar Ecol Prog Ser 106:41–55

Capone DG, Taylor DL, Taylor BF (1977) Nitrogen fixation (acetylene reduction) associated with macroalgae in a coral-reef community in the Bahamas. Mar Biol 40:29–32

Capper A, Tibbetts IR, O'Neil JM, Shaw GR (2006) Feeding preference and deterrence in rabbitfish *Siganus fuscescens* for the cyanobacterium *Lyngbya majuscula* in Moreton Bay, south-east Queensland, Australia. J Fish Biol 68:1589–1609

Charpy L, Casareto BE, Langlade MJ, Suzuki Y (2012) Cyanobacteria in coral reef ecosystems: a review. J Mar Biol 2012:1–9

Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304

Cissell EC, McCoy SJ (2021) Shotgun metagenomic sequencing reveals the full taxonomic, trophic, and functional diversity of a coral reef benthic cyanobacterial mat from Bonaire. Caribbean Netherlands Sci Total Environ 755:142719

Cissell EC, McCoy SJ (2022) Marine cyanobacteria in the anthropocene: are top-down paradigms robust to climate change? Clim Chang Ecol 3:100057

Cissell EC, Manning JC, McCoy SJ (2019) Consumption of benthic cyanobacterial mats on a Caribbean coral reef. Sci Rep 9:12693

Cissell EC, Eckrich CE, McCoy SJ (2022) Cyanobacterial mats as benthic reservoirs and vectors for coral black band disease pathogens. Ecol Appl. https://doi.org/10.1002/eap.2692

Clements KD, German DP, Piché J, Tribollet A, Choat JH (2017) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linn Soc 120:729–751

de Bakker DM, van Duyl FC, Bak RPM, Nugues MM, Nieuwland G, Meesters EH (2017) 40 Years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: the rise of slimy cyanobacterial mats. Coral Reefs 36:355–367

de Ribeiro FV, Caires TA, de Simões MAA, Hargreaves PI, Villela LB, de Fistarol GO, Caselgrandi AB, Pereira-Filho GH, de Moura RL, Pereira RC, Salomon PS (2022) Benthic cyanobacterial diversity and antagonistic interactions in abrolhos bank: allelopathy, susceptibility to herbivory, and toxicity. Front Mar Sci 8(1):13

Dell CLA, Longo GO, Burkepile DE, Manfrino C (2020) Few herbivore species consume dominant macroalgae on a Caribbean coral reef. Front Mar Sci 7:1–12

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128

Ford AK, Bejarano S, Nugues MM, Visser PM, Albert S, Ferse SCA (2018) Reefs under siege-the rise, putative drivers, and consequences of benthic cyanobacterial mats. Front Mar Sci 5:1–15

Ford AK, Visser PM, van Herk MJ, Jongepier E, Bonito V (2021) First insights into the impacts of benthic cyanobacterial mats on fish herbivory functions on a nearshore coral reef. Sci Rep 11:7147

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks, CA

Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7:1325–1330

Fricke A, Teichberg M, Beilfuss S, Bischof K (2011) Succession patterns in algal turf vegetation on a Caribbean coral reef. Bot Mar 54:111–126

Gauna MC, Cáceres EJ, Parodi ER (2015) Spatial and temporal variability in algal epiphytes on Patagonian *Dictyota dichotoma* (Dictyotales, Phaeophyceae). Aquat Bot 120:338–345

Grange JS, Rybarczyk H, Tribollet A (2015) The three steps of the carbonate biogenic dissolution process by microborers in coral reefs (New Caledonia). Environ Sci Pollut Res 22:13625–13637

Hartig F (2020) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa.

Herren LW, Walters LJ, Beach KS (2006) Fragment generation, survival, and attachment of *Dictyota* spp. at Conch Reef in the Florida Keys, USA. Coral Reefs 25:287–295

Kohler KE, Gill SM (2006) Coral point count with excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259–1269

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117

Lefévre CD, Bellwood DR (2011) Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. Mar Ecol Prog Ser 422:239–251

Lüdecke D, Makowski D, Waggoner P, Patil I (2020) Assessment of Regression Models Performance. CRAN. Available from https://easystats.github.io/performance/.

Manning JC, McCoy SJ (2022) Coprophagy in Caribbean parrotfishes. Ecology 103:e3657

Manning JC, McCoy SJ (2023) Territoriality drives patterns of fixed space use in Caribbean parrotfishes. Ecol Evol 13:e9833

McDermid KJ, Stuercke B (2003) Nutritional composition of edible Hawaiian seaweeds. J Appl Phycol 15:513–524

Nagle DG, Paul VJ (1998) Chemical defense of a marine cyanobacterial bloom. J Exp Mar Bio Ecol 225:29–38

Nagle DG, Paul VJ (1999) Production of secondary metabolites by filamentous tropical marine cyanobacteria: Ecological functions of the compounds. J Phycol 35:1412–1421

Nicholson GM, Clements KD (2020) Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. Coral Reefs 39:1313–1327

Nicholson GM, Clements KD (2021) Ecomorphological divergence and trophic resource partitioning in 15 syntopic Indo-Pacific parrotfishes (Labridae: Scarini). Biol J Linn Soc 132:590–611

Nicholson GM, Clements KD (2022) *Scarus spinus*, crustose coralline algae and cyanobacteria: an example of dietary specialization in the parrotfishes. Coral Reefs 41:1465–1479

Nieder C, Liao CP, Lee CL, Clements KD, Liu SL (2022) Novel field observations of coral reef fishes feeding on epiphytic and epizoic organisms associated with the allelopathic seaweed Galaxaura divaricata. Ecol Evol. https://doi.org/10.1002/ece3.9529

Paul VJ, Arthur KE, Ritson-Williams R, Ross C, Sharp K (2007) Chemical defenses: From compounds to communities. Biol Bull 213:226–251

Pickholtz R, Kiflawi M, Crossin GT, Pickholtz E, Zamsky R, Kahan I, Gavriel T, Belmaker J (2022) Highly repetitive space-use dynamics in parrotfishes. Coral Reefs 41:1059–1073

Puyana M, Prato J (2013) Overgrowth of reef organisms by benthic cyanobacteria in the Colombian Caribbean. Mutis 3:58–60

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. v. 4.0.2

Reverter M, Jackson M, Daraghmeh N, von Mach C, Milton N (2020) 11-yr of coral community dynamics in reefs around Dahab (Gulf of Aqaba, Red Sea): the collapse of urchins and rise of macroalgae and cyanobacterial mats. Coral Reefs 39:1605–1618

Reverter M, Helber SB, Rohde S, de Goeij JM, Schupp PJ (2022) Coral reef benthic community changes in the Anthropocene: Biogeographic heterogeneity, overlooked configurations, and methodology. Glob Chang Biol 28:1956–1971

Ritson-Williams R, Arnold SN, Paul VJ (2020) The impact of macroalgae and cyanobacteria on larval survival and settlement of the scleractinian corals *Acropora palmata*, *A. cervicornis* and *Pseudodiploria strigosa*. Mar Biol 167:1–12

Sammarco P (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. Mar Ecol Prog Ser 13:1–14

Sheppard CE, Williams GJ, Exton DA, Keith SA (2023) Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state. Glob Ecol Biogeogr 32:435–449. https://doi.org/10.1111/geb.13638

Smith KM, Quirk-Royal BE, Drake-Lavelle K, Childress MJ (2018) Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA). Mar Ecol Prog Ser 603:175–187

Steneck RS, Bellwood DR, Hay ME (2017) Herbivory in the marine realm. Curr Biol 27:R484–R489

Steneck RS, Arnold SN, Boenish R, de León R, Mumby PJ, Rasher DB, Wilson MW (2019) Managing recovery resilience in coral reefs against climate-induced bleaching and hurricanes: a 15 year case study from Bonaire, Dutch Caribbean. Front Mar Sci 6:1–12

Stuij TM, Cleary DFR, Gomes NCM, Mehrotra R, Visser PM, Speksnijder AGCL, Hoeksema BW (2023) High diversity of benthic cyanobacterial mats on coral reefs of Koh Tao, Gulf of Thailand. Coral Reefs 42:77–91

Thacker RW, Nagle DG, Paul VJ (1997) Effects of repeated exposures to marine cyanobacterial secondary metabolites on feeding by juvenile rabbitfish and parrotfish. Mar Ecol Prog Ser 147:21–29

Titlyanov EA, Yakovleva IM, Titlyanova TV (2007) Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. J Exp Mar Bio Ecol 342:282–291

Tribollet A, Langdon C, Golubic S, Atkinson M (2006) Endolithic microflora are major primary producers in dead carbonate substrates of Hawaiian coral reefs. J Phycol 42:292–303

Vergés A, Bennett S, Bellwood DR (2012) Diversity among macroalgae-consuming fishes on coral reefs: a transcontinental comparison. PLoS ONE 7:e45543

Wilkinson C, Sammarco P (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation*. Mar Ecol Prog Ser 13:15–19

Wilson S, Bellwood DR (1997) Cryptic dietary components of territorial damselfishes (Pomacentridae, Labroidei). Mar Ecol Prog Ser 153:299–310

Zubia M, Vieira C, Palinska KA, Roué M, Gaertner JC, Zloch I, Grellier M, Golubic S (2019) Benthic cyanobacteria on coral reefs of Moorea Island (French Polynesia): diversity response to habitat quality. Hydrobiologia 843:61–78