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Molina, Nury Elizabeth

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The Functional Roles of Herbivorous Fishes on Coral Reefs

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

Nury Elizabeth Molina

Committee in charge:

Professor Deron E. Burkepile, Chair

Dr. Thomas C. Adam, Researcher

Dr. Jennifer E. Caselle, Researcher

Professor Rebecca Vega Thurber

June 2026

The dissertation of Nury Elizabeth Molina is approved.

Thomas C. Adam

Jennifer E. Caselle

Rebecca Vega Thurber

Deron E. Burkepile, Committee Chair

March 2026

The Functional Roles of Herbivorous Fishes on Coral Reefs

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by

Nury Elizabeth Molina

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Completing a Ph.D. is a transformative experience, not only professionally but also personally. First, I would like to thank my advisor Dr. Deron Burkepile. This was my dream lab when I was applying to graduate school and I feel so lucky to have been a member of the Pile. Through your mentorship I've grown to be an independent leader. You give us the freedom to pursue our unique research interests even if it leads us to new and challenging places. The freedom to pursue these extremely challenging endeavors like working at a field site with no science station and our lab had no connections to, ended up being one of the best things that I could have experienced. Because you believed in me, it gave me the opportunity to grow. While you let us be independent, you were always there for me when I needed you. You've also been my advocate and stepped up when I needed extra help to ensure my success. You go above and beyond to cultivate an incredibly kind and supportive lab environment. It truly was a dream to be in the Pile. Second, I would like to thank the rest of my committee members. Tom, we are so lucky that you are part of the lab. Your willingness to engage deeply about ideas, experiments, and analyses with me was invaluable. Your mentorship also extended beyond scientific input. You really cared for all of us and treated us like family. Some of my favorite nights were the nights you grilled for us in Moorea. When you're out in the field for months at a time, it's moments like that, that make you feel like you have family. Your laugh was infectious and always made a tough field day better. You also have the incredible skill of talking underwater which is quite impressive. I also don't think there's anyone else that works as hard as you do in the field.

Becky, I also feel so lucky that I got to work so closely with you and your lab. You always made time to listen to me and provide guidance and encouragement. You also gave me the confidence to step outside of my comfort zone and learn new things in the field. Working and diving off of a boat day in and day out was new to me and I still remember you calling me super boaty when I tied up the mooring line to the boat at the Pile mooring. Perhaps an insignificant moment to others but getting those boosts of encouragement helped me grow my confidence in unfamiliar situations that I didn't grow up in. I always felt seen and acknowledged by you made which made me feel like I belonged. You could also tell when I was going through a hard time and took the time to sit down and talk with me and give me the support I needed. You have an incredible gift of providing rigorous feedback while simultaneously building me up. You are the type of person that uplifts people and I am truly so lucky to call you a mentor.

Jenn, you are truly an inspiration and someone I look up to. Your commitment to uplifting the next generation is remarkable. I'm so glad I got to be a part of onBoard and meet incredible students. You dedicate so much time and effort to pay it forward and it's had so many ripple effects on students including me. You also provide such insightful feedback and always make me think about why my work matters and real applications of it.

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Thank you to my colleagues and friends in American Samoa. Val, you've been an incredible mentor and friend to me. I deeply cherish my time with you in American Samoa. You are someone I really look up to. Tine, Sana, and Alisha, I feel like I gained the most incredible friendships from you. Thank you Max and Monyca for treating me like family.

I also want to thank Paul, Peggy, and Caitlin for believing in me in The Diversity Project. All I had was a love of the ocean but had no experience in research or diving and could barely swim. It is remarkable your dedication to supporting the next generation. Your mentorship truly changed the trajectory of my life. Thank you for opening up this world to me. There is no other program in marine science that is as life changing as The Diversity Project. I am eternally grateful for you and that I get to be part of The Diversity Project Family. Thank you, Shayna, for being an incredible mentor at UCLA. You helped me grow so much which ultimately led me to pursuing a PhD. Thank you Greg Hodgson for my first marine science experiences while at UCLA. You saw something in me, and I am so grateful.

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VITA OF NURY ELIZABETH MOLINA
March 2026

EDUCATION

Doctor of Philosophy in Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, June 2026 (expected)

Master of Arts, Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, June 2023

Bachelor of Science, Environmental Science and Conservation Biology, University of California, Los Angeles, June 2019

PROFESSIONAL AND ACADEMIC APPOINTMENTS

Sea Grant Knauss Fellow, June 2026- June 2027

NOAA Protected Area Policy Division Dr. Nancy Foster Visiting Scholar, March – June 2024

Teaching Assistant, Coral Reef Biology and Ecology, UCSB, September – December 2020 and 2021

Consultant, The Nature Conservancy, September 2020 – March 2021

PUBLICATIONS

Sura SA, **Molina NE**, Blumstein DT, Fong P. Selective consumption by herbivorous fishes suggests reduced functional complementarity on a fringing reef. *J. Exp. Mar. Bio. Ecol.* 2021

Fong CR, Sura SA, **Molina NE**, Ford AT, Howard HB, Smith NN, Fong P. Testing the conceptual and operational underpinnings of field herbivory assays *J. Exp. Mar. Bio. Ecol.* 2020

SELECTED AWARDS AND GRANTS

Sea Grant John A. Knauss Fellowship (\$73,100), 2026-2027

UCSB Academic Senate Doctoral Student Travel Award (\$900), 2025

NOAA Dr. Nancy Foster Scholarship (\$225,000), 2019-2025

UCSB Regents in the Ecology, Evolution, and Marine Biology Award (\$29,000), 2024-2025

UCSB Individualized Professional Skills Grant for Capitol Hill Ocean Week (\$1,200), 2024

Coral Reef Conservation Fund Grant – NFWF (\$61,068.18), 2020-2023

Schmidt Family Foundation Environmental Solutions Fellow (\$8,000), 2020

MENTORSHIP

Senior graduate student mentor for the UCSB EEMB Mentorship Program, 2024-2025

Graduate Mentor for the UCSB onBoard Program, 2023-2025

Supervised 12 undergraduates including overseeing a Senior Honors Thesis, 2020-2026

EarthEcho International StemExplore Mentor, 2019 – 2020

SERVICE AND PROFESSIONAL MEMBERSHIPS

Graduate Student Representative, UCSB Dive Control Board. (2021–2025).

The Explorer's Club (2023–present)

Founding Member, Moorea Coral Reef LTER Diversity, Equity, and Inclusion Committee (2021-2022)

SELECTED PANELS AND PRESENTATIONS

UCLA Physical Sciences Division New Student Welcome Invited Panelist (September 2024 and 2025) ~600 students attended

Molina, N.E. *Complementarity of resource use across multiple functional traits by herbivorous fish on coral reefs in Moorea, French Polynesia*. Society for the Advancement of Chicanos/Hispanics and Native Americans in Science. October 2025. Poster Presentation.

Molina, N.E. *Complementarity of resource use across multiple functional traits by herbivorous fish on coral reefs in Moorea, French Polynesia*. The Diversity Project Symposium. August 2025. Poster Presentation.

Molina, N.E. *Complementarity of resource use across multiple functional traits by herbivorous fish on coral reefs in Moorea, French Polynesia*. Indo-Pacific Fish Conference, Taiwan. June 2025. Poster Presentation.

Molina, N.E. *Role of herbivorous fish on coral reefs*. NOAA Ocean Guardian Youth 2023, 2024. Oral Presentation.

Molina, N.E. *Herbivorous fish foraging patterns on dead coral skeletons*. Moorea LTER All Investigators Meeting. December 2023. Oral Presentation.

Molina, N.E. *Species-specific impacts of herbivorous fishes on coral reefs in American Samoa*. NOAA Office of National Marine Sanctuaries Headquarters Staff Meeting, August 2023. Oral Presentation.

Molina, N.E. *Species-specific impacts of herbivorous fishes on coral reefs in American Samoa*. NOAA Office of National Marine Sanctuaries Research Coordinators Meeting, May 2023. Oral Presentation.

Molina, N.E. *Species-specific impacts of herbivorous fishes on coral reefs in American Samoa*. Department of Marine and Wildlife Resources, American Samoa, November 2022. Oral Presentation.

Abstract

The Functional Roles of Herbivorous Fishes on Coral Reefs

by

Nury Elizabeth Molina

Herbivorous fishes provide critical ecological roles on coral reefs. However, coral reefs are undergoing local and global stressors that can alter the dominant benthic organisms on reefs, often leading to reefs with abundant algae. Given the importance of herbivorous fishes in mediating coral-algal competition, it is essential to re-evaluate their functional roles in the age of the Anthropocene. This dissertation addresses three important knowledge gaps. 1) Studies increasingly show that herbivore foraging behavior varies along axes beyond food choice, underscoring the need to consider additional dimensions of foraging such as bite rates and space use to understand patterns of herbivory. While these important niche axes have been identified, there is a deficit of research evaluating across all of these ecological dimensions for a diverse suite of herbivorous fishes. 2) Many coral reefs across the globe are experiencing a loss of coral and increase in algae in response to global and local stressors. The increase in algae on reefs may alter the feeding behavior of herbivorous fishes, which play key roles in the dynamics of these ecosystems. Yet, few studies have explored how the foraging ecology of individual species of herbivorous fishes may differ across reefs with different benthic community states (abundant coral vs. abundant algae). 3) Following

disturbances to coral reefs, opportunistic species can displace corals as the dominant benthic organisms. The brown macroalga, *Turbinaria ornata*, has become increasingly abundant on coral reefs in the South Pacific and can persist as an alternative stable state on reefs. Thus, it is important to understand the drivers that facilitate the success of this opportunistic species following a disturbance, and especially the role of herbivory amidst a backdrop of overfishing, nutrient enrichment, and physical disturbance.

To address the first knowledge gap, in Chapter 1, I evaluated interspecific variation in herbivore foraging behaviors of eleven different species of herbivorous fish across multiple foraging niche axes (bite rates, feeding on food items and substrates, selectivity patterns, and maximum linear distance traveled) through focal behavioral observations of herbivore feeding on coral reef flats and a forereef in American Samoa. I found that the herbivorous fish species studied differed across all of the niche axes considered, thus highlighting the high levels of functional complementarity of the herbivore assemblage in American Samoa. To address the second knowledge gap, in Chapter 2, I conducted behavioral observations recording bite rates, foraging range, food item selectivity, and substrate selectivity of five herbivorous fish species *Acanthurus nigrofuscus*, *Zebrasoma scopas*, *Chlorurus spilurus*, *Scarus oviceps*, and *Scarus psittacus* on reefs with either abundant coral or abundant macroalgae in the lagoons of Moorea, French Polynesia. Several species of herbivorous fish exhibited differences in their foraging behaviors between reefs in the coral vs. algal state, although some foraging metrics were more dynamic than others. These results suggest that herbivorous fishes may be more flexible in their food choices on reefs with different benthic communities while not changing where on the reefs that they forage. Our work argues for

increased emphasis on understanding how state shifts in the benthic communities of coral reefs will alter the foraging ecology of ecologically important species. To address the third knowledge gap, in Chapter 3, we conducted a ~4-year factorial experiment that created a gradient of herbivory pressure using fish exclosures of different sizes (Very Low, Low, Medium, and High) and manipulated nutrient enrichment (Ambient vs. Enriched Nutrients) on a reef in Moorea, French Polynesia. I found that herbivory was the main driver of *T. ornata* percent cover and density, with only a minor and inconsistent effect of nutrient enrichment that was only present under the lowest herbivory conditions. Overall, I highlight the species-specific foraging behaviors of herbivorous fish and how that may differ on reefs with abundant algae. Further, I emphasize the critical role of herbivory in controlling the population dynamics of an opportunistic algal species on reefs experiencing intense local and global stressors.

I. High complementarity of herbivorous fishes across multiple foraging axes on coral reefs in American Samoa

Abstract

Herbivorous fishes provide critical ecological roles on coral reefs, and research in the last two decades has highlighted species-specific behaviors revealing the levels of complementarity and redundancy of the herbivorous fish community. Studies increasingly show that herbivore foraging behavior varies along axes beyond food choice (such as foraging range and foraging substrate), underscoring the need to consider additional dimensions of foraging to understand patterns of herbivory. While these important niche axes have been identified, there is a deficit of research evaluating across multiple foraging axes for a diverse suite of herbivorous fishes. In this study, we evaluated interspecific variation in herbivore foraging behaviors of eleven different species of herbivorous fish across multiple foraging niche axes (bite rates, feeding on food items and substrates, selectivity patterns, and maximum linear distance traveled) through focal behavioral observations of herbivore feeding on coral reef flats and a forereef in American Samoa. We found that the herbivorous fish species studied differed across all of the niche axes considered, thus highlighting the high levels of functional complementarity of the herbivore assemblage in American Samoa. Bite rates and movements displayed inverse relationships, with species with high bite rates exhibiting shorter distances moved and species with low bite rates moving greater distances. While we found high preferences for feeding on epilithic algal matrix (EAM) as a food item on both the reef flat and forereef, fishes that preferred EAM often exhibited different patterns in the substrates they fed on among bommies, rubble, dead coral, etc. Further we also found a

relationship between the degree of flexibility of food item and flexibility in substrate use with species that feed on a wider range of food items also show a wider range of substrate use. We also highlight that the patterns in the foraging metrics we used differed from prior studies for many species studied in other regions, emphasizing that local context may influence the functional roles of these herbivore species.

Introduction

Herbivorous fishes play critical ecological roles on coral reefs (Bellwood et al. 2004). By controlling algae that otherwise would compete with corals for space on the reef, herbivorous fishes can facilitate the recruitment, growth, and survivorship of reef building corals (Box and Mumby 2007, Burkepile and Hay 2008, Suchley and Alvarez-Filip 2017, Wakwella et al. 2020). However, herbivorous fishes vary in a number of traits that can influence how they affect algae and coral. For example, interspecific differences in diet (Fox et al. 2009, Kelly et al. 2016), movement (Adam et al. 2015, Eggertsen et al. 2020, Chow et al. 2021), and habitat selection (Adam et al. 2015; Eggertson et al. 2020) can all influence how and where herbivores impact algal assemblages (Adam et al. 2018). As a result of these differences, different species may contribute differentially to the removal of algae on reefs (Ruttenberg et al. 2019, Robinson et al. 2020, Eggertsen et al. 2020, Munsterman et al. 2021).

A key trait that differentiates different species of herbivores is their diet. Complementarity in diet can be important for removal of different macroalgal taxa (Burkepile and Hay 2008, 2011, Rasher et al. 2013). However, redundancy in behaviors across the herbivore guild is

also important because it provides potential compensation for a decrease in a particular function as populations of species fluctuate (Nash et al. 2012). In addition to diet, it may be important to understand how species vary in additional foraging axes to discern more finely how herbivores distribute their critical role of herbivory. Niche axes that can influence how and where the critical role of herbivory is distributed on reefs include: habitat preferences, substrate preferences, microhabitat use, and foraging area (Adam et al. 2015, Brandl and Bellwood 2016, Carlson et al. 2017, Semmler et al. 2021). Although these important niche axes have been identified, few studies evaluate all of these traits simultaneously across a diverse suite of herbivorous fishes (but see Adam et al. 2015, Allgeier et al. 2017, Eggertsen et al. 2020). By evaluating the foraging behavior of different herbivorous fish species across multiple foraging metrics concurrently, we can understand the unique roles of the species within the herbivore assemblage and their overall levels of complementarity and redundancy.

Previous studies evaluating the levels of functional diversity of herbivorous fishes on coral reefs found that multiple functional traits must be considered when assessing herbivore functional roles (Adam et al. 2015, Eggertsen et al. 2020). For example, in the Caribbean, parrotfish species that were similar in diet differed in the habitats they visited, substrates foraged on, and their spatial scale of foraging (Adam et al. 2015). Similarly, in the Western Indian Ocean, while both parrotfish species *Scarus ghobban* and *Scarus rubroviolaceus* preferred the epilithic algal matrix (EAM), *S. ghobban* targeted EAM on rocky substrate and *S. rubroviolaceus* targeted EAM on carbonate boulder (Eggertsen et al. 2020). Similarly, in the Great Barrier Reef, only a narrow subset of herbivores were found to access concealed microhabitats, further highlighting how different species even within the same functional

group differ in where they deliver critical ecological processes (Brandl and Bellwood 2016). Further, even when herbivorous fish species have similar diets they may differ in their foraging range (Adam et al. 2015, Chow et al. 2021), indicating that different species deliver their roles in distinct places on the reefs even if they exhibit similar foraging roles. By only assessing food items as an axis of differentiation among herbivore taxa, we may be overestimating the redundancy of species because they may feed on different locations or forage over different areas.

An additional valuable metric of feeding behavior is the niche breadth, defined as the range of resources a species uses (Slatyer et al. 2013, Hayden et al. 2019, Miller et al. 2019). This metric is especially useful as it can identify the degree of flexibility in resource use by consumers (Afeeworki et al. 2011). Further, through evaluation of the niche breadth we can obtain information on the degree of specialist or generalist behaviors. Evaluation of the levels of specialization of herbivorous fishes is important given recent modeling work highlighting that generalist herbivore communities provide the greatest reef resilience, since a greater range of functions are delivered that promote coral dominated states (Sura et al. 2025). Thus, characterizing how different herbivore species fall on the continuum of specialists to generalists fills an important knowledge gap given its implications in reef resilience.

Research on the functional diversity herbivorous fishes using multiple ecological metrics has not been conducted on reefs in American Samoa. Yet, the reefs in American Samoa represent a potential outlier in the dynamics of coral reefs in the Anthropocene given their continued resilience (ONMS 2022). Despite the drastic decline of live coral on many reefs globally

(Eddy et al. 2021), the reefs of American Samoa support healthy coral populations and stand out in contrast to global trends (ONMS 2022, Towle et al. 2022). In Fagatele Bay, one of several units of the National Marine Sanctuary of American Samoa, surveys in 2018 and 2024 found that corals were more abundant than when first surveyed in 1979, including healthy populations of coral recruits, and increasing coral colony population densities and (Green et al. 2022, Birkeland et al. 2024). However, the size structure of the herbivorous fish assemblage is skewed towards smaller individuals, with large herbivorous fish (> 30 cm) being rare in the main island of Tutuila sanctuary units (ONMS 2022). This may undermine the potential function of the herbivore assemblage given the unique role that larger herbivorous fishes can play (Bruggemann et al. 1994b, Shantz et al. 2020). Correspondingly, in most of the sanctuary units, the biomass of herbivorous fishes was found to be lower than their estimated biological potential for seemingly intact, resilient reefs (Heenan and Williams 2013). Over a decade later herbivore abundance is likely still lower than their estimated biological potential given low abundance and small size structure of herbivorous fish in recent surveys (Green et al. 2022). Thus, given the altered abundance and size structure of the herbivorous fish communities across American Samoa, there is a vital need to characterize the foraging behaviors of herbivorous fishes on these reefs in order to identify baseline herbivore foraging behaviors and identify key behaviors that are well represented or potentially vulnerable.

In this study, we evaluated interspecific variation in herbivore foraging behaviors using multiple different metrics through focal behavioral observations of herbivorous fishes on reef flats and a forereef in American Samoa. During focal behavioral observations of seven

surgeonfish species (*Acanthurus nigrofuscus*, *Acanthurus lineatus*, *Acanthurus nigricans*, *Zebrasoma scopas*, *Naso lituratus*, *Naso unicornis*, *Naso vlamingii*) and four parrotfish species (*Chlorurus spilurus*, *Chlorurus frontalis*, *Scarus oviceps*, and *Scarus psittacus*), we recorded their: (1) bite rates, (2) distance traveled while foraging, (3) bites taken on different food items (e.g., algal turf, macroalgae, coral), and (4) which substrates (e.g., dead coral, rubble, pavement) these food items occurred on fish. Our main aim was to investigate how the foraging behaviors of different herbivores species differed across multiple different ecological metrics. To address this overarching aim, we addressed the following specific questions: How do herbivorous fish species differ in their: (1) bite rates, (2) distance moved while foraging, (3) percentage of bites taken on food items and substrates, (4) selectivity patterns on food items and substrates, and (5) levels of specialization on food item and substrate use and how they are these related.

Methods

Study sites and focal species

We focused our work on Tutuila, the largest and most populated island of American Samoa. We conducted fish behavioral observations at two reef flat sites (Fatumafuti S14° 17.793' W170° 40.613', and Amaua/Auto S14° 16.714' W170° 37.672') and one forereef site (Fagatele Bay S14° 21.957' W170° 45.762') (Fig. 1). Fish behavioral observations were conducted in 2023, April – June on the reef flat and November for the forereef.

We focused our behavioral observations on the dominant species of herbivorous fishes, including grazing surgeonfishes from the genus *Acanthurus*, macroalgae browsing

surgeonfishes from the genus *Naso*, scraping parrotfishes from the genus *Scarus*, and excavating/bioeroding parrotfishes from the genus *Chlorurus* (Table 1). While *N. vlamingii* is typically considered a planktivore (Choat et al. 2004), we observed juveniles feeding on the benthos and thus included them in our study. The evidence for parrotfishes differing in diet and functional role depending on body size is significant (Bruggemann et al. 1994b, Bonaldo and Bellwood 2008, Lokrantz et al. 2008, Ong and Holland 2010, Adam et al. 2018, Lange et al. 2020). Thus, we divided parrotfish within a species between juveniles/subadults (< 15 cm) and adults (> 15 cm) (Eggertsen et al. 2020) for the analyses given the non-linear relationship between body size and function when parrotfish reach a size of 15 -20 cm (Lokrantz et al. 2008). Although there is some evidence of differences in feeding preferences of surgeonfishes across body size (Duran et al. 2019), we did not also focus analyses on different surgeonfish size classes given the range of individual sizes were narrower than for parrotfishes.

Quantification of the benthic community

To relate fish foraging behavior to the potential food items and substrates available to the fishes, we also quantified the benthic community composition. At each site, we quantified the abundance of benthic food items and substrates using point-intercept surveys with quadrats along four 30 m transects laid perpendicular to the shoreline. Benthic cover was assessed using the point-intercept method for 16 evenly spaced points within a 0.5×0.5 m quadrat. Quadrats were placed at 1 m intervals along the transects. At each point, we recorded both the cover type (epilithic algal matrix (EAM): a multi-species assemblage of filamentous algae, macroalgal propagules, and detritus (Wilson et al. 2003), macroalgae, turf within damselfish territories, live coral, cyanobacteria, crustose coralline algae) and the underlying substrate on which the cover type was located (Fig. S1). Macroalgae and corals were identified to species when possible, to genus when species was not possible, or functional group when even genus level was not possible. Substrates consisted of: (1) dead branching coral, (2) bommie, which was dead massive corals, mostly *Porites lobata* and *Porites rus*, (3) live coral, (4) pavement (bare substrate with limited topographic complexity), (5) rubble, which was pieces of unconsolidated dead coral, and (6) sand.

Fish Behavioral Observations

All observations were conducted between 1000-1600 hrs, the primary foraging times for herbivorous fishes (Bruggemann et al. 1994a). Observations were conducted on snorkel for the reef flat sites and on SCUBA for the forereef site at a distance of 2 - 3 m from the focal fish. We haphazardly selected focal individuals for observation and allowed 2-3 min for the fish to acclimate to the presence of the diver. The observer estimated the total length of the focal individual to the nearest cm. After acclimation, the diver followed the fish for 10 min. During this observation, the diver recorded each foraging bout, defined as a series of

repeated bites in a single area, usually targeted at a single food item (Bellwood and Choat 1990). The diver recorded the number of bites in each feeding bout, the food item targeted, which as identified to the lowest taxonomic level possible in the field, and the substrate on which the fish was foraging. Food items of macroalgae or coral were usually identifiable to genus or species. Because of the difficulty of identifying species targeted within the EAM, we simply classified all bites on EAM as such (Adam et al. 2015). We also differentiated bites on the EAM and the dense turf within damselfish territories given that the algal composition often differs between EAM and the turf within damselfish territories (Ceccarelli et al. 2001, 2005, 2011, Eurich et al. 2018). Further, to differentiate feeding on macroalgae, we categorized bites into two distinct categories: feeding on macroalgae and feeding on the epiphytes or epifaunal community on macroalgae (hereafter ‘epi macroalgae’). Bites classified as on macroalgae involved the removal of visible macroalgal tissue, indicating consumption of macroalgal biomass. In contrast, bites classified as ‘epi macroalgae’ were characterized by bites targeting the epibionts on the surface of the macroalgae, without obvious removal of the macroalgal tissue as is common for many non-browsing species when feeding on macroalgae (Dell et al. 2020).

We also identified the type of substrate on which the food items were growing using the same categories as the benthic surveys (i.e., dead branching coral, live coral, pavement, bommie, rubble, and sand) which provides further information about how species are using their habitat and potentially avoiding competition with other herbivore species. Live coral was included both as a food item and a substrate given its ability to be a direct foraging resource and substrate. Feeding observations on live coral were distinguished by two

behaviors with some parrotfish species observed scraping away live coral tissue, while other species, often surgeonfishes, observed feeding on live coral while not removing any coral skeleton. However, it was unclear whether these surgeonfish species were feeding on an epilithic biofilm, mucus, detritus, coral polyps, or other food item that was on the surface of the coral. Further, these distinctions were often challenging to discern in the field, thus we simply categorized any bite on live coral as such regardless of it removed coral skeleton or not.

Statistical analysis

How do herbivorous fish species differ in their bite rates and distance moved?

To assess whether overall bite rates differed among herbivorous fish species, we fit a model with a main effect of fish species and included size as a covariate. Bite rate data were log-transformed to homogenize variance.

To investigate whether herbivorous fish species moved different distances, we conducted a model with a main effect of fish species and included size as a covariate on log-transformed maximum linear distance traveled (m).

Separate models were run for the reef flat and forereef zones. For the reef flat, linear mixed models with site as a random effect were conducted. As there was only one site for the forereef, standard linear models were conducted. Model assumptions were visually evaluated through diagnostic plots and were met. We conducted post hoc pairwise

comparisons using Tukey's Honest Significant Difference (HSD) test with p-value adjustment for multiple comparisons using the *emmeans* package in R.

How do herbivorous fish species differ in their percentage of bites taken on food items and substrates?

To evaluate whether the percentage of bites differed among fish species based on food item and substrate type within each reef zone (reef flat and forereef), we conducted separate PERMANOVAs for each zone and response variable (food item and substrate). For the reef flat, we also controlled for site level structure by restricting permutations within site. Analyses were performed using the *adonis2* function in the *vegan* package in R with Bray-Curtis dissimilarities and 999 permutations on raw bite data.

How do herbivorous fish species differ in their selectivity patterns on food items and substrates?

To determine the preferences of different fish species for food items and substrates relative to their availability, we conducted a selectivity analysis using Manly's alpha (Chesson 1983) on bite data. Availability of food items and substrates were calculated for each site from the mean abundance based on point contact data. The selectivity index, Manly's alpha, ranged between 0 and 1 and was interpreted relative to the null selectivity ($\alpha = 1/m$, where m is the total number of resource types available and bitten). The null selectivity value is shown as a dashed red line in the figures. A 95% confidence interval above the null selectivity line indicates selection (preference), entirely below indicates

avoidance, and intervals overlapping the null line suggest no significant preference for or avoidance of a diet item.

The selectivity analyses were conducted within each reef zone (reef flats and forereef) for both food items and substrates for each species. To align resource use data with availability estimates, we collapsed the epibionts on macroalgae category into ‘Macroalgae’ in the bite data because we did not have estimates of the abundance of epibionts on macroalgae from the benthic data. Although most species were observed feeding on epibionts rather than removing macroalgal biomass directly, this behavioral nuance was simplified in the analysis and thus may underestimate the differences in foraging among some species. For the reef flat, the availability of resources was virtually the same between the two sites and resulted in near identical results, thus we pooled selectivities between the two sites. On the forereef, fewer herbivorous fish species were included for the analyses due to a limited number of individuals observed, which constrained the ability to use all of the species in the forereef analyses.

How specialized are fish species on food items and substrates and are these related?

While the selectivity analyses provide information on a species’ preferences, we were also interested in how flexible species are in their resource use by calculating their niche breadth. We used data only from fishes on the reef flat to evaluate niche breadth given the greater fish species diversity and number of individuals followed as compared to the forereef. To evaluate the breadth of the feeding niche for each herbivore species on food items and substrates, we used the proportional similarity index (PSI):

$$PSI_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where p_{ij} is the proportion of resource j used by individual i , q_j is the proportion of resource j available (Feinsinger et al. 1981). This metric ranges from 0 to 1 and considers the proportional use of resources to its relative availability, providing information on how generalized or specialized a species is. A higher PSI indicates more generalist behavior (i.e., broader niche breadth) and a lower PSI indicates more specialist behavior (i.e., narrower niche breadth). We calculated the PSI separately on the food item and substrate use.

To evaluate whether herbivorous fish species differed in their PSI on food items and substrates, we conducted a linear mixed model using the *lme4* package with a random effect of site. This was conducted for PSI on food items and PSI on substrates separately. Model assumptions were visually evaluated through diagnostic plots. We conducted post hoc pairwise comparisons using Tukey's Honest Significant Difference (HSD) test with p-value adjustment for multiple comparisons using the *emmeans* package in R.

Further, we evaluated if there was a relationship between PSI of food item and PSI of substrate through Spearman's correlation and visualized the patterns with a scatterplot and trend line was fit using locally estimated scatterplot smoothing with a 95% confidence interval. This allows us to evaluate for example whether specialists on food items are also specialists on substrates.

Results

How do herbivorous fish species in American Samoa differ in their bite rates and distance moved?

Bite Rate

The bite rate of herbivorous fishes was significantly different among fish species on both the reef flat ($F_{(11,65.9)} = 7.5$, $p < 0.001$; Fig. 2a, Table S1) and forereef ($F_{(4,40)} = 5.7$, $p < 0.001$; Fig. 2a, Table S2). In addition, on the forereef, the size covariate accounted for significant variation in bite rate ($F_{(1,40)} = 7.4$, $p = 0.01$, Table S2). On the reef flat, *Scarus psittacus* (adult; $26.5 \text{ min}^{-1} \pm 12.2$) and *Acanthurus lineatus* ($21.9 \text{ min}^{-1} \pm 4.6$) exhibited the highest bite rates, whereas *Naso lituratus* ($1.7 \text{ min}^{-1} \pm 0.7$), *N. unicornis* ($2.1 \text{ min}^{-1} \pm 1.1$), and *N. vlamingii* ($1.2 \text{ min}^{-1} \pm 0.9$) had the lowest bite rates. Post hoc Tukey comparisons indicated that *A. lineatus* had the highest bite rates as they had greater bite rates than several surgeonfish species (*N. lituratus*, *N. unicornis*, *N. vlamingii*, *Z. scopas*) and the juveniles/subadult life stage of *S. oviceps*. Bite rates of *Naso* species were significantly lower than those of *A. lineatus*, *S. psittacus* (adult), *C. spilurus* (juveniles/subadults) and several other acanthurids (all comparisons $p < 0.05$) (Table S3). On the forereef, *A. nigricans* ($20.5 \text{ min}^{-1} \pm 3.8$) had the highest bite rate, and *N. lituratus* ($6.1 \text{ min}^{-1} \pm 1.3$) and *S. oviceps* adults exhibited the lowest ($5.9 \text{ min}^{-1} \pm 1.6$). Although *N. lituratus* bite rates were higher on the forereef than on the reef flat, they were still significantly lower than those of *A. nigricans* ($p < 0.001$) and ($p = 0.02$) (Table S4).

Distance Moved

For both the reef flat and forereef, herbivorous fish species differed in their maximum linear distance traveled (reef flat: $F_{(11, 56.6)} = 3.7$, $p < 0.001$, Fig. 2b, Table S5; forereef: $F_{(4, 40)} = 3.4$,

$p = 0.02$, Fig. 3b, Table S6). For the reef flat, the covariate size accounted for significant variation in distance moved ($F_{(1,74.0)} = 4.8$, $p = 0.03$, Table S5). Tukey pairwise comparisons revealed *N. lituratus* and *N. unicornis* had greater maximum linear distance traveled than *A. lineatus* ($p < 0.05$) (Table S7). A pattern that emerged on the reef flat was that the species that displayed some of the lowest bite rates (*N. lituratus*), had higher maximum linear distance traveled ($25.5 \text{ m} \pm 5.4$), and similarly the species that had some of the highest bite rates (*A. lineatus*) had a smaller distance traveled ($8.0 \text{ m} \pm 1.4$) (Fig 2a and b). On the forereef, the significant pairwise comparisons showed that *N. lituratus* had a greater maximum linear distance traveled than *A. nigricans* and *Z. scopas* ($p < 0.05$). Thus, on the forereef similar patterns emerged where the species with one of the lowest bite rates (*N. lituratus*) had significantly greater distance traveled ($19.9 \text{ m} \pm 2.4$) than *A. nigricans* ($11.0 \text{ m} \pm 1.4$), which had the highest bite rates on the forereef (Fig 3a and b) (Table S8).

How do herbivorous fish species differ in their percentage of bites taken on food items and substrates?

Reef flat

Food Items

On the reef flat, the percentage of bites taken by herbivorous fishes differed significantly among species for food items (PERMANOVA, food item: $F_{(11,84)} = 2.6$, $p = 0.001$; Fig 4a). The epilithic algal matrix (EAM) was the most commonly targeted food item, constituting more than 40% of the bites by 8 out of 12 species and life stage.

Damselfish turf constituted a considerable percentage of the diet of many fishes, with *Acanthurus lineatus* displaying the highest percentage of bites on damselfish turf (58.7 %). Several parrotfish species were observed to feed on live coral. *Chlorurus spilurus* juveniles/subadults had 38.8% of their bites on live coral, and they were distributed on *Porites*, *Pavona*, and *Acropora*. *S. oviceps* juveniles/subadults had 15.7% of their bites on live coral, and they were distributed on *Porites*, *Acropora*, and *Pavona*. *S. oviceps* adults had 22% of their bites on live coral, and they occurred on *Porites* and *Pavona*. Two surgeonfish species were also observed to have a considerable percentage of their bites on live coral: *Z. scopas* had 28.0% of their bites on live coral on *Porites* and *Acropora*; *N. lituratus* had 34.3% of their bites on live coral and it was on *Porites*.

Only the *Naso* spp. and *Zebrasoma scopas* were observed to remove macroalgae. *Naso lituratus* removed macroalgae in 20.3 % of its bites, *N. unicornis* 35.4 %, *N. vlamingii* 8.5 %, and *Z. scopas* 7.9 % (Fig 4a). Other species observed feeding on macroalgae (*A. nigricans*, *A. nigrofuscus*, *C. spilurus* juvenile/subadult, and *S. psittacus* adult) were observed to feed only on epibionts associated with macroalgae. *Naso vlamingii* appeared to feed on both macroalgae and epibionts on macroalgae (Fig 4a). Specifically, *N. lituratus* fed on *Lobophora*, *Galaxaura*, and *Dictyota*. *N. unicornis* fed on *Dictyota*, *Lobophora*, and on an unidentified brown macroalgae. *Naso vlamingii* fed on red calcareous macroalgae, *Halimeda*, and *Dictyota*. *Z. scopas* mostly fed on an unidentified alga (Fig S2a).

Substrates

On the reef flat, the proportion of bites taken by herbivorous fishes differed significantly among species for substrates (PERMANOVA, $F_{(11,84)} = 3.1$, $p = 0.001$; Fig 4b). Rubble was the most frequently grazed substrate on the reef flat with the highest percentage of bites being from *Acanthurus nigricans* (70.5 %) and *Chlorurus frontalis* adults (72.6 %) (Fig 4b). All species fed on the bommie substrate, although the surgeonfish generally had a higher percentage of bites on bommie than did the parrotfish (Fig 4b). Feeding on the pavement substrate was variable among species with *S. oviceps* adult (25.7 %) and *S. oviceps* juvenile/subadult (30.5 %) having the greatest percentage of bites on pavement while *A. nigricans*, *Z. scopas*, *C. frontalis* adult, and *N. vlamingii* never fed on pavement. Only *C. spilurus* juvenile/subadult fed on the sand substrate, although this represented a low percentage of their bites (0.55 %).

Considering only bites involving macroalgae and epibionts on macroalgae, *N. unicornis* showed similar percentage of bites on rubble (45.9 %) and bommie (44.3 %), with fewer on dead coral (9.84 %), *N. vlamingii* fed primarily on bommies (61.0%), while *N. lituratus* fed across a more diverse set of substrates, with equal percentage of bites on pavement and rubble (33.3 % each), followed by dead branching coral (26.7 %), and bommies (6.7 %) (Fig S2b). In contrast, all bites on macroalgae by *Z. scopas* were observed on bommies (Fig S2b).

Forereef

Food Items

On the forereef, the patterns of bite proportions also differed significantly among species for food items (PERMANOVA, food item: $F_{(4, 41)} = 3.9$, $p = 0.001$; Fig 5a). As on the reef flat,

the epilithic algal matrix (EAM) was the most commonly targeted food item, although only *C. spilurus* adults had > 40% of their bites on EAM. Notably, cyanobacteria comprised a considerable percentage of bites on the different food items with *A. nigricans* (33.5 %) and *Z. scopas* (32.8 %) having the greatest percentage of bites on cyanobacteria (Fig 4a).

Damselfish turf generally constituted a lower percentage of bites than on the reef flat (Fig 5a). Only *C. spilurus* adults and *S. oviceps* adults were observed to feed on live coral as a food item (Fig 5a). For *C. spilurus* adults, these bites on live coral occurred on *Montipora*, *Acropora*, and unidentified encrusting corals. For *S. oviceps* adults, bites on live coral occurred on *Montipora* and unidentified encrusting corals.

On the forereef, only *N. lituratus* and *C. spilurus* adults were observed to remove macroalgae (Fig 5a). *Naso lituratus* removed macroalgae in 9.3% of their bites and *C. spilurus* adult in 1.5 % (Fig 5a). Specifically, *N. lituratus* fed on *Halimeda* and red calcareous algae, and *C. spilurus* adult also fed on *Halimeda* and red calcareous macroalgae, in addition to *Lobophora* (Fig S2c). Both species also fed on epibionts associated with macroalgae: *N. lituratus* (5.6 %) and *C. spilurus* adult (5.9 %). All other species observed to feed on macroalgae only fed on the epibionts: *A. nigricans* (7.3 %), *Z. scopas* (30.5 %), and *S. oviceps* adult (13.5 %) (Fig 5a).

Substrate

On the forereef, the patterns of bites also differed significantly among species for substrates (PERMANOVA, $F_{(4,41)} = 2.0$, $p = 0.043$; Fig 5b). Dead coral was the most commonly grazed substrate (Fig 5b), and represented a similar percentage of bites for most species, with *A.*

nigricans (34.7%) being the lowest and *S. oviceps* adults (48.1%) being the highest (Fig 5b). The percentage of bites on pavement was similar for *N. lituratus* (29.0 %), *C. spilurus* adults (24.0%), and *S. oviceps* adults (21.3 %), and higher for *A. nigricans* (39.0 %) and *Z. scopas* (40.7 %) (Fig 5b). Feeding on the rubble substrate was similar across most species (23.3% to 26.0%) except for *Z. scopas* (3.8%) (Fig 5b). Only *C. spilurus* adults (7.0%) and *S. oviceps* adults (5.7%) were observed to feed on live coral on the forereef.

Considering only bites involving macroalgae, *N. lituratus* had its highest percentage of macroalgae associated bites on the rubble substrate (42.1 %), followed by dead branching coral (36.8 %), and pavement (21.1 %) (Fig S2d). *Chlorurus spilurus* adult displayed its highest percentage of macroalgae associated bites on dead branching coral (53.2 %), followed by rubble (36.2 %), and pavement (10.6 %) (Fig S2d).

How do herbivorous fish species differ in their selectivity patterns on food items and substrates?

Reef flat

Selectivity patterns on food items varied across species. EAM was significantly preferred by five species, and fed in proportion to its availability by others with the exception of *N. vlamingii* which avoided EAM (Fig 6). *Acanthurus lineatus* and *N. lituratus* both preferred damselfish turf, while the rest of the species displayed neutral selection for damselfish turf. *Naso unicornis* and *N. vlamingii* were the only species to prefer macroalgae, while *A. nigricans*, *A. nigrofuscus*, *Z. scopas*, *N. lituratus*, and *S. psittacus* adults fed on macroalgae in

proportion to its availability, while the rest of the species avoided macroalgae. *Zebrasoma scopas*, *N. lituratus*, *C. spilurus* juveniles/subadults, and *S. oviceps* juveniles/subadults displayed neutral selection for live coral. All other species avoided live coral.

Selectivity on substrates also varied across species, although rubble was highly preferred by several species (Fig 7). Notably, only rubble, bommie, and dead branching coral were significantly preferred substrates among the fish species. Rubble was preferred by *A. nigricans*, *N. lituratus*, *N. unicornis*, and *C. frontalis* adults. Bommie was preferred by *A. lineatus* and *A. nigrofuscus*. Dead branching coral was preferred by *Z. scopas* and *S. oviceps* juveniles/subadults. *Chlorurus spilurus* juveniles/subadults, *S. oviceps* adults, and *S. psittacus* adults generally fed on substrates in proportion to their abundance except for sand. For the rest of the substrate categories, fishes either fed on the substrates in proportion to its availability or avoided them.

Forereef

For selectivity on food items, EAM was highly preferred by all observed fish species on the forereef (Fig 8). No other food item was preferred by the fish species. *Zebrasoma scopas* was the only species that did not avoid macroalgae. *Chlorurus spilurus* adults and *S. oviceps* adults avoided all other food items besides EAM (Fig 8).

For substrate selectivity, *A. nigricans* was the only species to prefer pavement while all other species displayed neutral selection on pavement (Fig 9). *Zebrasoma scopas* and *S. oviceps* adults preferred dead coral substrate while all other species displayed neutral selection for

dead coral. *Chlorurus spilurus* adults were the only species to prefer rubble substrate.

Zebrasoma scopas avoided rubble while all other species had neutral selection of rubble (Fig 9).

How specialized are fish species on food items and substrates and are these related?

For the food items, fish species significantly differed in their PSI (niche breadth) ($F_{(11, 64.6)} = 4.3, p < 0.001$) (Fig. 10a). The *Naso* spp., in particular *N. vlamingii* stood out as having significantly lower PSI than several surgeonfish and parrotfish species (Table S8). In general, parrotfish more often displayed higher PSI, indicating more generalist feeding patterns and surgeonfish displaying lower PSI suggesting more specialist feeding patterns. *Naso* spp. in particular appeared more specialized than other surgeonfishes.

For the substrate, species did not differ significantly in their PSI ($F_{(11, 79.8)} = 0.8, p = 0.688$) indicating most fish species display a similar degree of substrate use flexibility (Fig. 10b). Estimated marginal means of substrate PSI ranged from 0.3 to 0.4 on the lower to middle of the spectrum indicating they are not highly specialized nor highly generalized.

Spearman's correlation revealed that food item and substrate PSI were positively correlated ($\rho = 0.69, p = 0.02$), suggesting that species with a narrower food item niche breadth (lower PSI) also tended to have a narrower substrate niche breadth (lower PSI), and species with a broader niche breadth (higher PSI) tended to have broader substrate niche breadth (higher PSI) (Fig. 11). However, substrate PSIs were on the lower to middle of the scale (0.3 to 0.4) for all species.

Discussion

We found that the herbivorous fish species studied here differed across all of the niche axes considered (bite rates, distance moved, feeding on food items and substrates, selectivity patterns, and niche breadth), thus highlighting the high levels of functional complementarity of the herbivore assemblage in American Samoa. Bite rate and movement results reveal contrasting patterns with species with high bite rates exhibiting shorter distances moved and species with low bite rates having greater distance moved. While we found high preferences for feeding on EAM on both the reef flat and forereef, species often targeted different substrates, highlighting partitioning within the EAM feeders (Table 2). In addition, we found surprising utilization of live coral by both parrotfish and surgeonfish (Fig. 4), indicating live coral may be an underappreciated resource, although further investigation in the actual material fish were ingesting is needed. Further we also found a relationship between the degree of flexibility of food item and substrate use with species that feed on a wider range of food items also show greater flexibility in their substrate use. Overall, we add to the growing literature highlighting the important patterns in the functional diversity of coral reef fishes, highlighting how herbivorous fishes differentially exploit different resource dimensions on reefs (Adam et al. 2015, Eggertsen et al. 2020, Chow et al. 2021).

Naso spp. stood out relative to the other species by travelling longer distances while foraging, which aligns with data on browsers in general foraging over relatively large areas compared to other functional groups of herbivorous fishes (Nash et al. 2013, Welsh and Bellwood 2014,

Green et al. 2015). We found *A. lineatus* moved the smallest distance while foraging, likely because they are territorial surgeonfishes with small home ranges (Craig 1996, Green et al. 2015). While parrotfish can rove within their home range including activities of feeding, mating, spawning, and resting spanning (< 0.3 to 1 km long for *Scarus* and *Chlorurus* spp.; or 3 km for larger *Chlorurus* and *Scarus* spp.) (Green et al. 2015), their movement within feeding territories can be quite constrained (Davis et al. 2017). There is a plethora of literature now on the home ranges (movement encompassing feeding, resting, mating, migration) of herbivorous fishes (reviewed in Green et al. 2015). However, it would be beneficial to gain more fine scale knowledge on the extent of herbivore movement while exclusively feeding in order to understand the spatial distribution of herbivory (Tootell and Steele 2016, Carlson et al. 2017, Davis et al. 2017, Streit et al. 2019), especially given that many herbivores concentrate their feeding in smaller areas than that of their total home range (Welsh and Bellwood 2012, Davis 2016, Streit et al. 2019). While we did not directly link the behaviors of these fishes to their ultimate functional impact, spatially-explicit modeling simulations estimate that spatially constrained foraging may be more effective at conferring reef resilience, likely due to more intense, localized herbivory (Sandin and McNamara 2012, Eynaud et al. 2016). Thus, future studies should work towards linking herbivorous fish species-specific patterns of movement to their functional impact on reefs.

We found that many of the well-studied fish species displayed different foraging behaviors across the resource axes in our study, revealing substantial geographical variation in behaviors. For example, *Naso unicornis* have been found to consume *Turbinaria*, *Dictyota*, *Sargassum*, and *Padina* in other studies in the GBR, Fiji, Hawaii, and Moorea (Choat et al.

2002, 2004, Hoey and Bellwood 2009, Rasher et al. 2013, Kelly et al. 2016, Tebbett et al. 2020, Sura et al. 2021). Yet we did not observe *N. unicornis* to feed on any of these macroalgae even though they were all present (with the exception of *Sargassum*), instead feeding on *Lobophora* and *Galaxaura*. However, Tebbett et al. (2020) did also observe *N. unicornis* to also feed on *Galaxaura* in the GBR. Further, *Naso lituratus* is also known to feed on the brown macroalgae *Sargassum*, *Padina*, *Dictyota*, and *Turbinaria* in Hawaii and Fiji (Rasher et al. 2013, Kelly et al. 2016) as well as *Sargassum* and *Padina* in Moorea (Sura et al. 2021). Yet we only observed *N. lituratus* feeding on *Lobophora*, *Halimeda*, *Galaxaura*, and other red calcareous macroalgae.

Interestingly, according to the selectivity analysis, the browser *N. lituratus* avoided macroalgae on the forereef, instead targeting EAM, damselfish turf, and cyanobacteria. However, macroalgae on the forereef was dominated by red calcareous algae and the green calcareous alga *Halimeda*, and no brown macroalgae recorded in the benthic surveys. Even if the specific algal species preferred by *N. lituratus* differs across studies in different regions as described earlier, it appears *N. lituratus* does have a preference for brown macroalgae. Thus, they may especially dislike red calcareous algae and *Halimeda*, thus actively avoiding it on the forereef in American Samoa, although herbivory assays would be necessary to confirm this. The scarcity of preferred food may induce herbivores to consume less preferred but more abundant resources (Francini-Filho et al. 2010). Thus, if brown algae are their preferred food items, they may be forced to switch to other resources due to the low abundance of macroalgae and on the reefs studied in American Samoa where we did not record any brown macroalgae on the forereef in the benthic surveys.

Other variable patterns across regions are evident with *A. nigrofuscus* which was found to prefer the red alga *Asparagopsis* and have neutral selection for *Turbinaria* in Hawaii (Kelly et al. 2016) and prefer *Sargassum* in Moorea (Sura et al. 2021). Yet the only macroalgae we observed *A. nigrofuscus* to feed on was red calcareous macroalgae and *Halimeda*. Although, we did find some similarities with other studies, for example *Naso* spp. are often found to have low feeding rates and tend to feed on macroalgae (Choat et al. 2004). Gut content analysis of *A. nigricans* found a high proportion of red thallate algae (Choat et al. 2002). Our observations align as the only macroalgae we recorded them to feed on was red calcareous macroalgae. Overall, however, there appears to be more differences in herbivore foraging behavior across reefs and regions than similarities, underscoring the need to continue to evaluate localized foraging behaviors.

By evaluating substrate use, we found high complementarity even among behaviors that initially appear redundant. In particular, many species preferred EAM or had a neutral preference for EAM, yet they fed on distinct substrates. For example, *A. lineatus* preferred EAM, yet it was one of two species that preferred the bommie substrate. In contrast other fishes that targeted EAM, like *Z. scopas* or *C. frontalis* targeted dead coral and rubble, respectively. This pattern aligns with previous studies that show considering substrate use reveals greater complementarity among species that feed on similar food resources (Adam et al. 2015, Brandl and Bellwood 2016, Eggertsen et al. 2020). Similarly, even among the browsers, when only considering bites on macroalgae by *Naso* spp., we found *N. lituratus* exhibited 26.7% of their bites on dead coral substrates while *N. unicornis* had the lowest

proportion of bites at 9.8 % on dead coral substrates, again highlighting how even species within the same genus and functional group differ across other niche axes when substrate use is considered.

Only the *Naso* spp. and *Zebrasoma scopas* were observed to remove macroalgae while other species observed feeding on macroalgae (*A. nigricans*, *A. nigrofuscus*, *C. spilurus* juvenile/subadult, and *S. psittacus* adult) were observed to feed only on epibionts associated with macroalgae. *Naso vlamingii* appeared to feed on both macroalgae and epibionts on macroalgae. Thus, given the variety of species not normally considered as browsers were found to feed on the epibionts on macroalgae, the role of epibiont grazing warrants further study as previously suggested by Puk et al. (2016). Grazing of epibionts on macroalgae can potentially enhance the growth of macroalgae by increasing their potential for photosynthetic capacity (Fox and Bellwood 2008), however, high epibiont loads can also deter removal of macroalgal biomass by rabbitfish and unicornfish (Lefèvre and Bellwood 2010) yet attract feeding by parrotfish (Lefèvre and Bellwood 2011). Therefore, grazing of epibionts on macroalgae could potentially facilitate browsing on macroalgae given that browsers may be deterred by high epibiont loads. Thus, an increased focus on the causes and consequences of epibiont grazing on macroalgae would help illuminate both the functional roles of different herbivores species and the impact of their feeding on benthic dynamics.

We also documented both parrotfishes and surgeonfishes frequently feeding on live coral. Many parrotfish species have been shown to feed on live corals (Bonaldo and Rotjan 2018).

However, the frequent bites on live coral by the surgeonfishes *Z. scopas* and *N. lituratus* were surprising, however these fish were not removing coral skeleton during feeding as parrotfish often do. Further, it was unclear what these fish were targeting, but potentially could include resources such as coral polyps, biofilm, detritus, or coral mucus. Corals can host rich biofilm communities of microorganisms (Remple et al. 2021) which might represent significant resources for herbivores. Detritus on reefs can also represent a highly nutritious resource, sometimes having higher nutritional value than filamentous turf algae (Crossman et al. 2001). Mucus secretion is a common phenomenon by corals (Bythell and Wild 2011), and mucus can trap organic matter and be of high nutritional value (Wild et al. 2004). Clearly, more devoted study of the resources surgeonfishes are using while biting live coral is warranted as coral may present an underappreciated resource on coral reefs.

The niche breadth is a key functional trait describing a consumer's role in a community (Hayden et al. 2019). Our niche breadth analysis revealed an additional insight into the functional diversity of the herbivore community on American Samoa's reefs. Overall, we found that parrotfish, on average, appeared to behave more as generalists compared to most surgeonfish when considering food items. Within the surgeonfish, we found the browsers (*Naso* spp.) to be the most specialized and thus likely the least flexible in their food item use. However, some surgeonfish (e.g., *A. nigricans*, *A. nigrofuscus*) appeared to have similar flexibility in diets as compared to parrotfish. Given the variation in herbivore foraging behaviors we describe compared to other studies in different regions, it would be valuable to evaluate niche breadth in other regions. There may be a variety of reasons for the differences in behaviors across studies and regions, but could be due to different benthic

community composition. Identifying an herbivore's niche breadth in other regions would provide insight on whether they are true generalists or specialists or are just constrained by the resource availability at our sites.

The high degree of complementarity across most comparisons of the observed 11 species of herbivorous fish studied highlight the high level of resource partitioning of the herbivore assemblage in American Samoa. The results are in line with other studies showing that greater complementarity is found when considering multiple niche axes (Rosenfeld 2002, Brandl and Bellwood 2014, Adam et al. 2015, 2018, Kelly et al. 2016, Eggertsen et al. 2020), even among closely related species (Fox et al. 2009). For example, taxa targeting EAM often forage across many different substrates and even different *Naso* spp. that target macroalgae often forage from different substrates. Further, the evidence is overwhelming for the variation in foraging behavior across regions. This reveals a critical need for better synthesis of species feeding behaviors given the variation in foraging behaviors both that we found and others across regions in order to understand the underlying commonalities. The differences could reflect underlying ecological drivers such as the benthic community composition, resource quality, or even competition. Thus, it would be beneficial for future studies to understand the drivers of the different patterns across regions.

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Figures

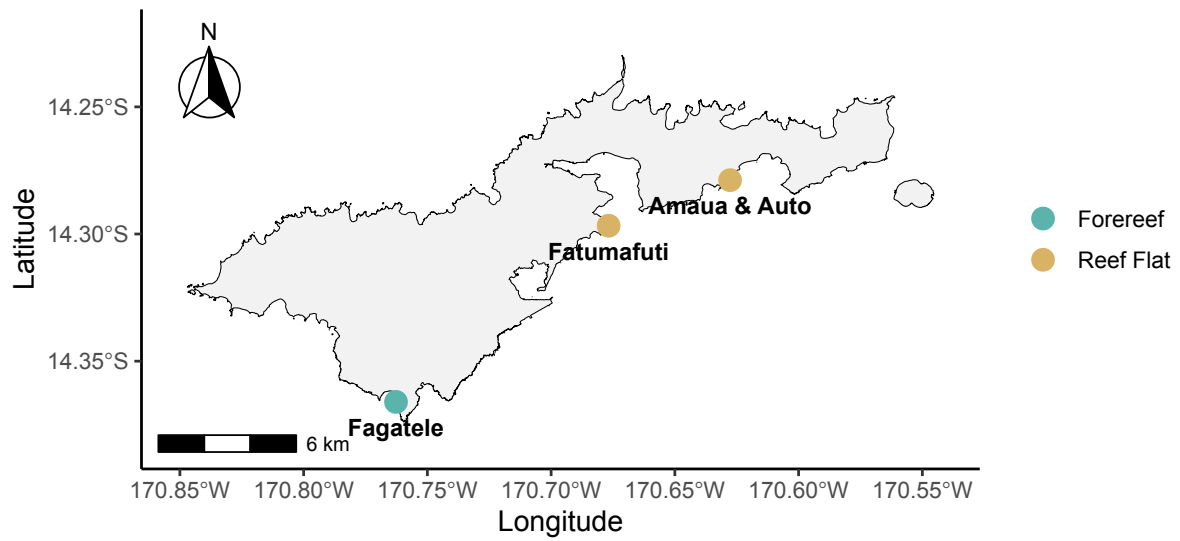


Figure 1. Map of study sites on Tutuila, American Samoa. Basemap shoreline data from NOAA Centers for Coastal Ocean Science (2001).

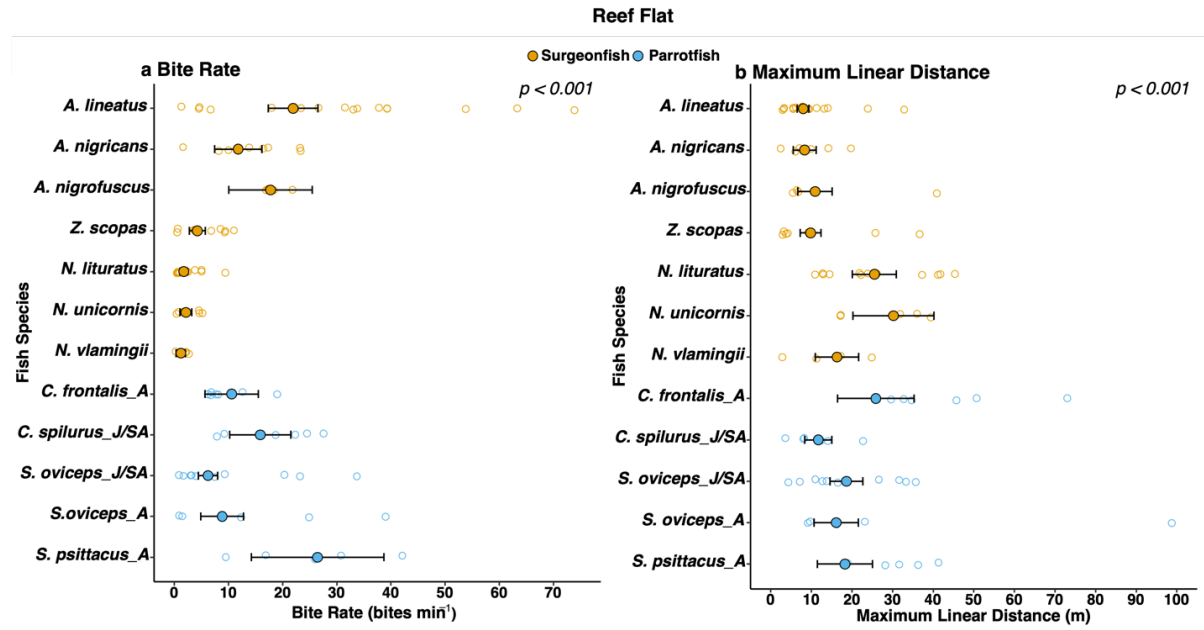


Figure 2. Estimated marginal means ($\pm$ SE) of size-adjusted **a)** bite rates for each species and **b)** maximum linear distance traveled (m) for each species for the reef flat. Open circles represent raw maximum linear distance traveled values and filled points represented the model predicted means. Surgeonfish indicated by orange circles and parrotfish indicated by blue circles. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. Statistics are from linear mixed models.

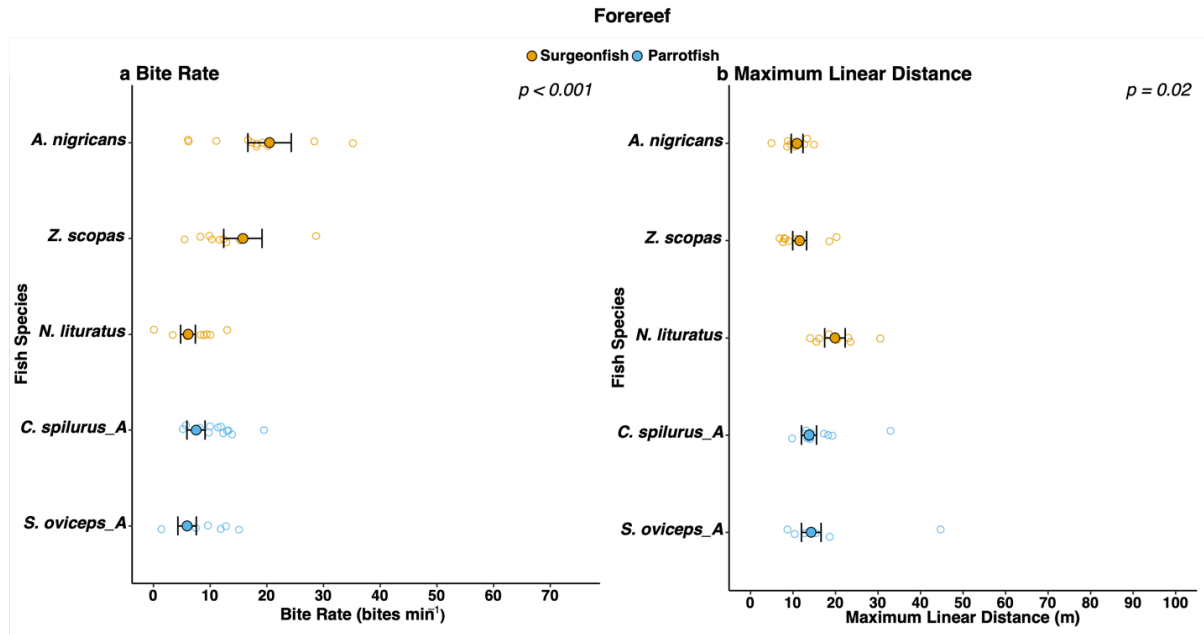


Figure 3. Estimated marginal means ($\pm$ SE) of size-adjusted **a)** bite rates for each species and **b)** maximum linear distance traveled (m) for each species for the forereef. Open circles represent raw maximum linear distance traveled values and filled points represented the model predicted means. Surgeonfish indicated by orange circles and parrotfish indicated by blue circles. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. Statistics are from the standard linear models.

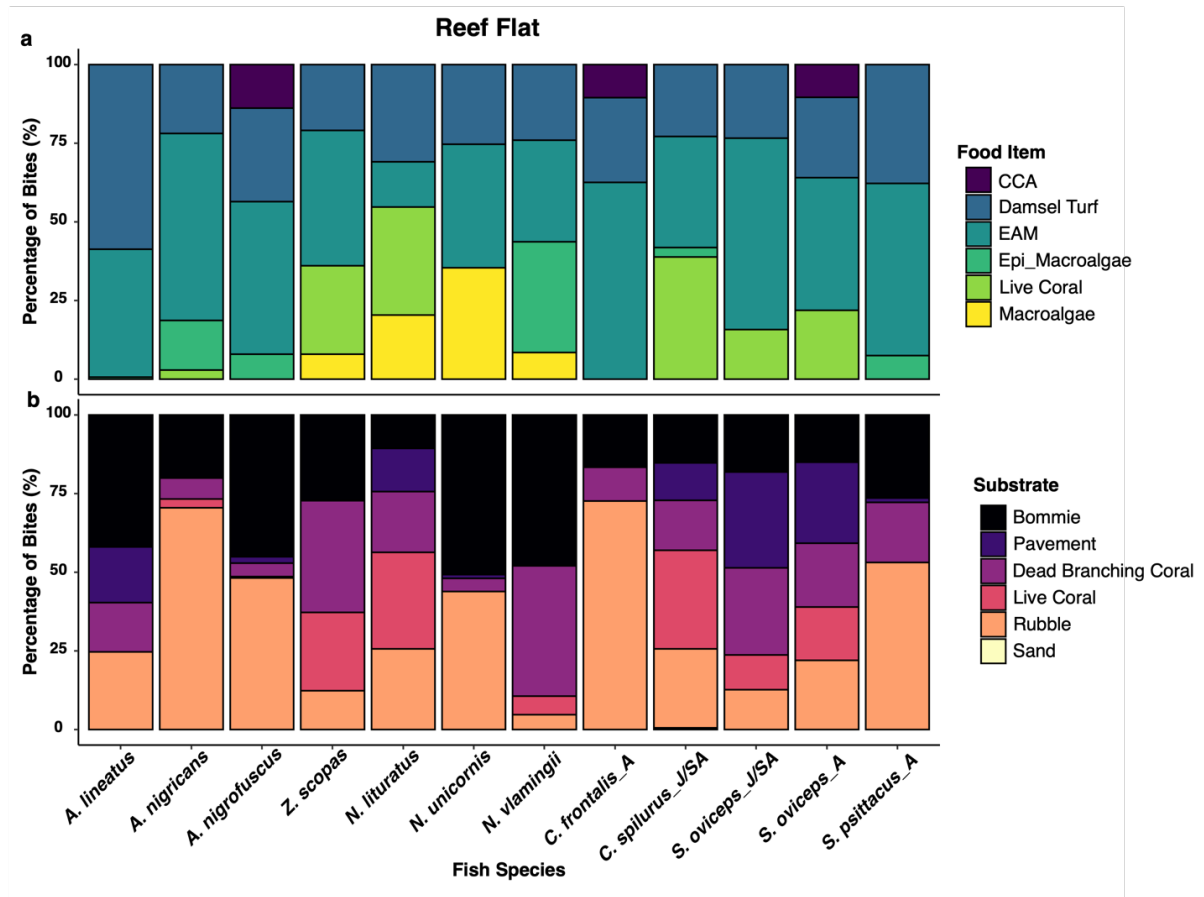


Figure 4. Mean percentage of bites taken by fish species in the reef flat on **a)** food items and **b)** substrates. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

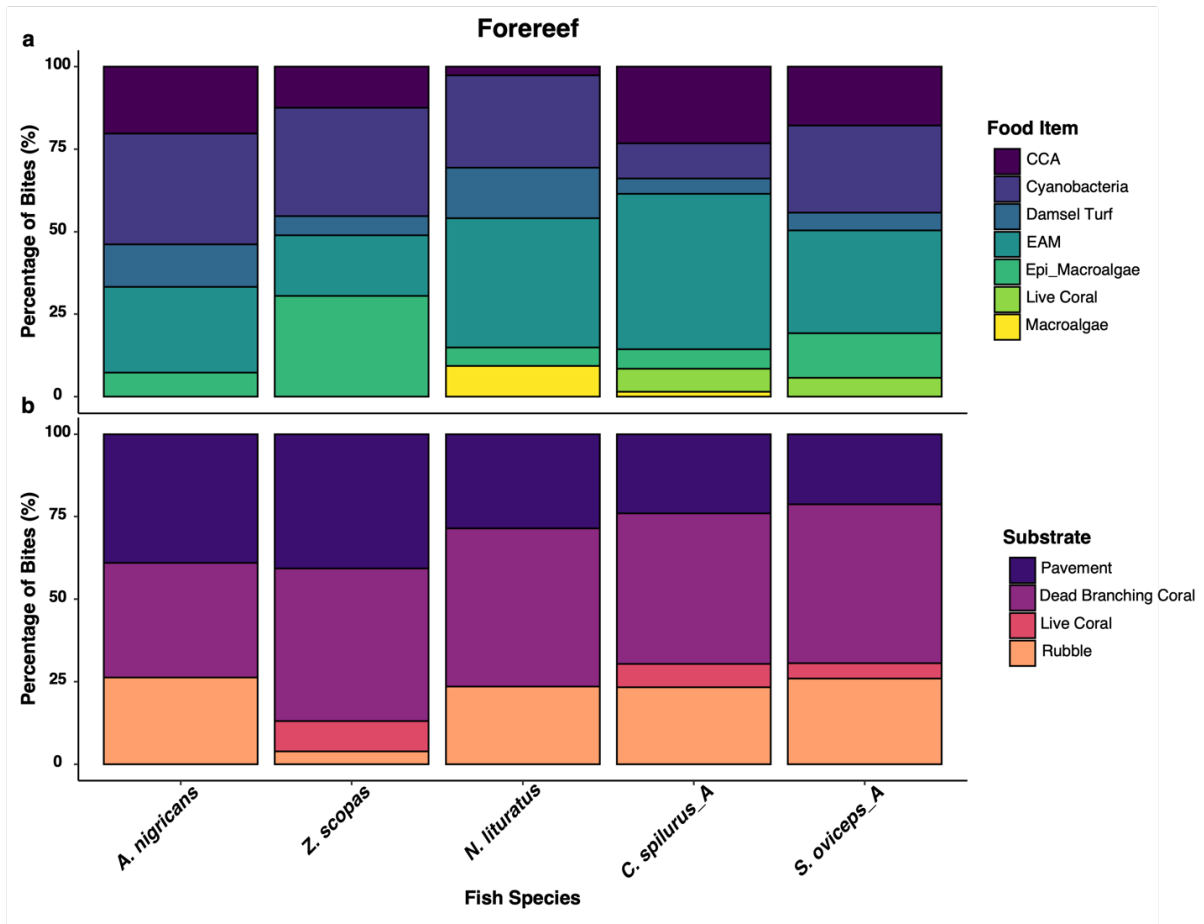


Figure 5. Mean percentage of bites taken by each observed fish species on the forereef on **a)** food items and **b)** substrates. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

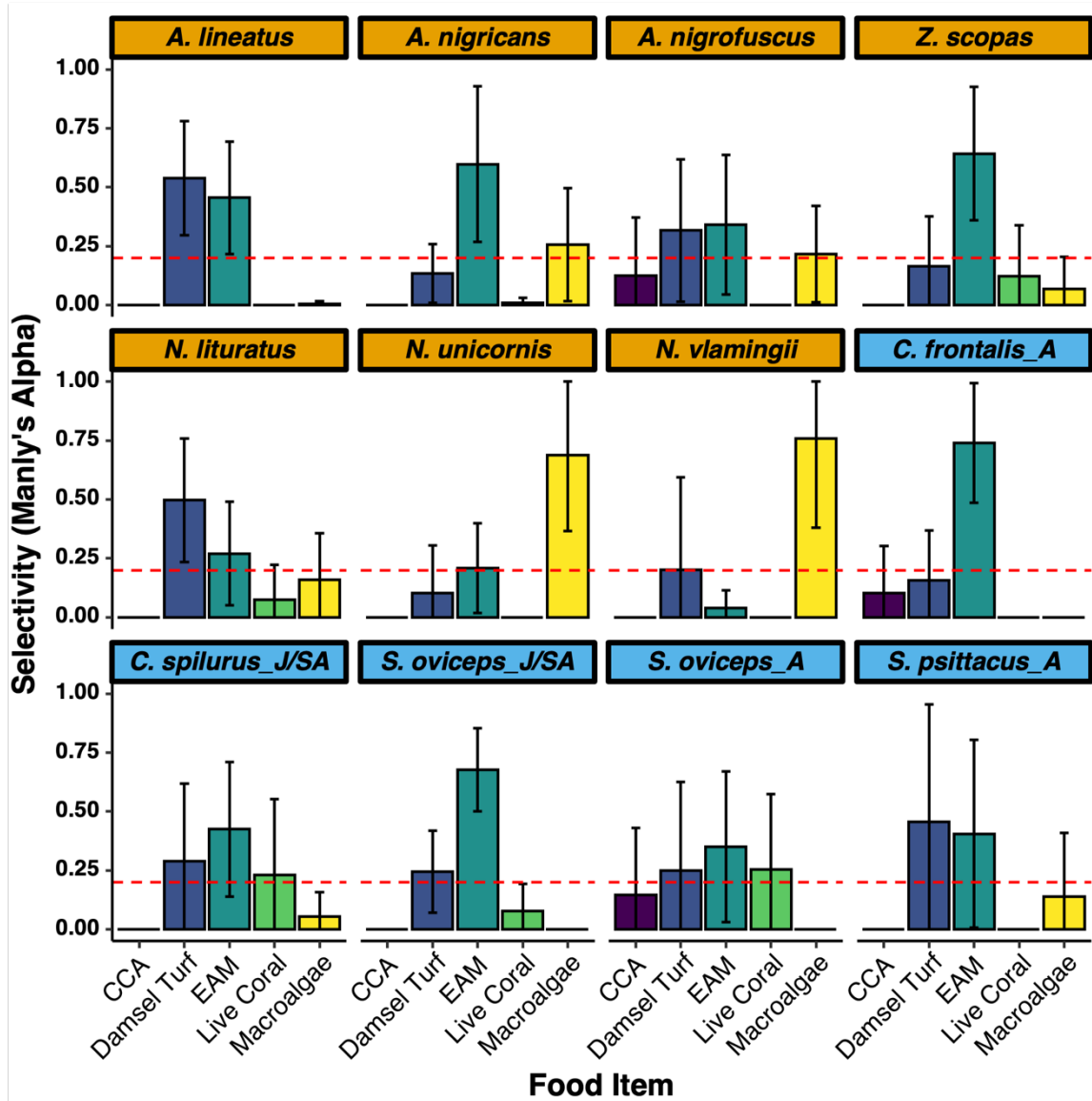


Figure 6. Manly selectivity index values ($\pm$ 95% Confidence Interval) on the reef flat of herbivorous fish species for the food items. Significant selectivity for or against the food item or substrate is indicated by the $\pm$ 95% CI being fully above or below the null selectivity (dashed red line). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

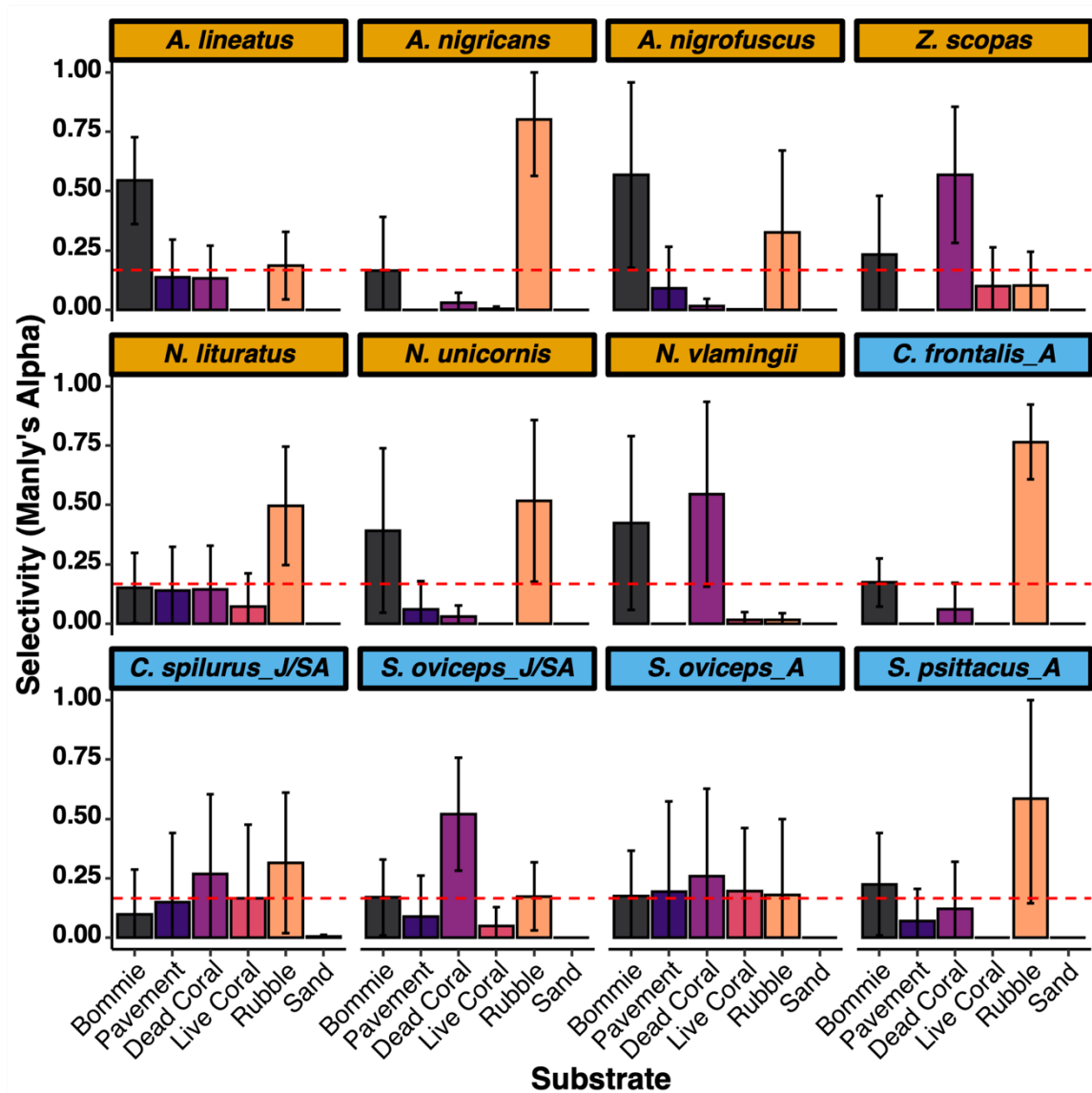


Figure 7. Manly selectivity index values ($\pm$ 95% Confidence Interval) on the reef flat of herbivorous fish species for the substrates. Significant selectivity for or against the food item or substrate is indicated by the $\pm$ 95% CI being fully above or below the null selectivity (dashed red line). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

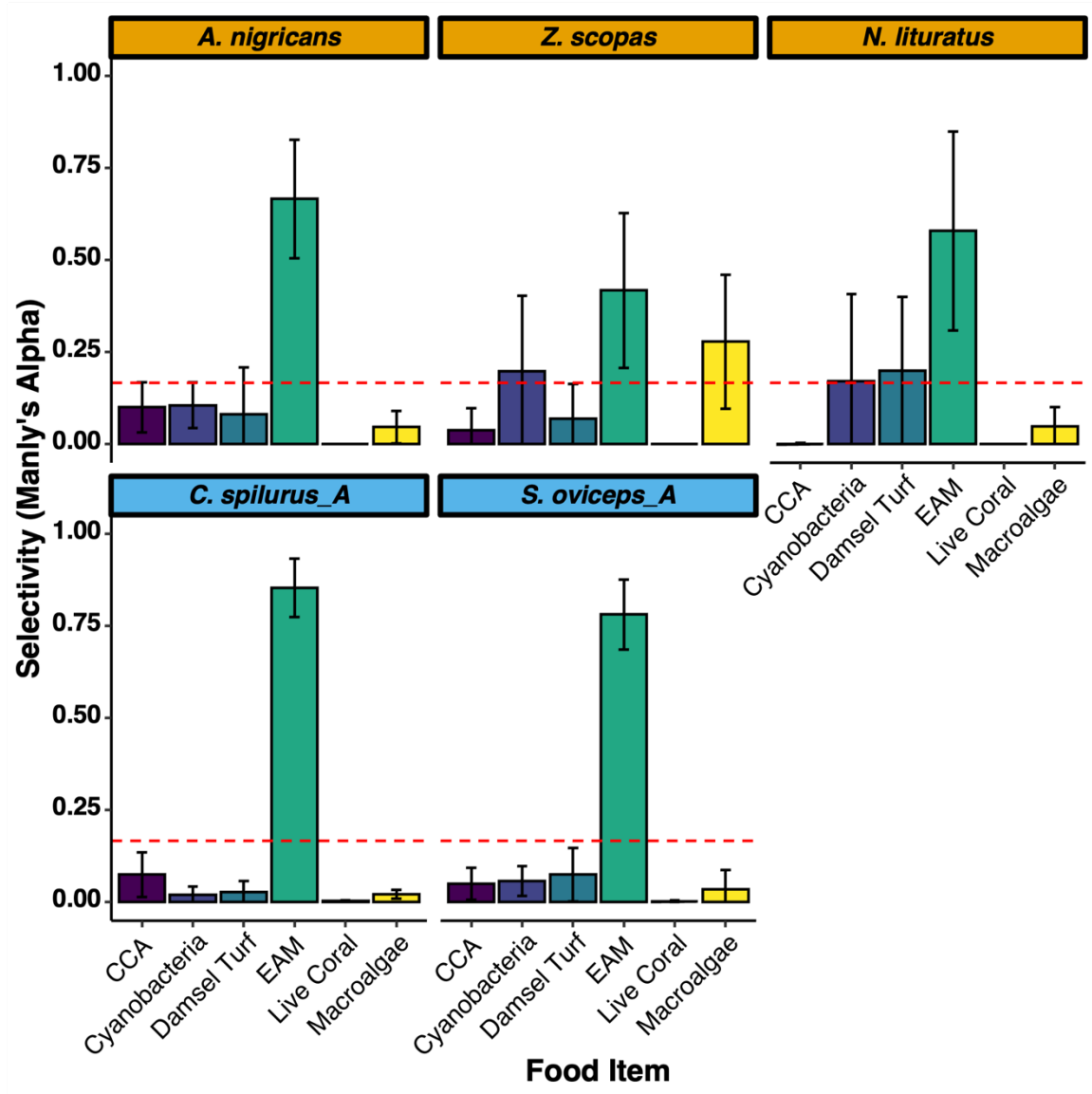


Figure 8. Manly selectivity index values ($\pm$ 95% Confidence Interval) on the reef forereef of herbivorous fish species for the food items. Significant selectivity for or against the food item or substrate is indicated by the $\pm$ 95% CI being fully above or below the null selectivity (dashed red line). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

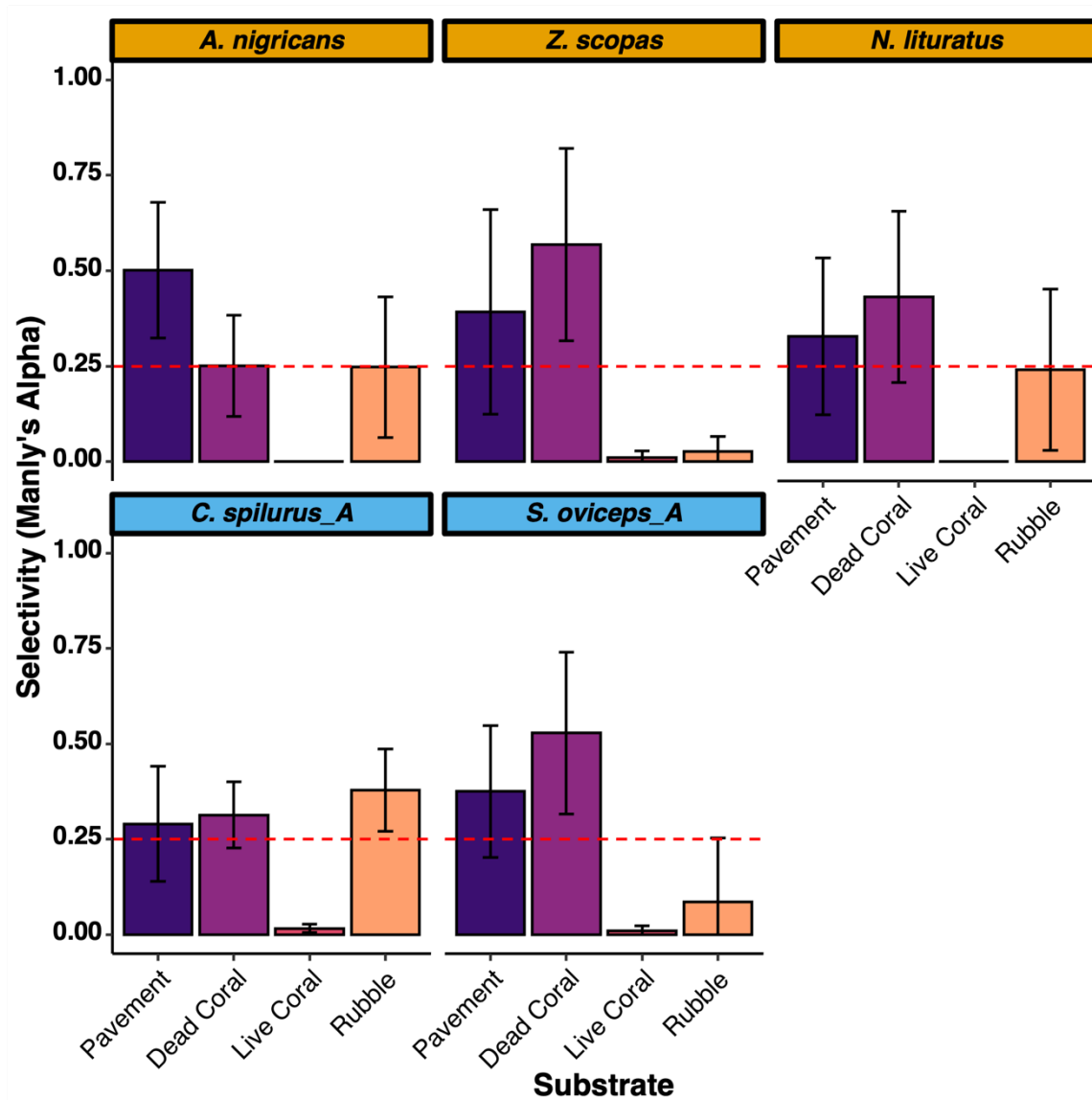


Figure 9. Manly selectivity index values ($\pm$ 95% Confidence Interval) on the forereef of herbivorous fish species for the food items. Significant selectivity for or against the food item or substrate is indicated by the $\pm$ 95% CI being fully above or below the null selectivity (dashed red line). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

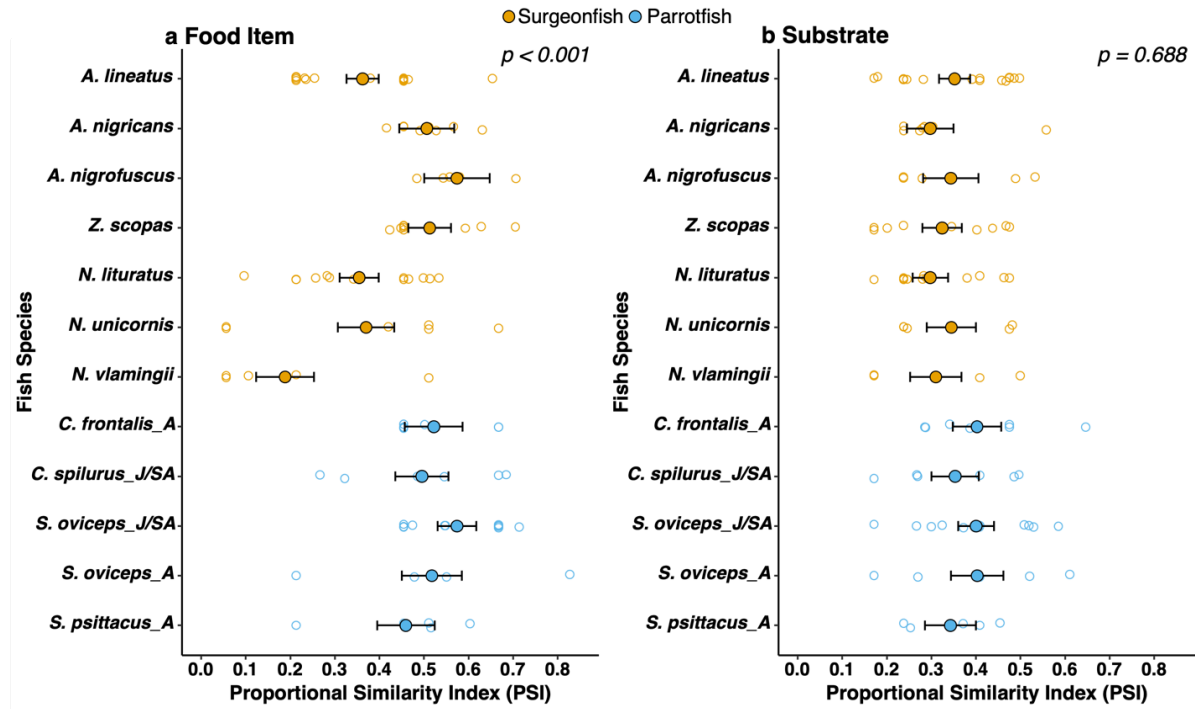


Figure 10. Estimated marginal means ($\pm$ SE) of PSI for feeding on **a)** food items and **b)** substrates. Open circles represent raw PSI values and filled points represented the model predicted means. Surgeonfish indicated by orange circles and parrotfish indicated by blue circles. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. Statistics are from linear mixed models.

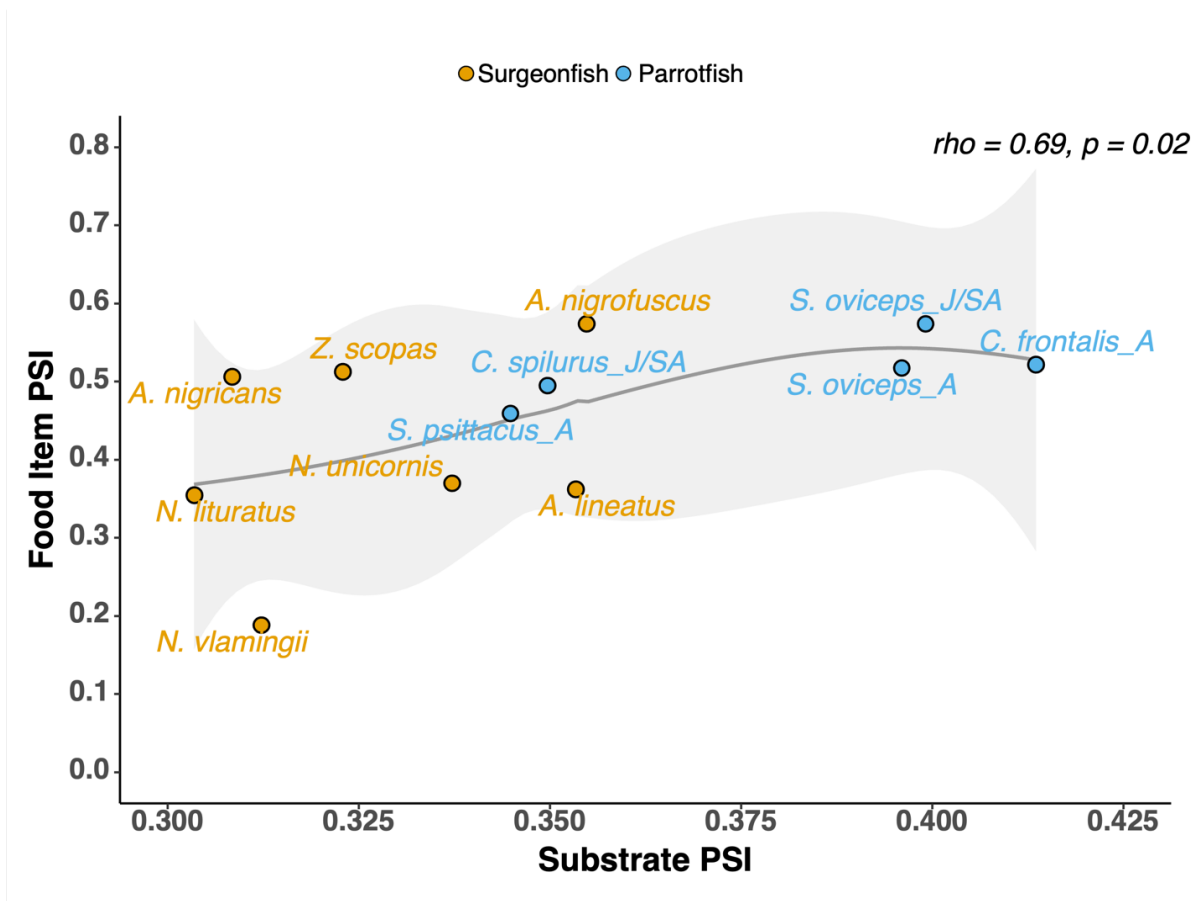


Figure 11. Spearman correlation between food item PSI and substrate PSI for the herbivorous fish species on the reef flat. Food item PSI and substrate PSI were positively correlated ($\rho = 0.69$, $p = 0.02$). The shaded region represents the 95% CI for the fitted LOESS curve. Surgeonfish indicated by orange circles and parrotfish indicated by blue circles. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

Table 1. The number of individuals followed per species in the two reef zones (Reef flat and Forereef). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

Fish Species	Reef Flat	Forereef
<i>Acanthurus lineatus</i>	16	0
<i>Acanthurus nigricans</i>	8	11
<i>Acanthurus nigrofuscus</i>	5	0
<i>Chlorurus frontalis_A</i>	7	0
<i>Chlorurus spilurus_J/SA</i>	6	0
<i>Chlorurus spilurus_A</i>	0	12
<i>Naso unicornis</i>	6	0
<i>Naso vlamingii</i>	5	0
<i>Scarus oviceps_A</i>	5	6
<i>Scarus oviceps_J/SA</i>	11	0
<i>Scarus psittacus_A</i>	5	0
<i>Zebrasoma scopas</i>	9	9

Table 2. The preferred food item and substrates for each observed species in the reef flat and forereef.

Scientific Name	Samoan Common Names	Preferred Food Item	Preferred Substrate	Reef Zone
<i>Acanthurus lineatus</i>	alogo	Damsel turf, EAM	Bommie	Reef flat
<i>Acanthurus nigricans</i>	gaitolama, i'usina, laulama	EAM	Rubble	Reef flat
<i>Acanthurus nigrofuscus</i>	ponepone	NA	Bommie	Reef flat
<i>Zebrasoma scopas</i>	pe'ape'a, pitopito	EAM	Dead Coral	Reef flat
<i>Naso lituratus</i>	ili'ilia, umelei	Damsel turf	Rubble	Reef flat
<i>Naso unicornis</i>	ume-isu	Macroalgae	Rubble	Reef flat
<i>Naso vlamingii</i>	ume-masimasi	Macroalgae	Dead Coral	Reef flat
<i>Chlorurus frontalis_A</i>	NA	EAM	Rubble	Reef flat
<i>Chlorurus spilurus_J/SA</i>	fuga-gutumu, fugausi-tuavela, laea-tuavela	EAM	NA	Reef flat

<i>Scarus</i> <i>oviceps_A</i>	fuga-alosina, laea-tuavela	NA	NA	Reef flat
<i>Scarus</i> <i>oviceps_J/SA</i>	fuga-alosina, laea-tuavela	EAM	NA	Reef flat
<i>Scarus</i> <i>psittacus_A</i>	fuga-matapua'a, fugausi- matapua'a, laea-matapua'a	NA	NA	Reef flat
<i>Acanthurus</i> <i>nigricans</i>	gaitolama, i'usina, laulama	EAM	Pavement	Forereef
<i>Zebrasoma</i> <i>scopas</i>	pe'ape'a, pitopito	EAM	Dead Coral	Forereef
<i>Naso lituratus</i>	ili'ilia, umelei	EAM	NA	Forereef
<i>Chlorurus</i> <i>spilurus_A</i>	fuga-gutumu, fugausi-tuavela, laea-tuavela	EAM	NA	Forereef
<i>Scarus</i> <i>oviceps_A</i>	fuga-alosina, laea-tuavela	EAM	Dead Coral	Forereef

Supplementary Figures and Tables

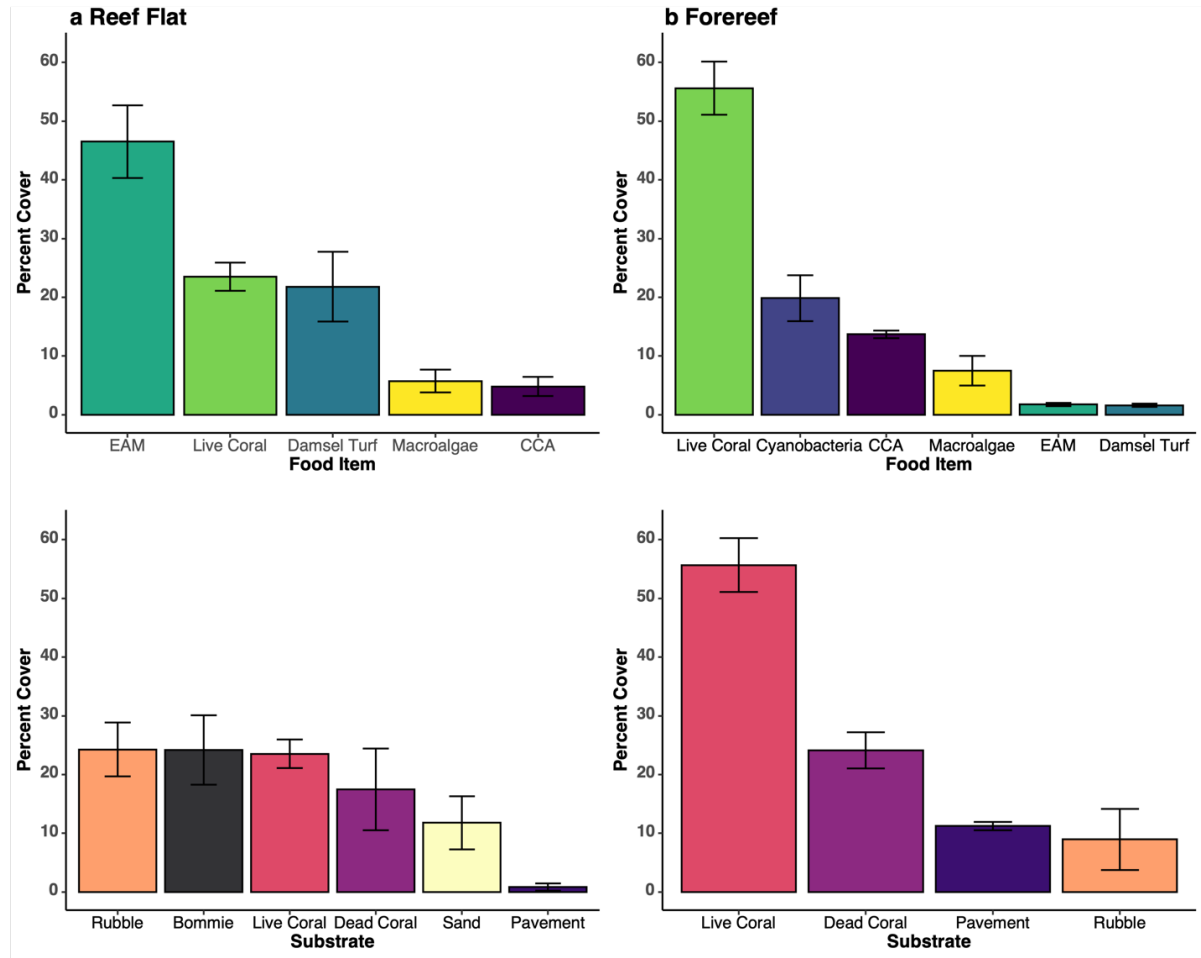


Figure S1. Percent cover (mean $\pm$ SE) of the different food items and substrates on the a) reef flat and b) forereef. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

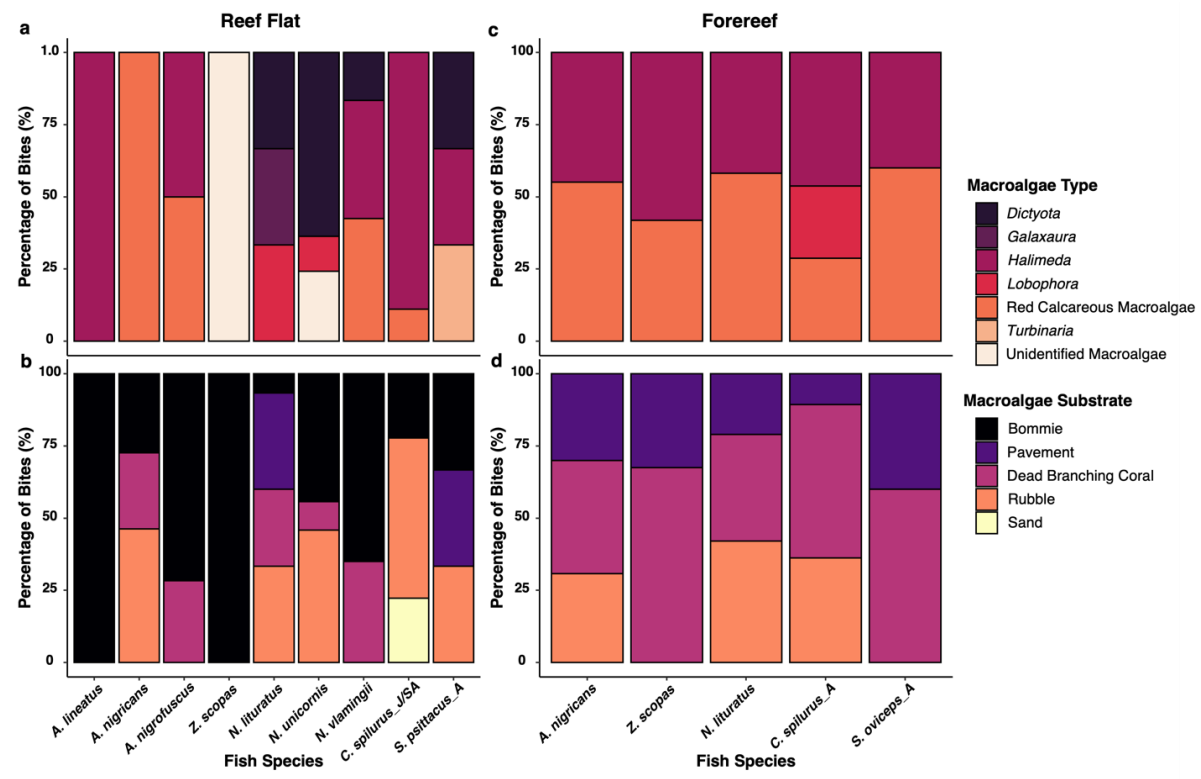


Figure S2. Mean percentage of bites on macroalgae for the different macroalgae taxa and the substrates that harbored the macroalgae on the a) reef flat and b) forereef. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

Table S1. ANOVA Type II table output based on the linear mixed model on log-transformed bite rate for the reef flat.

	<i>F</i>	<i>Df</i>	<i>Df.res</i>	<i>Pr(>F)</i>
Fish Species	7.48	11	65.93	<0.001
Size	0.34	1	82.97	0.561

Table S2. ANOVA Type II table output based on the linear model on log-transformed bite rate for the forereef.

	<i>Sum.Sq</i>	<i>Df</i>	<i>F</i>	<i>Pr(>F)</i>
Fish Species	5.98	4	5.70	<0.001
Size	1.85	1	7.06	0.011
Residuals	10.49	40	NA	NA

Table S3. Pairwise contrasts between species of bite rate on the reef flat based on linear mixed model.

<i>Contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>DF</i>	<i>t.ratio</i>	<i>p.value</i>
<i>Acanthurus lineatus</i> - <i>Acanthurus nigricans</i>	0.58	0.39	66.44	1.51	0.932
<i>Acanthurus lineatus</i> - <i>Acanthurus nigrofuscus</i>	0.20	0.45	73.67	0.45	1.000
<i>Acanthurus lineatus</i> – <i>Chlorurus frontalis_A</i>	0.68	0.45	82.51	1.52	0.930
<i>Acanthurus lineatus</i> - <i>Chlorurus spilurus_J/SA</i>	0.31	0.40	82.87	0.77	1.000
<i>Acanthurus lineatus</i> - <i>Naso lituratus</i>	2.12	0.32	81.84	6.62	<0.001
<i>Acanthurus lineatus</i> - <i>Naso unicornis</i>	1.99	0.41	80.87	4.82	<0.001
<i>Acanthurus lineatus</i> - <i>Naso vlamingii</i>	2.34	0.45	82.47	5.26	<0.001

<i>Acanthurus lineatus</i> – <i>Scarus oviceps</i> _A	0.85	0.45	78.72	1.89	0.760
<i>Acanthurus lineatus</i> - <i>Scarus oviceps</i> _J/SA	1.16	0.33	82.18	3.54	0.030
<i>Acanthurus lineatus</i> – <i>Scarus psittacus</i> _A	-0.18	0.47	82.21	-0.38	1.000
<i>Acanthurus lineatus</i> - <i>Zebrasoma scopas</i>	1.47	0.35	82.14	4.19	0.004
<i>Acanthurus nigricans</i> - <i>Acanthurus nigrofuscus</i>	-0.38	0.45	82.01	-0.85	0.999
<i>Acanthurus nigricans</i> – <i>Chlorurus frontalis</i> _A	0.10	0.49	82.44	0.20	1.000
<i>Acanthurus nigricans</i> - <i>Chlorurus spilurus</i> _J/SA	-0.28	0.50	59.33	-0.56	1.000
<i>Acanthurus nigricans</i> - <i>Naso lituratus</i>	1.54	0.37	83.00	4.19	0.004
<i>Acanthurus nigricans</i> - <i>Naso unicornis</i>	1.41	0.53	38.04	2.64	0.296
<i>Acanthurus nigricans</i> - <i>Naso vlamingii</i>	1.76	0.49	82.76	3.59	0.026
<i>Acanthurus nigricans</i> – <i>Scarus oviceps</i> _A	0.26	0.58	38.23	0.45	1.000
<i>Acanthurus nigricans</i> - <i>Scarus oviceps</i> _J/SA	0.57	0.42	64.16	1.35	0.969
<i>Acanthurus nigricans</i> – <i>Scarus psittacus</i> _A	-0.76	0.57	77.88	-1.34	0.971
<i>Acanthurus nigricans</i> - <i>Zebrasoma scopas</i>	0.89	0.44	68.01	2.01	0.683

<i>Acanthurus nigrofuscus</i> – <i>Chlorurus frontalis</i> _A	0.48	0.56	82.45	0.85	0.999
<i>Acanthurus nigrofuscus</i> - <i>Chlorurus spilurus</i> _J/SA	0.11	0.54	64.48	0.19	1.000
<i>Acanthurus nigrofuscus</i> - <i>Naso lituratus</i>	1.92	0.42	83.00	4.52	0.001
<i>Acanthurus nigrofuscus</i> - <i>Naso unicornis</i>	1.79	0.58	45.14	3.10	0.114
<i>Acanthurus nigrofuscus</i> - <i>Naso vlamingii</i>	2.14	0.53	82.79	4.06	0.006
<i>Acanthurus nigrofuscus</i> – <i>Scarus oviceps</i> _A	0.64	0.63	47.00	1.02	0.996
<i>Acanthurus nigrofuscus</i> - <i>Scarus oviceps</i> _J/SA	0.95	0.47	69.96	2.01	0.686
<i>Acanthurus nigrofuscus</i> – <i>Scarus psittacus</i> _A	-0.38	0.63	79.65	-0.60	1.000
<i>Acanthurus nigrofuscus</i> - <i>Zebrasoma scopas</i>	1.27	0.49	72.10	2.60	0.299
<i>Chlorurus frontalis</i> _A - <i>Chlorurus spilurus</i> _J/SA	-0.38	0.59	80.89	-0.64	1.000
<i>Chlorurus frontalis</i> _A - <i>Naso lituratus</i>	1.44	0.49	82.11	2.95	0.143
<i>Chlorurus frontalis</i> _A - <i>Naso unicornis</i>	1.31	0.61	72.22	2.14	0.594
<i>Chlorurus frontalis</i> _A - <i>Naso vlamingii</i>	1.66	0.63	82.48	2.65	0.270
<i>Chlorurus frontalis</i> _A – <i>Scarus oviceps</i> _A	0.16	0.56	56.54	0.29	1.000

<i>Chlorurus frontalis</i> _A - <i>Scarus oviceps</i> _J/SA	0.47	0.53	82.55	0.89	0.999
<i>Chlorurus frontalis</i> _A – <i>Scarus psittacus</i> _A	-0.86	0.49	81.06	-1.76	0.832
<i>Chlorurus frontalis</i> _A - <i>Zebrasoma scopas</i>	0.79	0.56	82.76	1.42	0.956
<i>Chlorurus spilurus</i> _J/SA - <i>Naso lituratus</i>	1.82	0.42	76.10	4.28	0.003
<i>Chlorurus spilurus</i> _J/SA - <i>Naso unicornis</i>	1.68	0.46	82.68	3.66	0.021
<i>Chlorurus spilurus</i> _J/SA - <i>Naso vlamingii</i>	2.04	0.50	82.93	4.09	0.005
<i>Chlorurus spilurus</i> _J/SA – <i>Scarus oviceps</i> _A	0.54	0.53	82.88	1.02	0.997
<i>Chlorurus spilurus</i> _J/SA - <i>Scarus oviceps</i> _J/SA	0.85	0.40	82.48	2.10	0.621
<i>Chlorurus spilurus</i> _J/SA – <i>Scarus psittacus</i> _A	-0.49	0.59	82.13	-0.82	1.000
<i>Chlorurus spilurus</i> _J/SA - <i>Zebrasoma scopas</i>	1.17	0.42	82.46	2.78	0.206
<i>Naso lituratus</i> - <i>Naso unicornis</i>	-0.13	0.45	55.92	-0.29	1.000
<i>Naso lituratus</i> - <i>Naso vlamingii</i>	0.22	0.43	82.42	0.51	1.000
<i>Naso lituratus</i> – <i>Scarus oviceps</i> _A	-1.28	0.52	59.22	-2.45	0.392
<i>Naso lituratus</i> - <i>Scarus oviceps</i> _J/SA	-0.97	0.35	79.92	-2.80	0.199
<i>Naso lituratus</i> – <i>Scarus psittacus</i> _A	-2.30	0.54	82.92	-4.24	0.003

<i>Naso lituratus</i> - <i>Zebrasoma scopas</i>	-0.65	0.36	81.00	-1.78	0.824
<i>Naso unicornis</i> - <i>Naso vlamingii</i>	0.35	0.52	79.03	0.68	1.000
<i>Naso unicornis</i> – <i>Scarus oviceps</i> _A	-1.14	0.52	82.11	-2.21	0.547
<i>Naso unicornis</i> - <i>Scarus oviceps</i> _J/SA	-0.84	0.42	82.58	-2.01	0.688
<i>Naso unicornis</i> – <i>Scarus psittacus</i> _A	-2.17	0.60	82.84	-3.64	0.023
<i>Naso unicornis</i> - <i>Zebrasoma scopas</i>	-0.52	0.43	82.71	-1.20	0.988
<i>Naso vlamingii</i> – <i>Scarus oviceps</i> _A	-1.50	0.61	79.69	-2.45	0.384
<i>Naso vlamingii</i> - <i>Scarus oviceps</i> _J/SA	-1.19	0.44	82.82	-2.71	0.242
<i>Naso vlamingii</i> – <i>Scarus psittacus</i> _A	-2.52	0.66	82.57	-3.82	0.013
<i>Naso vlamingii</i> - <i>Zebrasoma scopas</i>	-0.87	0.45	82.79	-1.93	0.734
<i>Scarus oviceps</i> _A - <i>Scarus oviceps</i> _J/SA	0.31	0.49	82.32	0.63	1.000
<i>Scarus oviceps</i> _A – <i>Scarus psittacus</i> _A	-1.03	0.54	82.94	-1.92	0.746
<i>Scarus oviceps</i> _A - <i>Zebrasoma scopas</i>	0.63	0.51	82.55	1.22	0.986
<i>Scarus oviceps</i> _J/SA – <i>Scarus psittacus</i> _A	-1.34	0.55	82.02	-2.43	0.396
<i>Scarus oviceps</i> _J/SA - <i>Zebrasoma scopas</i>	0.32	0.36	82.00	0.90	0.999
<i>Scarus psittacus</i> _A - <i>Zebrasoma scopas</i>	1.65	0.57	82.02	2.88	0.168

Table S4. Pairwise contrasts between species of bite rate on the forereef based on linear model.

<i>Contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>DF</i>	<i>t.ratio</i>	<i>p.value</i>
<i>Acanthurus nigricans</i> – <i>Chlorurus spilurus</i> _A	0.92	0.30	40	3.13	0.026
<i>Acanthurus nigricans</i> - <i>Naso lituratus</i>	1.10	0.25	40	4.42	<0.001
<i>Acanthurus nigricans</i> - <i>S.oviceps</i> _A	1.13	0.33	40	3.47	0.010
<i>Acanthurus nigricans</i> - <i>Zebrasoma scopas</i>	0.25	0.23	40	1.07	0.820
<i>Chlorurus spilurus</i> _A - <i>Naso lituratus</i>	0.18	0.27	40	0.68	0.960
<i>Chlorurus spilurus</i> _A – <i>Scarus oviceps</i> _A	0.21	0.26	40	0.81	0.926
<i>Chlorurus spilurus</i> _A - <i>Zebrasoma scopas</i>	-0.68	0.32	40	-2.14	0.223
<i>Naso lituratus</i> – <i>Scarus oviceps</i> _A	0.03	0.30	40	0.09	1.000
<i>Naso lituratus</i> - <i>Zebrasoma scopas</i>	-0.86	0.27	40	-3.23	0.020
<i>Scarus oviceps</i> _A - <i>Zebrasoma scopas</i>	-0.88	0.34	40	-2.57	0.096

Table S5. ANOVA Type II table output based on the linear mixed model on log-transformed maximum linear distanced moved for the reef flat.

	<i>F</i>	<i>Df</i>	<i>Df.res</i>	<i>Pr(>F)</i>
Fish Species	3.68	11	56.61	<0.001
Size	4.84	1	73.98	0.031

Table S6. ANOVA Type II table output based on the linear model on log-transformed maximum linear distanced moved for the forereef.

	<i>F</i>	<i>Df</i>	<i>Df.res</i>	<i>Pr(>F)</i>
Fish Species	1.49	4	3.43	0.02
Size	0.20	1	1.85	0.18
Residuals	4.34	40	NA	NA

Table S7. Pairwise contrasts between species on the maximum linear distanced moved on the reef flat.

<i>Contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>DF</i>	<i>t.ratio</i>	<i>p.value</i>
<i>Acanthurus lineatus</i> - <i>Acanthurus nigricans</i>	-0.04	0.34	60.89	-0.12	1.000
<i>Acanthurus lineatus</i> - <i>Acanthurus nigrofuscus</i>	-0.28	0.39	66.37	-0.73	1.000
<i>Acanthurus lineatus</i> – <i>Chlorurus frontalis</i> _A	-1.10	0.37	73.42	-2.94	0.148
<i>Acanthurus lineatus</i> - <i>Chlorurus spilurus</i> _J/SA	-0.35	0.31	73.68	-1.11	0.993
<i>Acanthurus lineatus</i> - <i>Naso lituratus</i>	-1.08	0.26	72.83	-4.15	0.005
<i>Acanthurus lineatus</i> - <i>Naso unicornis</i>	-1.25	0.36	64.65	-3.43	0.046
<i>Acanthurus lineatus</i> - <i>Naso vlamingii</i>	-0.66	0.35	73.65	-1.86	0.782
<i>Acanthurus lineatus</i> – <i>Scarus oviceps</i> _A	-0.64	0.35	71.29	-1.83	0.797
<i>Acanthurus lineatus</i> - <i>Scarus oviceps</i> _J/SA	-0.78	0.27	73.31	-2.93	0.152
<i>Acanthurus lineatus</i> – <i>Scarus psittacus</i> _A	-0.76	0.38	73.11	-2.03	0.670
<i>Acanthurus lineatus</i> - <i>Zebrasoma scopas</i>	-0.19	0.29	73.35	-0.64	1.000
<i>Acanthurus nigricans</i> - <i>Acanthurus</i> <i>nigrofuscus</i>	-0.24	0.40	73.01	-0.60	1.000
<i>Acanthurus nigricans</i> – <i>Chlorurus frontalis</i> _A	-1.06	0.42	73.39	-2.53	0.341

<i>Acanthurus nigricans</i> - <i>Chlorurus</i> <i>spilurus</i> _J/SA	-0.31	0.42	56.40	-0.74	1.000
<i>Acanthurus nigricans</i> - <i>Naso lituratus</i>	-1.04	0.32	74.00	-3.26	0.068
<i>Acanthurus nigricans</i> - <i>Naso unicornis</i>	-1.21	0.49	26.05	-2.45	0.409
<i>Acanthurus nigricans</i> - <i>Naso vlamingii</i>	-0.62	0.41	73.93	-1.51	0.933
<i>Acanthurus nigricans</i> – <i>Scarus oviceps</i> _A	-0.61	0.48	36.49	-1.26	0.979
<i>Acanthurus nigricans</i> - <i>Scarus oviceps</i> _J/SA	-0.74	0.37	56.79	-1.99	0.698
<i>Acanthurus nigricans</i> – <i>Scarus psittacus</i> _A	-0.72	0.47	69.97	-1.55	0.921
<i>Acanthurus nigricans</i> - <i>Zebrasoma scopas</i>	-0.15	0.39	58.77	-0.37	1.000
<i>Acanthurus nigrofuscus</i> – <i>Chlorurus</i> <i>frontalis</i> _A	-0.81	0.47	73.40	-1.73	0.847
<i>Acanthurus nigrofuscus</i> - <i>Chlorurus</i> <i>spilurus</i> _J/SA	-0.07	0.45	60.60	-0.14	1.000
<i>Acanthurus nigrofuscus</i> - <i>Naso lituratus</i>	-0.80	0.37	73.99	-2.19	0.562
<i>Acanthurus nigrofuscus</i> - <i>Naso unicornis</i>	-0.96	0.52	31.78	-1.84	0.786
<i>Acanthurus nigrofuscus</i> - <i>Naso vlamingii</i>	-0.37	0.44	73.95	-0.85	0.999
<i>Acanthurus nigrofuscus</i> – <i>Scarus oviceps</i> _A	-0.36	0.52	44.10	-0.70	1.000

<i>Acanthurus nigrofuscus</i> - <i>Scarus oviceps</i> _J/SA	-0.50	0.41	61.85	-1.21	0.986
<i>Acanthurus nigrofuscus</i> – <i>Scarus psittacus</i> _A	-0.48	0.52	71.39	-0.93	0.998
<i>Acanthurus nigrofuscus</i> - <i>Zebrasoma scopas</i>	0.10	0.43	62.75	0.22	1.000
<i>Chlorurus frontalis</i> _A - <i>Chlorurus spilurus</i> _J/SA	0.75	0.48	72.45	1.57	0.915
<i>Chlorurus frontalis</i> _A - <i>Naso lituratus</i>	0.01	0.40	73.16	0.03	1.000
<i>Chlorurus frontalis</i> _A - <i>Naso unicornis</i>	-0.15	0.53	53.78	-0.28	1.000
<i>Chlorurus frontalis</i> _A - <i>Naso vlamingii</i>	0.44	0.51	73.43	0.87	0.999
<i>Chlorurus frontalis</i> _A – <i>Scarus oviceps</i> _A	0.45	0.46	51.43	0.99	0.997
<i>Chlorurus frontalis</i> _A - <i>Scarus oviceps</i> _J/SA	0.31	0.44	73.18	0.71	1.000
<i>Chlorurus frontalis</i> _A – <i>Scarus psittacus</i> _A	0.33	0.40	72.50	0.84	0.999
<i>Chlorurus frontalis</i> _A - <i>Zebrasoma scopas</i>	0.91	0.47	73.33	1.95	0.723
<i>Chlorurus spilurus</i> _J/SA - <i>Naso lituratus</i>	-0.74	0.34	69.14	-2.19	0.565
<i>Chlorurus spilurus</i> _J/SA - <i>Naso unicornis</i>	-0.90	0.39	73.66	-2.30	0.485
<i>Chlorurus spilurus</i> _J/SA - <i>Naso vlamingii</i>	-0.31	0.39	73.93	-0.79	1.000
<i>Chlorurus spilurus</i> _J/SA – <i>Scarus oviceps</i> _A	-0.30	0.42	73.89	-0.72	1.000

<i>Chlorurus spilurus_J/SA - Scarus oviceps_J/SA</i>	-0.43	0.32	73.16	-1.36	0.968
<i>Chlorurus spilurus_J/SA – Scarus psittacus_A</i>	-0.42	0.47	73.12	-0.89	0.999
<i>Chlorurus spilurus_J/SA - Zebrasoma scopas</i>	0.16	0.34	73.10	0.48	1.000
<i>Naso lituratus - Naso unicornis</i>	-0.16	0.41	35.88	-0.40	1.000
<i>Naso lituratus - Naso vlamingii</i>	0.43	0.34	73.28	1.25	0.982
<i>Naso lituratus – Scarus oviceps_A</i>	0.44	0.41	53.75	1.06	0.995
<i>Naso lituratus - Scarus oviceps_J/SA</i>	0.30	0.29	69.84	1.05	0.996
<i>Naso lituratus – Scarus psittacus_A</i>	0.32	0.43	73.98	0.74	1.000
<i>Naso lituratus - Zebrasoma scopas</i>	0.90	0.31	70.56	2.92	0.155
<i>Naso unicornis - Naso vlamingii</i>	0.59	0.45	60.06	1.31	0.974
<i>Naso unicornis – Scarus oviceps_A</i>	0.60	0.42	73.20	1.43	0.954
<i>Naso unicornis - Scarus oviceps_J/SA</i>	0.46	0.36	70.92	1.28	0.980
<i>Naso unicornis – Scarus psittacus_A</i>	0.48	0.49	73.71	0.98	0.998
<i>Naso unicornis - Zebrasoma scopas</i>	1.06	0.38	72.08	2.82	0.195
<i>Naso vlamingii – Scarus oviceps_A</i>	0.01	0.48	70.65	0.02	1.000

<i>Naso vlamingii</i> - <i>Scarus oviceps</i> _J/SA	-0.13	0.35	74.00	-0.36	1.000
<i>Naso vlamingii</i> – <i>Scarus psittacus</i> _A	-0.11	0.52	73.59	-0.21	1.000
<i>Naso vlamingii</i> - <i>Zebrasoma scopas</i>	0.47	0.36	74.00	1.29	0.978
<i>Scarus oviceps</i> _A - <i>Scarus oviceps</i> _J/SA	-0.14	0.39	73.91	-0.35	1.000
<i>Scarus oviceps</i> _A – <i>Scarus psittacus</i> _A	-0.12	0.42	73.95	-0.28	1.000
<i>Scarus oviceps</i> _A - <i>Zebrasoma scopas</i>	0.46	0.41	74.00	1.13	0.992
<i>Scarus oviceps</i> _J/SA – <i>Scarus psittacus</i> _A	0.02	0.44	73.01	0.04	1.000
<i>Scarus oviceps</i> _J/SA - <i>Zebrasoma scopas</i>	0.60	0.29	73.01	2.03	0.674
<i>Scarus psittacus</i> _A - <i>Zebrasoma scopas</i>	0.58	0.46	73.02	1.25	0.982

Table S8. Pairwise contrasts between species on the maximum linear distanced moved on the forereef.

<i>Contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>DF</i>	<i>t.ratio</i>	<i>p.value</i>
<i>Acanthurus nigricans</i> – <i>Chlorurus spilurus</i> _A	-0.21	0.19	40	-1.10	0.803
<i>Acanthurus nigricans</i> - <i>Naso lituratus</i>	-0.55	0.16	40	-3.45	0.011
<i>Acanthurus nigricans</i> – <i>Scarus oviceps</i> _A	-0.24	0.21	40	-1.16	0.775
<i>Acanthurus nigricans</i> - <i>Zebrasoma scopas</i>	-0.05	0.15	40	-0.33	0.997
<i>Chlorurus spilurus</i> _A - <i>Naso lituratus</i>	-0.34	0.17	40	-2.01	0.280
<i>Chlorurus spilurus</i> _A – <i>Scarus oviceps</i> _A	-0.03	0.16	40	-0.20	1.000
<i>Chlorurus spilurus</i> _A - <i>Zebrasoma scopas</i>	0.16	0.20	40	0.79	0.931
<i>Naso lituratus</i> – <i>Scarus oviceps</i> _A	0.31	0.19	40	1.61	0.502
<i>Naso lituratus</i> - <i>Zebrasoma scopas</i>	0.51	0.17	40	2.97	0.038
<i>Scarus oviceps</i> _A - <i>Zebrasoma scopas</i>	0.19	0.22	40	0.88	0.904

Table S9. Pairwise contrasts between species on the PSI on food items on the reef flat.

<i>Contrast</i>	<i>Estimate</i>	<i>SE</i>	<i>DF</i>	<i>t.ratio</i>	<i>p.value</i>
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<i>Acanthurus lineatus</i> - <i>Acanthurus nigricans</i>	-0.14	0.07	69.41	-2.07	0.644
<i>Acanthurus lineatus</i> - <i>Acanthurus nigrofuscus</i>	-0.21	0.08	77.23	-2.65	0.270
<i>Acanthurus lineatus</i> – <i>Chlorurus frontalis</i> _A	-0.16	0.07	71.95	-2.21	0.545
<i>Acanthurus lineatus</i> - <i>Chlorurus spilurus</i> _J/SA	-0.13	0.07	83.97	-1.88	0.767
<i>Acanthurus lineatus</i> - <i>Naso lituratus</i>	0.01	0.06	83.69	0.14	1.000
<i>Acanthurus lineatus</i> - <i>Naso unicornis</i>	-0.01	0.07	78.26	-0.10	1.000
<i>Acanthurus lineatus</i> - <i>Naso vlamingii</i>	0.17	0.07	83.05	2.36	0.442
<i>Acanthurus lineatus</i> – <i>Scarus oviceps</i> _A	-0.16	0.08	81.67	-1.99	0.696
<i>Acanthurus lineatus</i> - <i>Scarus oviceps</i> _J/SA	-0.21	0.06	83.62	-3.73	0.017
<i>Acanthurus lineatus</i> – <i>Scarus psittacus</i> _A	-0.10	0.07	83.05	-1.32	0.974
<i>Acanthurus lineatus</i> - <i>Zebrasoma scopas</i>	-0.15	0.06	83.65	-2.49	0.360
<i>Acanthurus nigricans</i> - <i>Acanthurus</i> <i>nigrofuscus</i>	-0.07	0.08	83.00	-0.83	1.000
<i>Acanthurus nigricans</i> – <i>Chlorurus frontalis</i> _A	-0.02	0.07	83.00	-0.21	1.000
<i>Acanthurus nigricans</i> - <i>Chlorurus</i> <i>spilurus</i> _J/SA	0.01	0.09	54.35	0.12	1.000
<i>Acanthurus nigricans</i> - <i>Naso lituratus</i>	0.15	0.07	83.88	2.28	0.500

<i>Acanthurus nigricans</i> - <i>Naso unicornis</i>	0.14	0.10	33.90	1.40	0.956
<i>Acanthurus nigricans</i> - <i>Naso vlamingii</i>	0.32	0.09	81.79	3.67	0.021
<i>Acanthurus nigricans</i> – <i>Scarus oviceps</i> _A	-0.01	0.10	42.57	-0.11	1.000
<i>Acanthurus nigricans</i> - <i>Scarus oviceps</i> _J/SA	-0.07	0.08	58.65	-0.88	0.999
<i>Acanthurus nigricans</i> – <i>Scarus psittacus</i> _A	0.05	0.09	81.79	0.54	1.000
<i>Acanthurus nigricans</i> - <i>Zebrasoma scopas</i>	-0.01	0.08	60.79	-0.08	1.000
<i>Acanthurus nigrofuscus</i> – <i>Chlorurus</i> <i>frontalis</i> _A	0.05	0.08	83.00	0.62	1.000
<i>Acanthurus nigrofuscus</i> - <i>Chlorurus</i> <i>spilurus</i> _J/SA	0.08	0.10	63.67	0.80	1.000
<i>Acanthurus nigrofuscus</i> - <i>Naso lituratus</i>	0.22	0.08	84.00	2.84	0.183
<i>Acanthurus nigrofuscus</i> - <i>Naso unicornis</i>	0.20	0.11	44.39	1.94	0.728
<i>Acanthurus nigrofuscus</i> - <i>Naso vlamingii</i>	0.39	0.10	82.94	4.06	0.006
<i>Acanthurus nigrofuscus</i> – <i>Scarus oviceps</i> _A	0.06	0.11	52.18	0.53	1.000
<i>Acanthurus nigrofuscus</i> - <i>Scarus oviceps</i> _J/SA	0.00	0.09	69.35	0.00	1.000
<i>Acanthurus nigrofuscus</i> – <i>Scarus psittacus</i> _A	0.11	0.10	82.94	1.21	0.987
<i>Acanthurus nigrofuscus</i> - <i>Zebrasoma scopas</i>	0.06	0.09	70.24	0.69	1.000

<i>Chlorurus frontalis</i> _A - <i>Chlorurus spilurus</i> _J/SA	0.03	0.09	56.93	0.29	1.000
<i>Chlorurus frontalis</i> _A - <i>Naso lituratus</i>	0.17	0.07	83.95	2.42	0.407
<i>Chlorurus frontalis</i> _A - <i>Naso unicornis</i>	0.15	0.10	36.55	1.53	0.923
<i>Chlorurus frontalis</i> _A - <i>Naso vlamingii</i>	0.33	0.09	82.15	3.76	0.016
<i>Chlorurus frontalis</i> _A – <i>Scarus oviceps</i> _A	0.00	0.10	45.07	0.04	1.000
<i>Chlorurus frontalis</i> _A - <i>Scarus oviceps</i> _J/SA	-0.05	0.08	61.83	-0.66	1.000
<i>Chlorurus frontalis</i> _A – <i>Scarus psittacus</i> _A	0.06	0.09	82.15	0.71	1.000
<i>Chlorurus frontalis</i> _A - <i>Zebrasoma scopas</i>	0.01	0.08	63.57	0.11	1.000
<i>Chlorurus spilurus</i> _J/SA - <i>Naso lituratus</i>	0.14	0.08	76.00	1.82	0.803
<i>Chlorurus spilurus</i> _J/SA - <i>Naso unicornis</i>	0.13	0.08	83.66	1.49	0.938
<i>Chlorurus spilurus</i> _J/SA) - <i>Naso vlamingii</i>	0.31	0.09	84.00	3.45	0.039
<i>Chlorurus spilurus</i> _J/SA – <i>Scarus oviceps</i> _A	-0.02	0.09	83.43	-0.26	1.000
<i>Chlorurus spilurus</i> _J/SA - <i>Scarus oviceps</i> _J/SA	-0.08	0.07	83.49	-1.08	0.995
<i>Chlorurus spilurus</i> _J/SA – <i>Scarus psittacus</i> _A	0.04	0.09	84.00	0.40	1.000
<i>Chlorurus spilurus</i> _J/SA - <i>Zebrasoma scopas</i>	-0.02	0.08	83.40	-0.23	1.000

<i>Naso lituratus</i> - <i>Naso unicornis</i>	-0.02	0.08	55.32	-0.19	1.000
<i>Naso lituratus</i> - <i>Naso vlamingii</i>	0.17	0.08	83.77	2.17	0.573
<i>Naso lituratus</i> – <i>Scarus oviceps</i> _A	-0.16	0.09	64.95	-1.90	0.753
<i>Naso lituratus</i> - <i>Scarus oviceps</i> _J/SA	-0.22	0.06	80.16	-3.49	0.035
<i>Naso lituratus</i> – <i>Scarus psittacus</i> _A	-0.10	0.08	83.77	-1.37	0.966
<i>Naso lituratus</i> - <i>Zebrasoma scopas</i>	-0.16	0.07	80.69	-2.38	0.429
<i>Naso unicornis</i> - <i>Naso vlamingii</i>	0.18	0.09	81.49	1.97	0.711
<i>Naso unicornis</i> – <i>Scarus oviceps</i> _A	-0.15	0.09	83.03	-1.70	0.864
<i>Naso unicornis</i> - <i>Scarus oviceps</i> _J/SA	-0.20	0.08	83.60	-2.70	0.246
<i>Naso unicornis</i> – <i>Scarus psittacus</i> _A	-0.09	0.09	81.49	-0.97	0.998
<i>Naso unicornis</i> - <i>Zebrasoma scopas</i>	-0.14	0.08	83.83	-1.83	0.799
<i>Naso vlamingii</i> – <i>Scarus oviceps</i> _A	-0.33	0.10	82.94	-3.46	0.038
<i>Naso vlamingii</i> - <i>Scarus oviceps</i> _J/SA	-0.39	0.08	83.60	-4.94	<0.001
<i>Naso vlamingii</i> – <i>Scarus psittacus</i> _A	-0.27	0.09	83.00	-2.98	0.132
<i>Naso vlamingii</i> - <i>Zebrasoma scopas</i>	-0.32	0.08	83.63	-4.01	0.007
<i>Scarus oviceps</i> _A - <i>Scarus oviceps</i> _J/SA	-0.06	0.08	83.98	-0.71	1.000

<i>Scarus oviceps</i> _A – <i>Scarus psittacus</i> _A	0.06	0.10	82.94	0.61	1.000
<i>Scarus oviceps</i> _A - <i>Zebrasoma scopas</i>	0.00	0.08	84.00	0.06	1.000
<i>Scarus oviceps</i> _J/SA – <i>Scarus psittacus</i> _A	0.11	0.08	83.60	1.47	0.945
<i>Scarus oviceps</i> _J/SA - <i>Zebrasoma scopas</i>	0.06	0.06	83.01	0.95	0.998
<i>Scarus psittacus</i> _A - <i>Zebrasoma scopas</i>	-0.05	0.08	83.63	-0.66	1.000

II. Title: Coral reef phase shifts alter feeding behavior of herbivorous fishes

Abstract

Many coral reefs across the globe are experiencing a loss of coral and increase in algae in response to global and local stressors. The increase in algae on reefs may alter the feeding behavior of herbivorous fishes, which play key roles in the dynamics of these ecosystems. Yet, few studies have explored how the foraging ecology of individual species of herbivorous fishes may differ across reefs with different benthic community states (abundant coral vs. abundant algae). Here, we conducted behavioral observations, recording bite rates, foraging range, food item selectivity, and substrate selectivity of five herbivorous fish species *Acanthurus nigrofuscus*, *Zebrasoma scopas*, *Chlorurus spilurus*, *Scarus oviceps*, *Scarus psittacus*, on reefs with either abundant coral or abundant macroalgae in the lagoons of Moorea, French Polynesia. Several species of herbivorous fish exhibited differences in their foraging behaviors between reefs in the coral vs. algal state, although some foraging metrics were more dynamic than others. While most species did not differ in their bite rates or foraging range between reef states, we found a shift in the preferences for many food items. While fishes in coral state tended to show patterns of neutral selection (feeding on resources in proportion to their availability), fishes in the algal state showed stronger patterns of selectivity with clear preferences for (e.g., epilithic algae, macroalgae) and avoidance of (e.g., live coral, damselfish turf) food items. In contrast to patterns in selectivity for food items, fishes showed similar preference patterns for the substrates on which they fed (e.g., bommie, rubble, dead coral) between the two different reef states. These results suggest that herbivorous fishes may be more flexible in their food choices as the benthic communities of

reefs change while not changing where on the reefs that they forage. Our work argues for increased emphasis on understanding how state shifts in the benthic communities of coral reefs will alter the foraging ecology of ecologically important species.

Introduction

Herbivorous fishes are a major structuring force on benthic communities on coral reefs. They exert strong effects on algal dynamics on coral reefs, often removing up to 90% of daily algal production on reefs (Carpenter 1986). By providing this intense top-down pressure, herbivorous fishes can control the distribution, abundance, productivity, and diversity of algae (Lewis 1986, Mumby et al. 2006, Burkepile and Hay 2008, Marshall and Mumby 2015, Sheppard et al. 2023). However, herbivorous fish are not a monolithic group, with different species showing different feeding preferences and roles within the community (Mantyka and Bellwood 2007, Burkepile and Hay 2008, Rasher et al. 2013, Burkepile et al. 2022). For example, differences in diet often result in these fishes being divided into functional groups such as grazers, scrapers, or browsers (Green and Bellwood 2009). Yet even categorization into functional groups likely overlooks important nuances in diet and behavior among species that can differ within functional groups (Semmler et al. 2021). While research is progressing on defining and refining functional groups, it is less clear how, or even if, the feeding behavior of these herbivore species may change as the benthic communities of reefs change.

On many coral reefs worldwide, corals are declining in abundance (Eddy et al. 2021) while algae are increasing in abundance due to both global and local stressors (Adam et al. 2021, Souter et al. 2021). As the community composition of coral reefs changes in response to

global change, these changes could potentially alter the feeding preferences and behavior of herbivorous fishes. Although there have been few studies examining how benthic community composition shapes feeding patterns in coral reef herbivores, some studies have shown that herbivore species can alter their feeding preferences as algal resources change in abundance (Francini-Filho et al. 2010, Hanmer et al. 2017). Further, stable isotopes have suggested that some herbivores show different isotopic niches on coral vs. algal dominated reefs (Letourneur et al. 2017). When considering movement, herbivorous fish can also alter their foraging area in response to changes in resource availability (Nash et al. 2012, Carlson et al. 2017). Thus, there is increasing evidence that changes in the benthic community of reefs may alter the foraging behavior of herbivorous fishes.

Understanding how foraging behavior of herbivorous fishes changes as benthic communities of reefs change is increasingly important to understand as there is the potential for changes in feeding behavior to act as feedbacks that could support certain benthic regimes. For example, lower removal of algal biomass in algal states in the Eastern Tropical Pacific is a positive feedback that can contribute to algal dominated states (Muthukrishnan et al. 2016); yet higher macroalgal biomass removal on algal dominated areas conversely is a feedback that could contribute to the recovery of algal dominated reefs in Moorea (Bittick et al. 2020). In addition, one might expect fishes on reefs with abundant algae to forage over smaller distances, and spatially constrained feeding in algal dominated reefs could potentially support coral recovery (Sandin and McNamara 2012). Therefore, any changes in herbivore foraging behavior on reefs dominated by coral or algae could present important feedbacks that provide a competitive advantage to corals or algae. However, before we can concretely describe

herbivore foraging behaviors that acts as feedbacks that support coral or algal regimes, we must first understand if herbivore foraging behavior is different between reefs dominated by coral and reefs dominated by algae.

One key aspect of understanding how the feeding behavior of herbivorous fishes may change as benthic communities change is choosing the important aspects of feeding behavior that may be flexible. Previous studies evaluating the levels of functional diversity of herbivorous fishes on coral reefs found that multiple functional traits must be considered when assessing herbivore functional roles (Adam et al. 2015). Herbivores can differ in their resource use across multiple niche axes including habitat preferences, substrate preferences, microhabitat use, foraging area, and even the intestinal microbiome (Adam et al. 2015, Brandl and Bellwood 2016, Scott et al. 2020, Semmler et al. 2021). Yet, few studies have explored how multiple niche axes might change across reefs with different benthic communities (Eggertson et al. 2020), especially in the context of how reefs are shifting from abundant coral to abundant macroalgae. As coral reefs continue to shift in the benthic community in the face of global and local stressors, it is important to identify the flexibility in foraging behavior in response to shifts in the benthic community given their potential to act as feedbacks that alter benthic dynamics.

In this study, we evaluated how different species of herbivorous fishes alter their feeding behavior depending on benthic community structure by conducting focal behavioral observations of herbivore feeding on reefs with either abundant coral or abundant macroalgae in the lagoons of Moorea, French Polynesia. During focal behavioral observations of five

different species of herbivorous fish (*Acanthurus nigrofuscus*, *Zebrasoma scopas*, *Chlorurus spilurus*, *Scarus oviceps*, and *Scarus psittacus*), we recorded bites taken on different food items (e.g., algal turf, macroalgae, coral) as well as which substrates (e.g., dead branching coral, rubble, pavement) these food items occurred on. Our main aim was to quantify intraspecific differences in herbivore foraging behaviors between reefs in the coral vs. algal state by assessing bite rate, foraging range, food item use, and substrate use. We addressed how the following metrics of herbivore foraging differed between reefs in the coral vs. algal state: (1) herbivore feeding rates, (2) foraging range, (3) percentage of bites taken on food items and substrates, and (4) selectivity for food items and substrates between reef states.

Methods

Study sites and focal organisms

This research was conducted in Moorea, French Polynesia, and based out of the University of California Gump Research Station on the north side of the island. Fish behavioral observations were conducted in July and August 2022 at two sites with abundant coral (hereafter ‘coral state’) and two sites with abundant macroalgae (hereafter ‘algal state’) on reefs in the shallow (<3m) lagoon. While the epilithic algal matrix (EAM), a diverse assemblage including multi-species composition of filamentous algae, detritus, microbes, microalgae, macroalgal propagules, and sediment (Diaz-Pulido and McCook 2003, Wilson et al. 2003), was usually the dominant benthic cover at all sites, sites in the coral state vs. algal state differed in the abundance of coral and macroalgae. Sites in the coral state had $29.9\% \pm 3.7$ live coral cover and $8.9\% \pm 2.0$ cover of macroalgae while sites in the algal state

had $33.3\% \pm 3.7$ cover of macroalgae and $8.8\% \pm 0.8$ live coral cover (Fig. 1). Five species of herbivorous fish were followed which included two surgeonfish species (*Acanthurus nigrofusus*, *Zebrasoma scopas*) and three parrotfish species (*Chlorurus spilurus*, *Scarus oviceps* and *Scarus psittacus*) (Table S1). The evidence for parrotfishes differing in diet and functional role depending on body size is significant (Bruggemann et al. 1994, Bonaldo and Bellwood 2008, Lokrantz et al. 2008, Ong and Holland 2010, Adam et al. 2018, Lange et al. 2020). Thus, we divided parrotfish within a species between juveniles/subadults (< 15 cm) and adults (> 15 cm) for the analyses. Although there is some evidence of differences in feeding preferences of surgeonfishes across body size (Duran et al. 2019), we did not focus analyses on different surgeonfish size classes given fewer individuals of the smaller size class on our focal reefs.

Focal fish observations to quantify foraging behavior

The purpose of collecting fish behavioral observations was to evaluate how the preferences for food items and substrates may differ under different benthic community states. All behavioral observations were done on snorkel by the same two trained individuals. During 10 min focal observations, we recorded the number of bites the focal fish took per foray (series of consecutive bites), the food items bitten (EAM, macroalgae, coral, turf within damselfish territories) and the substrate (dead branching coral, rubble, pavement, bommie, sand) the food items. Observers maintained ~ 3 m distance from the fish being observed. Before data were recorded during the 10 min observation period, fish were followed for a 2 min acclimation period to allow them to become accustomed to the snorkeler's presence. Follows were ended and excluded from the dataset if fish behavior appeared affected by observer

presence such as the focal fish watching the observer or fleeing. During the follows, we towed a float with a GPS that recorded our position every 15 sec in order to record the distance moved by each fish (Carlson et al. 2017, Davis et al. 2017).

We note that the food items that these fishes were ingesting may be different than what they were assimilating from the material in their bites. For example, many herbivorous fishes, particularly parrotfishes, often ingest items, like macroalgae, not for the nutrition in the macroalgae but for the epiphytic algae living on the macroalgae or ingest epilithic algae in order to access the endolithic algae below them (Clements et al. 2016, Nicholson and Clements 2020). However, our goal was not to quantify the sources of nutrients to these fishes, which would require analyses of gut contents, stable isotopes, or fatty acid profiles. Our goal was to quantify how different benthic communities affect what these fishes ingest and thus remove from the benthos.

Quantification of the benthic community

To relate foraging behavior to the potential food and substrate availability, we also quantified the benthic community composition. At each site, we quantified the relative abundance of benthic food items and substrates using point-intercept surveys with quadrats along four 30 m transects laid perpendicular to the shoreline. Along each transect, benthic cover was assessed using the point-intercept method for 16 evenly spaced points within a 0.5×0.5 m quadrat placed at 1 m intervals along the transect. At each point, we recorded both the cover type (EAM, macroalgae, coral, turf within damselfish territories hereinafter ‘damsel turf’) and the underlying substrate (bommie, dead branching coral, live coral, rubble, pavement,

and sand) on which the cover type was located. Macroalgae and corals were identified to species when possible. Substrates included categories that consisted of: (1) dead branching coral, (2) rubble, which was pieces of unconsolidated dead coral, (3) bommie, which was dead massive corals, mostly *Porites lobata* and *Porites rus*, (4) live coral, (5) coral pavement, and (6) sand. Live coral was included both as a food item and a substrate given its ability to be a direct foraging resource and substrate. Feeding observations on live coral were distinguished by two behaviors with some parrotfish species observed scraping away live coral tissue, while other species, often surgeonfishes, observed feeding on the coral surface potentially on coral polyps, mucus, biofilm, or detritus without removing any coral skeleton. However, these distinctions were often challenging to discern in the field, thus we did not differentiate between the different types of feeding on live coral.

Quantification of herbivore assemblage

Previous research has suggested that reefs with either abundant coral or abundant algae can support different communities of herbivorous fishes (Munsterman et al. 2021). To quantify the herbivore assemblage at each of our sites, we conducted four belt transects (5 × 50 m). All roving herbivores within transects were identified to species and estimated to the nearest length in cm.

Statistical Analyses

Are herbivorous fish assemblages different between reefs in the coral vs. algal state?

To investigate whether the herbivorous fish assemblages differed between coral and algal states, we first evaluated whether herbivore densities differed between reef state. We included all roving herbivores species, not just our focal species, that were present in both coral and algal states (i.e., we removed species that were only present in one state as they could not provide a meaningful comparison). We conducted a linear mixed model with an interaction of fish species with reef state on log-transformed densities (individuals/100m²) and a random effect of site. Model was fitted with restricted maximum-likelihood (REML), type II Wald F-tests and Kenward-Rogers estimated degrees of freedom. Model assumptions were visually assessed through diagnostic plots. Tukey-adjusted pairwise contrasts between reef state within for each species (coral vs. algal state) using Kenward-Rogers estimated degrees of freedom were conducted using *emmeans*. To further assess whether the structure of herbivorous fishes differed between coral and algal states, we conducted a PERMANOVA using a Bray-Curtis dissimilarity matrix (999 permutations) on log-transformed herbivore densities. We also visualized differences in herbivorous fish community structure in non-metric multidimensional space using *metamds*.

Are there intraspecific differences in herbivore foraging rates between reefs in the coral vs. algal state?

To determine if fish species differed in their overall feeding rates between the two different reef states, we conducted a generalized linear mixed model on the effect of the reef state (Coral vs. Algal) with a negative binomial distribution, including fish size as a covariate and a random effect of site. Model assumptions were visually evaluated through the *DHARMa* package and were met. We used a type II Anova from the *car* package to assess the

significance of effects. Tukey-adjusted pairwise contrasts of bite rates between reef states within herbivore species was conducted using the *emmeans* package.

Are there intraspecific differences in the distance moved while foraging between reef states?

To investigate whether fish species moved different distances while foraging within coral or algal states, we conducted a linear mixed model on the effect of the reef state (Coral vs. Algal) on log-transformed maximum linear distance traveled (m) from our GPS tracks, including fish size as a covariate and a random effect of site, separately for each species. Model assumptions were visually evaluated through diagnostic plots. Post-hoc comparisons were conducted using *emmeans*.

Are there intraspecific differences in the percentage of bites by herbivorous fish for food items and substrates between reefs in the coral vs. algal state?

To visually assess whether species had different percentage of food items consumed between reef states, we visualized the multivariate patterns of the percentage of bites taken on food items using a canonical analysis of principal coordinates (CAP) on a Bray-Curtis dissimilarity matrix to identify the food items that associated with reef state. Reef state was the constraining variable while fish species was included as a conditional variable. The same analysis was also conducted on the percentage of bites taken on substrates.

How does the selectivity for food items and substrates change within herbivore species between reefs in the coral vs. algal state?

To determine the foraging preferences of fish species relative to the availability of benthic resources, we calculated selectivity indices using Manly's alpha on the bite rate data. The selectivity index ranges between 0 to 1, and reflects the proportional use of a resource relative to its availability, where r represents the bite rate on a given resource, and n represents the percent cover. The null selectivity was defined as $1/m$ where m is the number of food items or substrate categories available and bitten by the observed fish. For example, we had 6 substrate categories which meant that the null selectivity for substrates was 0.17. Confidence intervals were calculated for each selectivity index estimate. If the 95% confidence interval was entirely above the null selectivity, the resource was considered actively targeted. If the 95% confidence interval was entirely below the null selectivity the resource was considered actively avoided. Overlap of the confidence interval with the null selectivity value indicated feeding in proportion to the abundance of that type with no significant preference or avoidance. Selectivity analyses were conducted separately for each reef state, and were applied to both food item and substrate categories separately.

Results

Are the herbivorous fish communities different between reefs in the coral vs. algal state?

There was a significant interaction effect of fish species and reef state on fish abundance ($F_{(9,91.58)} = 2.8$, $p = 0.006$). However, Tukey adjusted pairwise contrasts revealed that none of the species had significantly different densities between coral and algal states (Fig S1). While the nMDS appeared to display clustering of species between reef states (Fig S1), the

PERMANOVA revealed that herbivore communities did not significantly differ between reef states ($F(1,2) = 1.4$, $p = 0.33$).

Are there intraspecific differences in herbivore foraging rates between coral and algal states?

Zebrasoma scopas and *S. oviceps* adults had significantly different bite rates between reef states (*Z. scopas*: z. ratio = 2.0, $p = 0.043$; *S. oviceps* adults: z. ratio = 2.5, $p = 0.013$) with greater bite rates in the algal state. *Zebrasoma scopas* had ~ 2 times the bite rate (14.1 vs. 7.2 bites min^{-1} in algal vs. coral state respectively) and *S. oviceps* adults had 2.5 times the bite rate (9.4 vs 3.7 bites min^{-1} in algal vs. coral state respectively) (Fig. 2a). Visually, there was a pattern of higher bite rates in the algal state (especially for *S. oviceps* juveniles/subadults: z. ratio = 2.1, $p = 0.077$) for most other species (except for *A. nigrofuscus*), however, they were not statistically significant.

Does the distance moved while foraging change between reef states within herbivore species?

Only *S. psittacus* juveniles/subadults displayed significant differences between reef states in the maximum linear distance traveled while feeding, with greater maximum linear distance traveled on reefs in the coral state ($F(1,2.3) = 30.8$, $p = 0.02$) (Fig 2b).

Are there intraspecific differences in the proportion of bites by herbivorous fish for food items and substrates between reefs in the coral vs. algal state?

Food Items

In the coral state, feeding on EAM ranged from 36 to 51 % of bites, while in the algal state feeding on EAM ranged from 22 to 86 % with several species displaying considerably greater percentage of bites on EAM in the algal state (*C. spilurus* adults: Algal state: 86%, *S. oviceps* adults: Algal state: 86%, *S. psittacus* adults Algal State: 79%, *Z. scopas*: Algal state: 78%) (Fig 3). The only species that did not show an increase in percentage of bites taken on macroalgae in the algal state were *C. spilurus* adults and *S. oviceps* adults. While all species fed on damsel turf in the coral state, only the juvenile/subadult stages of the three parrotfish species fed on damsel turf in the algal state. In the coral state, all fish species fed on live coral with several species having > 25% of bites taken on live coral (*A. nigrofuscus*: 40 %, *Z. scopas*: 26 %, *S. psittacus* juveniles/subadults: 29 %). However, in the algal state there was considerably less feeding on live coral with values ranging only from <1 to 5 % of bites (Fig 3). When combining all live coral feeding observations across both reef states, parrotfish took over 50% of their bites on live coral on *Montipora* and over 30% on *Porites* (mostly *P. lobata*). Surgeonfish took 60% of bites from live coral on *Montipora* and 20% on *Porites lobata* and 20% on *Porites rus*.

The canonical analysis of principle coordinates (CAP) revealed that overall, the percentage of bites taken on the different food items was structured by reef state (Fig. 4a) with the coral state clustered with the live coral and damsel turf food items and the algal state clustered with macroalgae (Fig 4a). When analyzed by fish species, most species followed similar clustering patterns with the food items that differentiate them between reef states being live coral and

damsel turf in the coral states and macroalgae in the algal states, although the clustering appeared to be weaker for *C. spilurus* adults and *S. psittacus* adults (Fig. 4b).

Substrates

The parrotfishes, *C. spilurus* juveniles/subadults, *S. oviceps* juveniles/subadults and *S. oviceps* adults all appeared to have a considerable increase in their percentage of bites on the bommie substrate in the coral state relative to the algal state (Fig. 3). Only, *A. nigrofuscus* and *Z. scopas* displayed an increase their percentage of bites taken on dead branching coral substrate in the algal state. For most species, the percentage of bites taken on rubble in the two reef states was similar except for *C. spilurus* adults (Coral state: 30 %, Algal state: 41 %), *S. oviceps* adults (Coral State: 4 %, Algal state: 13 %), *S. psittacus* adults (Coral state: 30 %, Algal state: 20 %), and *Scarus oviceps* juveniles/subadults did not feed on rubble at all in the algal state. In the coral state, only *S. psittacus* adults had > 10 % of their bites on pavement. While in the algal state, *S. psittacus* juveniles/subadults, *S. psittacus* adults, and *Z. scopas* had > 10 % of their bites on pavement. *Scarus psittacus* adults appeared to have a generous percentage of their bites on sand in both reef states (> 20 %). Only in the coral state did other species also have a meaningful percentage of bites on sand: *C. spilurus* adults (Coral state: 20 %), *S. oviceps* adults (Coral state: 30 %), *S. psittacus* juveniles/subadults (Coral state: 10 %,) (Fig 3).

The CAP on the percentage of bites taken on substrates revealed modest but consistent differentiation of substrate feeding with coral states clustering towards live coral and pavement and algal states clustering toward rubble and dead coral (Fig. 5a). For each fish

species, the pattern of the clustering of coral states towards live coral and algal states toward rubble and dead coral was visible although modest (Fig. 5b).

How does the selectivity for food items and substrates change within herbivore species between reefs in the coral vs. algal state?

Food Items

Selectivity in food items differed considerably between reef states for the observed fish species. In the coral state, there were considerably more neutral feeding selections across food items in general. However, in the algal state, a preference for EAM and macroalgae strongly emerged along with avoidance of other categories and fewer neutral responses. This pattern is especially evident with *A. nigrofuscus*, *Z. scopas*, and *S. oviceps* juveniles/subadults who did not select for or against any of the food items in the coral state, except for *A. nigrofuscus* avoiding live coral. However, in the algal state, *A. nigrofuscus* preferred EAM and macroalgae, *Z. scopas* preferred EAM, and *S. oviceps* juveniles/subadults preferred macroalgae. All three species avoided more food items in the algal state than in the coral state. Overall, fish species exhibited stronger preferences in the algal state including selecting both for and against food items while showing less preferences for food items in the coral state.

Substrates

In comparison to the patterns for food items, the selectivity patterns for feeding substrates appear to be more consistent between coral and algal states for most species. In general, most

fish species either selected for bommie substrate or maintained a neutral selection for it between coral and algal states. Similarly, fish tended to either have a neutral preference or select for rubble substrate and this remained consistent between coral and algal states. *Scarus psittacus* adults did not select for any substrate categories in both reef states while avoiding both live coral and dead branching coral. However, they were the only species to feed on pavement in proportion to its availability and did so consistently in both reef states. *Scarus psittacus* juveniles/subadults avoided pavement in the coral state but fed in proportion to its relative availability in the algal state. All other species avoided pavement substrate in both reef states.

Discussion

Previous work has shown that herbivorous fish species differ in their foraging traits such as bite rates, food items, substrate preferences, and foraging area (Nash et al. 2012, Adam et al. 2015, Brandl and Bellwood 2016, Kelly et al. 2016). Our work shows that some of these foraging traits can be different depending on the benthic community composition of reefs. In the two reef states (abundant coral vs. abundant algae), several species of herbivorous fish exhibit differences in foraging behaviors, although some behaviors appear more flexible while others appear more static. While most species did not show differences in bite rates or foraging range between reef states, we found many species showed differences in how they selected food items between reef states. Fishes in the coral state showed few strong preferences for food items, often feeding on resources in proportion to their availability. Yet, fishes in the algal state often showed stronger foraging choices with clear preferences for (such as EAM) or avoidance of food items. In contrast, fishes in both the coral and algal state

exhibited similar selectivities for the substrates on which they foraged, suggesting that what these fishes feed on appears more flexible than where these fishes feed. Our results show that some elements of the feeding behavior of herbivorous fishes appears more flexible across different benthic community composition while others appear to be more fixed. However, we did not capture changes in behavior immediately following the loss of coral, and experimental work would be necessary to confirm if immediate phase shifts from coral to algal dominance do stimulate changes in herbivore foraging behavior.

Despite differences in the abundance of corals and algae between reef states, herbivorous fishes generally did not considerably alter their feeding rates or the distance they traveled while feeding. Only the surgeonfish *Z. scopas* and the parrotfish *S. oviceps* adults displayed different bite rates between reef states, exhibiting higher bite rates in the algal state. In another study in Moorea, *C. spilurus* and *A. nigrofuscus* were also found to have relatively consistent foraging rates across a variety of reef sites (Tootell and Steele 2016). Similarly, only one species and life stage (*S. psittacus* juveniles/subadults) displayed significantly different foraging ranges between reef states with greater distance moved in coral states. Thus, at least in the lagoonal reefs in Moorea, most herbivorous fish species display relatively inflexible bite rates and movement patterns regardless if the reefs are abundant in coral or algae.

In the algal state, fish species displayed stronger choices for food items especially for *Z. scopas*, *C. spilurus* adults, *S. oviceps* juveniles/subadults, and *S. oviceps* adults. While we did not explore why they would have more deliberate foraging selections in the algal state, this could potentially be due to the algal state providing a wider range and more consistent

coverage of desirable food items allowing for more deliberate, targeted foraging. Optimal foraging theory predicts that consumers will not be selective in conditions of food scarcity (Perry and Pianka 1997). Thus, the coral state may have provided more limited and patchier food resources, resulting in more neutral selection (i.e., consuming resources as they are found). Surgeonfish in the Red Sea have been found to exhibit a diel shift from selective feeding in the morning when a preferred algal resource is present to a non-selective strategy in the afternoon when the preferred resource is diminished (Khait et al. 2013). Similarly, there is also evidence of herbivorous fish consuming the dominant resource when preferred food resources are scarce (Francini-Filho et al. 2010). Our study suggests the potential that herbivorous fish could modify their selectivity

The epilithic algal matrix (EAM) and macroalgae were the two food items that stood out as more preferred in the algal state. Even though the percent cover of EAM did not differ between coral and algal states, it still was a more preferred food item in the algal state. The epilithic algal matrix was also distinct from any other food item category as it was never avoided by any fish species in both reef states; it was either preferred or fed in proportion to its availability. Numerous other studies have found that herbivorous fish target the EAM (Francini-Filho et al. 2010, Kelly et al. 2016, Hanmer et al. 2017, Carlson et al. 2017, Leitão et al. 2023). However, the EAM is made up of a diverse assemblage including multi-species composition of filamentous algae, detritus, microbes, microalgae, macroalgal propagules, and sediment (Diaz-Pulido and McCook 2003, Wilson et al. 2003), which we did not distinguish. Gut content analyses have revealed that herbivorous fish do discriminate across different types of algal turf (Kelly et al. 2016). Thus, by categorizing it as one functional group and

not obtaining finer taxonomic resolution within the EAM, we likely underestimated how the different species partitioned their feeding within the epilithic community (Nicholson and Clements 2020). Further, the EAM community could have differed between reefs in the coral vs. algal state, a fact that could also have led us to underestimate potential changes in foraging patterns between reef states.

Surprisingly we found that non-browsing fishes (*A. nigrofuscus*, *C. spilurus* juveniles/subadults, and *S. oviceps* juveniles/subadults) displayed a preference for macroalgae in the algal state and macroalgae made up a considerable percentage of their food item bites. However, for most of the observations of feeding on macroalgae, we did not observe these fish to obviously remove pieces of macroalgae. Thus, these non-browsers are likely targeting the epibionts on macroalgae (Fong et al. 2018, Bittick et al. 2019, Dell et al. 2020, Nieder et al. 2022), and likely not removing meaningful macroalgal biomass. These macroalgae, in a sense, are acting as a substrate type themselves by harboring epibionts that these fishes feed on. In fact, in algal-dominated reefs in Moorea, the macroalga, *Turbinaria ornata* has been suggested by some to be a secondary foundational species, by providing habitat to epiphytes and supporting feeding by herbivorous fish on the epiphytes (Bittick et al. 2019). Further, increased macroalgal densities resulted in an increase supply of epiphytes and consequently greater feeding by herbivorous fish (Bittick et al. 2019). Thus, on reefs abundant with macroalgae, macroalgae may act as a newly abundant substrate harboring epibionts targeted by herbivorous fish. Future research on the role of different macroalgal types in harboring different types of epibionts and selection by herbivorous fish is warranted

especially given the fact that greater densities of macroalgae also result in an increase in epiphyte load (Bittick et al. 2019).

While the food item selectivity was different between reef states, substrate selectivity by fishes was more conserved with little differences in preferences between reef states. In the Red Sea, the parrotfish *S. ferrugineus* was also found to maintain its substrate selectivity which was primarily on hard coral substrates on reefs even with changes in macroalgal biomass throughout seasons (Afeworki et al. 2011). Thus, while different species of fish may target different substrates (Adam et al. 2015, Brandl and Bellwood 2016, Eggertsen et al. 2020), their preferences for substrates appear less likely to vary across reefs with different benthic communities. These relatively consistent uses of substrates across reef state revealed consistent differences among herbivore species on where on the reef they foraged. For example, *Scarus psittacus* adults exhibited unique substrate foraging by feeding on pavement and sand substrates which were avoided by all other species. In contrast, *S. oviceps* adults targeted or fed on dead branching coral substrates in proportion to its availability while *C. spilurus* adults targeted rubble. Thus, species clearly differ in the substrates they target, but this remains consistent between reef states.

Surprisingly, we found that all species we observed fed on live coral, although with different intensities and preferences. However, in the selectivity analyses which took into account the relative availability of resources, coral was avoided by all species except by *S. oviceps* juveniles/subadults and, interestingly, *Z. scopas* where they fed on live coral in proportion to its availability in the coral state. While feeding on corals by some parrotfish species is common (Rotjan and Lewis 2005, Ezzat et al. 2020, Huertas et al. 2021), feeding on coral by

surgeonfishes is rare with the only other report for *A. nigrofuscus* showing limited feeding on live coral in Okinawa (Nanami 2025). Unlike the feeding on live coral by parrotfishes, which clearly removed coral skeleton and coral tissue, feeding by surgeonfishes did not remove obvious coral skeleton. Thus, it was unclear what resource surgeonfishes were feeding on as they bit live coral. It is possible surgeonfishes were feeding on coral polyps or some form of epilithic layer on the coral, whether that is mucus, detritus, or a biofilm, although we were unable to make this discrimination. Not surprisingly, feeding on live coral was much more prevalent in the coral state with a higher proportion of fish feeding on live coral than the algal state.

Despite fishes in coral vs. algal reef states showing different patterns of selectivity for food items, we showed that EAM is an important foraging resource in both reef states. However, it would be beneficial to characterize the EAM community as it is not homogeneous and there is room to detect feeding preferences within EAM bites. This characterization would be relevant to understanding reefs in the Anthropocene as the epilithic algal community has increased on reefs widely across the globe (Tebbett et al. 2023a, 2023b), and the composition of the epilithic community is connected to reef health (Tebbett et al. 2025). Overall, we provide evidence that herbivorous fishes may be more flexible in their food choices while not changing their bite rate, movement patterns, or where on the reefs that they forage regardless of the benthic community composition of the reef. However, the reefs we studied diverged in community composition likely over the course of a decade or more (Adam et al. 2021). Thus, future studies should examine how sudden changes in the dominant benthic organisms such as following coral-killing disturbances such as cyclones or marine heat waves alters herbivore foraging behavior. Moreover, our work argues for increased emphasis on

understanding how state shifts in the benthic communities of corals reefs will alter the foraging ecology of ecologically important species.

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Figures

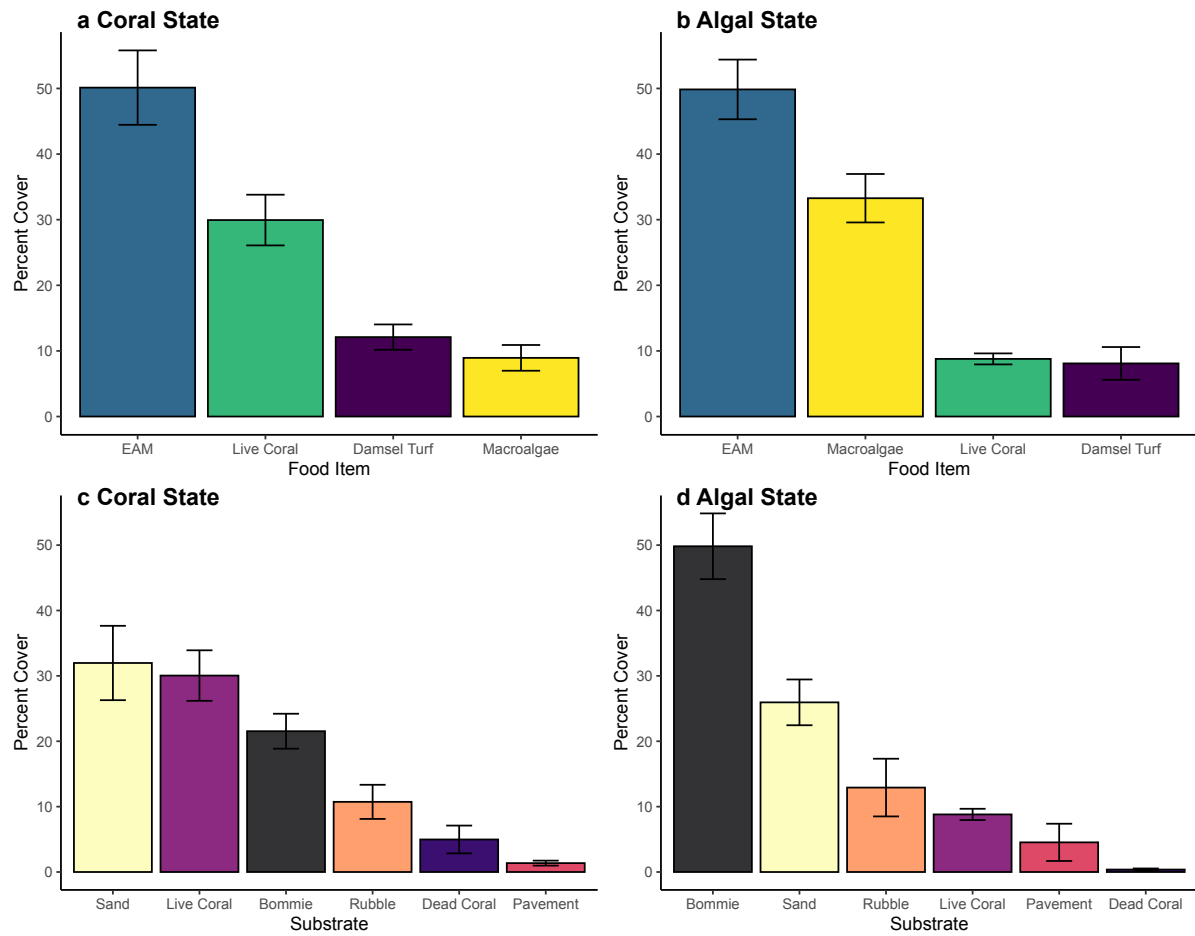


Figure 1. Percent cover (mean $\pm$ SE) of the different food items in the a) coral state and b) algal state and different substrates in the c) coral state and d) algal state at our study sites. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

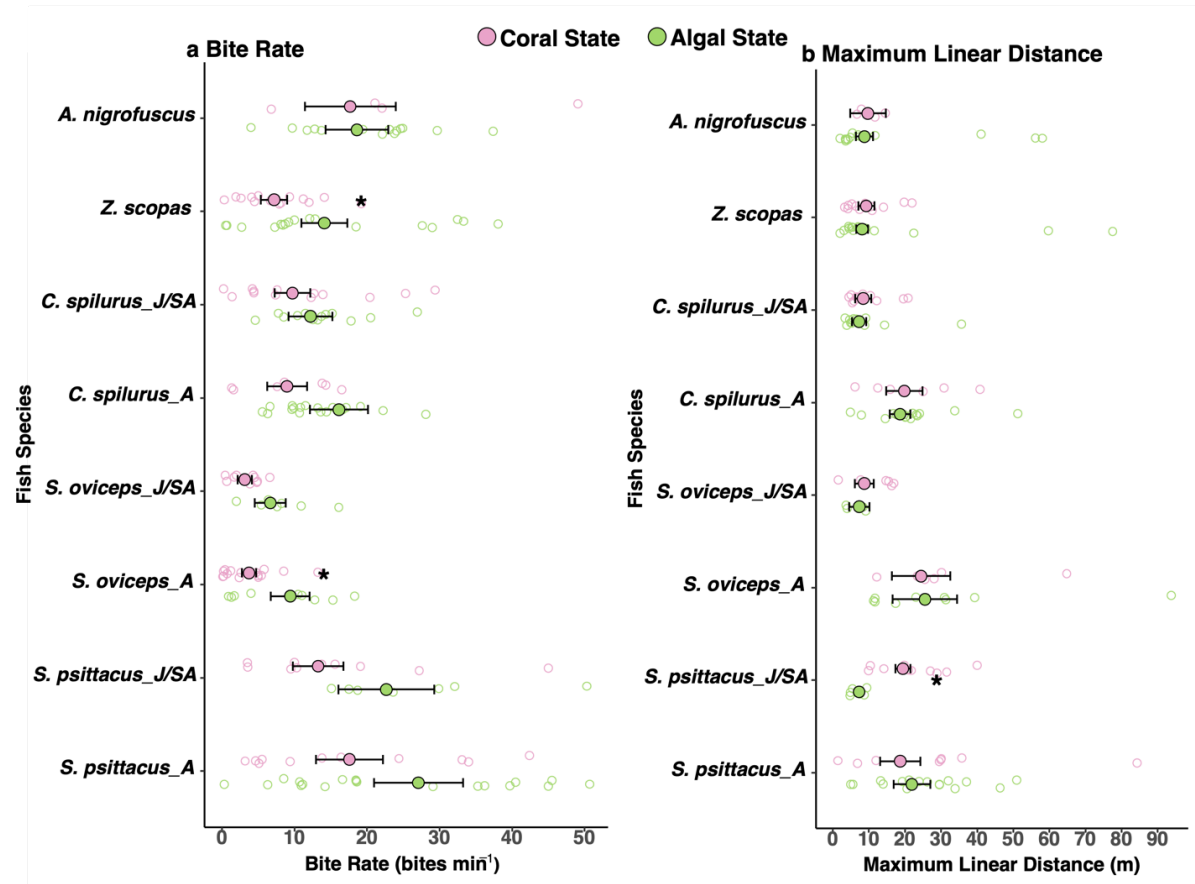


Figure 2. a) Estimated marginal means ($\pm$ SE) of size-adjusted bite rates for each species. Open circles represent raw bite rate values and filled points represented the model predicted means. b) Estimated marginal means ($\pm$ SE) of size-adjusted maximum linear distance traveled (m) for each species. Open circles represent raw maximum linear distance traveled values and filled points represented the model predicted means. Asterisks denote the species that had significantly different maximum linear distance traveled ($P < 0.05$) between coral (pink) and algal (green) states from the generalized linear mixed model for bite rates and linear mixed model for maximum linear distance moved. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

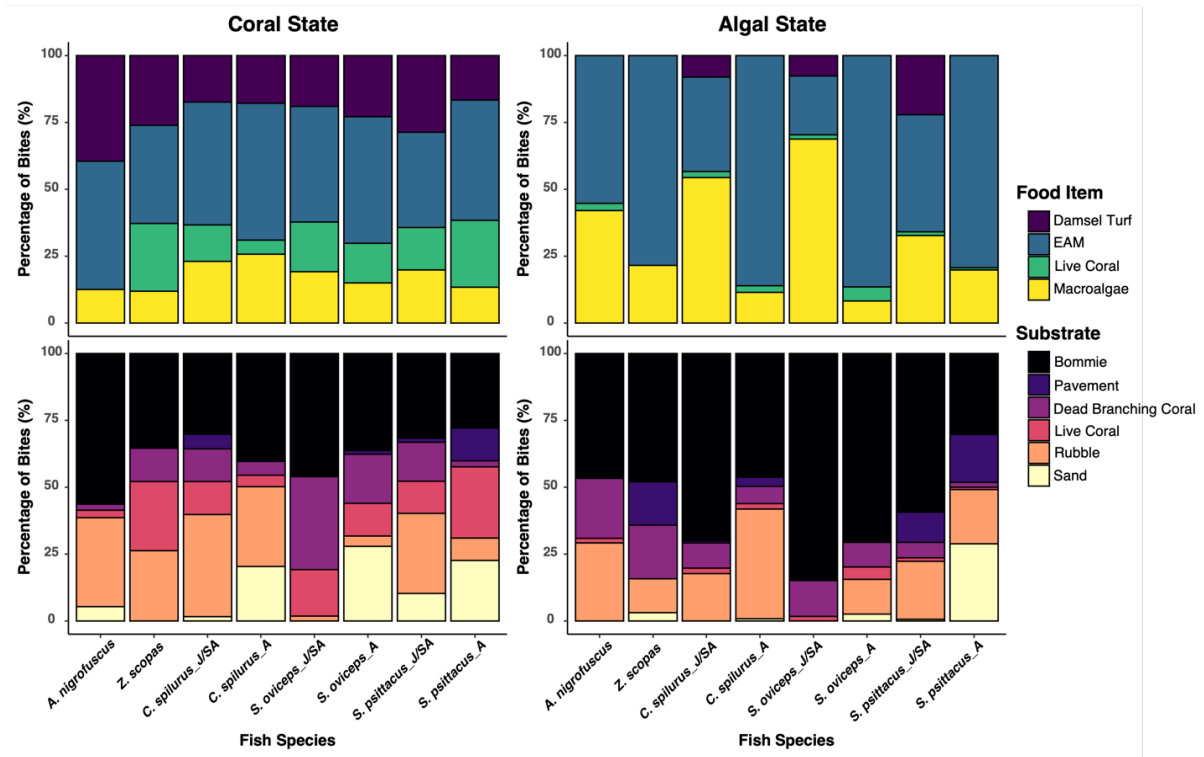


Figure 3. Mean percentage of bites taken by each species on the food items (top panels) and substrates (bottom panels) in the coral (left) and algal (right) states. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

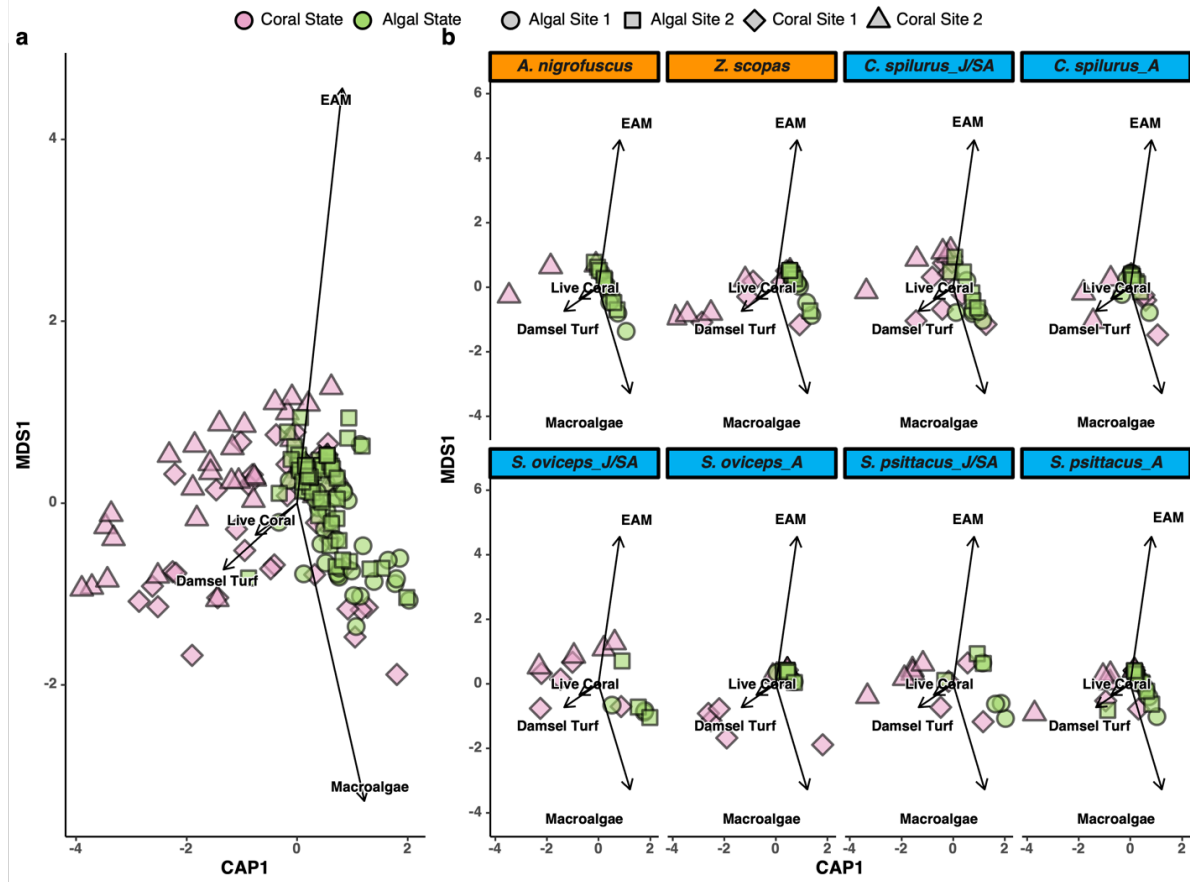


Figure 4. Canonical analysis of principle coordinates (CAP) on the Bray-Curtis dissimilarity matrix of the proportion of bites taken on food items between coral (pink) and algal (green) states for a) all of the fish species together and b) by species. Vectors represent the direction and strength of the food item's correlation with the ordination axes. Different shapes indicate the different sites (two per reef state). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

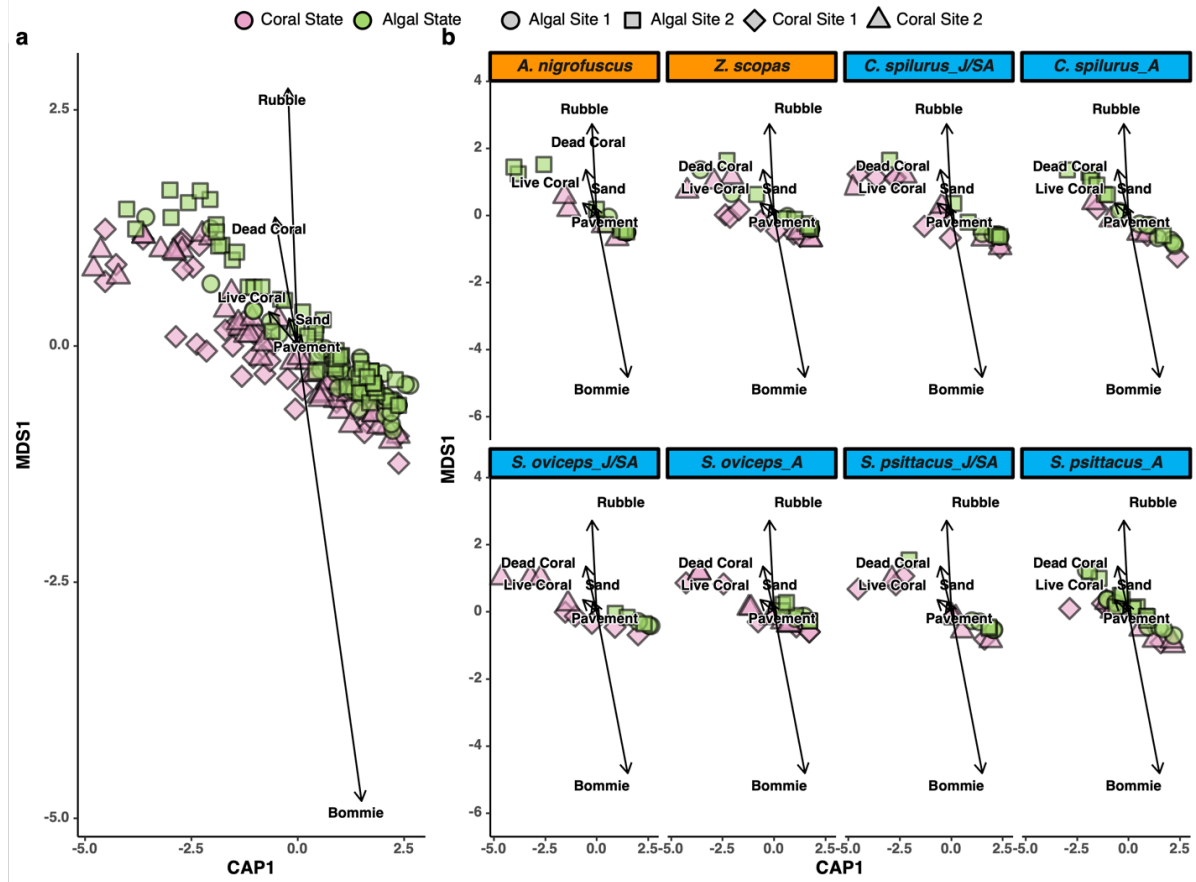


Figure 5. Canonical analysis of principle coordinates (CAP) on the Bray-Curtis dissimilarity matrix of the proportion of bites taken on substrates between coral (pink) and algal (green) states for a) all of the fish species together and b) by species. Vectors represent the direction and strength of the substrate's correlation with the ordination axes. Different shapes indicate the different sites (two per reef state). Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

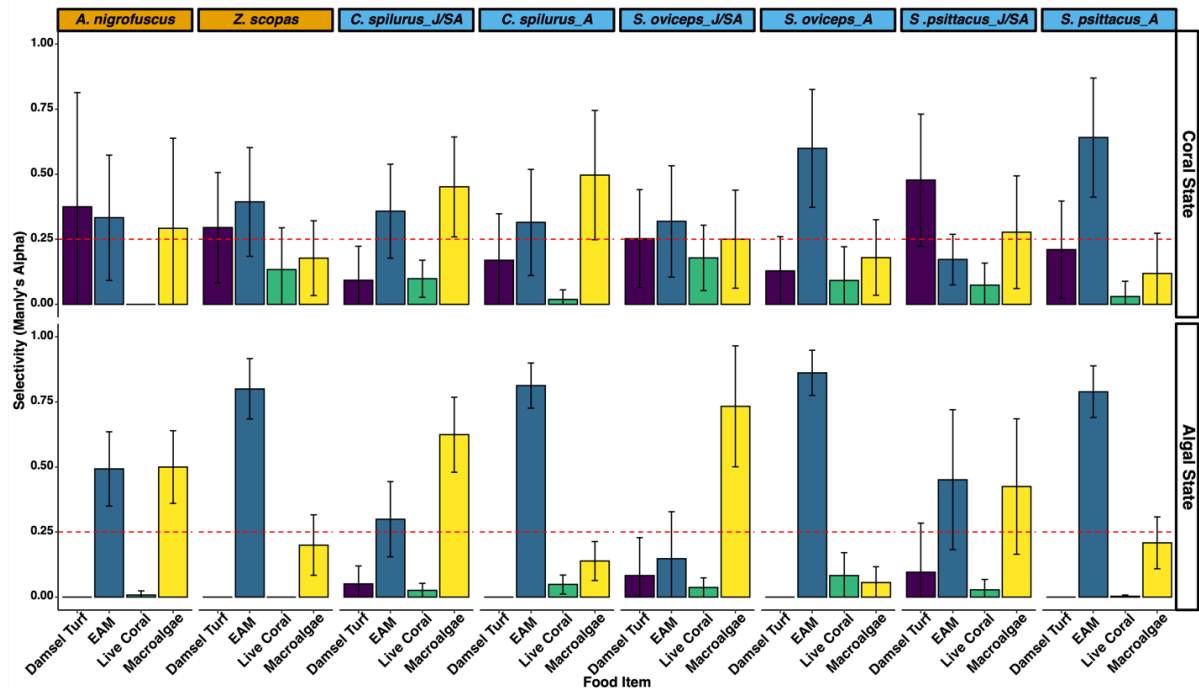


Figure 6. Selectivity (Manly's alpha) of each fish species for the food items on reefs in the coral state (top panel) or algal state (bottom panel). Error bars represent 95% Confidence Intervals (CI). CI fully above the null alpha line (dashed red line) indicates preference for item. CI fully below the null alpha line indicates avoidance of item. Overlap of CI with the null alpha line indicates feeding in proportion to item abundance. Orange headings represent surgeonfish and blue headings represent parrotfish. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm.

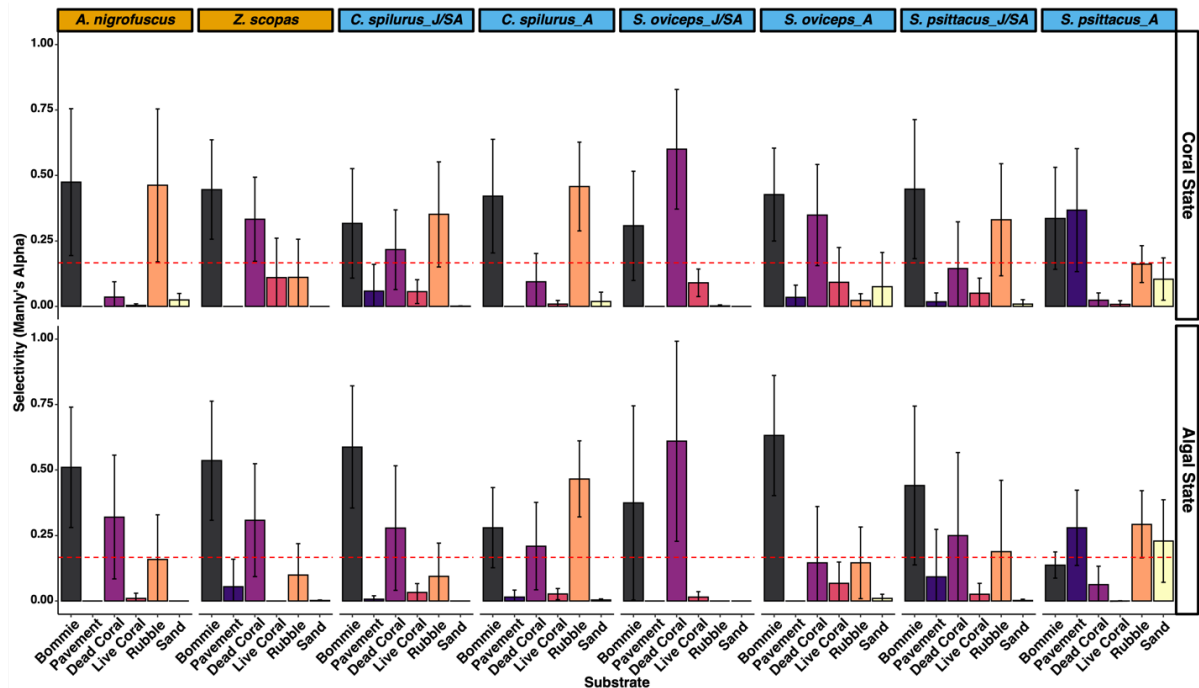


Figure 7. Selectivity (Manly's alpha) of each fish species for the substrates on reefs in the coral state (top panel) or algal state (bottom panel). Error bars represent 95% Confidence Intervals (CI). CI fully above the null alpha line (dashed red line) indicates preference for substrate. CI fully below the null alpha line indicates avoidance of substrate. Overlap of CI with the null alpha line indicates feeding in proportion to substrate abundance. Orange headings represent surgeonfish and blue headings represent parrotfish. Juveniles/subadults (J/SA) are parrotfish individuals < 15 cm and adults (A) are parrotfish individuals > 15 cm. To improve readability, the substrate category Dead Branching Coral was abbreviated to Dead Coral.

Supplementary Figures and Tables

Table S1. The number of individual fish followed per species in the coral and algal states.

<i>Fish Species</i>	<i>Coral State</i>	<i>Algal State</i>
<i>Acanthurus nigrofusus</i>	4	14
<i>Zebrasoma scopas</i>	13	16
<i>Chlorurus spilurus_J/SA</i>	13	12
<i>Chlorurus spilurus_A</i>	7	16
<i>Scarus oviceps_J/SA</i>	9	6
<i>Scarus oviceps_A</i>	15	9
<i>Scarus psittacus_J/SA</i>	9	7
<i>Scarus psittacus_A</i>	11	18

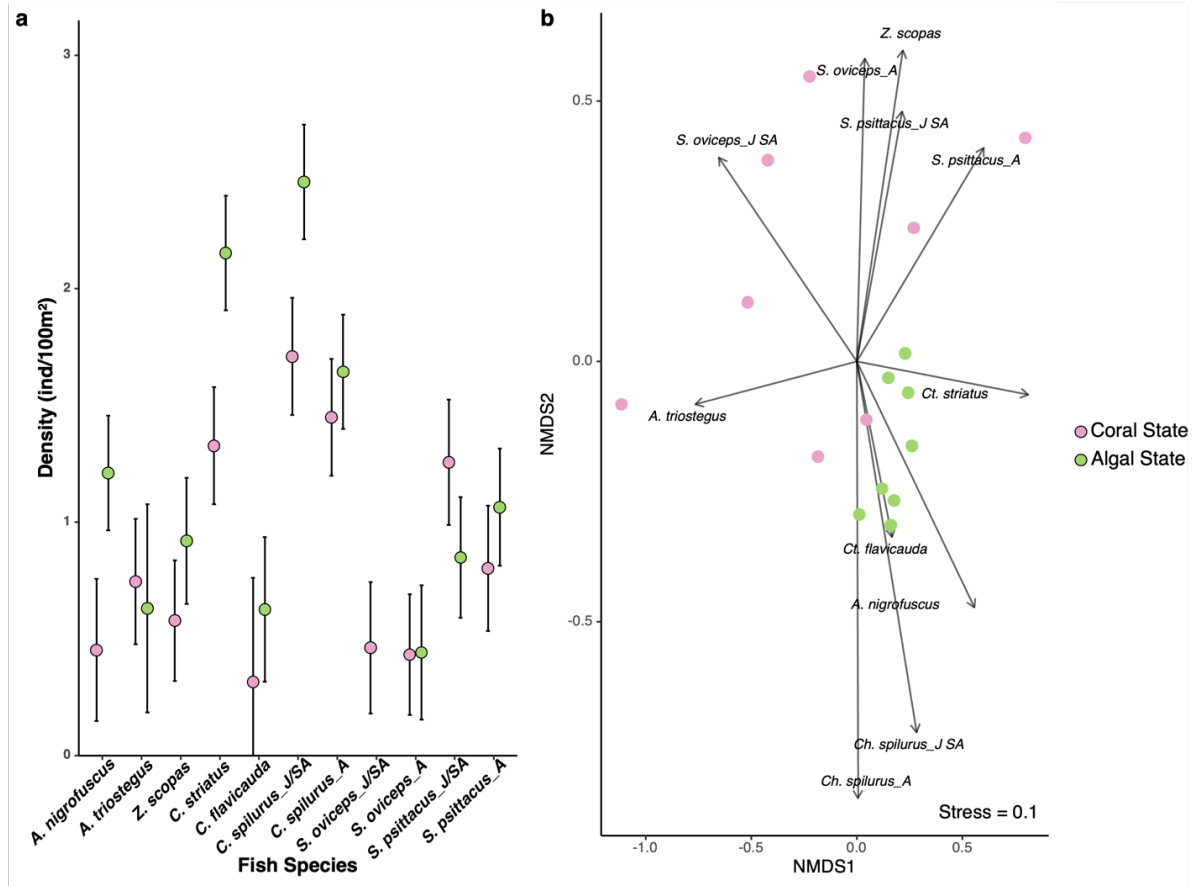


Figure S1. a) The density of herbivorous fish species (number of individuals/100m²) in the coral (pink) and algal (green) state. b) Non-metric multidimensional scaling analysis on the herbivore assemblage between coral (pink) and algal (green) state.

III. Effects of overfishing and nutrient enrichment on the population dynamics of the brown macroalga, *Turbinaria ornata* on coral reefs following a space clearing disturbance

Abstract

Following disturbances to coral reefs, opportunistic species can displace corals as the dominant benthic organisms. The brown macroalga, *Turbinaria ornata*, has become increasingly abundant on coral reefs in the South Pacific and can persist as an alternative stable state on reefs. Thus, it is important to understand the drivers that facilitate the success of this opportunistic species following a disturbance given the known direct negative effects of *T. ornata* on coral recruitment, growth, and microbiomes. As overharvesting of herbivorous fish and nutrient enrichment are known stressors on coral reefs, we set out to understand how these two stressors influence the population dynamics of *T. ornata* (measured as benthic cover, density, and recruitment timing) following a simulated disturbance that mimicked a cyclone. We conducted a ~4-year factorial experiment that created a gradient of herbivory pressure using fish exclosures of different sizes (Very Low, Low, Medium, and High) and manipulated nutrient enrichment (Ambient vs. Enriched Nutrients) on a reef in Moorea, French Polynesia. We found that herbivory was the main driver of *T. ornata* percent cover and density, with only a minor and inconsistent effect of nutrient enrichment that was only present under the lowest herbivory conditions. Surprisingly, this effect of nutrient enrichment at the lowest herbivory conditions resulted in less *T. ornata* density than under ambient nutrients. Further, we found that the highest levels of herbivory severely delayed the timing of *T. ornata* recruitment on the reef by at least two years after the experimental disturbance. These findings suggest that lower levels of

herbivory facilitate earlier recruitment of *T. ornata*, which could have important implications for reef population dynamics and community trajectory following disturbances. Browsing fishes were rare in our experiment, thus consumption of early life stages of *T. ornata* by other herbivorous fishes is likely important in preventing the establishment and growth of *T. ornata*. Overall, herbivory was the strongest factor in determining *T. ornata* benthic cover, density, and recruitment, suggesting that the overexploitation of herbivorous fish may give *T. ornata* a competitive advantage following disturbances.

Introduction

Coral reefs are increasingly impacted by anthropogenic stressors leading to an increase in opportunistic algal assemblages (Ledlie et al. 2007, Hughes et al. 2010, Roff et al. 2015b, Fukunaga et al. 2022). As these opportunistic species can displace corals, it is important to understand the drivers that facilitate the success of these opportunistic species. The brown macroalga, *Turbinaria ornata* is an opportunistic species that has become increasingly abundant on reefs in the South Pacific (Stiger and Payri 1999a, 1999b, 2005, Martinez et al. 2007, Zubia et al. 2015). For example, in the Society Islands, this alga was only documented in low densities before the 1980's (Payri and Naim 1982), but is now abundant on the benthos of many reefs and has been considered a secondary foundational species on reefs by some (Bittick et al. 2019).

Importantly, *T. ornata* patches can persist as an alternative stable state on reefs (Schmitt et al. 2022). *Turbinaria ornata*'s success is likely due to its quick maturity into a non-palatable stage due to its chemical and physical defenses that deter herbivores (Stiger and Payri 2004,

Davis 2018, Betancourt et al. 2023). In addition, *T. ornata* possess both an advantageous life history and key morphological traits that enhance their dispersal and survival (Stewart 2006b, 2008, Sirison and Burnett 2020, Zubia et al. 2020). Further, there are positive feedbacks that reinforce the dominance of *T. ornata*, including providing an associational refuge to conspecific recruits (Davis 2018) and ontogenetic variation in blade and thallus toughness that increases survivorship of adult thalli (Stiger and Payri 2005, Betancourt et al. 2023). Not only can adult *T. ornata* thalli facilitate recruitment of new *T. ornata*, but they can also promote the growth of other algal species, further contributing to a macroalgal-dominated state (Bittick et al. 2010). The proliferation of *T. ornata* may be problematic given its direct negative effects on coral recruitment (Bulleri et al. 2018) and growth (Bulleri et al. 2013, Clements et al. 2020) as well as the coral microbiome (Briggs et al. 2021). *Turbinaria ornata* may also alter the surrounding chemical and microbial environment in ways that may be unfavorable to corals (Pozas-Schacre et al. 2025). Thus, the establishment and growth of *T. ornata* following disturbance can potentially prevent recovery of corals and help transform reefs to algal dominance, which is often difficult to reverse (Schmitt et al. 2019).

Given that *T. ornata* has been increasing in abundance, it is key to address the potential factors that are influencing its dynamics. For example, herbivorous fishes often have strong influence on macroalgae on coral reefs (Lewis 1986, Burkepile and Hay 2006, Holbrook et al. 2016) and can suppress *T. ornata* during its palatable early life stages (Davis 2018). The experimental removal of herbivorous fish can result in an increase in abundance of macroalgae (Hughes et al. 2010, Holbrook et al. 2016) and a decline in abundance of adult and juvenile corals (Hughes et al. 2007, Zaneveld et al. 2016). Yet, most experiments

examining the role of herbivores do so by excluding all herbivorous fishes, which may not accurately represent how these fishes are lost to human fishing practices. Larger-bodied individuals are often disproportionately targeted resulting in shifts in the size-structure towards smaller individuals (Zgliczynski and Sandin 2017, Shantz et al. 2020). The herbivore functional groups are grazers, browsers, detritivores, scrapers and excavators, and the function of herbivores often correlates with their size. For example, large excavating parrotfishes are major agents of bioerosion, yet small excavators function similarly to scrapers by not removing as much of the substratum (Green and Bellwood 2009). Thus, the removal of larger herbivorous fish can severely impact the ability of the herbivore community to remove algae resulting in altered benthic dynamics (Fong et al. 2016, Shantz et al. 2020). Thus, understanding how reductions both in the abundance and body size of herbivorous fishes will impact the dynamics of algal communities is key to understanding the ecology of present-day coral reefs.

In addition to the importance of top-down control of algal communities by herbivores, bottom-up control by nutrient availability is another important driver of algal community dynamics on coral reefs (Smith et al. 2001, 2010, Littler and Littler 2007, Walsh 2011, Adam et al. 2021). Because coral reefs tend to be oligotrophic, algae often readily assimilate nutrients when nutrient availability increases (den Haan et al. 2016, Fong et al. 2020). For *T. ornata*, elevated nutrient concentrations can bolster physical defenses, making the alga more resistant to herbivores and increasing its survivorship (Bittick et al. 2016, Bergman et al. 2016, Sura et al. 2021a). In this way, nutrient enrichment may indirectly release *T. ornata* from herbivore control, even when herbivore populations remain intact. However, in natural

systems where nutrient enrichment coincides with reductions in herbivory due to fishing pressure, these effects may be compounded. Therefore, understanding how nutrient enrichment interacts with reductions in herbivory is critical to predicting *T. ornata* dynamics on coral reefs.

Our objective was to examine the effects of reductions in herbivory and increases in nutrient availability on the dynamics of the brown macroalga, *Turbinaria ornata*, after a significant space-clearing disturbance. Algae can rapidly expand and dominate reefs following disturbances due to the increase in newly available space that is easily colonized (Williams et al. 2001, Roff et al. 2015a, Fukunaga et al. 2022), and *T. ornata* is a successful opportunistic invader, often capitalizing on dead coral substrata (Ramesh et al. 2019). The period immediately following disturbances can be critical in shaping the trajectory of a coral reef as algae that quickly become established can inhibit future coral recruitment (Adam et al. 2022). Thus, the effects of herbivory and nutrients on algae may be amplified following space-clearing disturbances. To accomplish our objective, we conducted a ~4-year factorial experiment that created an incremental reduction of herbivory pressure (Very Low, Low, Medium, and High) using fish exclosures and manipulated nutrient enrichment (Ambient vs. Enriched Nutrients) on a forereef in Moorea, French Polynesia. To simulate a cyclonic disturbance, all live branching corals were removed and transplanted to other locations on the reef at the beginning of the experiment. We predicted that the higher levels of herbivory (High and Medium) would suppress *T. ornata* but that there would be a tipping point in the Low and Very Low treatments where *T. ornata* would escape herbivore control and proliferate. Further, we predicted that nutrient enrichment would increase the abundance of *T.*

ornata the most at the lowest levels of herbivory but also that nutrients would increase *T. ornata* somewhat even in the presence of herbivores as nutrients can increase anti-herbivore defenses in *T. ornata* (Bittick et al. 2016, Bergman et al. 2016).

Methods

Experimental Design

The experiment was located on the forereef on the north shore of Moorea, French Polynesia (S17° 28.386' W149° 49.059'). To test the effects of herbivory and nutrient enrichment on benthic community dynamics, we conducted a ~4-year factorial experiment (July 2018-July 2022). We deployed 32 1.25 m² fish exclosures of 112 cm × 112 cm × 50 cm dimensions (L × W × H) at 12 m depth. Each exclosure was constructed with plastic-coated wire mesh with 2.5 × 2.5 cm mesh size and attached to 50cm pieces of stainless steel all-thread that had been anchored into the reef substrate. The experiment was a randomized block design with 8 blocks each containing one plot of each of the four herbivory treatments (Very Low, Low, Medium, High). Four of the blocks were enriched with nutrients and four were left at ambient nutrients. Thus, each combination of herbivory and nutrients had n = 4. To simulate a disturbance by a cyclone we removed all of the live branching corals and transplanted them to different locations on the reef. Following the removal and transplanting of the live branching corals, the remaining encrusting corals were lightly scraped with wire brushes to mimic the scouring effect that a cyclone creates. All macroalgae, which were rare, were also removed.

To manipulate the size distribution of fishes that entered the experiment, and therefore the levels of herbivory, we cut openings of different sizes to create the four herbivory treatments: 1) Very Low Herbivory - exclosures with 2.5 cm × 2.5 cm openings, 2) Low Herbivory - exclosures with 5 cm × 5 cm openings, 3) Medium Herbivory - exclosures with 7.5 cm × 7.5 cm openings, and 4) High Herbivory exclosures with four sides (2.5 cm × 2.5 cm openings) but no top to allow access by all fishes.

Nutrient enrichment was achieved with slow-release fertilizer similar to methods used in previous studies (Zaneveld et al. 2016, Burkepile et al. 2020). Fertilizer diffusers were constructed of 15 cm diameter PVC tubes with 0.5cm holes drilled in them. The tubes were filled with 175g of Osmocote (19-6-12, N-P-K) fertilizer pellets and wrapped with plastic mesh to keep the fertilizer pellets inside the tubes but allow the diffusion of nutrients from the pellets out of the tubes. Diffusers were attached inside the nutrient treatment exclosures for a total of 5 diffusers per exclosure (one at each corner and one in the center of the plot). We replaced enrichment diffusers every 12-16 weeks except for two periods during the COVID-19 pandemic (01-30-2020 to 08-31-2020, and 08-31-2020 to 02-08-2021) where enrichment diffusers were not replaced until 08-31-2020 and not again until 02-08-2021 when travel to Moorea was not possible. Thus, enrichment tubes were deployed without replacement for longer than usual likely reducing the levels of enrichment during these periods. Nutrient enrichment was shown to be effective in increasing water column ammonium (NH_4^+) nitrate (NO_3^-) + nitrite (NO_2^-), and phosphate (PO_4^{3-}) concentration more than 2 fold compared to ambient treatments (Becker et al. 2021).

Quantification of fish community

To quantify how fishes used the different treatments of the experiment, we conducted 5 min surveys per enclosure. During the 5 min surveys, each fish that entered the enclosure was identified to species and the total length (to the nearest cm) of the fish was estimated. The total body length of each fish was converted to biomass using allometric scaling relationships (Brooks and Adam 2019). These surveys were done during three time points each year of the experiment (April, August, November), except for two time points missed due to the COVID-19 pandemic.

Quantification of the benthic community

At three time points each year (April, August, November - except for the two time points missed due to the COVID-19 pandemic noted above), we quantified benthic cover in each enclosure in our experiment via point contacts on photomosaics. We took ~64 individual photographs of each enclosure using Olympus TG cameras. Then, we generated photomosaics by combining the 64 individual photographs from each enclosure using Agisoft Metashape software. The high-resolution imagery created by this process allows for the identification of benthic space holders (i.e., coral, macroalgae, turf). We analyzed the photomosaics using CoralNet (Beijbom et al. 2015) by identifying the organisms at 225 evenly spaced point on each photomosaic. We used this to calculate the percent cover of *T. ornata*.

In addition to the cover data generated from the photomosaics, we also conducted *in situ* counts of individuals of *T. ornata* to assess the population structure. To determine the

abundance of *T. ornata*, we counted each individual thallus in each plot in both April 2021 and April 2022. We also measured the thallus length of each individual alga to the nearest cm using a ruler. The density of *T. ornata* in each enclosure was calculated based on the count data.

Statistical Analysis

Effect of experimental treatments on herbivore biomass and size

While the enclosures were visited by the entire fish community, here we focus only on the herbivores that accessed the plots as they are most relevant to algal dynamics. To test whether the experimental treatments (herbivory and nutrient enrichment) altered the biomass of the herbivorous fish that accessed the experiment, we conducted a linear mixed model with plot nested within block and the timepoint sampled as random effects. The block level random effect was dropped due to a singularity error. Biomass was log transformed to meet assumptions of homogeneity of variance. To distinguish whether changes in biomass across herbivore exclusion treatments were due to changes in body size, we conducted a linear mixed model on fish size (total length) with the herbivory treatments (Very Low, Low, Medium, and High) as a fixed effect with plot nested within block as random effects. Total length was log transformed to meet assumptions of homogeneity of variance.

Given, the unique functions of each of the herbivore functional groups, we also were interested in how the experimental treatments (herbivory and nutrient enrichment) altered the biomass of each herbivore functional group individually. The herbivore functional groups

evaluated were grazers, detritivores, scrapers, and excavators (Green and Bellwood 2009). A linear mixed model with the interaction of herbivory and nutrient treatments as the main effects and biomass of each respective functional group as the response with plot and timepoints as random effects was conducted. This was conducted for each herbivore functional group. Biomass was log transformed to meet assumptions of homogeneity of variance.

Effects of herbivory and nutrient treatments on *T. ornata* benthic cover, recruitment and density

To analyze the effects of the herbivory treatments, nutrient treatments, and time on the percent cover of *T. ornata* cover, we conducted a generalized linear mixed model. Herbivory treatments, nutrient treatments, and time (as days since start of the experiment) were treated as fixed effects with plot nested within block as a random effect to account for the nested and blocked experimental design. Random effects were dropped if there was a singularity error. We ran the model with a tweedie and zero-inflated beta distribution and used AIC values to pick the best-fitting model. The best model fit was given by the tweedie distribution (Table S1). The tweedie distribution provides a superior fit for overdispersed and zero-inflated data (Shono 2008).

To examine the effect of the herbivory and nutrient treatments on the timing of recruitment of *T. ornata*, we conducted a linear mixed model with plot nested within block as a random effect. Recruitment was defined as the year of first detection when percent cover of *T. ornata* exceeded zero and is represented in fractions of a year. Random effects were dropped as there

was a singularity error, thus the final model was a linear model. To test the significance of the main effects and their interaction, we conducted an ANOVA using the *car* package (Fox and Weisberg 2019). Model assumptions were checked through visual assessment of diagnostic plots. We used the *emmeans* package to perform post-hoc comparisons.

To analyze the effects of the herbivory and nutrient treatments on the density of *T. ornata*, we conducted a generalized linear mixed model. Herbivory and nutrient treatments were treated as fixed effects with plot nested within block as a random effect to account for the nested and blocked experimental design. Models were conducted on the overall *T. ornata* density and for the different *T. ornata* life stages (recruit < 2cm, juvenile $\leq$ 5cm, and adult > 5cm). We ran the model with a Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial, and tweedie distribution and used AIC values to pick the best-fitting model (Table S2 and S3). The random effects were dropped from the models if there was a singularity error. This analysis was conducted for both years in which the *in-situ* count data were collected (2021 and 2022). For the overall *T. ornata* density, the best model fit was given by a zero-inflated negative binomial model across both years. For the life stages across both years (2021 and 2022), the best model fit was given by the negative binomial distribution except for juveniles and recruits in 2022 for which the model with the zero-inflated negative binomial distribution was the best fit (Tables S4, S5, S6, S7, S8, S9). For *T. ornata* recruit densities in 2022, the zero-inflated Poisson model was not considered as the model did not converge. The presence of overdispersion was evaluated using the *performance* package in R (Lüdtke et al. 2021).

All linear mixed models were conducted using the *lme4* package (Bates et al. 2015). Model assumptions were checked through visual assessment of diagnostic plots. To assess the significance of the main effects and their interaction, we conducted a Type III Wald's F test with the Kenward-Rogers method of degrees of freedom estimation. We used the *emmeans* package to conduct post-hoc comparisons (Lenth 2024).

Generalized linear mixed models were conducted using the *glmmTMB* package in R (Brooks et al. 2017). Model residuals were examined using simulation-based model checking from the *DHARMA* package in R (Hartig 2022). To assess the significance of the main effects and their interactions, we conducted a Type III Wald chi-square analysis. Pairwise comparison analyses were performed using the *emmeans* package in R (Lenth 2024).

All statistical analyses were conducted in R version 4.4.1.

Results

Effects of fish exclusion treatments on herbivore biomass and size

The herbivory treatments created a reduction in herbivory (Fig. 1) that mimicked the effects of size-selective fishing similar to previous experiments (Holbrook et al. 2016, Shantz et al. 2020). There was a significant effect of herbivory treatments ($F_{(3,147.48)} = 26.91$, $p < 0.001$) but no significant effect of nutrient enrichment ($F_{(1,6.08)} = 0.06$, $p = 0.812$) or their interaction ($F_{(3,147.27)} = 1.44$, $p = 0.233$) on overall herbivorous fish biomass (Table S10). Overall herbivore biomass increased with greater consumer access (Fig. 1a). Pairwise comparisons

revealed that herbivore biomass was significantly lower in the Very Low and Low herbivory levels compared to the Medium and High ($p < 0.001$), with a more than an 8-fold increase in fish biomass from the Very Low to High treatments. Fish biomass was lower in the Very Low compared to the Low herbivory treatment ($t.ratio = -3.260$, $p = 0.008$), but there was no significant difference between the Medium and High herbivory treatments ($t.ratio = -0.404$, $p = 0.978$).

Similar to the overall biomass patterns, mean fish length increased with greater consumer access (Fig. 1b). There was a significant effect of the herbivory treatments on the length of fish ($F_{(3,482.83)} = 20.318$, $p < 0.001$) (Table S11). Pairwise comparisons revealed fish length was significantly lower in the Very Low treatment as compared to the Medium and High treatments (Very Low and Medium: $t.ratio = -5.497$, $p < 0.001$; Very Low and High: $t.ratio = -6.877$, $p < 0.001$). Fish size was also reduced in the Low treatment as compared to the Medium and High treatments (Low and Medium: $t.ratio = -3.641$, $p = 0.002$; Low and High: $t.ratio = -5.252$, $p < 0.001$).

Similar patterns were seen with increasing biomass across the herbivory treatments for the different herbivore functional groups (Fig. S1). For the biomass of grazers, detritivores, scrapers, and excavators, there was a significant effect of herbivory treatments ($p < 0.05$) but not a significant effect of nutrients nor their interaction ($p > 0.05$) (Table S12). For these functional groups, biomass increased with increasing consumer access (from Very Low to High herbivory treatments) (Fig S1). Notably, the Very Low and Low treatments completely excluded the scrapers and excavators as they were only present in the Medium and High

treatments. Finally, the only browser recorded (*Naso lituratus*) was only recorded once across the observed time periods and only in the High herbivory treatment.

Effects of herbivory and nutrients on *T. ornata* cover and recruitment over time

While visually over time, there appeared to be a trend of higher percent cover of *T. ornata* in the ambient treatments in the Very Low and Low treatments, there was no significant effect of nutrient enrichment or interaction between nutrients and herbivory, and time on the percent cover of *T. ornata* (Table S13). The lack of nutrient effect could be due increased variability in the lower herbivory treatments (Fig. 2). However, there was a significant interaction of herbivory and time on the cover of *T. ornata* (Herbivory $\times$ Time interaction, $\chi^2 = 9.008$, $df = 3$, $p = 0.029$; Fig. 2; Table S13) indicating that the effects of herbivory on the cover of *T. ornata* varied over the course of the experiment. There was a 9-fold difference between the mean percent cover of the Very Low and High herbivory treatments by the end of the experiment with the mean percent cover of *T. ornata* being higher in the lower herbivory treatments (Very Low: $8.02 \% \pm 2.95$; Low: $4.70 \% \pm 2.20$) than the higher herbivory treatments (Medium: $2.45 \% \pm 1.12$; High: $0.82 \% \pm 0.34$) (Fig. 2).

The timing of *T. ornata* recruitment was significantly affected by the herbivory treatments ($F_{(3,16)} = 17.0891$, $p < 0.001$; Fig. 3, Table S14). Recruitment occurred in the earlier part of the experiment in the lower herbivory treatments compared to the higher herbivory treatments (Very Low vs Medium: t-ratio= -4.803, $p = < 0.001$; Very Low vs High: t-ratio= -5.348 , $p = < 0.001$) and (Low vs Medium: t-ratio= -4.546, $p = 0.002$; Low vs High: t-ratio= -5.113 , $p = < 0.001$). Specifically, the lower herbivory treatments (Very Low and Low)

showed recruitment in the first two years compared to the higher herbivory treatments (Medium and High), which showed recruitment occur in the last two years of the experiment (Fig. 3). A number of exclosures never had colonization by *T. ornata* including three High (two enriched, one ambient), two Medium (one enriched, one ambient), one Low (ambient), and two Very Low herbivory replicates (one enriched, one ambient).

Effects of herbivory and nutrient treatments on the overall density of *T. ornata*

When we counted the density of individual thalli of *T. ornata* in 2021, herbivory treatment had a significant effect on the density of *T. ornata* with lower herbivory associated with higher densities (individuals/m²) ($\chi^2 = 23.816$, df = 3, $p < 0.001$). Nutrient enrichment also had a significant effect with lower densities in the enriched treatments ($\chi^2 = 4.296$, df = 1, $p = 0.038$) (Fig 4a), but there was no significant interaction between herbivory and nutrient treatment ($\chi^2 = 2.819$, df = 3, $p = 0.421$; Table S15). Pairwise comparisons revealed that density was higher in the both the Very Low and Low herbivory treatments compared to the Medium herbivory treatments (Very Low and Medium: z.ratio = 5.85, $p < 0.001$; Low and Medium: z.ratio = 5.85, $p < 0.001$; Table S16). The High herbivory treatment resulted in zero *T. ornata* thalli across all replicates. As a result, they were not included in the pairwise comparisons because the model could not provide meaningful estimates for this treatment level.

In 2022, herbivory treatment had a significant effect on the density of *T. ornata* (individuals/m²) ($\chi^2 = 9.985$, df = 3, $p = 0.019$) but there was no effect of nutrient treatment ($\chi^2 = 0.214$, df = 1, $p = 0.644$) and no significant interaction ($\chi^2 = 0.518$, df = 3, $p = 0.915$;

Fig 4b; Table S15). Pairwise comparisons with Tukey-adjustment across herbivory treatments revealed that *T. ornata* density was significantly higher in the Very Low and Low treatments compared to the High herbivory treatments (Very Low vs. High: z.ratio = 3.92, $p < 0.001$; Low vs. High: z.ratio = 4.01, $p < 0.001$). The only other significant difference was between the Low and Medium herbivory treatments (z.ratio = 2.64, $p = 0.041$; Table S17).

Effects of herbivory and nutrient treatments on the density of *T. ornata* by life stage

For 2021, there was only a significant effect of herbivory on the density of adult *T. ornata* ($\chi^2 = 16.131$, $df = 3$, $p = 0.001$; Fig. 4C; Table S18) with greater density in the Very Low and Low compared to the Medium herbivory treatments (Very Low and Medium: z.ratio = 4.809, $p < 0.001$; Low and Medium: z.ratio = 4.166, $p < 0.001$). For juvenile *T. ornata* density, there was also only a significant effect of herbivory ($\chi^2 = 12.786$, $df = 3$, $p = 0.005$; Fig. 4C; Table S18) with greater density in the Very Low and Low compared to the Medium herbivory treatments for juvenile *T. ornata* (Very Low and Medium: z.ratio = 4.368, $p < 0.001$; Low and Medium: z.ratio = 4.365, $p < 0.001$). For recruits of *T. ornata*, there was not a significant effect of the herbivory, nutrient treatments, nor their interaction on their density (Herbivory: $\chi^2 = 0.776$, $df = 3$, $p = 0.855$; Nutrients: $\chi^2 = 0.776$, $df = 1$, $p = 0.378$; Herbivory*Nutrients: $\chi^2 = 1.118$, $df = 3$, $p = 0.773$; Fig. 4C; Table S18).

For 2022, there was not a significant effect of herbivory, nutrient treatments, nor their interaction on the density of *T. ornata* adults (Herbivory: $\chi^2 = 7.050$ $df = 3$, $p = 0.070$; Nutrients: $\chi^2 = 0.008$, $df = 1$, $p = 0.927$; Herbivory*Nutrients: $\chi^2 = 2.467$, $df = 3$, $p = 0.481$; Fig 4D; Table S19). However, there was a significant effect of herbivory on the density *T.*

ornata juveniles in 2022 ($\chi^2 = 16.924$ df = 3, $p < 0.001$; Fig 4D; Table S19) with greater densities in the Very Low and Low compared to the Medium and High herbivory treatments (Very Low and Medium: z.ratio = 2.856, $p = 0.022$; Very Low and Open: z.ratio = 4.960, $p < 0.001$; Low and Medium: z.ratio = 2.875, $p < 0.001$; Low and High: z.ratio = 5.040, $p < 0.001$). Similarly, there was only an effect of herbivory on the density of *T. ornata* recruits in 2022 ($\chi^2 = 8.854$ df = 3, $p = 0.031$; Fig 4D; Table S19) with significant differences between the Very Low and High (z.ratio = 3.242, $p = 0.007$) and Medium and High treatments (z.ratio = 4.036, $p = 0.0003$).

Discussion

Our results reveal that herbivory is the dominant force in controlling *T. ornata* dynamics on disturbed coral reefs, with a minimal effect of nutrient enrichment, similar to patterns from other experiments on algal dynamics during early periods of succession (Jompa and McCook 2002, Sotka and Hay 2009). In particular, we found that herbivory had the strongest influence on determining *T. ornata* benthic cover, density, and recruitment. When herbivorous fishes had full access to the reef, they were able to delay recruitment of *T. ornata* by at least two years which reveals the critical role of herbivorous fish following disturbances. Therefore, herbivory slows recruitment, which could allow other benthic organisms such as corals time to establish first, leading to important priority effects that could facilitate coral abundance. Our research suggests that the ongoing exploitation of herbivores on coral reefs could facilitate recruitment of long-lived macroalgae, such as *T. ornata*, after disturbances that may begin the trajectory towards an algal-dominated state.

The manipulation of consumer access through the herbivory treatments (Very Low, Low, Medium, and High) in our experiment successfully created a gradient of overall herbivore biomass and individual herbivore size. This gradient allowed us to demonstrate that while herbivory is the main factor in controlling *T. ornata* population dynamics, the impact of herbivory is modulated by the abundance and size structure of the herbivore community. Our results are similar to others showing differential effects of different levels of herbivory depending on herbivore size. For example, an experiment in the Caribbean that created a gradient of herbivory found that removing medium and large parrotfishes resulted in a 4-fold increase in algal biomass and a 10-fold increase in macroalgal diversity, further highlighting the critical role of larger herbivores (Shantz et al. 2020). Similarly, another experiment in the Caribbean found that reduced herbivory by excluding only the largest herbivorous fish resulted in an increase in algal abundance and reduced coral recruitment (Steneck et al. 2014). Experiments in the lagoon of Moorea, French Polynesia that also created a reduction of herbivory found that the reduction in abundance and size of herbivorous fishes reduced their ability to control algal abundance (Fong et al. 2016). Further, Moorea-based forereef experiments that created a gradient of herbivory found a tipping point of where macroalgae escaped control of herbivores (Holbrook et al. 2016). Similar to Holbrook et al. (2016), ambient herbivory levels in our experiment (as represented by the High herbivory treatments) was sufficient to prevent the proliferation of macroalgae. Thus, larger herbivorous fish play unique roles on reefs and are important for effective top-down control of macroalgae.

Reductions in herbivory not only led to a higher abundance of *T. ornata* but also led to earlier algal recruitment. The Very Low and Low herbivory exclosures saw *T. ornata* recruiting to

exclosures over a year faster than the higher levels of herbivory. These differences in the timing of recruitment can be important because the order and timing of species colonization during a community reassembly can lead to drastically different community trajectories by preempting and modifying niches before other species arrive (Symons and Arnott 2014, Fukami 2015). On coral reefs, consumers are known to influence benthic community succession on coral reefs (McDevitt-Irwin et al. 2023) with herbivores often being the dominant driver shaping early algal recruitment and growth (Diaz-Pulido and McCook 2003). Indeed, when herbivores are excluded, priority effects may emerge (McDevitt-Irwin et al. 2023) with the early arrival of algae under low herbivory regimes giving algae a competitive advantage and inhibiting the recruitment of corals (Adam et al. 2022). While in this study we did not focus on the consequences for corals, the ability of *T. ornata* to colonize faster under low herbivory conditions after a disturbance sets the stage for important priority effects that could impact the recovery rate of corals over the long term in these communities. While it may be initially surprising that there was any recruitment in the higher herbivory treatments when the experimental factors remained unchanged, the experiment occurred during a backdrop of widespread coral mortality on the forereef following a 2019 coral bleaching event (Speare et al. 2022) with an eventual growth of macroalgae (Kopecky et al. 2024). Following coral mortality, algae colonize newly available substrate, leading to a dilution of herbivory intensity as herbivores need to graze over a larger area (Williams et al. 2001). Thus, macroalgae that were once easily excluded can become established. In the case of *T. ornata*, once it establishes and exceeds 2 cm, it is highly unpalatable to herbivorous fish, resulting in positive feedbacks that reinforce the *T. ornata* population (Davis 2018).

In our highest herbivory treatment, herbivores often inhibited recruitment of *T. ornata* until after the third year of the experiment, and in some cases completely prevented *T. ornata* from colonizing. These data suggest that the extant populations of herbivorous fishes on the forereef of Moorea can keep *T. ornata* from proliferating. Mature *T. ornata* is considered to be a highly unpalatable alga not readily consumed by most herbivorous fish (Bittick et al. 2010, Davis 2018, Sura et al. 2021b). But our results show that if there is sufficient herbivory following a disturbance, herbivores can prevent *T. ornata* from establishing. Interestingly, browsing herbivores (those that eat macroalgae) are generally rare on the forereefs of Moorea (Brooks 2025) and our data showed that browsers very rarely visited our experiment. This pattern indicates that herbivory by the other functional groups such as grazers, scrapers, and excavators were likely able to remove small recruits of *T. ornata* when they were likely still part of the low-lying algal community. Mortality of *T. ornata* can be quite high when they are small (Davis 2018, Gallagher 2025), which likely prevents mature *T. ornata* from establishing.

None of the densities of the algal life stages studied were affected by nutrient enrichment, again revealing the dominant role of herbivory in this highly oligotrophic system. Lower herbivory levels were associated with higher densities of the earlier life stages by the fourth year of the experiment reveal that the population of *T. ornata* is being sustained. Not only does reduced herbivory level lead to earlier recruitment of *T. ornata*, but also supports the continued production of new individuals which reinforces their persistence. Similar to the results on the overall density of *T. ornata*, herbivory rather than nutrient enrichment is the dominant force in shaping *T. ornata* population structure. Similarly, on the Great Barrier

Reef, herbivory strongly reduced the density and growth of *Lobophora* and *Sargassum* recruits, while nutrient enrichment only had minor effects on the growth of *Lobophora* recruits and no effects on *Sargassum* recruits (Diaz-Pulido and McCook 2003). Thus, it is important to consider the life stage of macroalgae. In particular, it is especially critical to understand the dynamics of the different *T. ornata* life stages as the ontogenetic changes they undergo that facilitate their own success (Stewart 2006a, 2008) in addition to the facilitation of younger cohorts (Davis 2018), is part of what makes *T. ornata* such a successful opportunistic species especially on disturbed reefs. Overall, our results demonstrate a sustained population of *T. ornata*, consisting of mature adults, likely contributes to ongoing recruitment, reinforcing their long-term persistence. Given the positive feedbacks that allow for *T. ornata*'s success, the persistence of *T. ornata* across the life stages of adults, juveniles, and recruits underscore how established populations can endure following disturbances.

While previous studies found that nutrient enrichment reduced the effect of herbivory on *T. ornata* (Bittick et al. 2016, Gallagher 2025), we did not find an increase in *T. ornata* cover or density when exposed to nutrient enrichment. In contrast, we found nutrient enrichment decreased overall *T. ornata* density, but only in 2021. This suggests an inconsistent, subtle negative effect of nutrient enrichment on *T. ornata* density. This result was somewhat surprising given that many previous experiments have shown a positive effect of nutrient enrichment (Smith et al. 2001, 2010, Jompa and McCook 2002, Zaneveld et al. 2016), although this effect is often modest as compared to the effects of removing herbivores (Burkepile and Hay 2006). In contrast, nutrients can sometimes inhibit algae as research from the Caribbean that shows nutrient enrichment can inhibit the percent cover, height, and

biomass of the brown macroalga *Dictyota* (Ramseyer et al. 2021). Other research has shown that nutrient additions can actually increase the rates of herbivory (Burkepile and Hay 2009) on algae, potentially leading to a suppression of overall algal abundance. Our data on fish abundance did not suggest this effect, although we did not quantify herbivory directly. Another potential mechanism influencing the slight negative effect of nutrients on *T. ornata* could be shifts in other members of the algal community that impact *T. ornata*. Nutrient enrichment often enhances the growth of filamentous algae and often facilitates its abundance (Zaneveld et al. 2016), which can outcompete and suppress macroalgal abundance (Farrell et al. 2025). There was statistically no effect of nutrient enrichment on the benthic cover of *T. ornata* even though graphically it appears that enriched treatments have lower percent cover of *T. ornata*. However, the replicates in the lower herbivory treatments appeared to be variable. Thus, even if nutrient enrichment did affect the percent cover of *T. ornata* in some replicates, it was not consistent across the experiment. Thus, there are several potential mechanisms that could have led to the subtle negative impact of nutrients on *T. ornata*.

There is a need for a more nuanced understanding of the interaction of overfishing and nutrient enrichment on the dynamics of opportunistic macroalgae following disturbances. We show that on the forereefs in Moorea, French Polynesia, following a disturbance, herbivory seems to be an overwhelming force preventing establishment of *T. ornata*, an important opportunistic algal becoming more abundant on Indo-Pacific reefs. Importantly, our work utilized a gradient of herbivory, which we argue should be used more often as it allows detection of herbivory limit where algae may gain hold and dominate (Holbrook et al. 2016,

Schmitt et al. 2019, Shantz et al. 2020). Our work provides insight on the how the consequences of overharvesting of herbivorous fish may be amplified following disturbances when an opportunistic species such as *T. ornata* may establish, persist, and dominate. Reductions in herbivory could magnify priority effects where the establishment of *T. ornata* could then suppress the recovery of corals (Bulleri et al. 2013, 2018, Adam et al. 2022). Further, given the range of the potential effects of nutrient enrichment on algae including increased macroalgal abundance (Smith et al. 2010), decreased algal growth (Ramseyer et al. 2021), or inconsistent negative effect as in our study, reveals there is still much to be disentangled on the effects of nutrient enrichment. Thus, more studies are needed that evaluate a gradient of both herbivory and nutrient enrichment on other opportunistic algal species and the consequences on the coral community allowing us to better understand the interaction of these two stressors on disturbed coral reef communities.

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Figures and Tables

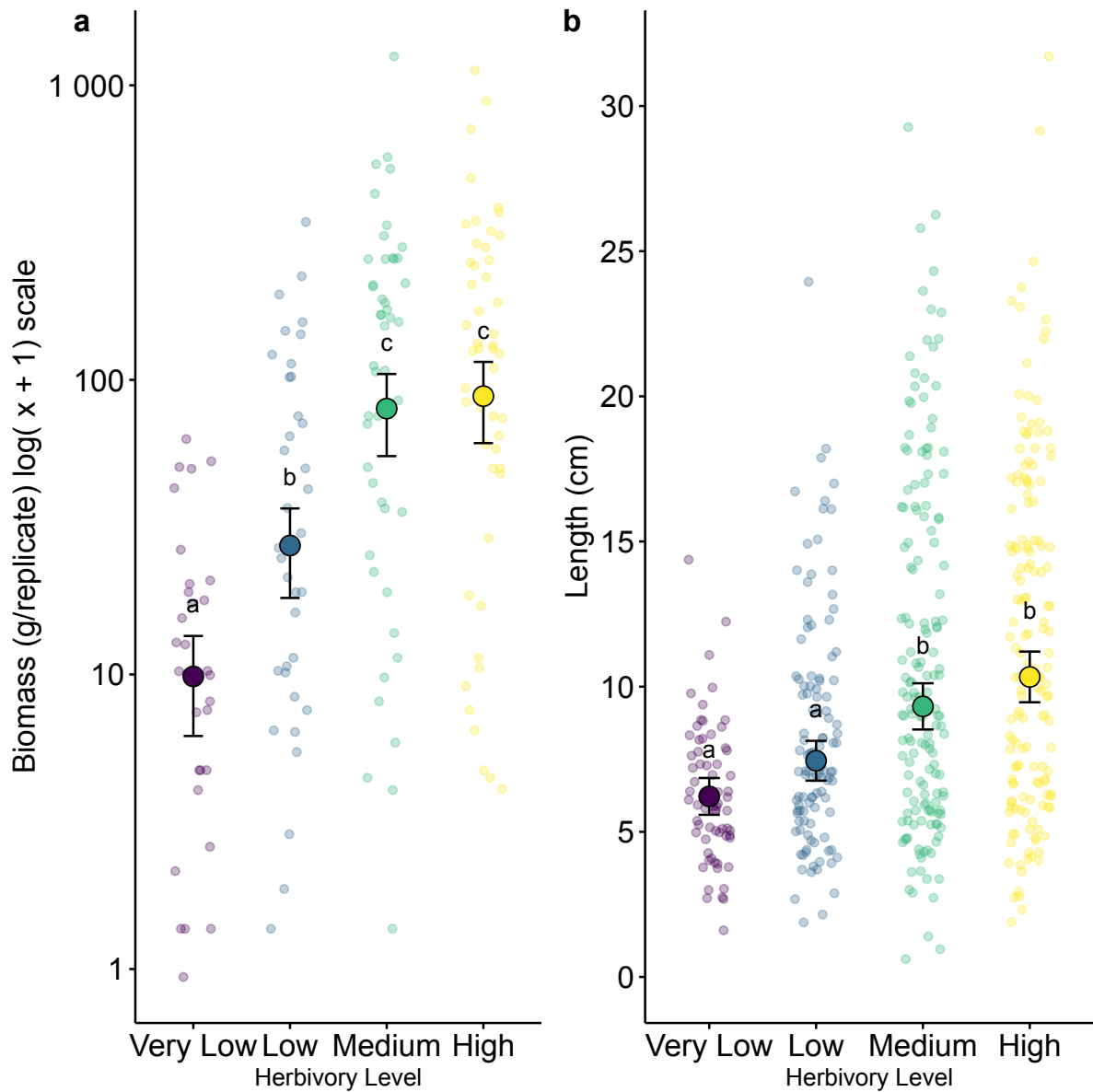


Figure 1. Estimated marginal means $\pm$ SE and raw data of a) overall herbivorous fish biomass (g/ cage replicate) on a log (x + 1) scale and b) total length of individual fish across herbivory treatments. Categories that do not share letters are significantly different from each other based on Tukey post-hoc analysis. Statistics are from linear mixed models.

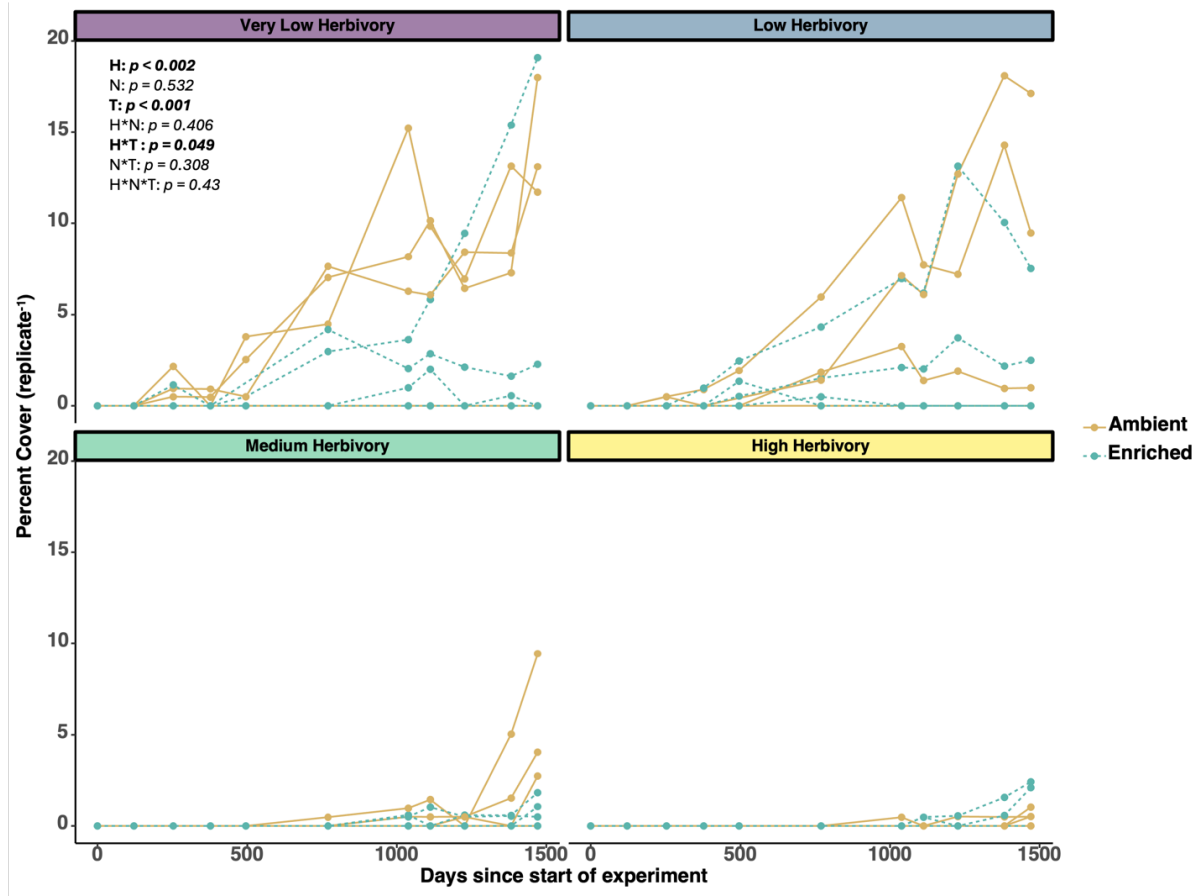


Figure 2. Benthic cover of *Turbinaria ornata* across the herbivory and nutrient enrichment treatments over time since the experiment began in 2018. Plots show the trajectories of individual replicates with treatments. (Herbivory treatments = H, Nutrient treatments = N, Time = T). Statistics are from the generalized linear mixed model.

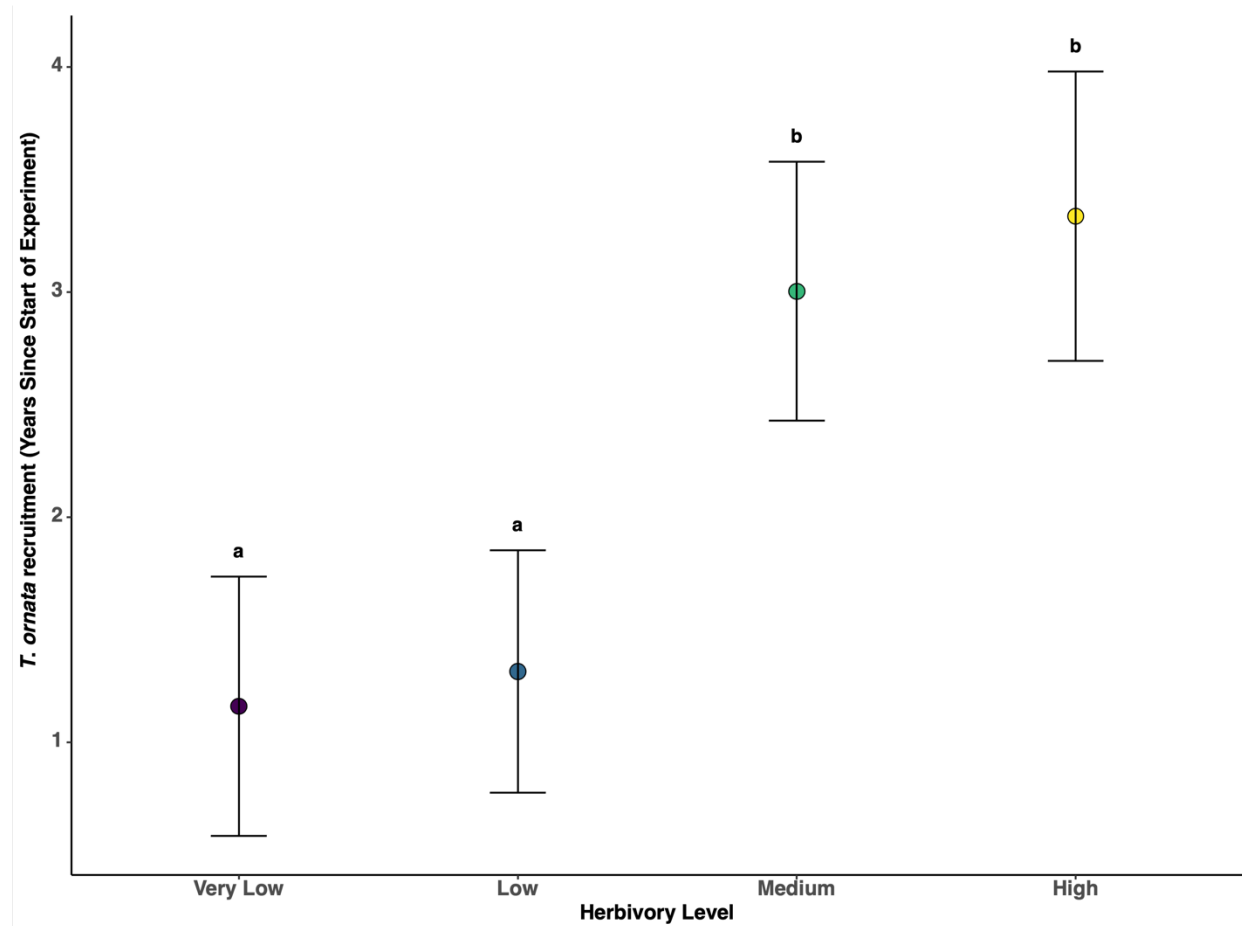


Figure 3. Estimated marginal means $\pm$ SE for number of years from the beginning of the experiment for which *T. ornata* first recruited across the herbivory treatments. Categories that do not share letters are significantly different from each other based on Tukey post-hoc analysis from the linear model.

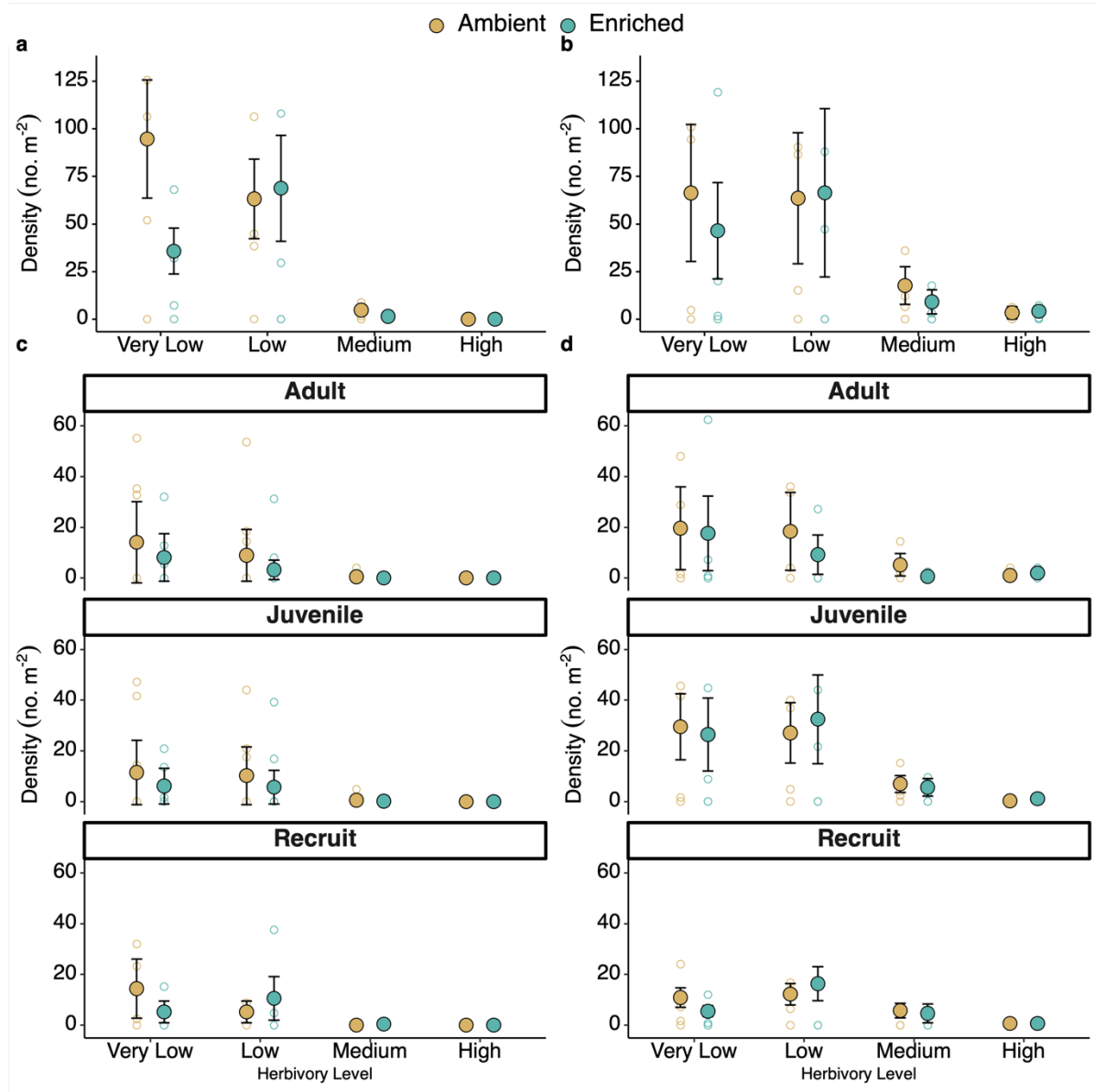


Figure 4. Estimated marginals $\pm$ SE and raw data of the overall density of *T. ornata* by herbivory level (Very Low, Low, Medium, High) and nutrient treatments (Ambient and Enriched) in (a) April 2021 and (b) April 2022, and separated by *T. ornata* life stage of adult, juvenile, and recruits in (c) April 2021, and (d) April 2022.

Supplementary Figures and Tables

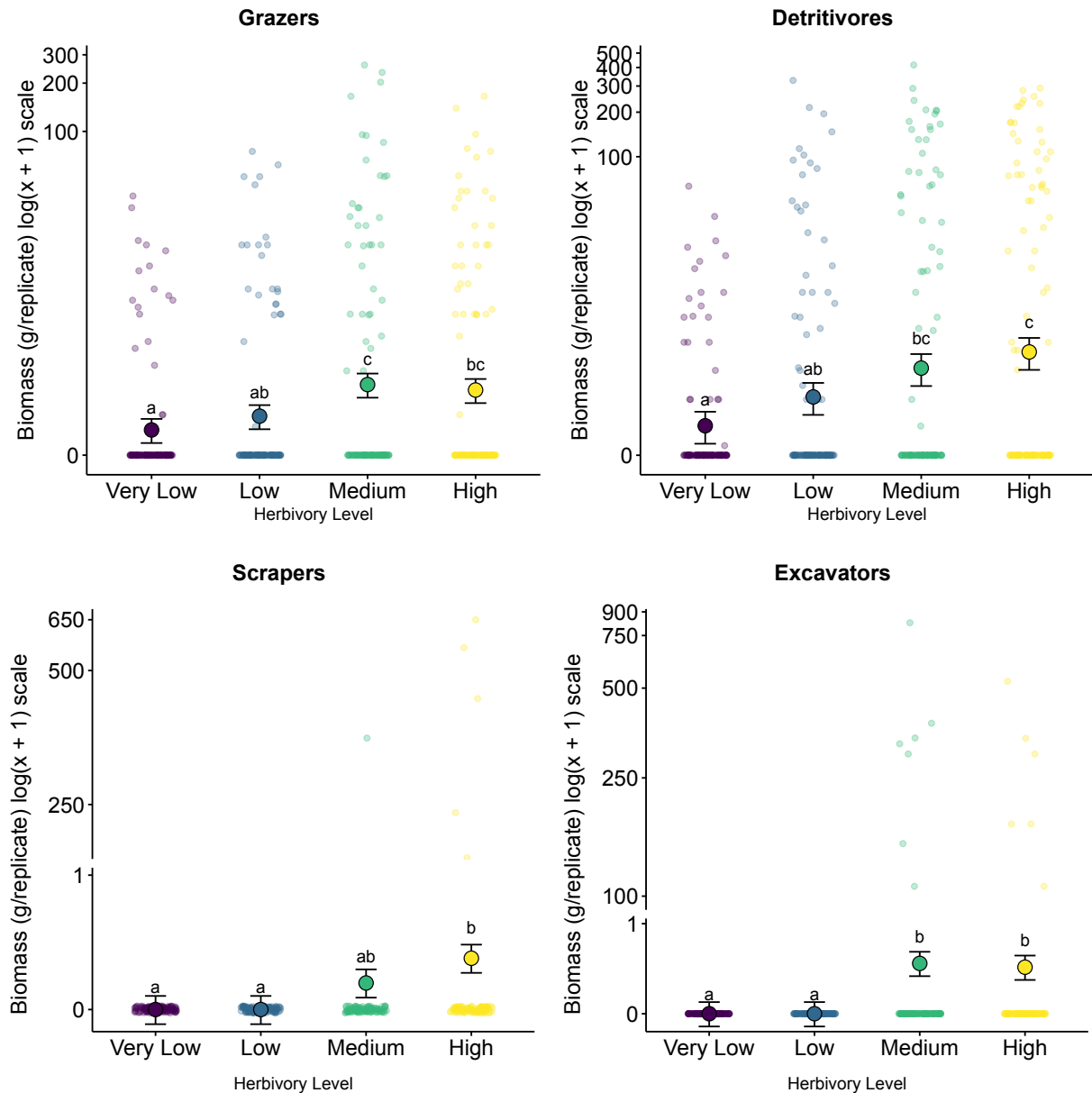


Figure S1. Estimated marginal means $\pm$ SE and raw data of biomass of each herbivore functional group (a) Grazers across herbivory treatments. Categories that do not share letters are significantly different from each other based on Tukey post-hoc analysis. Note different Y axes for each functional group and y-axis breaks for the Scraper and Excavator panels.

Table S1. AIC model selection of the effects of herbivory treatment, nutrient treatment, and time on the proportion of *T. ornata* cover.

	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LL</i>	<i>Cum.Wt</i>
Tweedie	19	-348.27	0.00	1.00	1.00	194.29	1
Zero-Inflated Beta	20	-112.22	236.05	0.00	0.00	77.39	1

Table S2. AIC model selection on the effects of herbivory and nutrient treatments on the overall density of *T. ornata* in 2021.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
zinbinom	10	184.28	0.00	1.00	1.00	-76.90	1.00
tweedie	11	198.65	14.37	0.00	0.00	-81.72	1.00
nbinom	10	198.78	14.50	0.00	0.00	-84.15	1.00
zipoiss	11	281.69	97.41	0.00	0.00	-123.24	1.00
poiss	10	343.76	159.48	0.00	0.00	-156.64	1.00

Table S3. AIC model selection on the effects of herbivory and nutrient treatments on the overall density of *T. ornata* in 2022.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
zinbinom	10	240.13	0.00	1.00	0.73	-104.83	0.73
nbinom	9	242.21	2.07	0.35	0.26	-108.01	0.99
tweedie	11	248.40	8.27	0.02	0.01	-106.60	1.00
zipoiss	10	544.72	304.59	0.00	0.00	-257.12	1.00
poiss	10	637.26	397.13	0.00	0.00	-303.39	1.00

Table S4. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* adults in 2021.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
nbinom	10	165.10	0.00	1.00	0.68	-67.31	0.68
tweedie	11	166.64	1.54	0.46	0.31	-65.72	1.00
zinbinom	12	175.04	9.95	0.01	0.00	-67.31	1.00
zipoiss	10	192.35	27.25	0.00	0.00	-80.94	1.00
poiss	10	201.82	36.73	0.00	0.00	-85.67	1.00

Table S5. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* juveniles in 2021.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
nbinom	10	167.25	0.00	1.00	0.77	-68.39	0.77
tweedie	11	170.93	3.68	0.16	0.12	-67.87	0.89
zinbinom	11	171.18	3.93	0.14	0.11	-67.99	1.00
zipoiss	10	184.11	16.86	0.00	0.00	-76.82	1.00
poiss	9	201.02	33.78	0.00	0.00	-87.42	1.00

Table S6. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* recruits in 2021.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
nbinom	9	128.17	0.00	1.00	0.55	-50.99	0.55
tweedie	10	129.12	0.95	0.62	0.34	-49.32	0.90
zinbinom	11	131.52	3.36	0.19	0.10	-48.16	1.00
poiss	9	178.89	50.72	0.00	0.00	-76.36	1.00

Table S7. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* adults in 2022.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
nbinom	9	193.06	0.00	1.00	0.78	-83.44	0.78
zinbinom	10	195.59	2.53	0.28	0.22	-82.56	1.00
tweedie	12	207.21	14.15	0.00	0.00	-83.39	1.00
zipoiss	11	334.59	141.53	0.00	0.00	-149.69	1.00
poiss	10	369.95	176.88	0.00	0.00	-169.74	1.00

Table S8. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* juveniles in 2022.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
zinbinom	10	193.39	0.00	1.00	0.87	-81.46	0.87
nbinom	9	197.19	3.80	0.15	0.13	-85.50	1.00
tweedie	12	214.17	20.78	0.00	0.00	-86.87	1.00
zipoiss	10	274.54	81.16	0.00	0.00	-122.03	1.00
poiss	10	349.24	155.85	0.00	0.00	-159.38	1.00

Table S9. AIC model selection on the effects of herbivory and nutrient treatments on the density of *T. ornata* recruits in 2022.

<i>Model</i>	<i>K</i>	<i>AICc</i>	<i>Delta_AICc</i>	<i>ModelLik</i>	<i>AICcWt</i>	<i>LogLik</i>	<i>CumWt</i>
zinbinom	10	160.04	0.00	1.00	0.77	-64.78	0.77
nbinom	9	163.17	3.13	0.21	0.16	-68.49	0.93
tweedie	11	165.10	5.06	0.08	0.06	-64.95	0.99
zipoiss	11	168.75	8.71	0.01	0.01	-66.77	1.00
poiss	10	186.87	26.84	0.00	0.00	-78.20	1.00

Table S10. Biomass of herbivorous fish analysis of deviance table from Wald's F Type III test on the linear mixed model of the interaction of herbivory and nutrient treatments.

	<i>Sum.Sq</i>	<i>Mean.Sq</i>	<i>NumDF</i>	<i>DenDF</i>	<i>F.value</i>	<i>Pr(>F)</i>
Herbivory	102.31	34.10	3	147.48	24.91	<0.001
Nutrients	0.08	0.08	1	6.08	0.06	0.812
Herbivory:Nutrients	5.92	1.97	3	147.27	1.44	0.233

Table S11. Length of herbivorous fish analysis of deviance table from Wald's F Type II test on the linear mixed model with the main effect of herbivory treatment.

	<i>Sum.Sq</i>	<i>Mean.Sq</i>	<i>NumDF</i>	<i>DenDF</i>	<i>F.value</i>	<i>Pr(>F)</i>
Herbivory	14.16	4.72	3	595.84	26.74	<0.001

Table S12. Biomass of herbivorous fish analysis of deviance table from Wald's F Type III test on the linear mixed model of the interaction of herbivory and nutrient treatments for each herbivore functional group.

	<i>Sum.Sq</i>	<i>Mean.Sq</i>	<i>NumDF</i>	<i>DenDF</i>	<i>F.value</i>	<i>Pr(>F)</i>
--Grazer--						
Herbivory	31.567	10.522	3	427	6.197	< 0.001
Nutrients	0.391	0.391	1	427	0.230	0.632
Herbivory:Nutrients	9.558	3.186	3	427	1.876	0.133
--Detritivore--						
Herbivory	85.132	28.377	3	427	9.756	< 0.001
Nutrients	3.833	3.833	1	427	1.318	0.252
Herbivory:Nutrients	2.930	0.977	3	427	0.336	0.799
--Scraper--						

Herbivory	5.426	1.809	3	427	3.283	0.021
Nutrients	1.235	1.235	1	427	2.242	0.135
Herbivory:Nutrients	1.668	0.556	3	427	1.009	0.389

--Excavator--

Herbivory	15.608	5.203	3	433	5.587	< 0.001
Nutrients	3.285	3.285	1	433	3.527	0.061
Herbivory:Nutrients	4.013	1.338	3	433	1.437	0.231

Table S13. Proportion of *T. ornata* cover analysis of deviance table from Wald's Chi-square Type III test on the generalized linear mixed model of the interaction of herbivory treatment, nutrient treatment, and time.

	<i>Chisq</i>	<i>Df</i>	<i>Pr(>Chisq)</i>
Intercept	39.546	1	<0.001
Herbivory	15.055	3	0.002
Nutrients	0.390	1	0.532
Time	52.261	1	<0.001
Herbivory:Nutrients	2.908	3	0.406

Herbivory:Time	7.837	3	0.049
Nutrients:Time	1.037	1	0.308
Herbivory:Nutrients:Time	2.758	3	0.43

Table S14. Analysis of deviance table on the effect of herbivory and nutrient treatments on time for *T. ornata* recruitment.

	<i>Df</i>	<i>Sum.Sq</i>	<i>Mean.Sq</i>	<i>F.value</i>	<i>Pr(>F)</i>
Herbivory	3	22.65	7.55	17.09	<0.001
Nutrients	1	0.62	0.62	1.40	0.253
Herbivory:Nutrients	3	1.61	0.54	1.21	0.336
Residuals	16	7.07	0.44	NA	NA

Table S15. Density of overall *T. ornata* (individuals m⁻²) analysis of deviance table from Wald's Chi-square type III test on the generalized linear mixed model for 2021 and 2022.

	<i>Chisq</i>	<i>Df</i>	<i>Pr(>Chisq)</i>
--2021--			
Intercept	192.491	1	<0.001
Herbivory	23.816	3	<0.001
Nutrients	4.296	1	0.038
Herbivory:Nutrients	2.819	3	0.42
--2022--			
Intercept	59.790	1	<0.001
Herbivory	9.985	3	0.019
Nutrients	0.214	1	0.644
Herbivory:Nutrients	0.518	3	0.915

Table S16. Pairwise comparisons with Tukey adjustment on the density of *T. ornata* between the herbivory treatments excluding the High treatment in 2021.

	<i>contrast</i>	<i>null.value</i>	<i>ratio</i>	<i>std.error</i>	<i>df</i>	<i>null</i>	<i>statistic</i>	<i>adj.p.value</i>
Herbivory	Very Low / Low	0	0.92	0.48	Inf	1	-0.16	0.986
Herbivory	Very Low / Medium	0	29.42	17.01	Inf	1	5.85	<0.001
Herbivory	Low / Medium	0	31.96	18.93	Inf	1	5.85	<0.001

Table S17. Pairwise comparisons with Tukey adjustment on the density of *T. ornata* between the herbivory treatments in 2022.

<i>term</i>	<i>contrast</i>	<i>null.value</i>	<i>ratio</i>	<i>std.error</i>	<i>df</i>	<i>null</i>	<i>statistic</i>	<i>adj.p.value</i>
Herbivory	Very Low / Low	0	0.85	0.49	Inf	1	-0.27	0.993
Herbivory	Very Low / Medium	0	4.38	2.58	Inf	1	2.51	0.059
Herbivory	Very Low / High	0	14.84	10.20	Inf	1	3.92	<0.001

Herbivory	Low / Medium	0	5.12	3.17	Inf	1	2.64	0.041
Herbivory	Low / High	0	17.36	12.36	Inf	1	4.01	<0.001
Herbivory	Medium / High	0	3.39	2.42	Inf	1	1.71	0.319

Table S18. Density of *T. ornata* (individuals m⁻²) by life stage analysis of deviance table from Wald's Chi-square type III test on the generalized linear mixed model in 2021.

	<i>Chisq</i>	<i>Df</i>	<i>Pr(>Chisq)</i>
--Recruit--			
(Intercept)	10.896	1	< 0.001
Herbivory	0.776	3	0.855
Nutrients	0.776	1	0.378
Herbivory:Nutrients	1.118	3	0.773
--Juvenile--			
(Intercept)	4.855	1	0.028
Herbivory	12.786	3	0.005

Nutrients	0.163	1	0.687
Herbivory:Nutrients	0.156	3	0.984
--Adult--			
(Intercept)	5.458	1	0.019
Herbivory	16.131	3	0.001
Nutrients	0.122	1	0.727
Herbivory:Nutrients	0.675	3	0.879

Table S19. Density of *T. ornata* (individuals m⁻²) by life stage analysis of deviance table from Wald's Chi-square type III test on the generalized linear mixed model in 2022.

	<i>Chisq</i>	<i>Df</i>	<i>Pr(>Chisq)</i>
--Recruit--			
(Intercept)	46.549	1	< 0.001
Herbivory	8.854	3	0.031
Nutrients	1.678	1	0.195
Herbivory:Nutrients	1.694	3	0.638
--Juvenile--			

(Intercept)	59.125	1	< 0.001
Herbivory	16.924	3	< 0.001
Nutrients	0.025	1	0.876
Herbivory:Nutrients	1.147	3	0.766
--Adult--			
(Intercept)	12.795	1	< 0.001
Herbivory	7.050	3	0.070
Nutrients	0.008	1	0.927
Herbivory:Nutrients	2.467	3	0.481
