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Selective consumption of macroalgal species by herbivorous fishes suggests reduced functional complementarity on a fringing reef in Moorea, French Polynesia

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Abstract

Worldwide, many coral reefs are at risk of shifting to degraded algal-dominated states, due to compromised ecological conditions. Functional diversity of herbivorous fishes maintains coral reef health and promotes reef resilience to disturbances. Given previous evidence, it appears the functional roles of herbivorous fishes differ across geographical locations, indicating a need for further assessment of macroalgal consumption by herbivorous fishes. We assessed functional diversity by examining foraging behavior of herbivorous fish species on macroalgae on a fringing reef in Moorea, French Polynesia. We video-recorded choice experiments containing seven common macroalgae and used Strauss' linear resource selection index to determine macroalgal selectivities. We used cluster analysis to identify any distinct groups within herbivorous fish species, given the macroalgal species they targeted, and fitted generalized linear mixed-effects models to identify factors that best predicted the number of bites taken on macroalgae. Seven species from 3 fish families/tribes took a total of 956 bites. Fish species differed in their selectivity with some species (*Naso lituratus*, *N. unicornis*, *Calatomus carolinus*) strongly preferring one or two macroalgal species, while other fish species (*Acanthurus nigrofuscus*, *Ctenochaetus striatus*, *Chlorurus sordidus*, *Balistapus undulatus*) were less selective. This resulted in fish species forming two clusters. Only 3 of 7 macroalgae were preferred by any fish species, with two fish species both preferring the same two macroalgae. The limited differences in fish species' preferences for different macroalgae suggests limited functional complementarity. Two models (macroalgal species identity+fish functional group, macroalgal species identity+fish species) best predicted the number of bites taken on macroalgae compared to models incorporating only a single explanatory factor or fish family. In the context of this Moorean fringing reef, there is greater functional redundancy than complementarity of herbivorous fishes consuming macroalgae, and the fishes grouped together according to their relative selectivity. We observed fish species that are not classified as browsers consuming macroalgae, suggesting diets of herbivorous fishes may be broader than previously thought. Finally, we observed macroalgal selectivities and consumption that differed from previous studies for the same fish species. Our results contribute to the understanding of functional diversity of herbivorous fishes across coral reefs, and also highlight

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the need for additional research to further elucidate the role of context and functional diversity of herbivorous fishes consuming macroalgae on coral reefs.

Keywords

functional redundancy; functional complementarity; herbivorous fishes; macroalgae; selectivity

1. INTRODUCTION

Coral reefs are one of the most diverse ecosystems on earth, yet many appear at risk of shifting from healthy, coral-dominated to degraded, algal-dominated states due to a combination of natural and anthropogenic disturbances (e.g., Hughes et al. 2010). Herbivorous fishes are critical for maintaining coral-dominated reefs because they consume algae that compete with coral (e.g., Mumby et al. 2006, Hughes et al. 2007, Fong and Paul 2011). Coral reefs contain a diversity of herbivorous fishes and algae, and herbivorous fishes can selectively forage on different algae (e.g., Mantyka and Bellwood 2007a, Rasher et al. 2013, Humphries et al. 2015). Complementary foraging facilitates healthy coral reefs by reducing algal cover, biomass, and diversity while promoting coral survival and growth (Burkepile and Hay 2008). On the other hand, redundancy in herbivore foraging promotes coral reef resilience (Bellwood et al. 2004, Nash et al. 2016), which is the ability to resist and recover from phase shifts following disturbance (Holling 1973, Hodgson et al. 2015). This is because functional redundancy safeguards functions even if some herbivore species are removed. It is important to assess the functional diversity of herbivorous fishes on coral reefs in order to understand the community's ability to promote a healthy coral reef.

To assess herbivore functional diversity on coral reefs, it is necessary to classify herbivorous fishes into groups at the appropriate resolution. Traditionally, herbivorous fishes were classified as grazers and browsers (e.g. Hiatt and Strasburg 1960, Horn 1989), referring to whether they consume crustose coralline algae (CCA) and turf algae (<2 cm height) versus macroalgae (>2 cm height, Littler and Littler 2011a,b), respectively. More recently Green and Bellwood (2009) defined four functional groups: 1) scrapers/small excavators, 2) large excavators/bioeroders, 3) grazers/detritivores, and 4) browsers. With either of these classifications, the functional group of browsers encompasses all herbivorous fishes that consume macroalgae. However, herbivory pressure can vary on different macroalgal species (e.g., Mantyka and Bellwood 2007a,b, Chan et al. 2012, Rasher et al. 2013, Humphries et al. 2015), on macroalgae of varying nutritional quality (e.g., Boyer et al. 2004, Fong et al. 2006, Chan et al. 2012, Bittick et al. 2016), and on macroalgal thalli of varying sizes (e.g., Hoey 2010, Davis 2018). In addition, individual species of herbivorous fishes can selectively forage on different macroalgal species (e.g., Mantyka and Bellwood 2007a, Rasher et al. 2013, Humphries et al. 2015), among different parts of macroalgal thalli (Streit et al. 2015), and among macroalgal thalli of different heights (Hoey 2010). This selective foraging on macroalgae can be attributed to the diversity of morphologies, chemical and physical defenses, and nutritional values of macroalgal species (e.g., Rasher et al. 2013). In addition, the size of macroalgal browser species can influence their selectivity of macroalgae (Feitosa and Ferreira 2015, Duran et al. 2019). Thus classifying herbivorous fishes as browsers may

be too coarse to capture the functional diversity of their foraging on macroalgae and further research may reveal the need for finer scale groupings (Mantyka and Bellwood 2007a, Rasher et al. 2013).

Coral reefs around the world vary in the composition of their herbivorous fish and macroalgal communities, making it difficult to generalize information on the functional diversity of fishes across locations. The functional diversity of herbivorous fishes that consume macroalgae can vary with biogeographic location (e.g., Tebbett et al. 2019), seasons (e.g., Lefèvre and Bellwood 2011), reefs within a location (e.g., Bauman et al. 2017), reef habitat (e.g., Cvitanovic and Bellwood 2009, Hoey and Bellwood 2009), reef condition (e.g., Chong-Seng et al. 2014), macroalgal density (e.g., Bauman et al. 2019), and macroalgal height (e.g., Hoey 2010), among others. Single-species transplants of macroalgae can be used to assess the functional diversity of herbivorous fishes across various contexts (all above references except Tebbett et al. 2019). However, to assess the types of algae consumed by herbivorous fishes, studies often use multiple-species choice assays (e.g., Mantyka and Bellwood 2007a,b, Rasher et al. 2013, Humphries et al. 2015, Tebbett et al. 2019), focal fish follows (e.g., Fox et al. 2009, Adam et al. 2015, 2018, Kelly et al. 2016, Smith et al. 2018), or stomach content analyses (e.g., Choat et al. 2002, Hoey et al. 2013). When focusing on the types of algae consumed, the functional diversity of herbivorous fishes has been studied on coral reefs in the Great Barrier Reef (e.g., Mantyka and Bellwood 2007a), the Caribbean (e.g., Adam et al. 2015), Kenya (Humphries et al. 2015), Fiji (Rasher et al. 2013), and the Hawaiian Islands (Kelly et al. 2016). The variation in herbivorous fish functional diversity across contexts, studies, and reefs indicates a continuing need to expand our understanding of the functional diversity of herbivorous fishes consuming macroalgae on coral reefs worldwide.

Our objective was to examine the functional diversity of herbivorous fish species in the context of their selectivity of macroalgae on a fringing reef in Moorea, French Polynesia. We had three questions:

1. What are the feeding selectivities of herbivorous fish species on macroalgae found on a fringing reef?
2. How do herbivorous fish species group together based upon their foraging on macroalgae?
3. What information (macroalgal species, herbivorous fish family, herbivorous fish species, functional group) best predicts the amount of foraging (number of bites) on macroalgae?

2. METHODS

2.1 Macroalgal Choice Experiments

We examined the behavior of herbivorous fishes foraging on macroalgae on Taahiamanu Reef (17°29'17.68"S, 149°50'55.07"W), a fringing reef of Moorea, French Polynesia. Similar to previous studies (e.g., Mantyka and Bellwood 2007a, Rasher et al. 2013, Humphries et al. 2015), we used videos to remove the effect of human observers (e.g.,

Nanninga et al. 2017) when examining fish foraging behavior. We deployed choice experiments consisting of seven common macroalgae that co-occur on fringing reefs and span a wide range of functional groups and palatabilities (Littler et al. 1983, Steneck and Dethier 1994). Our macroalgae included *Padina boryana* Thivy, *Dictyota* sp. J.V. Lamouroux, *Acanthophora spicifera* (M. Vahl) Børgesen, *Sargassum mangarevense* (Grunow) Setchell, *Turbinaria ornata* (Turner) J. Agardh, *Galaxaura* sp. J.V. Lamouroux, and *Halimeda* sp. J.V. Lamouroux. We used “proportional-sized” choices, following the methods of Mantyka and Bellwood (2007a), by visually standardizing intraspecific macroalgal volume to reflect individual species’ natural sizes and growth forms. We measured initial and final wet weights (biomass) to calculate percent change in biomass (see 2.2.1 below) and for use in the selectivity index (see 2.2.2 below).

We collected macroalgae from Taahiamanu Reef two days before deployment and stored them in flow through water tables. We constructed the experimental units the afternoon prior to deployment. Choice experiments (n=6 per day) and caged controls (n=3 per day) were deployed >5 m apart at Taahiamanu Reef on June 24 and 26, 2015 from approximately 0900 to 1400 hrs. We deployed GoPro Hero3 video cameras approximately 0.7 m from each experimental unit. A scale bar was included at the beginning of each recording to estimate fish sizes. One camera malfunctioned on June 24, so n = 11 experimental deployments.

We defined a fish visit as the interval between when a fish entered and left the video frame. Because fish may have left and then re-entered the frame, we cannot know if a fish visit represents a unique individual. For fish that took bites on at least one macroalga, we recorded fish species, size (5 cm size classes), and number of bites on each macroalga. We excluded data from the first 10 min after deployment to limit disturbance to behavior by our presence. Following the methods of Mantyka and Bellwood (2007a), we stopped recording data once any macroalgal species was too small to be visually detected in the videos. We analyzed approximately 50 h of videos. We had limited sample sizes for some observed fish species (Table 1). While we recognize these sample sizes are low, we used all species in our analysis to expand our ability to compare our work with previous studies. However, for transparency, sample sizes are reported for each species (Table 1).

2.2 Statistical Analyses

2.2.1 Loss of macroalgal biomass—We used initial and final wet weights (biomass) to calculate percent change in biomass ($(\text{final} - \text{initial}) / \text{initial} * 100$) of each macroalga for each choice experiment and calculated the mean \pm SE across choice experiments (n=11). We used caged controls to account for handling losses and macroalgal growth. We adjusted percent change in biomasses for experimental macroalgae by subtracting the average percent change in biomass calculated from caged controls. A thalli of *T. ornata* was lost during recovery for one choice experiment, resulting in n=10 for *T. ornata* change in biomass.

2.2.2 Selectivity—Previous studies assessing the foraging behavior of herbivorous fishes used several metrics and indices with no apparent standardized measure to quantify foraging behavior (e.g., Mantyka and Bellwood 2007a, Rasher et al. 2013, Adam et al. 2015, Humphries et al. 2015, Kelly et al. 2016, Adam et al. 2018, Burkepile et al. 2019, Smith

et al. 2018). Strauss' linear resource selection index (Strauss 1979) and Manly's alpha electivity index (Manly et al. 1972, Chesson 1978, Chesson 1983) are commonly used indices. However, Manly's alpha electivity index assumes food resources are not being depleted during the time of observation and is often used when following herbivores and observing their foraging behavior on natural substrates. Because we used choice experiments, the macroalgae were only available in limited quantities and, thus, could be depleted. Therefore, we used Strauss' linear resource selection index (Strauss 1979) to determine selectivity of macroalgae because it does not rely on the assumption of unlimited resources. Strauss' selection indices (L) were calculated as

$$L = r_i - p_i$$

where i is the focal macroalgal species, r_i is the proportion of the number of bites taken on that macroalgal species out of all macroalgal species during a fish visit, and p_i is the proportion of initial biomass available for that macroalgal species out of the total biomass available across all macroalgal species. We calculated L for each macroalgal species bitten during each fish visit. Then across all fish visits per fish species, we calculated the mean L and corresponding 95% confidence intervals (CI) for each macroalga for each fish species. Selectivity preference (positive) and avoidance (negative) of a macroalgal species by a fish species were indicated by 95% CI that did not overlap zero.

2.2.3 Similarities of Macroalgal Selectivities—To determine the similarities of our fish species based upon their macroalgal selectivities, we performed a cluster analysis on the mean L values calculated for each fish species on each macroalgal species. Thus, fish species within a cluster exhibit similar macroalgal selectivities, while different clusters of fishes exhibit distinct macroalgal selectivities. We used R 4.0.2 and RStudio (RStudio Team 2016, R Core Team 2016) and the 'hclust' function from the 'dendextend' package (Galili 2015) to determine the clustering of fish species based upon their macroalgal selectivities.

2.2.4 Bite Model—We compared generalized linear mixed-effects models (GLMMs) for bites to determine what information best predicted the number of bites taken on macroalgae. Our response variable was number of bites per fish visit, and because our bite data were overdispersed (variance greater than the mean), we fit our models using a negative binomial distribution. Also, we included fish visit ($N = 201$) as a random effect to account for individual variation.

Our predictor variables included macroalgal species, fish family, fish species, and fish functional group. We excluded fish size from the analyses because fish species strongly predicted fish size (ANOVA $F_{6,1400} = 1272$, $p < 0.0001$). We classified herbivorous fishes into four functional groups (Green and Bellwood 2009): 1) scrapers/small excavators, which are small (<35 cm standard length) parrotfishes that consume turf algae and scrape the substrate; 2) large excavators/bioeroders, which are large (> 35 cm standard length) parrotfishes that contribute to bioerosion through their excavating bites; 3) grazers/detritivores, which consume turf algae and/or associated detritus but do not scrape or excavate the substrate; and 4) browsers, which consume macroalgae.

Because fish species, fish family, and fish functional group were all nested together, none of these predictor variables were included in the same model. Our data were insufficient to fit interaction terms, so we compared seven main effects models to determine which variables best predicted the number of bites taken on macroalgae. Specifically, we tested models including (1) macroalgal species, (2) fish species, (3) fish family, (4) fish functional group, (5) macroalgal species + fish species, (6) macroalgal species + fish family, and (7) macroalgal species + fish functional group.

We compared Akaike Information Criterion scores corrected for small samples sizes (AICc) and AICc weights between the models to determine which information is most important (macroalgal species, fish species, fish family, or fish functional group) to predict the number of bites taken on macroalgae. To compare our models, we used differences in AICc scores ($\Delta AICc$), where the lowest calculated value is 0. Models with $\Delta AICc$ in the range of 2 – 7 have support (Burnham et al. 2011), so we used a more conservative value of $\Delta AICc > 4$ (e.g. Bittick et al. 2018) and the AICc weights to indicate differences between models. We used R 4.0.2 and RStudio (RStudio Team 2016, R Core Team 2016) and the `glmer.nb` function with the ‘bobyqa’ optimizer from the ‘lme4’ package (Bates et al. 2015) to fit our models. We used the `aictab` function from the ‘AICcmodavg’ package (Mazerolle 2020) to calculate AICc, $\Delta AICc$, and AICc weights for our models. We used the `r.squaredGLMM` function from the ‘MuMIn’ package (Barto 2019) to determine conditional R^2 values using the delta method (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017) for each of our models.

3. RESULTS

We observed 7 species from 3 fish families/tribes taking a total of 956 bites on the presented macroalgae (Table 1). The number of fish visits per species varied greatly.

3.1 Loss of macroalgal biomass

Four macroalgae (*Padina boryana*, *Dictyota sp.*, *Acanthophora spicifera*, and *Sargassum mangarevense*, in rank order of greatest to least loss) lost biomass due to herbivory during our choice experiments (Fig. 1).

3.2 Bites and Selectivity

Fish species differed in how many bites per visit they took on each macroalga (Fig. 2A–G); this resulted in differences in their selectivity of macroalgae (Fig. 2H–N). Two acanthurids, both in the genus *Naso* (*N. lituratus* and *N. unicornis*), took many bites on (Fig. 2A,B) and strongly preferred *P. boryana* (Fig. 2H,I) and avoided almost all other macroalgae. The exception was that *N. lituratus* bit *S. mangarevense* (Fig. 2A), although this did not result in a strong preference (Fig. 2H). One of the two Labridae (tribe Scarinae) species we observed, *Calatomus carolinus*, only took bites on (Fig. 2C) and preferred (Fig. 2J) *P. boryana* and *S. mangarevense* and avoided all other macroalgae. In comparison, two of the other acanthurids, *Ctenochaetus striatus* and *Acanthurus nigrofuscus*, were less selective as they bit many macroalgal species (Fig. 2D,E) and they did not exhibit preference or avoidance for at least 3 macroalgae (Fig. 2K,L). *C. striatus* was the least selective in that it

did not prefer any macroalgae and avoided two macroalgae: *P. boryana* and *Acanthophora spicifera* (Fig. 2L). Slightly more selective in its foraging, *A. nigrofuscus* preferred *S. mangarevense* and avoided three macroalgae (*P. boryana*, *Halimeda sp.*, *Galaxaura sp.*) while neither preferring nor avoiding the remaining macroalgal species (Fig. 2K). For the other Labridae (tribe Scarinae) species, *Chlorurus sordidus*, we observed very few fish visits ($n = 4$), so the calculated selectivity indices were highly variable (Fig. 2M). However, *C. sordidus* was only observed to bite *S. mangarevense* and *Turbinaria ornata* (Fig. 2F). One triggerfish (Balistidae) species, *Balistapus undulatus*, took bites on five of the seven macroalgae (Fig. 2G); however, it only preferred one species: *A. spicifera* (Fig. 2N).

3.3 Similarities of Macroalgal Selectivities

Cluster analyses indicated our herbivorous fish community was made up of two groups (Fig. 3). One group contained three species (*N. lituratus*, *N. unicornis*, and *C. carolinus*) that exhibited strong selectivity for at least one macroalga. They primarily consumed *P. boryana* and sometimes *S. mangarevense*, but avoided all other macroalgal species. In comparison, the second group contained four species (*C. striatus*, *A. nigrofuscus*, *C. sordidus*, and *B. undulatus*) that were less selective when biting macroalgae; they bit a variety of macroalgal species with minimal preferences or avoidances. The only observed preferences for these four fishes were *A. nigrofuscus* preferring *S. mangarevense*, and the triggerfish, *B. undulatus*, preferring *A. spicifera*.

3.4 Bite Model

Comparison of our bite models using AICc scores and weights indicated two models best predicted the number of bites taken on macroalgae ($AICc < 4$, Table 2). Specifically, models incorporating macroalgal species identity and either fish species or fish functional group are better predictors than models incorporating fish family and macroalgal species identity or any of the variables by themselves (Table 2, Table S1).

3.5 Fish Sizes

We primarily observed small fishes (<15 cm) taking bites on this fringing reef, although we did observe larger *C. carolinus* (Scarinae) individuals taking bites (Fig. 4). All *C. sordidus* were <10 cm and almost all *N. unicornis* and *N. lituratus* were <15.1 cm, with approximately half of them <10.1 cm (Fig. 4).

4. DISCUSSION

In the context of this fringing reef in Moorea, we found the fish community has greater functional redundancy than complementarity in terms of their selectivity of macroalgae. There was high functional redundancy for two species of macroalgae (*Padina boryana* and *Sargassum mangarevense*) because they were preferred by multiple fish species. *Acanthophora spicifera* was the only other macroalga preferred by any fish species, but since it was only preferred by one fish, the triggerfish *Balistapus undulatus*, this suggests limited functional redundancy for this macroalga. Our results suggest some functional complementarity in macroalgal selectivity as three macroalgae were preferred, with some differences in the fishes preferring them. However, complementarity in terms of macroalgal

selectivity on this reef appears limited since four macroalgae were never preferred. Our results are consistent with previous studies in terms of finding functional redundancy for some macroalgae (e.g., Mantyka and Bellwood 2007a, Rasher et al. 2013, Humphries et al. 2015). However, these previous studies often found stronger functional complementarity among herbivorous fishes consuming macroalgae than we observed. The implication of functional redundancy on this Moorean reef is that herbivory on these macroalgae should be maintained after disturbances, as long as the redundant fishes exhibit response diversity to disturbances (e.g., Elmqvist et al. 2003, Bellwood et al. 2004, Nash et al. 2016). However, the limited functional complementarity suggests some functional roles are not filled by the resident fish community, which may have negative effects on this fringing coral reef (e.g., Burkepile and Hay 2008).

The functional redundancy and complementarity we observed may be specific to the temporal, spatial, and resource availability context of our experiment. Among other factors, foraging preferences can vary depending upon which resources are available (e.g., Hanmer et al. 2017). For example, the parrotfish, *C. carolinus*, preferred *P. boryana* and *S. mangarevense*, while avoiding *T. ornata* in Moorea. However, when *P. boryana* and *S. mangarevense* were not options, this parrotfish strongly preferred *Turbinaria sp.* in Hawai'i (Kelly et al. 2016). Therefore, it is possible the fishes we observed as redundant could exhibit complementary foraging when a different number or composition of macroalgae is presented. Overall, although this is the first assessment of herbivorous fish functional diversity in terms of their macroalgal selectivity on coral reefs in Moorea, French Polynesia, additional research is necessary to further elucidate the functional diversity of Moorean herbivorous fishes in other contexts.

We did not find support for finer scale divisions for macroalgal selectivity within the broad grouping of browsers on this Moorean fringing reef. Herbivorous fishes grouped together according to their relative selectivity, with one group highly selective, albeit of the same macroalga, while the other group was less selective, eating several species of macroalgae. Our finding for this Moorean fringing reef contrasts with previous studies in Fiji (Rasher et al. 2013), Kenya (Humphries et al. 2015), and the GBR (Mantyka and Bellwood 2007a) that observed herbivorous fishes were functionally complementary because each selected a different macroalga, or different taxonomic groups of macroalgae (e.g., reds, greens, or browns). However, our two clusters reflect previous functional groups, as the fishes within our more selective cluster are usually classified as browsers (Green and Bellwood 2009). They exhibited high redundancy in their preference of *P. boryana* and limited complementarity in consuming other macroalgae. In comparison, the fishes within our less selective cluster encompass multiple other functional groups and primarily consumed macroalgae other than *P. boryana*. *Padina boryana* is one of the most abundant macroalgae on this fringing reef (Johnson et al. 2018) and another fringing reef in Moorea (Fong and Fong 2014). Thus, our clusters of herbivorous fishes on this fringing reef suggest high redundancy within browsers in terms of consuming one of the most abundant macroalgae, while there appears to be complementarity within herbivorous fishes more broadly as the second cluster of fishes provides supplemental removal of macroalgae other than *P. boryana*. Overall, the current classification scheme of grouping all browsers together appears sufficient in the context of this fringing reef in Moorea.

Fishes other than known herbivores may also play important roles in macroalgal removal on coral reefs. Triggerfishes are not considered herbivorous fishes, and they are not classified into one of the herbivorous fish functional groups since their trophic status has not been confirmed (Green and Bellwood 2009). However, we observed the triggerfish, *B. undulatus*, taking bites on multiple species of macroalgae and preferring one macroalga. Recently, Tebbett et al. (2019) also found a triggerfish species (*Melichthys niger*) to be the dominant remover of macroalgal biomass on Caribbean reefs. More research is needed to understand the roles of additional fish species in macroalgal removal on coral reefs.

We observed macroalgal selectivities that differed from herbivorous fishes in Hawai'i. In Hawai'i, *N. unicornis* strongly preferred *Turbinaria sp.* while *N. lituratus* preferred *Dictyota sp.* (Kelly et al. 2016). In contrast, even though we offered both *Turbinaria sp.* (*T. ornata*) and *Dictyota sp.*, both *Naso sp.* avoided these two macroalgae in Moorea. The grazer *A. nigrofuscus* preferred *S. mangarevense* in Moorea, while they preferred a different macroalga, *Asparagopsis sp.*, in Hawai'i (Kelly et al. 2016). Also, as stated earlier, the parrotfish, *C. carolinus*, preferred different macroalgae between Hawai'i and Moorea. Although we had some overlap with Kelly et al. (2016) in which macroalgae were available as options, the differences in which macroalgae were available between studies may explain the observed differences in macroalgal selectivities for these fish species (e.g., Hanmer et al. 2017). Kelly et al. (2016) is the only previous study to report macroalgal selectivities for the same fishes we observed. Further research assessing variation in resource availability will help improve our understanding of foraging preferences of herbivorous fishes.

We also observed differences in which macroalgae our observed fishes took bites on in Moorea versus other locations (for a complete list see Table 3). Both *Naso sp.* are some of the only fishes found to directly consume *Turbinaria sp.* in other studies, but neither species took bites on *T. ornata* in our study. Also, both *Naso sp.* predominantly consume brown macroalgae across locations; however, they also consumed red macroalgae in Hawai'i (both species) and in the GBR (*N. unicornis* only, Table 3), but did not in our study. Similarly, *C. carolinus* often consumes the brown macroalgae, *Padina sp.* and *Sargassum sp.*, as we found in our study, although, additionally, they consumed one green and two red macroalgae in GBR and Hawai'i, respectively. The detritivore *Ctenochaetus striatus* often consumes a diversity of macroalgae, including on this fringing reef in Moorea, whereas, in Fiji, *C. striatus* only took bites on the substrate (Rasher et al. 2013, Table 3). Although these coral reefs overlap in some species of fishes and macroalgae, herbivorous fishes exhibited differences in the macroalgae they consume. Our results support Tebbett et al. (2019) that assuming the functional roles of herbivorous fishes based upon previous work done in other reef systems may prove incorrect.

Study context, macroalgal characteristics, and fish size may help explain differences between studies. As previously stated, the functional diversity of herbivorous fishes consuming macroalgae can vary depending on the spatial, temporal, and resource availability contexts of studies (e.g., Lefèvre and Bellwood 2011, Bauman et al. 2017, Hanmer et al. 2017). Therefore, the specific macroalgae that fishes took bites on in various locations may relate to what options were available. Also, macroalgae are diverse in their morphologies, chemical and physical defenses, and nutritional content (e.g., Paul and Hay

1986, Steneck and Dethier 1994, Pereira and da Gama 2008, Fong and Paul 2011). Inter- and intraspecific variation in these characteristics between studies and locations likely influenced selectivity and consumption of macroalgae by fishes. Finally, recent studies found diet varied with fish size for herbivorous parrotfishes (e.g., Feitosa and Ferreira 2015, Adam et al. 2018, Smith et al. 2018) and surgeonfishes (Duran et al. 2019). However, these studies do not include any of the fish species we observed, and we could not test the role of size in fish foraging behavior within our study. Overall, our results identify the need for future studies that explore the relationships between fish size, macroalgal selectivity, macroalgal consumption, functional diversity, and algal biomass removal. This research will fill a critical knowledge gap for many herbivorous fish species that are common on coral reefs.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Literature Cited

- Adam TC, Kelley M, Ruttenberg BI, Burkepile DE, 2015. Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia*. 179, 1173–1185. [PubMed: 26245147]
- Adam TC, Duran A, Fuchs CE, Roycroft MV, Rojas MC, Ruttenberg BI, Burkepile DE, 2018. Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Mar. Ecol. Prog. Ser* 597, 207–220.
- Barto K, 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Maechler M, Bolker B, Walker S, 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Software* 67(1), 1–48. doi:10.18637/jss.v067.i01.
- Bauman AG, Hoey AS, Dunshea G, Feary DA, Low J, Todd PA, 2017. Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. *Sci. Rep* 7, 8352. doi:10.1038/s41598-017-08873-3 [PubMed: 28827630]
- Bauman AG, Seah JCL, Januchowski-Hartley FA, Hoey AS, Fong J, Todd PA, 2019. Fear effects associated with predator presence and habitat structure interact to alter herbivory on coral reefs. *Biol. Lett* 15, 20190409. 10.1098/rsbl.2019.0409 [PubMed: 31573428]
- Bellwood DR, Hughes TH, Folke C, Nyström M, 2004. Confronting the coral reef crisis. *Nature*. 429, 827–833. [PubMed: 15215854]
- Bennett S, Bellwood DR, 2011. Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Mar. Ecol. Prog. Ser* 426, 241–252.
- Bittick SJ, Clausing RJ, Fong CR, Fong P, 2016. Bolstered physical defences under nutrient-enriched conditions may facilitate a secondary foundational algal species in the South Pacific. *J. Ecol* 104, 646–653. doi: 10.1111/1365-2745.12539

- Bittick SJ, Sutula M, Fong P, 2018. A tale of two algal blooms: negative and predictable effects of two common bloom-forming macroalgae on seagrass and epiphytes. *Mar. Environ. Res* 140, 1–9. 10.1016/j.marenvres.2018.05.018 [PubMed: 29807625]
- Boyer KE, Fong P, Armitage AR, Cohen RA, 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. *Coral Reefs* 23, 530–538.
- Burkepile DE, Hay ME, 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *PNAS*. 105(42), 16201–16206. 10.1073/pnas.0801946105 [PubMed: 18845686]
- Burkepile DE, Adam TC, Roycroft M, Ladd MC, Munsterman KS, Ruttenberg BI, 2019. Species-specific patterns in corallivory and spongivory among Caribbean parrotfishes. *Coral Reefs*. 10.1007/s00338-019-01808-6
- Burnham KP, Anderson DR, Huyvaert KP, 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol* 65, 23–35.
- Chan AY, Lubarsky K, Judy KN, Fong P, 2012. Nutrient addition increases consumption rates of tropical algae with different initial palatabilities. *Mar. Ecol. Prog. Ser* 465, 25–31. doi:10.3354/meps09946
- Chesson J, 1978. Measuring preference in selective predation. *Ecol.* 59(2), 211–215. <https://www.jstor.org/stable/1936364>
- Chesson J, 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecol.* 64(5), 1297–1304. <https://www.jstor.org/stable/1937838>
- Choat JH, Clements KD, Robbins WD, 2002. The trophic status of herbivorous fishes on coral reefs. 1: Dietary analyses. *Mar. Biol* 140, 613–623. doi:10.1007/s00227-001-0715-3
- Chong-Seng KM, Nash KL, Bellwood DR, Graham NAJ, 2014. Macroalgal herbivory on recovering versus degrading coral reefs. *Coral Reefs* 33:409–419.
- Cvitanovic C, Bellwood DR, 2009. Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* 28, 127–133. doi:10.1007/s00338-008-0433-0
- Davis SL, 2018. Associational refuge facilitates phase shifts to macroalgae in a coral reef ecosystem. *Ecosphere* 9, e02272. 10.1002/ecs2.2272
- Duran A, Adam TC, Palma L, Moreno S, Collado-Vides L, Burkepile DE, 2019. Feeding behavior in Caribbean surgeonfishes varies across fish size, algal abundance, and habitat characteristics. *Mar. Ecol* DOI: 10.1111/maec.12561
- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J, 2003. Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ* 1(9), 488–494. <http://www.jstor.org/stable/3868116>
- Feitosa JLL, Ferreira BP, 2015. Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. *Mar. Ecol* 36, 462–474.
- Fong CR, Fong P, 2014. Why species matter: an experimental assessment of assumptions and predictive ability of two functional-group models. *Ecol.* 95, 2055–2061.
- Fong CR, Sura SA, Ford AT, Howard HB, Molina NE, Smith NN, Fong P, 2020. Testing the conceptual and operational underpinnings of herbivory assays: does variation in predictability of resources, assay design, and deployment method affect outcomes? *J. Exp. Mar. Biol. Ecol* 533, 151469.
- Fong P, Smith TB, Wartian ML, 2006. Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. *Ecol.* 87, 1162–1168.
- Fong P, Paul VJ, 2011. Coral Reef Algae. In: Dubinsky Z, Stambler N (eds) *Coral reefs: an ecosystem in transition*. Springer Science + Business Media B.V, pp 241–272.
- Fox RJ, Sunderland TL, Hoey AS, Bellwood DR, 2009. Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Mar. Ecol. Prog. Ser* 385, 261–269. doi:10.3354/meps08059
- Graba-Landry AC, Loffler A, McClure EC, Pratchett MS, Hoey AS, 2020. Impaired growth and survival of tropical macroalgae (*Sargassum* spp.) at elevated temperatures. *Coral Reefs* 39, 475–486. 10.1007/s00338-020-01909-7

- Green AL, Bellwood DR, 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific Region. IUCN, Glan, Switzerland.
- Galili T, 2015. dendextend: an R package for visualizing, adjusting, and comparing trees of hierarchical clustering. *Bioinformatics*. DOI: 10.1093/bioinformatics/btv428
- Hanmer J, White JW, Pawlik JR, 2017. Application of diet theory reveals context-dependent foraging preferences in an herbivorous coral reef fish. *Oecologia* 185, 127–137. doi:10.1007/s00442-017-3855-y
- Hiatt RW, Strasburg DW, 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr* 30(1), 65–127. <http://www.jstor.org/stable/1942181>
- Hodgson D, McDonald JL, Hosken DJ, 2015. What do you mean, 'resilient'? *Trend. Ecol. Evol* 30(9), 503–506. 10.1016/j.tree.2015.06.010
- Hoey AS, 2010. Size matters: macroalgal height influences the feeding response of coral reef herbivores. *Mar. Ecol. Prog. Ser* 411, 299–302.
- Hoey AS, Bellwood DR, 2009. Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12, 1316–1328.
- Hoey AS, Brandl SJ, Bellwood DR, 2013. Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs*. 32, 973–984. doi:10.1007/s00338-013-1043-z
- Holling CS, 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst* 4, 1–23.
- Horn MH, 1989. Biology of marine herbivorous fishes. *Oceanogr. Mar. Biol. Ann. Rev* 27, 167–272.
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskij N, Pratchett MS, Steneck RS, Willis B, 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol* 17, 360–365. doi: 10.1016/j.cub.2006.12.049 [PubMed: 17291763]
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS, 2010. Rising to the challenge of sustaining coral reef resilience. *Trend. Ecol. Evol* 25(11), 633–642. doi:10.1016/j.tree.2010.07.011
- Humphries AT, McQuaid CD, McClanahan TR, 2015. Context-dependent diversity-effects of seaweed consumption on coral reefs in Kenya. *PLoS ONE* 10(12), e0144204. doi:10.1371/journal.pone.0144204 [PubMed: 26673609]
- Johnson GC, Pezner AK, Sura SA, Fong P, 2018. Nutrients and herbivory, but not sediments, have opposite and independent effects on the tropical macroalga, *Padina boryana*. *J. Exp. Mar. Bio. Ecol* 507, 17–22.
- Kelly ELA, Eynaud Y, Clements SM, Gleason M, Sparks RT, Williams ID, Smith JE, 2016. Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. *Oecologia*. 182, 1151–1163. DOI 10.1007/s00442-016-3724-0 [PubMed: 27651229]
- Lefèvre CD, Bellwood DR, 2011. Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. *Mar. Ecol. Prog. Ser* 422, 239–251. doi:10.3354/meps08916
- Littler MM, Littler DS, Taylor PR, 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol* 19, 229–237.
- Littler MM, Littler DS, 2011a. Algae-macro. In: Hopley D (ed) *Encyclopedia of Modern Coral Reefs*. Springer Science + Business Media B.V., pp 30–38
- Littler MM, Littler DS, 2011b. Algae, Turf. In: Hopley D (ed) *Encyclopedia of Modern Coral Reefs*. Springer Science + Business Media B.V., pp 38–39
- Manly BFJ, Miller P, Cook LM, 1972. Analysis of a selective predation experiment. *Am. Nat* 106(952), 719–736. <https://www.jstor.org/stable/2459502>
- Mantyka CS, Bellwood DR, 2007a. Macroalgal grazing selectivity among herbivorous coral reef fishes. *Mar. Ecol. Prog. Ser* 352, 177–185.
- Mantyka CS, Bellwood DR, 2007b. Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs* 26,435–442. doi:10.1007/s00338-007-0214-1
- Mazerolle MJ, 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3–1. <https://cran.r-project.org/package=AICcmodavg>

- Michael PJ, Hyndes GA, Vanderklift MA, Vergés A, 2013. Identity and behavior of herbivorous fish influence large-scale spatial patterns of macroalgal herbivory in a coral reef. *Mar. Ecol. Prog. Ser* 482, 227–240.
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB, 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311, 98–101. doi:10.1126/science.1121129 [PubMed: 16400152]
- Nakagawa S, Schielzeth H, 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Meth. Ecol. Evo* 4, 133–142. doi: 10.1111/j.2041-210x.2012.00261.x
- Nakagawa S, Johnson PCD, Schielzeth H, 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14, 20170213. 10.1098/rsif.2017.0213 [PubMed: 28904005]
- Nanninga GB, Côte IM, Beldade R, Mills SC, 2017. Behavioural acclimation to cameras and observers in coral reef fishes. *Ethol.* 123, 705–711. DOI: 10.1111/eth.12642
- Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR, 2016. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *J. App. Ecol* 53, 646–655. DOI: 10.1111/1365-2664.12430
- Paul VJ, Hay ME, 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. *Mar. Ecol. Prog. Ser* 33, 255–264.
- Pereira RC, da Gama BAP, 2008. Macroalgal chemical defenses and their roles in structuring tropical marine communities. In: Amsler CD (ed) *Algal chemical ecology*. Springer-Verlag Berlin Heidelberg, pp 25–55.
- Plass-Johnson JG, Ferse SCA, Jompa J, Wild C, Teichberg M, 2015. Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnol. Oceanogr* 60, 1382–1391.
- Puk LD, Ferse SCA, Wild C, 2016. Patterns and trends in coral reef macroalgae browsing: a review of browsing herbivorous fishes of the Indo-Pacific. *Rev. Fish. Biol. Fisheries* 26, 53–70. DOI 10.1007/s11160-015-9412-z
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rasher DB, Hoey AS, Hay ME, 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecol.* 94(6), 1347–1358.
- RStudio Team, 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL: <http://www.rstudio.com/>.
- Smith KM, Quirk-Royal BE, Drake-Lavelle K, Childress MJ, 2018. Influences of ontogenetic phase and resource availability on parrotfish foraging preferences in the Florida Keys, FL (USA). *Mar. Ecol. Prog. Ser* 603, 175–187. 10.3354/meps12718
- Steneck RS, Dethier MN, 1994. A functional group approach to the structure of algal-dominated communities. *Oikos.* 69, 476–498.
- Strauss RE, 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans. Am. Fish. Soc* 108(4), 344–352. DOI: 10.1577/1548-8659(1979)108<344:REFIEI>2.0.CO;2
- Streit RP, Hoey AS, Bellwood DR, 2015. Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. *Coral Reefs.* 34, 1037–1047. DOI 10.1007/s00338-015-1322-y
- Tebbett SB, Hoey AS, Depczynski M, Wismer S, Bellwood DR, 2019. Macroalgae removal on coral reefs: realised ecosystem functions transcend biogeographic locations. *Coral Reefs.* 10.1007/s00338-019-01874-w
- Vergés A, Bennett S, Bellwood DR, 2012. Diversity among macroalgae-consuming fishes on coral reefs: a transcontinental comparison. *PLoS ONE* 7(9): e45543. doi:10.1371/journal.pone.0045543 [PubMed: 23029083]

Highlights:

- Fishes consuming macroalgae show more redundancy than complementarity in Moorea
- Herbivorous fishes showed differing selectivity across a range of macroalgal species
- Fishes exhibited different selectivities in this location compared to other locations
- Fishes not considered browsers consumed macroalgae

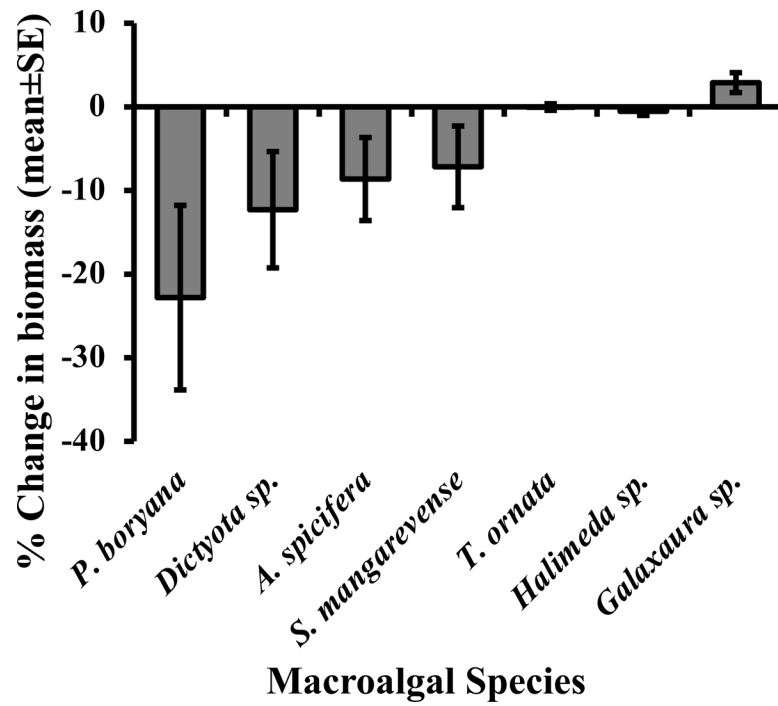


Figure 1. Percent change in biomass (mean±SE) for each macroalgal species presented in choice assays (n=11).

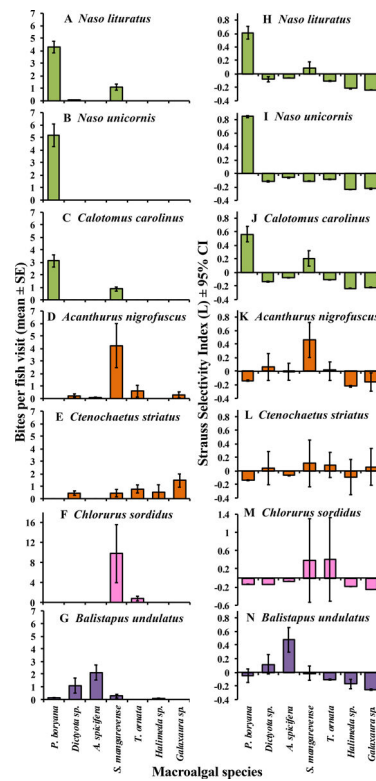


Figure 2.

Bites per fish visit (mean \pm SE, column 1) and Strauss selectivity index values (\pm 95% CI, column 2) for fish species taking bites on macroalgal choice experiments. Macroalgae are presented in order of increasing complexity and defenses against herbivory, according to Steneck and Dethier (1994). Fish species are color coded according to their functional group based on Green and Bellwood (2009): green = browser, orange = grazer/detritivore, pink = scraper/small excavator, and purple = unclassified. Note: panels F and M are on different scales than the rest. Sample sizes are the following: *Naso lituratus* n = 73, *Naso unicornis* n = 11, *Calotomus carolinus* n = 56, *Acanthurus nigrofuscus* n = 17, *Ctenochaetus striatus* n = 9, *Chlorurus sordidus* n = 4, *Balistapus undulatus* n = 31.

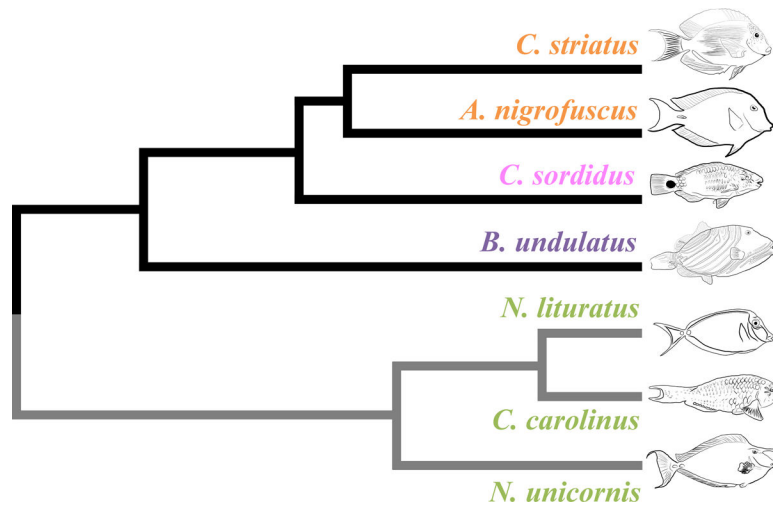


Figure 3. Clusters of fish species based upon their Strauss' selectivity indices for macroalgae presented in choice experiments. Black versus gray lines indicate which fish species group together into each cluster. Fish species names are color coded according to their functional group based on Green and Bellwood (2009): orange = grazer/detritivore, pink = scraper/small excavator, purple = unclassified, and green = browser. Fish drawings provided by Nury Molina.

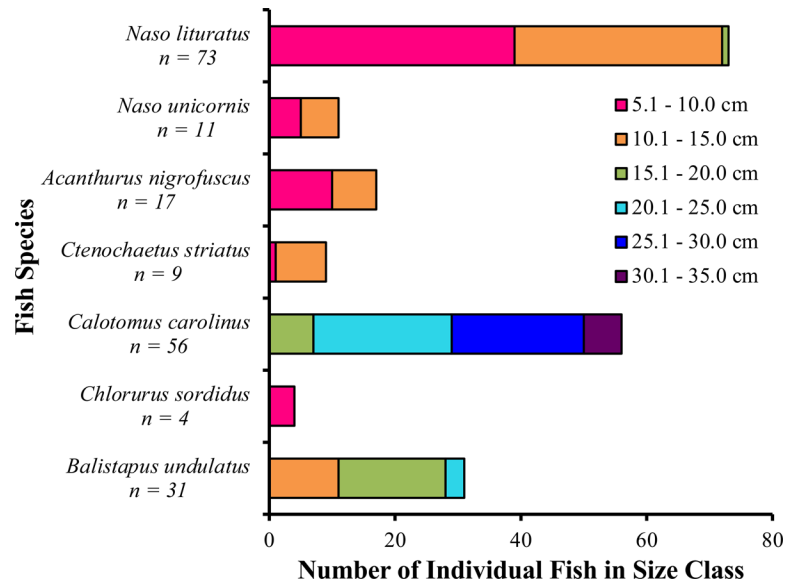


Figure 4. Number of individual fish of each fish species within different size classes. Total number of fish visits for each species is indicated below their name.

Table 1.

The fish species taking bites on macroalgae and the number of fish visits (replicates) per fish species. We classified our fish species into functional groups based upon Green and Bellwood (2009).

Fish Species (common name)	Fish Family (Tribe)	Functional Group	Fish Visits	Total Bites
<i>Balistapus undulatus</i> Park (Orange-lined triggerfish)	Balistidae	N/A	31	113
<i>Acanthurus nigrofuscus</i> Forsskål (Brown surgeonfish)	Acanthuridae	Grazer / detritivore	17	92
<i>Ctenochaetus striatus</i> Quoy & Gaimard (Striped bristletooth)	Acanthuridae	Grazer / detritivore	9	33
<i>Naso lituratus</i> Forster (Orangespine unicornfish)	Acanthuridae	Browser	73	397
<i>Naso unicornis</i> Forsskål (Bluespine unicornfish)	Acanthuridae	Browser	11	57
<i>Calotomus carolinus</i> Valenciennes (Stareye parrotfish)	Labridae (Scarinae)	Browser	56	222
<i>Chlorurus sordidus</i> Forsskål (Bullethead parrotfish)	Labridae (Scarinae)	Scraper / small excavator	4	42

Table 2.

We used AICc scores and weights to evaluate which GLMM best predicted the number of bites fish took on macroalgae. Fish functional group refers to the classifications according to Green and Bellwood (2009). All models were fitted with a negative binomial distribution and included fish visit as a random effect. Presented are conditional R^2 values calculated using the delta method (Nakagawa et al. 2017).

Model Formulation	R^2	K	AICc	AICc	AICc Weight
Number of Bites ~ Macroalgae + Fish Species	0.422	15	2036.3	0	0.8
Number of Bites ~ Macroalgae + Fish Functional Group	0.403	12	2039.0	2.7	0.2
Number of Bites ~ Macroalgae + Fish Family	0.325	11	2094.6	58.3	0.0
Number of Bites ~ Macroalgae	0.306	9	2116.4	80.0	0.0
Number of Bites ~ Fish Family	0.001	5	2365.0	328.7	0.0
Number of Bites ~ Fish Functional Group	0.002	6	2366.0	329.7	0.0
Number of Bites ~ Fish Species	0.003	9	2369.9	333.6	0.0

Table 3.

Fish species observed in this study and macroalgae they took bites on from this and previous studies.

Fish Species	Location	Sources	Methods	Macroalgae consumed
<i>Acanthurus nigrofuscus</i>	Moorea, French Polynesia	This study	Multiple-species assays	<i>Dictyota sp.</i> , <i>Acanthophora spicifera</i> , <i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i> , <i>Galaxaura sp.</i>
	GBR	Hoey and Bellwood 2009, Graba-Landry et al. 2020	Single-species assays	<i>Sargassum swartzii</i> *, <i>Sargassum sp.</i> *
	GBR	Tebbett et al. 2019	Multiple-species assays	<i>Sargassum sp.</i> *, <i>Turbinaria sp.</i> *, <i>Acanthophora sp.</i> *, <i>Galaxaura sp.</i> *, <i>Laurencia sp.</i>
<i>Balistapus undulatus</i>	Hawai'i	Kelly et al. 2016	Focal fish follows	<i>Amanzia sp.</i> , <i>Asparagopsis sp.</i> , <i>Tricleocarpa sp.</i> , <i>Turbinaria sp.</i> *
	Moorea, French Polynesia	This study	Multiple-species assays	<i>Padina boryana</i> , <i>Dictyota sp.</i> , <i>Acanthophora spicifera</i> , <i>Sargassum mangarevense</i> , <i>Halimeda sp.</i>
	Moorea, French Polynesia	Fong et al. 2020	Single-species assays	<i>Padina boryana</i> *
<i>Calatomus carolinus</i>	Moorea, French Polynesia	This study	Multiple-species assays	<i>Padina boryana</i> , <i>Sargassum mangarevense</i>
	GBR	Hoey and Bellwood 2009	Single-species assays	<i>Sargassum swartzii</i> *
	GBR	Tebbett et al. 2019	Multiple-species assays	<i>Sargassum sp.</i> *, <i>Halimeda sp.</i>
	Kenya	Humphries et al. 2015	Multiple-species assays	<i>Padina sp.</i> *
	Indonesia	Plass-Johnson et al. 2015	Single-species assays	<i>Padina pavonica</i> *
<i>Chlorurus sordidus</i>	Hawai'i	Kelly et al. 2016	Focal fish follows	<i>Amanzia sp.</i> , <i>Tolyptocladia sp.</i> , <i>Turbinaria sp.</i>
	Moorea, French Polynesia	This study	Multiple-species assays	<i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i>
	Moorea, French Polynesia	Fong et al. 2020	Single-species assays	<i>Padina boryana</i>
	GBR	Hoey and Bellwood 2009	Single-species assays	<i>Sargassum swartzii</i> *
	GBR	Bennett and Bellwood 2011	Single-species assays	<i>Sargassum myriocystum</i> *
<i>Ctenochaetus striatus</i>	Ningaloo Reef, Western Australia	Vergés et al. 2012, Michael et al. 2013	Single-species assays	<i>Sargassum myriocystum</i> *
	Fiji	Rasher et al. 2013	Multiple-species assays	<i>Sargassum polydictyon</i> *, <i>Galaxaura filamentosa</i> , <i>Amphiroa crassa</i> , substrate
	Seychelles, West Indian Ocean	Chong-Seng et al. 2014	Single-species assays	<i>Sargassum sp.</i> *
<i>Ctenochaetus striatus</i>	Moorea, French Polynesia	This study	Multiple-species assays	<i>Dictyota sp.</i> , <i>Sargassum mangarevense</i> , <i>Turbinaria ornata</i> , <i>Halimeda sp.</i> , <i>Galaxaura sp.</i>

Fish Species	Location	Sources	Methods	Macroalgae consumed
	Moorea, French Polynesia	Fong et al. 2020	Single-species assays	<i>Padina boryana</i>
	GBR	Hoey and Bellwood 2009, Graba-Landry et al. 2020	Single-species assays	<i>Sargassum swartzii</i> *, <i>Sargassum sp.</i> *
	GBR	Tebbett et al. 2019	Multiple-species assays	<i>Sargassum sp.</i> *, <i>Turbinaria sp.</i> *, <i>Acanthophora sp.</i> , <i>Halimeda sp.</i> , <i>Galaxaura sp.</i> *, <i>Laurencia sp.</i>
	Ningaloo Reef, Western Australia	Michael et al. 2013	Single-species assays	<i>Sargassum myriocystum</i> *
	Fiji	Rasher et al. 2013	Multiple-species assays	None - fed on substrate
	Kenya	Humphries et al. 2015	Multiple-species assays	<i>Cystoseira sp.</i> *, <i>Dictyota sp.</i> *, <i>Hypnea sp.</i> , and <i>Padina sp.</i>
	Moorea, French Polynesia	This study	Multiple-species assays	<i>Padina boryana</i> , <i>Dictyota sp.</i> , <i>Sargassum mangarevense</i>
	Moorea, French Polynesia	Fong et al. 2020	Single-species assays	<i>Padina boryana</i> *
	Ningaloo Reef, Western Australia	Vergés et al. 2012, Michael et al. 2013	Single-species assays	<i>Sargassum myriocystum</i> *
<i>Naso lituratus</i>	Fiji	Rasher et al. 2013	Multiple-species assays	<i>Sargassum polycystum</i> *, <i>Turbinaria conoides</i> , <i>Padina boryana</i> *, <i>Dictyota bartayresiana</i> *
	Indonesia	Plass-Johnson et al. 2015	Single-species assays	<i>Sargassum sp.</i> *, <i>Padina pavonica</i> *
	Hawai'i	Kelly et al. 2016	Focal fish follows	<i>Amansia sp.</i> , <i>Dictyota sp.</i> *, <i>Laurencia sp.</i> , <i>Tolypocladia sp.</i> , <i>Turbinaria sp.</i>
	Moorea, French Polynesia	This study	Multiple-species assays	<i>Padina boryana</i>
	Moorea, French Polynesia	Fong et al. 2020	Single-species assays	<i>Padina boryana</i> *
	GBR	Choat et al. 2002	Stomach contents	<i>Dictyota sp.</i> , <i>Turbinaria sp.</i> specified in text, otherwise macroalgal genera not specified.
	GBR	Hoey 2010, Streit et al. 2015, Puk et al. 2016-Review, Graba-Landry et al. 2020	Single-species assays	<i>Sargassum sp.</i>
<i>Naso unicornis</i>	GBR	Tebbett et al. 2019	Multiple-species assays	<i>Sargassum sp.</i> , <i>Turbinaria sp.</i> , <i>Acanthophora sp.</i> , <i>Galaxaura sp.</i> , <i>Laurencia sp.</i> , <i>Halimeda sp.</i>
	Ningaloo Reef, Western Australia	Puk et al. 2016 - Review	Single-species assays	<i>Sargassum myriocystum</i>
	Fiji	Rasher et al. 2013	Multiple-species assays	<i>Sargassum polycystum</i> , <i>Turbinaria conoides</i> , <i>Padina boryana</i> *, <i>Dictyota bartayresiana</i>
	Kenya	Humphries et al. 2015	Multiple-species assays	<i>Sargassum sp.</i>
	Seychelles, West Indian Ocean	Chong-Seng et al. 2014	Single-species assays	<i>Sargassum sp.</i>

Fish Species	Location	Sources	Methods	Macroalgae consumed
	Indonesia	Plass-Johnson et al. 2015	Single-species assays	<i>Sargassum</i> sp., <i>Padina pavonica</i> *
	Hawai'i	Kelly et al. 2016	Focal fish follows	<i>Amanoa</i> sp., <i>Chondrophycus</i> sp., <i>Laurencia</i> sp., <i>Pterocladia</i> sp., <i>Tolyptocladia</i> sp., <i>Tricleocarpa</i> sp., <i>Turbinaria</i> sp.

We included studies if 1) they observed at least one of the fish species from our study, 2) they included at least one of the macroalgae in our study as an option, and 3) they identified macroalgae to at least the genus level. We used an asterisk (*) to indicate macroalgae consumed in previous studies that coincide with macroalgae consumed in this study for each fish species.