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

## 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

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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, 2011b), 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, 2007b; 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, 2007b; 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, *Dictoya 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

**Table 1**
The fish species taking bites on macroalgae and the number of fish visits (replicates) per fish species.

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

We classified our fish species into functional groups based upon Green and Bellwood (2009).

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 h. 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 (final – initial / initial *100) of each macroalga for each choice experiment and calculated the mean ± 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

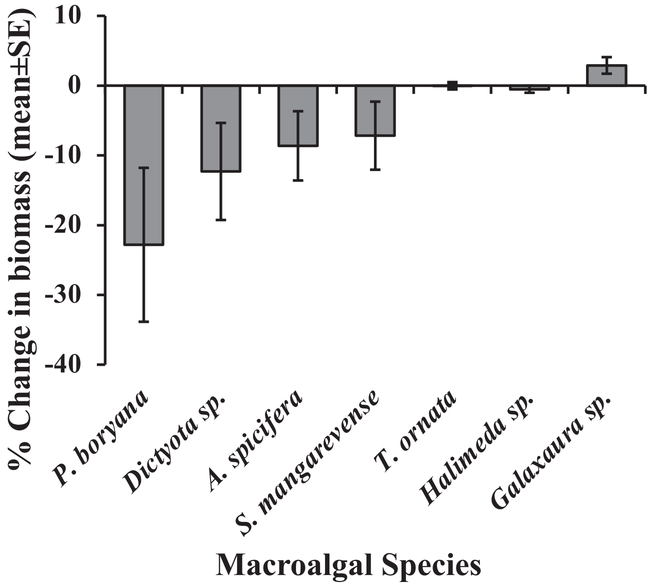

**Fig. 1.** Percent change in biomass (mean ± SE) for each macroalgal species presented in choice assays ($n = 11$).

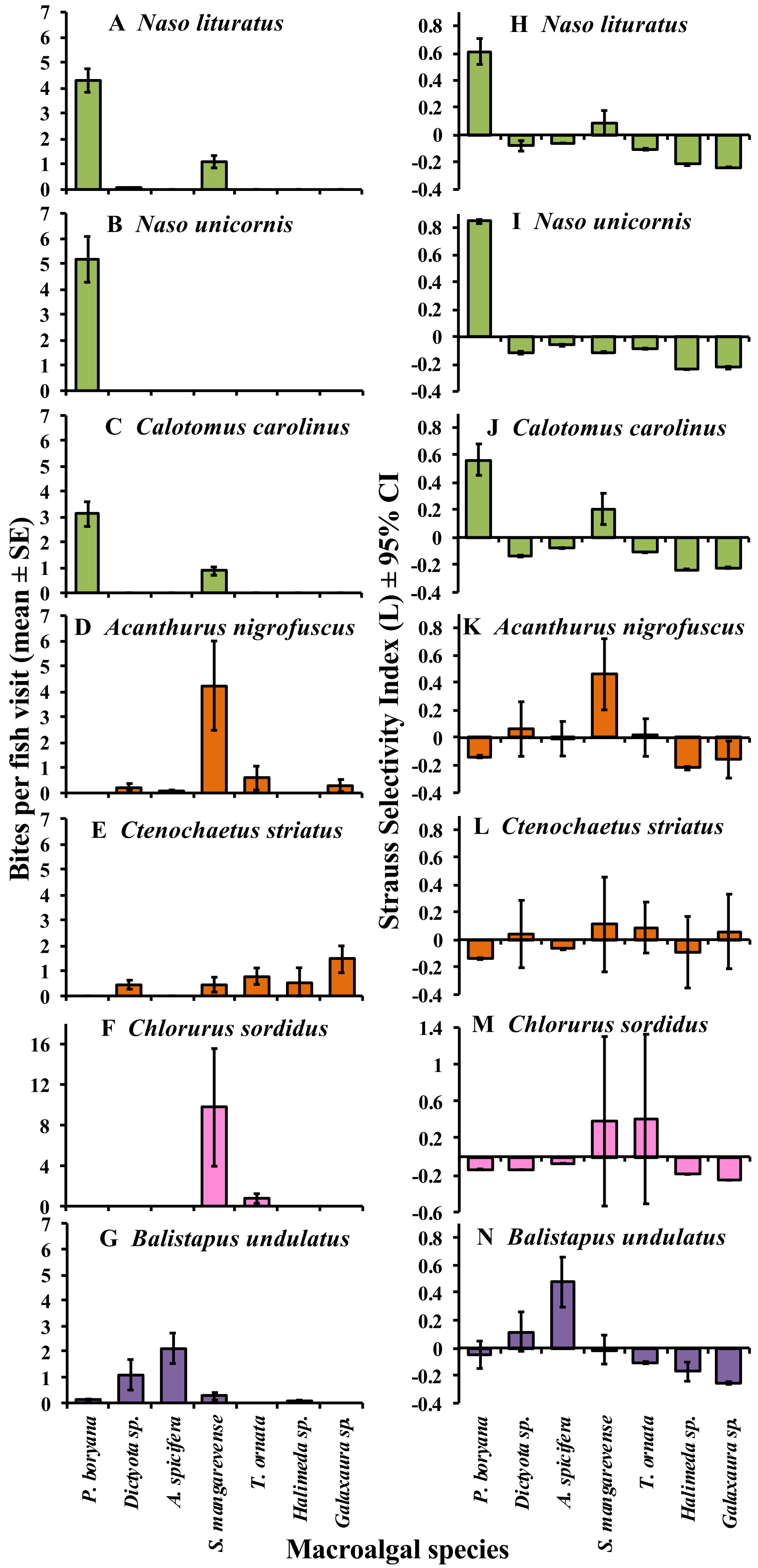

**Fig. 2.** Bites per fish visit (mean ± SE, column 1) and Strauss selectivity index values (±95% CI, column 2) for fish species taking bites on macroalgal choice experiments. Macroalgae are presented in order of increasing complexity and defenses against herbivory, according to Steneck and Dethier (1994). 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 (ΔAICc), where the lowest calculated value is 0. Models with ΔAICc in the range of 2–7 have support (Burnham et al., 2011), so we used a more conservative value of ΔAICc >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, ΔAICc, and AICc weights for our models. We used the r.squaredGLMM function from the 'MuMIn' package (Bartoń, 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).

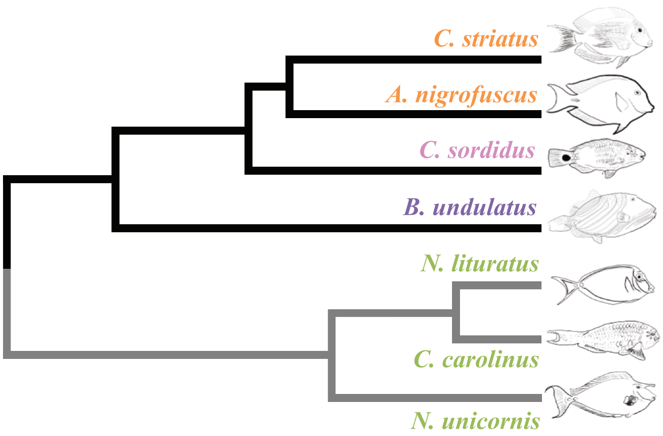

**Fig. 3.** Clusters of fish species based upon their Strauss' selectivity indices for macroalgae presented in choice experiments. Black versus gray lines indicate which fish species group together into each cluster. Fish species names are color coded according to their functional group based on Green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

### 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 (ΔAICc <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

**Table 2**
We used ΔAICc scores and weights to evaluate which GLMM best predicted the number of bites fish took on macroalgae.

| Model Formulation | $R^2$ | K | AICc | ΔAICc | 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 |

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).

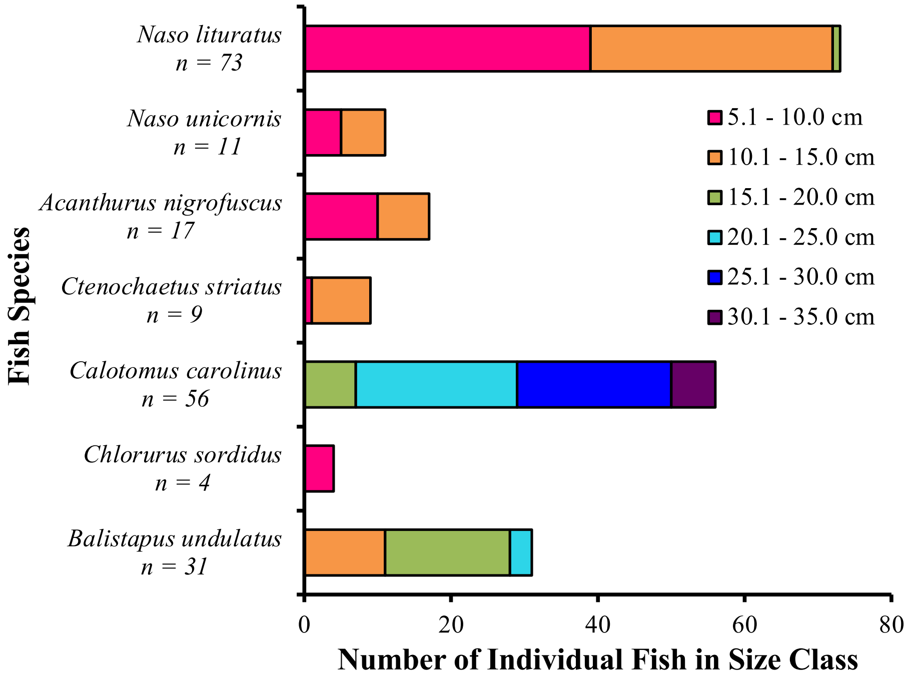

**Fig. 4.** Number of individual fish of each fish species within different size classes. Total number of fish visits for each species is indicated below their name.

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 group 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

**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 |
|---|---|---|---|---|
| ***Acanthurus nigrofuscus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Dictyota sp., Acanthophora spicifera, Sargassum mangarevense, Turbinaria ornata, Galaxaura sp.* |
| | GBR | Hoey and Bellwood, 2009,<br>Graba-Landry et al., 2020 | Single-species assays | *Sargassum swartzii*,*<br>*Sargassum sp.** |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | *Sargassum sp.*, Turbinaria sp.*, Acanthophora sp.*, Galaxaura sp.*, Laurencia sp.* |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | *Amansia sp., Asparagopsis sp., Tricleocarpa sp., Turbinaria sp.** |
| ***Balistapus undulatus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Padina boryana, Dictyota sp., Acanthophora spicifera, Sargassum mangarevense, Halimeda sp.* |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | *Padina boryana** |
| ***Calatomus carolinus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Padina boryana, Sargassum mangarevense* |
| | GBR | Hoey and Bellwood, 2009 | Single-species assays | *Sargassum swartzii** |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | *Sargassum sp.*, Halimeda sp.* |
| | Kenya | Humphries et al., 2015 | Multiple-species assays | *Padina sp.** |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | *Padina pavonica** |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | *Amansia sp., Tolypiocladia sp., Turbinaria sp.* |
| ***Chlorurus sordidus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Sargassum mangarevense, Turbinaria ornata* |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | *Padina boryana* |
| | GBR | Hoey and Bellwood, 2009 | Single-species assays | *Sargassum swartzii** |
| | GBR | Bennett and Bellwood, 2011 | Single-species assays | *Sargassum myriocystum** |
| | Ningaloo Reef, Western Australia | Vergés et al., 2012,<br>Michael et al., 2013 | Single-species assays | *Sargassum myriocystum** |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | *Sargassum polycystum*, Galaxaura filamentosa, Amphiroa crassa*, substrate |
| | Seychelles, West Indian Ocean | Chong-Seng et al., 2014 | Single-species assays | *Sargassum sp.** |
| ***Ctenochaetus striatus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Dictyota sp., Sargassum mangarevense, Turbinaria ornata, Halimeda sp., Galaxaura sp.* |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | *Padina boryana* |
| | GBR | Hoey and Bellwood, 2009,<br>Graba-Landry et al., 2020 | Single-species assays | *Sargassum swartzii*,*<br>*Sargassum sp.** |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | *Sargassum sp.*, Turbinaria sp.*, Acanthophora sp., Halimeda sp.*, Galaxaura sp.*, Laurencia sp.* |
| | Ningaloo Reef, Western Australia | Michael et al., 2013 | Single-species assays | *Sargassum myriocystum** |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | None - fed on substrate |
| | Kenya | Humphries et al., 2015 | Multiple-species assays | *Cystoseira sp., Dictyota sp.*, Hypnea sp.,* and *Padina sp.* |
| ***Naso lituratus*** | Moorea, French Polynesia | This study | Multiple-species assays | *Padina boryana, Dictoyta sp., Sargassum mangarevense* |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | *Padina boryana** |
| | Ningaloo Reef, Western Australia | Vergés et al., 2012,<br>Michael et al., 2013 | Single-species assays | *Sargassum myriocystum** |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | *Sargassum polycystum*, Turbinaria conoides, Padina boryana*, Dictyota bartayresiana** |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | *Sargassum sp.*, Padina pavonica** |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | *Amansia sp., Dictyota sp.*, Laurencia sp., Tolypiocladia sp., Turbinaria sp.* |
| ***Naso unicornis*** | Moorea, French Polynesia | This study | Multiple-species assays | *Padina boryana* |
| | Moorea, French Polynesia | Fong et al., 2020 | Single-species assays | *Padina boryana** |
| | GBR | Choat et al., 2002 | Stomach contents | *Dictyota sp., Turbinaria sp.* 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 | *Sargassum sp.* |
| | GBR | Tebbett et al., 2019 | Multiple-species assays | *Sargassum sp., Turbinaria sp., Acanthophora sp., Galaxaura sp., Laurencia sp., Halimeda sp.* |

(continued on next page)

Table 3 (*continued*)

| Fish Species | Location | Sources | Methods | Macroalgae consumed |
|---|---|---|---|---|
| | Ningaloo Reef, Western Australia | Puk et al., 2016 - Review | Single-species assays | *Sargassum myriocystum* |
| | Fiji | Rasher et al., 2013 | Multiple-species assays | *Sargassum polycystum, Turbinaria conoides, Padina boryana*, Dictyota bartayresiana* |
| | Kenya | Humphries et al., 2015 | Multiple-species assays | *Sargassum sp.* |
| | Seychelles, West Indian Ocean | Chong-Seng et al., 2014 | Single-species assays | *Sargassum sp.* |
| | Indonesia | Plass-Johnson et al., 2015 | Single-species assays | *Sargassum sp., Padina pavonica** |
| | Hawai'i | Kelly et al., 2016 | Focal fish follows | *Amansia sp., Chondrophycus sp., Laurencia sp., Pterocladiella sp., Tolypiocladia sp., Tricleocarpa sp., Turbinaria 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.

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.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151508.

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