Journal of Experimental Marine Biology and Ecology 533 (2020) 151469

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Testing the conceptual and operational underpinnings of field herbivory assays: Does variation in predictability of resources, assay design, and deployment method affect outcomes?

Caitlin R. Fong[a,*], Shayna A. Sura[b], Ashlyn T. Ford[c], Hunter B. Howard[d], Nury E. Molina[b], Nefertiti N. Smith[e], Peggy Fong[b]

[a] Department of Ecology, Evolution, Marine Biology, University of California, Santa Barbara, CA 93106, United States of America
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, United States of America
[c] School of the Environment, Florida Agricultural and Mechanical University, Tallahassee, FL 32307, United States of America
[d] Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, MD 21853, United States of America
[e] Department of Marine and Environmental Science, Hampton University, Hampton, VA 23668, United States of America

ARTICLE INFO

Keywords:
Herbivory
Herbivory assays
Out-plant experiments
Macroalgae
Palatability

ABSTRACT

Herbivory assays are a valuable tool used by field ecologists to understand many of the patterns and processes affecting herbivory, a widely recognized driving force in marine communities. However, methods vary substantially among studies in both design and operation, and the effect of these differences has yet to be evaluated. We assessed the effects of several key components of assay design on estimates of herbivory on a tropical reef, a system characterized by strong herbivory pressure by highly mobile grazers. Based on our results, we offer four recommendations. First, we found assays out-planted on sequential days in both predictable and random locations within a 60m2 site experienced temporal increases in herbivory by an increasingly diverse assemblage of fishes. Thus, we strongly advise against placing herbivory assays in the same site over a series of days. Second, we found while the amount of biomass consumed in assays was density-dependent, but the percent loss was not. Thus, it is our opinion that researchers should report percent consumption because this metric is robust to differences in biomass offered and will facilitate comparisons across studies. Third, we found associational effects, where proximity of species of differing palatabilities impacted estimates of herbivory rate on one or both species, but these impacts were not consistent across species or sites. Thus, we recommend the effect of association be directly tested for multi-species herbivory assays. Fourth, we found no effect of attachment method on estimates of herbivory rate and recommend researchers continue to use the attachment method in which they are most confident. We hope our experimental results prove useful in the future when designing, conducting, and interpreting herbivory assays.

1. Introduction

Herbivory assays are a valuable tool enabling field ecologists to understand many of the patterns and processes affecting herbivory. Herbivory assays typically entail out-planting known weights or lengths of macroalgae or seagrass and using loss and/or video recordings to compare rates, pressure, and selectivity. Herbivory assays have been used across a range of marine communities, including kelp forests (e.g. Vergés et al., 2016), rocky intertidal (e.g. Aguilera et al., 2015), seagrass meadows (e.g. Bourque and Fourqurean, 2013), and coral reefs (e.g. Hay et al., 1983). These assays have been used to compare spatial and temporal patterns in herbivory pressure (a few examples include Hay et al., 1983, Madin et al., 2011, Aguilera et al., 2015, Catano et al., 2016, Bourque and Fourqurean, 2013). They have also been used to assess differences in herbivory pressure on macroalgae of different quality, including differences in nutritional content (e.g. Chan et al., 2012; Shantz et al., 2017), collection location (Keeley et al., 2015), or developmental stage (e.g. Hoey, 2010). Cafeteria-style herbivory assays have been used to assess preferences and selectivity of individual fish species for different macroalgal species and to compare fish community structure and function (Mantyka and Bellwood, 2007a, 2007b; Rasher et al., 2013). Additionally, videos of these herbivory assays have been used to identify key grazers (Mantyka and Bellwood, 2007a; Vergés et al., 2016). In spite of intensive use, the effects of common differences

* Corresponding author.
E-mail address: cat.r.fong@gmail.com (C.R. Fong).

https://doi.org/10.1016/j.jembe.2020.151469
Received 10 June 2020; Received in revised form 18 September 2020; Accepted 18 September 2020

in methods have never been evaluated.

One possible effect to evaluate is whether predictability of a resource can impact the resulting levels of herbivory measured using algal assays. In order to achieve adequate replication, some researchers outplant herbivory assays in different locations within the same site over sequential days or within a few days (e.g. Mantyka and Bellwood, 2007a, 2007b; Rasher et al., 2013; Plass-Johnson et al., 2015; Keeley et al., 2015). This practice may result in the presence of the resource becoming predictable over time and may affect measures of herbivory. For example, a carnivorous coral reef fish responds to the occurrence of a regular resource provided through chumming (Sweatman, 1996). In this case, fish aggregated in greater abundances than what may be expected naturally. Further, the community composition of consumers measured at predictable versus unpredictable assays may differ. Although, to our knowledge, there are no studies of this topic in marine systems, evidence from terrestrial systems shows less competitive species with broader searches specialize on unpredictable resources and are readily observed at these unpredictable resources, while competitive dominants monopolize predictable resources (Cortés-Avizanda et al., 2012). Alternately, theory suggests the number of observed species may increase over time for predictable assays as more species that specialize on predictably available resources find and then return to the assays, only saturating once the entire community has been sampled (Efron and Thisted, 1976). Therefore, it is critical that we understand how the predictability of a resource alters the abundance and composition of herbivores, and the amount of resources that may be consumed.

Herbivory assays vary in size among studies, which may impact estimates of herbivory. For example, optimal foraging theory (OFT) predicts as resource patch size increases, foraging increases, with individuals leaving a patch when patch intake rates equal mean intake rates across the landscape (Charnov, 1976). Thus, herbivores should remove more biomass from larger or denser patches, resulting in herbivory pressure estimates that are density-dependent, making comparisons among studies using different initial biomasses problematic. There is some empirical evidence on coral reefs that herbivorous fish abundance and behavior do track spatial patterns of resource availability (Tootell and Steele, 2016). However, OFT may not govern herbivory dynamics. For example, previous research indicates larger assemblages of *Sargassum* experience reduced herbivory rates, likely due to fear of hidden predators in large algal masses (Hoey and Bellwood, 2010). Further, herbivory may be driven primarily by landscape characteristics rather than abundance (Madin et al., 2011; Fong et al., 2017; Gil and Hein, 2017). Reasons researchers vary the biomass of algae offered include attempting to standardize size by providing equal volumes of different species (e.g. Mantyka and Bellwood, 2007a, 2007b) or to equalize encounter rates, especially for less mobile herbivores (Sotka and Hay, 2002). Because the amount of resources provided in herbivory assays varies substantially across studies (Chan et al., 2012; Keeley et al., 2015; Madin et al., 2011; Mantyka and Bellwood, 2007a, 2007b; Plass-Johnson et al., 2015), the importance of assay quantity should be directly tested.

Associational effects occur when herbivory rate depends on proximity of species of different palatability, and may arise when multiple species are out-planted together. An associational defense occurs when a more palatable species experiences decreased herbivory when associated with a less palatable species (e.g. Hay, 1986). An associational susceptibility occurs when herbivory on a less palatable species increases when associated with a more palatable species (see Barbosa et al., 2009 for review). Many assays comprise a mixed assemblage where associational effects may arise, including cafeteria-style assays that are used to assess herbivore preference and selectivity (Mantyka and Bellwood, 2007a, 2007b; Chan et al., 2012; Keeley et al., 2015). While associational defenses are well established in marine communities (e.g. Littler et al., 1986; Littler et al., 1987; Fong et al., 2006; Bittick et al., 2010; Loffler et al., 2015), the frequency of associational susceptibilities is unclear. Regardless of directionality, whether associational effects of either type affect the outcome of herbivory assays has not been established and warrants direct assessment.

Operationally, herbivory assays must be attached to something for deployment, and it is possible the considerable variation in methods used may impact estimates of herbivory rate. For example, herbivorous fishes may rely on visual cues for foraging, and variation in attachment method may influence those cues, adding variation to estimates of herbivory pressure across methods. Attachment methods include cable ties and rope (e.g. Chan et al., 2012; Keeley et al., 2015; Plass-Johnson et al., 2015), clothes pins (Hay et al., 1983, Madin et al., 2011, Catano et al., 2016), rope twists (Sluka and Miller, 2001), rubber bands and lead weights (Hoey, 2010), and gardening wire (Bennett and Bellwood, 2011). While attachment methods vary substantially across studies, how this variation affects experimental outcomes has never been tested.

Although herbivory assays are commonly used, methodological variation has never been evaluated. However, both theoretical predictions and empirical evidence suggest varying the design of assays in ways that may alter resource predictability, optimal foraging, and associational context may affect resultant measures of herbivory. At a more operational level, methods for attachment and deployment of assays vary substantially among studies but comparisons of these methods are lacking. Here, we determined how 1) temporal and spatial predictability of resources, 2) resource quantity as different initial biomasses, 3) associational effects due to proximity of species of differing palatability, and 4) method of attachment affect measures of herbivory in the field.

2. Materials and methods

This study was conducted in Moorea, French Polynesia in January-February 2016 and June-July 2017. We chose to work on a tropical reef because herbivory is a strong structuring force (Lewis, 1986).

2.1. Study sites

We conducted our studies on four fringing reefs along Moorea's north shore to test the generalizability of our findings (Fig. 1). Taahiamanu reef is a patch reef and we worked on the seaward reef slope at approximately three m depth. Stone Pier is also a patch reef system approximately two m deep and we worked in the middle of the reef

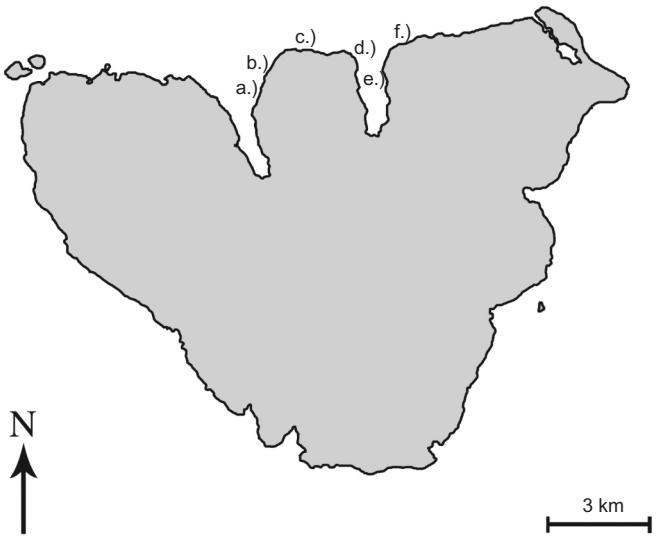

Fig. 1. Map of Mo'orea, French Polynesia with letters denoting our field sites: a.) Taahiamanu; b.) Stone Pier; c.) Hilton; d.) Green Marker; e.) Gump; and f.) Maharepa reefs. Scale bar is 3 km. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

away from the slope. Green Marker reef is a shallow reef with continuous hard structure and limited sand approximately two m deep before a drop off into the bay. Maharepa reef is also a continuous reef and we worked on the seaward slope ~ two m deep before a drop off into a boat channel. Previous research indicates these sites vary in herbivore abundance (Bergman et al., 2016). We used two additional sites for algal collection, Gump reef and Hilton reef, both patch reefs with high diversity and abundance of macroalgae.

2.2. Study species

We used different combinations of three species of macroalgae in our experiments to determine the generalizability of our findings across algal species of different morphologies. We used *Padina boryana, Sargassum mangarevense,* and *Galaxaura divaricate* (Guiry and Guiry, 2020) because they are common, vary in palatability, and have been used in other studies in Moorea (e.g. Fong and Fong, 2014; Fong, 2015; Keeley et al., 2015). *P. boryana* is a highly palatable foliose brown macroalga with light calcification (Fong and Fong, 2014). This species has been frequently used in herbivory assays in Moorea (e.g. Fong and Fong, 2014; Keeley et al., 2015). *S. mangarevense* is also a brown macroalga; it is in the thick/leathery functional form group (sensu Littler and Littler, 1980) and previous research indicates it is less palatable than *P. boryana* (Keeley et al., 2015). Our final species is a relatively unpalatable calcified red alga in the articulated calcified functional group (Steneck and Dethier, 1994; Fong and Fong, 2014), and previous research indicates *Galaxaura* congeners are less palatable than *Sargassum* congeners (Loffler et al., 2015).

2.3. Evaluating handling loss

We conducted a series of caged control experiments in 2017 to ensure the effectiveness of our herbivory assay experiments. In these assessments, we out-planted 5.0 g of *P. boryana* in cages at Maharepa in 2017 (n = 19). Algae were collected from Gump reef, cleaned of epibionts, spun in a salad spinner for 60 s, and wet weighed into 5.0 g subsamples. Subsamples were attached inside a cage and out-planted near our experiments. Cages were cylinders (ten cm diameter, ten cm height) constructed from hardware cloth with one x one cm openings. Prior studies confirmed that no herbivores were able to enter cages constructed from this material (Fong et al., 2016; Bittick et al., 2020). Cage controls were left in the field for between two and four hours, with an average deployment of 3.17 ± SD 0.668 h. Afterwards, cage controls were collected and algae respun and reweighed to quantify handling loss. Handling loss was calculated as percent loss per hour [(initial-final)/initial] x 100/h deployed.

2.4. Resource predictability

We evaluated whether temporal and spatial predictability affected herbivory rates at two sites. The two sites were Maharepa and Taahiamanu reefs, where we presented a single species of palatable macroalgae to herbivores in predictable and unpredictable locations within a 30 m by 2 m (60 m^2) experimental site. Qualitatively, Maharepa reef appeared to have a greater abundance of herbivorous fishes than Taahiamanu reef, though we did not conduct surveys.

The first experiment was conducted at ~two to three m depth along Taahiamanu fringing reef from 31 January to 5 February 2016. A palatable macroalga, *P. boryana*, was offered to herbivores daily between 900 and 1500 h. Each day, whole thalli of *P. boryana* were collected haphazardly at Gump reef. Thalli were cleaned of epibionts, spun in a salad spinner for 60 s, and wet weighed into 5.0 g subsamples. Each subsample was attached with cable ties to a 0.5 m length of rope and tied to the benthos, avoiding damselfish territories (Ceccarelli et al., 2005). Half the assays were assigned to be unpredictably available and deployed at new random locations chosen daily within the experimental site. The other half of the assays was assigned as predictably available and new assays were placed in the same locations every day for six days. Once a predictable marker was lost, the location was no longer used, resulting in uneven replication across days. For this and all subsequent experiments, replication is listed in figure captions. After two to four hours, assays were collected, spun, and wet weighed as above. Deployment time shortened over the course of the experiment as herbivory rate increased (see results); however, time deployed was the same within each day. Herbivory pressure was calculated as percent loss per hour [(initial-final)/initial] × 100/h deployed.

We conducted a second experiment on Maharepa reef from 9 to 14 July 2017 to determine the generalizability of this pattern. While our objective was the same, this second experiment expanded on the first in two ways. First, we video-recorded a subset of our predictably-available assays to determine which herbivorous fishes were responsible for loss of macroalgae and whether that changed over time. We only recorded predictable assays because these assays effectively went from unpredictable on the first day to increasingly predictable over the course of the experiment. We took a total of 15 videos of ~90 min each, with n = 2 or 3 for each of six days (some videos were not successful). Using these videos, we counted the number of fish species eating our predictable assays as well as number of bites. We were unable to enumerate individual fish because our video field of view was relatively small, and therefore, the same individual could swim in and out of the field of view, making it impossible to ensure we were counting individual fish. As before, once a predictable assay site marker was lost, the site was no longer used, resulting in uneven replication across days. Second, to determine if fish continued to respond to consecutive assay availability, after a six day break, we out-planted more assays in the same predictable and new unpredictable locations on a single day (20 July 2017).

We used a linear model to analyze herbivory pressure over the six day predictability experiment, with treatment and day as fixed effects and percent change per hour as our response variable; we did this for each experiment separately because both year and site varied between experiments. Data were square root transformed, after which residuals were normally distributed (see Table S1 for details). Data were analyzed with the 'car' package in R because lost replicates resulted in an unbalanced design (Fox and Weisberg, 2019). We also related fish species diversity to assay day with a linear model because our data was normally distributed (see Table S2 for details). To determine if the temporal pattern we observed at Maharepa reef over the course of our six day experiment (see results) was still detectable six days later, we conducted a *t*-test comparing herbivory pressure on day six versus day 12 across all predictable and unpredictable replicates. This test was appropriate because we found no effect of our predictability treatment in this site (see results).

2.5. Resource availability

To assess if macroalgal quantity, defined as differences in initial biomass, affected estimated rates of herbivory, we varied weight (g) offered in assays containing *P. boryana* or *S. mangarevense* in a total of five experiments. We conducted these experiments on Taahiamanu reef because this reef had abundant herbivorous fishes. We chose these two species of macroalgae because previous research has shown that, while both are palatable, *P. boryana* is more readily consumed than *S. mangarevense* (Keeley et al., 2015), and we wanted to determine if palatability affected response to resource availability. Assays comprised 5.0, 10.0, or 20.0 g of algae. *P. boryana* thalli were collected from Gump reef and offered to herbivores at Taahiamanu reef between 930 and 1330 h on 27 January 2016. Because of low availability on Gump reef, *S. mangarevense* was collected from Taahiamanu reef and offered to herbivores between 1030 and 1430 h on 28 January 2016. Experimental units for both species were deployed haphazardly at Taahiamanu reef on their respective dates. After four hours, algae were collected and

final weight was determined. For both species, we analyzed both grams consumed per hour and percent of initial mass consumed per hour because 1) both of these metrics are reported in the literature and 2) optimal foraging theory predicts herbivory rate should be highest on larger/denser resource patches (greater percent consumed). Thus, final weights of herbivory assays should be the same irrespective of initial weights because herbivores forage at a patch until the rate of return is equal to the landscape average. The *P. boryana* data met assumptions of parametric statistics (see Table S3 for details). Thus, we analyzed the data with a one-way ANOVA and subsequent Tukey HSD post hocs for both grams lost per hour and percent lost per hour. *S. mangarevense* data did not meet assumptions of parametric statistics, even after transformations, and was thus analyzed with a Kruskal-Wallis test with Dunn Test post hocs, with corrections for multiple comparisons.

To test the generalizability of the pattern we documented, we repeated the above experiment with just *P. boryana* at 3 additional sites in 2017: Maharepa, Green Marker, and Stone Pier reefs, on the 30th of June and the 3rd and 4th of July 2017, respectively. Methods for collection, assembly, deployment, and retrieval remained the same, and all thalli were collected from Gump reef. We deployed and then retrieved assays as before. Data for all three species across all three sites met assumptions of normality for both grams and percent after a square root transformation; prior to transforming, we added the minimum value to all data to ensure all responses were positive (See Table S3 for details). Thus, we analyzed each site separately with a one-way ANOVA for both grams consumed per hour and percent consumed per hour as separate response variables.

2.6. Associational defenses and susceptibility

We evaluated the impact of associational defenses, where the presence of a less palatable species decreases herbivory rate on a more palatable species, or associational susceptibility, where the presence of a more palatable species increases herbivory rate on a less palatable species, on estimates of herbivory. In our first two experiments, we tested for the presence of an associational effect. In our next three experiments, we varied distance between thalli to determine how far any associational effect extended.

In our first experiment, we used *P. boryana*, a more palatable species, and *S. mangarevense*, a less palatable species (Keeley et al., 2015). These species can co-occur on these reefs, with *P. boryana* growing near the holdfast of *S. mangarevense* (C. Fong, personal observation). Both species were collected haphazardly within the same area of Taahiamanu reef to minimize initial differences in susceptibility to herbivory that may be associated with location (Keeley et al., 2015). Algae were collected, cleaned of epibionts, spun, weighed, and assembled into assays. Experimental treatments were 10.0 g *P. boryana* > one m apart from any other assay, 10.0 g *S. mangarevense* > one m apart from any other assay, and 5.0 g of each species together, or zero cm apart, with thalli touching. Assays were deployed at Taahiamanu reef on 28 January 2016 from 1030 to 1430 h. Algae were then collected, spun, reweighed, and percent loss per hour was calculated.

In our second experiment, we used *P. boryana* and *G. divaricata*, a red alga that is less palatable than *S. mangarevense* (Mantyka and Bellwood, 2007a, 2007b for congeners). These species can co-occur, with species touching and with *P. boryana* even growing epiphytically on *G. divaricata* (C. Fong, personal observation). Both species were collected from Gump reef and assays were assembled as above. Experimental treatments were 6.0 g *P. boryana* > one m apart from any other assay, 6.0 g *G. divaricata* > one m apart from any other assay, or 3.0 g of each species zero cm apart. Assays were deployed at Taahiamanu reef on 4 February 2016 from 1100 h to 1400 h. Algae were then collected, spun, reweighed, and percent loss per hour was calculated.

To explore the spatial extent of any associational effects, we conducted similar experiments at three additional sites using four distance treatments to determine at what distance associational effects dissipated. We used *P. boryana* and *S. mangarevense* and had treatments where thalli were 0 cm, 10 cm apart, 20 cm apart, and > 1 m apart. Assays comprised 5.0 g of each species; *P. boryana* was collected at Gump reef while *S. mangarevense* was collected at the Hilton reef where it was readily available. Assays were deployed at Maharepa, Green Marker, and Stone Pier reefs on 5, 6, and 8th of July 2017 respectively. Assays were deployed between 1100 h and 1400 h, collected after two to four hours, reweighed, and calculated percent consumed per hour. Due to loss in the field, replication varied across treatment and sites (sample sizes are listed in figure captions).

For the first experiment with *P. boryana* and *S. mangarevense,* residuals were normally distributed and were thus analyzed with a two-way ANOVA with species and association as main effects. Because we had an unbalanced design, we used the car package in R (Fox and Weisberg, 2019). However, the data for the second experiment with *P. boryana* and *G. divaricata* did not meet assumptions, even after transformation. Thus, we analyzed grams remaining because these data were zero inflated due to total consumption of *P. boryana* in several assays. We used a GLM with a Poisson distribution, where species and association were main effects and grams remaining was the response variable. For the third and fourth experiments (*P. boryana* and *S. mangarevense*) at Maharepa and Stone Pier, data were assumed normal after a square root transformation (Table S4) while data at Green Marker were assumed normal after a log transformation. Thus, data from these three sites were analyzed with a two-way ANOVA with species and association as main effects.

2.7. Attachment

We determined if herbivory pressure varied with three methods of attachment: cable ties, clothespins, or twisted into a rope twine. We conducted this assay at three sites to ensure generalizability of the pattern: Stone Pier, Green Marker, and Maharepa reefs on the 16th, 21st, and 24th of July 2017, respectively. We used *P. boryana* collected haphazardly at Gump reef the day of each experiment. Algae were cleaned, spun, weighed, and 5.0 g subsamples were attached with one of the three methods, and out-planted haphazardly. As before, assays were offered between 930 and 1330, and collected before all algae were consumed. Algae were spun and reweighed, and percent loss in weight per hour calculated. Due to loss in the field, replication varied across treatments and among sites (see figure captions for details). Stone Pier residuals met assumptions of normality without transformation, while residuals from Green Marker met assumptions of normality after a square root transformation (see Table S5) and were thus analyzed with a one-way ANOVA. Data from Maharepa could not be successfully transformed. Herbivory rate was comparatively low. Amount lost (initial-final) was zero inflated due to this lower herbivory pressure; thus, these data were analyzed with a GLM with a Poisson distribution.

3. Results

3.1. Evaluating handling loss

Our average handling loss was 5.8 ± SE 0.8% of the macroalgal assay per hour.

3.2. Resource predictability

Herbivory increased over time in both of our resource predictability experiments, though this rate of increase did not statistically differ between our predictable and our unpredictable assays (day $p < 0.0001$ in both cases) (Fig. 2, Table S1). At Taahiamanu reef, herbivory on the first three days of the experiment was low and comparable between predictable or unpredictable resources (Fig. 2A). However, by day four, herbivory began to increase and appeared to diverge between treatments. By the end of the experiment (day six) overall herbivory almost

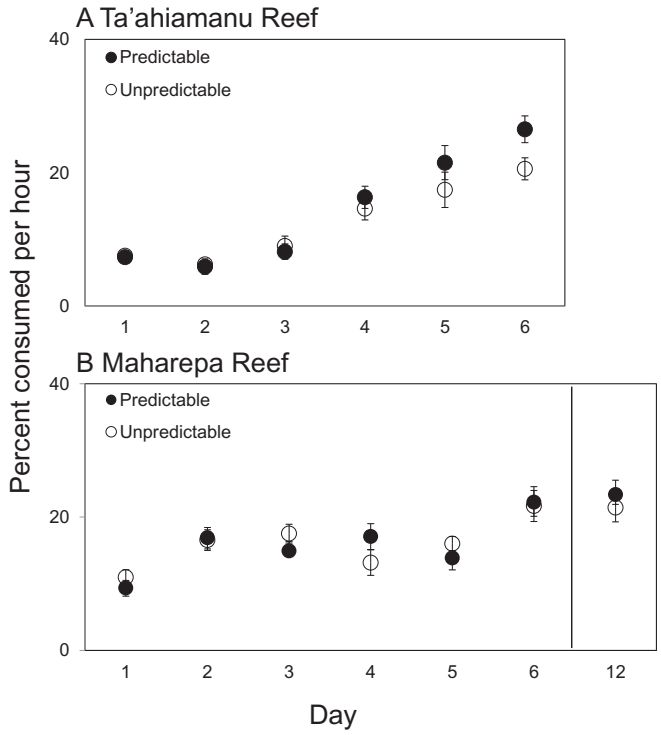

Fig. 2. Percent of *Padina boryana* consumed per hour for unpredictably (open) and predictably available resources (black) at a.) Taahiamanu in 2016 and b.) Maharepa in 2017. Points are means ± SE. At Taahiamanu reef, on days one through six, n = 14, 14, 14, 14, 12, 11 for predictable locations and 15, 15, 14, 15, 14, 14 for unpredictable locations. At Maharepa reef, on days days one through six, n = 15, 15, 14, 14, 14, 13 for predictable locations and 15, 13, 15, 15, 14, 15 for unpredictable locations. After six additional days (day 12), replication was n = 13 for predictable and 15 for unpredictable treatments.

tripled, and herbivory on predictably available resources was ~25% greater than on unpredictably available resources, though this difference was not significant. At Maharepa reef, herbivory was also lowest on the first day; however, herbivory rate increased more rapidly initially than at Taahiamanu reef and by day two, herbivory rate had already increased by > 50% per hour for both treatments (Fig. 2B). Overall, herbivory doubled by the end of both experiments.

We did not detect a difference in herbivory between the final day of our experiment and the assays out-planted six days after cessation of our experiment at Maharepa reef (*t*-test, p = 0.8488); rather, herbivory remained similar to the enhanced rate measured at the end of our six-day experiment, and elevated compared to the beginning of the experiment (Fig. 2 B).

At Maharepa reef, we documented a total of six species of fish taking bites on our assays: *Naso lituratus* (60% of bites), *Naso unicornis* (26% of bites), *Leptoscarus vaigiensis* (9.4% of bites), *Chlorurus sordidus* (3.6% of bites), *Balistapus undulatus* (0.1% of bites), and *Ctenochaetus striatus* (0.1% of bites) (Froese and Pauly, 2019). Over time, as our assays became more and more predictable, we found a significant positive, linear relationship between date of the experiment and number of species of fishes observed (p = 0.02181, Table S2, Fig. 3).

3.3. Resource availability

At Taahiamanu reef, grams of macroalgae consumed increased significantly with initial weight of algae offered for both *P. boryana* and *S. mangarevense*, though there was some variability in which treatments differed from each other (p < 0.0001, Table S3 A,B, Fig. 4 A,C. As expected, at Taahiamanu reef, *P. boryana* was consumed more rapidly than *S. mangarevense* (note Y axis scale change). Grams of *P. boryana*

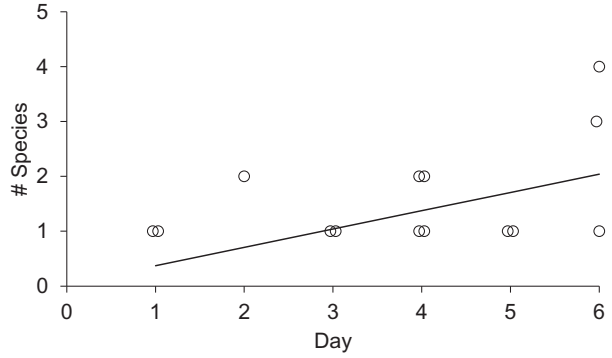

Fig. 3. Number of fish species observed in all videos over the six days of our predictable/unpredictable experiment (n = 15).

consumed per hour at Taahiamanu reef was highest for the 20 g assay while the 5 g and 10 g were consumed at a statistically similar rate (Table S3 A, Fig. 4 A). Similarly, grams of *S. mangarevense* consumed per hour increased with increasing assay weight; however, in this case, the 10 and 20 g assays were consumed at a similar rate with more than a five-fold increase over the rate of the 5 g assays (p = 0.03171, Table S3 B, Fig. 4 C). In contrast, we did not detect an effect of initial algal biomass on percent consumed per hour for either macroalgal species (p = 0.8826 and 0.05463 for *P. boryana* and *S. mangarevense*, respectively, Table S3 A,B, Fig. 4 B,D). For *P. boryana,* percent loss was statistically indistinguishable among treatments, with an average loss of 14.7 ± SE 1.1% per hour across treatments (Table S3A, Fig. 4 B). Like *P. boryana*, hourly percent loss per hour for *S. mangarevense* was the same among treatments, albeit at a much lower average of 3.6 ± SE 0.8% (Table S3B, Fig. 4 D).

Overall, we found similar patterns for consumption of *P. boryana* at Maharepa and Stone Pier reefs as at Taahiamanu reef, where grams consumed increased with increasing initial weights, though like before the specific treatments that differed varied (p = 0.00878 and 0.00045, respectively, Table S3 C,E, Fig. 5 A,E). However, this pattern was only marginally significant at Green Marker (p = 0.0546, Table S3 D, Fig. 5C). Across all three sites, herbivory on 20 g assays was at least three times greater than on 5 g treatments (Fig. 5 A,C,E). As in the prior experiments, we did not find a significant effect of initial amount offered on percent loss per hour (p = 0.799, 0.484, and 0.642 for Maharepa, Green Marker, and Stone Pier, respectively, Table S3 C,D,E, Fig. 5 B,D,F). However, herbivory rate appeared to vary across sites, with most rapid hourly consumption at Stone Pier, followed by Maharepa, and then Green Marker (Fig. 5). Hence, herbivores generally consume macroalgae in proportion to relative availability.

3.4. Associational defense and susceptibility

Our first two experiments testing for effects of interspecific associations by placing algae either adjacent (zero cm) or > one m apart had species-specific results (Fig. 6). While we found an interaction between association and species identity for *P. boryana* with *S. mangarevense* (p = 0.457, Table S4 A), there was no interaction in the *P. boryana* and *G. divaricata* experiment (p = 0.07558, Table S4 B). Association with the more palatable alga, *P. boryana*, more than doubled herbivory on the less palatable *S. mangarevense* (Fig. 6 A). However, there appeared to be no reciprocal effect of *S. mangarevense* on *P. boryana* as there appears to be equal herbivory on *P. boryana* with or without *S. mangarevense.* In contrast, we found a significant effect of species and association for our experiment with *P. boryana* and *G. divaricata,* but no interaction. In this experiment, *P. boryana* was more heavily grazed than *G. divaricata* both when alone and when associated (p = 0.02069, Table 4S B). However, overall herbivory rate was reduced for both species when together compared to when apart

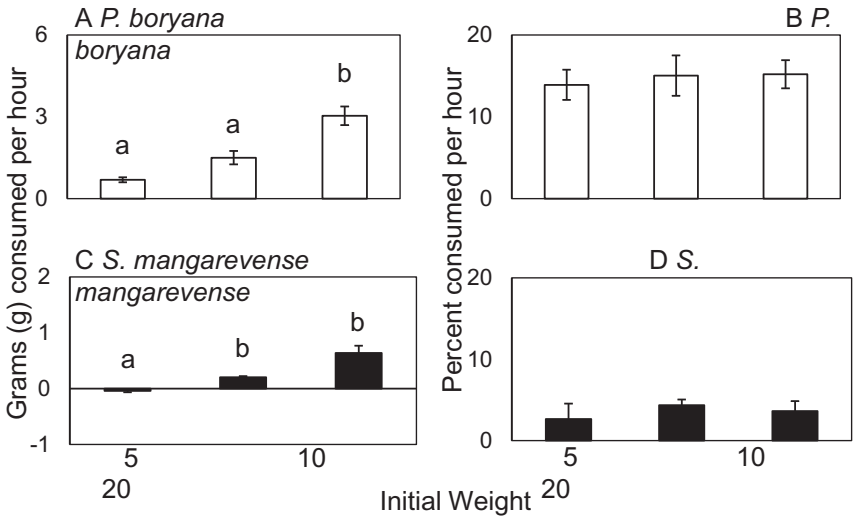

Fig. 4. Grams and percent macroalgae consumed per hour for a,b.) *Padina boryana* (n = 10, 9, 10 for 5, 10, and 20 g treatments respectively) and c,d.) *Sargassum mangarevense* (n = 10, 11, 8 for 5, 10, and 20 g treatments respectively) at Taahiamanu. Bars are means ± SE.

(p = 0.00159, Table 4S B, Fig. 6 B). The lack of interaction indicates the associational defense was equally positive for both species.

In our second set of experiments, where distance between species ranged from zero cm to > one m, the associational susceptibility *S. mangarevense* experienced when adjacent to *P. boryana* only occurred in one of the additional three sites (Fig. 7, Table 4S C-E). At Maharepa and Stone Pier we found no effect of distance on herbivory rate on *P. boryana* or *S. mangarevense* (p = 0.0922 and 0.2870 respectively, Table S4 C, D), just a species effect showing that *P. boryana* is more palatable than *S. mangarevense* (p < 0.001 for both, Fig. 7 A,C, Table S4 C,E). However, we did find an associational susceptibility at Green Marker, shown by a significant interaction between species identity and distance (p = 0.0219, Fig. 7 B, Table 4S 4D). As in all other experiments, herbivory on *P. boryana* was always greater than herbivory on *S. mangarevense* and equal across all levels of association. In contrast, herbivory on *S. mangarevense* depended on association, with herbivory rate increasing with increasing proximity to the more palatable *P. boryana*, at least in the zero to 20 cm range of distances. However, this pattern did not continue with the experimental units set at a distance of > one m; rather herbivory on these units was as high as the closest association.

3.5. Attachment

We found herbivory rate did not statistically differ with attachment method at any of the sites we tested (p > 0.3 for all, Table S5 A,B,C, Fig. 8 A,B,C). As in previous experiments, herbivory rate appeared to be highest at Stone Pier followed by Maharepa then Green Marker.

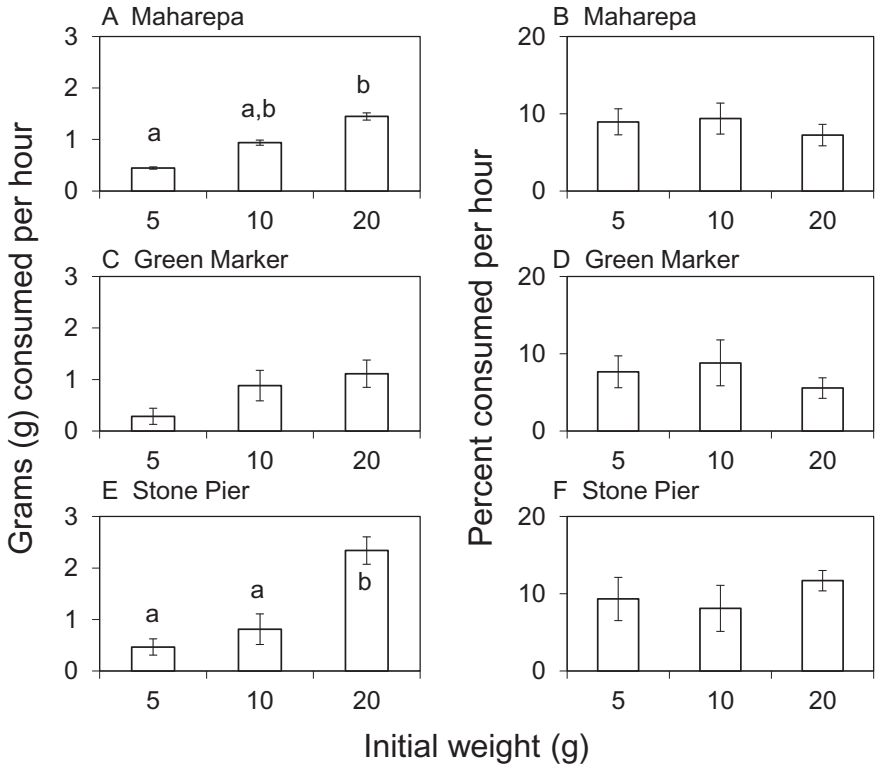

Fig. 5. Grams and percent macroalgae consumed per hour at Maharepa (a, b), Green Marker (c, d) and Stone Pier (e. f) sites. Bars are means ± SE. For 5, 10, and 20 g treatments, n = 9, 10, 9 at Maharepa; 9, 8, 10 at Green Marker; 9, 9, 8 at Stone Pier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

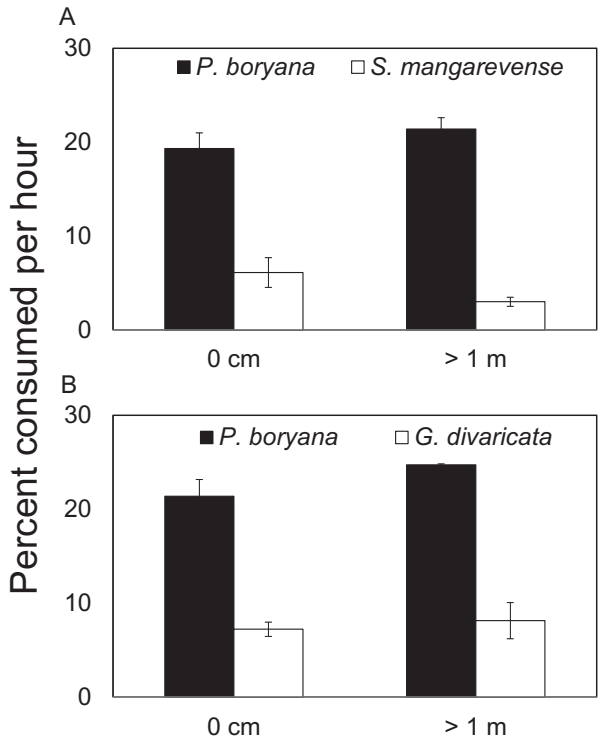

Fig. 6. a.) Percent macroalgae consumed per hour for a) *Padina boryana* (black) and *Sargassum mangarevense* (white) and b) *Padina boryana* (black) and *Galaxaura divaricata* (white) when offered in herbivory assays either alone or together. Replication for *P. boryana* and *S. mangarevense* was 9 while n = 9 for *P. boryana* alone, 10 for *G. divaricata* alone, and 9 for both when together.

4. Discussion

Our evaluation of current methodologies to estimate herbivory in the field revealed that existing variation among approaches in several critical components strongly impacts these estimates, limiting comparison across systems and studies. We found support for our theoretical predictions that assays that varied resource predictability and associational context influenced resultant measures of herbivory. In contrast, predictions from optimal foraging theory were not supported by our data, which may allow comparisons among assays of variable size. Similarly, we did not find that an operational source of variation, differences in attachment method, impacted estimates of herbivory. An important caveat to our findings is that the research was conducted on a tropical system characterized by strong herbivory by highly mobile herbivores; these results should be interpreted with some caution when applied to other systems. However, based on our results, we make four recommendations for future research, which we will discuss below. 1.) We recommend researchers not conduct herbivory assays in the same site over a series of days, especially if the study's objective is to compare results over space or time or to characterize fish communities. 2.) It is our opinion that researchers should report, either in the main text or supplement, percent consumption because this is a density-independent metric, facilitating comparisons among studies. 3.) We recommend researchers make an effort to explicitly test site and species-specific associational effects if herbivory assays must be assembled with multiple species in close proximity. 4.) Our data supports continued use of the attachment method in which you are most confident or adept. We hope our experimental results prove useful in the future when designing, conducting, and interpreting herbivory assays.

First, we strongly advise against placing herbivory assays in the same general location (i.e. a 30 × 2 m swath like this study) over a series of days if the objective of the study is to compare herbivory rates

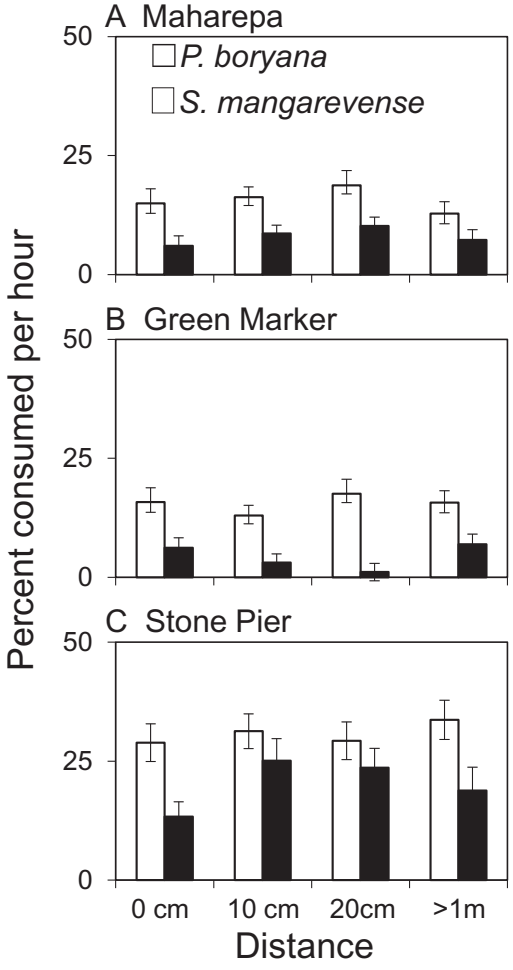

Fig. 7. Percent macroalgae consumed per hour for a) *Padina boryana* (white) and *Sargassum mangarevense* (black) when offered at varying distances from each other at Maharepa (a), Green Marker (b), and Stone Pier (c). Bars are means ± SE. For *P. boryana* > 100 cm away, *S. mangarevense* > 100 cm away, and *P. boryana* and *S. mangarevense* at 0, 10, and 20 cm apart, replication was 10, 8, 9, 10, 9 at Maharepa, 10, 10, 8, 8, 9 at Green Marker, and 10, 9, 10, 10, 10 at Stone Pier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

over space or time or to characterize fish communities. The consequences of repeating herbivory assays in the same location are boosted and more variable estimates of herbivory rates and fish diversity. Overall, our data implies that repeating assays in the same locations influences measurements of herbivory, and even randomly changing assay locations on sequential days within a site of the size we evaluated may not be sufficient to get independent, replicable measurements.

One pattern we discovered that may limit our ability to compare studies is that herbivory estimates increased and became more variable as resources in a given area became more predictable. Further, replication in the same location (i.e. the same attachment point) on sequential days can be even more problematic, though this pattern was weak and not consistent between sites. In previous studies, including our own work, assays were often out-planted on successive days in the same overall location to compare estimates of herbivory pressure between sites or species (e.g. Mantyka and Bellwood, 2007a, 2007b; Rasher et al., 2013; Plass-Johnson et al., 2015; Keeley et al., 2015; Fong et al., 2018). The practice of repeated assays within a site is a common solution to achieve adequate replication; however, our findings suggest that, going forward this practice be limited or even abandoned.

Another pattern that will limit our ability to compare measures of

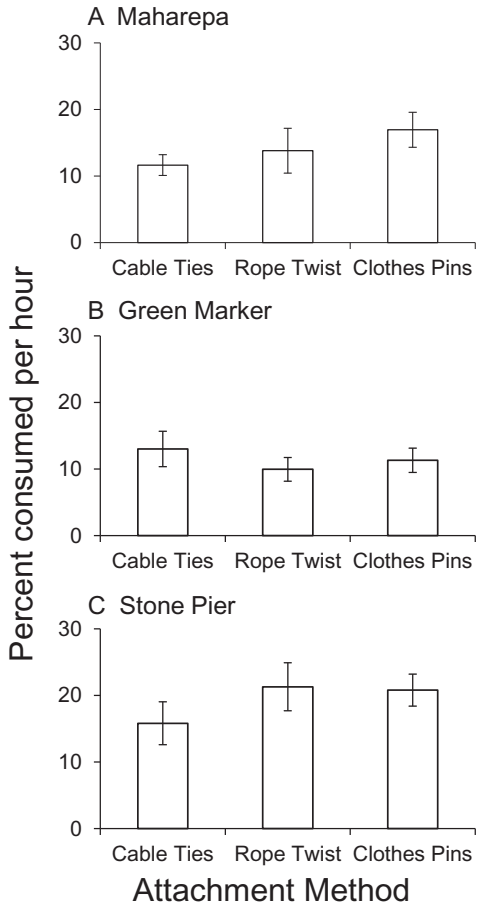

Fig. 8. Percent *P. boryana* consumed per hour when attached with different methods at Maharepa (a), Green Marker (b), and Stone Pier (c). Bars are means ± SE. For cable ties, clothespins, and rope twists, n = 9, 10, 9 at Maharepa, 9, 10, 8 at Green Marker, and 10, 10, and 8 at Stone Pier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fish diversity or components of fish behavior or function across repeated assays is that fish diversity increased as our assays became more predictable over time. This result can strongly affect the characterization of fish community structure and function if the underlying mechanisms are not taken into account. For example, it is possible that the increase in species diversity over time will resemble a species accumulation curve and eventually saturate when the full herbivore assemblage is observed (e.g. Efron and Thisted, 1976). In this case, the reason that diversity increases over time may be because some species are better at finding predictable resources (e.g. Cortés-Avizanda et al., 2012); thus over time, the full complement of good and bad searchers may be observed. One way to turn this into a positive outcome is to use repeated assays when assessing grazing selectivity, because repetition may allow researchers to increase the diversity of fishes observed (Fong et al., 2018). However, another possibility is that repetition may also generate competitive interactions, and exclusion may eventually arise, suggesting the increase in diversity over time may not persist. Regardless of the mechanism, our data implies that repeating assays in the same locations will change the fish community observed, and that this must be taken into account in future research.

If repeated assays in the same site are logistically necessary, we recommend that researchers explicitly evaluate how many days apart and how distant these assays must be deployed to ensure independence. We found herbivory rates remained elevated six days after our repeated assays, but did not evaluate longer intervals. Thus, additional research is needed to provide guidelines on how long researchers should wait before deploying further herbivory assays at a site.

Second, while the appropriate metric for reporting herbivory will depend on the overall objective of each specific study, we recommend researchers also report percent consumption because studies often offer different initial masses, and percentages will allow comparisons of estimates across studies as well as aid any potential future meta-analyses. Contrary to the predictions of optimal foraging theory (e.g. Charnov, 1976), we found herbivory rate was constant irrespective of biomass of algae out-planted when expressed as percent consumed per hour. This is not unexpected, as optimal foraging models are quite simplistic and assume only foraging is being optimized, while in reality, behavior is much more complex (Pierce and Ollason, 1987). Further, OFT assumes foraging behavior is the primary driver of fitness, which also may not be true (Pyke, 1984). We find it likely composition of the assay itself is the driver of our estimates of herbivory. For example, estimates of herbivory pressure can be driven by nutritional quality (e.g. Chan et al., 2012; Keeley et al., 2015) that can vary along an algal thallus. For example, apical portions of *P. boryana* can be nutrient-dense and less defended by calcification, and herbivores have been found to graze the high-quality apices, leaving the basal portions intact (Clausing et al., 2016). In this case, grazing may be a constant percent as fishes move on after eating the more nutritional/less defended portions. Thus, the nature or value of the resource offered is critical and known to effect estimates of herbivory (Chan et al., 2012, Keeley et al., 2015, Clausing et al., 2016). Whatever the mechanism, we found percent consumed proved to be a robust, density-independent metric of herbivory rate, and reporting this metric will facilitate comparisons across studies with varying initial masses.

Operationally, our finding is particularly useful for studies that use variable initial weights both within species and among species, which most often occurs for species with complex morphology that make matching initial weights difficult (e.g. Mantyka and Bellwood, 2007a, 2007b; Clausing et al., 2016). Further, some workers have varied the biomass of algae offered in an to attempt to standardize size by providing equal volumes or surface area to mass ratios of different species (e.g. Mantyka and Bellwood, 2007a, 2007b; Sotka and Hay, 2002), which our results indicate would have no effect on percent consumed. In summary, the lack of effect of initial weight on percent consumed facilitates comparisons of herbivory rates across sites, species, and amounts used within and between studies.

Third, we recommend site and species-specific evaluation of the effect of association if multi-species herbivory assays are employed. We found that, while associational effects could be strong, they were not generalizable across species pairs or sites. The presence of associational effects varied between macroalgal species pairs of differing palatability; further, patterns varied across sites. Prior research indicates associational relationships on reefs may be common, though the focus has generally been on defenses. For example, Bittick et al. (2010) found *Turbinaria ornata* stands harbored increased diversity of macroalgae because *T. ornata* protected palatable species from herbivores. Further, Littler et al. (1986) found the chemically defended *Stypopodium zonale* increased diversity of macroalgae within a ten cm radius by protecting associated species from herbivory, indicating this protective effect can extend some distance. Similarly, Fong et al. (2006) found association with epiphytic cyanobacteria decreased herbivory on the palatable *Acanthophora spicifera*. Finally, Loffler et al. (2015) found proximity of *Acanthophora spicifera* to *Galaxaura rugosa* protected *A. spicifera* from herbivory. Here, we present the first evidence known to us in the marine environment of an associational susceptibility (see Barbosa et al., 2009 for a review in terrestrial plant communities). In our assay, we found increased herbivory on a less palatable species due to association with a more palatable species, highlighting the need to consider increased susceptibility to herbivory with association. However, we found that this associational susceptibility was not consistent between species pairs or sites; thus, proximity effects should be tested and

considered when assembling multi-species herbivory assays, and patterns of association should continue to be evaluated.

Fourth, we recommend researchers continue to use the attachment method in which they are most confident or adept. We found attachment method did not affect the outcome of herbivory assays. This is good news, as attachment method is quite variable across studies (e.g. Hay et al., 1983; Sluka and Miller, 2001; Hoey, 2010; Bennett and Bellwood, 2011; Madin et al., 2011; Chan et al., 2012; Keeley et al., 2015; Plass-Johnson et al., 2015; Catano et al., 2016). Lack of an attachment method effect in our study indicates studies with different methods are comparable.

5. Conclusion

Herbivory is well established as a strong controlling process in many marine communities. Since herbivory assays are a common tool used in field ecology to build this body of knowledge, it is essential to understand the outcomes of methodological choices. We hope our experimental results prove useful in the future when designing, conducting, and interpreting herbivory assays in tropical systems and inspire similar work in temperate systems that may differ in intensity of herbivory and mobility of herbivores.

Declaration of Competing Interest

None.

Acknowledgements

We thank UC Berkeley's Gump South Pacific Research Station and staff. Thanks to the UC Office of the President (UCOP) UC-HBCU Initiative support to NNS, HBF, ATF; UCOP Dissertation Year Fellowship support to SAS; National Science Foundation (NSF) Graduate Research Fellowship Program 1144087 support to SAS; NSF Office of International Science and Engineering 1243541 support to NEM; and NSF Postdoctoral Research Fellowship Biology 1612308 support to CRF.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151469.

References

Aguilera, M.A., Valdivia, N., Broitman, B.R., 2015. Herbivore-alga interaction strength influences spatial heterogeneity in a kelp-dominated intertidal community. PLoS One 10 (9), e0137287. https://doi.org/10.1371/journal.pone.0137287.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., Szendrei, Z., 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annu. Rev. Ecol. Evol. Syst. 40, 1–20. https://doi.org/10.1146/annurev.ecolsys.110308.120242.

Bennett, S., Bellwood, D.R., 2011. Latitudinal variation in macroalgal consumption by fishes on the great barrier reef. Mar. Ecol. Prog. Ser. 426, 241–252. https://doi.org/10.3354/meps09016.

Bergman, J.L., Dang, B.N., Tabatabaee, M., McGowan, M.M., Fong, C.R., Bittick, S.J., Fong, P., 2016. Nutrients induce and herbivores maintain thallus toughness, a structural antiherbivory defense in *Turbinaria ornata*. Mar. Ecol. Prog. Ser. 559, 35–43. https://doi.org/10.3354/meps11884.

Bittick, S.J., Bilotti, N.D., Peterson, H.A., Stewart, H.L., 2010. *Turbinaria ornata* as an herbivory refuge for associate algae. Mar. Biol. 157 (2), 317–323. https://doi.org/10.1007/s00227-009-1319-6.

Bittick, S.J., Fong, C.R., Clausing, R.J., Harvey, J.D., Johnson, T.M., Frymann, T.A., Fong, P., 2020. The strength of herbivory is similar or even greater in algal- compared to coral-dominated habitats on a recovering coral reef. Mar. Ecol. Prog. Ser. 634, 225–229. https://doi.org/10.3354/meps13172.

Bourque, A.S., Fourqurean, J.W., 2013. Variability in herbivory in subtropical seagrass ecosystems and implications for seagrass transplanting. J. Exp. Mar. Biol. Ecol. 445, 29–37. https://doi.org/10.1016/j.jembe.2013.03.014.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85 (1), 146–156. https://doi.org/10.1111/1365-2656.12440.

Ceccarelli, D.M., Jones, G.P., McCook, L.J., 2005. Effects of territorial damselfish on an algal-dominated coastal coral reef. Coral Reefs 24 (4), 606–620. https://doi.org/10.1007/s00338-005-0035-z.

Chan, A.Y., Lubarsky, K., Judy, K.N., Fong, P., 2012. Nutrient addition increases consumption rates of tropical algae with different initial palatabilities. Mar. Ecol. Prog. Ser. 465, 25–31. https://doi.org/10.3354/meps09946.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9 (2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Clausing, R.J., Bittick, S.J., Fong, C.R., Fong, P., 2016. Sediments influence accumulation of two macroalgal species through novel but differing interactions with nutrients and herbivory. Coral Reefs 35 (4), 1297–1309. https://doi.org/10.1007/s00338-016-1477-1.

Cortés-Avizanda, A., Jovani, R., Carrete, M., Donázar, J.A., 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. Ecology. 93 (12), 2570–2579. https://doi.org/10.1890/12-0221.1.

Efron, B., Thisted, R., 1976. Estimating the number of unseen species: how many words did Shakespeare know? Biometrika 63 (3), 435–447. https://doi.org/10.1093/biomet/63.3.435.

Fong, C.R., 2015. An experimental assessment of herbivory and nutrient effects on a small-scale in a coral reef macroalgal community. Aquat. Bot. 123, 1–5. https://doi.org/10.1016/j.aquabot.2015.01.009.

Fong, C.R., Fong, P., 2014. Why species matter: an experimental assessment of assumptions and predictive ability of two functional-group models. Ecology 95 (8), 2055–2061. https://doi.org/10.1890/13-1557.1.

Fong, P., Smith, T.B., Wartian, M.J., 2006. Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. Ecology 87 (5), 1162–1168. https://doi.org/10.1890/0012-9658(2006)87[1162,ECMSTM]2.0.CO;2.

Fong, P., Frazier, N.M., Thompkins-Cook, C., Muthukrishnan, R., Fong, C.R., 2016. Size matters: experimental partitioning of the strength of fish herbivory on a fringing coral reef in Moorea, French Polynesia. Mar. Ecol. 37, 933–942. https://doi.org/10.1111/maec.12298.

Fong, C.R., Bittick, S.J., Clausing, R.J., Frias, M., Goody, N., Fong, P., 2017. Empirical data demonstrates risk-tradeoffs between landscapes for herbivorous fish may promote reef resilience. Mar. Environ. Res. 131, 1–5. https://doi.org/10.1016/j.marenvres.2017.11.001.

Fong, C.R., Chancellor, K.S., Rezni, J.J., Robinson, D.R., Barber, P.H., Habtes, S.Y., Fong, P., 2018. Epibionts on *Turbinaria ornata*, a secondary foundational macroalga on coral reefs, provide diverse trophic support to fishes. Mar. Environ. Res. 141, 39–43. https://doi.org/10.1016/j.marenvres.2018.08.001.

Fox, J., Weisberg, S., 2019. An {R} Companion to Applied Regression, Third ed. Sage, Thousand Oaks CA.

Froese, R., Pauly, D., 2019. FishBase. World Wide Web Electronic Publication. www.fishbase.org.

Gil, M.A., Hein, A.M., 2017. Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. Proc. Natl. Acad. Sci. 114 (18), 4703–4708. https://doi.org/10.1073/pnas.1615652114.

Guiry, M.D., Guiry, G.M., 2020. *AlgaeBase*. World-Wide Electronic Publication. National University of Ireland, Galway. http://www.algaebase.org (searched on 18 September 2020).

Hay, M.E., 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. Am. Nat. 128, 617–641. https://doi.org/10.1086/284593.

Hay, M.E., Colburn, T., Downing, D., 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. Oecologia 58 (3), 299–308. https://doi.org/10.1007/BF00385227.

Hoey, A.S., 2010. Size matters: macroalgal height influences the feeding response of coral reef herbivores. Mar. Ecol. Prog. Ser. 411, 299–302. https://doi.org/10.3354/meps08660.

Hoey, A.S., Bellwood, D.R., 2010. Cross-shelf variation in browsing intensity on the great barrier reef. Coral Reefs 29 (2), 499–508. https://doi.org/10.1007/s00338-010-0605-6.

Keeley, K.N., Stroh, J.D., Tran, D.S.C., Fong, C.R., Fong, P., 2015. 2015. Location, location, location: small shifts in collection site result in large intraspecific differences in macroalgal palatability. Coral Reefs 34 (2), 607–610. https://doi.org/10.1007/s00338-015-1274-2.

Lewis, S.M., 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol. Monogr. 56 (3), 183–200. https://doi.org/10.2307/2937073.

Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Natural. 116 (1), 25–44. https://doi.org/10.1086/283610.

Littler, M.M., Taylor, P.R., Littler, D.S., 1986. Plant defense associations in the marine environment. Coral Reefs 5 (2), 63–71. https://doi.org/10.1007/BF00270354.

Littler, M.M., Littler, D.S., Taylor, P.R., 1987. Animal-plant defense associations: effects on the distribution and abundance of tropical reef macrophytes. J. Exp. Mar. Biol. Ecol. 105, 107–121. https://doi.org/10.1016/0022-0981(87)90166-3.

Loffler, Z., Bellwood, D.R., Hoey, A.S., 2015. Associations among coral reef macroalgae influence feeding by herbivorous fishes. Coral Reefs 34 (1), 51–55. https://doi.org/10.1007/s00338-014-1236-0.

Madin, E.M., Madin, J.S., Booth, D.J., 2011. Landscape of fear visible from space. Sci. Rep. 1, 14. https://doi.org/10.1038/srep00014.

Mantyka, C.S., Bellwood, D.R., 2007a. Direct evaluation of macroalgal removal by herbivorous coral reef fishes. Coral Reefs 26 (2), 435–442. https://doi.org/10.1007/s00338-007-0214-1.

Mantyka, C.S., Bellwood, D.R., 2007b. Macroalgal grazing selectivity among herbivorous

coral reef fishes. Mar. Ecol. Prog. Ser. 352, 177–185. https://doi.org/10.3354/meps07055.
Pierce, G.J., Ollason, J.G., 1987. Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49, 111–118. https://doi.org/10.2307/3565560.
Plass-Johnson, J.G., Ferse, S.C., Jompa, J., Wild, C., Teichberg, M., 2015. Fish herbivory as key ecological function in a heavily degraded coral reef system. Limnol. Oceanogr. 60 (4), 1382–1391. https://doi.org/10.1002/lno.10105.
Pyke, G.H., 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. 15 (1), 523–575. https://doi.org/10.1146/annurev.es.15.110184.002515.
Rasher, D.B., Hoey, A.S., Hay, M.E., 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94 (6), 1347–1358. https://doi.org/10.1890/12-0389.1.
Shantz, A.A., Ladd, M.C., Burkepile, D.E., 2017. Algal nitrogen and phosphorus content drive inter-and intraspecific differences in herbivore grazing on a Caribbean reef. J. Exp. Mar. Biol. Ecol. 497, 164–171. https://doi.org/10.1016/j.jembe.2017.09.020.
Sluka, R.D., Miller, M.W., 2001. Herbivorous fish assemblages and herbivory pressure on Laamu atoll, Republic of Maldives. Coral Reefs 20 (3), 255–262. https://doi.org/10.1007/s003380100166.
Sotka, E.E., Hay, M.E., 2002. Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. Ecology 83, 2721–2735. https://doi.org/10.1890/0012-9658(2002)083[2721,GVAHPI]2.0.CO;2.
Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69 (3), 476–498. https://doi.org/10.2307/3545860.
Sweatman, H.P.A., 1996. Impacts of tourist pontoons on fish assemblages on the Great Barrier Reef. In: CRC Reef Research Centre Technical Report No. 5. CRC Reef Research Centre, Townsville (55pp).
Tootell, J.S., Steele, M.A., 2016. Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. Oecologia 181 (1), 13–24. https://doi.org/10.1007/s00442-015-3418-z.
Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M., Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y.M., 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proc. Natl. Acad. Sci. 113 (48), 13791–13796. https://doi.org/10.1073/pnas.1610725113.