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John M. Carroll
Georgia Southern University, jcarroll@georgiasouthern.edu

Amber D. Stubler
Occidental College, astubler@oxy.edu

Christopher M. Finelli
University of North Carolina Wilmington, finellic@uncw.edu

Bradley J. Peterson
Stony Brook University, bradley.peterson@stonybrook.edu

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SHORT COMMUNICATION

THE POTENTIAL USE OF SEAGRASS HERBIVORY PATTERNS AS AN INDICATOR OF HERBIVORE COMMUNITY CHANGE AFTER TROPICAL MARINE PROTECTED AREA ESTABLISHMENT

John M Carroll^{1,3*}, Amber D Stubler^{2,4}, Christopher M. Finelli¹, and Bradley J. Peterson²

¹Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC, 28407; ²School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY, 11794; ³Current address: Department of Biology, Georgia Southern University, Statesboro, GA, 30460; ⁴Current address: Biology Department, Occidental College, Los Angeles, CA, 90041; *Corresponding author: jcarroll@georgiasouthern.edu

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INTRODUCTION

In tropical seagrass systems, herbivores can greatly impact seagrasses and may even completely remove biomass (Unsworth et al. 2007, Peterson et al. 2013). Multiple factors affect seagrass herbivory, and the global decline of seagrass ecosystem health likely plays a major role in altering herbivory rates. In Caribbean seagrass beds and associated habitats, decades of overfishing, pollution, shoreline development, and climate change (Hughes 1994, Gardner et al. 2003) have impacted herbivory by altering both herbivore abundance, species interactions and habitat/macrophyte abundance. In particular, overharvest of fishes has led to shifts in dominant species within tropical systems (Knowlton 1992, Aronson and Precht 2000, Loh et al. 2015); in the Caribbean, this generally results in a loss of grazing pressure due to overharvest of herbivorous fishes (Mumby et al. 2006). To combat the loss of functionally important fish guilds, Marine Protected Areas (MPAs) have been established to reduce or restrict fishing pressure within their boundaries.

In many tropical MPAs, recovery of species across multiple taxa and trophic levels has been observed (McClanahan et al. 2007, Babcock et al. 2010, McClanahan 2014). Impacts of MPAs on herbivores are mixed, with some studies demonstrating an increase in herbivores (Noble et al. 2013, McClanahan 2014), while others report a decrease (Monaco et al. 2007). Protecting herbivores is important for tropical reef systems, as herbivores both reduce algal biomass which can outcompete corals (Mumby et al. 2006, Idjadi et al. 2006) while also offering a trophic subsidy from nearby shallow seagrass systems, transporting seagrass productivity to the reef (Peterson et al. 2013). The specific composition of herbivore communities may change after MPA establishment (McClanahan et al. 2007). Some larger tropical herbivores, such as parrotfish, can be important seagrass and algae consumers, and are often overharvested in areas that are not protected. When MPAs are established and fishing pressure is removed, parrotfish often recover rapidly (Noble et al. 2013). Therefore, we posit that changes in herbivore communities that result from MPA establishment will be reflected in herbivory patterns in seagrass

habitats (i.e., changes in overall herbivory and changes in bite size).

The north coast of Jamaica provides a well-studied reef and lagoon system with an extensive history of published studies on the degradation of the Discovery Bay (DB) reef complex. In 2009, the Discovery Bay Marine Lab (DBML), associated with the University of the West Indies, spearheaded the establishment of a Special Fishery Conservation Area (SFCA), a no fishing zone covering the entire lagoon (~1.65 km²), which is enforced by a local fishermen's cooperative group (C. Trench, DBML Chief Scientific Officer, pers. comm.). Although targeted quantitative assessments of fish communities pre- and post-establishment of the MPA in Discovery Bay are limited, anecdotally the presence and quantity of predators (e.g. mutton snapper and barracuda), which were rare prior to establishment, have increased (authors' pers. obs.). A seagrass herbivory study using tethers was performed in DB in 2007, indicating relatively high rates of herbivory over 24 h deployments that were likely due to small parrotfish (Peterson et al. 2012). In the absence of formal fish assessments, we sought to explore whether different herbivory patterns might support the hypothesis of community changes. Therefore, we compared data from Peterson et al. (2012) to our 2014 data collected in similar seagrass herbivory experiments at the exact same location. In particular, we expected that overall seagrass herbivory might increase if herbivore populations increase following MPA establishment. Alternatively, herbivory may decrease if predator populations increase which can affect herbivory both directly (consuming herbivores) and indirectly (changing behavior), or the overall herbivore community shifts away from seagrass specialists and toward generalist or algal herbivores. Regardless of the direction of the change, we expected protection to increase the overall size of herbivores within the reserve, leading to an increase in bite size metrics.

MATERIALS AND METHODS

Study site

Experiments from Peterson et al. (2012) and the present study were carried out in DB, a lagoon protected by a reef

crest, which receives nitrogen-enriched submarine groundwater discharge (Peterson et al. 2012). The experimental site is located in the interior of a continuous turtlegrass (*Thalassia testudinum* Koenig 1805) meadow in the western portion of DB (18.470969° N, -77.415848°W), a protected area ~0.8 km from the inlet and 180 m from the reef crest, accessible from DBML, and in an area of visible groundwater flux at ~2 m depth. While the site was not an MPA during 2007, the site is well within the established MPA boundaries. The groundwater discharge has no direct point source but instead percolates through the silt and sand into the water column. In 2007, the site was chosen due to the extensive, healthy turtlegrass bed, with mean densities of 466 ± 94 shoots/m² and biomass of 105.75 ± 26.75 g/m². For the 2014 tethering experiments, we returned to the same location selected by Peterson et al. (2012) at the same depth. Shoot density was measured by haphazardly tossing 5 quadrats (0.3 x 0.3 m) in our study area and counting all the shoots. We also did a quick biomass estimate in 2014 by measuring the weights of 3 sets of 10 shoots and multiplying by shoot density from quadrat counts at the site.

Seagrass Tethering Experiments

Seagrass grazing was quantified using a standard tethering technique adapted from Kirsch et al. (2002) and herbivory was recorded with Hero3 GoPros deployed on days 1-3 to capture an image every minute, and, on the 4th deployment day, to continuously record until the batteries died. Briefly, in both 2007 and 2014, whole seagrass shoots were collected from the field and returned to DBML for processing. Young, undamaged leaves were severed from their shoots and gently scraped with a razor blade to remove epiphytes (following Peterson et al. 2012). Leaves were then photographed with a scale bar, reassembled into 'shoots' with 2 leaves, and attached to a 0.25 m polypropylene tether line with a clothespin. Three shoots (n = 3) were then tethered to each line. Tethers were placed in the field for 24 h with the clothespins partially buried to allow the shoots to stand upright, after which time they were collected and replaced with a new tether. The recovered seagrass shoots were digitally photographed to determine herbivory on each leaf. Initial and final leaf areas were calculated using ImageJ image analysis software (Schneider et al. 2012) by tracing individual seagrass leaves before and after deployment. The difference in areas reflect grazing pressure (Goecker et al. 2005). This process was repeated for 4 consecutive days for the 2014 study and for 6 days for the Peterson et al. (2012) study.

Bite Size

Since there are no fish count data associated with the Discovery Bay MPA, we used bite size as a proxy for estimating the size and abundance of the herbivore community. Mouth size scales with fish length (Karpouzi and Stergiou 2003), and therefore the bite size of the herbivores in both studies were determined by measuring single bites on tethered seagrass blades. Only clearly distinct, single bites that occurred along

the edge of the blades were used for this analysis, resulting in 46 bites from 2007 and 45 bites from 2014. The bite area (area missing for each bite) and the bite width (diameter across the bite) were measured using ImageJ.

Analysis

Since we had right-skewed, continuous proportion data, the nonparametric Mann-Whitney test was used to determine whether herbivory rates differed by year (before or after MPA establishment). A number of tethers experienced no herbivory (no bite marks were present), which elevated the number of zeros in our data. We therefore ran tests on 2 datasets; first, the complete dataset including tethers with zero herbivory, and second, only the data from tethers which experienced some herbivory. The assumption for the second dataset was that tethers with no bites were not visited by herbivores, per Peterson et al. (2012). Additionally, Student t-tests were performed to determine whether bite width and bite area differed before and after MPA establishment. Due to differences in methods between studies, we could not make direct comparisons of shoot density and biomass metrics. GoPro videos were not analyzed due to the rarity of herbivory events.

RESULTS

During the 2014 surveys, shoot density at our study site was 708 ± 178 shoots/m², and our corresponding estimate for biomass was 195 g/m². These values were both higher than values recorded in 2007, although differences in methods preclude statistical analysis. Further, our qualitative fish observations in DB during 2014 identified predators that were either absent (mutton snapper, Figure S1) or rare (barracuda) during our early visits to the study site, as well as potential increases

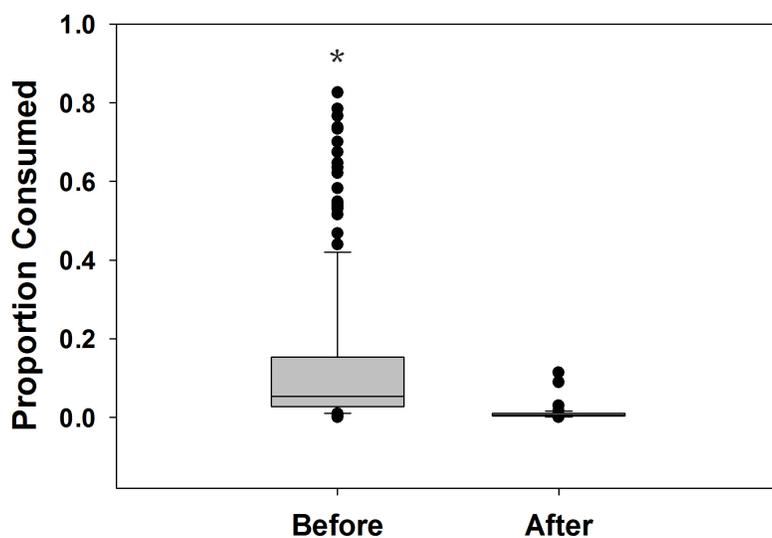


FIGURE 1. Box and whisker plot illustrating changes in herbivory over 24 h of *Thalassia testudinum* shoots on tethers which experienced herbivory from before the establishment of an MPA in Discovery Bay (Before, 2007) and after MPA establishment (After, 2014). The boundaries of the box represent the 25th and 75th percentiles, the solid line represents the median, the whiskers are the 10th and 90th percentiles, and the dots represent outliers. Star denotes significant differences (Mann-Whitney U test, $p < 0.001$).

in size and abundance of grazers, such as parrotfish.

In the 2007 herbivory experiments, performed before the 2009 MPA establishment, grazers consumed 7.7% of seagrass on tethers over a 24 hr period, whereas in 2014 after the MPA was established, consumption was reduced an order of magnitude to 0.8% of grass tethered over 24 h (Mann–Whitney $U = 10609$, $n_{\text{before}} = 360$, $n_{\text{after}} = 72$, $p = 0.012$). Excluding tethers with zero herbivory made the differences between herbivory in 2007 and 2014 even stronger (Mann–Whitney $U = 844.0$, $n_{\text{before}} = 205$, $n_{\text{after}} = 54$, $p < 0.001$; Figure 1). Interestingly, a larger number of seagrass tethers in 2014 (~75%) experienced grazing compared to tethers in 2007 (~57%), but the amount of grazing per shoot was significantly less. When herbivory did occur pre-MPA, it ranged from <1% to as high as 83% per shoot, whereas the largest loss post-MPA was ~11%. Further, bite size (both area and width) was significantly larger in 2014 compared to 2007 (bite area: $t_{88} = 6.857$, $p < 0.001$, Figure 2A; bite width: $t_{88} = 9.139$, $p < 0.001$ Figure 2B). Videos from GoPros confirmed larger bodied parrotfish were likely

responsible for the observed herbivory in 2014 (Figure 3).

DISCUSSION

It is possible that since a suite of ecological interactions are expected to change post-MPA establishment, we can potentially assess MPA success by taking advantage of data from studies that occur in these regions devoid of regular, standard monitoring. The dramatic reduction in grazing experienced by seagrass tethers deployed before and after MPA establishment in DB may be indicative of changes in fishing pressure within the bay. Numerous studies have highlighted the success of MPAs in conserving marine biodiversity and increasing biomass of numerous species (Lester et al. 2009, Babcock et al. 2010). Biomass of large predators can dramatically increase within reserves (McClanahan et al. 2007, Russ and Alcala 2011), although the impact of MPA establishment on herbivores has been ambiguous (McClanahan et al. 2007, Monaco et al. 2007, Gilby and Stevens 2014). While herbivore populations may be lower inside reserves due to an increase in piscivorous fish (Beets and Rogers 2002), other studies

have also demonstrated recoveries in herbivorous fish species, particularly larger-bodied species like parrotfish (Mumby et al. 2006, McClanahan et al. 2007, Noble et al. 2013). Disagreements between studies may be due to non-differentiation between different groups of herbivores (e.g., scarids vs. acanthurids), sizes of herbivores (e.g., small vs. large), or herbivore food preference (e.g., seagrass vs. macroalgae).

While overall herbivore biomass might increase within reserves (Stockwell et al. 2009, McClanahan 2014), this is likely due to a shift toward larger-bodied species or individuals (Mumby et al. 2006), rather than an increase in overall abundance. When compared between 2007 (Peterson et al. 2012) and the present study, the bite areas and widths are suggestive of a shift from smaller- to larger-bodied herbivores within DB over the past 8 years. The predominant turtlegrass grazers in 2007, before the MPA was established, were small, resident, seagrass-specialist herbivores, such as *Sparisoma radians* (Peterson et al. 2012), whereas the parrotfish observed consuming seagrass in the 2014 experiments, *Sparisoma aurofrenatum* and *Sparisoma viride*, are larger-bodied, generalist herbivores which consume both macroalgae and seagrass (McAfee and Morgan 1996, Overholtzer and Motta 1999). Since parrotfish are harvested in Jamaica (Figure S2), it is possible that populations of larger-bodied parrotfish have increased within the lagoon due to MPA status. Without formal fish assessments, we cannot say whether populations of *S. radians* have declined within the lagoon over this time period, or if they have just shifted behavior (Shears and Babcock 2003, Rizzari et al. 2014) in response to larger predators (i.e., barracuda, snapper) returning to the lagoon. Further, we cannot say with certainty that the abundance of the larger-bodied species we observed have increased dra-

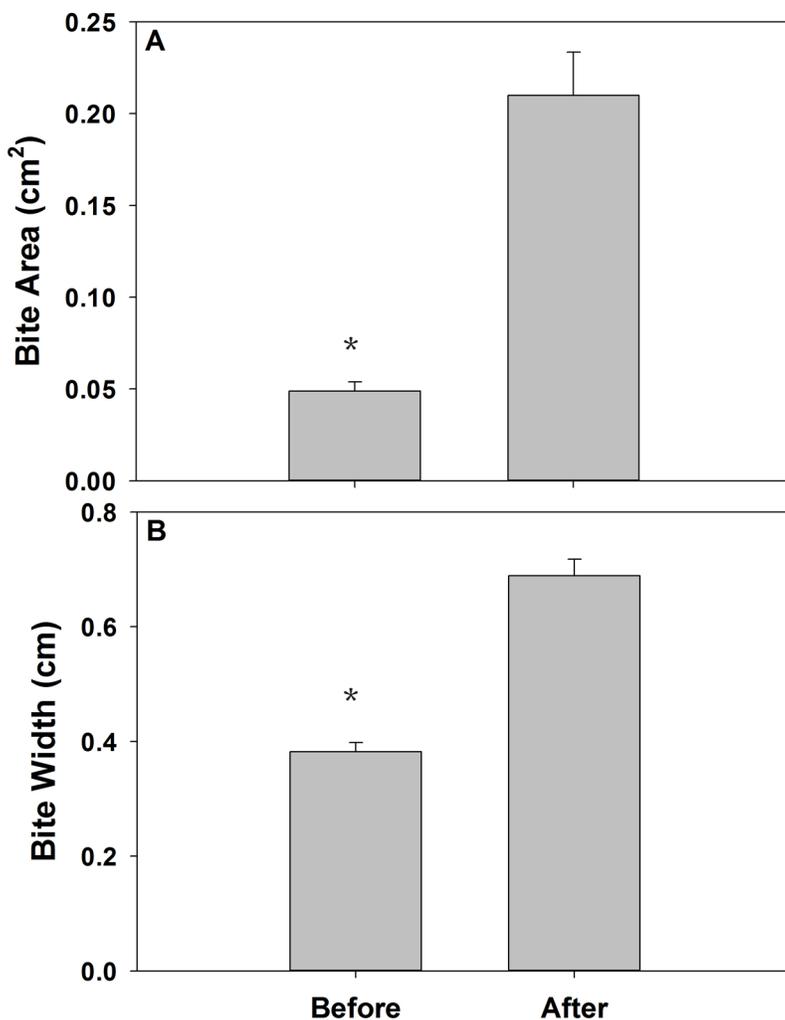


FIGURE 2. Mean bite area (cm²; A) and bite width (cm; B) on *Thalassia testudinum* shoots tethered in seagrass meadows before MPA (Before, 2007) and after MPA establishment (After, 2014). Error bars represent standard error. Stars denote significant differences (Student *t*-test, $p < 0.001$).



FIGURE 3. Screen-grabbed images of a Redband Parrotfish (*Sparisoma aurofrenatum*; top) and Stoplight Parrotfish (*Sparisoma viride*; bottom) consuming tethered seagrass from Hero3 GoPro videos.

matically, although the bite size analysis and frequency of bites (i.e., higher overall herbivory attempts but less herbivory) suggests that larger fish are the primary herbivores in the system now compared to 2007. Thus, the comparison of herbivory rates provides evidence that suggests a decline in overall herbivory rates which may have resulted from a shifting herbivore population structure toward larger, more generalist grazers, and/or changes in either abundance or behavior of the smaller seagrass-specialist even in the absence of fish counts.

The magnitude of change in the population of predominant herbivore guilds, as well as other members of the fish community in DB post-MPA is unclear due to the lack of fish counts or other monitoring activities, and that cannot be overstated. However, grazing assays may be useful in determining relative herbivore community and grazing intensity across reef locations (Hoey and Bellwood 2009, Cvitanovic and Hoey 2010), changes over time (Goatley et al. 2016), and MPA impacts (Bonaldo et al. 2017). The evidence from our seagrass assays suggests that herbivory rates have declined over the course of the study period and that the predominant turtlegrass herbivores are currently larger, based on bite metrics. Both of these conclusions are potentially indicative of MPA success, since indirect effects of MPAs can cascade down to basal resources (Gilby and Stevens 2014, McClanahan 2014). Algal cover and biomass tends to decline post-MPA establishment because populations of previously harvested large-bodied

herbivores (i.e., scarids) also recover and increase grazing (Mumby et al. 2006, Stockwell et al. 2009), although effects on seagrass are unclear. Although differences in method of calculation precluded statistical analysis, our recent estimates suggest that seagrass biomass may be almost double (195 g/m^2) what it was in 2007 (106 g/m^2 ; Peterson et al. 2012), likely due to the increase in shoot density at the site over that time period (466 ± 94 to 708 ± 178 shoots/ m^2). If these estimates are correct, seagrass metric changes are consistent with ecosystem changes post-MPA establishment likely occurring in Discovery Bay, Jamaica (i.e., reduced turtlegrass herbivory).

While we attribute much of the changes observed to the establishment of the MPA within DB, there could be other factors that could affect herbivory. We selected the same study location and the same depth as the 2007 experiment (Peterson et al. 2012) to eliminate the variability that might occur at a slightly different location within the seagrass meadow (Hammerschlag et al. 2010) or a different depth (Steele et al. 2014). Although we did not standardize leaf ranks (i.e., youngest to oldest leaves) between experiments when reassembling tethered shoots, we kept the method of selecting the youngest, inner leaves the same across experiments. However, nutritional quality of the turtlegrass, which can potentially reduce herbivory (Goecker et al. 2005), can be affected by leaf age and nitrogen inputs to the bay. We did not measure either groundwater flux or the resulting porewater, sediment, or seagrass nutrient content in 2014. Differences in flux could alter the delivery of nitrogen to the bay, affecting the nutritional content of the leaves and herbivory. While we are not sure whether groundwater flux and nitrogen delivery were altered between the 2 studies, historically turtlegrass herbivores at this location do not select for nitrogen-enriched grass (Peterson et al. 2012). Thus, it is unclear whether herbivory might be impacted by groundwater, a question beyond the scope of this experiment. In addition, the higher proportion of tethers receiving at least one bite in 2014, despite the lower overall herbivory, might indicate that fish were searching for more nutritious/different food resources than the local grass available, further supporting a potentially different suite of herbivores that can traverse distances to find suitable food. It is possible that other unmeasured parameters could be different between the 2 studies; regardless, we feel that examining seagrass herbivory could be a useful tool to evaluate MPA success in other regions.

In conclusion, MPA establishment may alter herbivore biomass, shift herbivore guilds, and/or alter herbivore behavior, due to overall increases in fish biomass within reserves. Since changes in herbivore communities should be reflected in herbivory patterns on basal resources such as seagrasses, our evidence suggests the possibility that fish communities within DB may have changed after establishing an MPA. Absent targeted quantitative fish assessments, a problem which plagues many MPAs in third-world regions, we suggest that it may be possible to deduce MPA success from experiments, such as macrophyte assays (Bonaldo et al. 2017), that examine changes in trophic interactions which might occur as a result of MPA establishment. This is a potentially useful tool that should be

investigated further, particularly in areas where it can be paired with fish counts and replicate sites inside and outside reserves, to establish this as a proxy for functional changes following MPA establishment before herbivory assays are considered for future monitoring efforts.

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