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Adrianna Parson
Augusta University, aparson@augusta.edu

Joseph M. Dirnberger
Kennesaw State University, jdirnber@kennesaw.edu

Troy Mutchler
Kennesaw State University, tmutchle@kennesaw.edu

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PATTERNS OF DISPERSION, MOVEMENT AND FEEDING OF THE SEA URCHIN *LYTECHINUS*, AND THE POTENTIAL IMPLICATIONS FOR GRAZING IMPACT ON LIVE SEAGRASS

Adrianna Parson¹, Joseph M. Dirnberger², and Troy Mutchler²

¹College of Allied Health Sciences, Augusta University, 1120 15th St, Augusta, GA 30912 USA; ²Department of Ecology, Evolution and Organismal Biology, Kennesaw State University, Kennesaw, GA 30144 USA; Corresponding author, email: jdimber@kennesaw.edu

ABSTRACT: The sea urchin *Lytechinus variegatus* is a known grazer of both living and dead tissue of turtlegrass, *Thalassia testudinum*, occasionally denuding large areas of seagrass. Field studies have attempted to assess effects of herbivory on seagrass by enclosing urchins at various densities. However, it is unclear how unrestricted urchins affect seagrass at lower densities more typically observed in the field. This study describes movement, feeding, and distribution of *L. variegatus* within beds of *T. testudinum* in St. Joseph Bay, Florida (USA) to quantify this urchin's impact as a seagrass grazer. Urchins were absent from portions of seagrass beds closest to shore, present at low densities midway across the bed, and at highest densities (up to ~5 individuals/m²) at the offshore edge of the bed. Urchins tended not to aggregate, moved twice as rapidly where seagrass cover was reduced, and moved > 20X faster when placed in areas of open sand. Dead seagrass tissue occurred 4–30X more frequently on oral surfaces than living seagrass tissue. Fecal pellets with dead seagrass tissue were > 3X more common than pellets with live seagrass tissue. Injury to seagrass leaves was more common along dead leaf sections than live sections (> 2–10X). Overall, spatial distributions, movement, and diet indicate that *L. variegatus* at densities observed in this study would tend to have minimal effects on living seagrass. Episodic periods of denuding grassbeds reported in the literature suggest *L. variegatus* switches to live seagrass tissue as dead tissue becomes scarce during times of high urchin density.

KEY WORDS: Echinoidea, *Thalassia*, diet, injury, detritivore

INTRODUCTION

The traditional paradigm that herbivory on living seagrass tissue is at most modest due to low palatability and nutritional quality (e.g., Ogden 1980, Klumpp et al. 1993) has shifted. Improved methodologies for estimating consumption of seagrass production indicate that rates vary greatly over time and space, from negligible (< 5%) to nearly 100% of leaf production (Cebrián and Duarte 1998, Heck and Valentine 2006). Larger seagrass grazers, including dugongs, green sea turtles, and many waterfowl, have experienced historic reductions (Jeremy et al. 2001, Heck and Valentine 2006), suggesting that these megaherbivores are unlikely to account for higher estimates of seagrass consumption. However, most seagrass beds still harbor diverse assemblages of species that consume primary production in the form of both live and dead seagrass tissue as well as epiphytic and drift algae (e.g., Greenway 1995, Scott et al. 2018). The degree to which these food types are consumed by different assemblages of grazers may help explain observed variability in impact of grazing on seagrass among sites and seasons (Scott et al. 2018). Discerning the overall effect of primary consumers on seagrass production requires a thorough understanding of the feeding behaviors, preferences, and consumption rates of common herbivores and omnivores (York et al. 2017). However, feeding ecologies are often not simple. Diet of any given member within a marine community is rarely centered on a single species or trophic level (e.g., Kitting 1980, Luczkovich et al. 2002, Valentine and Duffy 2006) and often shifts temporally and spatially with differences in food availability (e.g., Huh and Kitting 1985, Prior et al. 2016, Nakamoto et al. 2018).

The green or variegated urchin, *Lytechinus variegatus* (Lamarck, 1816; hereafter urchin) is often abundant in seagrass beds from North Carolina (USA) to Brazil (Greenway 1995, Watts et al. 2013). Published estimates suggest that densities are typically ≤ 20 individuals/m² (e.g. Vadas et al. 1982, Keller 1983, Beddingfield and McClintock 1994, Montague et al. 1995, Challener et al. 2019) though densities > 300 individuals/m² have been reported (Camp et al. 1973, Rose et al. 1999). Because of the widespread geographic distribution and extreme variation in population densities, these consumers have great potential to regulate seagrass biomass with indirect effects on trophic dynamics within the community and on the ability of seagrass meadows to provision ecosystem services. Previous studies on seagrass consumption by urchins have helped us understand the position of urchins in coastal food webs, but variability in urchin diets and outcomes of field experiments make it difficult to understand urchin impacts, especially at commonly observed densities. *Lytechinus variegatus* is an omnivore that consumes both living and dead seagrass tissue among other things (e.g., Watts et al. 2013, Parson 2018). The extent to which urchins feed on live or dead tissue and concentrate their grazing within a given area likely influences seagrass growth and survival with potential implications for the structure and function of seagrass systems. For example, intense grazing on live seagrass shoots may reduce existing photosynthetic tissue (e.g., Camp et al. 1973), perhaps to the point of creating seagrass barrens (Carnell et al. 2020). Loss of the seagrass canopy has been shown to affect carbon storage in sediments by modifying inputs of organic matter from seagrass

tissues and hydrodynamic settling of allochthonous carbon, and by reducing organic stocks via erosion and remineralization (Kennedy et al. 2010, Tanaya et al. 2018, Carnell et al. 2020). Less intense grazing of seagrass shoots may stimulate new shoot production (e.g., Valentine et al. 1997). On the other hand, consumption of dead tissue (whether still attached or decaying on the sea bottom) may not impact seagrass productivity directly, but microbial conditioning of dead tissue may facilitate energy transfer from seagrass tissues to consumers along detrital pathways (Klug 1980). The net contribution of sea urchins in seagrass food webs and carbon cycling hinges on their relative rates of grazing on live versus dead tissues and the factors that influence those rates.

In feeding studies on *L. variegatus*, dead leaf tissue was ingested more quickly (Montague et al. 1991), consumed in greater amounts by tethered and caged urchins (Marco-Méndez et al. 2012), and found more frequently in guts and mouths (Vadas et al 1982, Greenway 1995, Montague et al. 1995) than living seagrass tissue. However, *L. variegatus* can consume significant live seagrass biomass. In one study, live seagrass tissue comprised 85% of the volume of gut contents (Prado and Heck 2011). *Lytechinus variegatus* also has been observed to completely denude areas of seagrass beds when densities are extremely high (> 300 urchins/m²; Camp et al. 1973, Rose et al. 1999) and within field enclosures under certain conditions. Along the northeastern Gulf of Mexico (GOM), *L. variegatus* enclosed at densities of 20 urchins/m² or higher could remove all aboveground biomass of turtlegrass, *Thalassia testudinum* Banks ex König, though the ability for the seagrass to recover varied with season and duration of the experiment (Valentine and Heck 1991, Heck and Valentine 1995). Yet, at densities of 20 urchins/m², effects on leaf density/shoot, leaf width, and biomass were not always observed, and biomass and density of short shoots sometimes increased (Valentine et al 1997, 2000). Taken together, the results of feeding studies and enclosure experiments indicate that the relative consumption of dead and living tissue by *L. variegatus* may be quite variable, though it is unclear which forage type dominates seagrass consumption at the lower urchin densities (< 20 urchins/m²) observed in many systems.

Though enclosure experiments have been important in understanding conditions that lead to denuding, they may be less useful for quantifying the influence on seagrass beds of urchins at densities more typically observed in the field (i.e., ≤ 20 individuals/m²; e.g., Vadas et al 1982, Keller 1983, Beddingfield and McClintock 1994, Montague et al. 1995, Challener et al. 2019). Enclosures may overestimate urchin effects by interfering with the import of food items (such as detached dead seagrass tissue), export of regenerated nutrients, and recruitment of propagules (Eckman 1983). Enclosures limit urchin movement, potentially forcing urchins to switch to less palatable foods within enclosure boundaries. Confinement may prevent urchins from moving in response to induced seagrass defenses (Darnell and Heck 2013) or to increased predation risk associated with grazer-induced reduction in seagrass

cover (Heck and Valentine 1995). Experimental designs that permit urchins to exhibit natural behaviors and movement may reduce the potential to overestimate urchin herbivory and yield more accurate estimates of top-down effects on seagrass production (Valentine and Duffy 2006).

The goal of this study was to examine the potential for *L. variegatus* to directly influence turtlegrass beds through direct consumption of living tissue at urchin densities considerably lower than those observed during denuding events. To investigate this, *L. variegatus* distribution, movement, and feeding were examined collectively in the field to test 4 questions across multiple spatial scales: 1) Does consumption of seagrass tissue by urchins occur uniformly across the seagrass bed?; 2) Do urchins concentrate spatially in ways that would result in bare patches as observed in past denuding events?; 3) Do urchins *in situ* consume mostly live or dead seagrass tissue?; and 4) Do observed patterns in diet correspond to differences in nutritional value of the live or dead seagrass tissues?

MATERIALS AND METHODS

Study Site

All field data were collected in St. Joseph Bay, in the northeastern GOM along the Florida panhandle, USA (Figure 1). The bay receives no major freshwater input and contains an es-

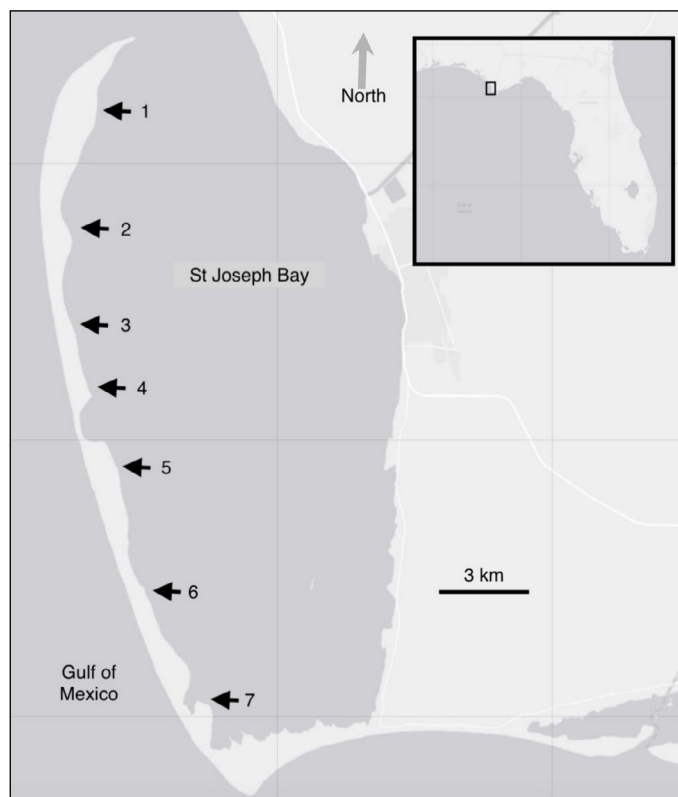


FIGURE 1. Sampling sites (1-7) in St. Joseph Bay, FL, USA. Rectangle on Florida map insert shows location of bay. At each site, 50 X 2 m transects ran parallel to the shore within each of 3 zones: nearshore (within 30-160 m from the shoreline), mid-shore (110-290 m), and offshore (180-540 m) in 10-12 June and 16-17 July 2014. An additional 500 m transect perpendicular to the shore was sampled at site 4 in May 2017, August 2017, and October 2018.

estimated 39 km² of seagrass beds (Florida Department of Environmental Protection 2008), mostly occurring along a narrow (typically < 500 m wide), shallow (< 2m) shelf adjacent to the shoreline of the bay. Water depth increases rapidly on the bayward side of the shelf (typically increasing to 5–10 m depth a few 100 m to the bayward side of the shelf and continues at these depths throughout most of the open bay). The dominant seagrass is *T. testudinum* forming dense, monospecific beds, though smaller areas of other seagrass species occur in the bay. *Halodule wrightii* (shoal grass) occupies the margins of grassbeds nearest to shore, and *Syringodium filiforme* (manatee grass) occurs sporadically mixed with *T. testudinum* or in monospecific patches.

Quantification of Urchin Abundance and Leaf Injury

Urchin abundance was visually surveyed by snorkeling along transects on 10–12 June and 16–17 July 2014 at 7 sites along the western shore of St. Joseph Bay (Figure 1; Lamle 2015). At each site, all urchins within belt transects (50 X 2 m) were tabulated. Single transects ran parallel to the shore within each of 3 zones: nearshore where seagrass coverage tended to be continuous (within 30–160 m from the shore depending on site), mid–shore near where large open patches within the seagrass bed became common (110–290 m), and offshore to the point where depth increased more rapidly and the seagrass bed became fragmented (180–540 m). Thus, a total of 21 transects, with 7 transects in each of the 3 zones, were surveyed during the course of this study.

To assess trends in urchin abundance and feeding activity in greater detail at a single site, and to examine variability among years, a 500 m transect was established in May and in August 2017 at Site 4 (Figure 1) perpendicular to the shore of Mosquito Point (29°46'45N 85°23'50W) and ending near the offshore margin of the seagrass bed. Water depth across most of the transect varied between 1–2 m, and dropped off rapidly beyond the offshore end of the transect to ~10 m within the next 200 m. Urchin abundance was estimated by slowly snorkeling along the 1 m wide belt transect and tallying the number of urchins within each 25 m interval of the 500 m transect.

To examine patterns across the seagrass bed of leaf injury and of live and dead tissues along leaves, 3 attached shoots of *T. testudinum* were sampled haphazardly over each 25 m interval; one at the beginning of the transect, one in the middle, and one at the end (n = 255 leaves for May, n = 271 for August). Individual leaves were photographed and examined for presence of injury (defined as tissue visually missing from the normally straight leaf edge) and dead tissue (defined as brown rather than green tissue) within each 1 cm section on each side along the leaf. The position of injury and of dead tissue along leaves were tabulated to examine the impact of urchin grazing on live and dead tissue along leaves. To examine persistence of trends in urchin abundance during seasonal temperature changes and storm events, the Mosquito Point transect at site 4 (Figure 1) was surveyed again in October 2018, 3 weeks after the passage of Hurricane Michael, a category 4 storm whose eye passed ~20 km to the north.

Quantification of Urchin Dispersion Patterns and Movement

Urchin dispersion and abundance relative to seagrass cover

was quantified within five 5 m transects parallel to the shoreline (August 2017) in an area of high urchin density at Site 4 (Figure 1) (~450 m from shore) as determined from the 500 m transect survey described above. The locations of transects were chosen to include areas that varied in seagrass cover. Two 0.25 m² quadrats were laid side by side along the transect at 10 consecutive 0.5 m points along each of the five 5 m transects (n=100 quadrats). Percent cover of seagrass was determined for each quadrat through visual estimation to the nearest 20%. Three shoots of *T. testudinum* were sampled from each quadrat to quantify injury to leaves.

To investigate the movement of urchins in response to changes in seagrass resource, field experiments were conducted in September 2017 and October 2018 ~450 m from shore at Site 4 (Figure 1). For each experimental plot, 4 urchins were placed ~2 cm apart around the base of a marker flag at the center of a plot. After 0.5 h, distance each urchin moved was estimated as the linear distance between the flag and the urchin's final position. Plots were randomly assigned to 5 treatments: 1) Undisturbed – no manipulation of seagrass leaves; 2) Detached leaves removed – leaf tissue not anchored by rhizomes (mostly dead leaves lying on bottom) gently raked away by hand; 3) Leaves clipped – Attached seagrass shoots clipped to ~3 cm to increase exposure of urchins while leaving basal shoots that are a potential structural obstacle to urchins moving along the bottom; 4) Both attached leaves (clipped) and detached leaves removed; and 5) Open sand – A nearby sandy patch containing no attached seagrass shoots prior to the study.

In September 2017, treatments were run sequentially in the order of treatments listed above using the same urchins within plots across all treatments (6 replicate plots per treatment x 4 urchins per plot = 24 individuals per treatment). Location of plots were chosen haphazardly within areas with dense seagrass cover and within an adjacent open sand patch (~15 x 64 m). In October 2018, 4 treatments were run simultaneously, with plots arranged in a 4 by 4 array in a Latin square design so that no orthogonal contained the same treatment (4 replicate plots per treatment x 4 urchins per plot x 4 treatments = 64 individuals). The treatment with both clipped and detached leaves (4) was not included in this second trial in order to allow observers to accurately monitor multiple treatments simultaneously while maintaining sufficient replication.

In situ Analyses of Diet

On each of 3 sampling dates (October 2016, August 2017, September 2017) at Site 4 (Figure 1, ~450 m from shore), ~200 urchins were examined in situ to obtain an instantaneous assessment of the type of food being consumed. Observers gently tilted all urchins encountered to view their oral surfaces and noted potential food items present among or over the teeth. Food was classified as dead seagrass (brown in color), live seagrass (green in color), other (not seagrass), or no food present. Care was taken not to dislodge urchins attached to anchored substrate (i.e. rooted seagrass shoots). Observers moved in a single direction parallel to shore to ensure no urchin was sampled twice.

Six urchins from each 5 m transect (at Site 4 where urchin dispersion was assessed as described above) were collected in Au-

gust 2017 for fecal pellet analysis ($n=30$ individuals). The urchins sampled had food cleared from their mouth, all items on their spines removed, and were gently rinsed with seawater to remove exterior debris. Each urchin was placed into a 500 ml jar containing filtered seawater. Screening was secured over the opening of each jar to allow gas exchange. All 30 urchins were placed in an insulated tank (to minimize temperature fluctuations) with aerated filtered seawater, and allowed to defecate for 18 h, after which fecal pellets in each jar were photographed. Digital images were analyzed by tabulating the type of fecal pellets contacting a line transect across the field of view. Fecal pellets were classified based on their color with brown corresponding to consumption of primarily dead tissue and green reflecting consumption of live seagrass leaves. To verify that live tissue did not change color during passage through the gut, urchins in the laboratory were fed only green leaves and fecal pellets were examined after 24 h.

Patterns in N and C Content in Live versus Dead Tissue

Live seagrass leaves attached to anchored rhizomes, detached leaves, and urchin tissues were collected in June 2017 for determination of carbon (C) and nitrogen (N). Detached leaves consisted of dead (brown) tissue, typically in a visible state of decay. Seagrass shoots and detached seagrass leaves were collected in summer 2017 in the 100–125 m, 225–250 m, and 475–500 m intervals of the 500 m transect at site 4. Individual shoots and detached leaves were collected haphazardly from the beginning, middle, and ends of the intervals, but only 2 seagrass shoots were collected from the 475–500 m interval. A mature leaf was removed from each shoot and bisected into distal and basal portions, and the epiphytic community was removed from the live and dead seagrass tissues by gently scraping with a scalpel. Three urchins were collected at the 475–500 m interval and dissected to remove the gut. The remaining tissue samples were dried to constant weight at 60° C and pulverized using a Wig-L-Bug Grinding Mill (Crescent). Ground tissues were wrapped in tin capsules and analyzed for C and N content at the University of California, Davis Stable Isotope Facility using a PDZ Europa ANCA–GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Statistical Analyses

Univariate analysis of variance (ANOVA) was used to detect effects of seagrass manipulations (bare, undisturbed, clipped, and raked) and plot position (position) on urchin movement (total distance moved from the plot center) when simultaneous treatments were used. Residuals from the fitted model indicated no departures from normality (Shapiro–Wilk, $p \geq 0.52$ for all treatments), and the assumption of homogeneity of variance was met (Levene's Test, $p=0.23$). One-way, repeated measures multivariate ANOVA was used to detect effects of seagrass manipulations on urchin movement when sequential treatments were used. Distances were log transformed to meet the normality assumption for residuals of the fitted model (Shapiro–Wilk, $p \geq 0.15$ for all treatments) and statistical significance was determined with Wilks' Lambda. Linear regression analysis was performed to

examine relationships between leaf injury and urchin density. Pattern of urchin dispersion was determined by comparing a Poisson distribution as an expected random distribution (calculated from the mean number of individuals per quadrat) to the observed distribution using a chi-squared analysis. A chi-square analysis was used to determine if injury coincided with dead tissue along leaves. Differences in the production of brown versus green fecal pellets among individual urchins was tested using a Student's *t*-test. Non-parametric Kruskal–Wallis tests were used to compare distributions of C and N contents for seagrass tissues across transect intervals, and Mann–Whitney U tests compared these same values across position on leaf and type of seagrass tissue (attached versus detached). All analyses were conducted using SPSS version 26 (IBM Corp. 2019).

RESULTS

At all 7 sites along the peninsula in summer 2014, no urchins were encountered within inshore zones (<160 m from shore), and highest urchin densities tended to occur further from shore (>180 m from shore; maximum density = 5.1 individuals/m² at 520 m from shore; Figure 2). Along the 500 m transect surveyed in 2017 and 2018, urchins were rarely observed within 300 m of the shoreline but increased in density further offshore on all 3 sample dates (maximum density = 4.5

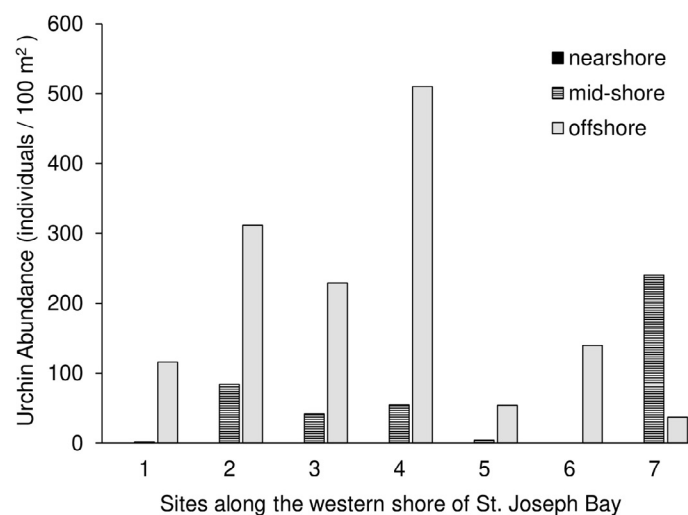


FIGURE 2. Number of *Lytechinus variegatus* sea urchins in 100 m² belt transects in 3 zones from inshore to offshore at 7 sites along the western shore of St. Joseph Bay, FL during June and July 2014. See Figure 1 for location of sites.

individuals/m²; Figure 3) though depth varied little across the transect. While urchin abundance was lower in the fall of October 2018 after the passage of Hurricane Michael, the trend of increasing abundance from inshore to offshore persisted (Figure 3). Offshore locations (>350 m) generally had higher incidences of injury along leaves. Mean number of leaf sections with injury dramatically increased 350–500 m from shore in May, though not in August. Injury was positively related to urchin density in May ($F_{20, 254} = 47.47$, $r^2 = 0.73$, $p < 0.0001$), but

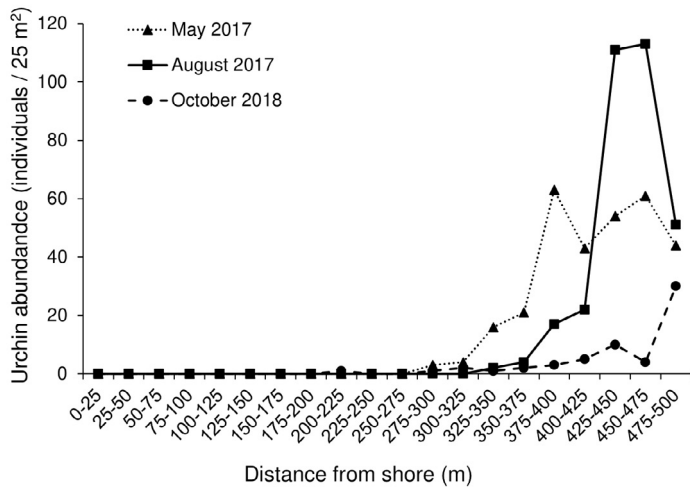


FIGURE 3. Number of *Lytechinus variegatus* sea urchins in 25 m² belt transects from inshore (0-25 m) to offshore (475-500 m) over 3 dates at Site 4. See Figure 1 for location of site. The October 2018 sampling date occurred 3 weeks after the passage of Hurricane Michael.

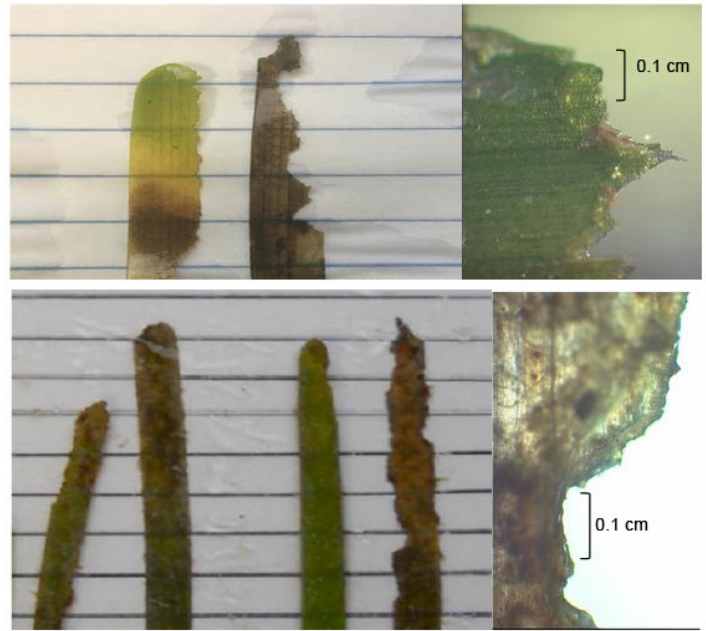


FIGURE 5. Injury to *Thalassia testudinum* leaves. Top: Injury induced by urchins in the laboratory. Bottom: Injury observed on leaves collected in situ in St. Joseph Bay, FL. Horizontal lines are 1 cm apart in images on the left. Images on the right show damage seen under the microscope.

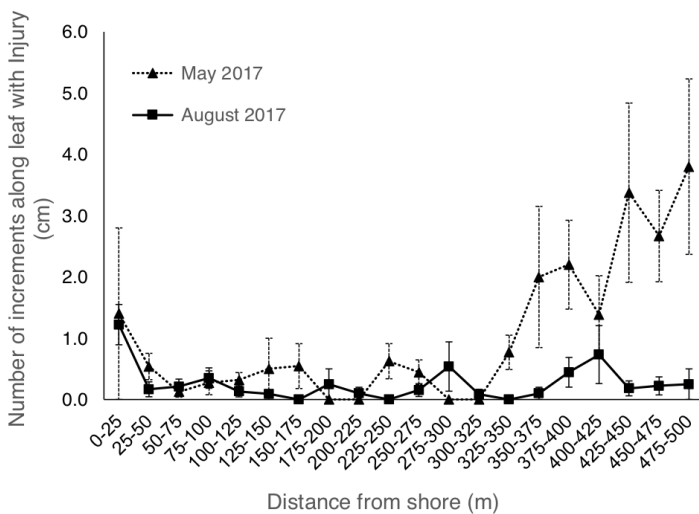


FIGURE 4. Number of injuries (mean \pm 1 se) on *Thalassia testudinum* leaves measured in 1 cm increments across a depth transect in St. Joseph Bay, FL during May and August 2017.

not related in August ($F_{20,270} = 0.16$, $r^2 = 0.01$; $p = 0.69$; $n = 20$) when injury tended to be less common across the transect (Figure 4). Leaf scar patterns of injury observed in the field were similar to injury patterns induced by urchins in the laboratory, both with jagged tears along leaf edges (Figure 5).

Based on analysis of one hundred 0.25 m² quadrat samples taken 450 m from shore, 87% of quadrats had 2 or fewer urchins (≤ 8 individuals/m; Figure 6) and mean urchin density for each of the 5 transects ranged from 4.2 to 6.4 individuals/m². Dispersion of urchins was clumped ($X^2_{100} = 14601.32$, $p < 0.001$, variance/mean = 1.95). However, the tendency toward clumping was driven by a single quadrat with 10 urchins (no other quadrat had more than 6 urchins, see Figure 6). This quadrat was in a transect that crossed a bare area and a patch

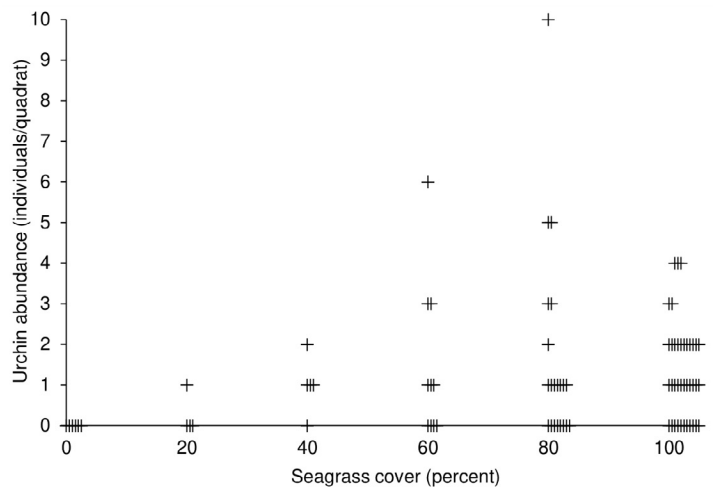


FIGURE 6. Number of *Lytechinus variegatus* sea urchins per 0.25 m² quadrat in St. Joseph Bay, FL versus percent cover of *Thalassia testudinum* (in 20% bins). Cross symbols for each percent cover class are slightly offset horizontally to show frequency of quadrats for a given number of individuals per quadrat within each seagrass cover class.

of *Halodule wrightii*. Removal of this quadrat from the analysis indicated urchin dispersion was not strongly clumped ($X^2_{95} = 8.96$, $p = 0.062$, variance/mean = 1.43). Across all quadrats, urchins were rare where seagrass percent cover was low. In quadrats with higher percent cover, number of urchins were variable (Figure 6). Urchin density and mean number of segments along the leaf with injury were not correlated ($r = 0.161$, $n = 100$, $p = 0.110$).

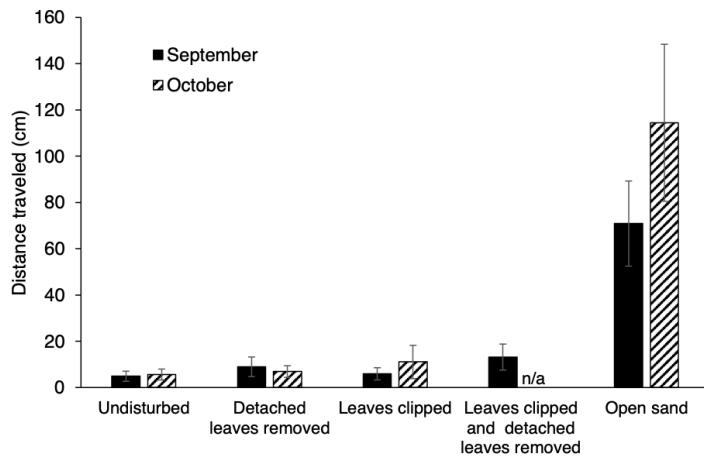


FIGURE 7. Mean (± 1 se) distance *Lytechinus variegatus* sea urchins moved during 5 sequentially run treatments in September 2017 and 4 simultaneously run treatments in October 2018.

In field manipulations of seagrass cover, urchins moved more rapidly with reduced cover. In the September 2017 experiment, mean distance of urchin movement, when compared to undisturbed plots, was nearly 3 times greater with reduced cover (live shoots clipped and detached leaves removed) and 8 times greater in areas of open sand ($F_{4,119} = 75.22$, $p = 0.013$; Tukey HSD $p = 0.018$ undisturbed plot and $p < 0.001$ in reduced cover plots; Figure 7). Even stronger differences among treatments were observed in the October 2018 experiment (Figure 7). Mean distance of urchins was >19 times greater in areas of open sand than in all other treatments ($F_{3,63} = 58.39$, $p < 0.001$, Tukey HSD $p < 0.01$), but in treatments where only one type of seagrass tissue (clipped live tissues or detached leaves) was removed, there was no difference in distance moved in comparison to undisturbed plots (Tukey HSD $p = 0.94$).

In May, most injuries were concentrated at the distal portion of leaves, furthest away from the base. Of 253 leaves examined, 66 leaves had the majority of injury closer to the distal end with 60 having injury that extended to the distal end, whereas only 2 leaves had the majority of injury closer to the basal end. On many leaves, injury occurred over several consecutive centimeters especially along leaves sampled further from shore. Dead tissue displayed a similar pattern, with the majority of dead tissue being concentrated along the distal portion of leaves. The percent of dead leaf tissue that was also injured (44.3%) was more than 10-fold greater than the percent of live leaf tissue injured (3.5%). Injury and dead tissue were more likely to co-occur than by chance alone ($X^2_{3487} = 701.42$, $p < 0.0001$).

As in May, most of the injury observed in August was concentrated at the distal portion of leaves, though injury was much less frequent. Of 271 leaves examined, 46 leaves had the majority of injury closer to the distal end with 38 having injury reaching to the distal end, whereas only 3 leaves had the majority of injury closer to the basal end. Dead tissue displayed a similar pattern, with the majority of dead tissue being

concentrated along the distal portion of leaves. The percent of dead tissue that was injured (2.1%) was more than twice the percent of live leaf tissue injured (1.0%). Injury and dead tissue were more likely to co-occur than by chance alone ($X^2_{5725} = 10.73$, $p = 0.0010$).

In field surveys, urchins concentrated feeding on dead seagrass tissue. On all 3 dates sampled, the frequency of urchins with brown seagrass within or over their oral opening was more than twice those with green seagrass or other food items (mostly bryozoans and macroalgae; Figure 8).

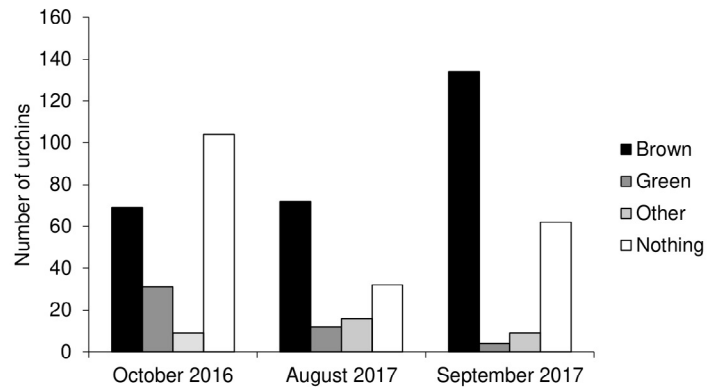


FIGURE 8. Feeding of *Lytechinus variegatus* sea urchins in St. Joseph Bay, FL over three dates. The bars indicate the number of urchins found with various food types at their oral openings. Brown—dead seagrass; Green—living seagrass; Other—bryozoans and macroalgae.

Urchins also produced brown fecal pellets more often than green when observed in temporary confinement (Student $t_{30} = -4.77$, $p < 0.001$; Figure 9). In contrast, urchins provided only green seagrass in the laboratory produced green fecal pellets in >99% of cases, so that percent brown pellets collected from field urchins are considered here as the percent brown (dead) seagrass tissue consumed.

Detached (dead) seagrass tended to have lower percentages of tissue N compared to live seagrass ($U_{25} = 118.5$, $p =$

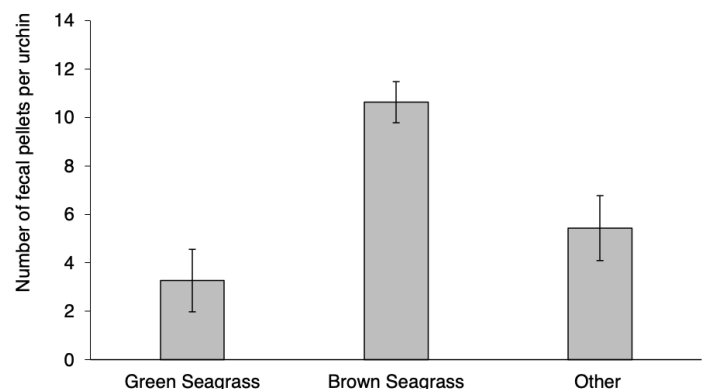


FIGURE 9. Mean (± 1 se) number of fecal pellets of *Lytechinus variegatus* sea urchins collected from St. Joseph Bay, FL in August 2017 separated by food items. Other—bryozoans and macroalgae.

TABLE 1. Mean (± 1 se) carbon (C) and nitrogen (N) values for sea urchins (*Lytechinus variegatus*) and turtlegrass (*Thalassia testudinum*) leaves collected across a 500 m offshore transect in St. Joseph Bay, FL in June 2017.

Transect segment	Tissue (n)	%C	%N	C:N
100-125 m	distal seagrass leaf (3)	0.35 \pm 0.02	0.02 \pm 0.01	19.38 \pm 3.46
	basal seagrass leaf (3)	0.32 \pm 0.01	0.02 \pm 0.00	15.61 \pm 2.13
	detached detrital seagrass (3)	0.31 \pm 0.01	0.01 \pm 0.00	25.38 \pm 1.27
225-250 m	distal seagrass leaf (3)	0.34 \pm 0.02	0.02 \pm 0.01	19.81 \pm 4.63
	basal seagrass leaf (2)	0.36 \pm 0.00	0.03 \pm 0.00	15.76 \pm 0.75
	detached detrital seagrass (1)	0.28	0.01	25.72
475-500 m	distal seagrass leaf (2)	0.35 \pm 0.00	0.02 \pm 0.00	25.47 \pm 2.47
	basal seagrass leaf (2)	0.34 \pm 0.02	0.02 \pm 0.00	20.43 \pm 1.39
	detached detrital seagrass (3)	0.34 \pm 0.02	0.01 \pm 0.00	38.03 \pm 2.08
475-500 m	Urchins (3)	0.2 \pm 0.02	0.02 \pm 0.00	14.96 \pm 0.89

0.007; Table 1) with mean values about 50% of those observed for attached (live) seagrass. However, detached and attached seagrass exhibited similar percentages of C ($U_{25} = 92.5$, $p = 0.251$; Table 1). Spatial patterns in C and N were not apparent along the 500 m transect ($KW_{25} = 1.88$, $p = 0.391$ and $KW_{25} = 2.80$, $p = 0.247$, respectively; Table 1), and distal versus basal portions of live seagrass leaves had comparable values for tissue C and N content ($KW_{25} = 2.64$, $p = 0.267$ and $KW_{25} = 0.71$, $p = 0.442$, respectively; Table 1).

DISCUSSION

Previously reported denuding events and field manipulations suggest that urchins alter seagrass biomass and production through consumption of live seagrass tissue (e.g. Camp et al. 1973, Heck and Valentine 1995). Urchins at lower densities observed in this study displayed patterns of dispersion, movement and feeding that would reduce grazing impact on live seagrass, and these patterns appear unrelated to food quality (as measured by N content of seagrass tissues). Urchins occurred mostly along the offshore margin of the seagrass bed, were not strongly clumped where they did occur, moved in response to reduced seagrass cover, and consumed mostly dead seagrass tissue. Potential shifts in grazing between live and dead tissue as a function of urchin population size likely contribute to variability in standing crop and carbon sequestration in seagrass systems.

The rarity of urchins and the lower frequency of leaf injury inshore indicate that effects of urchins are not equal across the seagrass bed. Spatial patterns in several abiotic and biotic factors (including seagrass cover) across the 500 m transect did not correspond to changes in urchin density across the transect. Mean water depth only differed by < 0.5 m between the nearest site inshore and the farthest site offshore, tending to become slightly shallower offshore near patches of open sand. Percent cover of seagrass and biomass of detached seagrass leaves showed no consistent trends across the seagrass bed (Parson 2018), and we found no spatial patterns in tissue nutrient content. However, water temperature provides a reasonable explanation for why urchin grazing is limited to offshore areas of the bed. Lower summer temperatures and coarser sed-

iments along the offshore portions of the seagrass bed (Parson 2018) suggest greater exchange of bay water with the offshore portions of the bed. Influxes of water from adjacent, deeper portions of the bay would likely moderate temperatures along the offshore edge of the seagrass bed, buffering urchins during summer and winter temperature extremes. Water temperature in the open bay ranges from 14.8–31.3°C (Port Saint Joe, Florida; NOAA 2018), falling within temperature tolerances for *L. variegatus* (11–35 °C; Watts et al. 2013), while temperature along the shallow inshore portions of the seagrass bed several hundred meters from the open bay are liable to fall outside of tolerance limits. We recorded a temperature of 34.4°C near our study site within the seagrass in June 2017 and Valentine and Heck (1991) reported winter temperatures as low as 8°C within seagrass beds of the bay. Beddingfield and McClintock (1994, 2000) documented mass mortality of *L. variegatus* in the shallower portions of the bay's seagrass beds during an intense cold front and attributed the northern range limit of the *L. variegatus* distribution to such low-temperature extremes.

While lower urchin density observed in October 2018 could be attributed to the passage 3 weeks prior of Hurricane Michael, higher densities of urchins were observed just offshore of the 500 m transect (pers. obs.), suggesting urchin distribution may shift further offshore later into autumn as a result of storm activity or seasonal decline in temperature. Challener et al. (2019) found no definitive impacts of the hurricane on *L. variegatus* abundance in St. Joseph Bay. Urchin temperature tolerances discussed above would support the idea that urchins move beyond the offshore end of the 500 m transect to avoid extremes in winter temperatures.

Grazing on attached seagrass leaves appeared to vary temporally as well as spatially. Injury was less frequent in August (1.3% of leaf length injured) than May (6.9% of leaf length injured), and, along with the increase in percent cover of seagrass offshore in August (Parson 2018), suggest a seasonal shift in diet away from attached leaves, potentially to detached dead leaves that accumulated along the bottom over the summer (pers. ob.). Because N content of dead leaves was lower than live seagrass tissue, a shift to consumption of dead tissue could represent selection of foods based on other factors af-

fecting nutritional characteristics, such as phosphorus, lipid, and carbohydrate content, or bacterial and epiphyte load and composition (Prado and Heck 2011). Alternatively, fewer injuries per leaf in August may be a function of higher leaf turnover rates (Zieman et al. 1984a).

It is possible that injury to leaves was due to contributions from other factors such as additional grazers or mechanical damage. However, > 95% of all injury observed in the field had a pattern of jagged, torn tissue along leaf edges similar to that produced by urchins in the laboratory, and jagged injury patterns have been associated with urchin grazing in other studies (e.g., Ogden et al. 1973). Fish herbivores in St. Joseph Bay (such as Emerald Parrotfish, *Nicholsina usta*) tend to leave smooth, regular bite marks (e.g., Ogden et al. 1973), and micro-invertebrates grazing on seagrass, such as amphipods, tend to consume epiphytes rather than seagrass tissue (Scott et al. 2018). In addition, > 80% of injured leaves collected in the field had injury present on both sides rather than one, as did leaves grazed by urchins in the laboratory. These patterns appear inconsistent with other possible sources of damage. Leaves injured by mechanical forces such as wave action or by megaherbivores in St. Joseph Bay (the green sea turtle, *Chelonia mydas*, and the West Indian manatee, *Trichechus manatus*) would likely be torn across the width (Burkholder et al. 2012) rather than having long stretches of injury along leaf margins on both sides (suggesting a single browsing event up and down leaf edges). Diseases, such as wasting disease, would likely manifest as black dots or streaks in leaf tissue (Short et al. 1988).

In the offshore area where urchins were abundant, urchins did not appear to concentrate feeding on whole seagrass shoots in a way that would denude above ground and below ground biomass within the seagrass bed. Our results showing increased movement of urchins in response to reduced leaf resources, scarcity of urchins in low cover areas, lack of correlation between urchin abundance and injury, and the tendency of urchins not to aggregate support this pattern. Random dispersion of *L. variegatus* over a scale of several meters has been noted within seagrass beds in southern Florida (Montague et al. 1995) and in St. Joseph Bay (Beddingfield and McClintock 2000), though aggregates have been noted where food resources are patchy (Vadas and Elnor 2003). While urchins tended toward random dispersion in our study, urchin density reached 10 individuals (40 individuals/m²) within one atypical quadrat. Though this density is within the range of densities that yielded impacts on seagrass biomass in enclosure experiments (Valentine and Heck 1991, Heck and Valentine 1995), our results indicate that when urchins are at lower ambient densities observed in this study and unrestricted by enclosures, urchin clumps disperse where seagrass biomass is reduced. Laboratory experiments indicate that *L. variegatus* disperse even when food is abundant, with fed urchins moving faster (~100 cm/h in erratic directions regardless of food location) than starved urchins (Klinger and Lawrence 1985).

In our study, urchin densities averaged up to ~5 individuals/m² along offshore transects, falling within ranges previous-

ly reported in St. Joseph Bay (Beddingfield and McClintock 2000, Challener et al. 2019). Where significant losses of seagrass biomass by *L. variegatus* have been documented, the ability of urchins to disperse was limited due to walls enclosing urchins at densities 4–16X greater than in our study (e.g., Valentine et al. 1997), or to abnormally high field densities ~100X greater with urchins forming aggregates up to 10 m across (Camp et al. 1973, Rose et al. 1999). Under such conditions, urchins decrease overhead seagrass canopy despite the cover that it provides. The importance of seagrass as a cover is suggested by higher rates of predation on urchins tethered in bare patches relative to those tethered within stands of seagrass, and the tendency for urchins to move out of areas left grazed from previously enclosed plots (Heck and Valentine 1995). In addition, *L. variegatus* commonly covers itself with detached leaves (pers. obs.) that likely become depleted where urchin densities are high.

The rarity of injury on basal portions of leaves suggests that urchins in our study were not foraging disproportionately near the actively growing, basal meristems. Our analysis of injury does not account for tissue lost when grazing severs leaves. However, if urchins feed preferentially on dead tissue of attached leaves, then segments severed are less likely to be living tissue, minimizing direct negative impacts of urchins on live seagrass and possibly resulting in stimulation of tissue growth by increasing light to living tissue. Preferential feeding on dead tissue is supported by the co-occurrence of injury and dead tissue along leaves and the low frequency of injury on leaves with tip intact. Alternatively, injury may induce tissue death and loss of tips. However, the preponderance of dead tissue along urchin oral surfaces and in fecal pellets in the field also indicate that urchins concentrate feeding on dead tissue over live seagrass tissue. In addition, urchins collected from St. Joseph Bay and presented with equal amounts of dead and live seagrass in laboratory choice trials consumed > 20x more dead seagrass than live seagrass (Parson 2018). This supports other feeding studies on *L. variegatus* that suggest preferential consumption of dead tissue (Vadas et al. 1982, Montague et al. 1991, Montague et al. 1995, Greenway 1995, Marco-Méndez et al. 2012).

Feeding on dead seagrass tissue may be nutritionally advantageous. Distal leaf ends, where dead tissue most frequently occurs, are less chemically and structurally defended against herbivory (e.g. McConnell et al. 1982, Zieman et al. 1984a, Vergés et al. 2011) and harbor greater bacterial and epiphytic algal biomass (Zieman et al. 1984b) relative to basal leaf ends where new tissue is produced. However, basal regions may have higher a proportion of nitrogen than do distal regions (Zieman et al. 1984b, Marco-Méndez et al. 2012), though this pattern was not observed in this study. In our study, percent of nitrogen in detached dead tissue was lower than in live attached leaves. If dead tissue is chemically and structurally less defended, increased consumption of such tissue could compensate for lower nutritional quality. For urchins unrestricted in the field, other factors such as accessibility and exposure to predators may also come into play in determining the type of

seagrass tissue consumed (e.g., Prado and Heck 2011).

Where urchins are artificially constrained or when dead tissue is depleted by unusually high urchin densities, urchins concentrate grazing on live tissue in a way that denudes areas of seagrass bed (e.g., Heck and Valentine 1995, Rose et al. 1999). However, our data indicate that urchins unconstrained and at lower densities move while consuming dead seagrass tissue, preferred as a forage and cover, rather than remaining in place and depleting live tissue. Avoidance of grazing along basal leaf areas as indicated by injury supports conclusions derived from feeding studies that *L. variegatus* is typically more important as a consumer of decomposing tissue than as a primary consumer of live seagrass tissue in transferring energy and matter to higher trophic levels (e.g., Vadas et al. 1982). This conclusion fits a more general synthesis that detrital pathways often dominate in seagrass systems where megaherbivores have been reduced or lost (Valentine and Duffy 2006). However, because urchins may shift to live seagrass tissue as increased urchin

densities deplete dead tissues, this paradigm must recognize that effects of herbivory on seagrasses may be periodic and non-linear with respect to consumer density. Future studies should examine conditions that lead to urchins reaching densities sufficient to exert direct negative effects on seagrass biomass. By understanding how factors such as variable larval recruitment and predation threat regulate urchin densities, management practices that account for herbivory can be developed to assist in conserving seagrass ecosystems. In addition, sediments in seagrass systems are widely recognized for their potential to sequester carbon (Fourqurean et al. 2012) but grazing by megaherbivores has the potential to influence future sequestration (Johnson et al. 2017). By consuming dead tissue, urchins also could play an important role in current and future carbon sequestration by decreasing the pool of dead tissue and modifying seagrass canopies to reduce passive settlement of carbon-rich particles.

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