

Gulf and Caribbean Research

Volume 30 | Issue 1

2019

Rapid Assessment of Post-Hurricane Michael Impacts on a Population of the Sea Urchin *Lytechinus variegatus* in Seagrass Beds of Eagle Harbor, Port Saint Joseph Bay, Florida

Roberta Challener
Bellarmino University, rchallener@bellarmine.edu

James B. McClintock
University of Alabama at Birmingham, mcclinto@uab.edu

Raymond Czaja Jr.
University of West Florida, rec46@students.uwf.edu

Christopher Pomory
cpomory@uwf.edu

Follow this and additional works at: <https://aquila.usm.edu/gcr>



Part of the [Marine Biology Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

DOI: 10.18785/gcr.3001.07

To access the supplemental data associated with this article, [CLICK HERE](#).

Recommended Citation

Challener, R., J. B. McClintock, R. Czaja Jr. and C. Pomory. 2019. Rapid Assessment of Post-Hurricane Michael Impacts on a Population of the Sea Urchin *Lytechinus variegatus* in Seagrass Beds of Eagle Harbor, Port Saint Joseph Bay, Florida. *Gulf and Caribbean Research* 30 (1): SC11-SC16. Retrieved from <https://aquila.usm.edu/gcr/vol30/iss1/7>

This Short Communication is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in *Gulf and Caribbean Research* by an authorized editor of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

GULF AND CARIBBEAN

R E S E A R C H

Volume 30
2019
ISSN: 2572-1410



Published by

**THE UNIVERSITY OF
SOUTHERN MISSISSIPPI**

GULF COAST RESEARCH LABORATORY

Ocean Springs, Mississippi

SHORT COMMUNICATION

RAPID ASSESSMENT OF POST-HURRICANE MICHAEL IMPACTS ON A POPULATION OF THE SEA URCHIN *LYTECHINUS VARIEGATUS* IN SEAGRASS BEDS OF EAGLE HARBOR, SAINT JOSEPH BAY, FLORIDA

Roberta C. Challener^{1*}, James B. McClintock², Raymond Czaja, Jr.³, and Christopher M. Pomory³

¹Bellarmine University, Biology Department, 2001 Newburg Road, Louisville, KY 40205; ²University of Alabama at Birmingham, Department of Biology, 1300 University Boulevard, Birmingham, AL 35294; ³University of West Florida, Biology Department, 11000 University Parkway, Pensacola, FL 32514; *Corresponding author, email: rchallener@bellarmine.edu.

KEY WORDS: echinoderms, seagrass ecosystem, storm events, climate change

INTRODUCTION

Echinoderms comprise an ecologically important group of marine invertebrates whose representatives inhabit coastal shorelines and bays of the northern Gulf of Mexico. Sea urchins, with their high densities and their capacity to rapidly graze a variety of algae and seagrasses, play a key role in structuring coastal communities (Valentine and Heck 1991, 1999, 2001, Valentine et al. 1997, Watts et al. 2013). For example, seasonal grazing by *Lytechinus variegatus* has been observed to stimulate seagrass production (Valentine et al. 1997, 2000) in part because they provide nutrients to the local community via their production of feces and ammonium (Greenway 1995, Watts et al. 2013). *Lytechinus variegatus* also influence the community through their preferential consumption of detrital seagrass leaves (Montague et al. 1991, Greenway 1995). Moreover, when aggregated in high density grazing fronts, *L. variegatus* can alter community structure through a dramatic loss of primary and secondary production that reduce fishery habitat and refugia (Rose et al. 1999, Maciá and Liman 1999). Therefore, *L. variegatus* serves important ecological roles and there is a need to better understand how physical disturbances such as increasingly powerful storms may impact their populations.

Studies that have examined the impacts of severe storms such as hurricanes on populations of echinoderms suggest that such events can cause a variety of outcomes (reviewed by Lawrence 1995). For example, Hurricane John (2006) had a significantly negative effect on coral reef communities in the Gulf of California that resulted in the complete loss of 6 species of echinoderms (Hernández et al. 2008). Hurricane Donna (1960) swept inland across north Florida Bay and displaced marine invertebrates including echinoderms inland where they died of aerial exposure (Tabb and Jones 1962). Hurricane Allen (1980) significantly reduced coral reef populations of the sea urchin *Diadema antillarum* in shallow water (≤ 10 m) of northern Jamaica (Woodley et al. 1981). Other studies found that some storms, despite the potential for mass mortality, had little to no effect on echinoderms.

For example, Hurricane Gilbert (1988) and Hurricane Hugo (1989) did not significantly alter abundances of ophiuroid or echinoid populations in backreef regions of Jamaica and St. Croix (Aronson 1993). Following the immediate passage of Hurricane Andrew (1992), seagrass communities and associated sea urchins at Lostman's River in Everglades National Park, in southwestern Florida generally survived intact (Dawes et al. 1995). Because it is almost impossible to predict and pre-sample a coastal site ahead of a hurricane strike, the number of studies providing pre- and post-hurricane comparisons is relatively small. Therefore, with limited numbers of such studies and a wide range of potential effects on echinoderms, it is important to study echinoderms that may be impacted by hurricanes whenever possible.

Saint Joseph Bay is a shallow, subtropical bay located on the northwestern panhandle of Florida that is semi-enclosed by the Saint Joseph Peninsula (Figure 1A). The bay contains large regions of luxuriant seagrass beds and patches of well-sorted sand (Valentine and Heck 1993), along with dense populations of the sea urchin *L. variegatus* (Beddingfield and McClintock 1994, Beddingfield 1997, Beddingfield and McClintock 2000, Challener and McClintock 2017). Hurricane Michael made landfall at Mexico City Beach, FL just west of Saint Joseph Bay as a category 5 storm (notably the most wind-intense hurricane to ever impact the Florida panhandle) on 10 October 2018. Sustained winds were measured at 250 km/h and peak storm surge was estimated at 4.2 m (National Weather Service 2018). A weather monitoring station in Apalachicola, located about 30 miles east of where the hurricane made landfall, registered lower wind speeds during the hurricane, yet winds still reached speeds as high as 100 km/h (www.ndbc.noaa.gov; NOAA station APCF1-8728690). Immediately following the hurricane's passage over the coast, aerial images indicated that the peninsula adjacent to Eagle Harbor in T.H. Stone Memorial Saint Joseph Peninsula State Park had been bisected by storm-generated currents creating a large passage (cut) to the Gulf of Mexico

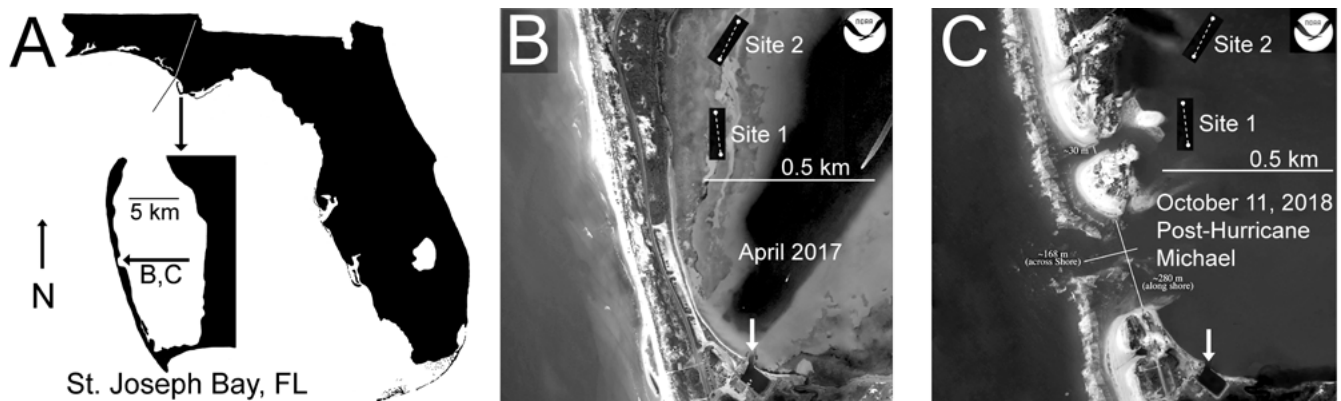


FIGURE 1. Sampling locations in Florida. A. Map of Florida with the location of Saint Joseph Bay enlarged along the panhandle of northwest Florida (black and white line indicates track of Hurricane Michael). B. Eagle Harbor within Saint Joseph Bay before Hurricane Michael. C. Damage and formation of a pass between Saint Joseph Bay and the Gulf of Mexico caused by Hurricane Michael. Dotted lines indicate seagrass beds that were sampled before and after Hurricane Michael (after Hurricane: Site 1 December 2018 and June 2019; Site 2 June 2019). White arrows in B and C indicate the location of Eagle Harbor boat ramp for reference. B and C images obtained from NOAA (<https://www.usgs.gov/media/images/and-after-photos-show-hurricane-michaels-destructive-power-2>).

(Figure 1B, C).

With climate change accelerating ocean warming, high intensity hurricanes are predicted to make coastal landfall in greater frequency (Knutson et al. 2010, IPCC 2014). Accordingly, understanding their potential impact on the ecology of coastal marine ecosystems that provide habitat for marine organisms and barriers to coastal erosion is important. The purpose of the present study was to conduct a rapid post-hurricane assessment of the status of a seagrass-associated population of the sea urchin *L. variegatus* in a high impact region of Saint Joseph Bay where population assessments had been periodically conducted in the 16 months leading up to the hurricane.

MATERIALS AND METHODS

Two study sites (Figure 1C) were selected because sea urchin densities had been sampled at both sites prior to Hurricane Michael monthly from June 2017 through April 2018 and again in June 2018. Site 1 was located 150 m from shore within the bay in Eagle Harbor (29°46'14.78" N, 85°24'9.8" W) and was about 250 m from the storm-generated cut created by Hurricane Michael. Site 1 was sampled twice post-hurricane, in December 2018 and again in June 2019. Site 2 was located 150 m from shore in Eagle Harbor (29°46'22.08" N, 85°24'7.82" W) and was about 300 m from the storm-generated cut. However, site 2 was located adjacent to the mouth of a small (25 m wide and 750 m long) tidal creek. Site 2 was sampled once post-hurricane in June 2019. Water depth at the study sites generally varied between 0.75 and 1.25 m, with air exposure only briefly occurring during the summer spring tides (R. Czaja, Jr., pers. obs.). More broadly, annual sea water temperature in Saint Joseph Bay ranges from 11–35°C, annual salinity from 26–36 (Beddingfield 1997), and pH from 7.4–8.3 (Challener et al. 2015). While *Thalassia testudinum* is the primary founda-

tion seagrass in the bay, other habitat-forming taxa occur including *Halodule wrightii*, Rhodophyta, and semi-infaunal bivalves including *Modiolus americanus* and *Atrina rigida* (Valentine and Heck 1993, Beddingfield 1997, Bologna 1998, Munguia 2006).

Individuals of *L. variegatus* were collected by hand using snorkel equipment from 1 m² quadrats placed sequentially along a 30 m transect line parallel to a seagrass bed edge and 3 m into the seagrass bed at sites 1 and 2 in Eagle Harbor, Saint Joseph Bay. Collections were made monthly from June 2017 through April 2018, in June 2018 (pre-hurricane), and June 2019 (250 d post Hurricane Michael). On each sampling date, all individuals within a quadrat were collected and test diameters of sea urchins were measured and assigned to 10-mm size classes. Salinity was measured with a refractometer and seawater temperature with a mercury thermometer. *Thalassia testudinum* shoot density and leaf lengths were measured in June 2018 (pre-hurricane) and June 2019 (post hurricane) via 5 randomly placed 0.25 m² quadrats at each of the 2 sites. The quadrat was divided into 16 subsections with string, creating 9 intersection points inside the quadrat. Shoots that were closest to a randomly selected intersection point were used in measures of leaf lengths. Leaves were snipped at the base and lengths were measured *in situ* using a ruler.

In December 2018 (70 d post Hurricane Michael), *L. variegatus* was sampled only at Site 1 in a similar manner as described above by placing 1 m² quadrats every 5 m along the length of a 50 m transect line (Fig. 1C). Images of all sea urchins collected from each quadrat were taken using a digital underwater camera and test diameters later obtained from images using ImageJ (Rasband 1997–2018). Seawater temperature (°C), dissolved oxygen (mg/L), and salinity were measured using a YSI handheld multimeter.

To standardize sampling methods and intensity between

pre- and post-hurricane urchin density surveys, every third quadrat from transects sampled between June 2017 and June 2018, as well as in June 2019, were used to compare to data collected from December 2018 at Site 1. With only one storm event, and one location sampled post-hurricane, there is no formal statistical test of storm impact. Instead, sea urchin density is presented as means with standard deviations and *t*-tests were used to compare months based on variation among quadrats sampled at Site 1 ($n=10$ months through June 2018, $n=11$ months for December 2018, $n=10$ months for June 2019) and Site 2 ($n=10$ months for June 2018 and 2019).

RESULTS

Sea water temperature at the study site in December 2017 (pre-hurricane sample) was 12°C and salinity was 32. Sea water temperature at the December 2018 post-hurricane sampling was slightly higher (14.2°C), dissolved oxygen was 11.21 mg/L, and salinity (28) was somewhat lower than that sampled at the same site in December 2017. Small pieces of the roadbed that had once straddled the nearby penin-

sula were observed along the December 2018 transect, lying within 5 cm of the surface sediments. Live leaves and shoots of *T. testudinum* were observed within all the quadrats sampled, indicating minimal storm disturbance to either above-ground or below-ground biomass within the seagrass bed.

At site 1 sea urchin density was similar between December 2017, prior to the hurricane (mean 2.90 ± 2.38 sd), and December 2018, just a little over 2 months after the hurricane (mean 2.82 ± 2.99 sd; $t_{19} = 0.07$, $p = 0.95$; Figure 2A). Mean sea urchin density sampled in December 2018 was also within the variation of densities (sd) measured in all the previous months except October 2017 (Fig. 2A). Sea urchin density was also similar at site 1 in June 2018 (mean 10.90 ± 7.02 sd) and June 2019 (mean 6.30 ± 3.37 sd; $t_{18} = 1.87$, $p = 0.08$) (Figure 2A), and at site 2 in June 2018 (mean 2.02 ± 2.74 sd) and June 2019 (mean 3.80 ± 3.52 sd; $t_{18} = 1.13$, $p = 0.27$) (Figure 2B). Mean sea urchin density sampled in June 2019 was also within the variation of densities (sd) measured in all the previous months at both sites.

Sea urchins at site 1 in December 2017 included individuals occupying all 6 of the 10-mm size classes (0–10 mm through 51–60 mm), whereas those sampled in December 2018 had diameters in only the 3 largest size classes (Figure 3A). While the 3 smallest 10-mm size classes of sea urchins were absent in December 2018, the percentage of sea urchins in the mid-size class (41–50 mm) was about three times greater than the same size class at site 1 in December 2017 (Figure 3A). In June 2018 at site 1, the second smallest size class (11–20 mm) comprised about 10% of the sea urchins sampled, whereas no sea urchins in this same size class were present in June 2019 (Figure 3B). Large sea urchins (41–50 mm size class) at site 1 were about 6 times more prevalent in June 2019 than in June 2018 (Figure 3B). At site 2, sea urchins in the 31–40 mm size class were most prevalent in June 2018 and June 2019. However, sea urchins in the 21–30 mm size class were about 5 times more prevalent in June 2018 than in June 2019 (Figure 3C).

Seagrass shoot density at site 1 was similar in June 2018 and in June 2019, with a difference in mean shoot density of only 10 shoots/0.25 m² (Table S1). At site 2, however, mean shoot density was 1.7 times greater in June 2019 than in June 2018 (Table S1). A similar trend was observed for leaf length, with leaf length at site 1 being only 0.4 cm greater in June 2019 than in June 2018; however, leaf length at site 2 was 2 times greater in June 2019 than in June 2018 (Table S1).

DISCUSSION

Although limited in scope, the results of this study indicate that *L. variegatus* populations in Saint Joseph Bay and possibly other impacted bays along the coast of the Gulf of Mexico may be resilient to intense storms such as Hurri-

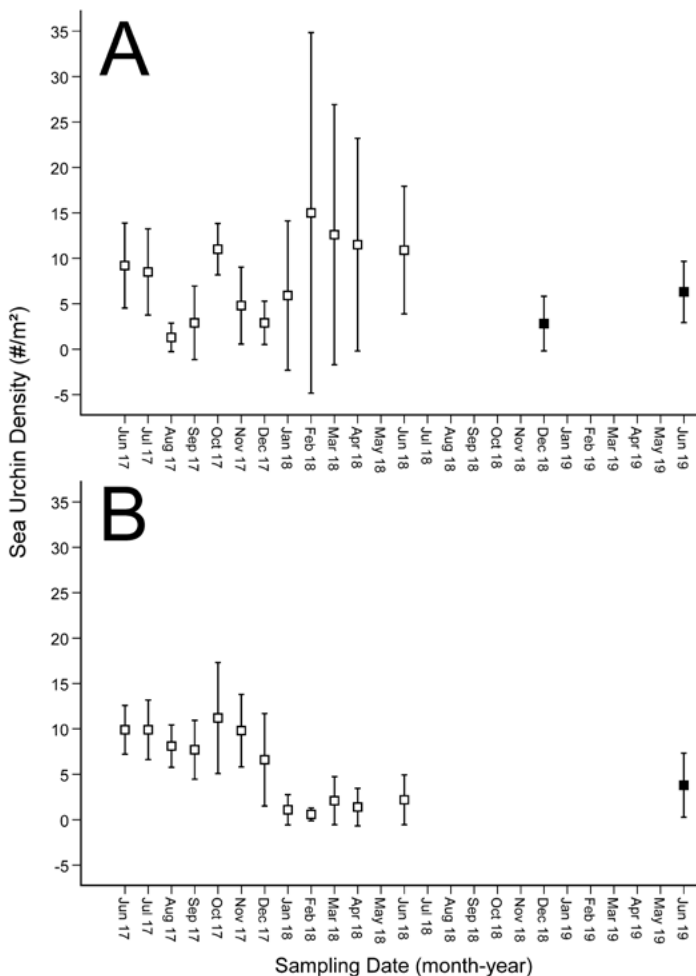


FIGURE 2. Mean monthly *Lytechinus variegatus* densities per square meter ($\bar{x} \pm sd$) pre-hurricane (2017-2018, open squares) versus post-hurricane (filled squares). A. Site 1. B. Site 2.

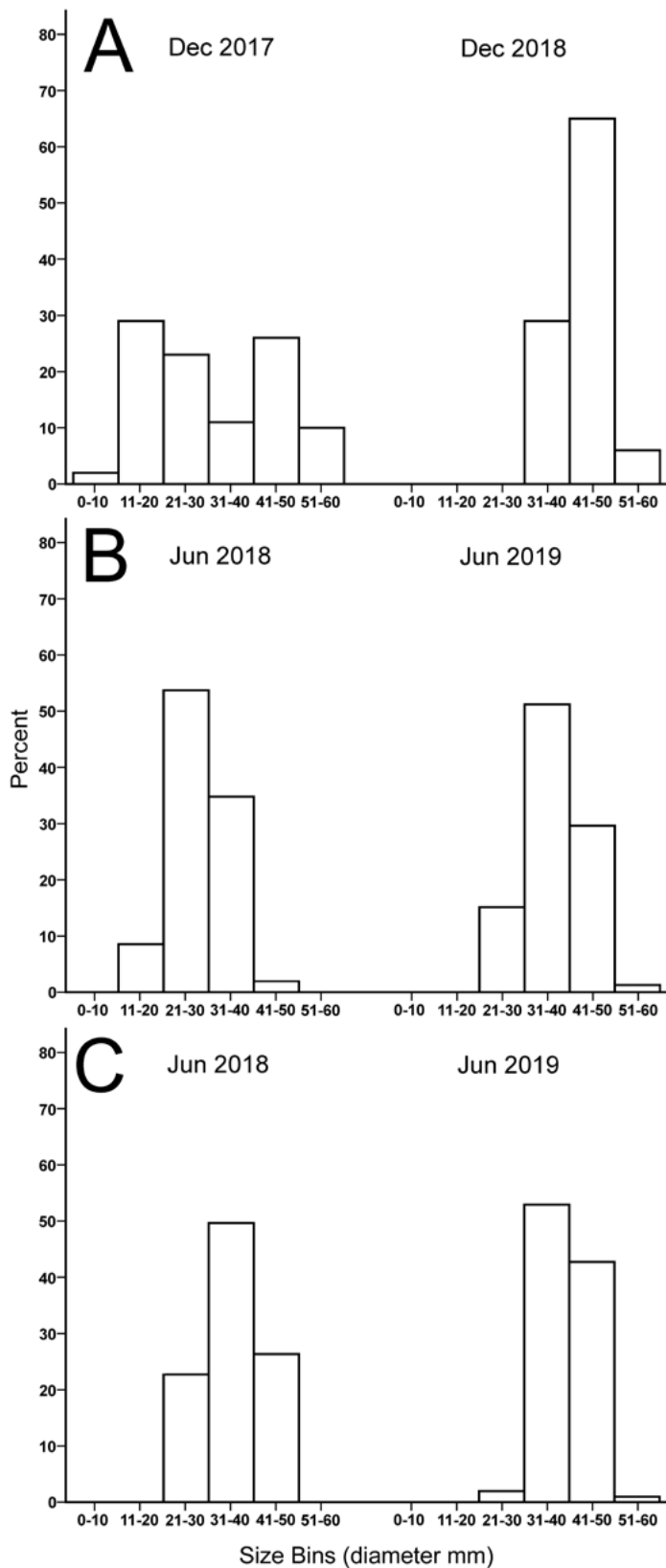


FIGURE 3. Percentage of *Lytechinus variegatus* individuals in each size class sampled before and after Hurricane Michael. A. Site 1, December (Dec) 2017 and December 2018. B. Site 1, June (Jun) 2018 and June 2019. C. Site 2, June 2018 and June 2019.

cane Michael. Despite the proximity of our sampling sites to the storm-generated cut in the Saint Joseph Peninsula, we

found no definitive post-hurricane impacts on the resident seagrass-associated population of the sea urchin *L. variegatus*. Similarly, there was no evidence that the seagrass itself was negatively impacted at either of our 2 sampling sites. Seagrass shoot density and shoot length were almost identical both pre- and post-hurricane at site 1 (samples taken in June 2018 and June 2019). In contrast, shoot density and shoot length doubled between June 2018 and June 2019 at site 2. This 2-fold post-hurricane increase could be the result of enhanced coastal nutrient productivity following the storm. In their review of the influence of hurricanes on coastal marine ecosystems of the northern Gulf of Mexico, Connor et al. (1989) concluded that over recorded history hurricanes generally enhance coastal nutrient productivity and that while some marine species may be reduced temporarily, they quickly recover. If nutrient productivity increased after Hurricane Michael, then both our sampling sites would have been expected to respond accordingly. Another possibility is the higher seagrass productivity detected in June 2019 at site 2 reflects inter-annual variability in nutrient input from the adjacent tidal creek at this site.

The post-hurricane densities of sea urchins measured in December 2018 and in June 2019 at both sampling sites fell within the range of sea urchin densities recorded over the year before our December 2018 sample. Moreover, the percentages of the 3 largest size classes of sea urchins measured in December 2018 at site 1 were similar to, or even greater than, urchins in those size classes measured a year earlier (December 2017) at the same site. It is possible the absence of the 3 smallest 10-mm size classes of sea urchins noted in December 2018 at site 1 (a little over 2 months after Hurricane Michael) could be attributable to small, lighter individuals being swept away by the storm-generated currents. However, it is not possible to rule out temporal or spatial differences in local recruitment or predation as causative agents. In addition, at site 1 there is a large proportion of individuals that fell into the 41–50 mm size cohort (~65%) in Dec 2018. In contrast, < 5% of individuals occurred in this same size class in June 2018. Some of this difference is attributable to the lack of smaller size classes in December 2018 which inflates the relative proportion of larger individuals. However, given estimates of rapid growth in *L. variegatus* in Saint Joseph Bay (Beddingfield and McClintock 2000), it is possible that individuals in the June 2018 31–40 mm cohort grew into the 41–50 mm December 2018 cohort over a 6 month period. A detailed population study of *L. variegatus* over a 2 year period in Saint Joseph Bay (mid-1992 to mid-1994) found mean densities varied greatly with habitat and season, with a mean of 13.4 individuals/m² for sea urchins living in seagrass beds (*Thalassia*), while sizes of individuals were more stable with mean test diameter ranging between 32–40 mm over the course of the study (Beddingfield and McClintock 2000). These densities and sizes are similar to those recorded in the

current study.

Hurricanes worldwide, enhanced by global climate warming, are predicted to increase in both intensity and frequency (Knutson et al. 2010, IPCC 2014). The Gulf of Mexico is no exception to this pattern. It is likely that regional climate warming contributed to the intensification of Hurricane Michael and the resultant destruction of the town of Mexico Beach, FL and neighboring regions of adjoining Saint Joseph

Bay (National Weather Service 2018). Despite the physical impacts to the human populations living in coastal areas, the present study provides further support that sea urchins such as *L. variegatus* residing in seagrass communities along the northern Gulf of Mexico are largely resilient to hurricanes, and in the present study remarkably so, given the intensity of Hurricane Michael.

ACKNOWLEDGEMENTS

Part of this research was funded by a Faculty Development Fellowship grant awarded to R.C. Challener by Belarmino University. James McClintock appreciates the financial support provided by an Endowed Professorship in Polar and Marine Biology at the University of Alabama at Birmingham.

LITERATURE CITED

- Aronson, R.B. 1993. Hurricane effects on backreef echinoderms of the Caribbean. *Coral Reefs* 12:139–142. <https://doi.org/10.1007/bf00334473>
- Beddingfield, S.D. 1997. The nutrition, growth, reproduction and population dynamics of *Lytechinus variegatus* (Lamarck) from contrasting habitats in St. Joseph Bay, Florida. Ph.D. thesis, University of Alabama at Birmingham, Birmingham, AL, USA, 187 p.
- Beddingfield, S.D. and J.B. McClintock. 1994. Environmentally induced catastrophic mortality of the sea urchin *Lytechinus variegatus* in shallow seagrass habitats of St. Joseph's Bay, Florida. *Bulletin of Marine Science* 55:235–240.
- Beddingfield, S.D. and J.B. McClintock. 2000. Demographic characteristic of *Lytechinus variegatus* (Echinodermata: Echinoidea) from three habitats in a north Florida bay, Gulf of Mexico. *PSZN Marine Ecology* 21:17–40. <https://doi.org/10.1046/j.1439-0485.2000.00688.x>
- Bologna, P. 1998. The effects of seagrass habitat architecture on associated fauna. PhD thesis. The University of South Alabama, Mobile, AL, USA, 225 p.
- Challener, R.C., and J.B. McClintock. 2017. *In situ* measurements of righting behavior of the sea urchin *Lytechinus variegatus* in the field: the importance of size, substrate type and covering material. *Aquatic Biology* 26:33–40. <https://doi.org/10.3354/ab00669>
- Challener, R.C., L.L. Robbins, and J.B. McClintock. 2015. Variability of the carbonate chemistry in a shallow, seagrass-dominated ecosystem: Implications for ocean acidification experiments. *Marine and Freshwater Research* 67:163–172. <https://doi.org/10.1071/MF14219>
- Connor, W.H., J.W. Day, Jr., R.H. Baumann, and J.M. Randall. 1989. Influence of hurricanes on coastal ecosystems along the northern Gulf of Mexico. *Wetlands Ecology and Management* 1:45–56. <https://doi.org/10.1007/BF00177889>
- Dawes, C.J., S.S. Bell, R.A. Davis, Jr., E.D. McCoy, H.R. Mushinsky, and J.L. Simon. 1995. Initial effects of Hurricane Andrew on the shoreline habitats of southwestern Florida. *Journal of Coastal Research Special Issue 21: Impacts of Hurricane Andrew on the Coastal Zones of Florida and Louisiana*: 22–26 August 1992. p. 103–110.
- Greenway, M. 1995. Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). *Bulletin of Marine Science* 56:719–736.
- Hernández, L., E.F. Balart, and H. Reyes–Bonilla. 2008. Effect of Hurricane John (2006) on the invertebrates associated with corals in Bahía de La Paz, Gulf of California. *Proceedings of the 11th International Coral Reef Symposium, Ft Lauderdale, FL USA, 7–11 July 2008*, p. 301–304.
- IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Core Writing Team, R.K. Pachauri and L.A. Meyer, eds.). IPCC, Geneva, Switzerland, 151 pp.
- Knutson, T.R., J.L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience* 3:157–163. <https://doi.org/10.1038/ngeo779>
- Lawrence, J.M. 1995. Mass mortality of echinoderms from abiotic factors. In: M. Jangoux and J.M. Lawrence, eds. *Echinoderm Studies*, Vol. 5. A.A. Balkema, Rotterdam, Netherlands, p. 103–138.
- Maciá, S. and D. Liman. 1999. Destruction of Florida Bay seagrasses by a grazing front of sea urchins. *Bulletin of Marine Science* 65:593–601.
- Montague, J.R., J.A. Aguinaga, K.A. Ambrisco, D.L. Vassil, and W. Collazo. 1991. Laboratory measurement of ingestion rate for the sea urchin *Lytechinus variegatus* (Lamarck). *Florida Scientist* 54:129–134. <https://www.jstor.org/stable/24320450>
- Munguia, P. 2006. Diversity patterns in pen shell (*Atrina ridiga*) communities. Ph.D. thesis. Florida State University, Tallahassee, FL, USA, 110 p.

- National Weather Service. 2018. Catastrophic Hurricane Michael Strikes Florida Panhandle October 10, 2018. <https://www.weather.gov/tae/HurricaneMichael2018> (viewed on 02/20/2019).
- Rasband, W.S. 1997–2018. ImageJ, U. S. National Institutes of Health, Bethesda, MD, USA. <https://imagej.nih.gov/ij/>
- Rose, C.D., W.C. Sharp, W.J. Kenworthy, J.H. Hunt, W.G. Lyons, E.G. Prager, J.F. Valentine, M.O. Hall, P.E. Whitfield, and J.W. Fourqurean. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Marine Ecology Progress Series* 190:211–222. <https://www.jstor.org/stable/24854640>
- Tabb, D.C. and A.C. Jones. 1962. Effect of Hurricane Donna on the aquatic fauna of North Florida Bay. *Transactions of the American Fisheries Society* 91:375–378. [https://doi.org/10.1577/1548-8659\(1962\)91\[375:eohdot\]2.0.co;2](https://doi.org/10.1577/1548-8659(1962)91[375:eohdot]2.0.co;2)
- Valentine, J.F. and K.L. Heck. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: Evidence from field manipulations in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 154:215–230. [https://doi.org/10.1016/0022-0981\(91\)90165-S](https://doi.org/10.1016/0022-0981(91)90165-S)
- Valentine, J.F. and K.L. Heck. 1993. Mussels in seagrass meadows: Their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. *Marine Ecology Progress Series* 96:63–74. <https://doi.org/10.3354/meps096063>
- Valentine, J.F. and K.L. Heck. 1999. Seagrass herbivory: Evidence for the continued grazing of marine grasses. *Marine Ecology Progress Series* 176:291–302. <https://doi.org/10.3354/meps176291>
- Valentine, J.F. and K.L. Heck. 2001. The role of leaf nitrogen content in determining turtlegrass (*Thalassia testudinum*) grazing by a generalized herbivore in the northeastern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 258:65–86. [https://doi.org/10.1016/S0022-0981\(00\)00342-7](https://doi.org/10.1016/S0022-0981(00)00342-7)
- Valentine, J.F., K.L. Heck, J. Busby, and D. Webb. 1997. Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. *Oecologia* 112:193–200. <https://doi.org/10.1007/s004420050300>
- Valentine, J.F., K.L. Heck, Jr., K.D. Kirsch, and D. Webb. 2000. Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA). *Marine Ecology Progress Series* 200:213–228. <https://doi.org/10.3354/meps200213>
- Watts S.A., J.B. McClintock, and J.M. Lawrence. 2013. *Lytechinus*. In: J.M. Lawrence, ed. *Sea Urchins: Biology and Ecology*, 3rd ed., Vol. 38 *Developments in Aquaculture and Fisheries Science*. Elsevier, Amsterdam, the Netherlands, p. 475–490. <https://doi.org/10.1016/c2011-0-06902-8>
- Woodley, J.D., E.A. Chornesky, P.A. Clifford, J.B.C. Jackson, L.S. Kaufman, N. Knowlton, J.C. Lang, M.P. Pearson, J.W. Porter, M.C. Rooney, K.W. Rylaarsdam, V.J. Tunnicliffe, C.M. Wahle, J.L. Wilff, A.S.G. Curtis, M.D. Dallmeyer, B.P. Jupp, M.A.R. Koehl, J. Neigel, and E.M. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749–755. <https://doi.org/10.1126/science.214.4522.749>