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Localized Placement of Breakwater Reefs Influences Oyster Populations and Their Resilience after Hurricane Harvey

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Abstract: Populations of the eastern oyster (*Crassostrea virginica*) have been historically declining due to both natural and anthropogenic stressors. In response, oyster reefs have been created with many different approaches. This study utilized intertidal reefs constructed with oyster shells recycled from local restaurants to provide oyster settlement substrate, reef-associated faunal habitat, and a barrier to prevent marsh erosion. The objective of this study was to determine how oyster population characteristics changed over four years (2016–2019) on five different reefs within Sweetwater Lake, Galveston Bay, Texas, with a secondary objective to examine how oyster populations responded after Hurricane Harvey. Over the study period, five different reefs were sampled each summer by removing five bags per reef to determine oyster abundance and size demography. For the three years of the study (2017–2019), we also quantified oyster spat recruitment to the reefs. Oyster abundance and size (shell height) varied interactively by year and reef number, whereas oyster recruitment was significantly lower following Hurricane Harvey and then returned to pre-storm levels. Our results further highlight the importance of reef placement for breakwater-style reefs, as it appears the hydrodynamics within Sweetwater Lake influenced both oyster abundance and size among individual reefs. While the created reefs receive limited larval influx due to the narrow opening between Sweetwater Lake and Galveston Bay proper, this limited connectivity seemed to prevent mass mortality from the freshwater influx from Hurricane Harvey. Therefore, projects creating oyster reefs should consider local and regional landscape factors for the long-term success of oyster populations and robustness to natural disasters.

Keywords: *Crassostrea virginica*; restored reefs; breakwater reefs; Hurricane Harvey; landscape; population dynamics

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1. Introduction

Akin to terrestrial habitats [1–6], the restoration of marine biogenic habitats, in response to habitat loss, has been approached on different scales to address theoretical ecological questions [7–11]. However, the vast majority of restoration efforts for these marine habitats have been centered around boosting ecological function, specifically focusing on increasing the abundance or population size [12–14], increasing the quantity of lost habitat [8,15,16], replacing lost biodiversity [13,17–21], and replenishing lost ecosystem services [22–24]. In many practical cases, restoration efforts for structured marine habitats are multifaceted and have sought to incorporate multiple aspects of theoretical and practical ecology to further perpetuate an understanding of the best practices and outcomes [25–28].

The eastern oyster, *Crassostrea virginica*, is an ecologically important species that provides many different ecosystem services. First, oysters create a structured habitat within estuarine systems along the Gulf of Mexico and the Atlantic coast of the United States. This ecologically important habitat is the result of the oyster's three-dimensional growth after settlement, which provides reefs in either intertidal or subtidal areas that would otherwise be open bottom. While these reef types have functional differences because of tidal dynamics [29–31], both are extremely valued, as they concentrate energy in one location and provide habitat for benthic-associated meiofauna, invertebrate macrofauna, and resident and transient fish [29,32–37]. Second, along with creating a physical structure, the vertical structure of oysters increases sedimentation on the reef by decreasing the water flow over it [37], enabling vertical growth of the entire reef. Third, the reefs created by oysters are valuable for energy dissipation within estuarine systems and for protecting coastal wetland habitats from erosion. This role in energy dissipation can help abate naturally occurring sources of erosion, such as a storm surge, or anthropogenically derived sources, such as boat wakes [38–40].

Along with providing ecosystem services, the eastern oyster has long been valued as a food commodity [41–44]. In this study, we utilized the Galveston Bay (GB) estuary, Texas, USA, as a model system because of the importance of the oyster fishery found within this estuary. The GB estuary is the 7th largest estuary in the USA, provides approximately 15% of the consumed oysters in the USA, and contributes approximately USD 50 million to the economy in the State of Texas annually [45]. However, the historic value of oysters as a food source has contributed to widespread population declines, not only in GB, but estuaries throughout its range within the USA [41–43]

Along with fishing pressure, oyster populations have also been reduced compared to historical numbers due to other natural stressors, such as large-scale storm events [39,46–48]. These periodic storms, specifically tropical storms and hurricanes, can quickly decimate oyster populations through sediment deposition, freshwater input, or a combination of both factors. Within the last several decades, the oyster populations of GB have been greatly impacted by two major storm events. In 2008, Hurricane Ike made landfall as a Category 2 storm. The associated Category 3–4 storm surge deposited significant quantities of sediment, burying approximately 70% of the oyster reefs in GB [49,50]. Then, in August 2017, Hurricane Harvey made landfall in Texas as a Category 4 hurricane, raining 824.7–1043.4 mm in three days within the Houston [51] and Galveston area (Figure 1).

The GB estuary was estimated to have received three times the Bay's normal volume in rain and freshwater run-off [52], which brought in 10.5 cm sediment across the Bay and some areas had over 50 cm of freshly deposited sediment [53]. This combination of decreased salinity from massive freshwater input (Figure 1) and sediment deposition caused the mortality rates of oysters in GB to drastically rise. For example, Du et al. [48] found the mean mortality rates on oyster reefs was up to 48%, with some locations experiencing 100% mortality after Hurricane Harvey, compared to historic mortality rates of 11%.

In efforts to regain lost ecosystem services from declining oyster populations, and to bolster harvestable stocks, there have been various methods to anthropogenically restore oyster reefs and abundances [12,15,19,25,43,54–60]. Commonly, this approach to restoration utilizes recycled oyster shell (cultch) for spat settlement [19,40,55,58,59,61], but other materials have also been utilized [54,62–64]. Oyster cultch can be deployed through directly deploying the shell onto the sediment or by placing the shells into aquaculture bags, which are then stacked on top of each other to create a breakwater reef that also provides shoreline protection [65–69]. While these breakwater reefs have a dual function in marsh protection and providing oyster settlement habitat, Morris et al. [65] highlight the need to understand the resilience of oyster populations on breakwater reefs. Using constructed oyster shell breakwater reefs in the GB estuarine system, the objectives of this study were to (1) evaluate how the population characteristics on individual reefs change over time; and (2) provide a comparison of the oyster populations before and after the impacts of Hurricane Harvey.

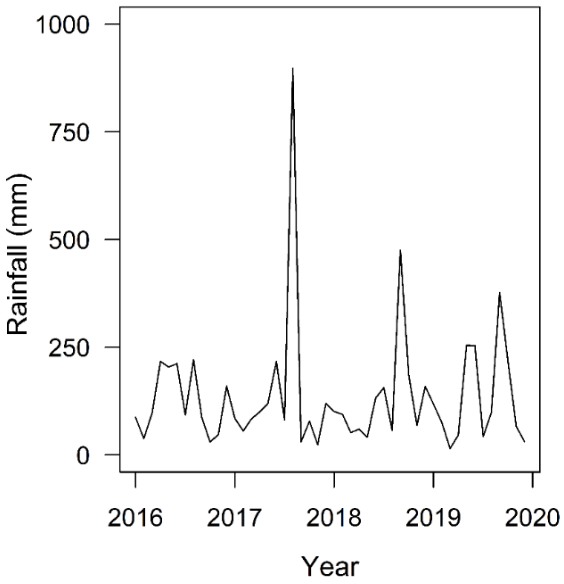

Figure 1. The monthly rainfall of Galveston County from January 2016 to December 2019, with the sharp increase representing the rainfall during August 2017 due to Hurricane Harvey. Data were acquired from the National Oceanographic and Atmospheric Administration's (NOAA) National Centers for Environmental Information for Galveston County, Texas, from 2016–2020. Data specifically acquired from https://www.ncdc.noaa.gov/cag/county/time-series/TX-167/pcp/all/1/2016-2020?base_prd=true&begbaseyear=1901&endbaseyear=2000 (accessed on 18 May 2022).

2. Materials and Methods

2.1. Study Site

This study was conducted in Sweetwater Lake, which is an anthropogenically built, semi-enclosed embayment that drains into West Galveston Bay Texas, USA (Figure 2).

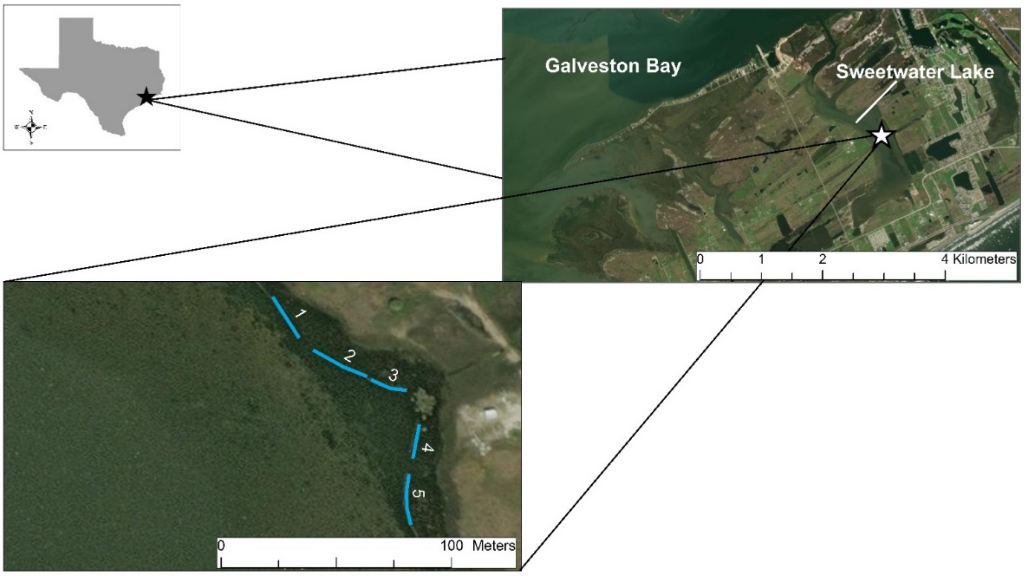

Figure 2. Sweetwater Lake (29.256233° N, −94.884030° W) is an anthropogenically constructed embayment off West Galveston Bay. The reefs utilized in the study, represented by blue lines overlaying the base layer imagery from ESRI ARC GIS, were labeled by proximity to the mouth of the embayment.

It was estimated the shoreline of Sweetwater Lake was eroding 1–2 ft (0.3–0.6 m) per year since the early 1990s. In response to this shoreline erosion, and the subsequent loss of marsh (*Spartina alterniflora*) habitat, the Galveston Bay Foundation (GBF) began constructing breakwater reefs in 2014. These breakwater reefs (henceforth referred to as created oyster reefs) were designed to mitigate shoreline erosion, and the subsequent marsh loss, while also providing structured habitat for oyster settlement and growth. Each created oyster reef was constructed with bagged oyster shells acquired through the GBF's Oyster Shell Recycling Program (galvbay.org/oysters). This Shell Recycling Program partners with local restaurants to collect shucked oyster shells, which are then sun cured for a minimum of six months on land to ensure the shell is pathogen free [70]. Once the shell was sun cured, groups of citizen scientists, including community volunteers, corporate teams, students, and scouts, assisted the GBF in the construction of the breakwater reefs in Sweetwater Lake. Approximately 30 pounds (13.6 kg) of shell was placed into a single mesh aquaculture bag. Volunteers then deployed the mesh bags with filled recycled oyster shells in a 4–2–1 pyramid, with four bags placed on the sediment, two bags on top of the bottom row, and one bag on the very top row (Figures 2 and 3). The length of each reef varied after construction, between 16 and 78 m (Table 1), due to the shape of the shoreline. To account of the variation in length among the reefs, specifically for the longest two reefs, Reef 1 and Reef 5, only distances equitable to other reefs were sampled [71]. Each reef was <5 m from the marsh edge, and since these reefs are intended to function as breakwater for marsh protection, there is minimal distance between the individual reefs (Figure 1).

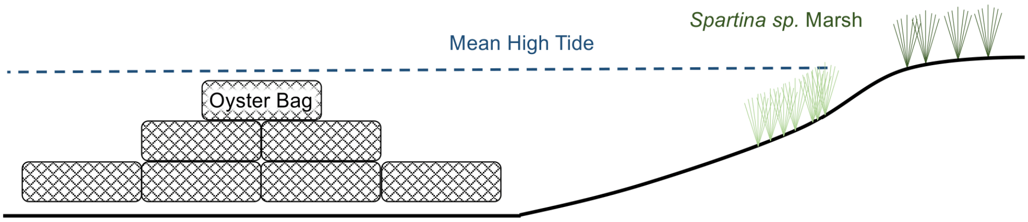

Figure 3. Conceptual cross section diagram of construction of each created intertidal oyster reef. Four aquaculture mesh bags filled with recycled oyster shells were placed on the sediment, a row of two bags were put down as the intermediate level, with the top row consisting of one row of bagged oyster shells.

Table 1. Time of construction and distance of each reef sampled. For the longest reefs (1 and 5), the entire reef was not sampled, to provide equitable lengths among all five reefs.

Reef Number	Time of Construction	Total Length (m)
1	June 2015	76
2	May 2014	39
3	May 2015	39
4	May 2014	16
5	May 2015	77

2.2. Oyster Abundance and Size Data Collection

Across 4 years (2016–2019), the five reefs (Figure 2 and Table 1) were sampled in July–August to quantify the oyster population characteristics. Five individual bags were haphazardly selected from each reef, placed in a bucket, and brought to shore. From each bag, the first 20 oysters were measured (shell height (SH) in mm) and then all remaining oysters were counted [7]. Laroche et al. [71] quantified the number of individual shells per bag during the first year of the study (2016) as a proxy for the quantity of habitat within each bag. Because there was no significant difference in the number of shells between bags or individual reefs, the shells were not counted in subsequent years. After counting and measuring the oysters, everything from the original bag was placed in a new bag and then immediately returned to the same location on the reef.

2.3. Oyster Spat Recruitment

Recruitment of oyster spat, a common term utilized for oyster larvae that have settled on benthic substrate after the pelagic life history stage, which represent larval settlement and mechanisms influencing survivorship [7,72], was measured across the five reefs for three years (2017–2019) of the study. Sampling began in June of each year and continued through either August (2017 and 2018) or November (2019). This differed timeframe was based on intra-annual recruitment experiments. Despite the temporal variance for sampling spat recruitment among years, this time frame captured peak settlement within the GB estuary [73]. Spat recruitment was quantified with 0.04 m^2 caged trays constructed from 1 × 1 cm hardware cloth, filled with ten pieces of similar-sized shells (70–90 mm), and then closed with a lid of the same type of hardware cloth to minimize predation [7]. Each individual tray was then secured to the reefs (Figure 4) and upon retrieval all spat were counted from each tray [7,15].

Figure 4. Spat recruitment trays attached to the created reefs in Sweetwater Lake, Galveston Bay, Texas.

2.4. Statistical Analysis

All data were analyzed using SAS Version 9.4 software (SAS Institute, Inc., Cary, NC, USA). Prior to analysis, data for oyster abundance and SH were tested for homogeneity of variance with Levene's test. Both data sets failed the homogeneity of variance test and the data were transformed (log(X + 1)) prior to analysis. Using the proc GLM in SAS, a two-way, repeated-measures analysis of variance (ANOVA) tested the hypothesis that year and/or reef number (proxy for location) had a significant contribution to variance in oyster abundance or oyster SH. Additionally, oyster spat recruitment did not meet homogeneity of variance and was log (X + 1) transformed prior to utilizing a two-way, repeated measures ANOVA, to test for differences among year and reef number. To find any significant interactions, we utilized a Student–Newman–Keuls post-hoc test.

3. Results

3.1. Oyster Abundance and Size

The data sets for oyster abundance and oyster SH failed the homogeneity of variance tests and were analyzed based on log (X + 1) data. Oyster abundances did not significantly differ ($p > 0.05$) by year (Table 2). Reef number (proxy for location) significantly influenced oyster abundance between years (Table 2). More importantly, there was a significant interaction between year and reef number (Table 2A and Figure 5). Independent, one-way ANOVAs, which compared reefs within year (Table 3A and Figure 5), demonstrated significant differences among reefs in 2016, 2017, and 2019. In 2016, Reefs 2 and 5 had significantly greater abundances (Figure 5); in 2017, Reef 4 was significantly greater than Reef 1; and in 2019, oyster abundance on Reef 4 was significantly greater than all other reefs (Figure 5).

Table 2. Results of a two-way, repeated measures ANOVA, analyzed on log (X + 1) data of (**A**) oyster abundance and (**B**) oyster shell height for the variables of year (2016–2019) and the reef number (1–5). The bold numbers are the significant values.

Effects	dF	F Value	*p* Value
A. Oyster Abundance			
Year	3	1.14	0.33
Reef Number	4	4.30	**0.0034**
Year × Reef Number	12	2.78	**0.0033**
B. Oyster Shell Height			
Year	3	37.13	**<0.001**
Reef Number	4	24.22	**<0.001**
Year × Reef Number	12	5.71	**<0.001**

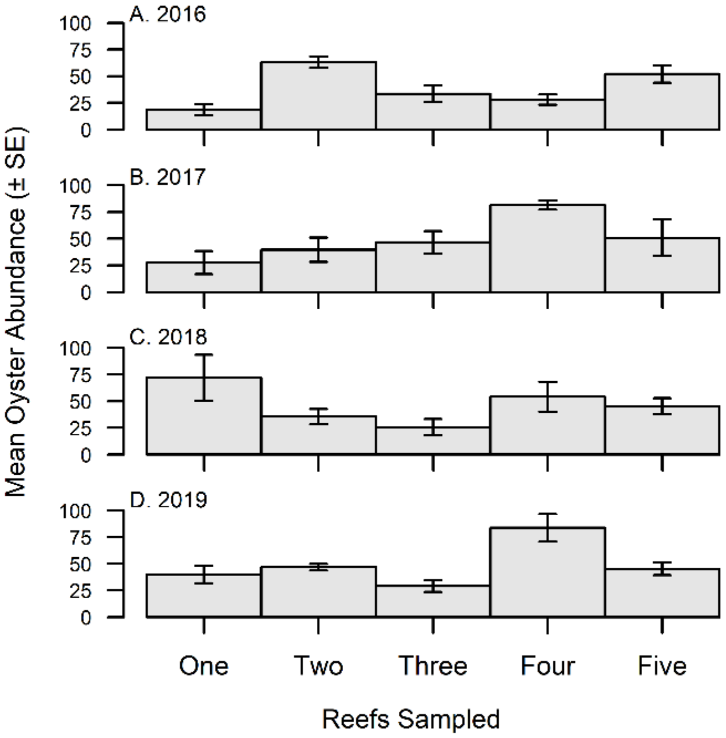

Figure 5. Oyster abundance (mean ± SE) from each reef (n = 5 bags sampled from each reef) for each year sampled in Sweetwater Lake, Galveston Bay, Texas. Reefs 2 and 4 were constructed in 2014 and the remaining reefs were constructed in 2015.

Oyster size varied significantly by year ($p < 0.001$) and reef number ($p < 0.001$), with a significant interaction also between year and reef number (Table 2). The subsequent one-way ANOVAs demonstrated a significant difference for all years by reef number (Table 3B). The SNK post-hoc results demonstrated varied differences among reef numbers by year. In 2016, Reef 2 was significantly greater than Reefs 3, 4, and 5, while Reef 1 had a significantly lower oyster size (Figure 6A). Reefs 2, 4, and 5 were significantly greater than Reefs 1 and 3 in 2017 (Figure 6A); in 2018, Reefs 2, 5, and 4 had the highest oyster SH size, while Reef 1 had significantly smaller oysters than all other reefs (Figure 6C). Finally, oyster SH in 2019 was significantly larger on Reefs 2, 3, and 5 compared to Reefs 1 and 4 (Figure 6D).

Table 3. Based on significant interactive effects of year by reef number, results for (**A**) oyster abundance and (**B**) oyster shell height, and the results of the one-way ANOVAs for reef number by year on log (X + 1) data. Reefs 2 and 4 were constructed in 2014 and the remaining reefs were constructed in 2015. The bold numbers are the significant values.

Effects	dF	F Value	*p* Value
A. Oyster Abundance			
2016	4	8.35	**0.0004**
2017	4	3.20	**0.04**
2018	4	1.71	0.18
2019	4	7.05	**0.001**
B. Oyster Shell Height			
2016	4	13.54	**<0.001**
2017	4	11.35	**<0.001**
2018	4	6.70	**<0.001**
2019	4	8.35	**<0.001**

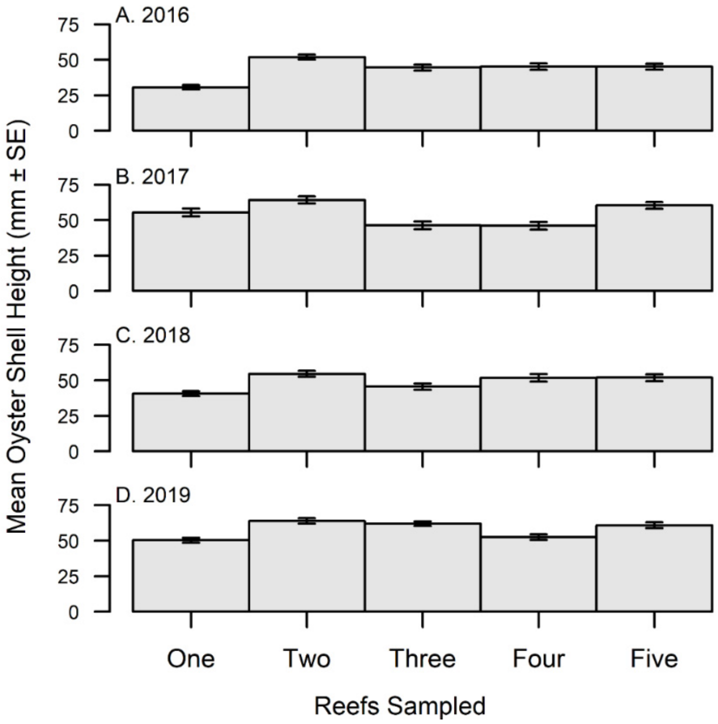

Figure 6. Oyster shell height (mean ± SE) from each reef (n = 5 bags sampled from each reef) for each year sampled in Sweetwater Lake, Galveston Bay, Texas. Reefs 2 and 4 were constructed in 2014 and the remaining reefs were constructed in 2015.

3.2. Oyster Spat Recruitment

Oyster spat recruitment significantly varied by year (Table 4), with counts significantly lower in the recruitment year sampled after Harvey (2018) compared to the years sampled prior to (2017) and after (2019) the storm (Figure 7). There was no overall significant difference for spat recruitment by reef number (as a proxy for location; Table 4); however, there was a significant interactive effect of year by reef (Tables 4 and 5).

Table 4. Results of a two-way, repeated measures ANOVA, analyzed on log (X + 1) data of spat count for periods of high recruitment during 2017–2019, sampled across the five reefs. The bold numbers are the significant values.

Effects	dF	F Value	*p* Value
Oyster Spat Recruitment			
Year	2	10.95	**<0.0001**
Reef Number	4	1.63	0.17
Year × Reef Number	12	2.42	**0.02**

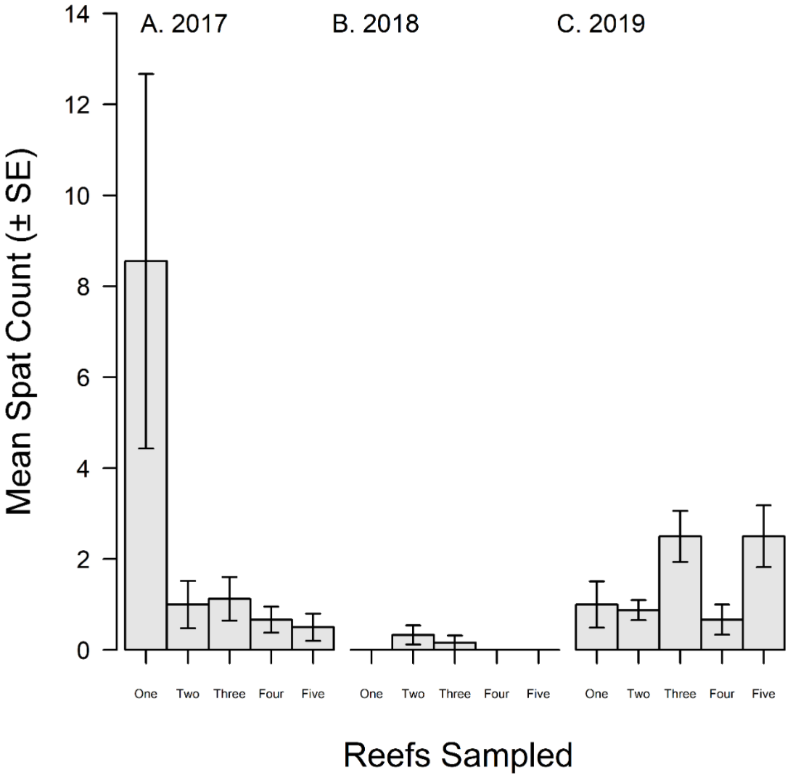

Figure 7. Spat count (mean ± SE) from each reef year sampled in Sweetwater Lake, Galveston Bay, Texas. There was a significantly lower spat count after Hurricane Harvey made landfall in Galveston compared to the years before and after.

Table 5. Based on significant interactive effects of year by reef number for oyster spat recruitment, the results of the one-way ANOVAs for reef number by year on log (X + 1) data. The bold numbers are the significant values.

Oyster Spat Recruitment			
2017	4	2.40	0.06
2018	4	1.54	0.22
2019	4	4.40	**0.04**

4. Discussion

Oyster population characteristics on created breakwater reefs in Sweetwater Lake, GB, appear to fluctuate based upon annual variation and the context of reefs in their landscape. This can be directly inferred from the high intra-annual variability in oyster abundances and the minimal impact on oyster abundances pre- versus post-Hurricane Harvey sampling events. Further, our results demonstrate that, over time, utilizing bagged oyster shell as a settlement habitat appears to limit the growth of oysters found within this created habitat, which suggests one or more mechanisms for these reefs may impede oyster growth after a certain size. Finally, the only difference we observed due to Hurricane Harvey was for larval recruitment, attributed to the hydrodynamics of the system at both the small and large landscape scales for these particular reefs and this system.

The created breakwater reefs in Sweetwater Lake had high variability for oyster abundances by year and reef location, suggesting the estuarine landscape influenced oyster abundances at multiple scales. Previous studies have demonstrated intra-reef landscape characteristics can influence oyster populations [7,74–76] and that the placement of created reefs can influence their functionality as habitat [7,18,34,77]. Reefs located closer to the mouth opening of Sweetwater Lake (reefs one and two) had the greatest abundances in 2016 and 2018. Reef four also experienced significantly higher abundances in some years, suggesting the tidal flux from West GB into Sweetwater Lake also facilitated high abundances of oysters. The tidal flux from the Bay proper likely facilitated higher abundances on these reefs due to greater larval supply from the Bay, which may not have been captured during the spat recruitment sampling, or due to increased phytoplankton being moved over the reefs as a food supply. Another factor that may have been driving oyster abundances within these bagged reefs is predation. Xanthid crabs are a common predator on small oysters [78–80]; however, in a study evaluating predator abundances of the oystershell mud crab (*Panopeus simpsoni*), Laroche et al. [71] quantified higher abundances of female oystershell mud crabs on Reefs 2 and 4. While their study was limited to one year, it suggests bottom-up factors are driving the variation in reefs, based on hydrodynamics, rather than a top–down mechanism from predation.

Previous work has demonstrated that oyster abundances had significant mortality in GB after Hurricane Harvey due to extremely low salinities [48]; however, oyster abundances on the reefs sampled in Sweetwater Lake did not have the same drastic loss after the storm. This lack of difference among the year is likely attributed to a combination of hydrodynamics, reef placement, and sampling regime. First, Sweetwater Lake only has access to West GB through a relatively small, man-made channel, mainly surrounded by *Spartina alterniflora* marsh complexes, and found in a narrow area of Galveston Island. Therefore, the freshwater runoff and flux into Sweetwater Lake appears to be limited and may have impacted oyster abundances. In turn, GB proper experienced high oyster mortality [48] due to the large quantity of freshwater runoff that entered and remained in the Bay [48,51]. It has been estimated that GB received 3x [53] to 5x [81] the Bay's volume in freshwater rainfall and runoff during and after the storm. The massive flux of freshwater into the Bay caused the entire Bay to become fresh for months before returning to normal salinities [52]. Thus, oyster populations in GB proper experienced high mortality rates from Hurricane Harvey, whereas, by comparison, the oyster abundances in Sweetwater Lake did not decline as drastically after the storm. Finally, due to logistical reasons, we were only able to sample the oyster reefs once per year. Therefore, the temporal timeframe of sampling would have missed the acute effects of the storm on the oyster populations in Sweetwater Lake but did demonstrate the resilience of oyster populations on created reefs after a large-scale disturbance.

Oyster size varied significantly over year, reef number, and interactively between the two variables. Interestingly, we also observed a relative threshold for oyster size. Not observing large-sized oysters in the bagged reefs suggests this style of reef construction may provide an threshold to an oyster's growth potential, as demonstrated by few oysters actually reaching the legal/harvestable size in Texas, which is 76 mm (available online: https://tpwd.texas.gov/regulations/outdoor-annual/fishing/shellfish-regulations/oyster-regulations#:~:text=Length%20and%20Possession%20Limits,greatest%20length%20of%20the%20shell, accessed 6 May 2022). While these oysters are not intended for harvesting, the impediment of growth may have implications for the population structure of oysters on each of the reefs. The smaller-sized oysters sampled suggest that the oyster spat recruiting onto the reefs could be mainly produced from adults in other areas of GB rather than the sampled reefs. This suggests the oyster populations on the created breakwater style reefs may not be self-reliant for larval supply and may represent a population sink because the upper sized oysters sampled represent the lower end for the reproductive size class of oysters [82,83]. Thus, these results indicate utilizing the breakwater reef method to provide multiple ecological benefits, such as a structure for oyster spat settlement, meiofauna and macrofauna habitat, and a barrier to protect marshes; however, this may limit oyster growth due to confinement.

The largest impact observed on the constructed breakwater reef oyster populations from Hurricane Harvey was decreased spat recruitment the following year (2018). The decline in spat recruitment after the storm could be attributed to the decreased larval supply. After the storm, reproductive-age oysters experienced high mortality rates [48], which would subsequently reduce the overall population's reproductive output. Further, the breakwater reefs were constructed in an extremely protected area, but the small channel may have limited larval influx to the reefs compared to the naturally occurring reefs in the area. Thus, reef development over time may be hindered due to the limited larval flux into the restoration site, although our data demonstrates that Hurricane Harvey had a significant impact on the larval output within GB.

In conclusion, constructing breakwater reefs has become a common technique by organizations, such as the GBF, who operate oyster shell recycling programs, to incorporate recycled oyster shell to increase oyster populations and protect shorelines. While the use of bagged oyster shell is successful in terms of oyster spat recruitment and abundance, the confinement of new oyster growth may be a limiting factor to the long-term success of these restoration efforts and there should be a comparative study of breakwater reefs compared to loose-shell planting. Finally, our results demonstrate that, under certain highly localized environmental conditions, oyster development on breakwater reefs may be robust to large-scale disturbances caused by natural disasters, such as Hurricane Harvey. Thus, restoration managers should consider the impact of large-scale events when developing restoration projects.

Author Contributions: Conceptualization, M.H.H. and H.L.; methodology, M.H.H.; software, M.H.H.; validation, M.H.H., R.A.S.L. and S.M.; formal analysis, M.H.H. and S.M.; investigation, M.H.H., H.L., R.A.S.L., E.C.-M., R.S., N.B. and S.M.; resources, M.H.H., H.L; data curation, M.H.H.; writing—original draft preparation, M.H.H.; writing—review and editing, M.H.H., H.L., R.A.S.L., E.C.-M., R.S., N.B. and S.M. visualization, M.H.H. and S.M.; supervision, M.H.H. and H.L.; project administration, M.H.H. and H.L.; funding acquisition, M.H.H., H.L., R.A.S.L., E.C.-M., R.S., N.B. and S.M. All authors have read and agreed to the published version of the manuscript.

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