LONG-TERM ECOLOGICAL ASSESSMENT OF FAUNAL DYNAMICS AND PRODUCTION ON A LARGE RESTORED OYSTER REEF IN THE GULF OF MEXICO

A Thesis

by

ABBY ELIZABETH WILLIAMS

BS, University of Missouri, 2017

Submitted in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

in

MARINE BIOLOGY

Texas A&M University-Corpus Christi
Corpus Christi, Texas

May 2019

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This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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May 2019

ABSTRACT

Crassostrea virginica oyster reefs, which are valued for providing essential fish habitat and other ecosystem services, were historically abundant throughout the Western Atlantic and U.S. Gulf of Mexico, yet have been severely degraded throughout their native range over the past century. The potential for oyster reefs to recover lost ecosystem services is a field that requires further research, in part due to the complex food webs that oyster reefs support by way of provision of high abundances of prey resources and habitat for vulnerable life stages of many fish and invertebrates. Because the majority of oyster reef restoration experiments are small-scale, it is unclear how fisheries benefits scale up for much larger restored reefs. Better understanding is needed on whether previous experimental findings are able to translate to large-scale restoration practices to advance our knowledge of oyster reef restoration. Half Moon Reef in Matagorda Bay, TX, was a large, historically productive reef rendered functionally extinct in the early 1900s due to overharvesting. In 2013, 23 of the original 200 ha were restored, followed by 4.5 years of ecological monitoring to assess faunal development and fisheries enhancement benefits. On a seasonal basis from July 2014 to January 2019, oysters were collected by hand from the restored reef while fish and macroinvertebrate samples were collected via suction sampling and modified epibenthic sled surveys on and off the reef. These data were used to assess oyster population and faunal community dynamics, including estimates of oyster disease and augmented faunal production from the restored reef. Data were also used to develop monitoring recommendations for key restoration metrics such as oyster population dynamics, oyster disease development, and faunal community development. Oyster population growth was typical of newly restored reefs, with the highest densities of newly settled oysters immediately post-restoration. Prevalence and

severity of oyster infection by *Perkinsus marinus* were relatively low and indicative of early stage infection. After 1.5 years, faunal community composition on the restored reef was distinct from unrestored sites. Estimations of enhanced production were similar to previous studies except for stone crabs (*Menippe adina*), which were an order of magnitude higher than previous estimates (11.0 kg 10 m^{-2} y^{-1} versus 1.0 kg 10 m^{-2} y^{-1}). Because restored reefs are generally small scale and monitored over a short timeframes of 1-2 years, this study provided the unique opportunity to assess longer-term thresholds of change in faunal metrics. Results indicated that monitoring timeframes of greater than 1 year may be required to properly document oyster population dynamics, faunal community succession, and seasonal dynamics of restored reef fauna. When reservoir reefs are distant from the restored reef, it may require greater than 4.5 years to observe the full onset of *P. marinus* (Dermo) disease within the restored oyster population. This study builds on previous meta-analyses of relatively small reefs monitored for short time scales encompassing a large geographic range by calculating the per-unit-area enhanced production of a large restored reef monitored over a relatively long time scale. Resource managers planning for future restoration projects in the Gulf of Mexico, particularly with the goal of enhancing faunal production of higher trophic levels, will benefit from assessments of large-scale restoration projects.

DEDICATION

For my dad, who taught me how to study for math in elementary school, led my high school calculus study group, took day trips to my undergraduate university to help me study for stats, answered countless phone calls about R code, and so much more. Thank you.

ACKNOWLEDGEMENTS

Thank you so much to my committee members for helping me through this process. Dr. Pollack, it has been an amazing experience to learn how to be a woman in science from you every day. Dr. Grabowski, thank you for taking the time to walk me through the production portion of this study – we would have been so lost without you. Dr. Withers, thank you for teaching me about estuarine organisms; I would still be in the lab identifying my samples if it wasn't for you and your estuarine class.

Thank you to The Nature Conservancy for restoring Half Moon Reef, and for funding this project. Thank you especially to Julie Sullivan for being such a wonderful addition to our field crew, and for telling the best stories.

Thank you to my funding sources: the Constance E. Boone Grant from the Houston Conchology Society, the Gulf Estuarine Research Society student travel awards, and the Hans & Patricia Suter Endowment from the Center for Coastal Studies.

Thank you to Terry Palmer and Tasha Breaux for spending so many grueling hours in the field doing the hardest work. Terry, I have learned so much from you about what it means to be dedicated to your work. Thank you for always being the first person to offer help whenever I've struggled with something. Tasha, thank you for giving the best advice, for always being so excited to teach me new things, and for letting me talk your ear off when we're in the lab.

A huge thank you to my fellow grad students (past and present) of the Pollack lab. Meghan Martinez and Abe Margo, the two of you have been such an incredible support system and I am so grateful for your friendship. Thank you to Danielle Zimmerman, for being my first lab bench

buddy and for being so positive and encouraging through this entire experience. Thank you to Danielle Marshall for teaching me so much about Half Moon Reef and helping me to jump into this project as quickly as possible.

Thank you so much to my family for being such a solid support system. To Kyle Kopp, thank you for always believing in me; you knew I was capable even when I doubted myself. I know the last two years have not been the easiest, but thank you for sticking it out with me. Finally, to my parents Kim and Stan, and my sister Jenna, thank you for your constant love and support throughout my life and my academic career. I couldn't have done this without you.

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INTRODUCTION

Degradation of estuarine and coastal ecosystems has been substantial over the past 150 years, driven by rapid human population growth in coastal areas (Lotze et al. 2006, Jackson et al. 2001). Many ecosystems that were once intact now exist in degraded states with reduced biodiversity and resilience (Lotze et al. 2006), and have lost vast quantities of the key habitats they support. An example of this is *Crassostrea virginica*, the Eastern oyster, the global populations of which are rapidly declining (Beck et al. 2009, 2011, zu Ermgassen et al. 2012, 2013). Oyster reefs have faced exploitation dating back nearly 125,000 years, with overharvesting largely a problem over the past two centuries (Kirby 2004, zu Ermgassen et al. 2012). Shell removal from common harvesting practices such as tonging and dredging limits the cultch available for future generations (Bayne 2017), thereby impeding reef formation recovery (Breitburg et al. 2000), reducing habitat heterogeneity, and contributing to overall estuarine and coastal ecosystem degradation (Brown et al. 2013). Globally, oyster reef loss is estimated to be as much as 91% due to unsustainable harvest, habitat degradation, and disease (Jackson 2008, Beck et al. 2011). Coincident with oyster reef degradation, key ecosystem services such as habitat provisioning for fish and macroinvertebrates and increased faunal and food web diversity are also lost (Bahr & Lanier 1981, Breitburg 1999, Peterson et al. 2003, Coen et al. 2007, Grabowski et al. 2012, Nevins et al. 2014, Rezek et al. 2017, Blomberg et al. 2018).

Habitat restoration has emerged as a best management practice to combat oyster reef loss (Brown et al. 2013), with goals ranging from enhanced fisheries (Coen & Luckenbach 2000, Breitburg et al. 2000), to improved ecosystem functions (Dunn et al. 2014). Oyster restoration efforts to date generally have been relatively smaller in scale (< 0.4 ha) due to the challenges associated with restoring larger oyster reefs (e.g., lack of shell material, siting and permitting constraints, limited

funding and expensive costs associated with restoration). In addition, these experimental efforts often have been studied within short-term grant funding periods of 1—2 years (Blomberg et al. 2018, Ziegler et al. 2018). The results from larger-scale restoration projects and longer-duration monitoring periods are needed to better understand which metrics should be monitored, and over what timescales, for assessing project success (La Peyre et al. 2014). Moreover, given the scale of habitat degradation, ecosystem recovery will rely on the capacity of larger-scale restoration efforts to return lost ecosystem services.

Structured coastal habitats such as oyster reefs support enhanced abundances of small fish and macroinvertebrates compared to adjacent unstructured areas (Wells 1961, Graham et al. 2016, De Santiago et al. 2019). Using meta-analyses of small (< 1 m^2) reefs from a number of studies across a broad geographic area, recent studies have estimated augmented production of fish and macroinvertebrate species from oyster reef habitat at 2.6 kg y^{-1} per 10 m^2 of reef (Peterson et al. 2003) to 4.0 ± 1.2 kg y^{-1} for 10 m^2 of reef (zu Ermgassen et al. 2016). The current study provided the opportunity to quantify the expected enhancement of production by small fish and macroinvertebrates from a relatively large (23 ha) restored oyster reef that was monitored seasonally over a longer (4.5 year) time scale. Quantification of ecosystem services provided by habitat restoration can help improve the ability of resource managers to estimate the return on future restoration investments (Peterson & Lipcius 2003).

The overarching goal of this study is to determine the long-term dynamics of reef restoration on oyster reef fauna by (1) examining the dynamics of oyster populations and faunal community development, (2) assessing the onset and progression of *Perkinsus marinus* (Dermo) infection within the restored oyster population, and (3) estimating the augmented production of fish and macroinvertebrates from the restored reef.

METHODS

Study Site

Matagorda Bay is part of the Lavaca-Colorado Estuary, the second largest of seven estuaries along the Texas-Gulf of Mexico coastline (Moore 1907; Figure 1). Matagorda Bay has an area of 1100 km^2 and an average depth of approximately 3 meters (Kraus et al. 2000). Shoals, many associated with natural oyster reefs, are abundant throughout the eastern arm of the bay (Orlando 1993).

The Colorado and Lavaca rivers are the main sources of freshwater inflow to Matagorda Bay (Kraus et al. 2000). Historically, the Colorado River had been diverted from Matagorda Bay to the Gulf of Mexico in the late 1920's, before finally being rediverted back to Matagorda Bay in 1992 (Wilber & Bass 1998, Kraus et al. 2000). The bay is directly connected to the Gulf of Mexico through Pass Cavallo and the Matagorda Ship Channel, located in the southwest end of the bay.

Half Moon Reef was a historic, 200 ha *Crassostrea virginica* reef in Matagorda Bay that experienced collapse of oyster populations in the early 1900s due to intensive dredging that destroyed the infrastructure of the reef (Moore 1907). Moore (1915) stated one oysterman was capable of harvesting 7 barrels of oysters per day from Half Moon Reef. After many years of this unsustainable pressure, Half Moon Reef was rendered functionally extinct with no oysters remaining (Galtsoff 1931). Pre-restoration surveys revealed that the area where Half Moon Reef was once located was primarily shell hash with a lack of complex structure (De Santiago et al. 2019).

In 2013, 23 ha of historic Half Moon Reef was restored by The Nature Conservancy using approximately 18 ha of Missouri limestone and 5 ha of concrete. The reef comprises a series of 189 m wide x 1 m high rows spaced with a repeating pattern of 9 m, 18 m, and 27 m distance between rows. The surrounding bay bottom is relatively unstructured and composed of shell hash and mud.

Study Design

Field sampling occurred seasonally (January, April, July, October) from April 2014 to January 2019. Data from April 2014 to May 2015 and from July 2015 to May 2017 were previously reported by De Santiago et al. (2019) and Marshall et al. (2019), respectively. De Santiago et al. (2019) sampled paired trays of concrete and limestone at six restored (HMA-HMF) and six unrestored (CA-CF) sites and found no significant difference between the limestone and concrete substrates (Figure 1). After determining no significant difference between substrates, Marshall et al. (2019) halted sampling of limestone trays after July 2016. In October 2017, HMF was found to be filled with shell hash;therefore, sampling of HMF and CF was discontinued.

Water Quality Measurements

Water quality parameters including temperature, conductivity, dissolved oxygen, salinity, pH, and turbidity were measured at each site during each sampling event using a YSI data sonde 0.1 m below the water surface and 0.3 m above the benthos. One-liter amber bottles were used to collect bottom water at each reef site for chlorophyll-*a* analysis. Chlorophyll-*a* samples were processed using the EPA Method 445.0 (Arar & Collins 1997). Water was filtered on GF/F filters in the field, which were then placed on ice in the dark. In the laboratory, filters were placed individually into tubes with 10 mL of 90% acetone and vortexed for 30 seconds. The

tubes were refrigerated overnight for an extraction period before being vortexed again. Tubes were then centrifuged and chlorophyll-*a* measurements were determined using a fluorometer.

Reef Community Characterization

Encrusting macrofauna

At least two pieces of substrate were retrieved from each restored site (HMA to HME) by SCUBA divers during each sampling event. Encrusting fauna were identified to the lowest practical taxon and quantified in the field using a 60 cm^2 mesh to estimate percent areal coverage. The mesh was overlaid on two areas of each substrate piece determined to be representative of the reef, and percent cover was estimated using the ratio of mesh units with fauna present to total mesh units. The number of living *C. virginica* oysters was counted and the shell height of each oyster was measured. Subsequently, substrate pieces were placed back on the reef.

Reef-resident assemblages

Paired sampling trays (46 x 61 cm; 0.28 m^2) were deployed at the five restored (HMA-HME) and the five control sites (CA-CE). The restored trays were filled with concrete cobble at the restored sites and with soft sediment in the unrestored sites (150 m from reef), representative of the larger areas on and off the reef. During each sampling period, divers collected fauna from trays using a suction sampler (Honda 160cc semi-trash pump with 5.1 cm ports). Sampling alternated between the paired trays present at each site, one per sampling event, to minimize disturbance to fauna. Trays remained in position throughout the study period due to their large size and weight.

Reef-associated fauna assemblages

Reef-associated fauna were collected using a modified epibenthic sled (0.72 m wide x 0.30 m high x 0.45 m deep) towed the length of the reef (200 m), at 4 adjacent sites between reef rows (SH1-SH4, 13 m from reef) and were compared to organisms collected at 4 distant sites in unrestored areas (SC1-SC4, 150 m from reef, Figure 1). The modified epibenthic sled is a canvas-covered rectangular steel frame with a row of attached steel teeth (2.2 cm wide x 4.3 cm high, spaced 4.0 cm apart) along the front bottom edge to efficiently sample epibenthic organisms (Stunz et al. 2002). The organisms were retained in a 1 mm mesh plankton net attached to the back of the sled. Tow samples were taken quarterly from April 2014 to April 2016 before changing to biannual samples from October 2016 to April 2018. Tow samples were unable to be conducted in April 2015, and they were discontinued after April 2018.

Reef resident and reef associated faunal samples were fixed in 10% buffered formalin in the field and brought back to the laboratory where they were sorted, counted, and identified to the lowest taxonomic level possible. Dry weights of organisms were obtained by placing samples in an oven at 55 °C for at least 24 hours. Mollusk shells were removed prior to biomass measurements using 1 mol L^{-1} HCl.

Perkinsus marinus

Perkinsus marinus is a protozoan parasite that thrives in warm water and high salinity conditions and causes severe oyster mortalities in the Gulf of Mexico (Chu & Volety 1997). The proportion of oysters infected with *P. marinus* (prevalence) and the relative severity of infection (weighted prevalence) in oysters was assessed for each restored site during each sampling period. A 5 mm x 5 mm section of mantle was excised and incubated in Ray's fluid thioglycollate media and kept

in the dark for 2 weeks before being refrigerated (Ray 1966). Tissues were gently blotted dry, placed on a microscope slide, and stained with Lugol's solution. Infection intensity was scored from 0-5 using methods adapted from Mackin & Hopkins (1962) and Craig et al. (1989). The prevalence of *P. marinus* infection was calculated as the number of infected oysters per site divided by the total number of living oysters per site. Severity of *P. marinus* infection was calculated by multiplying the mean infection intensity per site by the prevalence.

Reef community statistical analysis

Community trends in associated and resident reef assemblages were examined using non-metric multidimensional scaling analysis (nMDS; Clarke and Warwick 1994) with a Bray-Curtis similarity matrix and overlays from a cluster analysis. Similarity profile analysis (SIMPROF) was used to test for significance within clusters. For reef-resident faunal communities, abundance data were log(x+1) transformed and biomass data were fourth root transformed. Abundance and biomass data were square root transformed for reef-associated faunal communities. Similarity percentage analyses (SIMPER) were used to examine taxa that were characteristic of, and different among, treatments and dates.

Hydrological data (conductivity, salinity, temperature, DO measurements, and turbidity) were log(x+1) transformed and then were normalized along with pH and examined using a Principle Component Analysis (PCA). A BIO-ENV was used to examine the relationship between the hydrological and faunal data by calculating dissimilarity between physical and biological data using Spearman rank correlations (Clarke & Ainsworth 1993, Clarke et al. 2008). PRIMER v6 was used for all multivariate community analyses (Clarke & Garley 2006).

Effects of date and treatment on faunal density, species richness, diversity, and biomass were tested using separate two-way ANOVAs. Effects of date on oyster density, size, and areal coverage were tested using one-way ANOVAs. Data normality was assessed using the Shapiro-Wilk normality test. Homogeneity of variance was examined using a residuals vs. fitted plot with Breusch-Pagan and Brown-Forsythe tests. To meet ANOVA assumptions for normality, reef resident Hill's N1 diversity was log(x+1) transformed. Reef resident and reef associated species richness along with reef associated Hill's N1 diversity did not require transformations. Tukey's multiple comparison tests were used to examine data for potential differences in treatment and date where significant. For response variables where transformation for normality was not possible, non-parametric Kruskal-Wallis tests were used to examine any significant relationships. R version 3.4.3 was used to calculate all univariate statistical analyses (R Foundation for Statistical Computing 2017).

Oyster Reef Augmentation of Fish and Mobile Invertebrate Productivity

To estimate fish and invertebrate production augmented by the restored reef, a modification of methods from Peterson et al. (2003) and zu Ermgassen et al. (2016) were used. First, organisms were identified whose recruitment was considered to be enhanced by the oyster reef. This was achieved by ensuring the density of the species was greater on the restored reef than in the unrestored areas, and by the species being more abundant on the restored reef than in the unrestored areas in more than half of the sampling events. Life history information was then examined to determine obligate association with structured benthic habitat. Species which met these criteria were *Petrolisthes* sp. porcelain crabs, *Panopeus herbstii* mud crabs, *Alpheus heterochaelis* snapping shrimp, Xanthoidea mud crabs, *Gobiesox strumosus* skilletfish, *Hypsoblennius hentz* feather blennies, *Opsanus beta* toadfish, and *Menippe adina* stone crabs.

Selected species were separated into three categories: primary and secondary consumers (*Petrolisthes* sp., *P. herbstii*, *A. heterochaelis*, and Xanthoidea), annual tertiary consumers (*G. strumosus* and *H. hentz*), and tertiary consumers with lifespans greater than one year (*O. beta* and *M. adina*). For primary and secondary consumers, augmented biomass was calculated by taking the difference in biomass between the restored reef sites and the control soft sediment sites. Enhanced production for annual and long-lived tertiary consumers utilized an estimate of density enhancement, calculated by taking the difference in density between restored reef sites and control soft sediment sites. To calculate enhanced production for annual species, the estimate of density enhancement was multiplied by the average biomass of that species. For long-lived species, enhanced production was calculated using life tables with the estimate of density enhancement. Life tables were species-specific for stone crabs (*M. adina*) and toadfish (*O. beta*); sex ratios were assumed to be 50/50.

S_i, the proportion of individuals i-1 surviving to age class i, with M being the mortality rate for age class i, was calculated using the formula:

$$\boldsymbol{S_i = S_0 \times e^{(-M_i \times i)}}$$

S_{x_i}, the survival rate for age class i, was calculated using the formula:

$$\boldsymbol{S_{x_i} = S_i / S_{(i-1)}}$$

N_i, the estimated augmented density, was multiplied by S_{x_i} for each age class.

$$\boldsymbol{N_i = N_{(i-1)} \times S_{x_i}}$$

Next, the von Bertalanffy growth equation was utilized to calculate the average individual length of each age class *i*. L_∞ is the asymptotic maximum length, *K* is the Brody growth coefficient, and t_0 is the age at length 0.

$$\boldsymbol{L_i = L_\infty \times \left\{1 - e^{[-K \times (i - t_0)]}\right\}}$$

L_i is then converted to weight W_i using the length-weight relationship formula, where a and b are constants found in the literature:

$$\boldsymbol{W_i = a \times L_i^b}$$

The annual production per individual of age class *i* is calculated using the change in weight as age class progresses.

$$\boldsymbol{P_i = W_i - W_{(i-1)}}$$

Finally, the annual production of age class *i* is calculated by multiplying the annual production per individual age class P_i by the estimate of density enhancement N_i.

$$\boldsymbol{P_y = N_i \times P_i}$$

Graphical representations of enhanced production were created using the cumulative sum of the total annual production reaching a steady state as the populations mature and the birth and death rates reach equilibrium (zu Ermgassen et al. 2016).

RESULTS

Water Quality Measurements

Salinity fluctuated widely over the course of the study, ranging from 6.9 ± 2.0 (mean ± standard error) in October 2018 to 31.2 ± 0.0 in October 2014 (Figure 2A). Salinity was influenced by seasonal precipitation fluctuations and was typically higher in the winter and lower in the spring and summer, with greater variation in the fall. A halocline was present in October 2018 and January 2019; the top and bottom salinities were 0.9 ± 0.2 and 16.8 ± 2.3 and 1.9 ± 0.2 and 19.8 ± 1.9, respectively. Dissolved oxygen concentrations (mg L^{-1}) ranged from 4.7 ± 0.0 mg L^{-1} in July 2014 to 10.8 ± 0.0 mg L^{-1} in January 2018 and were inversely related to temperature, which fluctuated from 12.0 ± 0.1 ºC in January 2018 to 30.9 ± 0.2 ºC in July 2017 (Figure 2B; Figure 2C). The pH levels were fairly stable, ranging from 8.0 ± 0.0 in February 2017 to 8.7 ± 0.0 in July 2014 (Figure 2D). Turbidity ranged from 1.8 ± 0.5 NTU in January 2018 to 54.7 ± 5.6 NTU in April 2017 (Figure 2E). Chlorophyll-*a* concentrations ranged from 1.6 ± 0.4 µg L^{-1} in April 2016 to a peak of 40.7 ± 2.1 µg L^{-1} in April 2017 (Figure 2F).

Water quality parameters were merged using Principal Component Analysis (PCA; Figure 3; Appendices

Appendix ***1***). The first and second principal components (PC1 and PC2) explained 33.2% and 25.9% of the variation in the data set, respectively (total 59.2%). Temperature had the strongest negative correlation with PC1, opposite of dissolved oxygen (mg L^{-1}), which had the strongest positive correlation with PC1. Turbidity and chlorophyll-*a* had the strongest positive correlations with PC2 while salinity had the strongest negative correlation with PC2. Turbidity and

chlorophyll-*a* were grouped on PC2, as were salinity and pH. Temperature and dissolved oxygen had no significant correlation with PC2.

Reef Community Characterization

Encrusting macrofauna

Average percent areal coverage of substrate by oysters gradually increased between July 2014 and April 2018, before sharply decreasing during the subsequent two sampling events (Figure 4A). Average oyster percent cover ranged from 22.5% ± 2.9 in October 2018 to 100% ± 0.0 in April 2018. Average overall oyster percent cover was 48.9% ± 1.7. Average oyster percent cover differed by date ($p<0.0001$; Appendix 5) Average oyster abundance also differed by date ($p<0.0001$; Appendix 4) and declined steadily throughout the study (July 2014) to the last sampling date in January 2019. Average oyster abundance ranged from a maximum 2627.9 ± 247.2 oysters m^{-2} in July 2014 to a minimum of 66.7 ± 0.0 oysters m^{-2} in October 2018 (Figure 4B). Overall, average oyster abundance was 793.8 ± 48.7 oysters m^{-2}. Average market oyster size was 98.7 ± 1.0 mm, average sub-market oyster size was 46.2 ± 0.7 mm, and average oyster spat size was 14.4 ± 0.1 mm. Average adult oyster size ranged from 79.9 ± 0.0 mm in January 2015 to 116.5 ± 7.3 mm in January 2019 (Figure 4B). Average sub-market oyster size ranged from 27.8 ± 0.5 mm in July 2014 to 69.5 ± 2.2 mm in October 2017. Average oyster spat size ranged from 7.1 ± 1.0 mm in July 2016 to 25.7 ± 0.0 mm in February 2017. Average overall oyster size ranged from 13.5 ± 0.1 mm in July 2014 to 94.7 ± 4.5 mm in July 2017.

Perkinsus marinus infection

Infection of oysters by *P. marinus* was variable on Half Moon Reef. Infection was first observed with low prevalence ~3 months post-restoration (8.3%), in January 2015 and again in July 2015

(2.4%; Figure 5A). Infection was not observed again until October 2017 (68.1%), disappeared by July 2018, and then reappeared in the following sampling period, October 2018 at 73.3%. In January 2019, prevalence was 3.3%. Weighted prevalence of *P. marinus* infection remained low throughout the study, at or near zero for the first three years post-restoration (Figure 5B). Weighted prevalence increased to 0.6 in October 2017 before declining back down to zero July 2018 and then increasing again the following sampling period. Weighted prevalence was 0.0 in January 2019.

In sampling events where *P. marinus* was present, the parasite exhibited an aggregated distribution within the Half Moon Reef oyster population. When infection intensity was averaged by date, 45.7% of oysters were not found to be infected while another 21.0% of oysters had infection intensities less than 0.67 (Figure 6A). When averaged by date and site, 26.3% of oysters were not infected and 18.5% of oysters had intensities less than 0.67 (Figure 6B).

Reef-resident community

Faunal abundance of resident species was generally higher on the restored reef than in unrestored areas. In general, faunal abundances were highest and demonstrated the greatest variability between sampling dates immediately following restoration. Reef-resident faunal abundance differed within treatment-date combinations ($p<0.001$; Appendix 6). High (> 1000 individuals in restored sites and ~2000 individuals in unrestored sites) resident faunal abundance was observed in both the restored and unrestored sites immediately following the restoration of the reef (Figure 7A). Resident fauna on the unrestored sites peaked in May 2015 due to a pulse in *Astyris* sp. dove snails. Average resident faunal abundance was 531.2 ± 115.7 individuals m^{-2} in the restored sites and 523.0 ± 145.7 individuals m^{-2} in the unrestored sites. Resident faunal abundance in the

restored sites ranged from an average of 148.5 ± 30.7 individuals m^{-2} in July 2015 to 1317.4 ± 350.3 individuals m^{-2} in July 2014 (immediately post-restoration). In the unrestored sites, resident faunal abundance ranged from an average of 16.6 ± 4.5 individuals m^{-2} in July 2015 to an average 3340.0 ± 991.4 individuals m^{-2} May 2015. The highest abundances in the restored sites occurred in the summer. The greatest contributors to abundance in the restored sites were *Petrolisthes* sp. porcelain crabs, while small *Astyris* sp. and *Parvanachis ostreicola* snails contributed to the majority of unrestored faunal abundance.

Reef-resident faunal biomass did not follow the same pattern as resident faunal abundance. Biomass on soft-sediment controls remained low throughout the duration of this project, while restored reef resident biomass was generally much greater, especially in winter samples (Figure 7B). Resident faunal biomass differed by treatment-date combinations ($p<0.001$; Appendix 9) and was greatest at restored sites. Average resident faunal biomass was 17.7 ± 8.0 g m^{-2} in the restored sites and 1.6 ± 0.8 g m^{-2} in the unrestored sites. Biomass in the unrestored sites remained consistently low (from average 0.4 ± 0.2 g m^{-2} in February 2017 to 3.0 ± 1.4 g m^{-2} in July 2015), whereas biomass in the restored sites was highly variable, (from average 3.0 ± 0.9 g m^{-2} in July 2015 to 77.9 ± 35.8 g m^{-2} in January 2016) with several peaks in biomass observed in winter samples attributed to the presence of large adult stone crabs (*Menippe adina*).

Similar to patterns observed with faunal abundance, richness was greatest in both the restored and unrestored sites immediately after restoration, with no clear pattern among seasons (Figure 8B). In contrast to species richness, N1 diversity was influenced by date and treatment with no discernable trend over the course of the study. From this, it is possible to infer that there were similar numbers of species in both treatments, but a few species consistently dominated in the restored sites while there was generally a more even species distribution in the unrestored sites

(Figure 8A). Species richness differed by date ($p<0.001$; Appendix 7) but not treatment. Average species richness was 8.2 ± 0.8 species in the restored sites and 7.8 ± 1.0 species in the unrestored sites. Species richness in the restored sites ranged from an average of 4.8 ± 0.5 species in July 2015 to 13.3 ± 0.6 species in July 2014. In the unrestored sites, richness ranged from an average of 2.8 ± 0.7 species in July 2015 to 13.3 ± 5.4 species in October 2014. Hill's N1 diversity differed by combinations of both date and treatment ($p<0.001$; Appendix 8). Diversity was highest on restored sites immediately post-restoration while simultaneously being much lower in the unrestored sites (Figure 8C). Average Hill's N1 diversity was 3.8 ± 0.4 in the restored sites and 4.2 ± 0.6 in the unrestored sites. Average N1 diversity on the restored sites ranged from 2.4 ± 0.2 in July 2015 to 5.9 ± 0.5 in July 2014. On the unrestored sites, average N1 diversity ranged from 2.5 ± 0.4 in October 2017 to 6.8 ± 1.7 in April 2018.

Abundances of resident faunal communities separated into six main groups at 55% similarity ($p<0.05$; Figure 9A). Community composition at restored sites was similar to that at unrestored sites during early reef development (2014-15) and became more distinct 1 year post-restoration. Differences in abundance-based community composition were largely driven by *Petrolisthes* sp., *Panopeus herbstii* and other Xanthoidea crabs in the restored sites, and *Astyris* sp., *P. ostreicola*, and *Petrolisthes* sp. at unrestored sites (Appendix 14). There was no significant relationship between environmental data and resident faunal abundance data in the BIOENV analysis using Spearman correlations (Appendix 2).

Biomass of resident faunal communities separated into four main clusters at 50% similarity ($p<0.05$; Figure 9B). Similar to the abundance-based results, community biomass was similar between restored and unrestored sites until 1-year post-restoration. Differences in community composition using biomass were largely driven by *Petrolisthes* sp., *M. adina*, and *P. herbstii* at

restored sites and *Petrolisthes* sp. and *Asytris* sp. at unrestored sites (Appendix 15). Temperature and chlorophyll-*a* had the strongest correlation with resident faunal biomass in the BIOENV analysis using Spearman correlations (rho=0.203, $p<0.05$; Appendix 3).

Reef-associated community

Compared to resident fauna collected in sampling trays, abundance of reef-associated fauna collected in epibenthic sled tows were generally 1 – 2 orders of magnitude less. In contrast to resident fauna, associated faunal abundance was not measurably higher immediately post-restoration. Reef-associated faunal abundance differed by date ($p<0.001$; Appendix 10) but not treatment. Abundance was generally highest in the spring and was overall much less than that of reef- residents (Figure 10A). Faunal abundance from adjacent (13 m from reef) tow samples ranged from 0.1 ± 0.0 individuals m^{-2} in July 2015 to 14.0 ± 7.7 individuals m^{-2} in April 2016. Abundance in distant (150 m from reef) samples ranged from 0.0 ± 0.0 individuals m^{-2} in July 2015 to 27.6 ± 15.9 individuals m^{-2} in April 2016. Average abundance was 3.4 ± 1.6 individuals m^{-2} in the adjacent samples and 4.7 ± 2.5 individuals m^{-2} in the distant samples. Overall, abundance patterns were primarily driven by changes in the number of mysid shrimp in both treatments (Appendix 16).

Species richness of associated fauna was highest in the 5 months following restoration, and in this time period was much higher than species richness of resident fauna. In the months prior to July 2015, species richness declined to similar levels in both the associated and resident faunal communities. Species richness for reef-associated fauna differed by date ($p<0.001$; Appendix 11) but not treatment. Similar to species richness, associated faunal diversity was highest until 5 months post-restoration before declining to levels below resident faunal abundance. N1 diversity

differed within treatment-date combinations ($p<0.001$; Appendix 12). Average species richness was 11.4 ± 1.6 species at the adjacent sites and 4.7 ± 1.6 species at the distant sites. Richness varied over the course of the study and ranged from 3.0 ± 1.5 species in July 2015 to 24.0 ± 1.7 species in July 2014 at adjacent sites, and from 1.5 ± 0.5 species in July 2015 to 25.8 ± 3.1 species in April 2014 at distant sites (Figure 10B). Average Hill's N1 diversity was 3.6 ± 0.6 at the adjacent sites and 3.4 ± 0.5 at the distant sites. Diversity also varied throughout the study period and ranged from 1.3 ± 0.1 in July 2015 to 8.3 ± 1.1 in April 2014 at adjacent sites and from 1.2 ± 0.2 in July 2015 to 7.8 ± 0.6 in April 2014 at distant sites (Figure 10C).

Biomass of associated fauna was greatest immediately following restoration before decreasing by about 40 mg m^{-2} by July 2014, following patterns similar to species richness and diversity. After this decrease, associated faunal biomass followed an observable seasonal pattern similar to resident faunal biomass, despite resident biomass being 3-5 magnitudes greater. Species contributing the most to associated faunal biomass include juvenile *Callinectes sapidus* crabs and *Busycon sinistrum* snails, which were much smaller species than those contributing the most to reef-resident biomass. Reef-associated faunal biomass also differed by date ($p<0.001$; Appendix 13). Biomass at the adjacent and distant sites varied in a similar way, with peaks occurring most often in the winter (Figure 10D). Average biomass of reef-associated fauna was 7.4 ± 2.8 mg m^{-2} at the adjacent sites, and 7.9 ± 3.5 mg m^{-2} at the distant sites. Biomass of reef-associated fauna collected from epibenthic sled tows was much lower than that of reef residents and ranged from 0.2 ± 0.1 mg m^{-2} in October 2016 to 43.1 ± 6.3 mg m^{-2} in April 2014 at adjacent sites and from 0.0 ± 0.0 mg m^{-2} in July 2015 to 39.2 ± 17.8 mg m^{-2} in April 2014 at distant sites. Changes in overall biomass were primarily driven by changes in Mysidacea biomass for both treatments (Appendix 17).

Abundance-based reef-associated faunal communities separated into four main groups at 40% similarity ($p<0.05$; Figure 11A). Community composition was more similar by date than by treatment. Biomass-based community composition separated into two main clusters at 25% similarity, with no clear separation due to treatment or date ($p<0.05$; Figure 11B).

Productivity Enhancement

Nine species of fish and crustaceans were identified, the productivity of which is enhanced by the reef (Table 5). Five of those species were crustaceans we considered to be primary or secondary consumers (*Alpheus heterochaelis*, *Eurypanopeus* sp., *P. herbstii*, *Petrolisthes* sp., and other miscellaneous Xanthoidea mud crabs). Two fish that are tertiary consumers with annual lifespans (*Gobiesox strumosus* and *Hypsoblennius hentz*) and two species of long-lived tertiary consumers (*O. beta* and *M. adina*) were also determined to be enhanced by the reef.

For the primary and secondary consumers, average augmented biomass (g 10 m^{-2}) was calculated. The augmented biomass of these low trophic status consumers ranged from 4.0 g 10 m^{-2} (miscellaneous Xanthoidea crabs) to 26.9 g 10 m^{-2} (*Petrolisthes* sp.). Estimates of augmented production from tertiary species were substantial. Average enhanced production (kg 10 m^{-2}) for annual tertiary species *G. strumosus* and *H. hentz* was 0.1 kg 10 m^{-2} and 1.8 kg 10 m^{-2}, respectively. Meanwhile, augmented productivity of both long-lived species increased rapidly initially before reaching a carrying capacity (Figure 12). For *O. beta*, enhanced productivity begins close to 0.1 kg 10 m^{-2} y^{-1} in 2014, before reaching carrying capacity around 2020 at 2.5 kg 10 m^{-2} y^{-1}. *Menippe adina* begins at 1.3 kg 10 m^{-2} y^{-1} in 2014 before arriving at carrying capacity around 2019 at 11.0 kg 10 m^{-2} y^{-1}. Enhanced productivity for both species is assumed to remain oscillating at or around carrying capacity unless influenced by random events.

DISCUSSION

Effects of Restoration

Post-restoration monitoring is critical to understanding the establishment, evolution, and dynamics of the associated communities of restored habitats. Unfortunately, less than one-quarter of oyster reef restoration projects in the Gulf of Mexico and less than 40% of projects in the Chesapeake Bay have been monitored (NASEM 2017). In addition, individual oyster reef restoration projects frequently occur within short-term grant funding periods of 1—2 years (EOBRT 2007). Information from longer-term, continually monitored projects is incredibly important for improved assessment of restoration efforts (Kennedy et al. 2011) and increased understanding of regional drivers of local restoration outcomes such as climate change and extreme weather events (NASEM 2017). Results of long-term monitoring can also support adaptive resource management (La Peyre et al. 2014); indicating whether restoration investments are providing anticipated benefits to ecosystems and society. By examining a large-scale restoration project using consistent sampling methods with seasonal monitoring over a relatively long (4.5 years) monitoring duration, this study provides new insights into the dynamics of restored reef fauna.

After 1.5 years, the restored reef shifted from an oyster population dominated by many small oysters to a population of relatively few large oysters, which remained consistent for the remainder of the 4.5-year study period. Results indicate that monitoring periods of >1 year may be required to capture oyster population stability—a relatively longer time period than included in most oyster reef monitoring programs to date (Blomberg et al. 2018, Zeigler et al. 2018). This high mortality rate appears to be density-dependent and is characteristic of newly recruited oysters (Knights & Walters 2010). Juvenile oysters are very susceptible to predation, particularly

by some decapod crustaceans that were found in large densities (e.g., mud and stone crabs; Gosselin & Qian 1997), which likely contributed to post-settlement oyster mortality. Areal coverage of restoration substrates by oysters continued to increase until salinities dropped in October 2018, coincident with an increase in freshwater inflow. Oyster abundances and settlement dynamics can be temporarily affected by low salinity events in Gulf of Mexico estuaries (Pollack et al. 2010, La Peyre et al. 2009). Results indicate that monitoring of oyster areal coverage should continue to occur beyond 4 years post-restoration, or within a period that encompasses both wet and dry years at the restored site.

Perkinsus marinus infection in oyster populations is related to salinity and temperature; at low salinities and low temperature, infection prevalence and intensity decrease (Craig et al. 1989, La Peyre et al. 2003). In the current study, reduced salinity in October 2018 corresponded with an absence of *P. marinus* from oyster samples. However, because Half Moon Reef is relatively isolated (~1-10 km) from natural oyster populations, disease dynamics may have been influenced more by a lack of nearby hosts to maintain the infection, regardless of environmental conditions (Wright & Gompper 2005, Gompper & Williams 1998). *Perkinsus marinus* infection increases as oysters age (Paynter et al. 2010), as seen on Half Moon Reef where prevalence and severity increased approximately three years after restoration. The extremely variable prevalence and severity of *P. marinus* infection is indicative of *P. marinus* infection not yet being well established in the restored oyster population on Half Moon Reef. The average severity of infection on Half Moon Reef was much lower than the proportion of infected individuals, such that the majority of infected individuals have low underlying levels of infection and very few individuals had more severe infections, supporting previous studies indicating the majority of individual parasites are aggregated within a small percentage of hosts (May & Anderson 1978,

Ford et al. 1999). Results indicate that to be able to study the full development of *P. marinus* infection on reefs that are relatively isolated from infected host populations, >4.5 years of monitoring may be needed, and that most post-restoration monitoring projects do not have the longevity required. Due to the presence of *P. marinus* on reefs throughout Matagorda Bay and the Gulf of Mexico (Craig et al. 1989, La Peyre et al. 2009, Powell 2017, Soniat & Ray 2018), it is likely the parasite will continue to persist on Half Moon Reef, however continued regular flushing may serve to moderate infection within the oyster population (Pollack et al. 2010).

Resident faunal communities were similar between restored and unrestored habitats until 9 months post-restoration, indicating monitoring durations of 1 year or greater may be needed to observe faunal community succession on restored reefs. As oysters increased in size, the restored reef became more structurally complex and the faunal communities became less similar, supporting previous studies demonstrating that oyster reefs support distinct macrofaunal assemblages compared to other estuarine habitat types (Stunz et al. 2010, Nevins et al. 2014). Early similarities between faunal communities in restored and unrestored sites may have been due to opportunistic species from the unrestored sites colonizing the reef before more reef-dependent species became established. Indeed, colonization of over-dredged oyster reefs depends on the amount of time since the reef was disturbed and the distance between the study site and a source of colonizers (Cranfield et al. 2004). Half Moon Reef has exhibited rapid development of habitat complexity post-restoration compared to similar studies (Cranfield et al. 2004), with rapid oyster population development facilitating the development of unique macrofaunal community (De Santiago et al. 2019).

While differences in overall faunal biomass were influenced by both treatment and date, reef-resident faunal biomass was influenced by season (BIO-ENV), indicating that monitoring

periods of >1 year may be needed to fully understand seasonal dynamics of restored reef fauna. Seasonal influences on faunal biomass are likely due to seasonal recruitment patterns and seasonal environmental changes influencing food resource availability (Tolley & Volety 2005). In the current study, seasonal peaks of biomass were driven by stone crabs (*M. adina*), a species that resides on oyster reefs (zu Ermgassen et al. 2016). Whereas decapods (larger, heavier individuals) dominated in restored sites, a mix of gastropods (smaller, lighter individuals) and some smaller decapods dominated in unrestored sites, supporting previous studies showing decapods to be much more abundant on oyster reefs than in surrounding unstructured muddy habitat (Bahr & Lanier 1981, Zimmerman et al. 1989, Plunket & La Peyre 2005, Rodney & Paynter 2006).

Enhanced productivity and biomass of reef-resident fish and motile crustaceans resulting from restoration benefits larger resident or transient species that may utilize the reef as nursery or foraging habitat (Harding & Mann 2003, Peterson et al. 2003, McCoy et al. 2017). Indeed, in a concurrent study on Half Moon Reef, residency of spotted seatrout (*Cynoscion nebulosus*) increased with fish size, a pattern attributed to shifts in foraging behavior (TinHan et al. 2018). Mud crabs and porcelain crabs—the most abundant macroinvertebrates at Half Moon Reef – are important links to higher trophic levels (Yeager & Layman 2011). Additional research is needed to determine how enhancement of important prey species provides long-term foraging benefits to recreationally and commercially important fish species with known reef associations (Peterson et al. 2003, zu Ermgassen et al. 2016) such as red drum *Sciaenops ocellatus* and southern flounder *Paralichthys lethostigma*.

Compared to previous estimates of restoration-produced faunal enhancement, calculated from meta-analyses (Peterson et al. 2003, zu Ermgassen et al. 2016), only the estimates of enhanced

productivity of gulf stone crabs (*M. adina*) were dissimilar. Both papers estimated average enhanced productivity for stone crabs at less than 1.0 kg 10 m^{-2} y^{-1}, while conservative estimates from this study estimated enhanced productivity of stone crabs at about 11.0 kg 10 m^{-2} y^{-1}. These results support the concept of regional specificity of production enhancement, and in particular the assertion that crustaceans are more greatly enhanced by oyster reefs in the Gulf of Mexico than in the US Atlantic (zu Ermgassen et al. 2016). Quantifying regionally-specific production enhancement for economically important species such as for stone crabs is important for resource managers or restoration practitioners aiming to improve fishery production through restoration approaches.

The ability to calculate the value of ecosystem services provided by oyster reefs is invaluable for determining the scope of restoration and the amount of money stakeholders are willing to invest in restoration (Grabowski et al. 2012). Combining fishery landing values with enhanced production estimates (Grabowski & Peterson 2007) can provide coarse estimates of the value of oyster reefs as habitat for fish and crustaceans. When scaled up to 23 ha and only including the 4 tertiary species utilized for this study, it is estimated the entirety of restored Half Moon Reef could support 356,500 kg of enhanced fishery production per year relative to the unrestored bay bottom at its maximum potential.

The necessity of long-term studies to better understand the development of communities on oyster reefs has long been recognized (Coen & Luckenbach 2000). This project provided the unique opportunity to assess long-term development and dynamics of faunal communities of a large-scale restored oyster reef in the Gulf of Mexico and to provide recommendations of appropriate monitoring timelines for common ecological metrics. Results support previous estimates of enhanced faunal production determined from meta-analyses of small-scale reefs

monitored over short time periods, and demonstrate that crustacean enhancement is relatively greater in the Gulf of Mexico as compared to the US Atlantic. This study demonstrated the importance of continuing to study highly productive reefs in the Gulf of Mexico due to the observed differences between productivity levels in the Gulf of Mexico and the US Atlantic. Information acquired from this study can be used to inform resource managers in future restoration planning, in particular in predicting enhancement benefits generated by reef restoration for resident fish and motile macrofauna, and those effects on large transient fish species.

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1

FIGURES

Figure 1

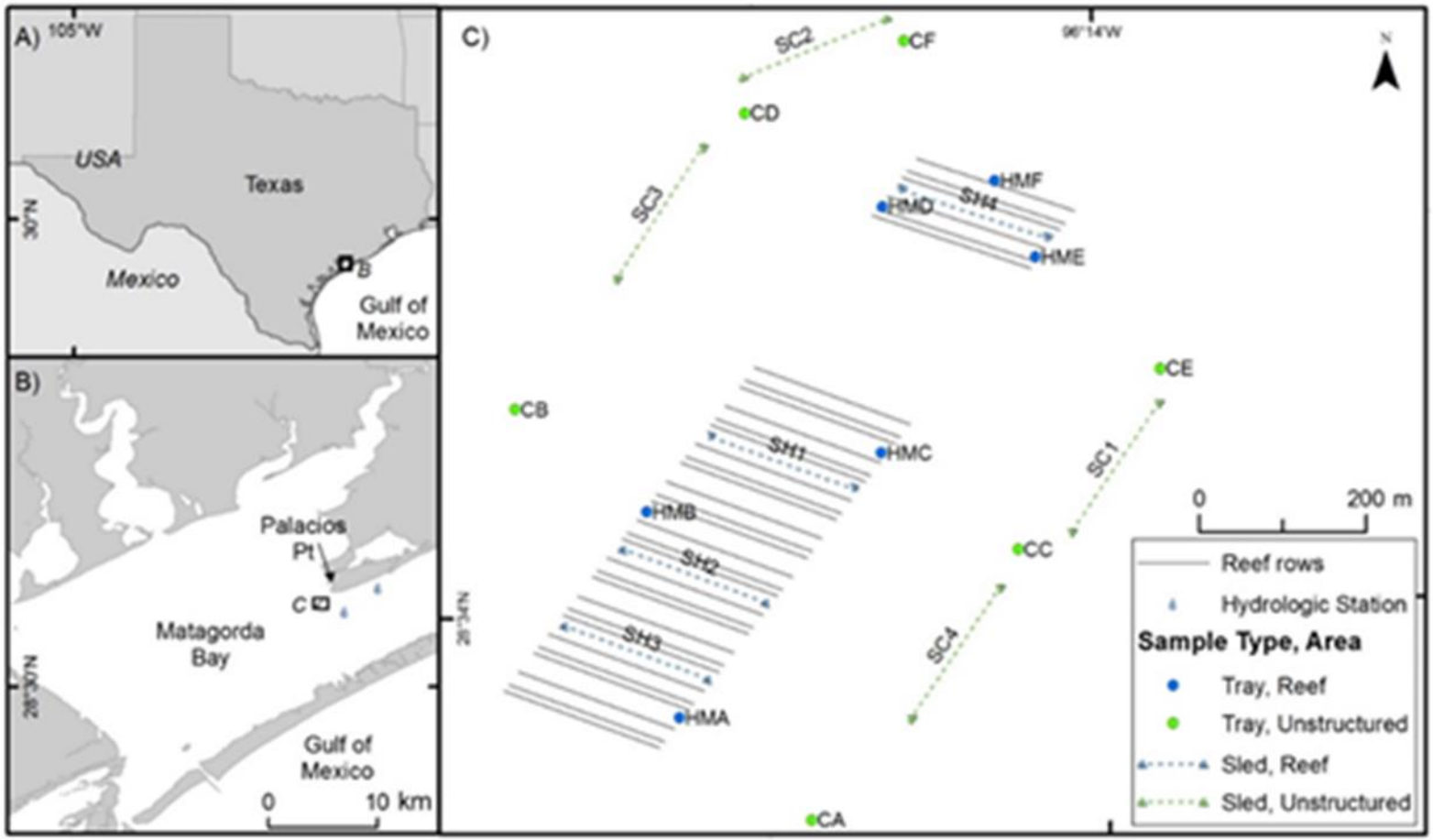


Figure 2

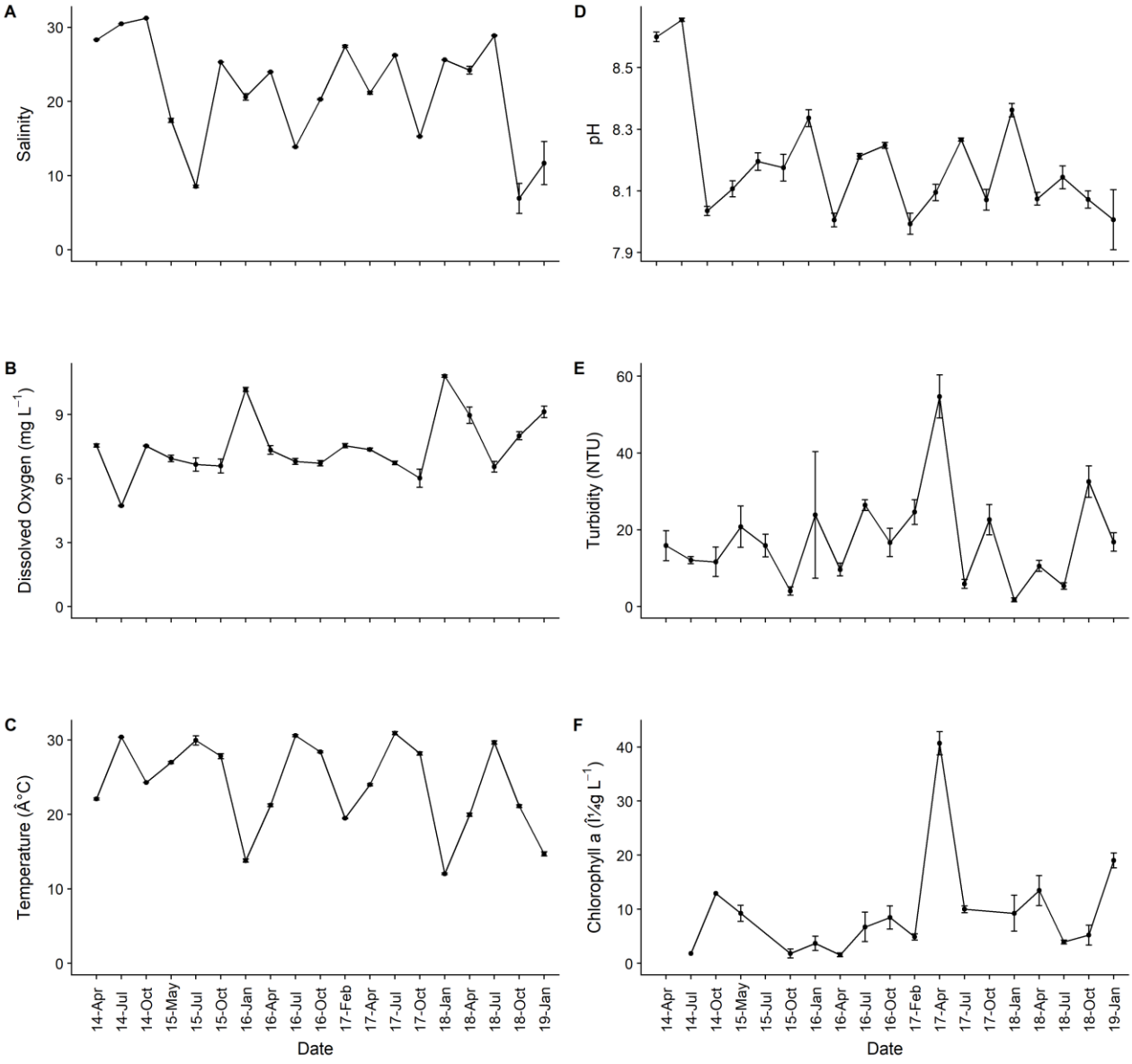

A
Salinity
30
20
10
0
D
pH
8.5
8.3
8.1
7.9
B
Dissolved Oxygen (mg L^{-1})
9
6
3
0
E
Turbidity (NTU)
60
40
20
0
C
Temperature (Â°C)
30
20
10
0
F
Chlorophyll a (Î¼g L^{-1})
40
30
20
10
0
14-Apr
14-Jul
14-Oct
15-May
15-Jul
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-Apr
17-Jul
17-Oct
18-Jan
18-Apr
18-Jul
18-Oct
19-Jan
Date

Figure 3

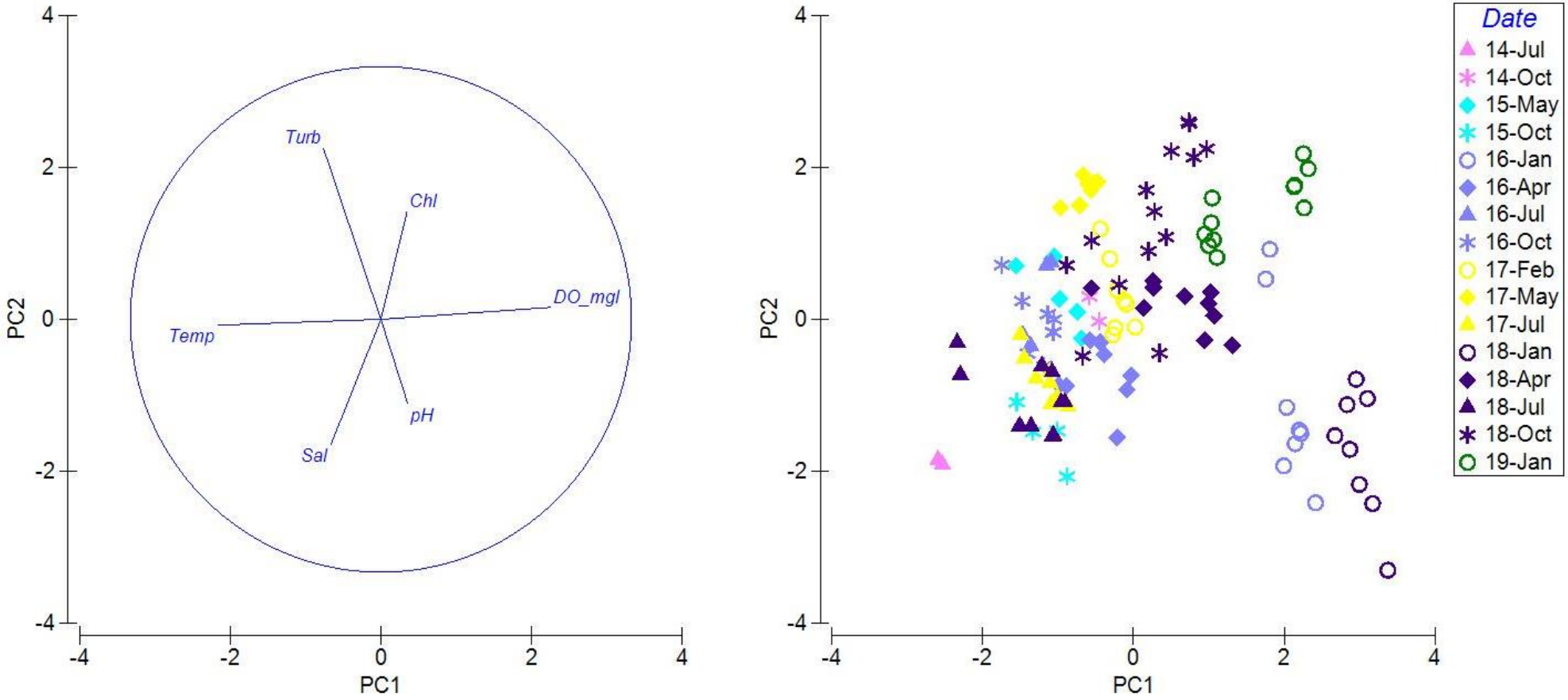

Turb
Chl
DO_mgl
Temp
pH
Sal
PC1
PC2
Date
14-Jul
14-Oct
15-May
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-May
17-Jul
18-Jan
18-Apr
18-Jul
18-Oct
19-Jan

Figure 4

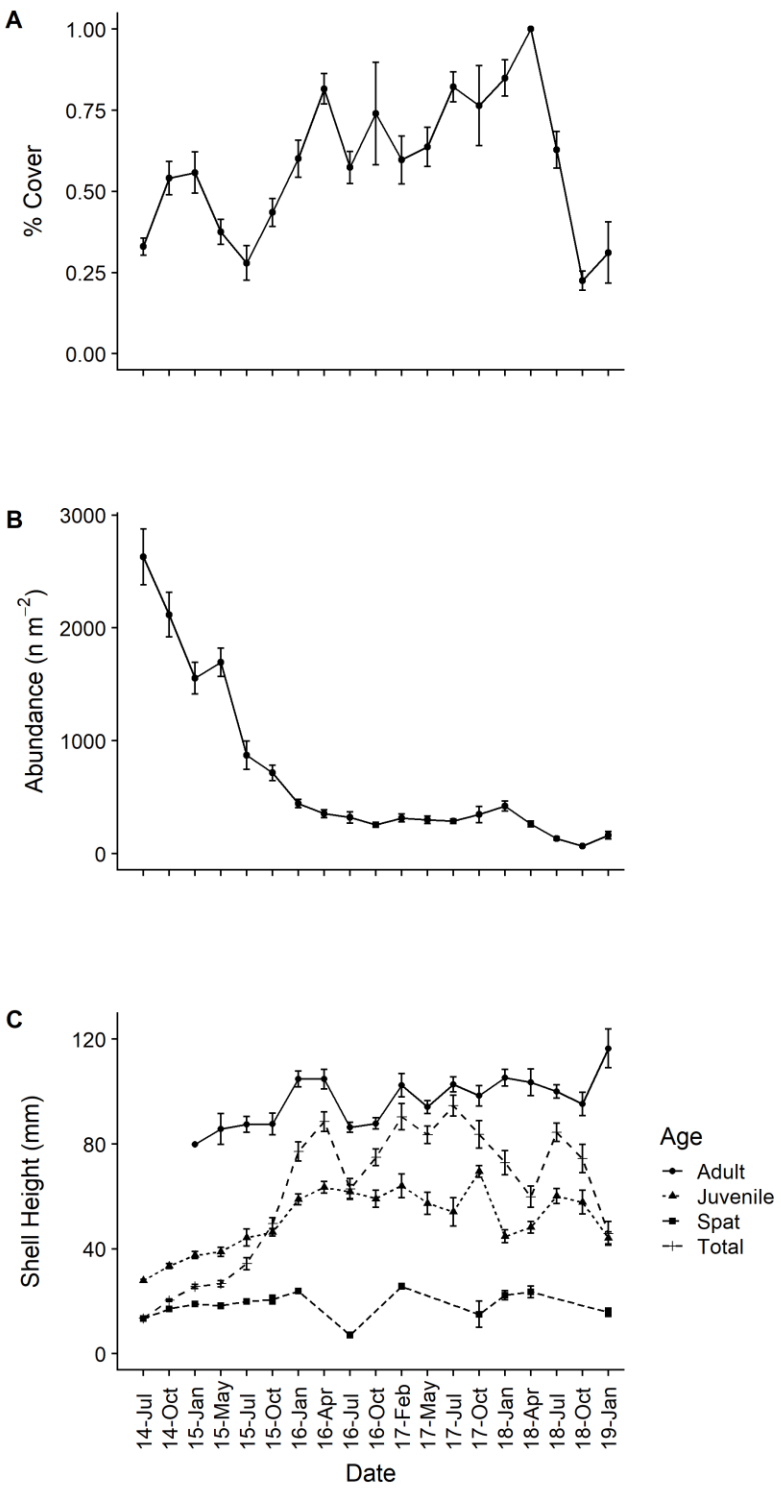

A
% Cover
1.00
0.75
0.50
0.25
0.00
B
Abundance (n m^{-2})
3000
2000
1000
0
C
Shell Height (mm)
120
80
40
0
14-Jul
14-Oct
15-Jan
15-May
15-Jul
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-May
17-Jul
17-Oct
18-Jan
18-Apr
18-Jul
18-Oct
19-Jan
Date
Age
Adult
Juvenile
Spat
Total

Figure 5

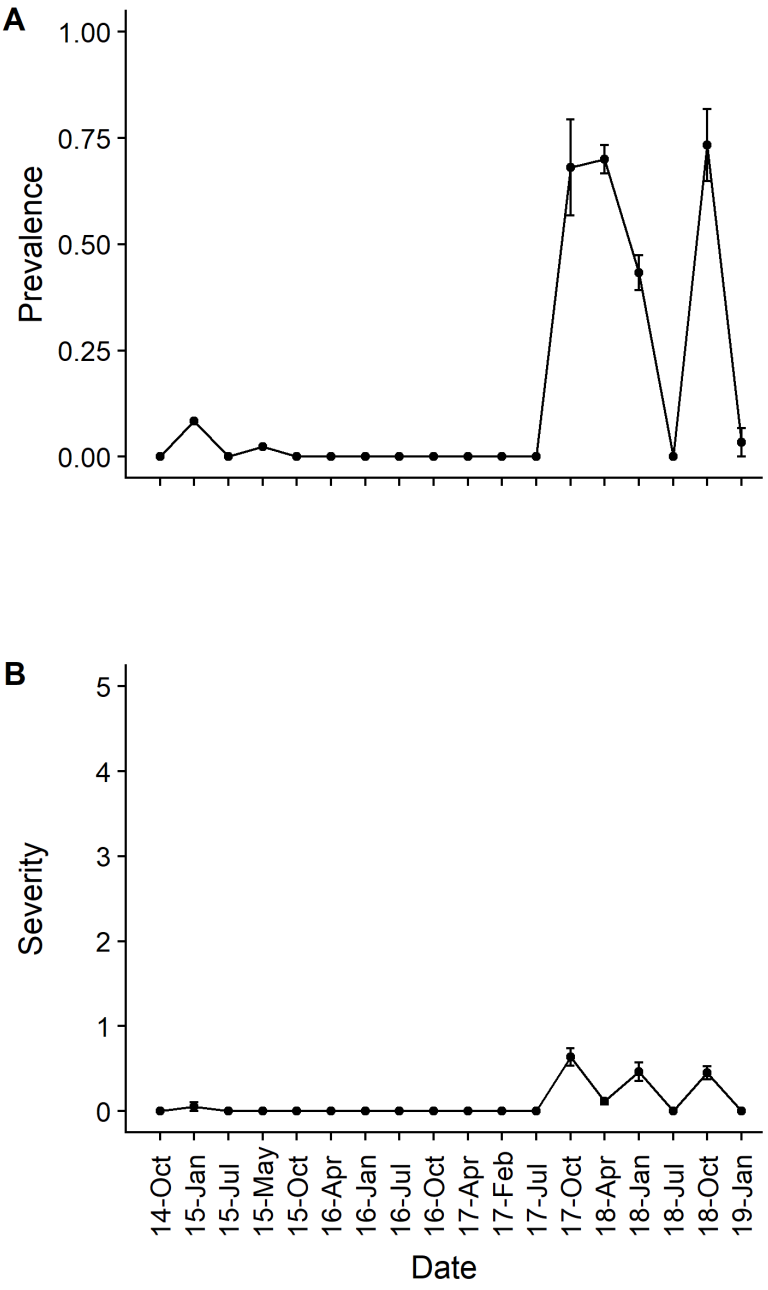

A
1.00
0.75
0.50
0.25
0.00
Prevalence
B
5
4
3
2
1
0
Severity
14-Oct
15-Jan
15-Jul
15-May
15-Oct
16-Apr
16-Jan
16-Jul
16-Oct
17-Apr
17-Feb
17-Jul
17-Oct
18-Apr
18-Jan
18-Jul
18-Oct
19-Jan
Date

Figure 6

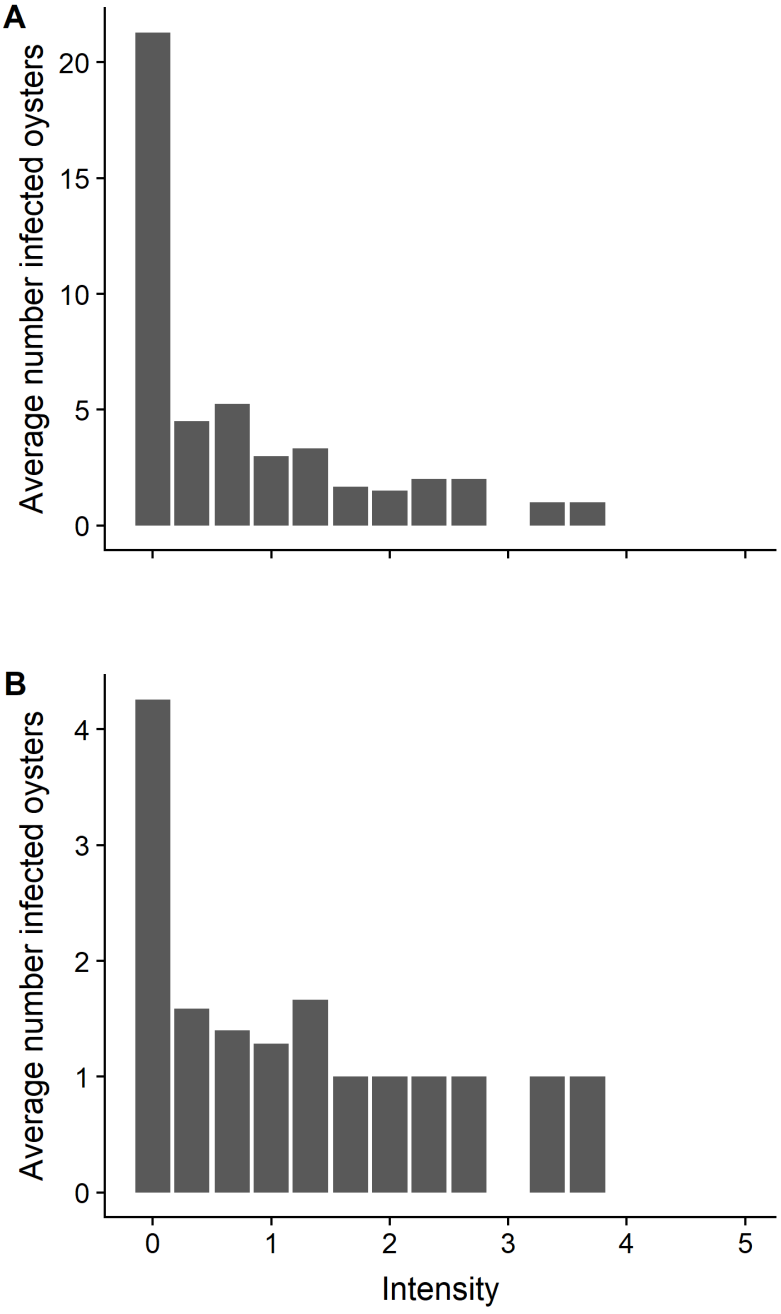

A
Average number infected oysters
20
15
10
5
0
B
Average number infected oysters
4
3
2
1
0
0
1
2
3
4
5
Intensity

Figure 7

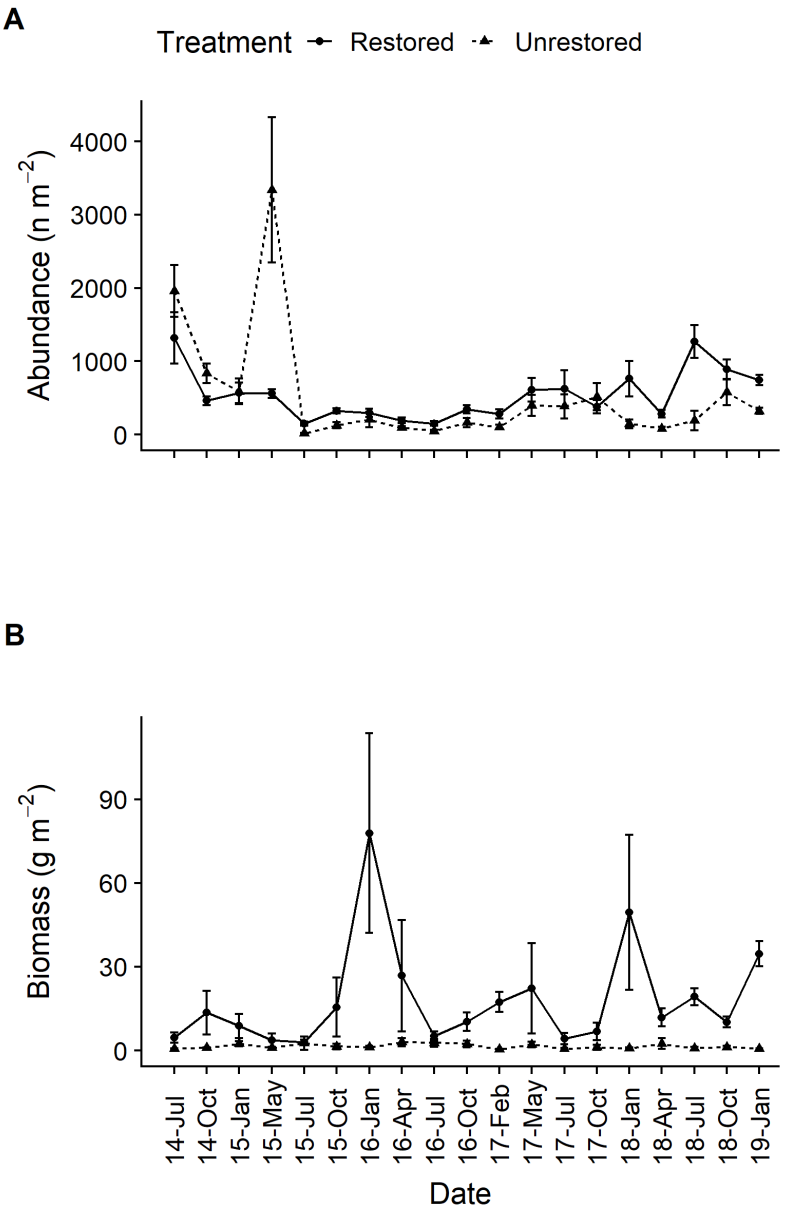

A
Treatment
Restored
Unrestored
Abundance (n m^{-2})
4000
3000
2000
1000
0
B
Biomass (g m^{-2})
90
60
30
0
14-Jul
14-Oct
15-Jan
15-May
15-Jul
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-May
17-Jul
17-Oct
18-Jan
18-Apr
18-Jul
18-Oct
19-Jan
Date

Figure 8

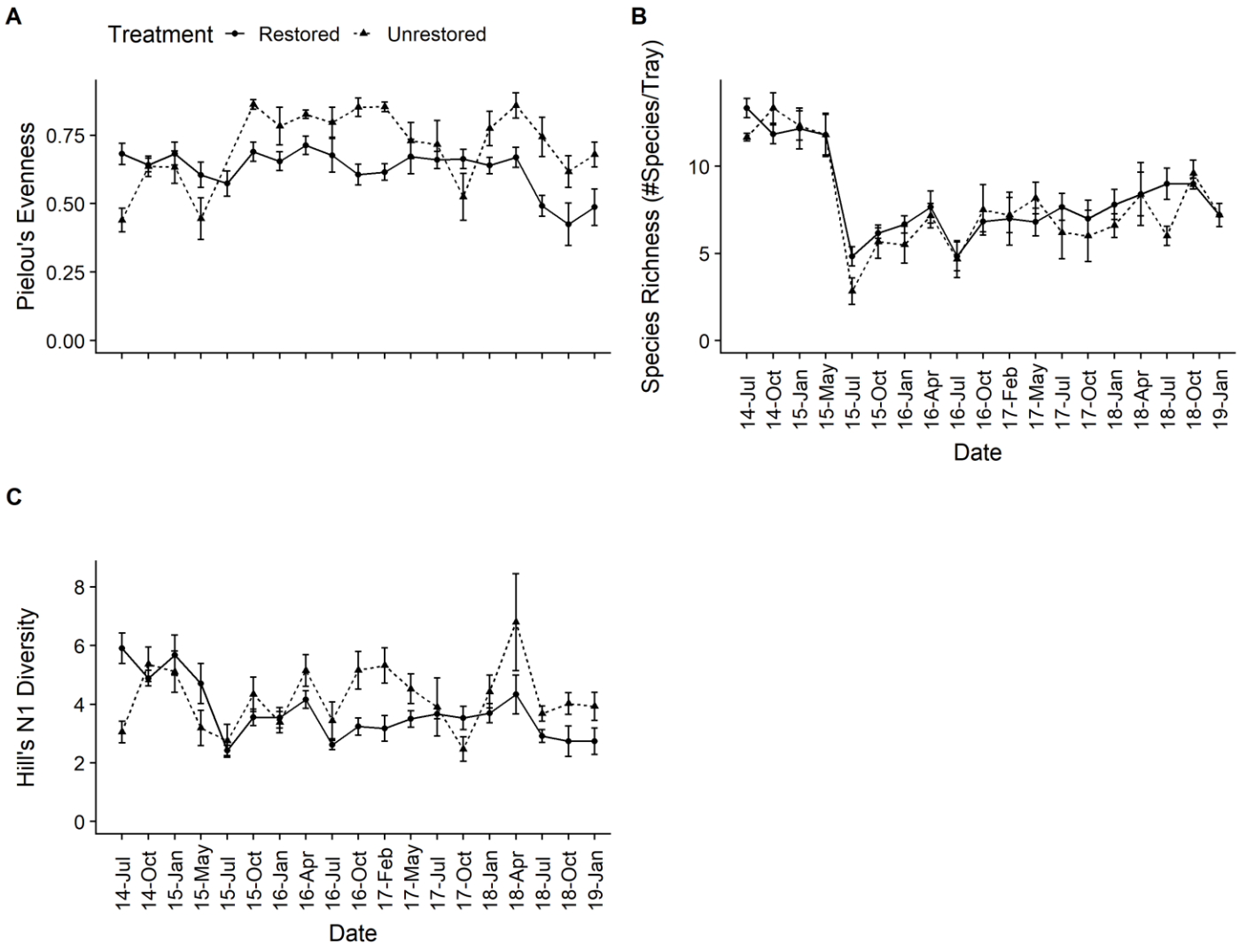

A
Treatment
Restored
Unrestored
Pielou's Evenness
0.00
0.25
0.50
0.75
B
Species Richness (#Species/Tray)
0
5
10
C
Hill's N1 Diversity
0
2
4
6
8
14-Jul
14-Oct
15-Jan
15-May
15-Jul
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-May
17-Jul
17-Oct
18-Jan
18-Apr
18-Jul
18-Oct
19-Jan
Date

Figure 9

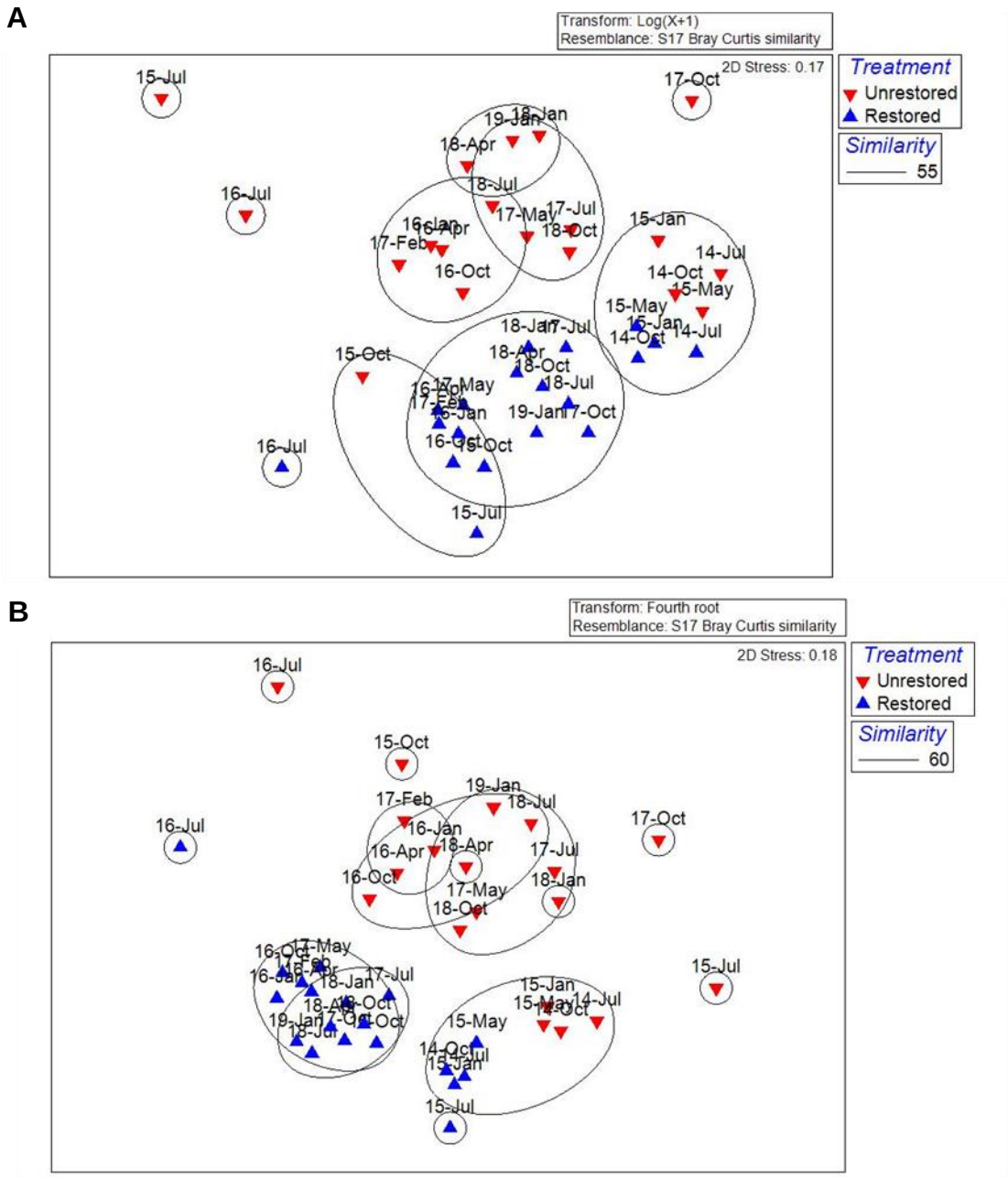

A
Transform: Log(X+1)
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.17
Treatment
Unrestored
Restored
Similarity
55
B
Transform: Fourth root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.18
Treatment
Unrestored
Restored
Similarity
60

Figure 10

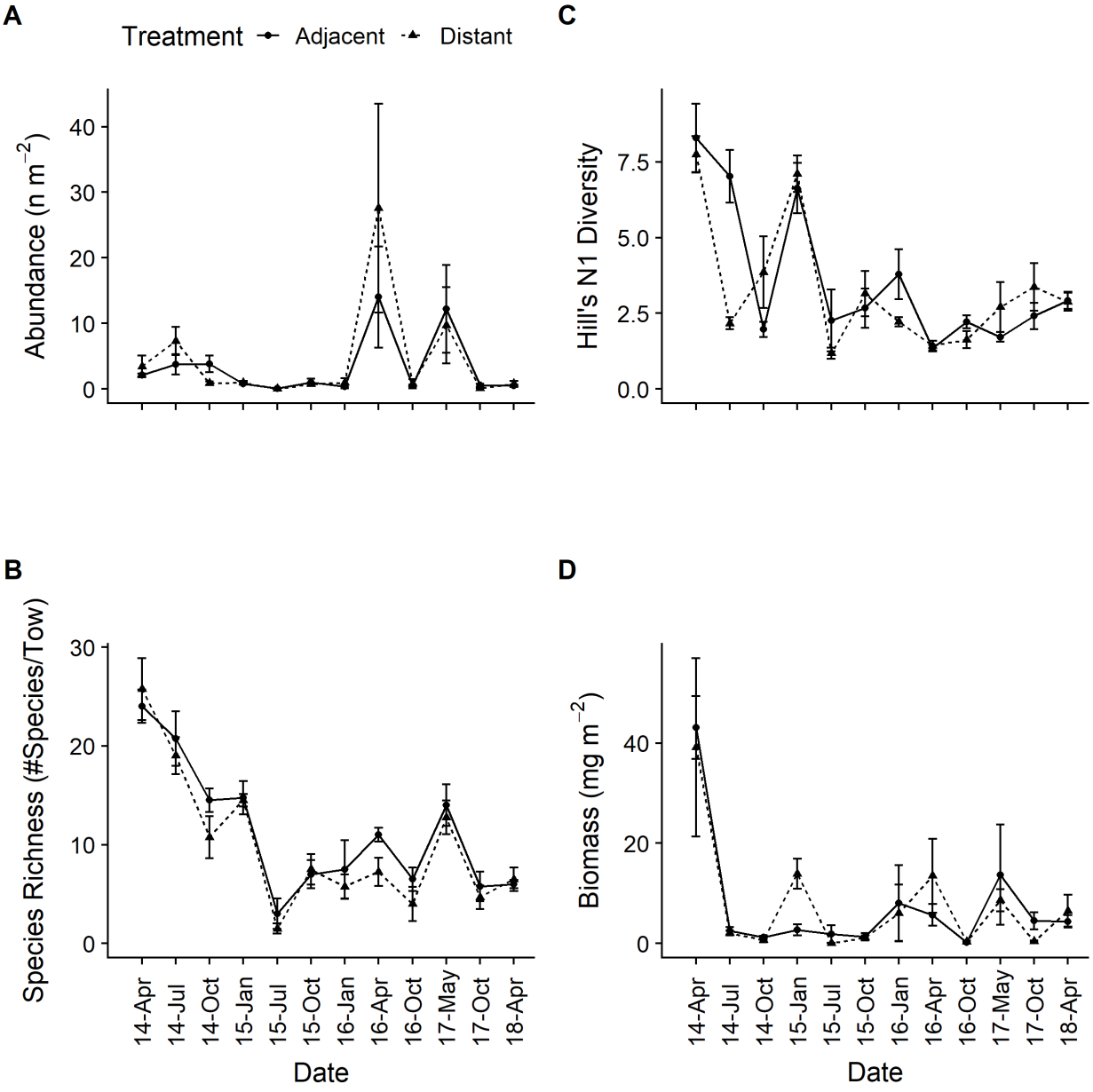

A
Treatment
Adjacent
Distant
Abundance (n m^{-2})
0
10
20
30
40
C
Hill's N1 Diversity
0.0
2.5
5.0
7.5
B
Species Richness (#Species/Tow)
0
10
20
30
14-Apr
14-Jul
14-Oct
15-Jan
15-Jul
15-Oct
16-Jan
16-Apr
16-Oct
17-May
17-Oct
18-Apr
Date
D
Biomass (mg m^{-2})
0
20
40
14-Apr
14-Jul
14-Oct
15-Jan
15-Jul
15-Oct
16-Jan
16-Apr
16-Oct
17-May
17-Oct
18-Apr
Date

Figure 11

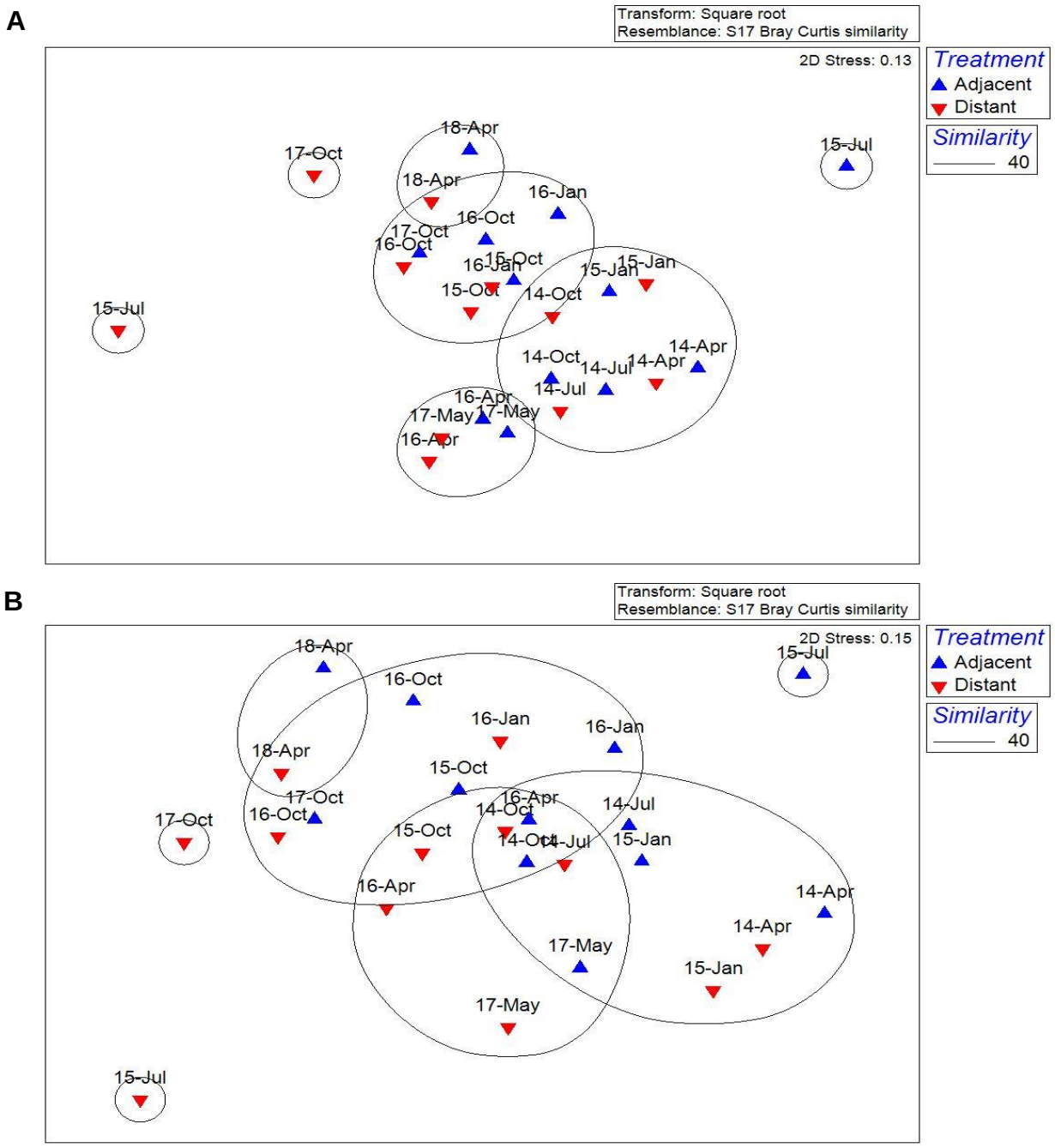
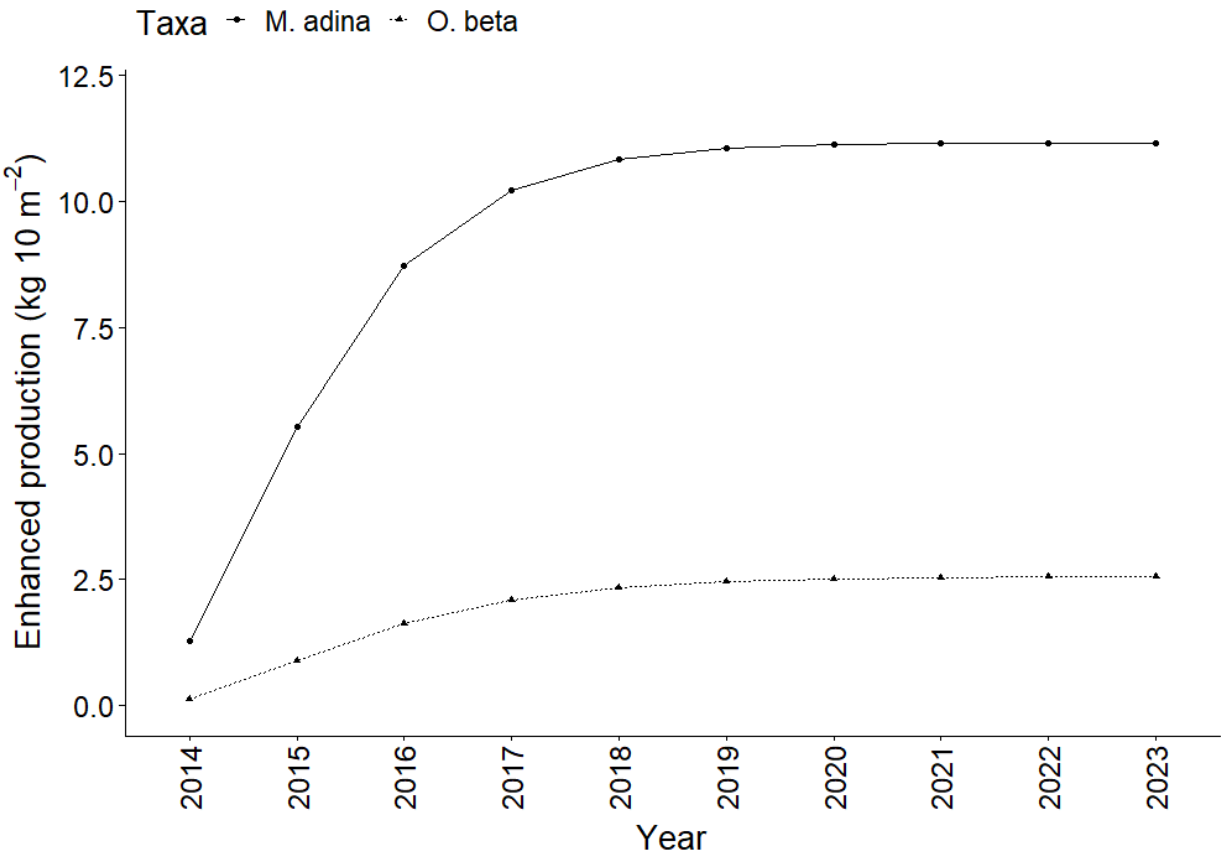

A
Transform: Square root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.13
Treatment
Adjacent
Distant
Similarity
40
18-Apr
17-Oct
15-Jul
18-Apr
16-Jan
16-Oct
17-Oct
16-Oct
16-Jan
15-Oct
15-Jan
15-Jan
15-Oct
14-Oct
15-Jul
14-Oct
14-Apr
14-Jul
14-Apr
14-Jul
16-Apr
17-May
17-May
16-Apr
B
Transform: Square root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.15
Treatment
Adjacent
Distant
Similarity
40
18-Apr
16-Oct
15-Jul
16-Jan
16-Jan
18-Apr
15-Oct
17-Oct
16-Apr
14-Jul
17-Oct
16-Oct
14-Oct
15-Oct
14-Oct
14-Jul
15-Jan
16-Apr
14-Apr
14-Apr
17-May
15-Jan
17-May
15-Jul

Figure 12


Taxa
M. adina
O. beta
Enhanced production (kg 10 m^{-2})
12.5
10.0
7.5
5.0
2.5
0.0
2014
2015
2016
2017
2018
2019
2020
2021
2022
2023
Year

TABLES

Table 1

		Restored				Unrestored			
Taxa	Higher Taxon	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Petrolisthes sp.	Decapoda	103	221.1	27.2	39.7	85	45.8	7.7	7.2
Panopeus herbstii	Decapoda	74	130.4	12.8	16.8	45	24.2	3.0	2.0
Parvanachis ostreicola	Gastropoda	59	146.1	33.0	15.0	69	139.6	24.5	17.7
Xanthoidea	Decapoda	67	91.2	10.4	10.7	52	36.7	5.7	3.5
Costoanachis sp.	Gastropoda	59	47.2	9.1	4.9	42	79.6	25.6	6.2
Astyris sp.	Gastropoda	56	39.5	7.9	3.9	74	365.1	94.9	49.7
Menippe adina	Decapoda	76	17.6	2.4	2.3	30	8.6	1.9	0.5
Alpheus heterochaelis	Decapoda	71	10.3	1.3	1.3	13	8.2	1.6	0.2
Aeolidiidae	Gastropoda	8	17.4	3.3	0.2	17	67.1	19.2	2.1
Nassarius acutus	Gastropoda	11	5.5	1.0	0.1	35	28.8	11.8	1.9

Table 2

		Restored				Unrestored			
Taxa	Higher Taxon	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Menippe adina	Decapoda	76	15.4	4.0	61	30	0.9	0.4	15.9
Petrolisthes sp.	Decapoda	103	3.0	0.3	15.9	85	0.3	0.0	13.3
Panopeus herbstii	Decapoda	74	2.6	0.4	10.0	45	0.2	0.0	5.0
Stramonita haemastoma	Gastropoda	16	4.2	1.1	3.5	9	2.6	0.7	14.3
Xanthoidea	Decapoda	67	0.6	0.2	2.1	52	0.2	0.1	6.3
Alpheus heterochaelis	Decapoda	71	0.5	0.1	1.8	13	0.1	0.0	0.5
Eurypanopeus sp.	Decapoda	12	2.0	0.6	1.3	5	0.4	0.1	1.2
Diogenidae	Decapoda	14	1.4	0.3	1.0	18	1.3	0.4	14.9
Astyris sp.	Gastropoda	56	0.0	0.0	0.0	74	0.1	0.1	5.5
Paguroidea	Decapoda	41	0.0	0.0	0.0	66	0.1	0.1	4.8
Clibanarius vittatus	Decapoda	9	1.5	0.4	0.7	2	3.2	0.6	4.0
Costoanachis sp.	Gastropoda	59	0.2	0.0	0.5	42	0.1	0.0	2.6
Palaemonetes sp.	Decapoda	24	0.2	0.1	0.3	31	0.1	0.0	2.0
Parvanachis ostreicola	Gastropoda	59	0.1	0.0	0.2	69	0.0	0.0	1.7
Cantharus cancellarius	Gastropoda	-	-	-	-	3	0.8	0.8	1.5
Pelia mutica	Decapoda	13	0.1	0.01	0.0	17	0.1	0.0	1.1

Table 3

		Impact				Control			
Taxa	Higher Taxon	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Mysidacea	Pericarida	42	3.0	1.1	80.3	42	4.2	1.8	82.9
Parvanachis ostreicola	Gastropoda	24	0.3	0.1	4.9	15	0.1	0.0	1.0
Paguroidea	Decapoda	28	0.2	0.1	3.3	29	0.2	0.1	2.5
Xanthoidea	Decapoda	29	0.1	0.0	1.7	13	0.0	0.0	0.2
Fish Larvae	Teleostei	11	0.2	0.1	1.1	12	0.4	0.2	2.2
Astyris sp.	Gastropoda	22	0.1	0.0	0.9	18	0.1	0.0	1.0
Turbonilla sp.	Gastropoda	11	0.0	0.0	0.1	15	0.4	0.3	2.5
Anchoa mitchilli	Teleostei	7	0.1	0.1	0.6	8	0.3	0.1	1.2

Table 4

		Impact				Control			
Taxa	Higher Taxon	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Callinectes sapidus	Decapoda	11	10.0	4.0	37.2	4	10.0	4.0	17.7
Busycon sinistrum	Gastropoda	4	9.0	3.0	12.4	1	20.0	-	5.5
Xanthoidea	Decapoda	29	0.7	0.4	7.2	13	0.3	0.1	1.1
Micropogonias undulatus	Teleostei	8	2.0	0.4	4.7	10	4.0	2.0	14.1
Mysidacea	Pericarida	42	0.3	0.1	4.4	42	0.3	0.1	4.7
Paguroidea	Decapoda	29	0.4	0.2	4.3	32	0.2	0.1	2.1
Sciaenidae juvenile	Teleostei	1	10.0	-	4.1	-	-	-	-
Farfantapanaeus aztecus	Decapoda	1	10.0	-	3.8	1	0.9	-	0.3
Panopeus herbstii	Decapoda	10	0.8	0.5	2.6	2	0.1	0.0	0.04
Palaemonetes sp.	Decapoda	14	0.4	0.2	2.1	11	0.3	0.1	1.1
Heterocrypta granulata	Decapoda	6	0.9	0.2	1.8	4	0.5	0.3	0.7
Gobiosoma bosc	Teleostei	19	0.3	0.1	1.7	7	0.4	0.2	0.9
Anchoa mitchilli	Teleostei	7	0.7	0.3	1.5	8	2.0	0.6	4.7
Parvanachis ostreicola	Gastropoda	24	0.2	0.1	1.4	15	0.1	0.0	0.3
Ophiurida	Echinodermata	3	1.0	1.0	1.2	5	0.1	0.0	0.1
Luidia clathrata	Decapoda	-	-	-	-	1	20.0	-	7.4
Brevoortia patronus	Teleostei	-	-	-	-	4	5.0	2.0	7.4
Persephona mediterranea	Decapoda	-	-	-	-	2	8.0	7.0	5.7
Etropus crossotus	Teleostei	2	0.1	0.1	0.1	5	3.0	2.0	5.6
Prionotus tribulus	Teleostei	-	-	-	-	2	6.0	0.3	4.3
Litopenaeus setiferus	Decapoda	-	-	-	-	1	10.0	-	3.5
Symphurus plagiusa	Teleostei	-	-	-	-	3	2.0	1.0	2.5
Busycotypus spiratus	Gastropoda	-	-	-	-	1	4.0	-	1.4
Trachypenaeus sp.	Decapoda	-	-	-	-	5	0.8	0.3	1.3

Table 5

Taxa	Higher Taxon	Trophic Status	Estimate of density enhancement (n 10 m^{-2})	Number of samples (positive samples)	Augmented biomass (g m^{-2})	Overall enhanced production (kg 10 m^{-2} y^{-1})
Alpheus heterochaelis	Decapoda	secondary	21.2	19 (15)	4.2	-
Eurypanopeus sp.	Decapoda	secondary	326.1	5 (4)	16.3	-
Panopeus herbstii	Decapoda	secondary	1061.3	14 (14)	23.9	-
Petrolisthes sp.	Decapoda	secondary	1752.7	19 (18)	26.9	-
Xanthoidea	Decapoda	secondary	545.6	17 (15)	4.0	-
Gobiesox strumosus	Teleostei	tertiary annual	17.8	4 (4)	11.9	0.2
Hypsoblennius hentz	Teleostei	tertiary annual	35.6	3 (3)	51.2	1.8
Menippe adina	Decapoda	tertiary long-lived	90.8	18 (14)	144.9	11.0
Opsanus beta	Teleostei	tertiary long-lived	35.6	7 (7)	2.5	2.5

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Appendix 3 BIOENV output for correlating water quality variables to reef-resident faunal biomass. 55

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Appendix 8 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal diversity 60

Appendix 9 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal biomass. 62

Appendix 10 ANOVA output of date, treatment, and treatment-date effect on reef-associated faunal abundance. 63

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APPENDICES

Appendix 1 Principle Component Analysis (PCA) resulting from analysis of water quality data.

PCA
Principal Component Analysis

Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	2.0	33.2	33.2
2	1.6	25.9	59.2
3	1.1	18.3	77.5
4	0.9	14.4	91.9
5	0.3	5.8	97.7

Eigenvectors
(Coefficients in the linear combinations of variables making up PC'S)

Variable	PC1	PC2	PC3	PC4	PC5
Temp	-0.7	-0.0	-0.2	-0.2	-0.3
DO_mgl	0.7	0.0	-0.0	-0.0	0.1
Sal	-0.2	-0.5	0.6	-0.2	0.5
pH	0.1	-0.3	-0.6	-0.6	0.3
Turb	-0.2	0.7	-0.1	0.0	0.7
Chl	0.1	0.4	0.4	-0.7	-0.3

Appendix 2 BIOENV output for correlating water quality variables to reef-resident faunal abundance.

BEST
Biota and/or Environment matching

Parameters
Rank correlation method: Spearman
Method: BIOENV
Maximum number of variables: 5
Resemblance:
Analyze between: Samples
Resemblance measure: D1 Euclidean distance

Variables
1 Temp
2 DO_mgl
3 Sal
4 pH
5 Turb
6 Chl

Global Test
Sample statistic (Rho): 0.161
Significance level of sample statistic: 7.3%
Number of permutations: 999 (Random sample)
Number of permuted statistics greater than or equal to Rho: 72

Best results

No.Vars	Corr.	Selections
3	0.161	1,4,6
3	0.158	4-6
4	0.158	1,4-6
2	0.145	1,6
2	0.143	4,6
3	0.139	1,5,6
2	0.139	5,6
4	0.133	1,2,4,6
4	0.133	2,4-6
5	0.132	1,2,4-6

Appendix 3 BIOENV output for correlating water quality variables to reef-resident faunal biomass.

BEST
Biota and/or Environment matching

Parameters
Rank correlation method: Spearman
Method: BIOENV
Maximum number of variables: 5
Resemblance:
Analyze between: Samples
Resemblance measure: D1 Euclidean distance

Variables
1 Temp
2 DO_mgl
3 Sal
4 pH
5 Turb
6 Chl

Global Test
Sample statistic (Rho): 0.203
Significance level of sample statistic: 3.60%
Number of permutations: 999 (Random sample)
Number of permuted statistics greater than or equal to Rho: 35

Best
results

No.Vars	Corr.	Selections
2	0.203	1,6
3	0.188	1,5,6
3	0.181	1,4,6
4	0.178	1,4-6
3	0.164	1,2,6
4	0.161	1,2,5,6
5	0.154	1,2,4-6
4	0.154	1,2,4,6
2	0.153	2,6
2	0.149	5,6

Appendix 4 ANOVA output of date effect on oyster abundance.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	19	487.5	25.7	91.9	<0.0001

Appendix 4. 1 Tukey grouping for date effect on oyster abundance.

Date	Mean	Tukey Groups				
14-Jul	4.0	A				
14-Oct	2.4		B			
15-May	2.3		B			
15-Jan	2.1		B			
15-Jul	1.4			C		
15-Oct	1.4			C		
16-Jan	0.9			C	D	
18-Jan	0.8				D	
19-Jan	0.8				D	E
16-Apr	0.6				D	E
18-Jul	0.6				D	E
17-Feb	0.5				D	E
17-Oct	0.5				D	E
17-Jul	0.5				D	E
16-Jul	0.5				D	E
16-Jul	0.5				D	E
17-May	0.5				D	E
18-Apr	0.4				D	E
16-Oct	0.3				D	E
18-Oct	0.0					E

Appendix 5 ANOVA output of date effect on oyster % cover.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	19	3.3	0.2	12.5	<0.0001

Appendix 5. 1 Tukey grouping for date effect on oyster % cover.

Date	Mean	Groups				
18-Apr	1.0	A				
18-Jan	0.9	A	B			
17-Jul	0.9	A	B			
16-Apr	0.9	A	B			
16-Oct	0.9	A	B	C		
16-Jul	0.9	A	B	C		
18-Jul	0.9	A	B	C		
17-May	0.9		B	C		
17-Oct	0.9		B	C	D	
16-Jan	0.9		B	C	D	
17-Feb	0.8		B	C	D	
15-Jan	0.8		B	C	D	
14-Oct	0.8		B	C	D	
15-Oct	0.8			C	D	E
16-Jul	0.8			C	D	E
15-May	0.8			C	D	E
14-Jul	0.7				D	E
19-Jan	0.7				D	E
15-Jul	0.7					E
18-Oct	0.7					E

Appendix 6 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal abundance.

	DF	Type III SS	Mean Square	F value	Pr (>F)
Date	18	151.0	8.4	4.0	<0.0001
Treatment	1	19.0	18.7	8.9	0.00285
Treatment-Date	18	85.0	4.7	2.3	0.00182

Appendix 6. 1 ANOVA output of combined factor treatment-date effect on reef-resident faunal abundance.

	DF	Type III SS	Mean Square	F value	Pr (>F)
Treatment-Date	37	255.0	6.9	3.3	<0.0001

Appendix 6. 2 Kruskal-Wallis results for resident faunal abundance treatment-date combination.

Kruskal-Wallis rank sum test
data: nm2 by TreatmentDate
Kruskal-Wallis chi-squared = 98.85, df = 37, p-value = 1.536e-07

Appendix 7 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal species richness.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	18	1373.1	76.3	15.8	<0.0001
Treatment	1	9.8	9.8	2.0	0.156
Treatment-Date	18	65.7	3.7	0.8	0.749

Appendix 7. 1 Tukey groupings for date effect on reef-resident faunal species richness.

Date	Mean	Tukey Groups					
14-Oct	12.6	A					
14-Jul	12.5	A					
15-Jan	12.3	A					
15-May	11.8	A	B				
18-Oct	9.3	A	B	C			
18-Apr	8.4		B	C	D		
17-May	7.5			C	D	E	
18-Jul	7.5			C	D	E	
16-Apr	7.4			C	D	E	
19-Jan	7.2			C	D	E	
18-Jan	7.2			C	D	E	
16-Oct	7.2			C	D	E	
17-Jul	7.1			C	D	E	
17-Feb	7.1			C	D	E	F
17-Oct	6.6			C	D	E	F
16-Jan	6.1			C	D	E	F
15-Oct	5.9				D	E	F
16-Jul	4.8					E	F
15-Jul	3.8						F

Appendix 8 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal diversity.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	18	132.9	7.4	4.6	<0.0001
Treatment	1	11.0	11.0	6.9	0.009518
Treatment-Date	18	82.0	4.6	2.8	0.000221

Appendix 8. 1 ANOVA output of combined factor treatment-date effect on reef-resident faunal diversity.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Treatment-Date	37	225.8	6.1	3.8	<0.0001

Appendix 8. 2 Tukey grouping for date effect on reef-resident faunal diversity.

Treatment-Date	Mean	Tukey Groups			
Unrestored.18-Apr	6.8	A			
Restored.14-Jul	5.9	A	B		
Restored.15-May	5.7	A	B		
Unrestored.14-Oct	5.4	A	B	C	
Unrestored.17-Feb	5.3	A	B	C	D
Unrestored.16-Oct	5.2	A	B	C	D
Unrestored.16-Apr	5.2	A	B	C	D
Unrestored.15-May	5.1	A	B	C	D
Restored.14-Oct	4.9	A	B	C	D
Restored.15-May	4.7	A	B	C	D
Unrestored.17-May	4.5	A	B	C	D
Unrestored.18-Jan	4.4	A	B	C	D
Unrestored.15-Oct	4.3	A	B	C	D
Restored.18-Apr	4.3	A	B	C	D
Restored.16-Apr	4.2	A	B	C	D
Unrestored.18-Oct	4.0	A	B	C	D
Unrestored.19-Jan	3.9	A	B	C	D
Unrestored.17-Jul	3.9	A	B	C	D
Restored.18-Jan	3.7	A	B	C	D
Unrestored.18-Jul	3.7	A	B	C	D
Restored.17-Jul	3.7		B	C	D
Restored.15-Oct	3.6		B	C	D
Restored.16-Jan	3.5		B	C	D
Restored.17-Oct	3.5		B	C	D
Restored.17-May	3.5		B	C	D
Unrestored.16-Jul	3.4		B	C	D
Unrestored.16-Jan	3.4		B	C	D
Restored.16-Oct	3.2		B	C	D
Unrestored.15-May	3.2		B	C	D
Restored.17-Feb	3.2		B	C	D
Unrestored.14-Jul	3.1		B	C	D
Restored.18-Jul	2.9		B	C	D
Unrestored.15-Jul	2.8			C	D
Restored.18-Oct	2.7			C	D
Restored.19-Jan	2.7			C	D
Restored.16-Jul	2.6			C	D
Unrestored.17-Oct	2.5			C	D
Restored.15-Jul	2.4				D

Appendix 9 ANOVA output of date, treatment, and treatment-date effect on reef-resident faunal biomass.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	18	19.8	1.1	7.3	<0.0001
Treatment	1	28.4	28.4	188.4	<0.0001
Treatment-Date	18	10.1	0.6	3.7	<0.0001

Appendix 9. 1 ANOVA output of combined factor treatment-date on reef-resident faunal biomass.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Treatment-Date	37	58.3	1.6	10.4	<0.0001

Appendix 9. 2 Kruskal-Wallis results for resident faunal biomass treatment-date combination.

Kruskal-Wallis rank sum test
data: gm2 by bio.int
Kruskal-Wallis chi-squared = 255.15, df = 37, p-value < 2.2e-16

Appendix 10 ANOVA output of date, treatment, and treatment-date effect on reef-associated faunal abundance.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	11	15.3	1.4	14.2	<0.0001
Treatment	1	0.0	0.0	0.0	0.887
Treatment-Date	11	0.9	0.1	0.8	0.626

Appendix 10. 1 Tukey grouping for date effect on reef-associated faunal abundance.

Date	Mean	Groups					
16-Apr	1.9	A					
17-May	1.7	A	B				
14-Jul	1.5	A	B	C			
14-Apr	1.2		B	C	D		
14-Oct	1.1		B	C	D	E	
15-Jan	0.9			C	D	E	F
15-Oct	0.9				D	E	F
18-Apr	0.9				D	E	F
16-Oct	0.8				D	E	F
16-Jan	0.7				D	E	F
17-Oct	0.7					E	F
15-Jul	0.						F

Appendix 11 ANOVA output of date, treatment, and treatment-date effect on reef-associated species richness.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	11	3679.0	334.4	27.9	<0.0001
Treatment	1	35.0	34.6	2.9	0.0939
Treatment-Date	11	61.0	5.6	0.5	0.9176

Appendix 11. 1 Tukey grouping for date effect on reef-associated faunal species richness.

Date	Mean	Groups					
14-Apr	24.9	A					
14-Jul	19.9	A	B				
15-Jan	14.6		B	C			
17-May	13.4			C			
14-Oct	12.6			C	D		
16-Apr	9.1			C	D	E	
15-Oct	7.3				D	E	F
16-Jan	6.6					E	F
18-Apr	6.3					E	F
17-Oct	5.3					E	F
16-Oct	5.3					E	F
15-Jul	2.4						F

Appendix 12 ANOVA output of date, treatment, and treatment-date effect on reef-associated species diversity.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	11	360.2	32.8	21.3	<0.0001
Treatment	1	2.1	2.1	1.4	0.242586
Treatment-Date	11	64.3	5.9	3.8	0.000289

Appendix 12. 1 ANOVA output of combined treatment-date effect on reef-associated species diversity.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Treatment-Date	23	426.7	18.6	12.0	<0.0001

Appendix 12. 2 Tukey grouping for treatment-date effect on reef-associated faunal diversity.

Treatment-Date	Mean	Groups			
Adjacent.14-Apr	8.3	A			
Distant.14-Apr	7.8	A			
Distant.15-Jan	7.1	A	B		
Adjacent.14-Jul	7.0	A	B		
Adjacent.15-Jan	6.6	A	B	C	
Distant.14-Oct	3.9		B	C	D
Adjacent.16-Jan	3.8		B	C	D
Distant.17-Oct	3.4			C	D
Distant.15-Oct	3.1				D
Adjacent.18-Apr	2.9				D
Distant.18-Apr	2.9				D
Distant.17-May	2.7				D
Adjacent.15-Oct	2.7				D
Adjacent.17-Oct	2.4				D
Adjacent.15-Jul	2.3				D
Distant.16-Jan	2.2				D
Adjacent.16-Oct	2.2				D
Distant.14-Jul	2.2				D
Adjacent.14-Oct	2.0				D
Adjacent.17-May	1.7				D
Distant.16-Oct	1.6				D
Distant.16-Apr	1.4				D
Adjacent.16-Apr	1.3				D
Distant.15-Jul	1.2				D

Appendix 13 ANOVA output of date, treatment, and treatment-date effect on reef-associated faunal biomass.

	DF	Type III SS	Mean Square	F value	Pr(>F)
Date	11	0.000305	2.769e-05	3.939	<0.0001
Treatment	1	0.000001	1.093e-06	0.156	0.639
Treatment-Date	11	0.000062	5.660e-06	0.805	0.635

Appendix 13. 1 Kruskal-Wallis results for associated faunal biomass treatment-date combination.

Kruskal-Wallis rank sum test
data: gm2 by Date
Kruskal-Wallis chi-squared = 123.98, df = 11, p-value < 2.2e-16

Appendix 14 SIMPER results for reef-resident faunal abundance.

Group Unrestored
Average similarity: 17.3

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Astyris sp.	72.9	4.8	0.5	27.7	27.7
Parvanachis ostreicola	26.0	3.6	0.5	21.1	48.8
Petrolisthes sp.	10.5	3.2	0.6	18.5	67.2
Paguroidea	6.4	1.5	0.4	8.9	76.1
Panopeus herbstii	2.9	1.5	0.3	8.4	84.6
Xanthoidea	5.1	0.8	0.4	4.8	89.3
Costoanachis sp.	9.0	0.4	0.3	2.5	91.8

Group Restored
Average similarity: 33.6

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes sp.	59.2	16.3	1.2	48.3	48.3
Panopeus herbstii	25.1	8.3	0.7	24.6	72.9
Xanthoidea	15.9	4.3	0.6	12.7	85.6
Parvanachis ostreicola	22.4	1.5	0.4	4.6	90.2

Groups Unrestored & Restored
Average dissimilarity: 85.1

Species	Group Unrestored Av.Abund	Group Restored Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Petrolisthes sp.	10.5	59.2	20.9	1.1	24.6	24.6
Astyris sp.	72.9	5.8	13.6	0.7	16.0	40.6
Panopeus herbstii	2.9	25.1	12.8	0.9	15.0	55.6
Parvanachis ostreicola	26.0	22.4	10.8	0.8	12.6	68.2
Xanthoidea	5.1	15.9	8.2	0.7	9.6	77.9
Costoanachis sp.	9.0	7.2	4.1	0.5	4.8	82.6
Paguroidea	6.4	0.8	2.9	0.5	3.4	86.0
Menippe adina	0.7	3.5	1.8	0.5	2.1	88.1
Nassarius acutus	2.7	0.2	1.3	0.3	1.5	89.6
Aeolidiidae	3.1	0.4	1.2	0.3	1.4	91.0

Appendix 15 SIMPER results for reef-resident faunal biomass.

Group Unrestored
Average similarity: 12.4

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes sp.	0.1	5.3	0.5	42.7	42.7
Astyris sp.	0.0	1.4	0.3	10.9	53.7
Panopeus herbstii	0.0	1.1	0.3	8.7	62.3
Xanthoidea	0.0	0.8	0.3	6.7	69.0
Paguroidea	0.0	0.8	0.3	6.3	75.4
Parvanachis ostreicola	0.0	0.6	0.4	5.1	80.5
Menippe adina	0.1	0.6	0.2	4.6	85.1
Costoanachis sp.	0.0	0.5	0.3	4.4	89.5
Palaemonetes sp.	0.0	0.3	0.2	2.7	92.1

Group Restored
Average similarity: 21.6

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes sp.	0.8	10.1	0.9	46.7	46.7
Menippe adina	3.0	4.4	0.4	20.1	66.8
Panopeus herbstii	0.5	3.8	0.5	17.5	84.3
Xanthoidea	0.1	1.3	0.3	5.9	90.2

Groups Unrestored & Restored
Average dissimilarity = 90.7

Species	Group Unrestored Av.Abund	Group Restored Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Menippe adina	0.1	3.0	22.8	0.8	25.1	25.1
Petrolisthes sp.	0.1	0.8	21.7	1.1	24.0	49.1
Panopeus herbstii	0.0	0.5	12.3	0.8	13.6	62.7
Xanthoidea	0.0	0.1	6.9	0.5	7.6	70.3
Stramonita haemastoma	0.1	0.2	4.7	0.4	5.2	75.5
Diogenidae	0.1	0.1	3.8	0.4	4.2	79.7
Alpheus heterochaelis	0.0	0.1	3.7	0.7	4.0	83.7
Eurypanopeus sp.	0.0	0.1	2.8	0.3	3.1	86.9
Costoanachis sp.	0.0	0.0	1.6	0.5	1.7	88.6
Astyris sp.	0.0	0.0	1.4	0.3	1.5	90.1

Appendix 16 SIMPER results for reef-associated faunal abundance.

Group Distant
Average similarity: 17.7

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mysidacea	3.9	14.2	0.8	80.3	80.3
Paguroidea	0.1	0.8	0.4	4.3	84.6
Nassarius acutus	0.0	0.6	0.2	3.5	88.1
Astyris sp.	0.1	0.3	0.3	1.9	90.0

Group Adjacent
Average similarity: 18.8

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mysidacea	2.7	14.4	0.7	77.0	77.0
Parvanachis ostreicola	0.2	1.2	0.3	6.1	83.1
Paguroidea	0.1	0.7	0.3	3.8	86.9
Xanthoidea	0.1	0.5	0.4	2.6	89.5
Engraulidae larvae	0.0	0.3	0.1	1.6	91.1

Groups Distant & Adjacent
Average dissimilarity: 81.7

Species	Group Distant Av.Abund	Group Adjacent Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mysidacea	3.9	2.7	45.1	1.4	55.2	55.2
Parvanachis ostreicola	0.1	0.2	4.9	0.6	6.1	61.2
Paguroidea	0.1	0.1	4.4	0.7	5.4	66.6
Engraulidae larvae	0.0	0.0	3.2	0.4	3.9	70.5
Fish larvae	0.1	0.0	2.2	0.4	2.7	73.2
Astyris sp.	0.1	0.0	2.1	0.4	2.5	75.7
Turbonilla sp.	0.1	0.0	2.0	0.3	2.5	78.1
Xanthoidea	0.0	0.1	1.5	0.5	1.8	80.0
Micropogonias undulatus	0.0	0.0	1.3	0.4	1.6	81.5
Aeolidiidae	0.0	0.0	1.3	0.4	1.5	83.0
Anchoa mitchilli	0.1	0.0	1.2	0.3	1.5	84.6
Nassarius acutus	0.0	0.0	1.2	0.3	1.5	86.1
Brevoortia patronus	0.0	0.0	1.1	0.2	1.4	87.5
Acteocina sp.	0.0	0.0	1.0	0.2	1.2	88.6
Portunidae	0.0	0.0	0.9	0.5	1.1	89.7
Gobiosoma bosc	0.0	0.0	0.9	0.3	1.0	90.7

Appendix 17 SIMPER results for reef-associated faunal biomass.

Group Distant
Average similarity: 9.7

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mysidacea	0.3	6.0	0.6	61.2	61.2
Nassarius acutus	0.0	0.9	0.2	9.0	70.2
Fish larvae	0.0	0.4	0.1	4.5	74.6
Micropogonias undulatus	0.9	0.4	0.2	4.5	79.1
Paguroidea	0.1	0.4	0.3	4.2	83.3
Anchoa mitchilli	0.3	0.3	0.1	2.8	86.1
Engraulidae larvae	0.0	0.2	0.1	2.0	88.1
Gobiidae larvae	0.0	0.1	0.3	1.5	89.6
Brevoortia patronus	0.5	0.1	0.1	1.3	90.8

Group Adjacent
Average similarity: 10.4

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mysidacea	0.3	5.4	0.6	51.9	51.9
Xanthoidea	0.5	0.6	0.4	5.9	57.8
Callinectes sapidus	2.4	0.6	0.1	5.3	63.2
Paguroidea	0.3	0.4	0.3	4.2	67.4
Gobiosoma bosc	0.1	0.4	0.2	3.8	71.1
Palaemonetes sp.	0.1	0.4	0.2	3.8	74.9
Panopeus herbstii	0.2	0.4	0.1	3.6	78.5
Costoanachis sp.	0.1	0.4	0.3	3.5	82.0
Parvanachis ostreicola	0.1	0.3	0.3	2.7	84.7
Micropogonias undulatus	0.3	0.3	0.1	2.5	87.2
Portunidae	0.0	0.2	0.2	1.6	88.7
Engraulidae larvae	0.0	0.2	0.1	1.5	90.3

Groups Distant & Adjacent
Average dissimilarity: 90.6

Species	Group Distant Av.Abund	Group Adjacent Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mysidacea	0.3	0.3	12.9	0.8	14.2	14.2
Callinectes sapidus	1.1	2.4	9.6	0.5	10.6	24.9
Micropogonias undulatus	0.9	0.3	6.8	0.5	7.5	32.3
Anchoa mitchilli	0.3	0.1	5.1	0.4	5.6	37.9

Paguroidea	0.1	0.3	4.5	0.4	5.0	42.9
Xanthoidea	0.1	0.5	4.3	0.4	4.7	47.7
Palaemonetes sp.	0.1	0.1	3.5	0.4	3.9	51.5
Brevoortia patronus	0.5	0.0	3.1	0.3	3.4	55.0
Panopeus herbstii	0.0	0.2	2.9	0.3	3.2	58.2
Etropus crossotus	0.4	0.0	2.8	0.3	3.0	61.2
Engraulidae larvae	0.0	0.0	2.6	0.3	2.8	64.0
Gobiosoma bosc	0.1	0.1	2.3	0.5	2.5	66.6
Busycon sinistrum	0.4	0.8	2.0	0.3	2.2	68.8
Costoanachis sp.	0.0	0.1	1.5	0.4	1.7	70.4
Farfantapanaeus aztecus	0.0	0.2	1.4	0.2	1.6	72.0
Luidia clathrata	0.5	0.0	1.4	0.2	1.6	73.6
Parvanachis ostreicola	0.0	0.1	1.4	0.5	1.6	75.2
Nassarius acutus	0.0	0.0	1.4	0.4	1.6	76.7
Menippe sp.	0.0	0.0	1.3	0.2	1.4	78.2
Heterocrypta granulata	0.0	0.1	1.2	0.3	1.4	79.5
Portunidae	0.0	0.0	1.1	0.4	1.2	80.7
Fish larvae	0.0	0.0	1.1	0.3	1.2	82.0
Diogenidae	0.1	0.0	1.1	0.2	1.2	83.2
Bairdella chrysoura	0.0	0.1	1.0	0.1	1.1	84.3
Gobiidae larvae	0.0	0.0	1.0	0.5	1.1	85.3
Litopenaeus setiferus	0.2	0.0	0.9	0.2	0.9	86.3
Acteocina sp.	0.0	0.0	0.8	0.2	0.9	87.1
Petrolisthes sp.	0.0	0.0	0.7	0.4	0.8	87.9
Cynoscion nebulosus	0.0	0.0	0.6	0.1	0.7	88.6
Sciaenidae juvenile	0.0	0.3	0.6	0.2	0.7	89.3
Astyris sp.	0.0	0.0	0.6	0.4	0.7	90.0