SALINITY DISTURBANCE AFFECTS COMMUNTY STRUCTURE AND ORGANIC MATTER ON A RESTORED *CRASSOSTREA VIRGINICA* OYSTER REEF IN MATAGORDA BAY, TEXAS

A Thesis

by

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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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ABSTRACT

Oyster reefs are one of the most degraded marine habitats, with estimated 85-91% global habitat loss compared to historic levels (Beck et al. 2011, Lotze et al. 2006). However, the restoration of oyster reefs is becoming a widely recognized tool to ameliorate the effects of habitat loss. Half Moon Reef, once a highly-productive 2 km^2 *Crassostrea virginica* oyster reef located in Matagorda Bay, Texas, was harvested to depletion in the early 20^{th} century. In 2014, The Nature Conservancy restored 0.23 km^2 of reef—one of the largest oyster reef restorations in the country. In the three years following reef restoration, two salinity disturbances (prolonged salinities <10) provided a unique opportunity to determine the effects of large salinity variations on oyster reef community structure and quality of organic matter.

Oyster growth generally increased over the 3-year study period, enhancing habitat provisioning for reef fauna. Reef-resident species metrics showed strong positive correlations with salinity. Following a low salinity event (25 to 9) one year post-restoration, the reef-resident fauna shifted from a community dominated by pioneer organisms to one comprising larger and more resilient crustaceans and gastropods. A second low salinity event two years post-restoration did not show a similar response, indicating the presence of larger oysters facilitated species that may otherwise not exist in high disturbance environments. Fauna from adjacent areas showed no patterns with distance from the reef, indicating restoration did not influence faunal communities away from the physical reef structure. As salinity decreased, suspended particular organic matter became more ^{13}C-depleted whereas surface sediment organic matter did not show significant change. Carbon/chlorophyll *a* and carbon/nitrogen ratios of suspended particulate organic matter indicated the quality of organic matter was higher following low salinity events, implying pulses

of freshwater inflow increased autochthonous production. Surface sediment organic matter and suspended particulate organic matter contributed nearly equally to assimilation by oysters. Results were integrated into a conceptual diagram to visualize the effects of salinity on oyster reef communities, providing a tool that natural resource managers can use for a broader perspective on the effects of salinity variations on oyster reef communities.

DEDICATION

To Stephen Marshall, my best friend. You never stop believing in me.

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INTRODUCTION

The eastern oyster, *Crassostrea virginica* (Gmelin 1791), is an ecologically and economically important species (Grabowski et al. 2012, Grabowski and Peterson 2007). Oysters provide many ecosystem services, such as food, habitat provision, shoreline protection (Grabowski et al. 2012), and increased water quality through consumption of phytoplankton (Kirby 2004) and nitrogen removal (Grabowski and Peterson 2007, Beseres Pollack et al. 2013). In addition, oysters are economically important as a commercially harvested species—Gulf of Mexico harvests generated nearly $100 million in 2015 (NOAA 2017). Oyster reefs are one of the most degraded marine habitats, due in part to their high value and sessile nature (Lotze et al. 2006, Jackson 2008). It is estimated that 85-91% of oyster reef habitat has been lost globally compared to historic levels (Beck et al. 2011, Lotze et al. 2006). This decrease is mainly attributed to overharvesting (Gross & Smyth 1946, Kirby 2004), although disease, predation, pollution, and salinity levels have also contributed (Gross & Smyth 1946, Rothschild et al. 1994).

One way to combat the steady decline in oyster abundance is through the restoration of reefs, which creates complex structure and supports similar or greater densities of nekton than natural reefs, and markedly greater densities than mud-bottom habitat (Brown et al. 2013, George et al. 2015, Humphries & La Peyre 2015). Within estuaries, oyster reefs are high quality habitats due to the services they provide, which facilitate increased species abundance, biomass, and diversity (Harding and Mann 1999, Harding and Mann 2001, Meyer and Townsend 2000, Tolley and Volety 2005a, Wells 1961). Their complex three-dimensional structures provide refuge for resident macrofauna, increase larval retention, enhance foraging, and reduce competition (Humphries et al. 2011, Peterson et al. 2003, Soniat et al. 2004, Tolley & Volety

2005a). Oyster reef restoration is becoming widely recognized as a reasonable and feasible response to ameliorating the effects of past habitat destruction.

Suspended particulate organic matter (SPOM) is the main food source for oysters (Abeels et al. 2012, Lebreton et al. 2016). While these particles often have allochthonous origin, there is increasing recognition of autochthonous organic matter contribution to oyster food resources following freshwater inflow events (Lebreton et al. 2016, Reyna et al. 2017). Freshwater inflow brings nutrients of terrestrial origin into estuaries (Conkright and Sackett 1986, Riera and Richard 1997, Simenstad and Wissmar 1985), spurring autochthonous phytoplankton production (Lebreton et al. 2016, Reyna et al. 2017), and producing higher quality organic matter. Changes to the composition and quality of SPOM can affect the general functioning of the reef as energy is transferred up various trophic linkages (Fry 2002). Stable isotope analyses can be used to determine the different food sources utilized by the oysters (Fry 2006), with stable isotopes of carbon permitting determination of the origin (i.e., benthic vs. pelagic) of food resources. Many studies have evaluated the composition ($\delta^{13}C$ and $\delta^{15}N$ values) of SPOM along estuarine gradients, primarily relating results to freshwater inflow (Hughes and Sherr 1983, Mooney and McClelland 2012, Stephenson and Lyon 1982). However, relatively few studies have examined the quality of SPOM and its relevance to salinity within estuarine systems.

Freshwater inflow pulses, and associated salinity variability, can act as a disturbance in coastal environments (Van Diggelen and Montagna 2016). Large variations in salinity, a proxy for freshwater inflow, can influence the functioning of oyster reefs through effects on oyster recruitment, growth, and survival (Coen and Luckenbach 2000, Davis 1958, La Peyre et al. 2003, La Peyre et al. 2013c). Less is known on how reef-resident organisms respond to such disturbance events. For example, many studies examine changes to benthic or macrofaunal

communities along a salinity gradient (see Mannino and Montagna 1997, Tolley et al. 2006, and others), but few examine structure of reef communities experiencing large *in situ* salinity variations. Likewise, a limited number of studies have investigated relationships between organic matter and salinity (i.e., freshwater inflow). In 2013 and 2014, a historic oyster reef in Matagorda Bay, Texas, was partially restored. Post-restoration, intermittent low salinity (<10) events provided the opportunity to examine the effects of large salinity variations on two major ecological parameters: reef community structure and organic matter composition and quality.

METHODS

Study Site

Matagorda Bay, part of the larger Lavaca-Colorado Estuary, is the third largest (1100 km^2) of seven major estuaries along the Texas coast (NOAA 1990). The bay is shallow, with an average depth of 2 m, and protected from the Gulf of Mexico by Matagorda Peninsula. The combination of a shallow bay and strong winds ensure that vertical stratification within the bay is not common (Ward et al. 1980). The bay bottom is characterized by numerous shoals, many of which are natural oyster reefs (Orlando et al. 1993).

The dominant source of freshwater inflow to Matagorda Bay is the Colorado River, which naturally flowed into the bay until the late 1920s, when the Colorado River was shifted to empty directly into the Gulf of Mexico (Ward et al. 1980). The River was rediverted back to Matagorda Bay in the early 1990s with the construction of Tiger Island Channel (Wilber & Bass 1998). Other sources of freshwater inflow to the system include the Tres Palacios River and Lavaca River (Figure 1).

Half Moon Reef (Figure 1; N 28°34’98” W 96°14’166”) was a historically productive subtidal *Crassostrea virginica* oyster reef spanning nearly 2 km^2 in Matagorda Bay (Moore

1907). Although productive from 1904-1905 (Moore 1907), years of unsustainable harvest caused the reef to be void of oysters by a 1926 survey (Galtsoff 1931). Surveys in 2011 indicated the historic footprint of Half Moon Reef was composed of mostly mud and shell hash (De Santiago 2016). From October 2013 to April 2014, 0.23 km^2 of Half Moon Reef were restored by The Nature Conservancy, comprising 0.18 km^2 of limestone substrate in the southern part of the reef (23 October to 3 December 2013), and 0.05 km^2 of concrete substrate in the northern part of the reef (6 March to 14 April 2014, De Santiago 2016). The restored reef complex includes 33 reef rows, each 189 m long and 1 m high, separated by a repeating pattern of 9 m, 18 m, and 27 m.

Field sampling on and around Half Moon Reef occurred seasonally from April 2014, the month restoration was completed, to May 2017. Samples collected from April 2014 to May 2015 were processed by Kevin De Santiago for a previous study (De Santiago 2016). All later samples were processed by the author of this study.

Water quality measurements

Water quality measurements, including dissolved oxygen, salinity, temperature, turbidity, and pH were taken at the surface and near the bottom of the water column at multiple sites during each sampling event using a YSI Pro DSS or Hydrolab MS5 sonde. Daily temperature and salinity data were retrieved from the Lower Colorado River Authority (LCRA; http://waterquality.lcra.org/). LCRA data was collected daily at Site 6984 in West Bay at Channel 4 until May 2014, then from Site NCM4 (6984 Replacement) from August 2014 to May 2017.

Reef community characterization

Sampling of encrusting macrofauna

During each sampling event, at least two pieces of reef substrate (size varied) were collected from each of six reef sites (HMA to HMF, Figure 1) by SCUBA divers to monitor recruitment and spatial coverage of encrusting organisms, as well as height of oysters. A 60 cm^2 mesh with a mesh size of 2.5 cm x 2 cm was overlaid on representative areas of the substrates, and percent cover was determined using the proportion of mesh units colonized relative to the total number of mesh units. Species were identified to the lowest practical taxon and enumerated for abundance estimations. In addition, shell height of all *C. virginica* greater than 5mm within the mesh was recorded.

Sampling of reef-resident and reef-associated faunal assemblages

Reef-resident fauna were sampled from July 2014 to May 2017. To monitor reef-resident faunal assemblages, two sampling trays (61 cm long x 46 cm wide) were placed at six sites on the reef (HMA-HMF), and at six control sites (CA-CF) (i.e., unrestored reef, Figure 1) in April 2014. Trays were filled with the same concrete substrate used in reef restoration at reef sites and material matching the surrounding bottom sediments at the control sites. Having two trays per site allowed for each tray to be sampled once every six months, to minimize disturbance of reef-resident fauna. Epifauna from the tray samples were recovered by a diver using a trash pump-powered suction sampler.

Reef-associated fauna were sampled from April 2014 to May 2017. To monitor reef-associated faunal assemblages, a modified epibenthic sled (MES) was towed for the length of the reef, approximately 200 meters, at four sites between reef rows (adjacent habitats, 13 m from reef; SH 1-4), and at four sites in unrestored areas (distant habitats, 150 m from reef; SC 1-4;

Figure 1). The MES is a canvas-covered rectangular steel frame (0.72 m wide x 0.30 m high x 0.45 m deep) with a row of attached steel teeth along the front bottom edge to agitate and dislodge demersal nekton and benthic crustaceans (see Stunz et al. [2002] and Nevins et al. [2014] for details). Tow samples were not collected during May 2015, July 2016, and February 2017 due to logistical issues.

All faunal samples were fixed in 10% buffered formalin in the field and brought back to the lab where they were sorted, identified to the lowest practical taxon, and enumerated. 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 2 mol L^{-1} HCl for small shells, and 12 mol L^{-1} HCl for large, thick shells. When necessary, mysids, larval fish and decapods from tow samples were subsampled using a Folsom plankton splitter to estimate densities (McEwen et al. 1954).

Perkinsus marinus *monitoring*

Presence and severity of *Perkinsus marinus* was assessed for oysters at each reef site on each sampling date. Using the culture method of Ray (1966), a section of mantle was excised and incubated in fluid thioglycollate medium for 1 week. Tissues were then placed on a microscope slide, stained with Lugol's solution, and given a ranking of 0-5 for infection intensity using methods adapted from Mackin (1962) and Craig et al. (1989). Prevalence (% infection) and weighted prevalence (severity) of *P. marinus* infection were then determined.

Reef community statistical analysis

Non-metric multidimensional scaling (nMDS; Clarke and Warwick 1994) analysis using a Bray-Curtis similarity matrix was used to describe spatial and temporal community trends, with overlays from a cluster analysis using the group average method. Similarity profile analysis

(SIMPROF) was used to test for significant similarities within clusters ($p<0.05$). Abundance data were log(x+1) transformed and biomass data were fourth-root transformed for reef-resident faunal communities, and abundance and biomass data were square-root transformed for reef-associated faunal communities. Similarity percentage (SIMPER) analyses were used to describe taxa that were characteristic of, and different among treatments (restored and unrestored) and dates. Hydrological measurements were normalized to comparable scales and analyzed using principal component analysis (PCA). The BIO-ENV analysis, which calculates dissimilarity between physical and biotic data, was used to relate environmental parameters to community assemblage data with weighted Spearman rank correlations (Clarke and Ainsworth 1993; Clarke et al. 2008). Multivariate community analyses were conducted using PRIMER v6 (Clarke and Garley 2006).

A one-way ANOVA was used to test the effect of the fixed factor date on oyster abundance and percent cover. A two-way ANOVA was used to test the effects of the fixed factors date and treatment (restored and unrestored) on the response variables abundance, species richness, and diversity of resident and associated fauna. Homogeneity of variance was examined using a residuals vs. fitted plot. Data normality was assessed using the Shapiro-Wilk and Kolmogorov-Smirnov normality tests. To meet ANOVA assumptions for normality, oyster abundance data were log(x+1) transformed and percent cover data were square-root transformed. Reef-resident and reef-associated abundance data were fourth-root transformed. Hill's N1 diversity index were square-root transformed for reef-associated species data. Tukey's multiple comparison test was used to determine differences among dates and between treatment levels when significant differences were found ($p < 0.05$). Because shell height data and biomass data for reef-resident and reef-associated fauna were not normal under any transformation, non-parametric Kruskal-

Wallis and Wilcoxon tests were used to test the effects of date and site on shell height, and date and treatment on reef-resident and reef-associated biomass. Dunn's test with Bonferroni adjustment was used to determine significant differences among and between treatment levels when significant differences were found ($p < 0.05$). Spearman rank correlations were fit for overall macrofaunal abundance, biomass, diversity, and richness, to water quality variables. Spearman correlations and non-parametric tests were performed using R 3.4.1 (R Foundation for Statistical Computing 2017). All other univariate analyses were performed using SAS 9.4 (SAS Institute Inc. 2014).

Composition, quality, and utilization of SPOM and SSOM

Stable isotope and chlorophyll a *analyses of SPOM and SSOM*

Bottom water samples were collected 0.1 m above the sediment-water interface at each sampling site using an amber collection bottle for quantification of chlorophyll *a* and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of suspended particulate organic matter (SPOM). All samples were sieved on a 250 µm screen to eliminate large detrital particles and zooplankton and then filtered on three different precombusted Whatman GF/F glass fiber filters (0.7 µm porosity) to determine carbon and nitrogen isotopic compositions of SPOM and chlorophyll *a* concentration. Filters were stored at -20 °C in the dark until analysis. Filters for carbon and nitrogen analyses were freeze dried. Carbonates were removed from filters for $\delta^{13}C$ and %C analyses by contact with HCl fumes in a vacuum-enclosed system for four hours; $\delta^{15}N$ and %N analyses were carried out on raw filters.

One cylindrical sediment core (37.4 cm^2) was collected by divers from each site (HMB-HME, Figure 1, 4 cores in total per sampling event) for stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of surface sediment organic matter (SSOM) and chlorophyll *a* measurements. Cores were collected

and handled with minimal disturbance; the top 2 cm were sliced and stored at -20 °C in the dark until processing in the laboratory. Samples were thawed and sieved wet on a 500 µm mesh screen to eliminate macrofauna, shell pieces and large detrital particles. Sieved sediment was freeze dried and ground using a mortar and pestle. Carbonates were removed from sediment for $\delta^{13}C$ and %C analyses using 2 mol L^{-1} HCl. HCl was added drop by drop until cessation of bubbling. Samples were then dried at 65 °C using a dry block heater under a fume hood. Dried samples were re-homogenized into ultrapure water using an ultrasonic bath, freeze dried and ground again. $\delta^{15}N$ and %N measurements, as well as chlorophyll *a* analyses, were carried out on raw samples.

Chlorophyll *a* was extracted from filters and sediment overnight using a non-acidification technique and read on a Turner Trilogy fluorometer (Turner Designs, Sunnyvale, USA) (Welschmeyer 1994; EPA method 445.0 1997).

Stable isotope analyses of Crassostrea virginica

Three different-sized oysters (20 mm < shell height < 160 mm) were collected from the top and near the base of the reef at each site (HMB-HME, Figure 1) by divers for stable isotope analyses. Oysters were stored on ice for transport to the laboratory and then scrubbed and kept for 36 hours in aerated seawater for evacuation of gut contents (Blomberg et al. 2017, Dubois et al. 2007). The oysters were then frozen at -20 °C before being dissected to collect the digestive gland material. Digestive gland samples were freeze dried and ground to a homogenous powder using a ball mill (MM400, Restch, Germany). Lipids were extracted from samples for $\delta^{13}C$ and %C analyses using two successive extractions with cyclohexane. Samples were then dried at 45 °C and ground again. $\delta^{15}N$ and %N analyses were carried out on raw samples.

Determination of isotopic compositions

Elemental and isotopic compositions were determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Milan, Italy) coupled to an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Analyses were conducted at the Littoral, Environment and Societies (LIENSs) Joint Research Unit stable isotope facility at the University of La Rochelle, France. Results are expressed in the δ notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Calibration was completed using reference materials (USGS-24, IAEA-CH6, -600 for carbon; IAEA-N2, -NO-3, -600 for nitrogen). Analytical precision based on the analyses of acetanilide (Thermo Scientific) and peptone (Sigma Aldrich) used as laboratory internal standard was <0.15‰.

Elemental composition and stable isotope data statistical analyses

C/Chl *a* and C/N ratios are often used as proxies to estimate the quality of organic matter (Cifuentes et al. 1989, Harmelin-Vivien et al. 2010, Lebreton et al. 2016, Malet et al. 2007, Savoye et al. 2003). C/Chl *a* ratios were calculated using the total organic carbon quantity from the acidified sample (μg L^{-1} SPOM; μg g^{-1} SSOM) and dividing by the concentration of Chl *a* (μg L^{-1} SPOM; μg g^{-1} SSOM). C/N ratios were calculated using the total organic carbon quantity from the acidified sample ((μg g^{-1})/12 g mol^{-1}) and dividing by the total nitrogen organic quantity of the raw sample ((μg g^{-1})/14 g mol^{-1}). SPOM C/Chl *a* ratios and C/N ratios were correlated with mean salinity using Spearman's rank correlations. Additionally, isotopic compositions of SPOM ($\delta^{13}C$ and $\delta^{15}N$) were correlated with all water quality parameters.

Contributions of SPOM and SSOM as food resources to oysters were estimated by solving mixing models within a Bayesian framework (R package SIMMR; Parnell 2016). Separate models were created for each sampling date. Isotope compositions of oysters and food sources were compared considering trophic fractionation factors of 0.39 ± 1.30‰ (mean ± standard deviation [SD]) for $\delta^{13}C$ values (Post 2002) and of 2.5 ± 2.5‰ for $\delta^{15}N$ values (Vander Zanden and Rasmussen 2001). Theoretical oyster food resource use was computed by subtracting the trophic fractionation factors from observed $\delta^{13}C$ and $\delta^{15}N$ values of oysters to correct for fractionation. Mixing models were run for 10,000 iterations with the first 1,000 iterations discarded. Means and credibility intervals (CI) of 95% were reported. Statistical analyses on stable isotope data were performed using R 3.4.1 (R Foundation for Statistical Computing 2017).

RESULTS

Water quality measurements

Mean salinity values from July 2014 to May 2017 fluctuated over 22 units, ranging from 8.6 ± 0.2 (mean ± standard error [SE]) in July 2015 to 31.0 ± 0.1 in October 2014 (Figure 2A). Salinities at HMR were on average 2.8 above that of LCRA station NCM4. Salinity at Half Moon Reef decreased from 16 to 9.1 from May to July 2015, although it is possible that the salinity was lower at the reef in June 2015. A similar magnitude salinity decrease at the LCRA station occurred in April to May 2016, although the same decrease was not observed during the sampling event at HMR in July 2016 due to rebounding salinities following the disturbance. Daily salinities from nearby LCRA stations were <10 during extended periods in late spring 2015 (28-58 days, missing June salinity data) and late spring 2016 (38 consecutive days) prior to the July sampling events, allowing us to observe the effects of these salinity variations. Mean temperature showed expected seasonal patterns, ranging from 9.6 ± 0.2 °C in January 2015 to

31.0 ± 0.3 °C in July 2014 (Figure 2B). Dissolved oxygen concentrations were greatest during the coolest sampling periods, and ranged from 5.8 ± 0.2 mg L^{-1} in July 2014 to 10.2 ± 0.1 mg L^{-1} in January 2016 (Figure 2C). pH was fairly consistent, ranging from 8.0 ± <0.1 in April 2016 to 8.7 ± <0.1 in July 2014 (Figure 2D). Mean turbidity was variable and ranged from 4.7 ± 0.9 NTU in October 2015 to 38.2 ± 2.3 NTU in May 2017 (Figure 2E). Chlorophyll *a* was also variable and ranged from 1.6 ± 0.4 μg L^{-1} during April 2016 to a peak of 40.7 ± 2.1 μg L^{-1} during May 2017, coinciding with the greatest turbidity (Figure 2F).

The first and second principal components (PC1 and PC2) for the water quality variables explained 38% and 27% (65% total) of the variation in the data, respectively (Figure 3, Appendix 1.1). Dissolved oxygen and salinity were strongly negatively correlated with temperature on PC1, indicating seasonal effects. Turbidity and chlorophyll *a* were closely coupled and negatively correlated with salinity and pH, indicating freshwater inflow effects. The highest dissolved oxygen concentrations and lowest temperatures occurred in winter, while lower overall dissolved oxygen concentrations and higher temperatures occurred in summer.

Reef community characterization

Encrusting macrofauna

Oysters were found in 85% of the encrusting macrofauna samples. Measured shell heights (>5 mm) ranged from 5.1 to 153.0 mm and generally increased over time (Figure 4A). Shell height was significantly different among date-site combinations ($p < 0.0001$; Appendix 2.1, Appendix 2.1e). Oyster spat dominated the population in the first six months since reef completion; 99% of oysters collected in July 2014, and 76% of oysters collected in October 2014 were spat (Figure 4B). No spat were observed after January 2016. The first market-sized oyster (>76 mm) was seen in January 2015, with market oysters making up 72% of the population in

February 2017, and 71% in May 2017.

Mean abundance was 886 ± 59 n m^{-2}, with a maximum of 7313 oysters m^{-2} observed during the first monitoring period in July 2014 (Figure 4B, Appendix 2.3). Mean oyster abundance was significantly different among date-site combinations but was generally higher in the first year of sampling (July 2014-July 2015, $p < 0.0001$; Appendix 2.1, Appendix 2.1b).

Mean percent coverage of substrate by oysters was 45.2 ± 2.0% (Figure 4C). Oyster coverage of 100% was observed from at least one replicate from one site in January 2015, 9 months post-restoration, and during every sampling from January 2016 through the final sampling in May 2017 (Appendix 2.3). Oyster percent cover was significantly different among date-site combinations ($p < 0.0001$, Figure 4C, Appendix 2.1, Appendix 2.1d). In general, samples collected in 2014 and 2015 had less oyster coverage than those collected in 2016 and 2017. There were no easily interpretable patterns among sites for shell height, abundance, or percent cover.

Eleven other encrusting species were observed, with barnacles and serpulid worms the next most abundant species after oysters (present in 52% and 43% of samples, respectively; Appendix 2.3).

Perkinsus marinus

A total of 403 oysters ranging in size from 26.2 mm to 160.7 mm were assessed for presence of *Perkinsus marinus* (approx. 36 oysters / sampling period, Appendix 2.4). *Perkinsus marinus* infection was not detected from any oysters examined.

Reef-resident community

Reef-resident faunal abundance and diversity were significantly different among treatment-date combinations ($p < 0.001$ and $p < 0.0001$, respectively; Appendix 2.2, Appendix

2.2b, Appendix 2.2d). In general, there were higher faunal abundances early in the study that decreased through time; the exception was May 2015, when a large recruitment of *Astyris* sp. (a dove snail species) was observed in the unrestored area (Figure 5A). Following the first low salinity event in late spring 2015, the restored reef had twice the density of organisms (average 299 individuals m^{-2}) than in the unrestored habitat (144 individuals m^{-2}). Species richness and N1 diversity were generally highest prior to the first low salinity event (Figure 5C, D). Species richness declined from ~12 species in April 2015 to ≤ 5 species in July 2015 at the restored and unrestored areas. N1 diversity in the unrestored area became consistently higher than in the restored reef in July 2015 although this difference was not significant. Panopeid mud crabs and porcelain crabs were the most abundance reef-resident species, with 39% and 26% abundance relative to the total (Appendix 2.5). In the unrestored habitat, the gastropod *Astyris* sp. was numerically dominant (57% relative abundance).

Biomass was generally higher in the restored reef and was significantly different among treatment-date combinations ($p < 0.0001$; Figure 5B, Appendix 2.2, Appendix 2.2j). Following the low salinity event in late spring 2015, the restored reef had ten times more biomass (average 22,500 mg m^{-2}) than the unrestored habitat (average 2,030 mg m^{-2}). In January 2016, extraordinarily high biomass (78,800 mg m^{-2}) in the restored reef was generated by a few stone crabs, *Menippe adina,* one of which had a dry weight greater than 60,000 mg. Overall, stone crabs made up 68% of relative biomass in the restored reef, with the largest individual making up 5% of all reef-resident biomass. Paguroidea (hermit crabs) were 25% of relative biomass in the unrestored habitat, with stone crabs, mud crabs, and the oyster drill, *Stramonita haemastoma* following with 18, 14, and 13% relative biomass, respectively (Appendix 2.6).

Abundance-based reef-resident community composition generally clustered into three

main groups with at least 55% similarity within each group ($p < 0.05$; Figure 7A). The first group, on the left of the nMDS plot, includes communities from both habitats in the first year post-restoration, prior to the initial low salinity event, and was dominated by *Astyris* sp., *Parvanachis ostreicola*, and *Costoanachis* sp. dove snails, porcelain crabs, and *Petrolisthes* sp. The second two groups separated generally by treatment, with faunal community on the restored reef dominated by panopeid mud crabs and porcelain crabs, compared to a community dominated by mud crabs, hermit crabs, porcelain crabs, and *Astyris* sp. and *Parvanachis* sp. dove snails in the unrestored habitat. The faunal community from the unrestored habitat in July 2015 grouped separately, and was dominated by gobiidae (mainly larval *Gobiosoma* sp.) and hermit crabs (Appendix 2.9).

Biomass-based reef-resident community composition clustered into four main groups with at least 55% similarity within each group ($p < 0.05$; Figure 7B). Similar to the abundance-based results, one cluster includes communities from both habitats prior to the 2015 salinity decrease. For subsequent dates, faunal communities from the restored habitat and unrestored grouped separately, with the July 2015 faunal community from the unrestored habitat grouping alone. Biomass-based community composition during the initial year was dominated by panopeid mud crabs, stone crabs, porcelain crabs, and dove snails in both restored and unrestored habitats. One year post-construction, and following the low salinity event in late spring 2015, community composition on the restored reef was characterized by stone crabs and mud crabs, whereas the unrestored sites were characterized by mud crabs, hermit crabs, porcelain crabs, and oyster drills. Biomass-based community composition in the unrestored habitat in July 2015 was dominated by stone crabs (Appendix 2.10).

The best water quality descriptor of reef-resident abundance-based community composition is the combination of salinity and dissolved oxygen (Rho = 0.284, $p \leq 0.05$; Appendix 1.2). Reef-resident biomass-based community composition is best described by salinity, although this is not significant (Rho = 0.148, p = 0.39; Appendix 1.3). Salinity was positively correlated with faunal abundance, biomass, species richness, and N1 diversity in both the restored and unrestored habitats (Table 1). In both the restored and unrestored areas, salinity was positively correlated with crustacean abundance, as well as gastropod abundance and biomass (Table 2). Biomass was significantly correlated with temperature in both the restored and unrestored habitats (Table 1). N1 diversity was negatively correlated with temperature and pH in the unrestored habitat, and turbidity and chlorophyll *a* in the restored habitat (Table 1). Also in the restored habitat, species richness was negatively correlated with turbidity, and chlorophyll *a* was negatively correlated with biomass (Table 1).

Reef-associated community

There were significant differences in reef-associated faunal abundance and species richness across sampling dates but not by treatment ($p < 0.05$; Figure 6A, C, Appendix 2.2, Appendix 2.2f, Appendix 2.2i). In areas adjacent (~13 m) and distant (~150 m) to the restored reef, mysidacea were the most abundant reef-associated species group collected, making up 78.8% and 83.0% of relative abundance (Appendix 2.7), and with over 43,000 individuals collected over the study period. Abundance of reef-associated organisms in adjacent and distant areas was generally <5 individuals m^{-2} except during two large recruitment periods in April 2016 (28 and 14 individuals m^{-2} in the distant and adjacent habitats, respectively) and May 2017 (10 and 12 individuals m^{-2} in the distant and adjacent habitats, respectively; Figure 6A). Species richness decreased from a peak of 25.0 and 22.8 species per tray (unrestored and restored,

respectively) immediately post-restoration to 0.8 (unrestored) in July 2015 coincident with the 2015 low salinity event; species richness then increased in both areas but was generally less than the first year of reef development (Figure 6C). Hill's N1 diversity was significantly different among treatment-date combinations ($p < 0.0001$; Figure 6D, Appendix 2.2, Appendix 2.2h). The highest inter-date variability in diversity occurred prior to the 2015 low salinity event and stabilized at lower diversities for the remainder of the study period. Biomass was significantly different among treatment-date combinations ($p < 0.0001$; Appendix 2.2, Appendix 2.2k). Biomass of organisms in both the adjacent and distant areas was highest during the first monitoring period in April 2014 (38 mg m^{-2} and 42 mg m^{-2}, respectively), and decreased to below 20 mg m^{-2} in both areas for the remainder of the study (Figure 6B). In adjacent areas, biomass of reef-associated species was dominated by portunid crabs (35.7% relative biomass). Distant areas were characterized by mysids, portunid crabs and the Atlantic croaker, *Micropogonias undulatus* (17.1%, 15.6%, and 12.2% relative biomass respectively; Appendix 2.8).

The abundance-based community composition of the restored and unrestored sites were at least 55% similar to each other, except for those from July 2015, which were at least 7% and 17% similar in the restored and unrestored habitats, respectively (Figure 8A). Restored and unrestored treatments were generally grouped by date pairs, with mysid abundance characterizing differences between treatments. Biomass-based community composition is generally consistent with the abundance-based community nMDS plot, with April 2014 and July 2015 grouping separately, and no distinction between treatments observed (Figure 8B).

The best water quality descriptors of abundance-based community composition in adjacent and distant areas are the combination of turbidity, salinity and dissolved oxygen (Rho =

0.485, $p < 0.04$, Appendix 1.4). Biomass-based community composition was best described by the combination of salinity and dissolved oxygen (Rho = 0.531, $p < 0.01$, Appendix 1.5). Salinity was positively correlated with faunal abundance, biomass, Hill's N1 diversity, and species richness in both the adjacent and distant areas (Table 1). In adjacent areas, salinity was positively correlated with crustacean abundance, gastropod abundance and biomass, and teleost biomass (Table 2). In distant areas, salinity was positively correlated with crustacean abundance and biomass, and gastropod abundance and biomass (Table 2). Faunal biomass was negatively correlated with temperature in in both adjacent and distant areas, and positively correlated with dissolved oxygen in distant areas (Table 1). N1 diversity was negatively correlated with temperature in distant areas, and positively correlated with pH in adjacent areas (Table 1).

Composition, quality, and utilization of SPOM and SSOM

Organic matter sources

Mean $\delta^{13}C$ values of SPOM ranged from -26.7 ± 0.2 ‰ (mean ± SD) in October 2016 to -24.9 ± 0.3 ‰ in April 2017; mean $\delta^{15}N$ values ranged from 6.1 ± 2.0 ‰ in February 2017 to 8.9 ± 0.3 ‰ in October 2016 (Table 3). Mean $\delta^{13}C$ values of SSOM ranged from -25.9 ± 3.4 ‰ in October 2016 to -22.5 ± 0.7 ‰ in April 2017; mean $\delta^{15}N$ values ranged from 7.3 ± 0.3 ‰ in February 2017 to 8.6 ± 0.2 ‰ in April 2016. Mean chlorophyll *a* concentrations for SPOM ranged from 1.6 ± 0.7 μg L^{-1} (mean ± SD) in April 2016 to 40.7 ± 4.2 μg L^{-1} in April 2017 (Table 4). For SSOM, mean chlorophyll *a* concentrations ranged from 0.01 ± 0.01 μg g^{-1} in July 2016 to 35.4 ± 12.5 μg g^{-1} in April 2017. C/Chl *a* ratios of SPOM ranged from 158 ± 30 to 498 ± 325 at its most degraded quality. C/Chl *a* ratios of SSOM ranged from 79 ± 13 in April 2017 to 1086 ± 210 in October 2016. C/N ratios of SPOM and SSOM ranged from 5.8 ± 2.1 to 14.0 ± 1.7, and from 8.8 ± 1.5 to 15.6 ± 2.4, respectively.

SPOM $\delta^{13}C$ values were positively correlated with salinity (Rho = 0.601, p = 0.005; Table 5, Figure 9), going from -26.1 to -25.0 ‰ for a salinity increasing from 14 to 28, and $\delta^{15}N$ values were negatively correlated with mean salinity (Rho = 0.656, p = 0.002; Table 5, Figure 9), going from 8.5 to 6.1 ‰ for the same variation of salinity. SPOM C/Chl *a* and C/N ratios were both positively correlated with mean salinity (Rho = 0.580, p = 0.009; Rho = 0.754, p < 0.001; Figure 10). As a result, for a salinity variation going from 14 to 28, the C/Chl *a* and C/N ratios increased from 259 to 515 and from 5.77 to 13.95, respectively.

The isotopic compositions of SPOM were also significantly correlated with some other water quality variables: $\delta^{13}C$ values were negatively correlated with temperature (Rho = -0.601, p = 0.005; Table 5) and pH (Rho = -0.577, p = 0.008), and positively correlated with dissolved oxygen (Rho = 0.758, p < 0.0001). $\delta^{15}N$ values were positively correlated with temperature (Rho = 0.656, p = 0.002; Table 5), pH (Rho = 0.742, p < 0.0001), and chlorophyll *a* concentration (Rho = 0.815, p < 0.0001). SSOM $\delta^{13}C$ and $\delta^{15}N$ values, as well as C/Chl *a* and C/N ratios, were not significantly correlated with any water quality variables.

C. virginica

Oysters from the top and bottom of the reef had similar $\delta^{13}C$ and $\delta^{15}N$ values (p > 0.05) and were therefore combined for analyses (Figure 11). Mean $\delta^{13}C$ values of *C. virginica* ranged from -24.2 ± 0.2 ‰ in July 2016 to -22.8 ± 0.2 ‰ in February 2017; mean $\delta^{15}N$ values were relatively stable, ranging from 9.8 ± 0.3 ‰ in April 2016 to 10.9 ± 0.2 ‰ in October 2016 (Table 3). SIMMR mixing model results indicated SSOM as the dominant source of organic matter assimilated by oysters across all sampling dates except July 2016 (Table 6). With the exception of July 2016, the mean 95% credibility interval for contribution of SPOM ranged from 0.29 to 0.58, while the mean 95% credibility interval for contribution of SSOM was higher, ranging

from 0.43 to 0.71 (Table 6). The median contribution of SPOM was negatively correlated with salinity (Rho = -0.935, $p < 0.0001$, Figure 12).

DISCUSSION

Reef community characterization

Changes in the oyster population

Initially high oyster abundances (over 2400 individuals m^{-2} in July 2014) steadily decreased and eventually stabilized in early 2016 at around 250 oysters m^{-2}. Observed patterns were likely due to a combination of gregarious settlement behavior at shorter time scales and competition and predation at longer time scales (Michener and Kenny 1991). Abundance did not show any relationship with environmental variables.

Percent cover of oysters increased by nearly 200% over the course of the study, with the influence of salinity apparent. The initial low salinity event (salinity 9) in 2015 resulted in the lowest oyster cover recorded (24%), whereas April 2016 (salinity 24) showed the highest percent cover (82%), indicating population recovery with increasing salinities. Low salinity events in late spring 2015 and 2016 appear to have had delayed effects on the oyster population, spurring growth following a flush of freshwater. This study supports previous findings that prolonged low salinities can cause oyster mortality, but that pulses of freshwater can promote oyster growth through decreased predation and disease (Beseres Pollack et al. 2011, La Peyre et al. 2013b, La Peyre et al. 2015).

Mean shell height of oysters increased 400% over the three-year study, demonstrating oyster growth and reef development despite changing environmental variables (i.e., salinity and temperature). Spat were not observed beyond the first 21 months of monitoring, which may be due to two major factors. First, low salinity events may have had a negative influence on

reproductive activity. Development and settlement of oyster larvae are influenced by salinity, with egg development having an optimal range of 10 to 22.5 (Davis 1958), and settlement being optimal during periods of high salinity (Hopkins 1935). Second, predation is a constant stressor for oyster spat, which are the target of many reef organisms, such as mud crabs and oyster drills (Galtsoff 1964, MacKenzie 1970), which were more abundant in later sampling periods.

Perkinsus marinus, which causes the oyster disease Dermo, was not detected in any of the oysters sampled, likely due to the relatively young age of the reef and annual low salinity periods which suppress parasite growth (La Peyre et al. 2003, Savage 2017). Increased flow rate, freshets, and extended wet conditions have all been negatively correlated with decreased oyster disease (Beseres Pollack et al. 2011, Lenihan 1999, La Peyre et al. 2003, Ray 1987, Savage 2017). Although no Dermo was identified in HMR, most Texas reefs have some amount of Dermo infection (Savage 2017), and oyster disease is becoming increasingly important as estuaries are subjected to drier conditions. Dermo is spread when the *Perkinsus marinus* parasite is released into the water via infected host feces, pseudofeces, or decomposing tissue (Bushek et al. 2002). I suspect that the distance of HMR from other infected reefs (Andrews and Ray 1988) and lack of commercial harvest and movement of stocks have limited disease progression.

Reef-resident and reef-associated faunal community patterns

Community composition of reef-resident fauna differed before versus after the low salinity event in late spring 2015, accompanied by a reduction in species richness and diversity. The BIO-ENV analysis indicated that salinity contributed to changes in faunal composition, supporting the results of previous studies among oyster populations (Abeels et al. 2012, Livingston et al. 2000, Wells 1961) and estuarine communities in general (Greenwood et al. 2007, Gunter 1961, Kim and Montagna 2009, Montagna and Kalke 1992). One study on oyster

reef communities within three estuaries in Florida found that community structure differed along a salinity gradient, with stations near high-flow tributaries dominated by flatback mud crabs and gobiids, and stations near low-flow tributaries dominated by panopeid mud crabs and porcelain crabs (Tolley et al. 2006). In the present study, gobiids and panopeid mud crabs contributed nearly 45% of abundances in July 2015 (salinity 9) and porcelain crabs and panopeid mud crabs contributed over 38% of abundances during the first year of study (mean salinity 27), supporting the findings of Tolley et al. These results also collaborate a study of benthic macrofauna along a salinity gradient in Nueces Bay, Texas, that found that higher abundance, biomass, and diversity of macrofauna were observed at higher salinities (Mannino and Montagna 1997). A second low salinity event in late spring of 2016 registered only small changes in species richness and diversity, which quickly rebounded with increasing salinity. Although the cause of this varying response is undetermined, I suspect the salinity disturbance experienced on the reef co-occurred with a critical community transition from pioneer organisms to those that thrive with substrate forming species such as bivalves (Cranfield et al. 2004). At this stage of succession, colonizers on the reef may not have been able to survive the initial salinity disturbance, opening niches that were filled by more resilient organisms associated with adult oyster communities (Cranfield et al. 2004, Lundquist et al. 2010). In July 2015, oysters (mean shell height 35 mm) may not have provided sufficient protection from disturbance that oysters in July 2016 (mean height 75 mm) provided. The presence of oysters facilitate other species that may not be able to exist in high disturbance environments (Kimbro and Grosholz 2006).

Faunal communities from areas adjacent (13 m) and distant (150 m) from the reef were more similar by date than by treatment. This supports the theory that the reef structure provides a unique community that does not extend beyond the reef edges (Brown et al. 2013, Humphries et

al. 2011). Reef restoration did not appear to influence faunal communities in adjacent or distant areas.

Relationships between salinity and faunal community measurements

Higher salinities create an environment favorable for increased faunal community abundance, biomass, diversity, and species richness. These community metrics were positively correlated with salinity for both reef-resident and reef-associated fauna supporting a number of other studies (Drake et al. 2002, Mannino and Montagna 1997, Montagna and Kalke 1992, Palmer and Montagna 2015). The most abundant organisms collected on the reef were mud crabs (Panopeidae, >38%), porcelain crabs (*Petrolisthes* sp., >26%), and dove snails (*Parvanachis ostreicola*, >13%). Although the mud crab *Panopeus herbstii* can tolerate reduced salinities, it is typically found in greater numbers at higher salinities, as are *Petrolisthes* sp. (Shumway 1983). The size of organisms can also increase along a salinity gradient (Gunter 1961). Stone crabs, contributing the greatest biomass to the restored reef, are generally restricted to salinities >12 (Menzel et al. 1958). Crustaceans and gastropods were also positively correlated with salinity, whereas teleosts were not, probably due to relatively low abundances for the duration of the study. Previous studies have shown positive correlations between fish assemblages (e.g., abundance, species richness, diversity) and salinity (Barletta et al. 2003, Martino and Able 2003, Peterson and Ross 1991, Thiel et al. 1995). In the present study, higher salinities allowed for crustacean and gastropod taxa groups to proliferate, leading to a richer reef faunal community.

Faunal communities supported by higher salinities can negatively affect oyster populations. Increased salinities (greater than the mean) have been correlated with more abundant or diverse faunal communities and suboptimal oyster populations (Gunter 1955, Tolley et al. 2005b). Many reef organisms prey upon oysters and can make a significant negative impact

on oyster populations under favorable salinity conditions (Brisker and Castagna 1987, Galtsoff 1964, Mathiessen 1971, Menzel and Hopkins 1956). Platyhelminthes flatworm species that prey upon oyster larvae flourish at salinities >15 (Pearse and Wharton 1938). Oyster drill *Stramonita haemastoma* cannot tolerate salinities <12-15 (Garton and Stickle 1980, MacKenzie 1981). Other common predators of oysters, such as the boring sponge, pea crabs, and sea stars were found on HMR, but in relatively small abundances. Oyster space competitors, hooked mussels and barnacles (Galtsoff 1964, Kennedy 1980, Osman et al. 1989), and oyster food resource competitors such as snapping shrimp and other seston-feeders (Abeels et al. 2012) were also observed on the reef. As salinities increase, oyster interactions with predators and competitors are likely to increase, influencing oyster survival.

Quality of food resources

Relationships between salinity, composition, quality of SPOM

SPOM had relatively low $\delta^{13}C$ values (-26.7 ± 0.2 ‰ to -24.9 ± 0.3 ‰), indicating it was mostly made of organic matter of terrestrial origin. I found that as salinity increased, SPOM became more ^{13}C-enriched, and C/Chl *a* and C/N ratios of SPOM increased. The response of $\delta^{13}C$ values to salinity was not unexpected, as it has already been shown that progressive mixing of marine and terrestrial sources exists along the estuarine gradient, with more ^{13}C-depleted material coming from terrestrial sources (e.g., riverine phytoplankton, C_3 plants such as *Batis maritima* and *Salicornia* sp., $\delta^{13}C$ value range -23 to -30‰, Fry and Sherr 1984, Lebreton et al. 2016), and more ^{13}C-enriched matter coming from sources of marine origin (e.g., marine phytoplankton, C_4 salt marsh plants; Bishop et al. 2017, Cifuentes et al. 1988, Harmelin-Vivien et al. 2008, Hughes and Sherr 1983, Riera and Richard 1996). The lowest SPOM $\delta^{13}C$ value was measured in October 2016, after a summer of increased precipitation and extremely low

salinities, indicating a larger importance of terrestrial organic matter in SPOM composition. The highest $\delta^{13}C$ values were measured in February and April 2017, which both followed periods of decreased precipitation and increasing salinity, indicating a larger influence of marine phytoplankton on SPOM composition. $\delta^{15}N$ values of SPOM varied by about 3‰ over the course of the study, with $\delta^{15}N$ values decreasing with an increase in salinity. The lowest $\delta^{15}N$ value was measured in February 2017 (i.e., low precipitations), while the highest $\delta^{15}N$ value was measured in October 2016 (i.e., high precipitations). The ^{15}N-enrichment in SPOM in October 2016 may be due to increased nitrogen loading from sewage effluent (Costanzo et al. 2001).

SPOM C/Chl *a* ratios were generally high (>200), indicating that SPOM was mostly made of degraded material. Mean C/N ratios for SPOM ranged between 5 and 14 for all sampling events. Combination of these ratios indicate that the SPOM was not dominated by fresh phytoplankton or fresh plant material, but the relatively high proportions of N suggests this material could contains a high load of bacteria, enriched in N (Thornton and McManus 1994).

At higher salinities, the quality of the SPOM (based on C/Chl *a* and C/N ratios) became more degraded, which was relatively surprising. One would expect lower salinities to indicate greater loads of terrestrial organic matter (i.e., generally degraded) in estuaries (Riera and Richard 1997, Savoye et al. 2012), leading to a lower quality SPOM pool. This was observed by Cifuentes et al. (1988) in the Delaware estuary, with an increase of C/Chl *a* ratios when approaching the source of fresh water. As previously stated, the opposite pattern was observed in the Lavaca-Colorado estuary. Low salinity events are related to greater inputs of fresh water, which contain nutrients (Montagna and Kalke 1992, Montagna and Yoon 1991). Lebreton et al. (2016) and Reyna et al. (2017) suggested that pulses of freshwater inflow or episodic rain events allow for an increase in autochthonous phytoplankton production due to the increase in nutrient

availability. Autochthonous plankton is of higher quality than detrital organic matter, thereby increasing the overall quality of the SPOM.

Assimilation of food resources

$\delta^{13}C$ values of *C. virginica,* which varied by about 1.4 ‰ over the course of the study, indicated food resources were a mixture of material from the water column (i.e., SPOM) and sediment origin (i.e., SSOM). July and October 2016 oysters, collected after periods of freshwater inflow and low salinity, had the most negative $\delta^{13}C$ values (-24.2 ± 0.2 ‰); February 2017 had the least negative $\delta^{13}C$ values (-22.8 ± 0.2 ‰) following a dry period with higher salinity, so oyster carbon isotopic compositions followed a similar pattern of enrichment as the SPOM. As a result, a larger contribution of SPOM as a food resource for oysters was observed when salinity was decreasing, which is probably related to the higher quality of SPOM during low salinity events.

As previously stated, autochthonous phytoplankton is of higher quality than terrestrial organic matter, which decays as it is drained into rivers and eventually the estuary. This makes autochthonous phytoplankton more likely to be assimilated by oysters (Newell and Jordan 1983). Several studies have shown that food sources available to oysters come in different sizes and nutritional qualities (Jorgenson 1990), and indicate that *C. virginica* can preferentially ingest particles of higher nutritional quality and reject less nutritional food sources as pseudofeces (Newell and Jordan 1983). If lower salinities promote autochthonous phytoplankton production, this may explain the higher contribution of SPOM to oyster assimilation at lower salinities. Freshwater inflow can therefore affect phytoplankton composition and concentration within estuaries, impacting energy transfer to higher trophic levels (Cloern and Dufford 2005, Savoye et al. 2012).

Significance of SSOM contribution

C. virginica consumed organic matter from both water column and sediment almost equally throughout the study. In fact, greater than 50% of SSOM was assimilated in all sampling months except July 2016. High freshwater inflow from the late spring and early summer of 2016 likely led to a larger nutrient load in the estuary, probably increasing the SPOM quality and its assimilation by oysters, to the detriment of SSOM.

$\delta^{13}C$ values of SSOM (-25.9 ± 3.4 ‰ to -22.5 ± 0.7 ‰) fluctuated more than $\delta^{13}C$ values of SPOM, while $\delta^{15}N$ (6.1 ± 2.0 ‰ to 8.9 ± 0.3 ‰) values fluctuated less (overall SSOM more enriched in both cases). The relatively large range of SSOM $\delta^{13}C$ values indicated that it was potentially made of a high diversity of sources, from terrestrial organic matter (generally lower than -23.0 ‰) to trapped phytoplankton (-20 ± 2.8 ‰, Winemiller et al. 2007; -22.1 ‰, Rezek et al. 2017), and possibly microphytobenthos (-22.0 to -12.0 ‰, Lebreton et al. 2016; -18.4 ± 2.3 ‰, Winemiller et al. 2007). The different combinations of these different food sources cannot be estimated just based on SSOM $\delta^{13}C$ values. The slightly higher $\delta^{15}N$ values of SSOM than of SPOM suggest a higher bacterial activity in the sediment, with bacteria relying in trapped organic matter, rather than in SPOM. Neither $\delta^{13}C$ or $\delta^{15}N$ values of SSOM showed a significant relationship with salinity. With only three data collections for SSOM chlorophyll *a* concentration analysis, I cannot interpret patterns in benthic chlorophyll. In addition, C/N ratios did not show any patterns. Neither C/Chl *a* nor C/N ratios were related to salinity.

While SSOM did not show significant patterns relating to water quality parameters, it is important to note that the high relief (1 m) of reef rows and exposure to southerly winds (often 15-25 km h^{-1} over the bay) may contribute to increased re-suspension of SSOM and vertical

mixing within the water column. Therefore, it is difficult to evaluate the influence of SSOM within this reef system.

Conceptual diagram

Salinity variability following large-scale oyster reef restoration of HMR provided an opportunity to evaluate the effects on a critical estuarine resource that is valued for habitat provisioning and numerous ecosystem services (Coen and Luckenbach 2000). Past work indicates successful reef development occurs in areas where freshwater flow can exert influence (Patillo et al. 1997). Episodic low salinity events can improve conditions for oysters (Beseres Pollack et al. 2011, La Peyre et al 2013c, Wilber 1992). Although the rate and duration of salinity change are important factors to consider (Beseres Pollack et al. 2011, McLeod and Wing 2008), evidence indicates that intermittent pulses of freshwater will enhance oyster populations on HMR.

Contributions of freshwater to estuaries can influence $\delta^{13}C$ values and C/Chl *a* ratios of primary producers and therefore primary consumers (Simenstad and Wissmar 1985). Pulses of freshwater spur fresh autochthonous phytoplankton production, which oysters prefer to detritus (Riera and Richard 1996). On HMR, the sources of organic matter appear to be composed of mainly degraded material, independent of season. However, the quality of organic matter was highest following low salinities, indicating episodic flooding can improve food resources for suspension feeders, thereby having a positive effect on oysters (Lebreton et al. 2016) and higher trophic levels.

By integrating the results of the current study with those from previous work, I created a conceptual diagram to visualize the effects of salinity on oyster reef communities similar to HMR (Figure 13; Copeland and Hoese 1966, Dekshenieks et al. 1993, La Peyre et al. 2003, La

Peyre et al. 2013a,b,c, La Peyre et al. 2016, Loosanoff 1965, Savage 2017). For example, crustacean abundance is greatest at higher salinities, with more than 75% of organisms collected in the current study at salinities >20. To limit the proportion of oysters infected with *P. marinus* to less than 50% among Texas estuaries, salinities <20 are recommended (Savage 2017). Finally, the quality of organic matter in the current study was greatest (C/Chl *a* < 200) at salinities below 16. Further research is warranted to examine how pulses of freshwater affect dynamics within oyster reef faunal communities over greater temporal and spatial scales.

This conceptual diagram can be used as a tool for resource managers and restoration practitioners to predict how reef communities may change as a function of changing salinity. For example, this diagram can be used during restoration planning and site selection based on specific goals (enhanced oyster versus faunal populations), or to predict how salinity variations may affect reef communities. It has already been shown that the composition of SPOM in Texas estuaries is affected by freshwater inflow (Bishop et al. 2017, Blomberg et al. 2017, Reyna et al. 2017). While there is a predicted shift towards autochthonous-production dominated estuaries due to future climate predictions (Lebreton et al. 2016), it is unknown how this shift would affect the functioning of estuaries. This diagram can be used to better understand the functioning of oyster reef communities following predicted increased salinity variability in estuaries.

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FIGURES

Figure 1. Map

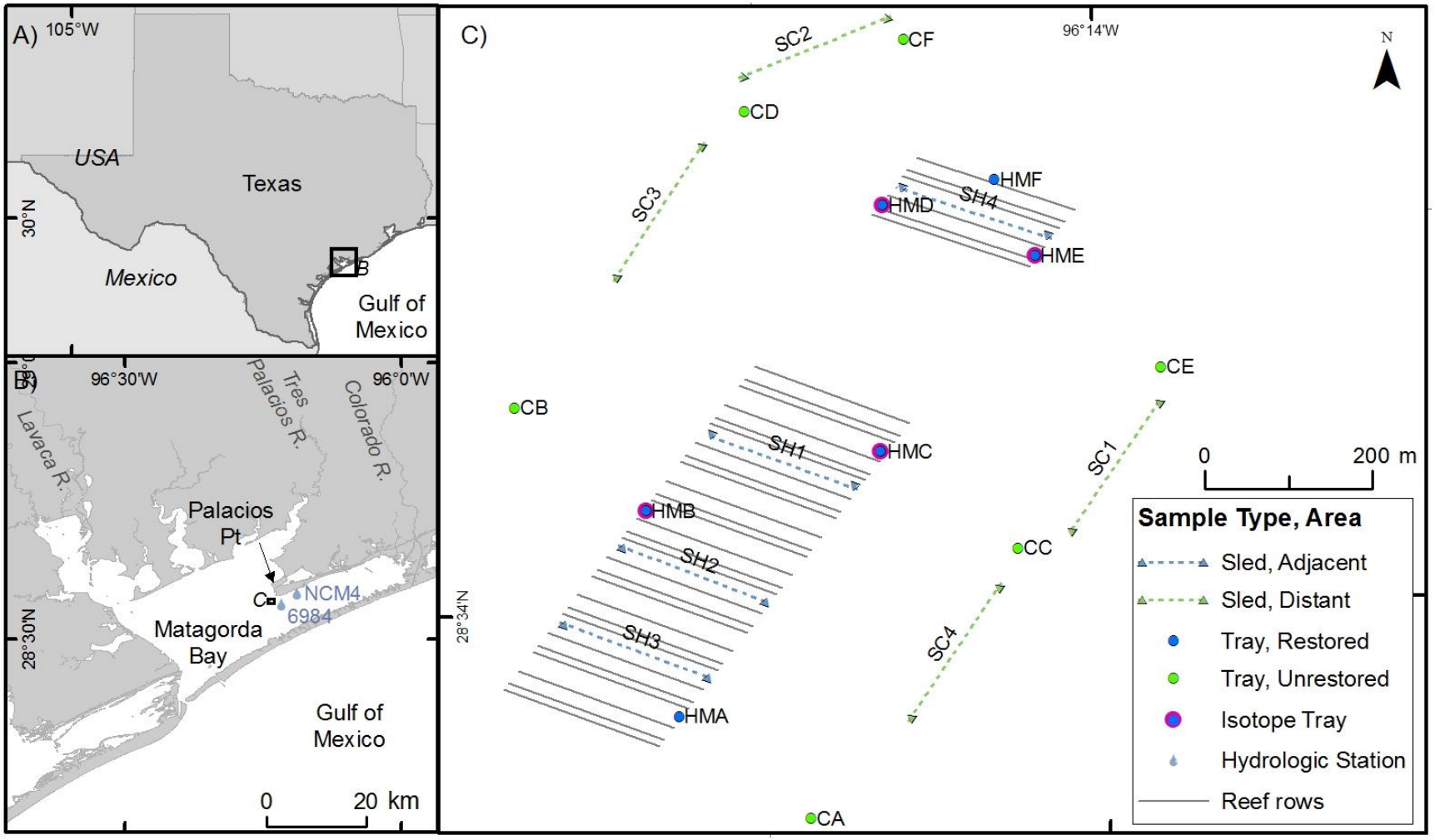

A)
105°W
USA
Texas
Mexico
Gulf of Mexico
30°N
B
B)
96°30'W
96°0'W
Lavaca R.
Tres Palacios R.
Colorado R.
Palacios Pt
C
NCM4
6984
Matagorda Bay
Gulf of Mexico
28°30'N
0
20 km
C)
96°14'W
N
28°34'N
SC2
CF
CD
SC3
HMF
HMD
SH4
HME
CB
SH1
HMC
HMB
SH2
SH3
HMA
CE
SC1
CC
SC4
CA
0
200 m
Sample Type, Area
Sled, Adjacent
Sled, Distant
Tray, Restored
Tray, Unrestored
Isotope Tray
Hydrologic Station
Reef rows

Figure 2.

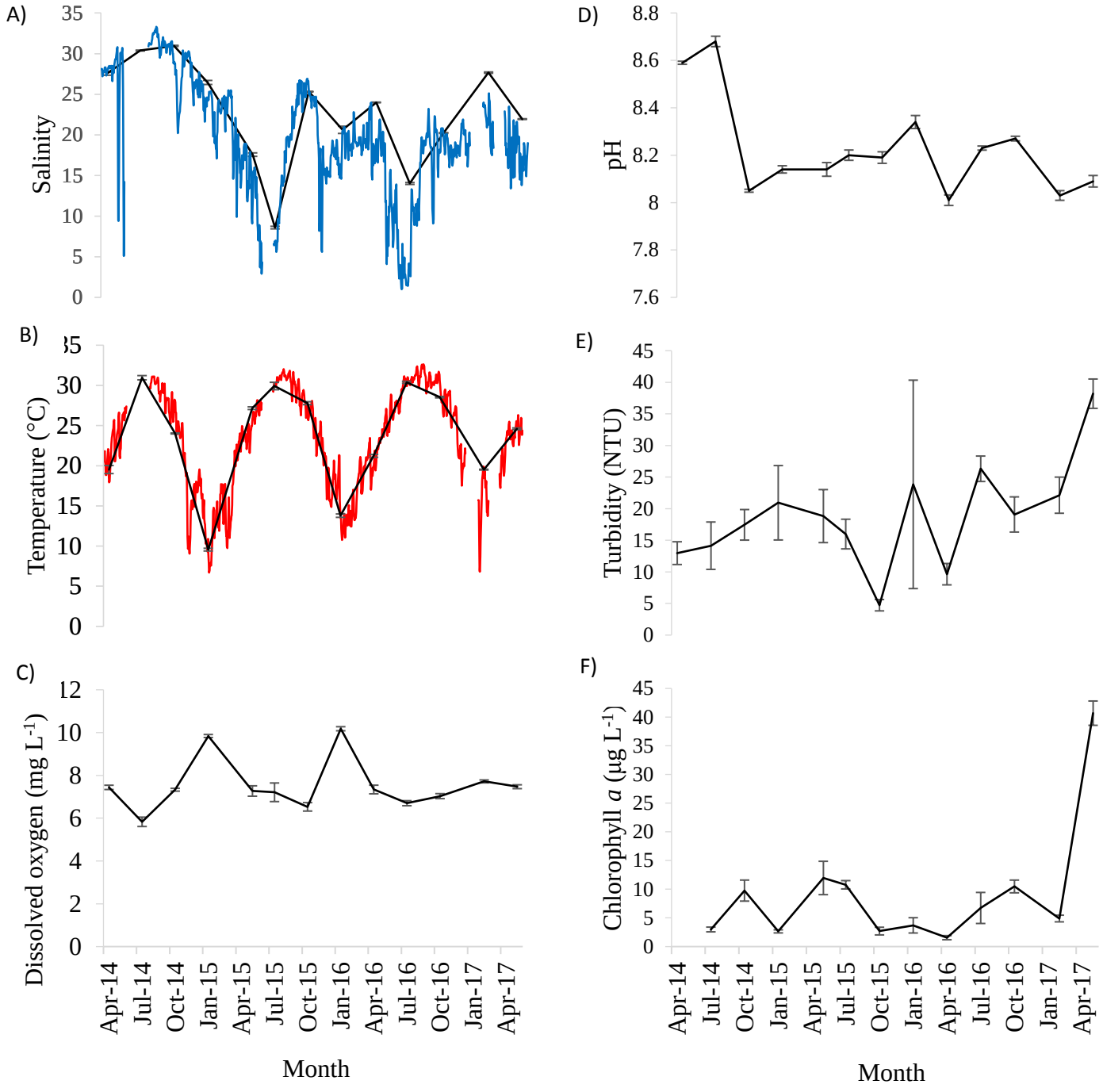

A)
Salinity
35
30
25
20
15
10
5
0
B)
Temperature (°C)
35
30
25
20
15
10
5
0
C)
Dissolved oxygen (mg L-1)
12
10
8
6
4
2
0
Apr-14
Jul-14
Oct-14
Jan-15
Apr-15
Jul-15
Oct-15
Jan-16
Apr-16
Jul-16
Oct-16
Jan-17
Apr-17
Month
D)
pH
8.8
8.6
8.4
8.2
8
7.8
7.6
E)
Turbidity (NTU)
45
40
35
30
25
20
15
10
5
0
F)
Chlorophyll a (µg L-1)
45
40
35
30
25
20
15
10
5
0
Apr-14
Jul-14
Oct-14
Jan-15
Apr-15
Jul-15
Oct-15
Jan-16
Apr-16
Jul-16
Oct-16
Jan-17
Apr-17
Month

Figure 3.

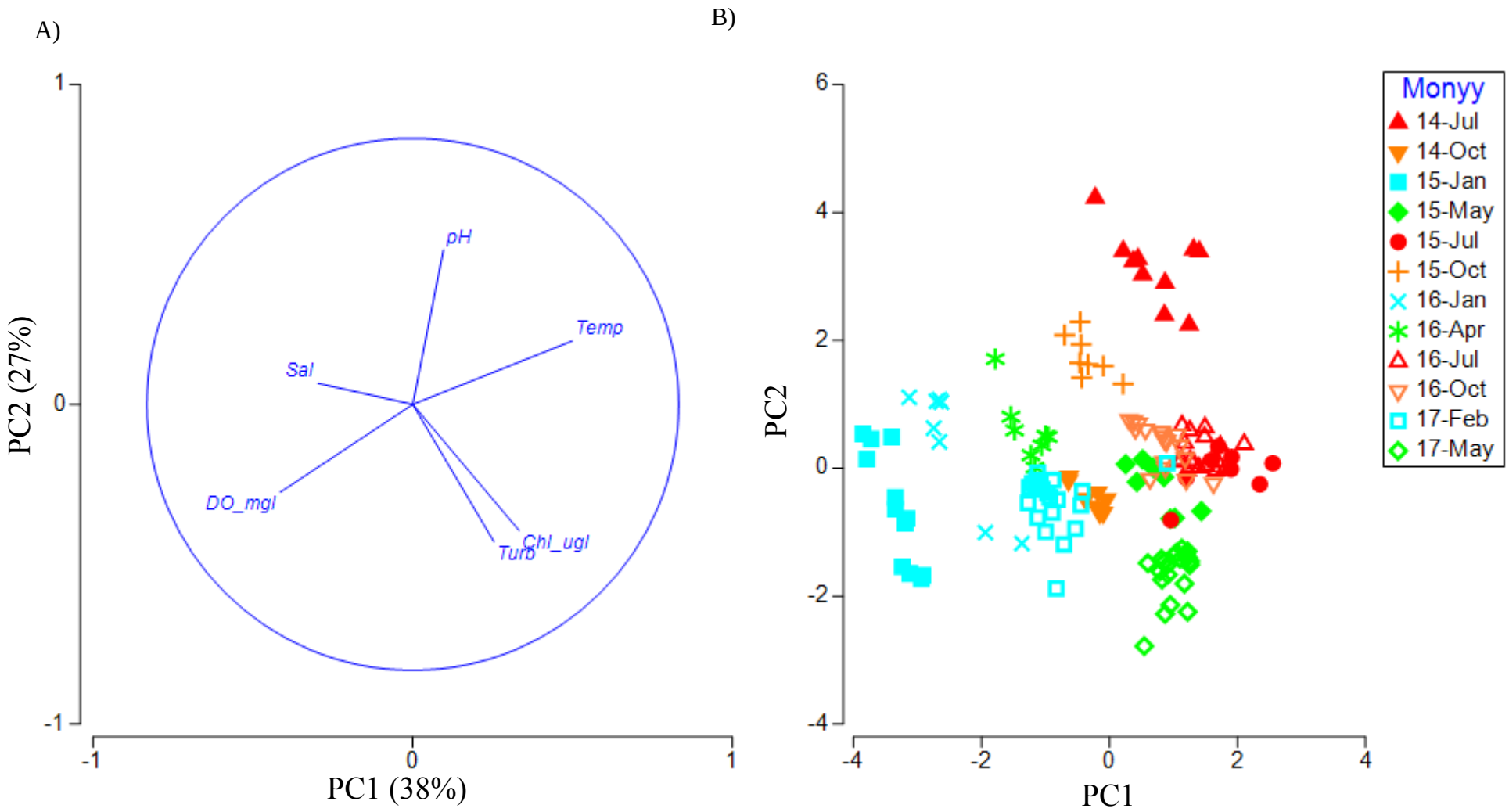

A)
B)
pH
Temp
Sal
DO_mgl
Turb
Chl_ugl
PC2 (27%)
PC1 (38%)
PC2
PC1
Monyy
14-Jul
14-Oct
15-Jan
15-May
15-Jul
15-Oct
16-Jan
16-Apr
16-Jul
16-Oct
17-Feb
17-May

Figure 4. Shell height, abundance, and percent cover of oysters on substrates. Shell height and abundance of oysters categorized by size class. Percent cover shown represents all oysters. Error bars represent standard error.

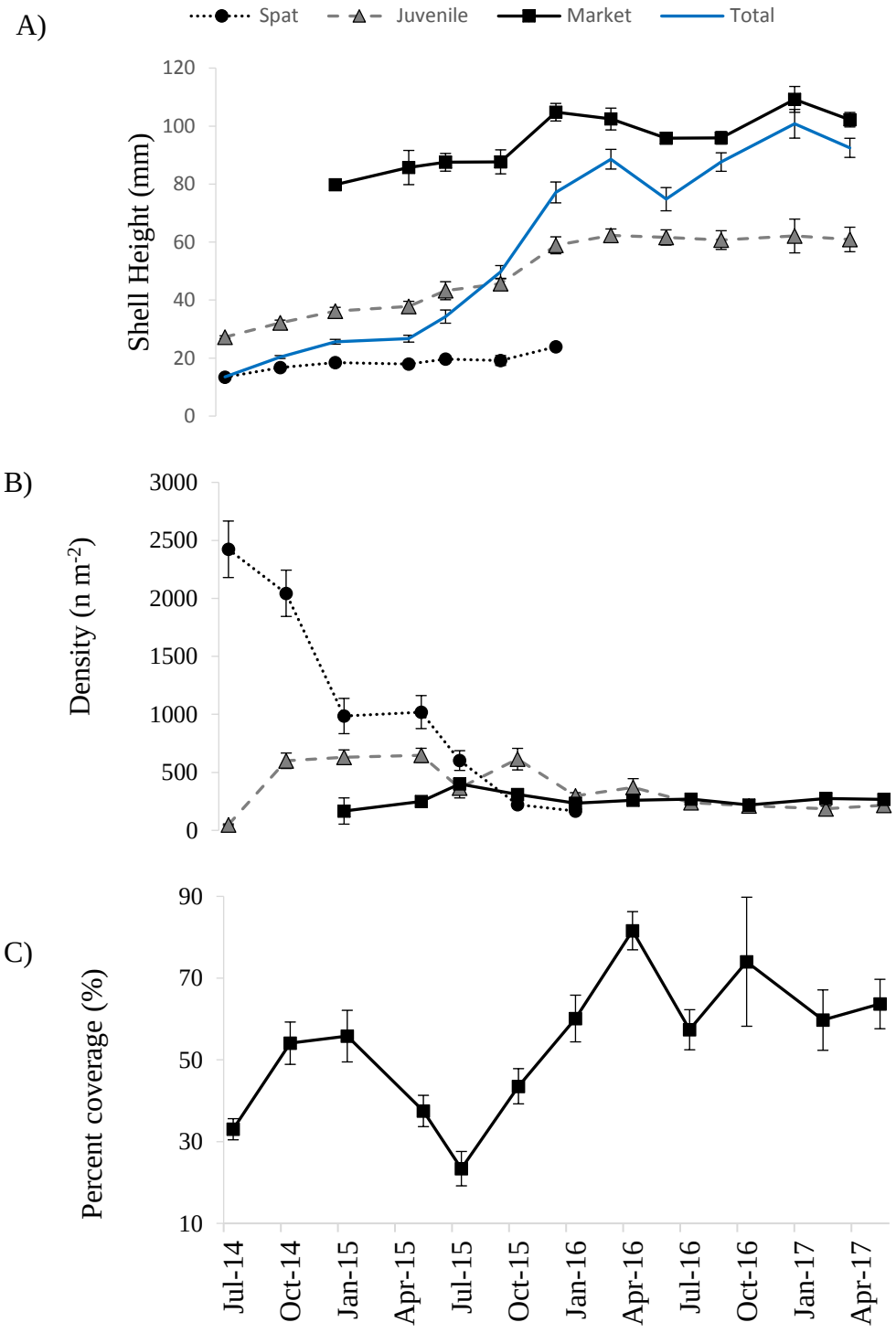


Figure 5.

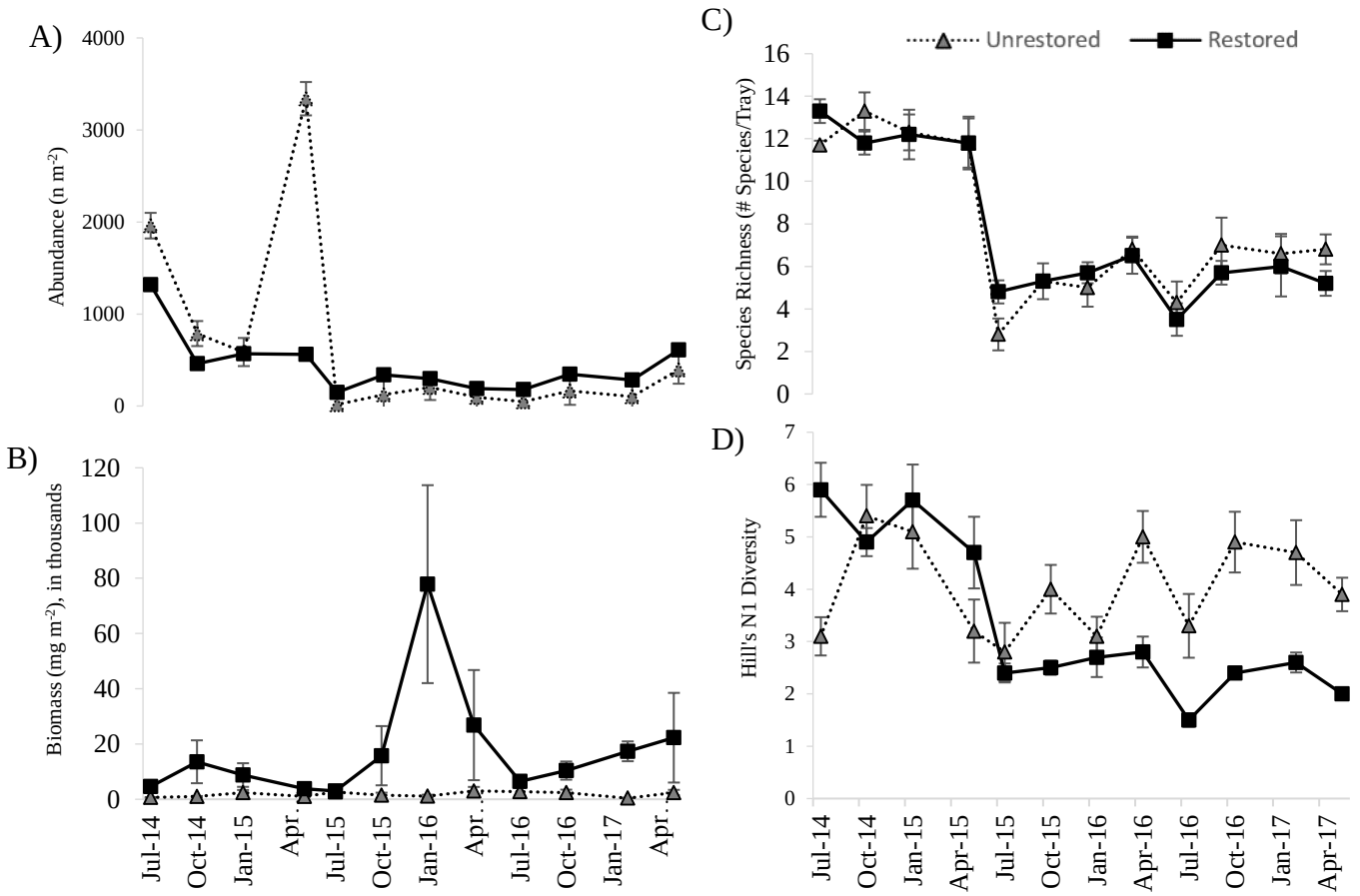

A)
Abundance (n m-2)
4000
3000
2000
1000
0
B)
Biomass (mg m-2), in thousands
120
100
80
60
40
20
0
Jul-14
Oct-14
Jan-15
Apr.
Jul-15
Oct-15
Jan-16
Apr.
Jul-16
Oct-16
Jan-17
Apr.
C)
Unrestored
Restored
Species Richness (# Species/Tray)
16
14
12
10
8
6
4
2
0
D)
Hill's N1 Diversity
7
6
5
4
3
2
1
0
Jul-14
Oct-14
Jan-15
Apr-15
Jul-15
Oct-15
Jan-16
Apr-16
Jul-16
Oct-16
Jan-17
Apr-17

Figure 6.

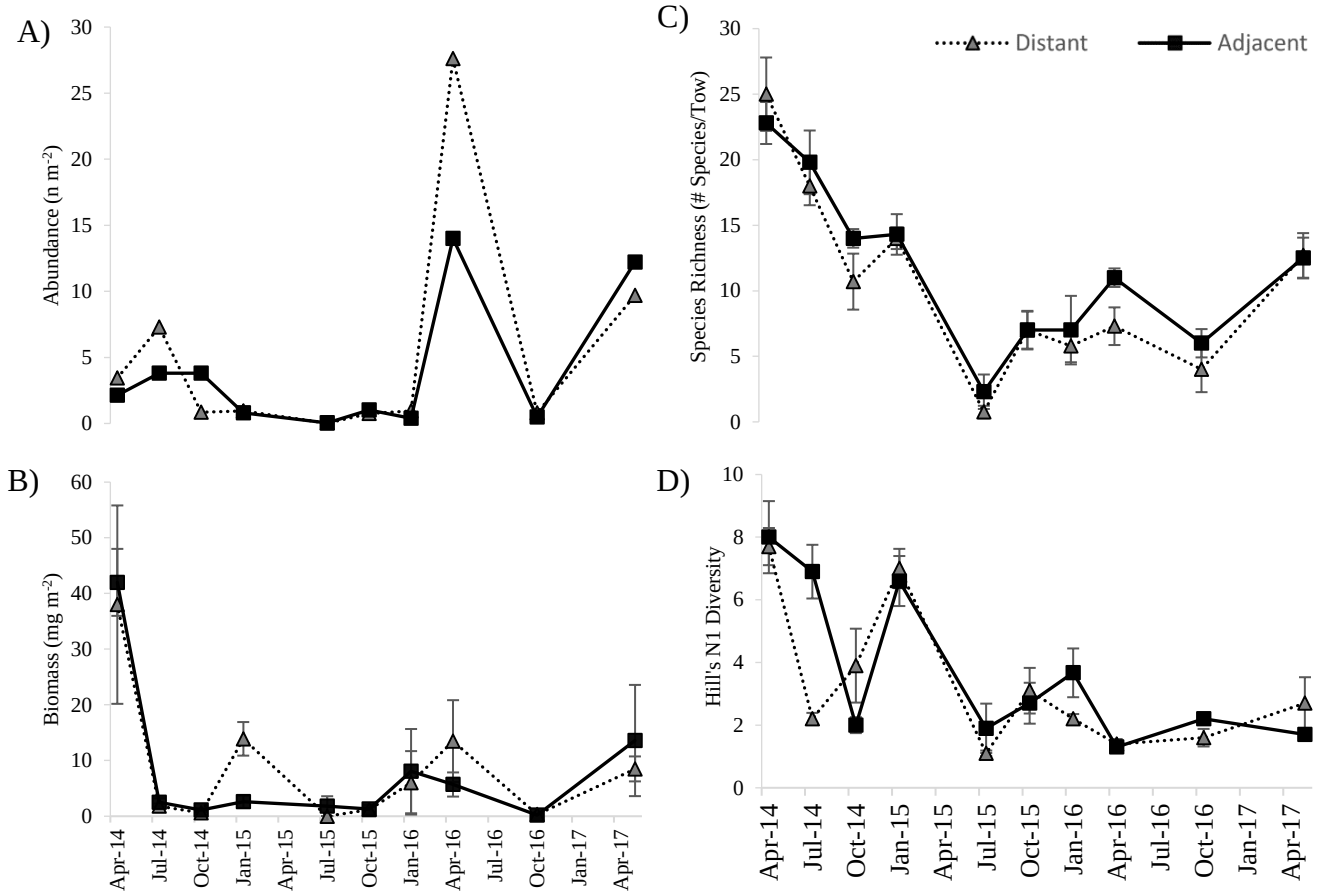
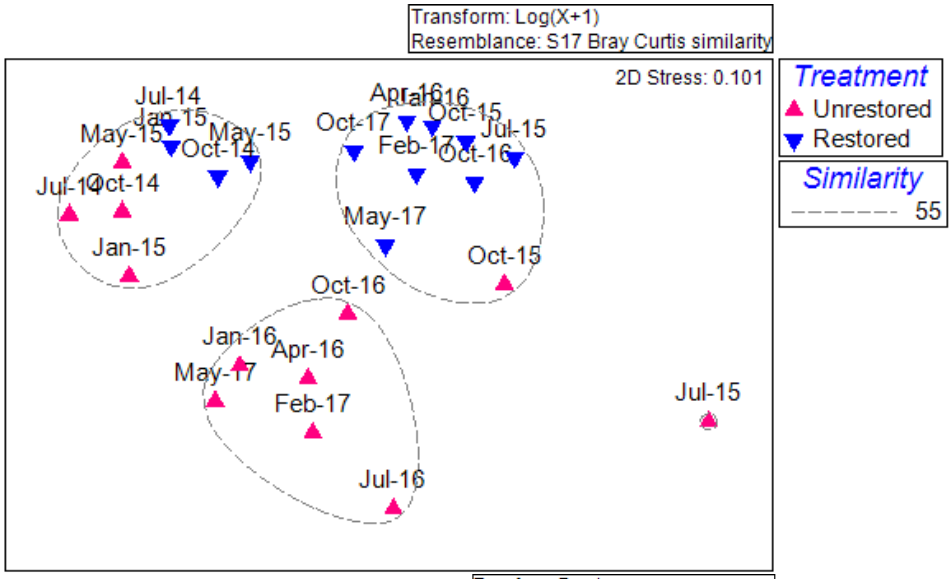

A)
Abundance (n m-2)
B)
Biomass (mg m-2)
C)
Species Richness (# Species/Tow)
Distant
Adjacent
D)
Hill's N1 Diversity
Apr-14
Jul-14
Oct-14
Jan-15
Apr-15
Jul-15
Oct-15
Jan-16
Apr-16
Jul-16
Oct-16
Jan-17
Apr-17

Figure 7.

A)


Transform: Log(X+1)
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.101
Treatment
Unrestored
Restored
Similarity
55
Jul-14
Jan-15
May-15
May-15
Oct-14
Jul-14
Oct-14
Jan-15
Apr-16
Jan-16
Oct-17
Oct-15
Jul-15
Feb-17
Oct-16
May-17
Oct-15
Oct-16
Jan-16
Apr-16
May-17
Feb-17
Jul-16
Jul-15

B)

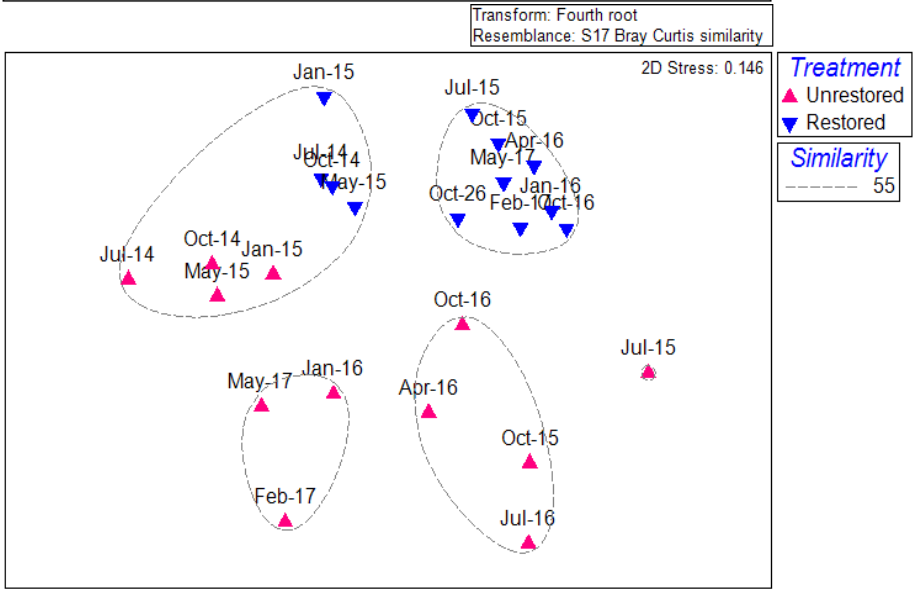
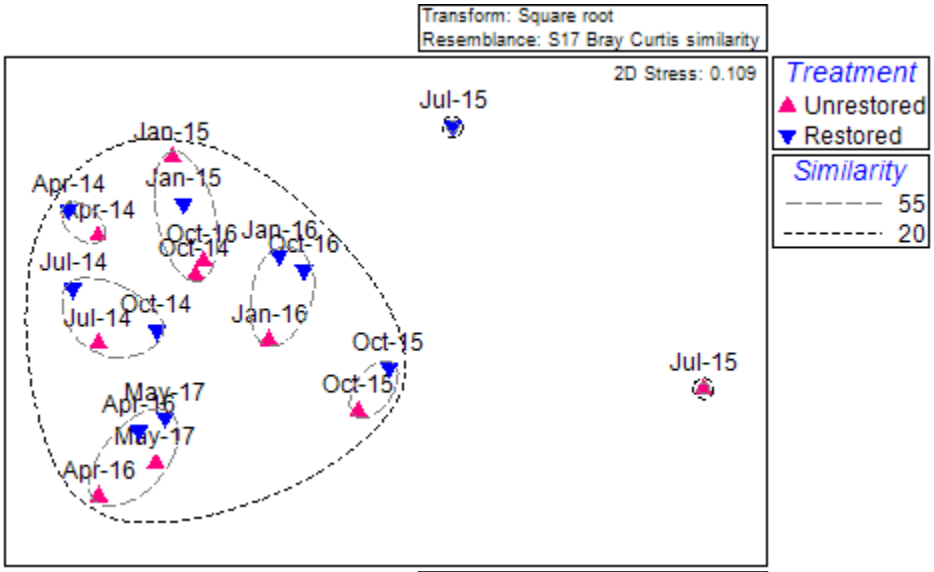

Transform: Fourth root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.146
Treatment
Unrestored
Restored
Similarity
55
Jan-15
Jul-14
Oct-14
May-15
Jul-14
Oct-14
Jan-15
May-15
Jul-15
Oct-15
Apr-16
May-17
Jan-16
Oct-26
Feb-17
Oct-16
Oct-16
Jul-15
May-17
Jan-16
Apr-16
Oct-15
Feb-17
Jul-16

Figure 8.

A)


Transform: Square root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.109
Treatment
Unrestored
Restored
Similarity
55
20
Jul-15
Jan-15
Apr-14
Jan-15
Apr-14
Oct-16
Oct-14
Jan-16
Oct-16
Jul-14
Oct-14
Jul-14
Jan-16
Oct-15
Jul-15
Oct-15
May-17
Apr-16
May-17
Apr-16

B)

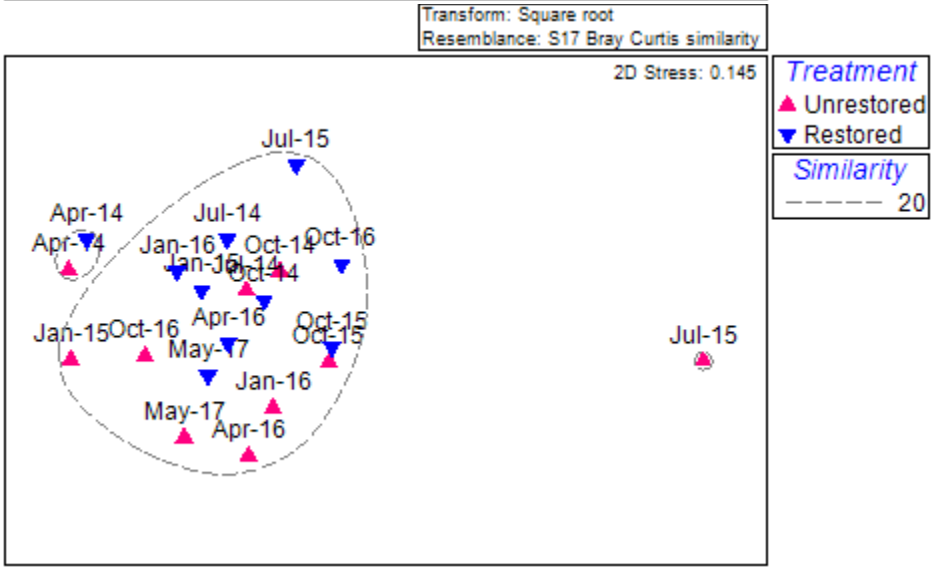

Transform: Square root
Resemblance: S17 Bray Curtis similarity
2D Stress: 0.145
Treatment
Unrestored
Restored
Similarity
20
Jul-15
Apr-14
Jul-14
Apr-14
Jan-16
Oct-14
Oct-16
Jan-16
Oct-14
Apr-16
Jan-15
Oct-16
Oct-15
Oct-15
Jul-15
May-17
Jan-16
May-17
Apr-16

Figure 9.

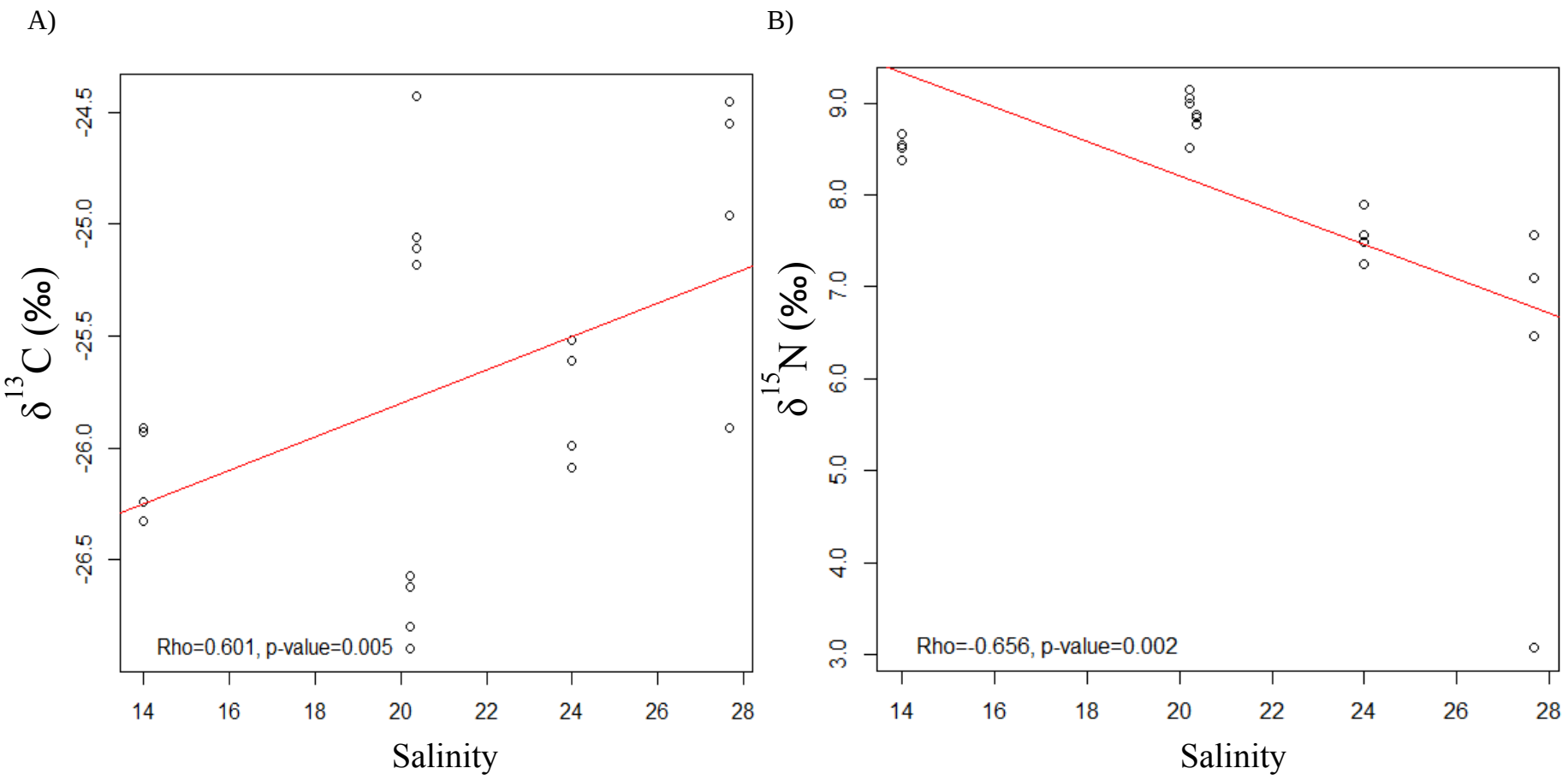

A)
B)
δ13C (‰)
δ15N (‰)
Salinity
Salinity
Rho=0.601, p-value=0.005
Rho=-0.656, p-value=0.002
-24.5
-25.0
-25.5
-26.0
-26.5
9.0
8.0
7.0
6.0
5.0
4.0
3.0
14
16
18
20
22
24
26
28

Figure 10.

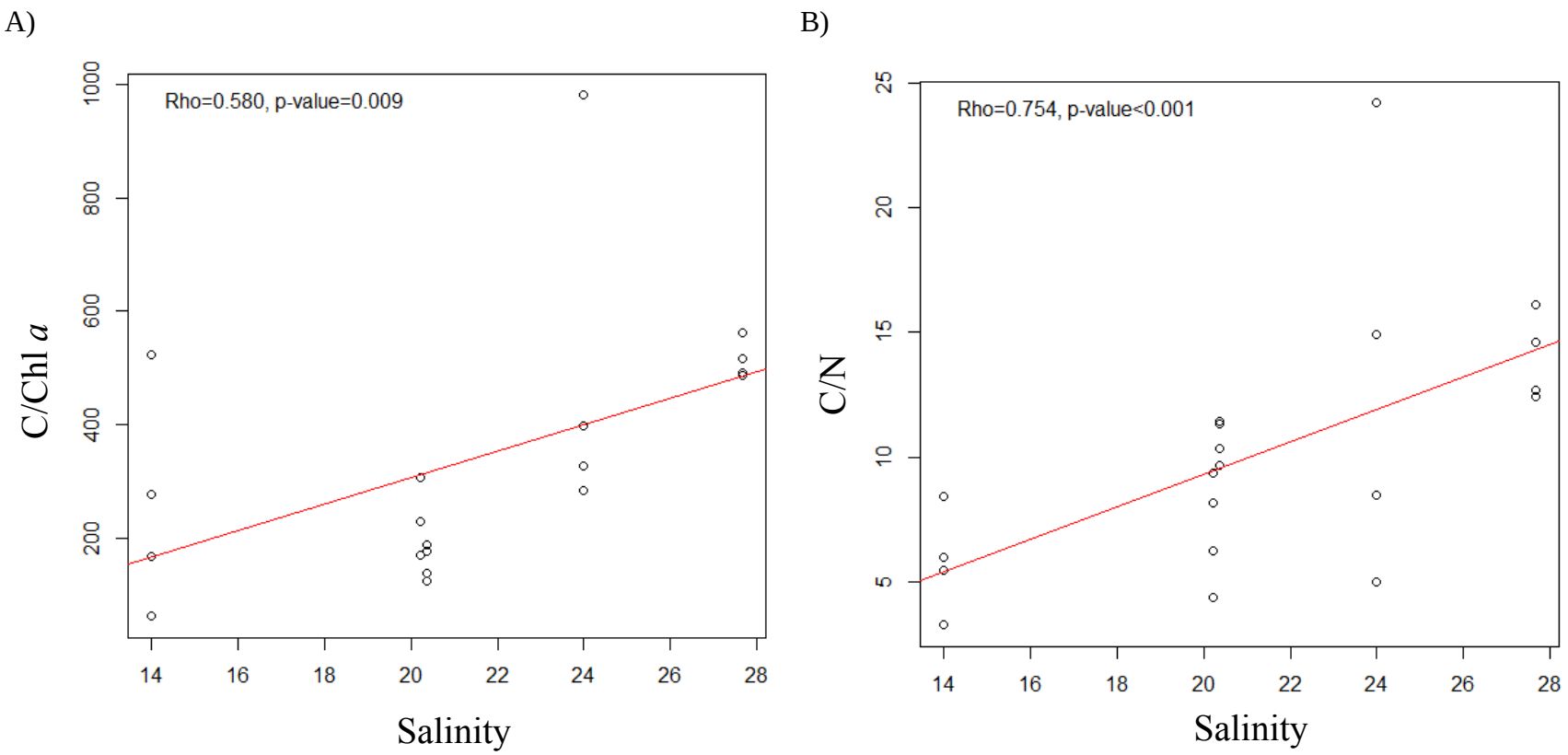

A)
Rho=0.580, p-value=0.009
C/Chl *a*
Salinity
B)
Rho=0.754, p-value<0.001
C/N
Salinity

Figure 11.

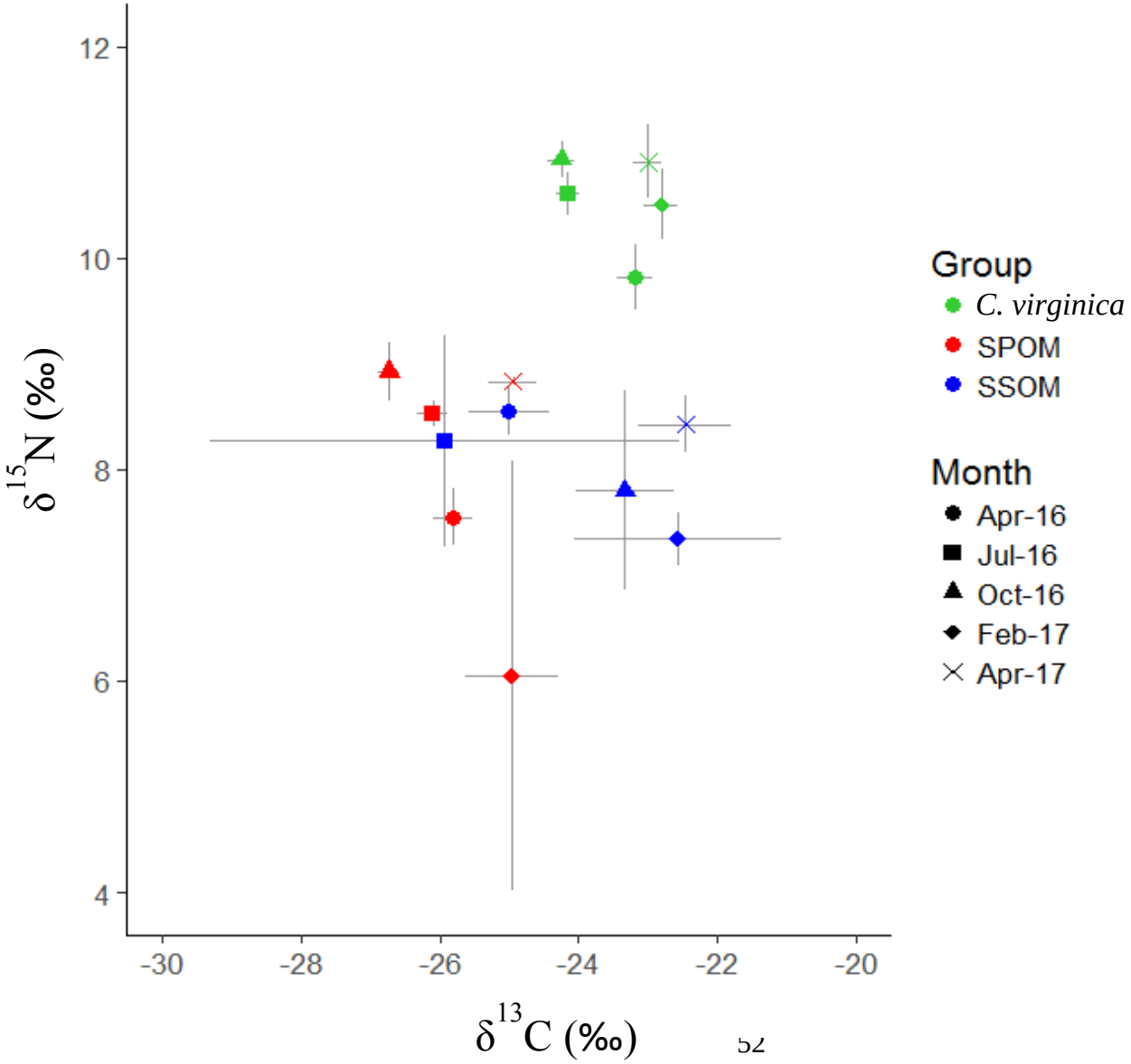

12
10
8
6
4
δ15N (‰)
-30
-28
-26
-24
-22
-20
δ13C (‰)
Group
C. virginica
SPOM
SSOM
Month
Apr-16
Jul-16
Oct-16
Feb-17
Apr-17

Figure 12.

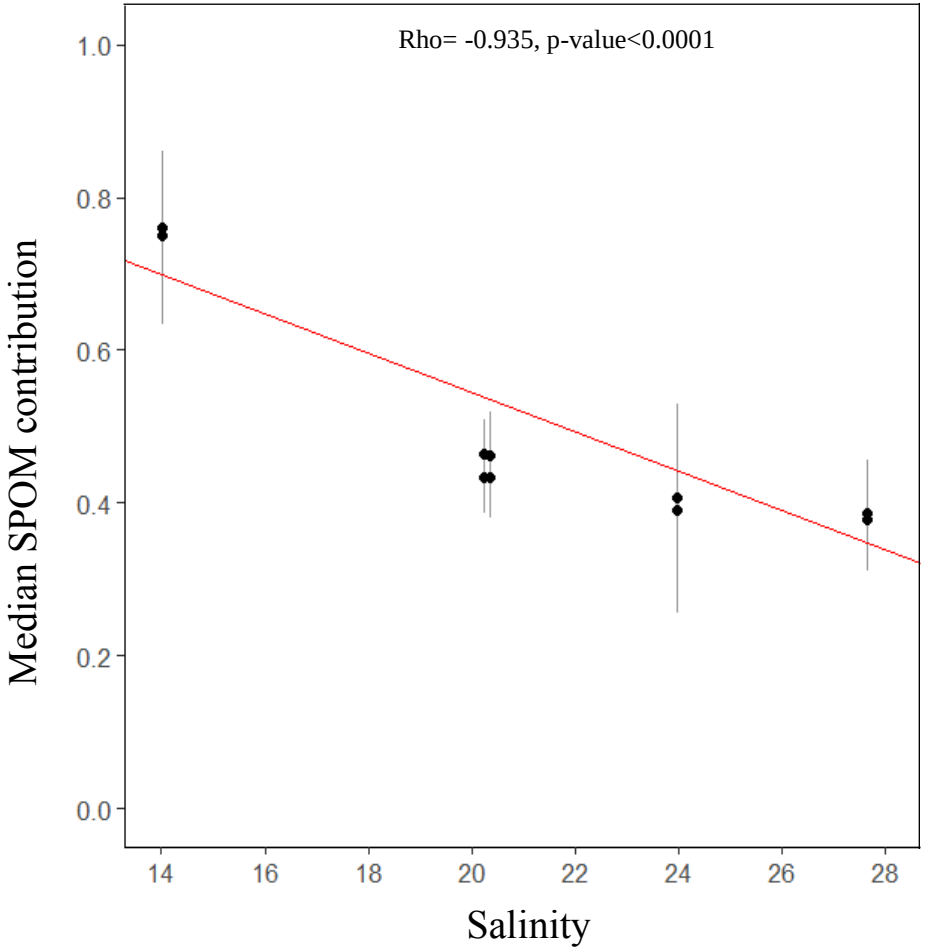
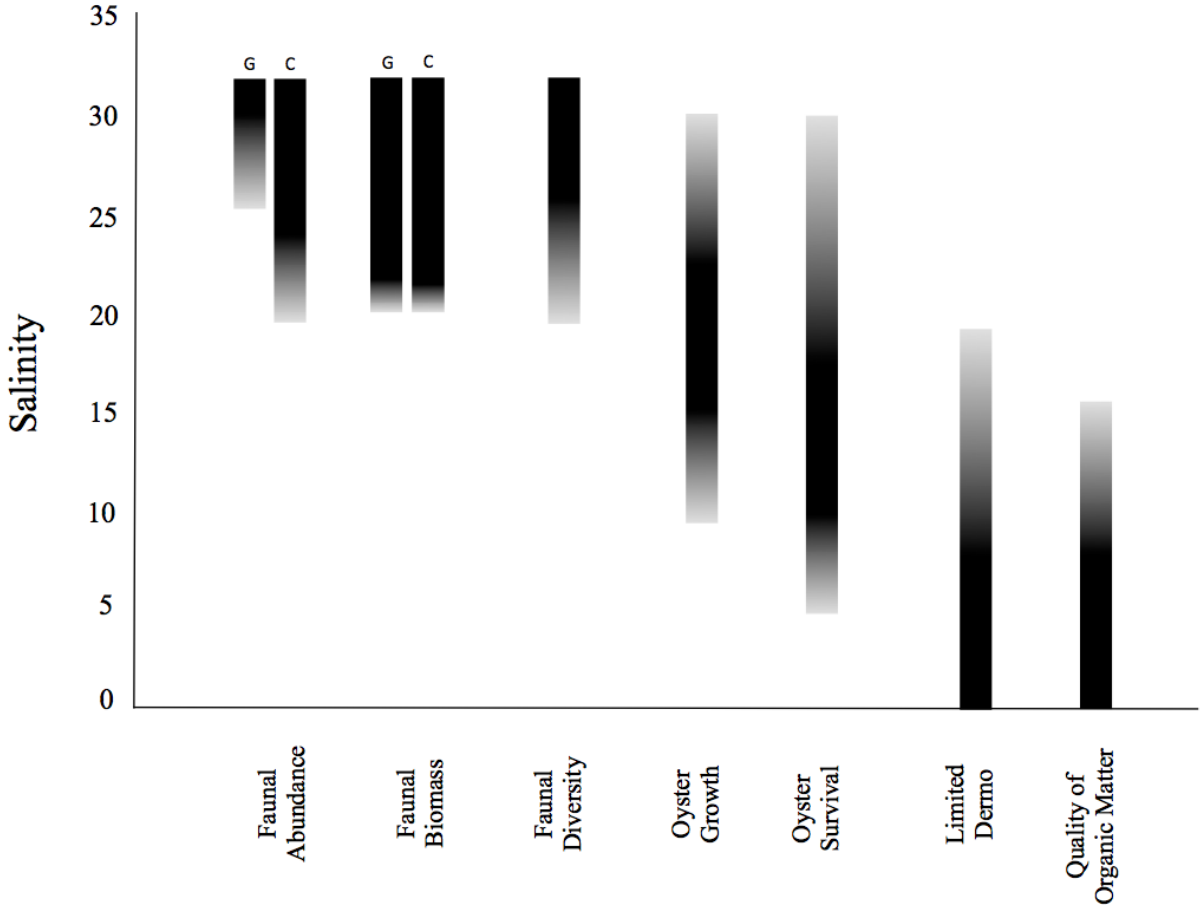

Rho= -0.935, p-value<0.0001
Median SPOM contribution
1.0
0.8
0.6
0.4
0.2
0.0
14
16
18
20
22
24
26
28
Salinity

Figure 13.


Salinity
35
30
25
20
15
10
5
0
G
C
G
C
Faunal Abundance
Faunal Biomass
Faunal Diversity
Oyster Growth
Oyster Survival
Limited Dermo
Quality of Organic Matter

TABLES

Table 1. Spearman rank correlation coefficients showing relationship among macrofaunal community measurements and water quality parameters. Significant correlations are bolded ($p < 0.05$).

		Variable (unit)		Salinity	Temperature (°C)	Turbidity (NTU)	pH	Dissolved Oxygen (mg L^{-1})	Chl *a*
Reef-resident fauna	**Restored**	Abundance (n m^{-2})	rho	**0.573**	-0.138	-0.206	-0.017	0.021	-0.122
			p	**0.000**	0.259	0.090	0.893	0.866	0.317
		Biomass (g m^{-2})	rho	**0.461**	**-0.310**	-0.073	-0.021	0.227	**-0.251**
			p	**0.000**	**0.010**	0.551	0.866	0.061	**0.038**
		Hill's Diversity (N1)	rho	**0.566**	-0.202	**-0.365**	-0.049	0.055	**-0.268**
			p	**0.000**	0.096	**0.002**	0.690	0.655	**0.026**
		Species Richness (S)	rho	**0.525**	-0.140	**-0.248**	-0.048	0.027	-0.142
			p	**0.000**	0.252	**0.040**	0.696	0.827	0.245
	Unrestored	Abundance (n m^{-2})	rho	**0.545**	-0.153	-0.111	-0.124	0.038	-0.031
			p	**0.000**	0.206	0.359	0.305	0.753	0.798
		Biomass (g m^{-2})	rho	**0.391**	**-0.237**	-0.062	-0.190	0.134	-0.067
			p	**0.001**	**0.048**	0.610	0.116	0.270	0.581
		Hill's Diversity (N1)	rho	**0.306**	**-0.331**	-0.035	**-0.395**	0.204	-0.169
			p	**0.010**	**0.005**	0.775	**0.001**	0.090	0.162
		Species Richness (S)	rho	**0.567**	-0.196	-0.113	-0.180	0.069	-0.102
			p	**0.000**	0.104	0.352	0.135	0.568	0.402

Table 1. cont.

		Variable (unit)		Salinity	Temperature (°C)	Turbidity (NTU)	pH	Dissolved Oxygen (mg L^{-1})	Chl *a*
Reef-associated fauna	**Adjacent**	Abundance (n m^{-2})	rho	**0.505**	-0.060	-0.138	-0.276	-0.022	-0.130
			p	**0.001**	0.715	0.404	0.089	0.894	0.457
		Biomass (g m^{-2})	rho	**0.529**	**-0.362**	-0.025	0.106	0.244	-0.202
			p	**0.001**	**0.024**	0.880	0.522	0.134	0.244
		Hill's Diversity (N1)	rho	**0.400**	-0.218	0.025	**0.654**	0.064	-0.201
			p	**0.012**	0.182	0.879	**0.000**	0.698	0.246
		Species Richness (S)	rho	**0.742**	-0.279	-0.072	0.179	0.074	-0.221
			p	**0.000**	0.085	0.665	0.275	0.655	0.202
	Distant	Abundance (n m^{-2})	rho	**0.346**	-0.053	-0.167	-0.043	-0.005	-0.266
			p	**0.033**	0.754	0.317	0.798	0.978	0.128
		Biomass (g m^{-2})	rho	**0.455**	**-0.483**	0.011	0.134	**0.328**	-0.292
			p	**0.004**	**0.002**	0.947	0.421	**0.044**	0.093
		Hill's Diversity (N1)	rho	**0.508**	**-0.525**	0.017	0.211	0.282	-0.216
			p	**0.001**	**0.001**	0.917	0.204	0.087	0.221
		Species Richness (S)	rho	**0.687**	-0.264	-0.050	0.262	0.073	-0.165
			p	**0.000**	0.109	0.765	0.112	0.663	0.350

Table 2. Abundance and biomass Spearman correlations with mean salinity for higher taxa groups within A) reef-resident fauna and B) reef-associated fauna. Significant correlations are bolded ($p < 0.05$).

A)

		Reef-resident fauna					
		Restored sites			**Unrestored sites**		
		n	**Rho**	**p**	**n**	**Rho**	**p**
Crustaceans	n m^{-2}	46	**0.321**	**0.007**	47	**0.463**	**0.000**
	g m^{-2}	46	0.036	0.769	47	0.036	0.769
Gastropods	n m^{-2}	46	**0.516**	**0.000**	47	**0.411**	**0.000**
	g m^{-2}	46	**0.416**	**0.000**	47	**0.330**	**0.005**
Teleosts	n m^{-2}	46	-0.121	0.321	47	-0.231	0.054
	g m^{-2}	46	-0.055	0.652	47	-0.216	0.072
Other	n m^{-2}	46	-0.158	0.196	47	-0.184	0.128
	g m^{-2}	46	-0.106	0.388	47	-0.164	0.176

B)

		Reef-associated fauna					
		Adjacent sites			**Distant sites**		
		n	**Rho**	**p**	**n**	**Rho**	**p**
Crustaceans	n m^{-2}	24	**0.420**	**0.007**	24	**0.398**	**0.011**
	g m^{-2}	24	**0.275**	**0.086**	24	**0.413**	**0.008**
Gastropods	n m^{-2}	24	**0.819**	**0.000**	24	**0.673**	**0.000**
	g m^{-2}	24	**0.737**	**0.000**	24	**0.475**	**0.002**
Teleosts	n m^{-2}	24	0.207	0.201	24	0.173	0.285
	g m^{-2}	24	**0.391**	**0.013**	24	0.254	0.114
Other	n m^{-2}	24	0.161	0.321	24	0.218	0.176
	g m^{-2}	24	0.039	0.813	24	0.217	0.179

Table 3. $\delta^{13}C$ and $\delta^{15}N$ values (‰, mean ± standard deviation) of *C. virginica* digestive gland, suspended particulate organic matter (SPOM), surface sediment organic matter (SSOM), and *C. virginica* digestive gland.

Month	***C. virginica***			**SPOM**			**SSOM**	
	n	**$\delta^{15}N$**	**$\delta^{13}C$**	n	**$\delta^{15}N$**	**$\delta^{13}C$**	n	**$\delta^{15}N$**	**$\delta^{13}C$**
Apr-16	24	9.8 ± 0.3	-23.2 ± 0.3	4	7.5 ± 0.3	-25.8 ± 0.3	4	8.6 ± 0.2	-25.0 ± 0.6
Jul-16	25	10.6 ± 0.2	-24.2 ± 0.2	4	8.5 ± 0.1	-26.1 ± 0.2	4	8.3 ± 1.0	-25.9 ± 3.4
Oct-16	24	10.9 ± 0.2	-24.2 ± 0.2	4	8.9 ± 0.3	-26.7 ± 0.2	4	7.8 ± 0.9	-23.3 ± 0.7
Feb-17	24	10.5 ± 0.3	-22.8 ± 0.2	4	6.1 ± 2.0	-25.0 ± 0.7	4	7.3 ± 0.3	-22.6 ± 1.5
Apr-17	24	10.9 ± 0.3	-23.0 ± 0.2	4	8.8 ± <0.1	-24.9 ± 0.3	4	8.4 ± 0.3	-22.5 ± 0.7

Table 4. Chlorophyll *a* (Chl *a*) concentrions, carbon/chlorophyll *a* (C/Chl *a),* and carbon/nitrogen (C/N) ratios (mean ± standard deviation) for suspended particulate organic matter (SPOM) and surface sediment organic matter (SSOM).

Source	**Month**	**Chlorophyll *a****	**C/Chl *a***	**C/N**
SPOM	Apr-16	1.6 ± 0.7	498 ± 325	13.1 ± 8.4
	Jul-16	6.7 ± 5.4	259 ± 197	5.8 ± 2.1
	Oct-16	10.5 ± 1.9	236 ± 69	7.9 ± 2.2
	Feb-17	4.9 ± 1.2	515 ± 34	14.0 ± 1.7
	Apr-17	40.7 ± 4.2	158 ± 30	10.7 ± 0.8
SSOM	Apr-16	-	-	15.6 ± 2.4
	Jul-16	-	-	12.1 ± 6.0
	Oct-16	2.4 ± 0.7	1086 ± 210	9.2 ± 1.2
	Feb-17	4.4 ± 2.6	561 ± 186	8.9 ± 1.1
	Apr-17	35.4 ± 12.5	79 ± 13	8.8 ± 1.5

* SPOM values reported in µg L^{-1}, SSOM values reported in µg g^{-1}

Table 5. Spearman rank correlation coefficients and p-values showing relationship between isotopic compositions of suspended particulate organic matter (SPOM) and surface sediment organic matter (SSOM) and water quality parameters. Significant correlations are bolded ($p < 0.05$).

	Variable		Salinity	Temperature (°C)	Turbidity (NTU)	pH	Dissolved oxygen (mg L^{-1})	Chl *a**
SPOM	**$\delta^{13}C$**	rho	**0.601**	**-0.601**	0.432	**-0.577**	**0.758**	-0.028
		p	**0.005**	**0.005**	0.057	**0.008**	**0.000**	0.908
	$\delta^{15}N$	rho	**-0.656**	**0.656**	0.331	**0.742**	-0.116	**0.815**
		p	**0.002**	**0.002**	0.154	**0.000**	0.625	**0.000**
SSOM	**$\delta^{13}C$**	rho	0.245	-0.245	0.411	0.135	0.348	0.409
		p	0.297	0.297	0.072	0.571	0.133	0.073
	$\delta^{15}N$	rho	-0.258	0.258	0.012	-0.129	0.238	0.171
		p	0.273	0.273	0.959	0.589	0.312	0.471

SPOM values reported in µg L^{-1}, SSOM values reported in µg g^{-1}

Table 6. Contributions (medians and 95% credibility intervals (CI)) of suspended particulate organic matter (SPOM) and surface sediment organic matter (SSOM) as oyster food sources from Bayesian mixing model outputs.

Source	Month	Lower CI	Median	Upper CI
SPOM	Apr-16	0.12	0.41	0.66
	Jul-16	0.54	0.80	0.97
	Oct-16	0.36	0.45	0.54
	Feb-17	0.35	0.45	0.54
	Apr-17	0.34	0.45	0.57
SSOM	Apr-16	0.34	0.59	0.88
	Jul-16	0.03	0.21	0.46
	Oct-16	0.46	0.55	0.64
	Feb-17	0.46	0.55	0.65
	Apr-17	0.44	0.55	0.66

APPENDICES

Appendix 1. Detailed results of PRIMER analyses

Appendix 1.1. Detailed results of Principal Component Analysis (PCA) resulting from analysis of modified water quality data.

PCA
Principal Component Analysis

Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	2.26	37.6	37.6
2	1.59	26.5	64.1
3	0.873	14.5	78.7
4	0.673	11.2	89.9
5	0.49	8.2	98.0

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

Variable	PC1	PC2	PC3	PC4	PC5
Turb	0.305	-0.516	-0.285	0.400	0.618
Temp	0.600	0.238	-0.056	-0.169	-0.167
Sal	-0.356	0.079	-0.865	0.124	-0.274
DO_mgl	-0.498	-0.330	0.395	0.331	-0.186
pH	0.115	0.581	0.105	0.793	-0.016
Chl_ugl	0.399	-0.474	-0.008	0.242	-0.693

Appendix 1.2. Detailed results of BEST BIO-ENV procedure correlating water quality variables to reef-resident abundance. Analysis performed on data averaged by Treatment-Date.

BEST
Biota and/or Environment matching

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

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

Global Test
Sample statistic (Rho): 0.284
Significance level of sample statistic: 5%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 4

Best results

No.Vars	Corr.	Selections
2	0.284	3,4
3	0.284	3-5
1	0.278	3
2	0.247	3,5
3	0.245	2,3,5
4	0.244	2-5
2	0.237	2,3
3	0.236	2-4
3	0.177	1,3,4
4	0.175	1,3-5

Appendix 1.3. Detailed results of BEST BIO-ENV procedure correlating water quality variables to reef-resident biomass. Analysis performed on data averaged by Treatment-Date.

BEST
Biota and/or Environment matching

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

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

Global Test
Sample statistic (Rho): 0.148
Significance level of sample statistic: 39%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 38

Best results

No.Vars	Corr.	Selections
1	0.148	3
2	0.124	3,4
3	0.116	3-5
2	0.103	3,5
2	0.092	2,3
3	0.091	1,3,4
3	0.088	2,3,5
2	0.088	1,3
4	0.088	1,3-5
4	0.087	2-5

Appendix 1.4. Detailed results of BEST BIO-ENV procedure correlating water quality variables to reef-associated abundance. Analysis performed on data averaged by Treatment-Date.

BEST
Biota and/or Environment matching

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

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

Global Test
Sample statistic (Rho): 0.485
Significance level of sample statistic: 4%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 3

Best results

No.Vars	Corr.	Selections
3	0.485	1,3,4
2	0.476	1,3
3	0.464	1-3
2	0.462	2,3
3	0.460	2,3,5
2	0.456	3,4
4	0.453	1,3-5
4	0.452	2-5
3	0.452	2-4
3	0.450	1,3,5

Appendix 1.5. Detailed results of BEST BIO-ENV procedure correlating water quality variables to reef-associated biomass. Analysis performed on data averaged by Treatment-Date.

BEST
Biota and/or Environment matching

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

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

Global Test
Sample statistic (Rho): 0.531
Significance level of sample statistic: 1%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 0

Best results

No.Vars	Corr.	Selections
2	0.531	3,4
3	0.521	3-5
1	0.502	3
3	0.501	2,3,5
4	0.490	2-5
2	0.490	2,3
3	0.488	2-4
2	0.463	3,5
4	0.303	1-3,5
5	0.301	1-5

Appendix 2. Supplementary tables.

Appendix 2.1. P-values from ANOVA tests on oyster metrics. Significant results ($p < 0.05$) are bolded.

2-Way ANOVA

	Abundance (Log (n m^{-2}))	**Cover √(%)**
Date	**<0.0001**	**<0.0001**
Site	0.1341	**0.0011**
Date*Site	**0.0247**	**0.012**
Main-Effects ANOVA		
Date-Site	**<0.0001**	**<0.0001**

Non-parametric analyses

	Shell Height
Date	**<0.0001**
Site	**<0.0001**
Date-Site	**<0.0001**

Appendix 2.1a. ANOVA output of date, site, and date*site effect on oyster abundance (Log (n m^{-2})).

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	11	37.85028118	3.44093465	66.55	<0.0001
Site	5	0.44154651	0.0883093	1.71	0.1341
Date*Site	53	4.10250234	0.0774057	1.5	0.0247

Appendix 2.1b. ANOVA output of combined factor date-site effect on oyster abundance.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date-Site	69	41.819637	0.60608	11.72	<0.0001

Tukey Grouping															Mean	N	Date-Site
								A							3.4867	5	HMB-JUL2014
		B						A							3.4855	4	HMB-OCT2014
		B						A			C				3.4668	6	HMA-JUL2014
		B		D				A			C				3.438	5	HMD-JUL2014
		B		D				A			C				3.4191	6	HME-JUL2014
	E	B		D				A			C				3.357	4	HMD-OCT2014
	E	B		D				A			C				3.3482	6	HMF-JUL2014
	E	B		D				A			C				3.3321	4	HMC-OCT2014
	E	B		D				A			C		F		3.3158	4	HME-OCT2014
	E	B		D				A		G	C		F		3.2982	4	HMD-JAN2015
	E	B		D				A		G	C		F		3.2877	4	HMC-MAY2015
	E	B		D		H		A		G	C		F		3.2757	2	HMB-MAY2015
	E	B	I	D		H		A		G	C		F		3.2542	4	HMB-JAN2015
	E	B	I	D		H		A		G	C		F		3.2125	3	HME-MAY2015
	E	J	B	I	D		H		A		G	C		F	3.1695	4	HMF-JAN2015
	E	J	B	I	D		H		A		G	C		F	3.1676	4	HMD-MAY2015
K	E	J	B	I	D		H		A		G	C		F	3.145	4	HMF-MAY2015
K	E	J	B	I	D		H		A		G	C		F	L	3.1303	4	HME-JAN2015
K	E	J	B	I	D		H		A		G	C	M	F	L	3.1039	4	HMA-OCT2014
K	E	J	B	I	D		H		A		G	N	C	M	F	L	3.0575	3	HMA-JUL2015
K	E	J	B	I	D		H		A	O	G	N	C	M	F	L	3.044	2	HMB-OCT2015
K	E	J	B	I	D		H		A	O	G	N	C	M	F	L	3.0404	4	HMA-JAN2015
K	E	J	B	I	D		H	P	A	O	G	N	C	M	F	L	2.9914	8	HMC-JUL2014
K	E	J	B	I	D		H	P	A	O	G	N	C	M	F	L	2.9713	4	HMC-JAN2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.942	4	HMF-OCT2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.9243	4	HMF-OCT2014
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.8368	5	HMB-JUL2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.8268	5	HME-JUL2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.8246	1	HMD-JUL2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.8176	4	HMC-OCT2015

K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.8106	2	HMD-OCT2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.792	4	HMC-JUL2015
K	E	J	B	I	D	Q	H	P	A	O	G	N	C	M	F	L	2.7737	4	HMF-JUL2015
K	E	J	B	I	D	Q	H	P		O	G	N	C	M	F	L	2.7552	4	HME-OCT2015
K	E	J		I	D	Q	H	P		O	G	N	C	M	F	L	2.7425	4	HME-JAN2016
K	E	J		I	D	Q	H	P		O	G	N		M	F	L	2.731	4	HMC-JAN2016
K	E	J		I		Q	H	P		O	G	N		M	F	L	2.6873	4	HMA-OCT2015
K	E	J		I		Q	H	P		O	G	N		M	F	L	2.6489	6	HMC-MAY2017
K	E	J		I		Q	H	P		O	G	N		M	F	L	2.6413	3	HMA-JAN2016
K		J		I		Q	H	P		O	G	N		M	F	L	2.5994	4	HMC-APR2016
K		J		I		Q	H	P		O	G	N		M	F	L	2.5944	5	HMA-APR2016
K		J		I		Q	H	P		O	G	N		M		L	2.581	4	HMC-FEB2017
K		J		I		Q	H	P		O		N		M		L	2.5536	6	HME-APR2016
K		J		I		Q	H	P		O		N		M		L	2.5536	6	HMD-JAN2016
K		J		I		Q		P		O		N		M		L	2.5243	4	HMC-JUL2016
K		J		I		Q		P		O		N		M		L	2.5243	4	HMA-JUL2016
K		J		I		Q		P		O		N		M		L	2.5242	2	HMF-JAN2016
K		J		I		Q		P		O		N		M		L	2.5242	3	HMB-OCT2016
K		J				Q		P		O		N		M		L	2.4492	4	HME-JUL2016
K		J				Q		P		O		N		M		L	2.4492	4	HME-MAY2017
K		J				Q		P		O		N		M		L	2.4394	5	HMB-FEB2017
K		J				Q		P		O		N		M		L	2.4394	5	HME-FEB2017
K						Q		P		O		N		M		L	2.4182	4	HMF-APR2016
K						Q		P		O		N		M		L	2.4149	6	HMB-JUL2016
						Q		P		O		N		M		L	2.4043	5	HME-OCT2016
						Q		P		O		N		M			2.3829	3	HMD-APR2016
						Q		P		O		N		M			2.3829	3	HMD-MAY2017
						Q		P		O		N		M			2.3743	2	HMB-JAN2016
						Q		P		O		N		M			2.3743	4	HMA-OCT2016
						Q		P		O		N					2.3443	5	HMB-MAY2017
						Q		P		O		N					2.3433	4	HMA-MAY2017
						Q		P		O		N					2.3433	4	HMC-OCT2016
						Q		P		O		N					2.3433	4	HMD-JUL2016
						Q		P		O							2.3244	3	HMF-OCT2016
						Q		P									2.2994	4	HMF-JUL2016
						Q											2.2244	3	HMF-FEB2017
						Q											2.2244	2	HMB-APR2016
						Q											2.2244	1	HMD-FEB2017
						Q											2.2244	3	HMF-MAY2017
						Q											2.2244	2	HMD-OCT2016

Means with the same letter are not significantly different

Appendix 2.1c. ANOVA output of date, site, and date*site effect on oyster percent cover (√%).

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	11	273.1385	24.8307727	7.83	<0.0001
Site	5	66.820787	13.3641574	4.21	0.0011
Date*Site	53	267.043016	5.0385475	1.59	0.012

Appendix 2.1d. ANOVA output of combined factor date-site effect on oyster percent cover.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date-Site	69	681.516911	9.8770567	3.11	<0.0001

Tukey Grouping				Mean	N	Date-Site
		A		11.783	3	HMB-OCT2016
B		A		9.858	3	HMD-APR2016
B		A	C	9.268	4	HME-MAY2017
B	D	A	C	9.206	4	HMF-APR2016
B	D	A	C	9.184	6	HME-APR2016
B	D	A	C	9.082	6	HMC-MAY2017
B	D	A	C	8.895	5	HMA-APR2016
B	D	A	C	8.844	4	HME-JAN2016
B	D	A	C	8.837	4	HMC-APR2016
B	D	A	C	8.832	4	HMC-JAN2016
B	D	A	C	8.74	3	HMA-JAN2016
B	D	A	C	8.654	5	HME-FEB2017
B	D	A	C	8.494	4	HMB-OCT2014
B	D	A	C	8.437	4	HMC-JUL2016
B	D	A	C	8.391	4	HMA-JUL2016
B	D	A	C	8.287	5	HME-OCT2016
B	D	A	C	8.254	4	HME-OCT2014
B	D	A	C	8.211	4	HMA-OCT2016
B	D	A	C	8.16	4	HME-JUL2016
B	D	A	C	8.1	2	HMB-OCT2015
B	D	A	C	8.038	4	HMD-JAN2015
B	D	A	C	7.887	4	HMA-JAN2015
B	D	A	C	7.866	5	HMB-FEB2017
B	D	A	C	7.539	4	HMF-JAN2015
B	D	A	C	7.489	4	HMC-FEB2017
B	D	A	C	7.352	4	HMC-OCT2016
B	D	A	C	7.325	4	HMA-MAY2017
B	D	A	C	7.167	4	HMD-JUL2016
B	D	A	C	7.16	4	HMC-OCT2014
B	D	A	C	7.127	5	HMB-MAY2017

B	D	A	C	7.071	1	HMD-FEB2017
B	D	A	C	7.069	4	HME-JAN2015
B	D	A	C	7.051	3	HMD-MAY2017
B	D	A	C	6.969	2	HMB-JAN2016
B	D	A	C	6.969	2	HMF-JAN2016
B	D	A	C	6.783	4	HMF-JUL2016
B	D	A	C	6.705	4	HMD-OCT2014
B	D	A	C	6.703	5	HMD-JUL2014
B	D	A	C	6.665	4	HME-OCT2015
B	D	A	C	6.595	3	HME-MAY2015
B	D	A	C	6.446	4	HMB-JAN2015
B	D	A	C	6.422	2	HMD-OCT2015
B	D	A	C	6.422	2	HMB-APR2016
B	D	A	C	6.404	4	HMA-OCT2014
B	D	A	C	6.312	4	HMD-MAY2015
B	D	A	C	6.302	4	HMA-OCT2015
B	D	A	C	6.114	2	HMD-OCT2016
B	D	A	C	6.087	4	HMF-OCT2015
B		A	C	6.079	6	HMF-JUL2014
B	D		C	6.049	6	HMB-JUL2016
B	D		C	6.033	4	HMC-JAN2015
B	D		C	5.951	6	HME-JUL2014
B	D		C	5.921	4	HMC-OCT2015
B	D		C	5.854	4	HME-JUL2015
B	D		C	5.838	4	HMC-MAY2015
B	D		C	5.829	5	HMB-JUL2014
B	D		C	5.829	6	HMA-JUL2014
B	D		C	5.749	3	HMF-OCT2016
B	D		C	5.711	4	HMF-MAY2015
B	D		C	5.696	6	HMD-JAN2016
B	D		C	5.502	4	HMF-OCT2014
B	D		C	5.387	2	HMB-MAY2015
B	D		C	5.21	3	HMF-MAY2017
B	D		C	5.183	4	HMC-JUL2015
B	D		C	4.781	3	HMA-JUL2015
B	D		C	4.553	3	HMF-FEB2017
	D		C	4.104	5	HMB-JUL2015
	D		C	4.082	1	HMD-JUL2015
	D		C	3.684	8	HMC-JUL2014
	D			3.485	4	HMF-JUL2015

Means with the same letter are not significantly different

Appendix 2.1e. Kruskal-Wallis output of date and the combined factor date-site effect on oyster shell height.

Kruskal-Wallis rank sum test
data: Height by Date
Kruskal-Wallis chi-squared = 1535.2, df = 11, p-value < 2.2e-16

Kruskal-Wallis rank sum test
data: Height by Site
Kruskal-Wallis chi-squared = 90.005, df = 5, p-value < 2.2e-16

Kruskal-Wallis rank sum test
data: Height by date_site
Kruskal-Wallis chi-squared = 1724.2, df = 69, p-value < 2.2e-16

Appendix 2.2. P-values from ANOVA tests on univariate metrics of associated and resident communities. Main-Effects ANOVA results only shown when applicable. Significant results ($p < 0.05$) are bolded.

Resident Communities 2-Way ANOVA

	Abundance ($\sqrt{\sqrt{}}$ (n m^{-2}))	**Hill's N1 Diversity**	**Species Richness**
Date	**<0.0001**	**<0.0001**	**<0.0001**
Treatment	**0.0179**	0.1762	0.6334
Treatment*Date	**<0.0001**	**<0.0001**	0.6914
Resident Communities Main-Effects ANOVA			
Treatment-Date	**<0.0001**	**<0.0001**	-

Associated Communities 2-Way ANOVA

	Abundance ($\sqrt{\sqrt{}}$ (n m^{-2}))	**Hill's N1 Diversity ($\sqrt{}$N1)**	**Species Richness**
Date	**<.0001**	**<.0001**	**<.0001**
Treatment	0.8903	0.1187	0.1056
Treatment*Date	0.6066	**0.0038**	0.8805
Associated Communities Main-Effects ANOVA			
Treatment-Date	-	**<0.0001**	-

Resident Communities Non-parametric Analyses

	Biomass
Wilcoxon	
Treatment	**<0.0001**
Kruskal-Wallis	
Date	0.392
Treatment-Date	**<0.0001**

Associated Communities Non-parametric Analyses

	Biomass
Wilcoxon	
Treatment	0.851
Kruskal-Wallis	
Date	**<0.0001**
Treatment-Date	**<0.0001**

Appendix 2.2a. ANOVA output of date, treatment, and treatment*date effect on resident faunal abundance ($\sqrt{\sqrt{n}}$ m^{-2}).

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	11	161.2459919	14.6587265	24.67	<0.0001
Treatment	1	3.4310601	3.4310601	5.78	0.0179
Treatment*Date	11	37.00388	3.3639891	5.66	<0.001

Appendix 2.2b. ANOVA output of combined factors treatment-date effect on resident faunal abundance.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Treat-Date	23	202.2376606	8.7929418	14.8	<0.0001

Tukey Grouping						Mean	N	Treatment-Date
			A			7.2224	5	Unrestored-MAY15
	B		A			6.5269	6	Unrestored-JUL14
	B		A	C		5.8192	6	Restored-JUL14
	B		D	C		5.3031	6	Unrestored-OCT14
	B	E	D	C		4.8452	5	Restored-MAY15
	F	E	D	C		4.7635	6	Unrestored-JAN15
	F	E	D	C		4.7553	6	Restored-JAN15
G	F	E	D	C		4.6778	5	Restored-MAY17
G	F	E	D	C		4.5894	6	Restored-OCT14
G	F	E	D	C		4.2711	6	Restored-OCT15
G	F	E	D	C		4.2527	6	Restored-OCT16
G	F	E	D	C	H	4.1892	6	Unrestored-MAY17
G	F	E	D		H	4.0791	6	Restored-JAN16
G	F	E	D		H	3.9714	5	Restored-FEB17
G	F	E	D		H	3.6437	6	Restored-APR16
G	F	E			H	3.5473	6	Restored-JUL16
G	F	E	I		H	3.4019	6	Restored-JUL15
G	F	E	I		H	3.3053	6	Unrestored-JAN16
G	F	E	I		H	3.2855	6	Unrestored-OCT16
G	F		I		H	3.1127	6	Unrestored-OCT15
G	F		I		H	3.0878	5	Unrestored-FEB17
G			I		H	3.0423	6	Unrestored-APR16
			I		H	2.5036	6	Unrestored-JUL16
			I			1.7307	6	Unrestored-JUL15

Means with the same letter are not significantly different

Appendix 2.2c. ANOVA output of date, treatment, and treatment*date effect on resident faunal Hill's N1 diversity.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Treatment	11	87.75870861	7.97806442	5.57	<0.0001
Date	1	2.65103566	2.65103566	1.85	0.1762
Treatment*Date	11	62.32027077	5.66547916	3.96	<0.0001

Appendix 2.2d. ANOVA output of combined factors treatment-date effect on resident faunal Hill's N1 diversity.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Treat-Date	23	152.5643692	6.6332334	4.64	<0.0001

Tukey Grouping				Mean	N	Treatment-Date
		A		5.9088	6	Restored-JUL14
	B	A		5.6788	6	Restored-JAN15
	B	A	C	5.3612	6	Unrestored-OCT14
	B	A	C	5.3196	5	Unrestored-FEB17
	B	D	A	C	5.1557	6	Unrestored-OCT16
	B	D	A	C	5.151	6	Unrestored-APR16
	B	D	A	C	5.1093	6	Unrestored-JAN15
E	B	D	A	C	4.8853	6	Restored-OCT14
E	B	D	A	C	4.7089	5	Restored-MAY15
E	B	D	A	C	4.5209	6	Unrestored-MAY17
E	B	D	A	C	4.3354	6	Unrestored-OCT15
E	B	D	A	C	4.0825	6	Restored-APR16
E	B	D	A	C	3.5511	6	Restored-OCT15
E	B	D	A	C	3.5286	6	Restored-JAN16
E	B	D	A	C	3.4988	5	Restored-MAY17
E	B	D	A	C	3.4439	6	Unrestored-JUL16
E	B	D	A	C	3.4297	5	Restored-OCT16
E	B	D	A	C	3.3897	6	Unrestored-JAN16
E	B	D		C	3.1859	5	Unrestored-MAY15
E	B	D		C	3.1734	5	Restored-FEB17
E	B	D		C	3.1037	5	Unrestored-JUL15
E		D		C	3.051	6	Unrestored-JUL14
E		D			2.6101	6	Restored-JUL16
E					2.423	6	Restored-JUL15

Means with the same letter are not significantly different

Appendix 2.2e. ANOVA output of date, treatment, and treatment*date effect on resident faunal species richness.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	11	1304.705017	118.609547	25.62	<0.0001
Treatment	1	1.0584	1.0584	0.23	0.6334
Treatment*Date	11	38.039747	3.458159	0.75	0.6914

Tukey Grouping		Mean	N	Date
	A	12.5833	12	22Oct2014
	A	12.5000	12	22Jul2014
	A	12.2500	12	05Jan2015
	A	11.8000	10	18May2015
	B	7.5455	11	02May2017
	B	7.4167	12	05Apr2016
	B	7.2500	12	06Oct2016
	B	7.1000	10	08Feb2017
C	B	6.0833	12	19Jan2016
C	B	5.9167	12	12Oct2015
C	B	4.7500	12	15Jul2016
C		3.9167	12	13Jul2015

Means with the same letter are not significantly different

Appendix 2.2f. ANOVA output of date, treatment, and date*treatment effect on associated faunal abundance ($\sqrt{\sqrt{n}}$ m^{-2}).

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	9	16.85488973	1.87276553	17.14	<0.0001
Treatment	1	0.00209787	0.00209787	0.02	0.8903
Treatment*Date	9	0.79910977	0.08878997	0.81	0.6066

Tukey Grouping			Mean	N	Date
	A		1.9042	8	05Apr2016
B	A		1.6663	8	02May2017
B	A	C	1.4689	8	21Jul2014
B	D	C	1.2478	8	22Apr2014
B	D	C	1.1496	8	22Oct2014
	D	C	0.9481	8	05Jan2015
	D		0.9059	8	12Oct2015
E	D		0.7533	8	06Oct2016
E	D		0.7471	8	19Jan2016
E			0.279	8	13Jul2015

Means with the same letter are not significantly different

Appendix 2.2g. ANOVA output of date, treatment, and date*treatment effect on associated faunal Hill's N1 diversity (√N1).

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	9	27.3330357	3.03700397	20.95	<0.0001
Treatment	1	0.3632627	0.3632627	2.51	0.1187
Treatment*Date	9	4.08150289	0.45350032	3.13	0.0038

Appendix 2.2h. ANOVA output of combined factor treatment-date effect on associated faunal Hill's N1 diversity.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Treat-Date	19	31.77780129	1.67251586	11.54	<0.0001

Tukey Grouping				Mean	N	Treatment-Date
		A		2.8543	4	Restored- APR14
		A		2.7808	4	Unrestored-APR14
B		A		2.6514	4	Unrestored-JAN15
B		A		2.6234	4	Restored-JUL14
B		A	C	2.55	4	Restored-JAN15
B	D	A	C	1.911	4	Restored-JAN16
B	D	A	C	1.8862	4	Unrestored-OCT14
B	D		C	1.7405	4	Unrestored-OCT15
	D		C	1.5985	4	Unrestored-MAY17
	D		C	1.5952	4	Restored-OCT15
	D	E		1.4872	4	Unrestored-JAN16
	D	E		1.4831	4	Restored-OCT16
	D	E		1.4651	4	Unrestored-JUL14
	D	E		1.3915	4	Restored-OCT14
	D	E		1.3082	4	Restored-MAY17
	D	E		1.26	4	Unrestored-OCT16
	D	E		1.1909	4	Unrestored-APR16
	D	E		1.1585	4	Restored-APR16
	D	E		1.0743	4	Restored-JUL15
		E		0.5411	4	Unrestored-JUL15

Means with the same letter are not significantly different

Appendix 2.2i. ANOVA output of date, treatment, and date*treatment effect on associated faunal species richness.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
Date	9	3512.0125	390.223611	30.01	<0.0001
Treatment	1	35.1125	35.1125	2.7	0.1056
Treatment*Date	9	56.5125	6.279167	0.48	0.8805

Tukey Grouping			Mean	N	Date
	A		24.750	8	22Apr2014
B	A		19.375	8	21Jul2014
B	C		14.375	8	05Jan2015
B	C		13.875	8	02May2017
D	C		12.500	8	22Oct2014
D	C	E	9.125	8	05Apr2016
D	F	E	7.250	8	12Oct2015
D	F	E	6.625	8	19Jan2016
	F	E	5.250	8	06Oct2016
	F		1.500	8	13Jul2015

Means with the same letter are not significantly different

Appendix 2.2j. Wilcoxon and Kruskal-Wallis output of treatment, date, and the combined factors treatment-date effect on resident community biomass.

Wilcoxon rank sum test with continuity correction
data: Tray_biomass by Treatment
W = 4114, p-value = 8.358e-13
alternative hypothesis: true location shift is not equal to 0

Kruskal-Wallis rank sum test
data: Tray_biomass by Date
Kruskal-Wallis chi-squared = 11.627, df = 11, p-value = 0.3923

Kruskal-Wallis rank sum test
data: Tray_biomass by treat_date
Kruskal-Wallis chi-squared = 73.203, df = 23, p-value = 3.856e-07

Appendix 2.2k. Wilcoxon and Kruskal-Wallis output of treatment, date, and the combined factor treatment-date effect on associated community biomass.

Wilcoxon rank sum test with continuity correction
data: Tow_biomass by Treatment
W = 820, p-value = 0.8512
alternative hypothesis: true location shift is not equal to 0

Kruskal-Wallis rank sum test
data: Tow_biomass by Date
Kruskal-Wallis chi-squared = 51.226, df = 9, p-value = 6.33e-08

Kruskal-Wallis rank sum test
data: Tow_biomass by treat_date
Kruskal-Wallis chi-squared = 54.357, df = 19, p-value = 2.914e-05

Appendix 2.3. Abundance and percent cover of encrusting species.

Taxa	**Freq.**	**Abundance (n m^{-2})**			**Coverage (%)**		
		mean ± SE	**max.**	**min.**	**mean ± SE**	**max.**	**min.**
Crassostrea virginica	278	886 ± 59	7313	0	45.2 ± 2	100.0	0.0
Thoracica	170	477 ± 57	10667	0	4.1 ± 0.4	54.3	0.0
Serpulidae	139	237 ± 31	4500	0	1.0 ± 0.2	25.0	0.0
Ischadium recurvum	55	75 ± 13	1667	0	1.0 ± 0.2	33.3	0.0
Brachidontes exustus	54	214 ± 46	8333	0	0.4 ± 0.1	20.8	0.0
Crepidula sp.	53	35 ± 5.8	833	0	0.5 ± 0.1	16.6	0.0
Anomia simplex	21	9 ± 2	333	0	0.2 ± 0.1	39.0	0.0
Bryozoa	7	-	-	-	<0.1 ± <0.1	0.8	0.0
Encrusting sponge	4	-	-	-	0.2 ± 0.2	50.0	0.0
Sabellidae	3	5 ± 3	667	0	0.1 ± 0.1	25.0	0.0
Stramonita haemastoma (eggs)	2	-	-	-	0.1 ± 0.1	33.3	0.0
Tunicata	2	4 ± 3	833	0	0.1 ± 0.1	16.7	0.0

Freq. = # of substrate samples taxa was observed on out of 327 total samples

Appendix 2.4. Number of oysters inspected for *Perkinsus marinus* along with shell height (SH) range and mean ± SE, mean oyster condition ± SE, and prevalence of disease from October 2014 to April 2017.

Date	# Inspected	SH Range	Mean SH ± SE	Mean Cond. ± SE	Presence
Oct-14	42	26.2-59.6	42.8 ± 1.1	4.3 ± 0.2	N
Jan-15	35	38.8-77.4	55.6 ± 2.1	3.4 ± 0.2	N
May-15	23	48.4-96.4	67.5 ± 2.5	2.6 ± 0.3	N
Jul-15	42	56.3-100.3	78 ± 1.8	2.2 ± 0.2	N
Oct-15	34	65.9-115.4	85.4 ± 2.1	3.8 ± 0.2	N
Jan-16	44	63.2-129.4	99.3 ± 2.6	3.0 ± 0.1	N
Apr-16	47	44.9-160.7	94 ± 4.0	1.7 ± 0.1	N
Jul-16	33	42.2-131.7	93.3 ± 4.0	3.3 ± 0.1	N
Oct-16	37	70.2-146.7	98.4 ± 3.0	3.3 ± 0.1	N
Feb-17	30	70.4-139.7	112 ± 3.0	2.3 ± 0.1	N
Apr-17	36	55.7-136	103.9 ± 3.6	1.8 ± 0.1	N
Overall	403	26.2-160.7	84.6 ± 1.3	2.9 ± 0.1	N

Appendix 2.5. Mean abundance of resident species comprising >1% relative abundance.

		Restored				Unrestored			
Species	Higher Taxa	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Panopeidae	Decapoda	69	170.7	16.9	38.8	60	39.3	5.0	6.3
Petrolisthes sp.	Decapoda	64	114.7	15.0	26.1	57	40.9	9.1	6.5
Parvanachis ostreicola	Gastropoda	29	59.8	24.6	13.6	44	87.9	21.2	14.0
Astyris sp.	Gastropoda	31	25.8	6.9	5.9	47	358.1	101.0	57.2
Costoanachis sp.	Gastropoda	31	24.0	7.4	5.4	31	28.6	9.7	4.6
Alpheus heterochaelis	Decapoda	48	8.3	1.4	1.9	10	1.0	0.4	0.2
Synalpheus fritzmuelleri	Decapoda	18	6.8	1.9	1.5	9	1.3	0.6	0.2
Menippe adina	Decapoda	40	6.7	1.2	1.5	20	1.6	0.4	0.3
Paguroidea	Decapoda	41	5.5	1.0	1.2	59	19.9	3.7	3.2
Aeolidiidae	Gastropoda	8	2.0	0.8	0.5	17	16.3	5.7	2.6
Nassarius acutus	Gastropoda	7	0.5	0.2	0.1	20	8.9	5.7	1.4

Freq = # of samples taxa was observed out of 69 total samples for Restored reef, 70 total samples for Unrestored reef

Appendix 2.6. Mean biomass of resident species comprising >1% relative biomass.

		Restored				Unrestored			
Species	Higher Taxa	Freq.	Mean (mg m^{-2})	SE	R%	Freq.	Mean (mg m^{-2})	SE	R%
Menippe adina	Decapoda	40	12022.3	3976.7	68.0	20	311.3	167.5	17.5
Panopeidae	Decapoda	69	2525.5	387.2	14.3	60	249.7	61.4	14.0
Petrolisthes sp.	Decapoda	64	1607.6	260.6	9.1	57	192.4	40.2	10.8
Stramonita haemastoma	Gastropoda	6	392.6	227.4	2.2	6	227.5	119.7	12.8
Alpheus heterochaelis	Decapoda	48	287.9	59.1	1.6	10	8.6	4.3	0.5
Paguroidea	Decapoda	41	285.2	96.4	1.6	59	447.2	139.8	25.2
Hypsoblennius hentz	Teleostei	3	222.4	133.3	1.3	.	.	.	.
Costoanachis sp.	Gastropoda	31	73.6	24.0	0.4	31	46.3	12.1	2.6
Palaemonetes sp.	Decapoda	18	41.7	16.2	0.2	22	25.8	7.5	1.5
Pelia mutica	Decapoda	13	9.8	3.4	0.1	17	25.6	8.8	1.4
Astyris sp.	Gastropoda	31	8.5	2.4	0.0	47	116.4	50.8	6.5
Portunidae	Decapoda	9	6.1	5.5	0.0	22	25.2	10.9	1.4
Cantharus cancellarius	Gastropoda	.	.	.	.	3	2155.0	2073.0	2.0

Freq = # of samples taxa was observed out of 69 total samples for Restored reef, 70 total samples for Unrestored reef

Appendix 2.7. Mean abundance of associated species comprising >1% relative abundance.

		Adjacent				Distant			
Species	Higher Taxa	Freq.	Mean	SE	R%	Freq.	Mean	SE	R%
Mysidacea	Decapoda	30	3.0	1.2	78.8	31	4.3	1.9	83.0
Parvanachis ostreicola	Gastropoda	21	0.2	0.1	5.0	14	0.1	0.0	1.0
Paguroidea	Decapoda	30	0.1	0.0	3.3	30	0.1	0.0	2.5
Penaeidae	Decapoda	14	0.1	0.1	2.6	13	0.1	0.0	1.5
Panopeidae	Decapoda	32	0.1	0.0	1.9	14	0.0	0.0	0.3
Sciaenidae	Teleostei	21	0.0	0.0	1.2	23	0.1	0.1	2.4
Anchoa mitchilli	Teleostei	7	0.0	0.0	0.6	8	0.1	0.0	1.3
Turbonilla sp.	Gastropoda	10	0.0	0.0	0.1	13	0.1	0.1	2.5

Freq = # of samples taxa was observed out of 40 total samples

Appendix 2.8. Mean biomass of associated species comprising >1% relative biomass.

		Adjacent				Distant			
Species	Higher Taxa	Freq.	Mean (mg m^{-2})	SE	R%	Freq.	Mean (mg m^{-2})	SE	R%
Portunidae	Decapoda	26	2.8	1.2	35.7	14	1.3	0.9	15.6
Busycon sinistrum	Gastropoda	4	0.9	0.5	11.7	1	0.4	0.4	4.7
Mysidacea	Decapoda	30	0.8	0.3	10.3	31	1.4	0.7	17.1
Panopeidae	Decapoda	32	0.7	0.3	9.2	14	0.1	0.0	1.0
Micropogonias undulatus	Teleostei	8	0.3	0.1	4.4	10	1.0	0.5	12.2
Sciaenidae	Teleostei	21	0.3	0.3	4.2	23	0.1	0.1	1.5
Paguroidea	Decapoda	30	0.3	0.1	4.1	30	0.2	0.1	2.5
Penaeidae	Decapoda	14	0.3	0.3	4.0	13	0.1	0.0	1.0
Palaemonetes sp.	Decapoda	13	0.1	0.1	1.9	11	0.1	0.0	1.0
Gobiidae	Teleostei	26	0.1	0.0	1.7	20	0.1	0.0	1.2
Heterocrypta granulata	Teleostei	6	0.1	0.1	1.7	4	0.0	0.0	0.6
Anchoa mitchilli	Teleostei	7	0.1	0.1	1.5	8	0.3	0.2	4.1
Parvanachis ostreicola	Gastropoda	21	0.1	0.0	1.3	14	0.0	0.0	0.3
Ophiurida	Echinodermata	2	0.1	0.1	1.1	5	0.0	0.0	0.1
Etropus crossotus	Teleostei	2	0.0	0.0	0.1	5	0.4	0.3	4.8
Luidia clathrata	Echinodermata	.	.	.	.	1	0.5	0.5	6.4
Brevoortia patronus	Teleostei	.	.	.	.	4	0.5	0.3	6.4
Persephona mediterranea	Decapoda	.	.	.	.	2	0.4	0.4	4.9
Prionotus tribulus	Teleostei	.	.	.	.	2	0.3	0.2	3.7
Litopenaeus setiferus	Decapoda	.	.	.	.	1	0.3	0.3	3.0
Symphurus plagiusa	Teleostei	.	.	.	.	3	0.2	0.1	2.1
Busycotypus spiratus	Gastropoda	.	.	.	.	1	0.1	0.1	1.2
Trachypenaeus sp.	Decapoda	.	.	.	.	5	0.1	0.1	1.1

Freq = # of samples taxa was observed out of 40 total samples

Appendix 2.9. SIMPER similarity output for reef-resident species abundance. Analysis was performed on untransformed data.

Group Remainder_Unrestored (October 2015-May 2017)
Average similarity:
43.38

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	9.06	13.75	2.26	31.7	31.70
Paguroidea	5.55	10.22	1.48	23.55	55.25
Astyris sp.	11.32	6.92	1.31	15.94	71.19
Petrolisthes sp.	4.58	5	0.91	11.53	82.72
Parvanachis ostreicola	7.11	4.27	0.95	9.84	92.56

Group Year 1 (July 2014-May 2015)
Average similarity:
40.73

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Astyris sp.	162.14	12.6	1.17	30.95	30.95
Petrolisthes sp.	39.23	9.59	1.07	23.54	54.49
Parvanachis ostreicola	55.55	6.3	1.22	15.47	69.96
Panopeidae	28	6.19	1.61	15.19	85.15
Costoanachis sp.	21	2.5	1.49	6.13	91.28

Group July15
Average similarity:
12.95

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Gobiidae	1.42	3.6	-	27.78	27.78
Paguroidea	0.75	2.88	-	22.22	50.00
Panopeidae	15.42	2.16	-	16.67	66.67
Menippe adina	0.75	1.44	-	11.11	77.78
Petrolisthes sp.	2.75	1.44	-	11.11	88.89
Palaemonetes sp.	0.5	0.72	-	5.56	94.44

Group Remainder_Restored (October 2015-May 2017)
Average similarity:
72.40

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	58.25	47.73	5.78	65.92	65.92
Petrolisthes sp.	25.44	20.67	3.43	28.55	94.46

Appendix 2.10. SIMPER similarity output for reef-resident species biomass. Analysis was performed on untransformed data.

Group Remainder_Unrestored (October 2015-May 2017)
Average similarity: 32.60

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	0.06	9.12	2.57	27.99	27.99
Paguroidea	0.18	9.09	0.86	27.89	55.88
Petrolisthes sp.	0.07	6.03	0.99	18.51	74.39
Stramonita haemastoma	0.11	5.38	0.55	16.51	90.90

Group Year 1 (July 2014-May 2015)
Average similarity: 30.54

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeidae	0.18	7.09	1.24	23.23	23.23
Menippe adina	0.42	6.86	0.66	22.47	45.70
Petrolisthes sp.	0.16	6.45	1.51	21.13	66.84
Astyris sp.	0.03	3.03	0.58	9.92	76.76
Costoanachis sp.	0.04	2.73	1.27	8.95	85.71
Alpheus heterochaelis	0.06	1.01	0.61	3.32	89.03
Pelia mutica	0.02	0.88	0.74	2.87	91.90

Group July15
Average similarity: 26.62

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Menippe adina	0.36	25	-	93.89	93.89

Group Remainder_Restored (October 2015-May 2017)
Average similarity: 50.59

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Menippe adina	5.26	29.88	1.58	59.07	59.07
Panopeidae	0.97	12.79	1.67	25.27	84.35
Petrolisthes sp.	0.59	4.8	1.12	9.49	93.83

Appendix 3. Supplementary figures

Appendix 3.1. $\delta^{13}C$ and $\delta^{15}N$ values of *C. virginica* (mean ± standard deviation) for top and bottom oysters, suspended particulate organic matter (SPOM), and surface sediment organic matter (SSOM) collected from sites HMB-HME for each sampling month.