REEF RESTORATION FACILITATES HABITAT PROVISIONING FOR OYSTERS AND MOTILE EPIFAUNA

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

Severe degradation of oyster reef habitat over the past century has led to associated losses in ecological and economic benefits. Common oyster reef restoration goals target replacement of lost ecosystem services, including habitat provision, by replacing the ecological functions of lost reef habitats. The goal of this study was to monitor development of faunal communities on a restored oyster reef in the Gulf of Mexico. In July 2017, more than 1 M tons of reclaimed oyster shell were used to restore 1.83 ha of oyster reef complex (~610 linear m) in St. Charles Bay, Texas. Oysters, epifauna, and infauna were sampled monthly for the first three months after construction, and then were sampled quarterly for a total of 19 months at the restored reef and nearby reference sites. Within the first three months after construction, mean oyster densities increased by more than three times, growth rates peaked at 0.41 mm d^{-1}, and the restored oyster population shifted from 100 % spat to more than 90 % submarket size oysters. Although *Perkinsus marinus* infection was detected on every sampling date on the reference reef, only a single infected oyster was observed on the restored reef. Reef location—away from infected source populations— and other hydrological factors such as current speed and direction, may have impeded disease development. Epifaunal density, biomass, and diversity, became similar to that of the reference reef within four months after construction, but a shift in epifaunal community assemblages occurred between the first and the second year after construction, indicating monitoring periods of more than one year are necessary to capture faunal community development on a restored reef. The structure provided by the restored reef was conducive to oyster and epifaunal community development and may have supported ecological resistance since minimal impacts to reef structure were observed in the wake of Hurricane Harvey. Infaunal

density, diversity, and biomass did not differ between sites adjacent (less than 5 m) versus distant (~30 m) from the restored reef and were governed more by salinity than presence of the restored reef. The recruitment and densities of oysters indicate that the restored reef met proposed success metrics within 19 months after construction, and that restored reefs can successfully replace ecosystem services, such as habitat provision, lost due to degradation.

DEDICATION

To my grandmother Ogdalia Montana Anchondo (Grandma Lala). Thank you for your unwavering love, support, and guidance. You are forever in our hearts and missed dearly.

March 17, 1941 – May 6, 2018

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INTRODUCTION

Oysters are conspicuous ecosystem engineers in temperate soft-sediment, coastal and marine environments, and provide numerous ecological benefits including enhanced secondary production of estuaries, filtration of coastal waters, and stabilization of sediments and shorelines (Newell, 1988; Meyer and Townsend, 2000; Nelson et al., 2004; Scyphers et al., 2011). As suspension feeders, oysters contribute to benthic-pelagic coupling in estuaries by removing large amounts of plankton and seston from the water column and transferring undigested and unassimilated material to the sediments in the form of pseudo-feces (Grizzle et al. 2008; Newell and Jordan 1983). The physical reef structure can directly and indirectly modulate resources used by reef-associated species, increasing the diversity of organisms via support for foraging, spawning, refuge, and providing substrate for attachment of sessile organisms (Jones et al., 1997; Humphries et al., 2011; Blomberg et al. 2017; Rezek et al. 2017). By increasing sedimentation rates, reducing turbidity and producing nutrient-rich biodeposits, oysters may also enhance benthic microalgal production and influence adjacent soft sediment infauna (Larsen 1985; Dame et al. 1980; Dame et al. 1989; Newell et al. 2002). Economically, Eastern oysters (*Crassostrea virginica*) are the most important group of wild-harvested mollusks in the United States (FAO, 2019).

Degradation of reef habitats has been extensive over the past century, with an estimated 85 % of native oyster habitat lost globally (Beck et al. 2011). Habitat loss has primarily been driven by anthropogenic impacts such as overharvest, dredging, changes to hydrology and salinity regimes, and disease (zu Ermgassen et al., 2012; Remacha-Trivino et al., 2008; Baggett et al., 2015). Over time, the loss of biogenic structure can have detrimental effects on ecological function and sustainability of these productive ecosystems (Lotze et al, 2006; Bricker et al., 2008). Increasing recognition of the magnitude of reef loss has motivated an increase in habitat restoration efforts in recent decades, with publications increasing more than 50-fold since the early 1990s (Web of Science, 2019). Common oyster reef restoration goals target replacement of ecosystem services, including regulatory (shoreline stabilization and water filtration), provisioning (food commodity), cultural (aesthetics and recreational opportunities), and supporting services (creation and enhancement of habitat) (Peterson et al., 2003; Weslawski et al., 2004).

Physical habitat structure and location can affect the outcome and long-term resiliency of oyster reef restoration efforts through controls on local environmental conditions and species interactions (Gregalis et al., 2009; Camp et al., 2015; Beseres Pollack et al. 2012; Humphries and La Peyre, 2015; Colden et al. 2017). In estuaries, which often demonstrate strong environmental gradients, reef location can regulate hydrological variability and subsequent production of oysters (Livingston et al. 2000; Klinck et al. 2002). Vertical relief can also influence reef success through effects on local physical variables, spat recruitment, and oyster density (Lenihan 1999; Powers et al. 2009). Monitoring and evaluation of restoration efforts are critical for assessment of project success, can improve our ability to manage and restore degraded reef habitats, and can be used to support an adaptive resource management framework.

The goal of this study was to monitor development of faunal communities on a restored oyster reef in the Gulf of Mexico. Specifically, the quantification of oyster density, size, and *Perkinsus marinus* infection as well as density, biomass, and diversity of reef-associated epifauna, compared to a nearby natural reference reef. We also quantified density, biomass, and diversity of infauna at sites adjacent to and distant from the restored reef until 19 months after reef construction as an indicator of the influence of oyster-mediated benthic-pelagic coupling on infauna communities. Monitoring successional patterns as a function of habitat provided by restored reefs, in comparison to existing natural counterparts, can inform resource management and restoration decision-making to maximize the benefits of restored habitats for estuarine species.

METHODS

Study Site

St. Charles Bay is a relatively shallow (less than 2 m) secondary bay within the Mission-Aransas Estuary along the Texas Gulf Coast (Longley, 1994) (Figure 1a, 1b). The estuary is microtidal with low mixing efficiency (< 0.05) and long residence times (~360 days; Solis and Powell, 1999), with an average annual rainfall of 81 cm y^{-1} (1941-1999; Tolan, 2007). Salinity regimes in St. Charles Bay are primarily influenced by freshwater inflow (FWI) from Cavasso Creek and Salt Creek (Chen, 2010; Figure 1b). The most common sediment type is sand to sandy silt (White, 1989). The surrounding watershed is approximately 530 km^2 and is relatively undeveloped compared to neighboring estuaries (Asquith et al., 2007). Southeasterly trade winds are predominant in this area and influence hydrological processes (Montagna et al., 2011).

Reef Construction

In July 2017, ~1.83 ha of oyster reef complex (~610 linear m) were restored in St. Charles Bay, TX (N 28°9’14’’ W 96°58’20’’; Figure 1c). The restoration site is adjacent to Goose Island State Park and has been identified as an area of interest to support critical gaps in Gulf Coast conservation and to ameliorate the effects of erosion (Texas Parks and Wildlife Department, personal communication). The reef was restored using reclaimed oyster shells provided by the “Sink Your Shucks” oyster shell recycling program (http://oysterrecycling.org/). Prior to use, shells were sun-bleached for a minimum of six months to eliminate bacteria and parasites (Bushek et al., 2004). Shells were deployed by barge as a series of seven rectangular mounds 40 m long x 10 m wide x 0.33 m high, oriented parallel to the shoreline along the 1-meter depth contour (Figure 1c). Hurricane Harvey passed directly over this area on 25-26 August 2017 as a category 4 hurricane.

Field Experimental Design

Reef development was monitored to determine if density and size of oysters, and density and diversity of reef-associated mobile epifauna on the restored reef (restored habitat) would become more similar to a natural reef (reference habitat) ~two km north of restored reef (Figure 1c). Eight sampling trays (each 45 cm long x 30 cm wide; 0.135 m^2) were deployed at four sites within each habitat (hereafter termed restored and reference trays) on 7 and 8 August 2017. The restored trays were filled with recycled oyster shells and the reference trays were filled using the surrounding natural reef material to mimic the surrounding oyster reefs. The sampling trays were anchored to the reef with steel reinforcing bar (rebar). Epifauna and oysters were collected monthly from 18 September (three weeks after Hurricane Harvey hit) to 13 November 2017, and quarterly thereafter (February 2018-February 2019) for a total of eight sampling events.

To assess whether infaunal densities, biomass, and diversity would be higher at adjacent sites (< 5 m, adjacent treatment) than control sites (~ 30 m from the reef; distant treatment), sediment cores were collected haphazardly at three adjacent sites and three distant sites. In addition, sediment cores were collected for sediment grain size distribution, and organic matter content (Figure 1c). Infauna samples were collected prior to reef construction in May and July 2017 to determine baseline community composition. Sampling after construction occurred monthly from September to November 2017, and quarterly from February 2018 to February 2019. Sediment cores were collected for grain size analyses prior to restoration in July 2017, monthly from September to November 2017, and quarterly from February 2018 to February 2019; cores for organic matter content analyses were collected quarterly for one year (February 2018 to February 2019).

Water quality

Surface and bottom temperature (°C), dissolved oxygen (mg l^{-1}), salinity, pH, and turbidity (NTU)—were measured using a YSI Pro DSS multiparameter sonde (YSI Incorporated, Yellow Springs, OH, United States). Water quality data were collected at three or four sites within each habitat on every sampling date (May 2017 to February 2019).

Faunal Sampling

Oysters and Dermo

Oysters were enumerated and the shell heights (SH) of 20 live oysters from each tray were measured to assess reef recruitment and growth of oyster populations. Prior to May 2018, spat (SH < 26 mm) were included in the 20 live oysters measured. However, spat were excluded from the 20 live oysters measured from May 2018 to February 2019, and their heights and densities were estimated after measuring the number and heights of spat on a subsample of five haphazardly selected post-spat oysters. Ten sub-market oysters (SH 26-75 mm) and ten market sized oysters (SH ≥ 76 mm) were collected from each habitat to characterize infection by *Perkinsus marinus*; an intracellular protozoan parasite that causes Dermo disease in the eastern oyster (Andrews and Ray 1988; Powell et al., 1996).

Reef-Associated Epifauna

Reef-associated mobile epifauna (> 1 mm) were collected using sampling trays that were deployed at restored and reference habitats (Figure 1c). During each sampling event, one haphazardly-selected sampling tray was sampled from each site without replacement. All collected fauna were fixed in 10 % buffered formalin. Vertebrates were placed on ice for a minimum of 20 minutes before being placed in buffered formalin and brought back to the laboratory for processing.

Infauna and Sediment

Infaunal macrobenthos and sediment (≥500 μm) were sampled using a 35.4 cm^2 cylindrical core tube to a depth of 10 cm. For infaunal macrobenthos, three replicate cores were collected per site, sectioned into 0-3 cm and 3-10 cm depths, fixed in 10 % buffered formalin, and stained with rose bengal. Two additional cores were collected per site and were sectioned into 0-3 cm depth for organic content, and 0-3 and 3-10 cm depth for sediment grain size analyses.

Laboratory analysis

Oysters and Dermo

To assess the presence of *Perkinsus marinus*, a 5 mm x 5 mm (dime-sized) piece of mantle-edge tissue was excised from just over the palps and placed into pre-labeled fluid thioglycollate media for one week following Ray (1966). After incubation, tissue was stained with Lugol's iodine solution and examined under a compound microscope for enumeration of *P. marinus* hypnospores. *Perkinsus marinus* intensity was scored using a 6-point scale (uninfected [0] to heavily infected [5]) adapted from Mackin (1962) by Craig et al. (1989). The proportion of oysters infected with *P. marinus* (prevalence) was calculated by dividing the number of infected oysters by the number of oysters sampled. Mean infection intensity (II) of individuals on the reef was calculated (Soniat et al., 2012), and weighted prevalence, a measure of the relative severity of *P. marinus* infection in a population, was calculated by multiplying mean infection intensity by prevalence.

Faunal Communities

Fauna collected from sampling trays and cores were sorted, identified to lowest possible identifiable level (usually species), and enumerated. Fauna were dried in a 60 °C oven for a minimum of 24 hours, then weighed to the nearest 0.01 g. Mollusks were placed into 2 M HCl to dissolve small shells prior to weighing, and 12 M HCL for large shells.

Sediment Grain Size

Sediment grain size was analyzed for 0-3 cm and 3-10 cm depths following the methods of Folk (1964). A homogenous 20 cm^3 subsample of each section was mixed with 50 ml hydrogen peroxide and 75 ml deionized water for 96 hours to digest organic materials. Supernatant was removed, and the sample was wet-sieved to remove sand and rubble using a vacuum pump and a Millipore Hydrosol SST filter holder fitted with a 62 µm stainless steel mesh screen; the resulting sand and rubble were dried and weighed. Silt and clay fractions of sieved material were determined through pipette analysis, with clay and silt portions dried and weighed. Percent of total mass for sand, rubble, clay, and silt was calculated for each site and sediment depth interval.

Sediment Organic Matter

To estimate sediment organic matter, a homogenous sediment sample was placed in a labeled pre-weighed aluminum boat and dried for 36 hours at 60 °C. Samples were weighed to obtain dry weight biomass and then placed in a muffle furnace for four hours at 450°C. The difference in sample weight before and after ignition in the muffle furnace represents the amount of the organic matter that was present in the sample.

Data Analysis

To characterize spatial and temporal trends in communities, non-metric multidimensional scaling (nMDS; Clarke and Warwick 1994) analyses were performed using a Bray-Curtis similarity matrix. Hierarchical cluster analyses were conducted using the group average method to highlight similarities and differences in community composition. A similarity profile (SIMPROF) analysis was used to test for statistical evidence of structure among samples. Abundance and biomass data were square-root transformed for reef-associated epifauna and infauna communities. Similarity percentage (SIMPER) analyses were used to describe taxa that were characteristic of habitats (restored and reference), treatments (adjacent and distant), and dates. Environmental parameters were normalized to comparable scales and analyzed using principal component analysis (PCA). BIO-ENV analysis was used to relate hydrological parameters to community assemblage data using weighted Spearman rank correlations (Clarke and Ainsworth, 1993).) The expectation-maximization algorithm was used to estimate turbidity values when actual values could not be determined. Multivariate community analyses were conducted using PRIMER v7 (Clarke and Gorley, 2006).

Two-way analysis of variance (ANOVA) tests were used to test the effect of the fixed factors date and habitat (restored or reference) on oyster and epifaunal density, biomass, and diversity, using the nlme package in R (Pinhiero et al., 2019). Two-way ANOVA tests were used to test the effects of fixed factors date and treatment (distant or adjacent) on infaunal density, biomass, and diversity (Pinheiro et al., 2019). Normality of residuals were assessed with Shapiro–Wilk tests, and homoscedasticity was assessed with residual vs fitted value plots. To meet ANOVA assumptions for normality, the Box-Cox (1964) procedure was used to determine effective transformations for residuals, using the MASS package in R (Venables and Ripley, 2002). Oyster density was log-transformed to meet the assumptions of normality. Reef-associated epifaunal density was square-root transformed and biomass was log-transformed. Infaunal biomass data were log-transformed, and Hill's N1 diversity data were square-root transformed. Non-parametric Kruskal-Wallis tests were used to test the effects of sampling date and treatment on infaunal density, and effects of date and habitat on water quality variables because the data did not meet normality assumptions under any transformation. If necessary, corrected Akaike Information Criterion (AICc) in the MuMIn package in R (Barton, 2019), was used to compare weighted regression terms to minimize the sum of the weighted squared residuals and account for heteroscedasticity. Tukey's multiple comparison test was used to determine differences among or between treatments when significant differences were found ($p < 0.05$), using the multcomp package in R (Hothorn et al., 2008). Pearson correlations were fit between biotic and environmental data using PROC CORR in SAS 9.4 (SAS Institute Inc. 2016). All univariate analyses except Pearson correlations were performed using R 3.5.2 (R Foundation for Statistical Computing, 2018).

RESULTS

Environmental Variables

Mean salinities ranged from 6.0 ± 0.0 (mean ± standard error [SE]) in September 2017 (23 days after Hurricane Harvey) to 30.0 ± 0.3 in August 2018 **(**Figure 2). Mean temperature displayed expected seasonal patterns, ranging from 9.9 ± 0.3 °C in November 2018 to 30.1 ± 0.2 °C in August 2017. Mean dissolved oxygen patterns were opposite those for temperature, ranging from 4.5 ± 0.4 mg L^{-1} in August 2018 to 10.9 ± 0.1 mg L^{-1} in November 2018. pH ranged from 8.0 ± 0.0 in May 2017 to 8.3 ± 0.0 in February 2018. Turbidity ranged from 5.5 ± 0.7 NTU in February 2019 to 55.9 ± 6.6 NTU in September 2017. All water quality variables differed among date-habitat combinations (p-value < 0.01; appendix 2.1.), but generally were more similar between habitats (restored and reference oyster reefs) than among dates.

Fauna

Oysters and Dermo

Oyster shell height on the restored reef ranged from 3 to 93 mm, and on the reference reef from 6 to 122 mm (Figure 3). Oysters on the restored reef grew rapidly during the early period after reef construction, with average growth rates ranging from 0.29-0.41 mm d^{-1} from August-November 2017, decreasing to 0.1 mm d^{-1} in December 2017 (Appendix 4.1). Except for the first sampling date, where the restored reef was dominated by 100 % spat oysters (shell height 3-25 mm), both the restored and reference reefs were dominated by sub-market size oysters (shell height 26-75 mm; Figure 4). Market size oysters (shell height ≥76) were first observed on the restored reef ten months after construction in May 2018, and peaked at 9.3 % (105 m^{-2}) on the last sampling date in February 2019 (Appendix 4.2; Figure 4). On the reference reef, market size oysters were present every sampling date, but proportions were highest in February 2018 at 15.0 % (29 m^{-2}). Oyster densities differed among date-habitat combinations ($p < 0.0001$; Appendix 2.2). Oyster densities were lowest on the restored reef in September 2017, and in February 2018 on the reference reef (188 ± 72 n m^{-2} and 143 ± 35 n m^{-2}, mean ± SE respectively) and generally increased throughout the project period (Figure 5). Mean oyster densities peaked on the restored reef at 1532 ± 247 n m^{-2} in May 2018, compared to 583 ± 63 n m^{-2} on the reference reef in November 2018. Spat (>800 %) and submarket (>600 %) densities were greatly enhanced on the restored reef relative to the reference reef in May 2018 (Appendix 4.3). On the last sampling date (February 2019), market size oyster densities increased >100 %, with an overall increase of 57 % across all size classes.

A total of 270 oysters (180 reference reef; 90 restored reef), ranging in height from 31 mm to 124 mm, were collected and assessed for the presence of *P. marinus*. At the reference reef, *P. marinus* was present on every sampling date. Prevalence and weighted prevalence were highest (100 %, 1.58 respectively) on the reference reef in August 2017, and lowest (5 %, 0.03 respectively) on the final sampling date in February 2019 (Figure 6; Appendix 3.1). Restored reef oysters were assessed for *P. marinus* starting in February 2018, after allowing time for oyster populations to grow to sizes larger than spat. Of the 90 oysters collected from the restored reef, only one oyster (in February 2018) was recorded with dermo infection, which was low (infection intensity 0.33). *Perkinsus marinus* distribution was grouped based on the infection intensity scale, with 60.7 % of oysters not diseased (infection intensity of 0), and 30.4 % having infection intensities less than 1.67 (Figure 7).

Reef-Associated Epifauna

A total of 7,554 organisms (4,236 on the restored and 3,318 on the reference reef) were collected, consisting of 24 epifaunal species (20 restored, 20 reference) (Figure 8). Reef-associated epifaunal density, biomass, and diversity differed among date-habitat combinations ($p < 0.0001$; Appendix 2.3). Epifaunal densities on the restored reef were least in September 2017 (357 ± 64 n m^{-2} (mean ± SE)), and generally increased to 1983 ± 652 n m^{-2} on the final sampling date in February 2019 (Figure 8). On the reference reef, one individual sheepshead fish (*Archosargus probatocephalus*), was collected on the last three sampling dates (August 2018, November 2018, and February 2019). As sheepshead are not considered reef-associated organisms, results were also analyzed excluding the fish (n-3; Figure 8). Epifaunal densities were lowest in February 2018 (389 ± 54 n m^{-2} (mean ± SE)) and were also highest in February 2019 (1102 ± 216 n m^{-2} (mean ± SE)); 1104 ± 215 n m^{-2} (mean ± SE)) including the sheepshead (Appendix 4.4). Starting in May 2018, epifaunal densities on the restored reef exceeded those on the reference reef and were consistently larger thereafter (Figure 8). On the restored reef, the flatback mud crab *Eurypanopeus depressus*, the Atlantic mud crab *Panopeus herbstii*, and the green porcelain crab *Petrolisthes armatus* contributed 22.7 %, 18.7 %, and 17.6 % to the total density, respectively (Table 1**).** On the reference reef, *P. armatus* and *P. herbstii* were the greatest contributors, supplying 34.9 % and 28.5 % of the total density, respectively. In the first 3 months after restoration, restored reef epifaunal biomass increased from 10.0 ± 2.6 to 40.2 ± 2.0 g m^{-2} (mean ± SE), whereas epifaunal biomass on the reference reef declined from 130.2 ± 39.0 to 50.4 ± 14.7 g m^{-2} (Figure 8). Biomass on the restored reef exceeded that of the reference reef and became similar by the last sampling date (February 2019; Figure 8), whereas the opposite occurred when the sheepshead fish were accounted for (Appendix 4.4). Restored reef epifaunal biomass was dominated by *E. depressus*, the hooked mussel *Ischadium recurvum*, and *P. armatus* (47.7 ± 6.2, 8.8 ± 4.3, 6.9 ± 1.4, respectively; Table 1). Reference reef epifaunal biomass was dominated by *E. depressus* (30.4 ± 4.0), *P. herbstii* (20.2 ± 3.2), and A. *probatocephalus* 18.9 ± 13.8 (Table 1). Hill's N1 diversity was slightly lower at the restored reef (3.1 ± 0.2) than the reference reef (3.9 ± 0.3) on the first sampling date in September 2017. Mean diversity fluctuated until August 2018, when diversity on the restored reef (5.4 ± 0.3) exceeded that on the reference reef and it remained higher for the duration of the study (Figure 8).

Epifaunal abundance community composition generally clustered into three main groups with at least 60 % similarity within each group ($p < 0.05$; Figure 9A). The cluster on the far left of the nMDS plot (September 2017) includes only the first sampling date after construction for the restored oyster reef, and was dominated *by P. herbstii*, the naked goby *Gobiosoma bosc*, the marsh grass shrimp *Palaemonetes vulgaris*, and *P. armatus* (Appendix 1.1). The other two clusters separated generally by date (Figure 9A). Community composition for both habitats for the first year (middle cluster) were characterized by *E. depressu*s, *P. herbstii*, *P. armatus*, and *G. bosc* with the addition of the big claw snapping shrimp, *Alpheus heterochaelis*, for the restored reef (Appendix 1.1). For the second year after restoration (right cluster), *P. armatus* dominated the communities of both habitats and were joined by *E. depressu*s, *P. herbstii, I. recurvum,* and the impressed odostome *Boonea impressa* (Appendix 1.1). Community composition was 75 % similar within habitats in the second year, with *G. bosc* (on the restored reef) and the Gulf stone crab, *Menippe adina* (on the reference reef) contributing to the inter-habitat differences. There were marginal differences in SIMPER analyses for abundance community composition between all epifauna and the exclusion of the three *A. probatocephalus* (Appendix 1.1; Appendix 1.2).

Epifaunal biomass community composition clustered into two main groups with 55 % similarity within each group (Figure 9B). Epifaunal community biomass on the restored reef from the first sampling date in September 2017, separated from all other date-habitat combinations, mirroring the abundance-based community composition results, and was dominated by *G. bosc*, *P. herbstii*, *P. vulgaris,* and Panopeidae (Appendix 1.4). The second cluster includes the remaining restored and reference reef communities (Figure 9B), and are characterized by *E. depressus, P. herbstii, P. armatus, G. bosc,* and *P. vulgaris*. When all epifauna were analyzed (inclusion of *A. probatocephalus*), community composition clustered into three main groups with 55 % similarity within each group (Appendix 4.5), with the first sampling date separating from the other clusters (September 2017; Appendix 1.5). The middle cluster includes all subsequent sampling dates for the restored reef, and September 2017 to May 2018 for the reference reef (Appendix 4.5). Epifaunal community biomass for the restored reef dates were characterized by *E. depressus*, *P. herbstii*, *G. bosc*, *P. armatus*, *A. heterochaelis,* and the skillet fish, *Gobiesox strumosus*; the reference reef by *E. depressus*, *P. herbstii*, *P. armatus,* and *G. bosc* (Appendix 1.5). The right cluster includes only reference reef samples from August 2018 to February 2019 (Appendix 4.5). Community biomass at the reference reef was characterized by *E. depressus*, *P. herbstii*, *G. bosc*, and *P. armatus*, and were joined by *I. recurvum*, and *M. adina* (Appendix 1.5). There were no significant correlation patterns among salinity, dissolved oxygen, or turbidity and epifauna metrics at either reef (Table 2).

Infauna

A total of 4,706 infaunal organisms were collected (2,496 from reef-adjacent sites, 2,210 from distant sites), representing 58 species (50 adjacent, 43 distant) (Table 3). Infaunal densities differed among date-treatment combinations ($p < 0.0001$; Appendix 2.4a) but generally exhibited more similarities between treatment sites (adjacent and distant) than among dates (Figure 10). At both reef-adjacent and distant sites, the most dominant species were polychaetes *Mediomastus* spp., *Streblospio benedicti*, and tanaid *Leptochelia rapax*. Infaunal biomass, and diversity differed by sampling dates ($p < 0.0001$ for both; Appendix 2.4). Total infaunal biomass was similar between treatment types (Figure 10), however the composition by species differed. At reef-adjacent sites, infaunal biomass was dominated by polychaetes Maldanidae 0.5 ± 0.5, Nereididae 0.4 ± 0.4, and *Haploscoloplos foliosus* 0.5 ± 0.3 (mean ± SE). At distant sites, infaunal biomass was dominated by the minor jackknife clam *Ensis minor* (0.2 ± 0.1), *H. foliosus* (0.2 ± 0.1), *L. culveri* (0.3 ± 0.1), and *Nereis* spp. (0.2 ± 0.1). Hill's N1 diversity fluctuated over time for both treatments, and ranged from 2.6 ± 0.7 to 6.3 ± 0.2 at the adjacent sites, and 3.1 ± 0.4 to 5.5 ± 0.3 at the distant sites.

Infaunal abundance community composition generally clustered into three main groups by date, with at least 60 % similarity within each group ($p < 0.05$; Figure 11A). The left cluster included a combination of spring and summer seasons and was dominated by *Mediomastus* spp., *L. rapax*, Ampeliscidae, and *Capitella capitata* (Appendix 1.7). The middle cluster was characterized by *L. rapax*, *Mediomastus* spp., *S. benedicti*, Ampeliscidae, Aoridae, and Nemertea for winter months (February 2017 and February 2018) and August 2018. The right cluster included fall dates (September – November 2017 and November 2018) and was characterized by *S. benedicti*, *Mediomastus* spp., and *L. rapax* (Appendix 1.7).

Infaunal biomass community composition clustered into two main groups corresponding to date, with at least 40 % similarity within each group ($p < 0.05$; Figure 11B). The right cluster includes the pre-construction sampling dates and was dominated by polychaetes *Mediomastus* spp., *Parandalia fauveli*, *L. culveri*, *Scolelepis squamata*, *H. foliosus*, and crustacean *L. rapax* (Appendix 1.8). The left cluster includes all subsequent sampling dates, with infaunal community biomass characterized by *L. rapax*, *Mediomastus* spp., *S. benedicti*, *P. fauveli*, *C. capitata*, Ampeliscidae, Aoridae, and Nemertea (Appendix 2.11).

The best water quality indicator of infauna abundance-based community composition was the combination of salinity and turbidity (Rho = 0.435, $p = 0.01$; Appendix 1.9). Infauna biomass-based community composition was also best described by salinity and turbidity (Rho = 0.448 $p = 0.03$; Appendix 1.10). Examining Pearson's rank correlation coefficients, salinity was positively correlated with epifaunal density and biomass for both treatment types, and turbidity was negatively correlated with infauna diversity for both treatment types (Table 4). pH was negatively correlated with infauna diversity for the adjacent sites as well as density and biomass for the distant sites. There were no significant correlations for dissolved oxygen or temperature with any infauna metrics.

Sediment Analyses

A principal component analysis (PCA) was performed on the percent of total mass for silt, sand, rubble, and clay for each treatment and sampling date from July 2017 to February 2019 (Appendix 4.6). The vector plot on the left shows that the PC 1 and PC 2 axis explains a total of 64 % of the variation. The factor plot on the right shows adjacent and distant treatments primarily clustering along the PC 1 axis for sand and silt, and that grain size between treatment generally did not vary as a function of distance from the restored reef. An additional PCA was performed on both grain size and organic content between February 2018 to February 2019 (Appendix 4.7). The vector plot shows that the PC 1 and PC 2 axis explains a total of 68 % of the variation, and the factor plot shows adjacent and distant treatments primarily clustering along the PC 2 axis for clay and silt, and similarly the treatments also did not vary as a function of distance from the restored reef.

DISCUSSION

Development of restored oyster reef

Rapid development of the restored oyster reef was observed in the first few months following reef construction. During this early period, oyster growth rates exceeded 0.4 mm d^{-1} and oyster densities increased more than three times; densities continued to increase to a high of more than 1500 oysters m^{-2} at ten months after construction and remained greater than 800 oysters m^{-2}. Densities for the current study were much higher compared to densities reported on other restored reefs in the Gulf of Mexico, estimated from 0 to 392 oysters m^{-2} for 11 restored reefs across seven bay systems from Louisiana to Alabama (La Peyre et al., 2014), and from 0 to 212 oysters m^{-2} in the northwest region of Florida (Frederick et al., 2016). Densities in the current study were within range of previously restored reefs in Texas estuaries, ranging from 900 - 1500 oysters m^{-2} on restored reefs in Aransas Bay (George et al. 2015; Graham et al. 2016) to 2000 oysters m^{-2} on a restored reef in Matagorda Bay (DeSantiago et al. 2019).

The shift in dominant size class of oysters on the restored reef from 100 % spat to more than 90 % submarket size in the first four months demonstrates their rapid growth; market size oysters occurred just ten months after construction (May 2018). Fast growth rates for small oysters are promoted by the warm temperatures typically observed in Gulf estuaries (Menzel, 1951; Butler 1954; Dame 1972); water temperatures remained greater than 15 ^{o}C for the first year after construction. Growth rates of oysters on the restored reef peaked within the first three months post restoration (0.41 mm d^{-1}), as compared to six months (0.40 mm d^{-1}) in a study conducted in Georgia (Manley et al., 2010). Growth rates of the current study (0.29-0.41 mm d^{-1}) exceeded previously published growth rates in Virginia studies, for both diploid and triploid *C. virginica* (0.1–0.2 mm d^{-1}; Harding 2007), and 0.12–0.16 mm d^{-1} in response to sediment burial (0 % control treatment) of *C. virginica* (Colden & Lipscius, 2015). Oyster spat experienced the highest increase in densities within the first year after construction, and results support previous evidence of accelerated oyster reef development in Gulf of Mexico estuaries following substrate provision (De Santiago et al. 2019; Marshall et al. 2019) and indicates substrate limitation may present a substantial impediment to oyster population development (Roughgarden et al., 1985).

Epifauna community development

Increased oyster density and size is an indicator of habitat complexity, and structured marine habitats can influence physical and biological processes and are often associated with more abundant and diverse species assemblages (Crooks, 2002; Grabowski, 2004; Gratwicke & Speight 2005; Nestlerode et al., 2007; Bouma et al., 2009). Habitat complexity may have influenced the corresponding increases in epifaunal density, biomass, and diversity observed, all becoming similar to the reference reef within four months after construction. The high densities of epifauna we observed on the restored reef (1983 mean n m^{-2}) demonstrate the habitat value of subtidal oyster reef in the Gulf of Mexico estuaries. Extraordinarily high densities of epifauna may have also been promoted by the relatively high vertical relief (approximately 0.3 m) of the reef, which may have facilitated epifaunal recruitment and increases in density and diversity (Coen and Luckenbach, 2000; Sueiro, et al., 2011; Karp et al., 2018). Decapods and fishes ranged from ~80 to 100 n m^{-2} on live oyster clusters in Tarpon Bay, Florida (Tolley and Volety,

2005) and from 17 to 62 n m^{-2} on subtidal oyster reef in Galveston Bay, Texas (Stunz et al. 2010). Similarity of the restored reef epifaunal community to that of the nearby reference reef is also important because oyster reef supports a unique community of fish and crustaceans compared to other estuarine habitats (Nevins et al., 2014), and because habitat provision is a key goal for many restoration efforts. Indeed, decapod crustaceans (green porcelain crabs and mud crabs) are known for positive association with reefs and were the most abundant taxa observed on both reef types (Margiotta et al., 2016).

Structural complexity of the reef may have also promoted resistance of the restored reef to an extreme event. On 25 August 2017, less than one-month after construction, Hurricane Harvey made landfall in South Texas as a Category 4 storm, and passed directly over the study area. The storm moved slowly across coastal Texas for six days, delivering up to 130 cm of rain. Because monitoring of oysters and epifauna had not yet begun, it was not possible to understand how early reef development may have been affected by the storm. However, observations from our first sampling event in September 2017 indicated that the physical structure of the reef was intact—no changes to reef height or areal extent were detected—and high densities of oyster spat were present. The three-dimensional structure and surface complexity of an oyster reef can slow current velocities (Widdows et al., 2002), promote larval recruitment and provide refuge from predation (Whitman and Reidenbach, 2012), and supply particulate matter from the water column to suspension feeders (Nelson et al. 2004; Crimaldi et al. 2007), all which may have contributed to rapid oyster recruitment and growth in the wake of an extreme event. Environmental factors affected by the hurricane, such as the rapid decline in salinity may also have been conducive to a spawning event and the subsequent growth of spat observed on the restored reef (Livingston et al., 1999; Soniat et al., 2012).

A shift in epifaunal community assemblages on the restored reef occurred after the first year after construction, when mussels *(I. recurvum*) and gastropods (*B. impressa*) became dominant. Whereas mussels may provide an important habitat resource benefit for reef fauna (Hadley et al., 2010), *B. impressa* is an ectoparasite that may reduce growth rates in parasitized oysters (White et al. 1984). *B. impressa* was found in higher densities on the restored reef than on the reference reef, possibly due to reduced wave energy or decreased distance between oysters (Powell et al., 1987). Additional research is warranted to understand the influence of these later successional species on the restored oyster population. The observed shift in epifaunal community composition one year after reef construction indicates that monitoring periods of more than one year are needed to adequately assess epifaunal community dynamics on restored reefs.

Reef location has the potential to influence success of a restored oyster population via controls on local environmental conditions that may affect biological interactions. Transmission of the parasite *P. marinus* occurs via dead oysters or feces/pseudofeces (Bushek et al., 2002) and infection varies by location (Craig et al. 1989). Minimizing *P. marinus* on restored reefs is desirable, to the extent possible, because infection is a major cause of mortality among Gulf of Mexico oysters (Soniat, 1996). In the current study, although *P. marinus* was present every sampling date on the reference reef, only a single infected oyster was observed on the restored reef during 19 months of monitoring, likely due to its location ~2 km from the nearest infection center. Although physical transport of infected oysters via harvest activities is another potential source of transmission, St. Charles Bay is closed to oyster harvesting, minimizing these effects. Because *P. marinus* infection can complicate restoration efforts by decreasing survival rates (Paynter et al., 2010), when choosing potential sites for reef restoration, consideration should be given to the location of infection centers to decrease the potential for disease transmission during early reef development.

Infauna community development and sediment analyses

It was hypothesized that the restored reef would enhance infaunal density, diversity, and biomass at reef-adjacent sites compared to distant control sites due to benthic-pelagic coupling (Lin and Grant, 2008). However, neither the amount of organic matter nor sediment grain size varied as a function of distance from the restored reef, indicating there was not a substantial nutrient subsidy provided by the reef. Alternatively, wind-wave resuspension, characteristic of shallow-water, microtidal estuaries along the Texas Gulf Coast, may have influenced estuarine sedimentation processes or redistributed biodeposits (Shideler 1984; Dame et al. 1991; Reisinger et al. 2017). The role of restored reef structure on changing local hydrodynamics and sedimentation patterns warrants additional research. To assess whether infaunal predators were more prevalent near the reef structure and were limiting infaunal production, an exploratory epibenthic sled survey was conducted in February 2018. There were no differences in predator density or biomass related to distance from the reef, indicating minimal effects of predation, similar to previous results on artificial reefs (Ambrose and Anderson, 1990). However, the influence of artificial reefs on predator foraging is equivocal, with other studies reporting significant effects (Bortone et al., 1998; Posey and Ambrose, 1994).

In the current study, infaunal density and biomass on both restored and reference reef sites were positively correlated with salinity. Indeed, salinity is one of the most important factors influencing infaunal distribution in Gulf of Mexico estuaries (Rakocinski et al., 1997), and increases in infaunal density with salinity are characteristic of Texas estuaries (Palmer et al.

2011; Van Diggelen and Montagna, 2016). Infaunal response in the current study appears to be driven less by the presence of the restored reef and more by prevailing salinity patterns.

CONCLUSION

There is strong interest in defining and standardizing monitoring metrics and timeframes for measuring restoration success (Wortley et al., 2013), including persistence of physical structure, presence of oysters, and evidence of successful recruitment (Coen et al., 2004). Within the first year after construction, oyster and epifaunal densities on the restored reef were similar to, or exceeded those at the reference habitat, however, a shift in epifaunal community composition was observed in the second year. Results indicate that monitoring periods of more than one year are needed to adequately assess reef development, with monitoring periods of more than two years recommended for assessment of long-term dynamics, supporting existing guidelines (Baggett et al., 2014; 2015). In all cases, nearby reference reefs should be used to provide a baseline for comparison. Using proposed success criteria for reef restoration—vertical relief greater than 20 cm, living oysters (>10 m^{-2}), and evidence of recent recruitment in 1 of 2 years of the survey (Powers et al., 2009)—the current restoration project met or exceeded all expectations within 19 months of reef construction. Success may have been facilitated by the location of the reef away from *P. marinus* infection centers, minimizing oyster mortalities during early reef development, as well as the effects of structural complexity on resistance to an extreme event. Results indicate that provision of hard substrate for reef restoration can expedite the replacement of lost habitat benefits due to natural reef loss, and that physical complexity and reef location are important factors to consider for early reef development, resistance to disturbance, and restoration success.

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FIGURES

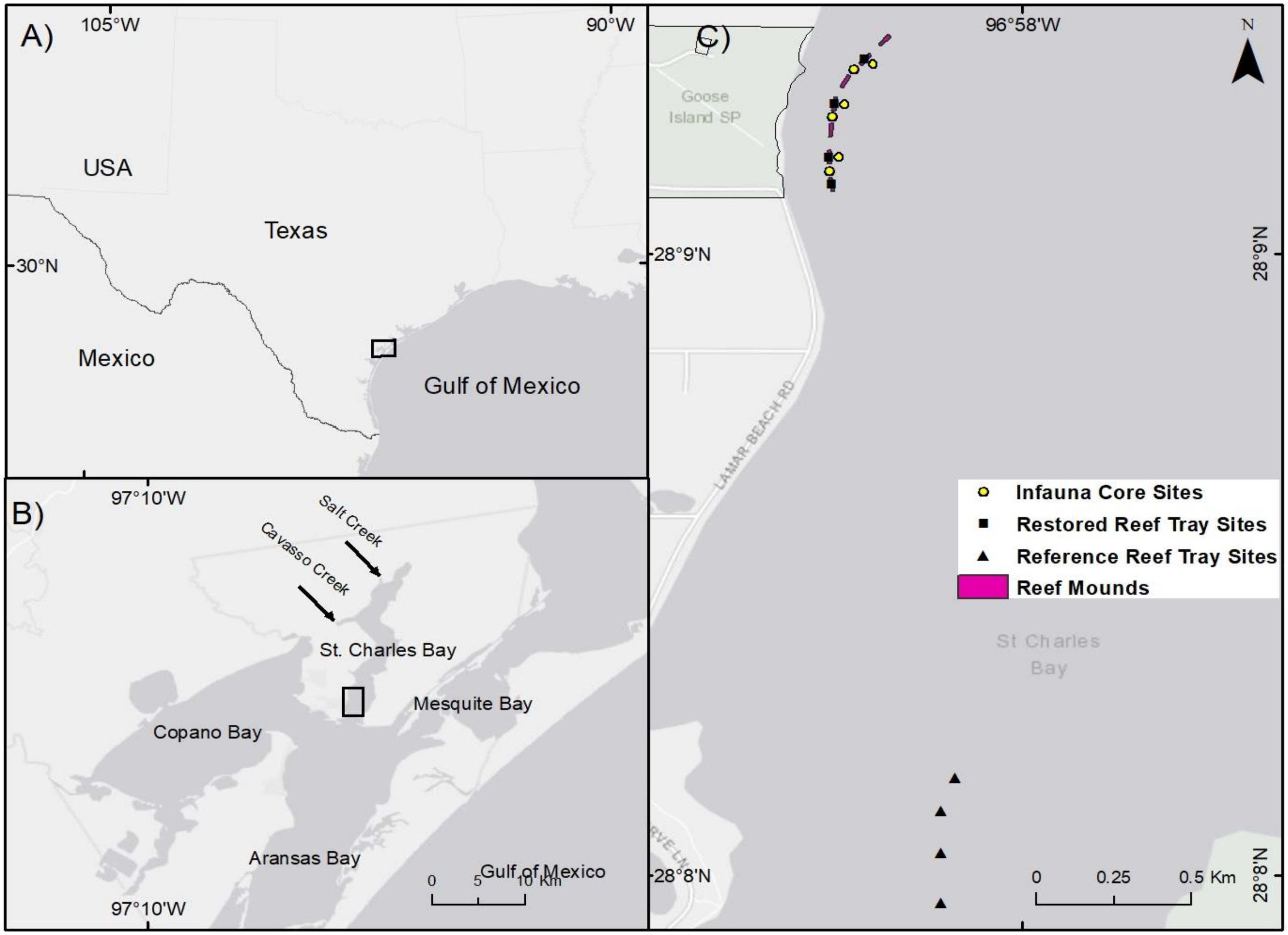


Figure 1. Map of the study area. A) Texas coastline and Gulf of Mexico B) The Mission-Aransas Estuary TX C) Sampling locations within St. Charles Bay.

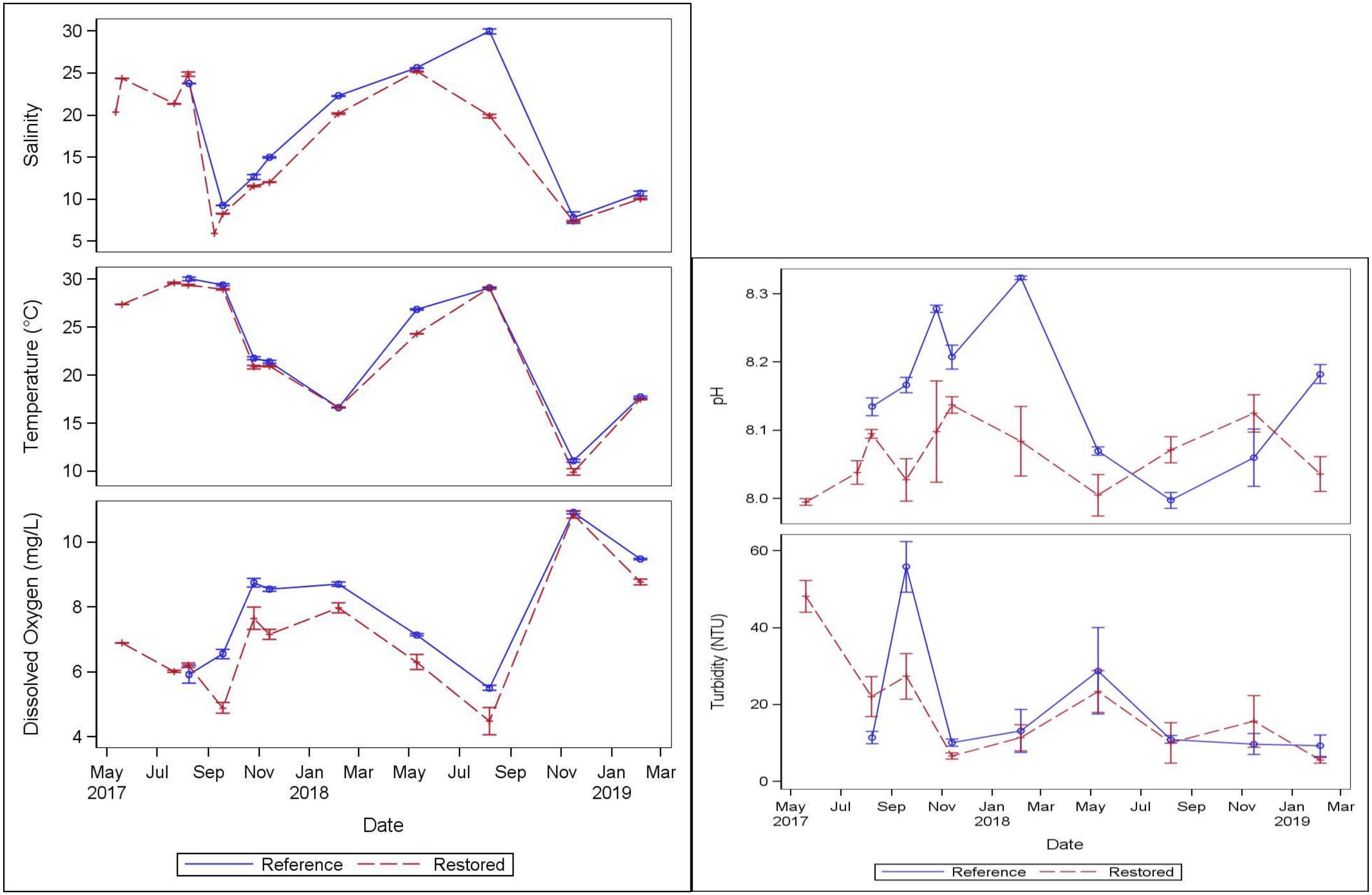


Figure 2. Salinity, temperature, dissolved oxygen, pH, turbidity (mean ± SE) during sampling events from May 2017 to February 2019.

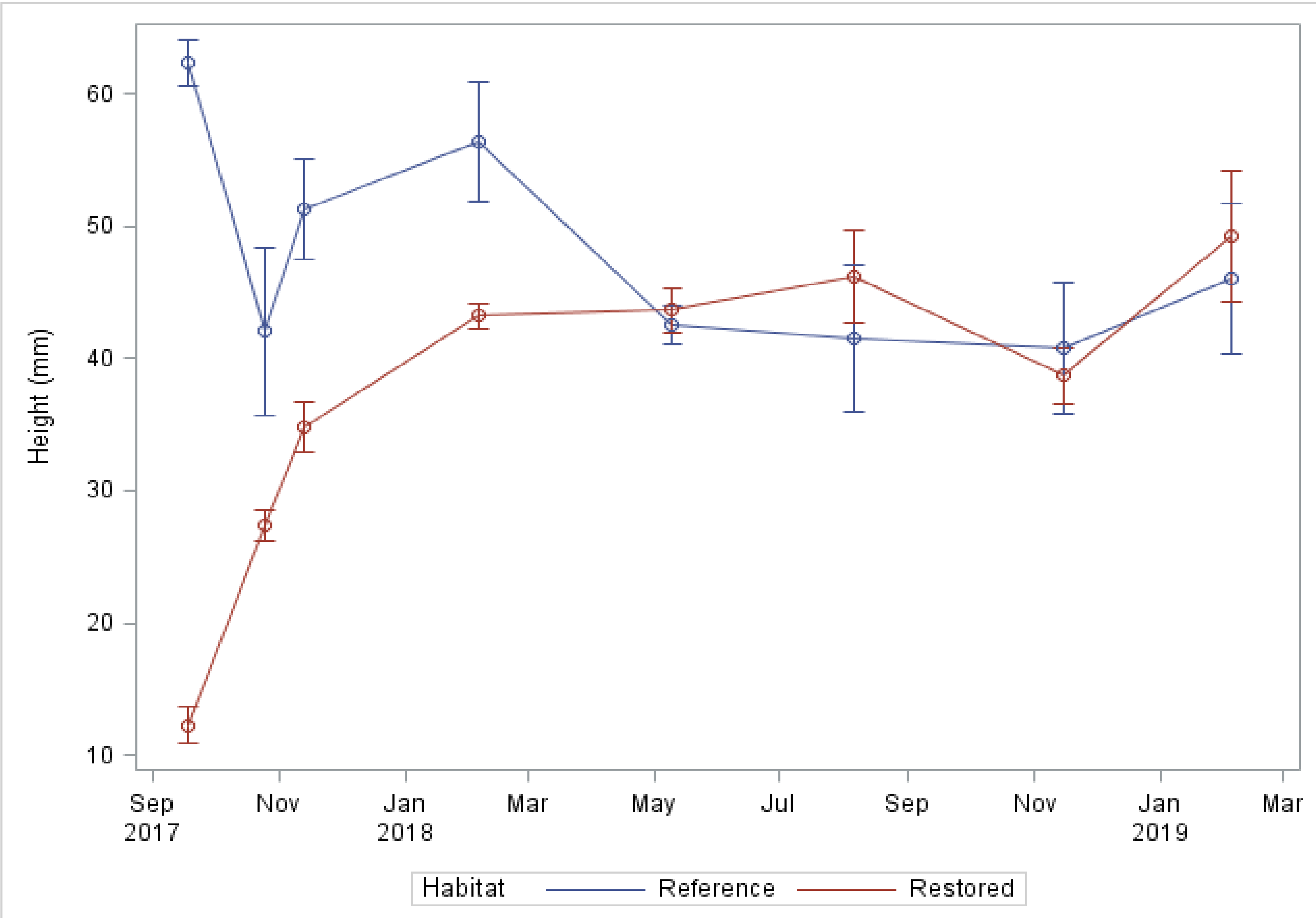


Figure 3. Mean shell height (mm) of oysters found on reference and restored oyster reefs from September 2017 to February 2019. Error bars represent standard error.

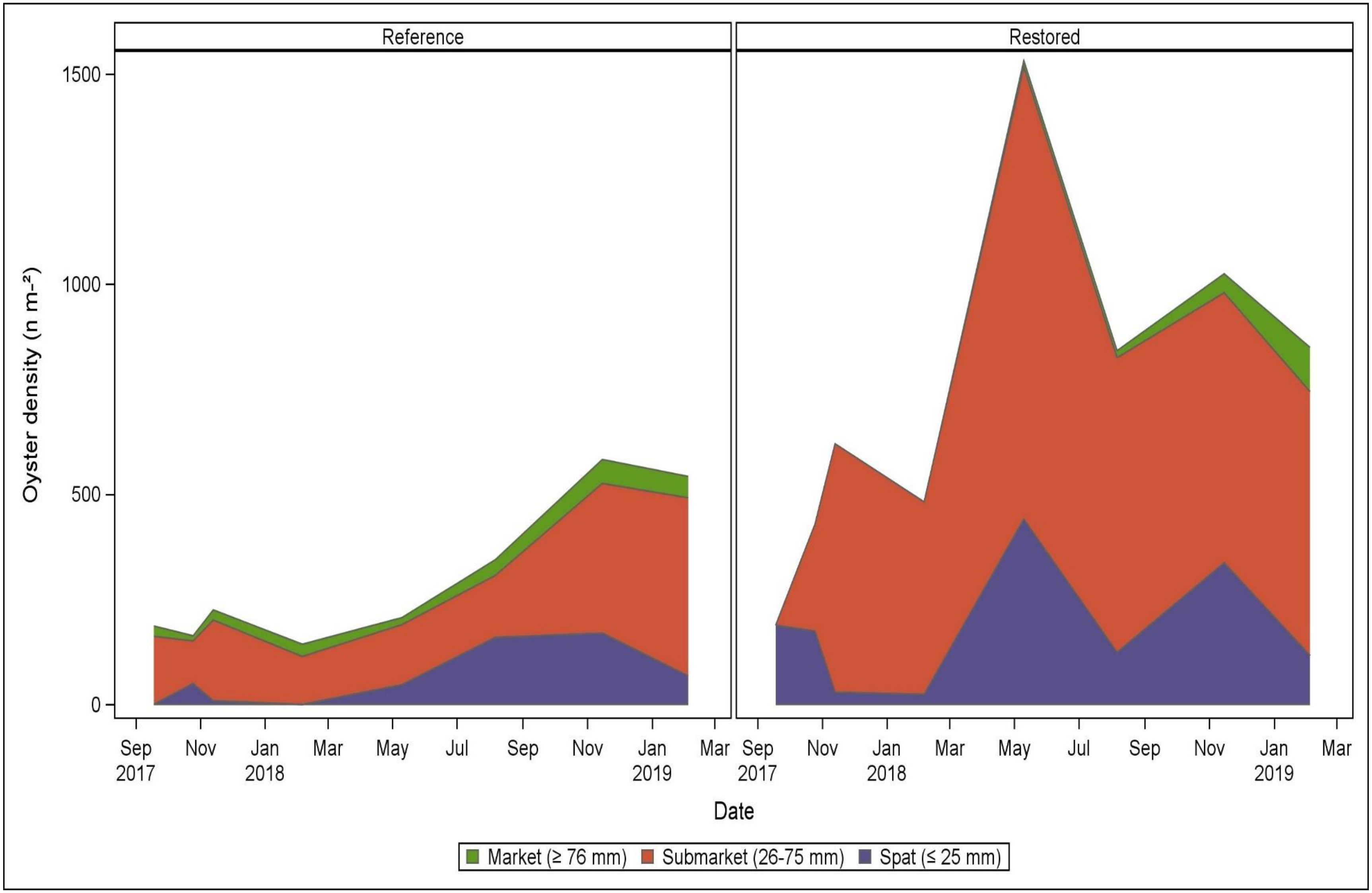


Figure 4. Oyster density percentage (n m^{-2}) of spat (≤ 25mm), sub-market (26-75mm), and market-sized oysters (≥76mm) on reference (left) and restored (right) oyster reefs from September 2017 to February 2019.

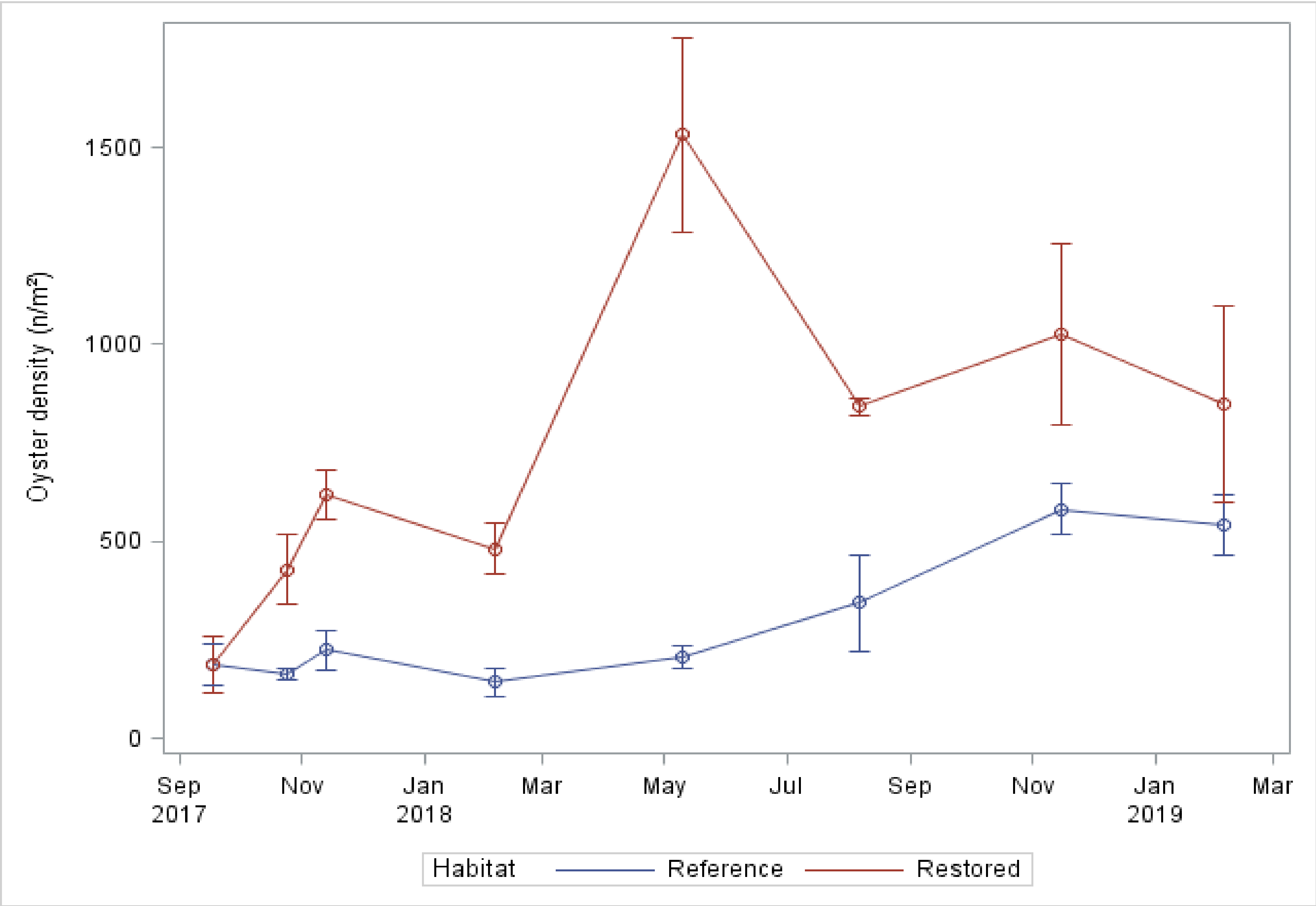


Figure 5. Mean oyster density of reference and restored oyster reefs from September 2017 to February 2019. Error bars represent standard error.

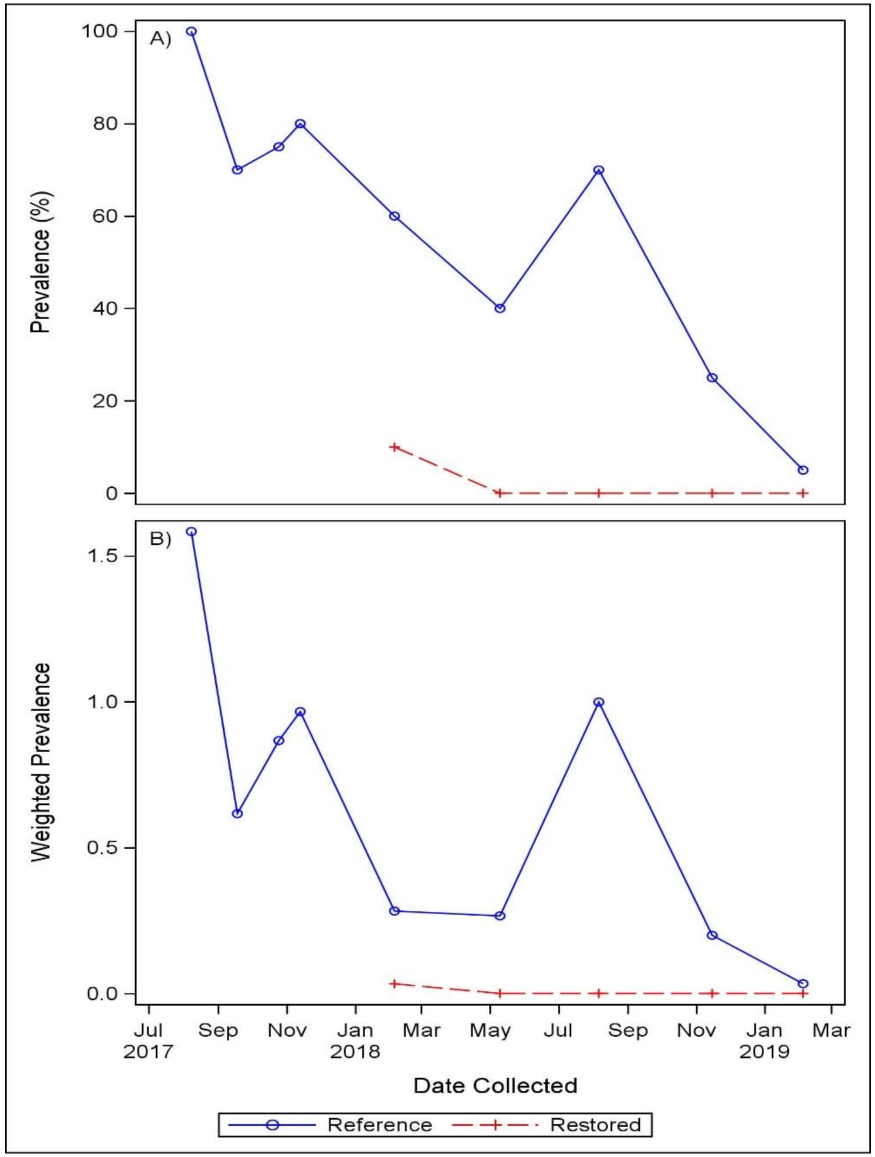


Figure 6. Proportion of oysters infected with *P. marinus* (prevalence) and severity of infection (weighted prevalence) for oysters at the restored and reference reefs from August 2017 to February 2019.

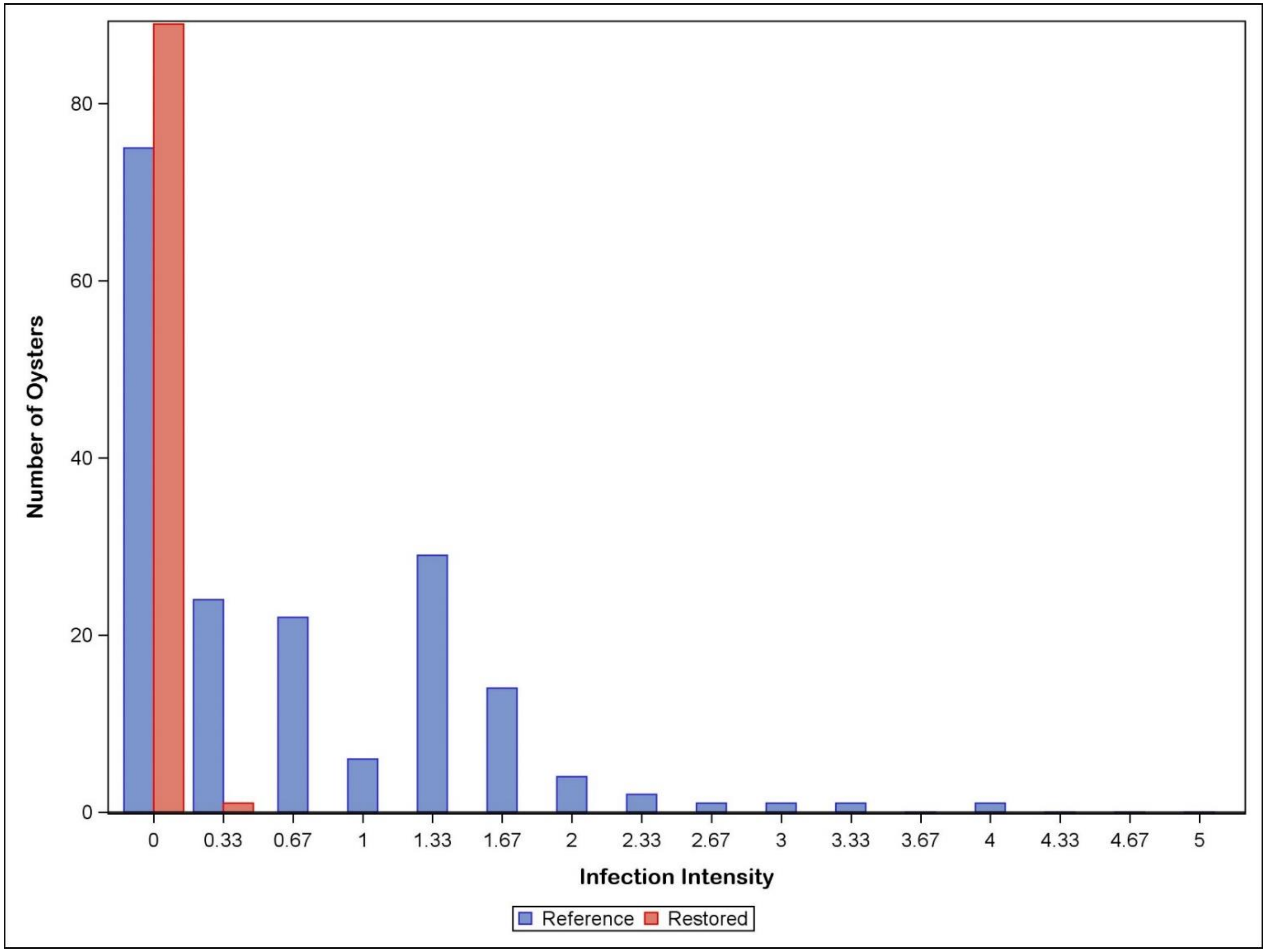


Figure 7. ***Perkinsus marinus*** **infection intensities (uninfected [0] to heavily infected [5] adapted from Mackin (1962) by Craig et al. (1989)) and corresponding number of oysters for the restored and reference reefs from August 2017 to February 2019.**

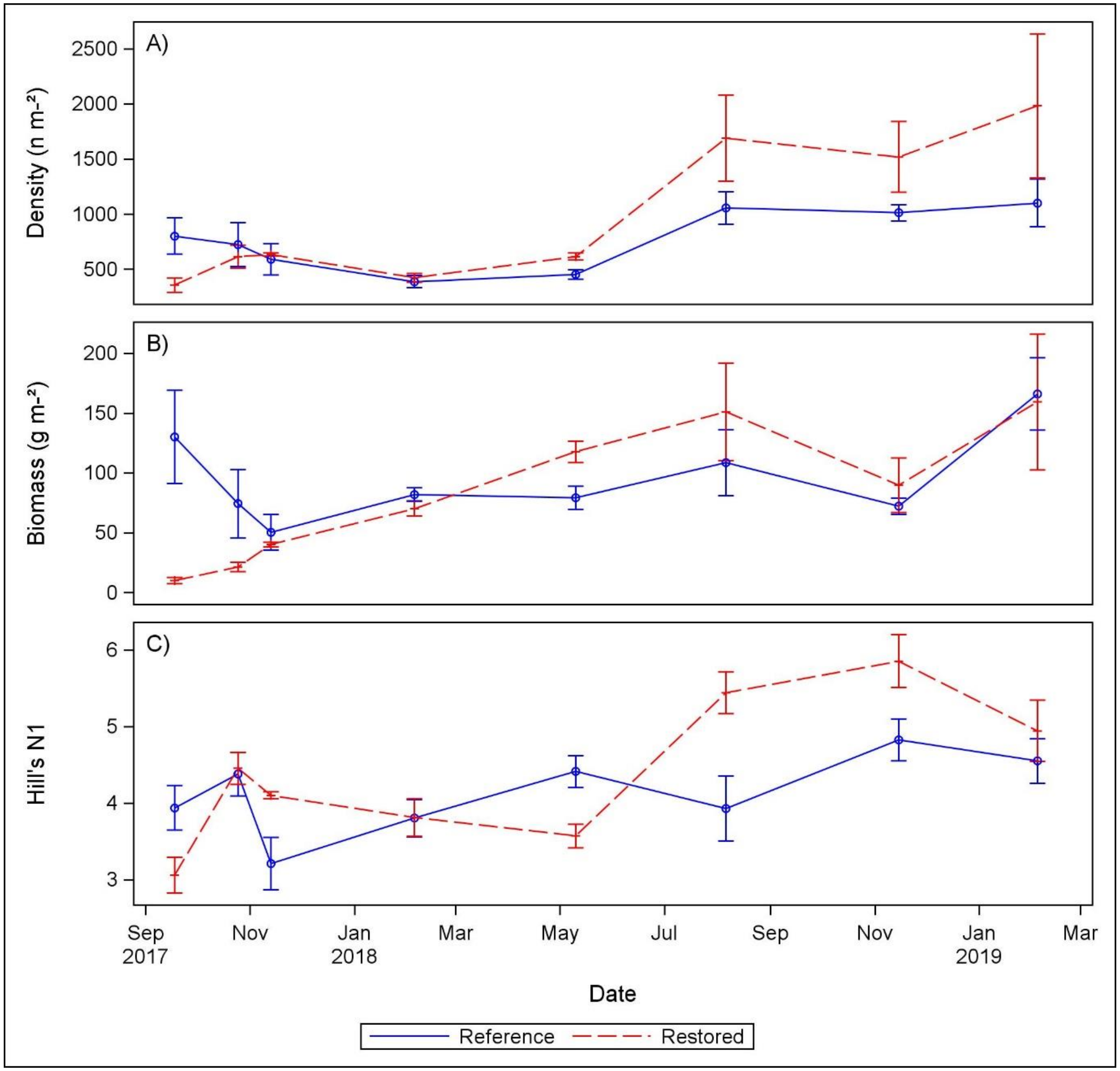
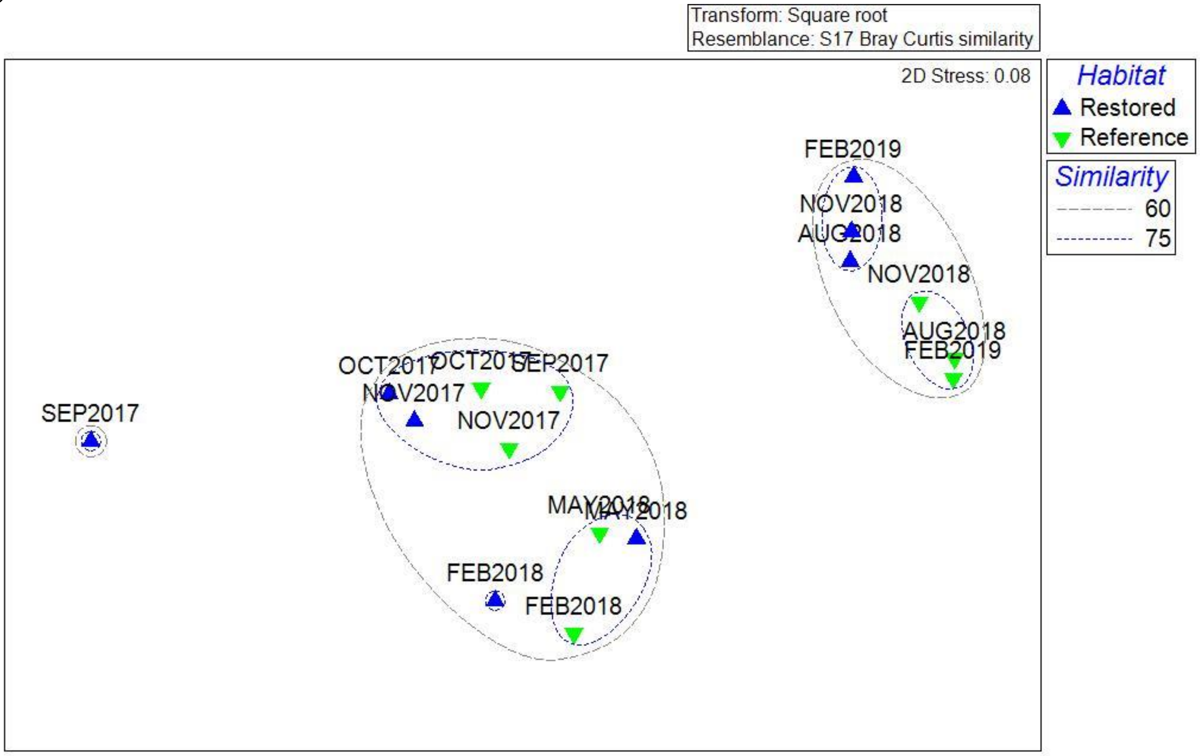


Figure 8. Mean density, biomass, and diversity (Hill's N1) of epifauna communities from August 2017 to February 2019 at restored and reference reefs (excluding *A. probatocephalus*; n-3). Error bars represent standard error.

A)



B)

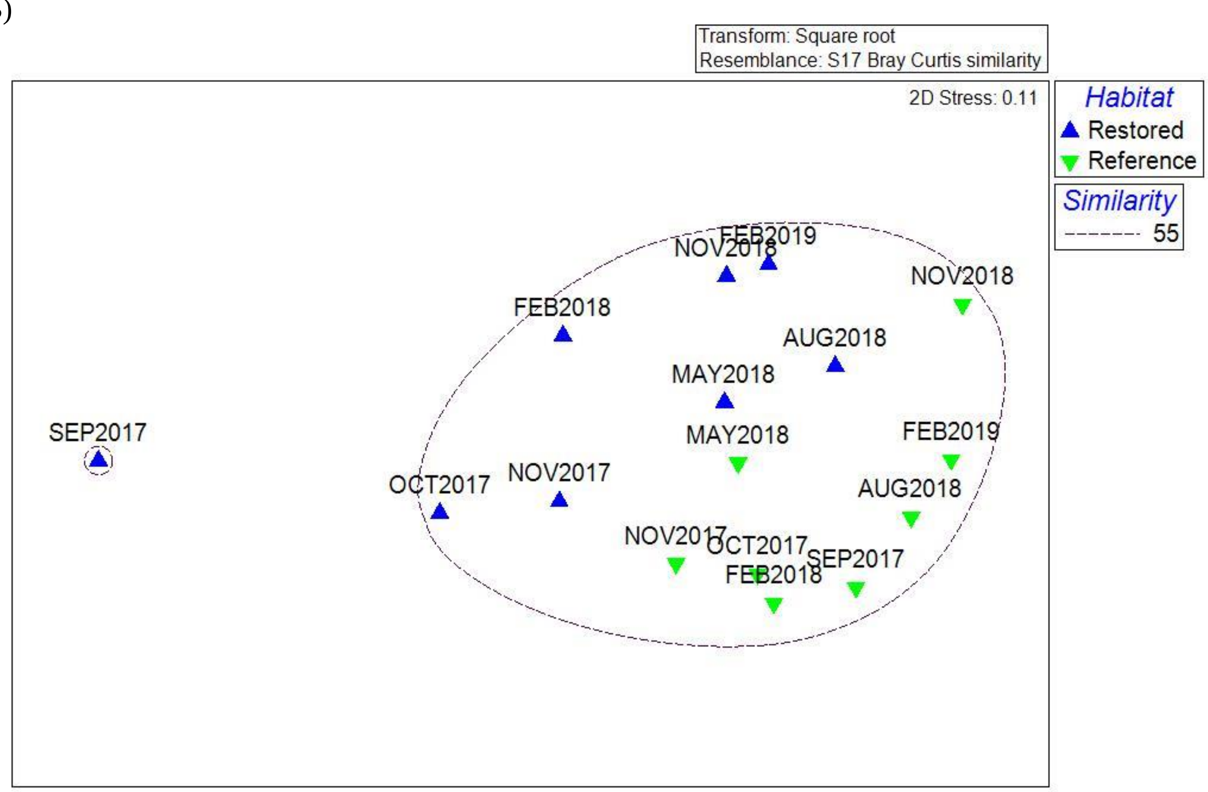


Figure 9. Nonmetric multidimensional scaling (nMDS) for epifauna communities (excluding *A. probatocephalus*; n-3). averaged by Treatment-Habitat. A) Abundance. B) Biomass.

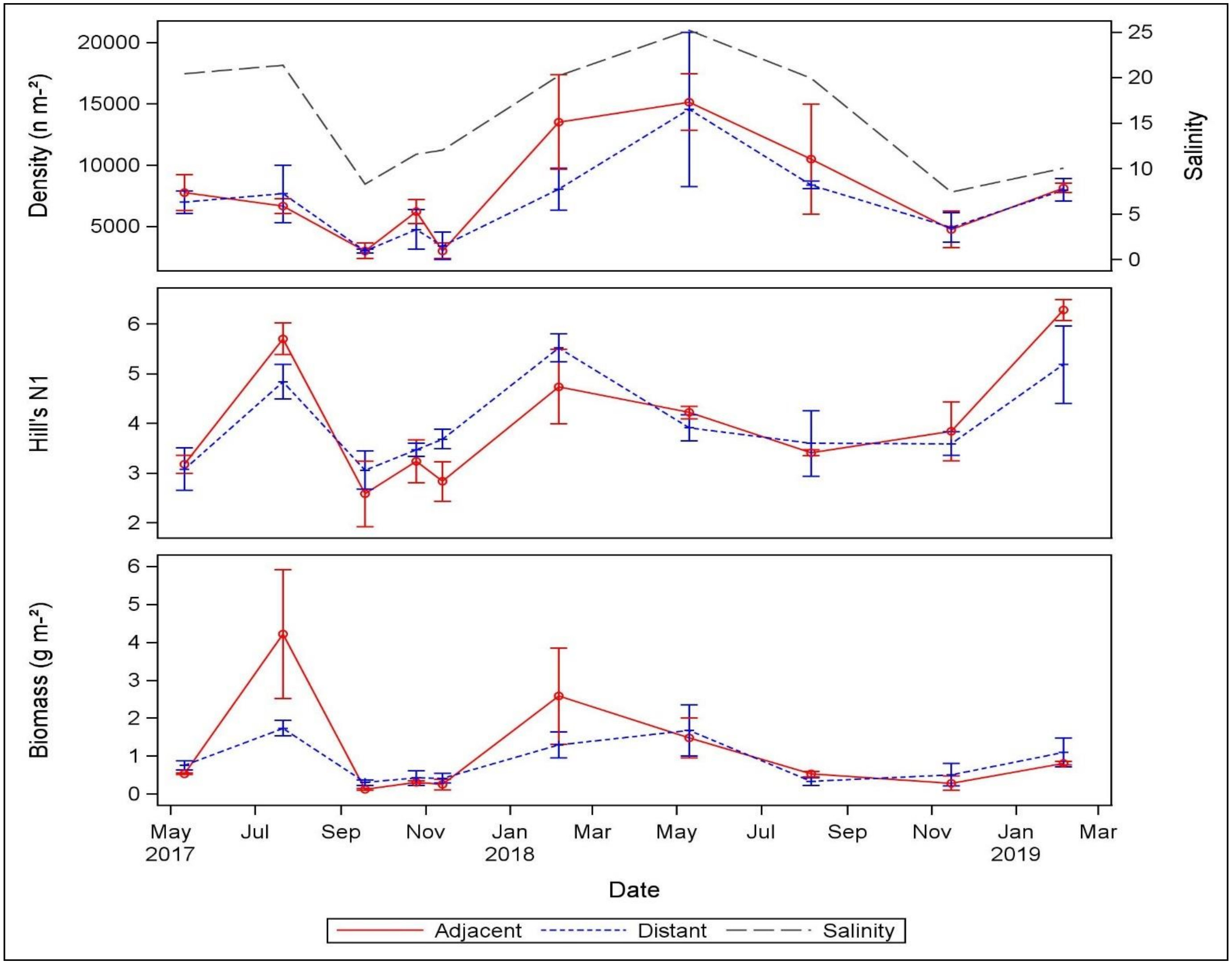
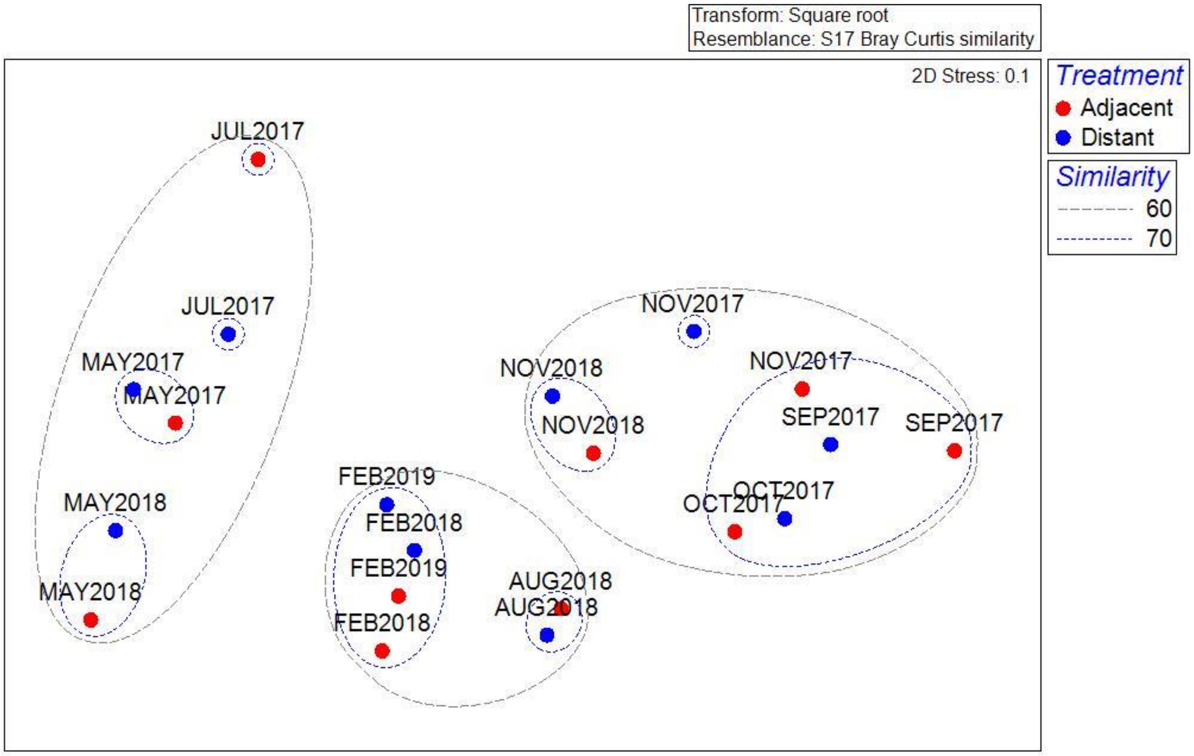


Figure 10. Mean density, biomass, and diversity (Hill's N1) of infauna communities, with mean salinity as secondary y-axis at restored and reference reefs. Error bars represent standard error.

A)



B)

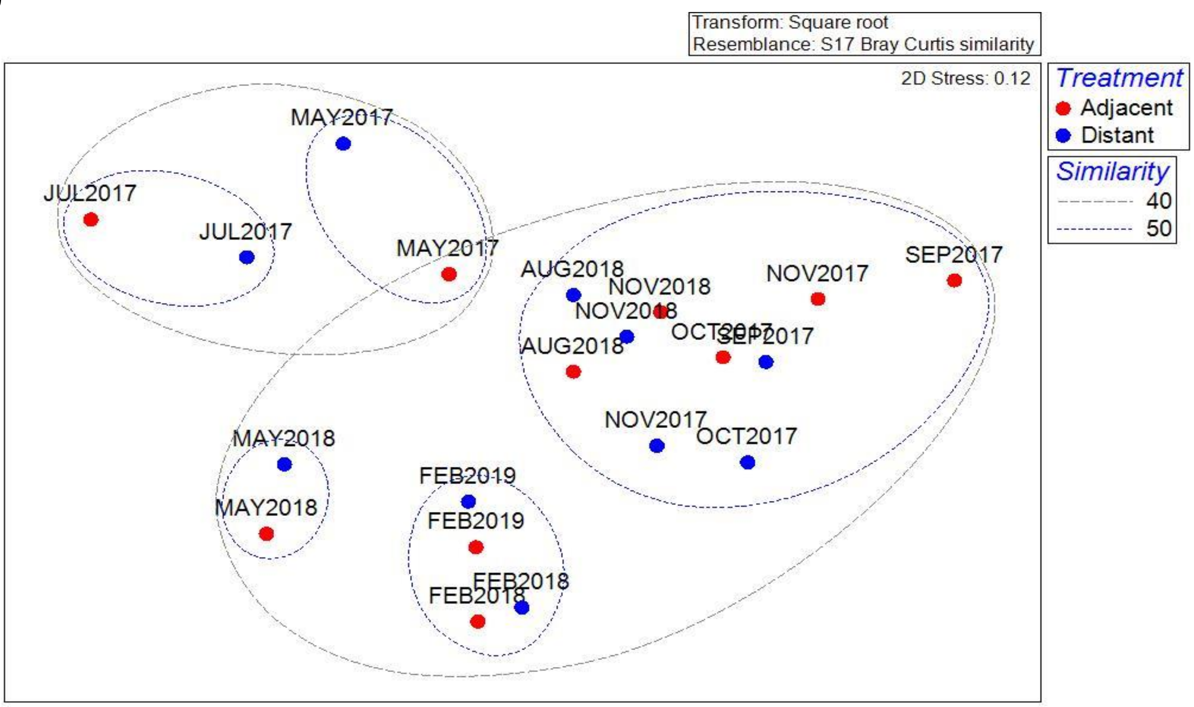


Figure 11. nMDS plot for infauna communities averaged by Date-Treatment. A) Abundance. B) Biomass.

TABLES

Table 1. Total number, densities (mean ± SE), and biomass (mean ± SE) of epifauna for the restored and reference reefs.

	Reference			Restored		
Taxa	Total # Collected	Density (n m-²)	Biomass (g m-²)	Total # Collected	Density (n m-²)	Biomass (g m-²)
Fish						
Gobiosoma bosc	104	24.1 ± 4.1	1.33 ± 0.22	261	60.4 ± 6.2	2.80 ± 0.24
Gobiesox strumosus	6	1.4 ± 0.6	0.58 ± 0.31	35	8.1 ± 2.2	1.67 ± 0.37
Opsanus beta	16	3.7 ± 1.2	13.38 ± 4.98	6	1.4 ± 0.6	2.39 ± 1.11
Chasmodes longimaxilla	11	2.5 ± 0.8	1.37 ± 0.53	3	0.7 ± 0.4	0.55 ± 0.31
Hypleurochilus bermudensis	3	0.7 ± 0.4	0.28 ± 0.27	2	0.5 ± 0.3	0.02 ± 0.01
Archosargus probatocephalus	3	0.7 ± 0.4	18.87 ± 13.78	—	—	—
Hypleurochilus ionthas	1	0.2 ± 0.2	0.12 ± 0.12	—	—	—
Hypsoblennius hentz	—	—	—	1	0.2 ± 0.2	0.44 ± 0.44
Hypsoblennius multifilis	1	0.2 ± 0.2	0.37 ± 0.37	—	—	—
Sygnathus scovelli	—	—	—	1	0.2 ± 0.2	0.01 ± 0.01
Crustacea						
Petrolisthes armatus	1158	268.1 ± 46.2	16.06 ± 2.57	746	172.7 ± 43.7	6.91 ± 1.42
Panopeus herbstii	945	218.8 ± 23.1	20.22 ± 3.20	791	183.1 ± 17.0	4.98 ± 0.51
Eurypanopeus depressus	529	122.5 ± 12.7	30.45 ± 4.00	960	222.2 ± 22.6	47.65 ± 6.16
Panopeidae	55	12.7 ± 5.7	0.08 ± 0.04	152	35.2 ± 12.0	0.64 ± 0.29
Palaemonetes vulgaris	98	22.7 ± 6.2	1.37 ± 0.47	69	16.0 ± 5.1	0.80 ± 0.28
Alpheus heterochaelis	28	6.5 ± 2.3	0.53 ± 0.20	45	10.4 ± 2.0	0.98 ± 0.18
Menippe adina	39	9.0 ± 2.4	7.55 ± 2.34	5	1.2 ± 0.5	3.64 ± 3.56
Dyspanopeus texanus	15	3.5 ± 1.6	0.06 ± 0.04	13	3.0 ± 1.1	0.05 ± 0.02
Stylochus spp.	2	0.5 ± 0.5	0.01 ± 0.01	3	0.7 ± 0.4	0.02 ± 0.02
Argulis sp.	—	—	—	1	0.2 ± 0.2	3.47E-05 ± 3.47E-05

Bivalvia						
Ischadium recurvum	206	47.7 ± 12.6	1.69 ± 0.77	649	150.2± 57.0	8.80 ± 4.27
Gastropoda						
Boonea impressa	96	22.2 ± 8.2	0.01 ±0.01	492	113.9 ± 48.0	0.15 ± 0.11
Costoanachis semiplicata	2	0.5 ± 0.3	0.001 ± 0.001	—	—	—
Nassarius acutus	—	—	—	1	0.2 ± 0.2	2.08E-04 ± 2.08E-04

Table 2. Pearson rank correlation coefficients (rho) between epifaunal community measurements and water quality variables for reference and restored reefs.

		Reference			Restored		
Variable (unit)	**Correlation**	**Density ($n\ m^{-2}$)**	**Biomass ($g\ m^{-2}$)**	**Hill's Diversity (N1)**	**Density ($n\ m^{-2}$)**	**Biomass ($g\ m^{-2}$)**	**Hill's Diversity (N1)**
Salinity	rho	-0.214	0.119	-0.183	-0.137	0.305	-0.219
	p	0.24	0.515	0.317	0.455	0.09	0.229
pH	rho	-0.391	-0.21	-0.294	-0.143	-0.229	0.123
	p	0.027	0.249	0.103	0.436	0.207	0.502
Dissolved Oxygen ($mg\ L^{-1}$)	rho	0.056	-0.236	0.278	0.175	0.021	0.348
	p	0.759	0.194	0.124	0.338	0.907	0.051
Temperature (°C)	rho	-0.066	0.174	-0.25	-0.202	-0.064	-0.419
	p	0.718	0.34	0.168	0.267	0.727	0.017
Turbidity (NTU)	rho	-0.24	-0.079	0.033	-0.174	-0.254	-0.083
	p	0.218	0.689	0.868	0.376	0.192	0.675

Table 3. Total number, densities (mean ± SE), and biomass (mean ± SE) of infauna for adjacent and distant treatments at the restored oyster reef.

	Adjacent			Distant		
Taxa	Total # Collected	Density (n m-²)	Biomass (g m-²)	Total # Collected	Density (n m-²)	Biomass (g m-²)
Polychaeta						
Mediomastus spp.	771	7289.5 ± 1062.7	0.299 ± 0.044	560	5294.6 ± 512.9	0.220 ± 0.025
Streblospio bendicti	507	4793.5 ± 1037.4	0.114 ± 0.021	349	3299.7 ± 752.0	0.074 ± 0.015
Parandalia fauveli	49	463.3 ± 86.5	0.255 ± 0.064	62	586.2 ± 116.9	0.213 ± 0.048
Capitella capitata	54	510.6 ± 206.0	0.023 ± 0.009	42	397.1 ± 95.8	0.018 ± 0.005
Laeonereis culveri	16	151.3 ± 72.9	0.264 ± 0.143	10	94.5 ± 45.8	0.277 ± 0.146
Scolelepis squamata	13	122.9 ± 64.8	0.029 ± 0.015	11	104.0 ± 44.0	0.023 ± 0.011
Haploscoloplos foliosus	18	170.2 ± 77.6	0.468 ± 0.274	5	47.3 ± 23.9	0.187 ± 0.144
Polydora cornuta	6	56.7 ± 31.6	0.002 ± 0.001	6	56.7 ± 28.5	0.024 ± 0.021
Nereididae	6	56.7 ± 34.4	0.357 ± 0.357	3	28.4 ± 15.8	0.029 ± 0.023
Nereis spp.	1	9.5 ± 9.5	0.032 ± 0.032	8	75.6 ± 33.1	0.166 ± 0.092
Hypereteone heteropoda	—	47.3 ± 23.9	0.026 ± 0.017	3	28.4 ± 15.8	0.001 ± 0.001
Capitellidae	5	47.3 ± 27.5	0.002 ± 0.001	2	18.9 ± 13.1	4.0E-04 ± 3.0E-04
Goniadidae	4	37.8 ± 17.9	0.005 ± 0.003	3	28.4 ± 15.8	0.006 ± 0.005
Americonuphis magna	—	—	—	4	37.8 ± 29.6	0.106 ± 0.099
Podarke obscura	—	—	—	4	37.8 ± 26.3	0.010 ± 0.007
Syllidae	2	18.9 ± 13.1	0.001 ± 4.0E-04	2	18.9 ± 13.1	0.001 ± 0.004
Hesionidae	1	9.5 ± 9.5	4.0E-04 ± 4.0E-04	3	28.4 ± 20.8	3.0E-04 ± 2.0E-04
Maldanidae	2	18.9 ± 18.9	0.530 ± 0.530	1	9.5 ± 9.5	0.065 ± 0.065
Hypereteone lactea	1	9.5 ± 9.5	0.008 ± 0.008	2	18.9 ± 13.1	0.023 ± 0.022
Polydora spp.	2	18.9 ± 18.9	1.0E-04 ± 1.0E-04	—		
Magelona pettiboneae	1	9.5 ± 9.5	0.004 ± 0.004	1	9.5 ± 9.5	0.003 ± 0.003
Onuphis eremita oculata	1	9.5 ± 9.5	0.001 ± 0.001	1	9.5 ± 9.5	0.005 ± 0.005
Marphysa aransensis	1	9.5 ± 9.5	0.018 ± 0.018	—	—	—

Pectinaria gouldii	1	9.5 ± 9.5	0.013 ± 0.013	—	—	—
Armandia agilis	—	—	—	1	9.5 ± 9.5	1.0E-04 ± 1.0E-04
Lysidice ninetta	1	9.5 ± 9.5	0.005 ± 0.005	—		
Polydora websteri	—	—	—	1	9.5 ± 9.5	5.0E-04 ± 5.0E-04
Oligochaeta						
Oligochaeta	10	94.5 ± 58.2	0.006 ± 0.003	10	94.5 ± 31.4	0.012 ± 0.005
Nemertea						
Nemertea	40	378.2 ± 79.7	0.092 ± 0.024	28	264.7 ± 52.6	0.106 ± 0.029
Crustacea						
Leptochelia rapax	634	5994.3 ± 1134.4	0.244 ± 0.077	644	6088.8 ± 1220.8	0.224 ± 0.047
Ampeliscidae	150	1418.2 ± 440.3	0.102 ± 0.026	173	1635.7 ± 479.8	0.140 ± 0.044
Aoridae	65	614.6 ± 167.7	0.069 ± 0.022	68	642.9 ± 159.7	0.069 ± 0.021
Corophiidae	10	94.5 ± 36.8	0.005 ± 0.002	111	1049.5 ± 848.7	0.051 ± 0.037
Cumacea	30	283.6 ± 99.0	0.028 ± 0.011	27	255.3 ± 61.3	0.026 ± 0.010
Mysidae	22	208.0 ± 82.6	0.057 ± 0.029	7	66.2 ± 26.1	0.018 ± 0.009
Ostracoda	15	141.8 ± 60.4	0.011 ± 0.005	7	66.2 ± 40.1	0.004 ± 0.002
Amphipoda	—	—	—	12	113.5 ± 113.5	0.003 ± 0.003
Isopoda	5	47.3 ± 23.9	0.014 ± 0.012	5	47.3 ± 30.7	0.011 ± 0.007
Caprellidae	—	—	—	2	18.9 ± 18.9	1.0E-04 ± 1.0E-04
Panopeidae	1	9.5 ± 9.5	0.032 ± 0.032	—	—	—
Megalop crab larvae	1	9.5 ± 9.5	0.001 ± 0.001	—	—	—
Gastropoda						
Fargoa gibbosa	12	113.5 ± 76.4	0.004 ± 0.002	12	113.5 ± 71.4	0.004 ± 0.003
Acteocina canaliculata	4	37.8 ± 22.5	0.004 ± 0.003	—	—	—
Vitrinellidae	4	37.8 ± 22.5	0.002 ± 0.001	—	—	—
Eulimastoma harbisonae	1	9.5 ± 9.5	4.0E-04 ± 4.0E-04	2	18.9 ± 18.9	0.004 ± 0.004
Evalea emeryi	2	18.9 ± 18.9	2.0E-04 ± 2.0E-04	—	—	—
Acteon candens	1	9.5 ± 9.5	1.0E-04 ± 1.0E-04	—	—	—
Cerithiidae	—	—	—	1	9.5 ± 9.5	0.002 ± 0.002
Bivalvia						
Mactra fragilis	9	85.1 ± 43.3	0.059 ± 0.040	3	28.4 ± 20.8	0.001 ± 0.001

Mulinia lateralis	4	37.8 ± 17.9	0.109 ± 0.091	7	66.2 ± 26.1	0.061 ± 0.038
Tagelus plebeius	1	9.5 ± 9.5	0.023 ± 0.023	4	37.8 ± 17.9	0.211 ± 0.135
Ischadium recurvum	1	9.5 ± 9.5	0.008 ± 0.008	—	—	—
Mercenaria campechiensis	1	9.5 ± 9.5	0.003 ± 0.003	—	—	—
Bivalvia	1	9.5 ± 9.5	0.001 ± 0.001	—	—	—
Ensis minor	—	—	—	2	18.9 ± 13.1	0.155 ± 0.128
Cnidaria						
Cnidaria	2	18.9 ± 18.9	1.0E-04 ± 1.0E-04	1	9.5 ± 9.5	4.0E-04 ± 4.0E-04
Fish						
Larval mugiliidae	1	9.5 ± 9.5	0.008 ± 0.008	—	—	—
Arthropoda						
Arthropoda	1	9.5 ± 9.5	4.0E-04 ± 4.0E-04	—	—	—

Table 4. Pearson correlation coefficients (rho) between infaunal community measurements and water quality variables for adjacent and distant sites at a restored oyster reef.

		Adjacent			Distant		
Variable (unit)	**Statistic**	**Density ($n\ m^{-2}$)**	**Biomass ($g\ m^{-2}$)**	**Hill's Diversity (N1)**	**Density ($n\ m^{-2}$)**	**Biomass ($g\ m^{-2}$)**	**Hill's Diversity (N1)**
Salinity	rho	0.461	0.316	0.152	0.351	0.318	0.136
	p	<.0001	0.002	0.154	0.001	0.002	0.202
pH	rho	-0.189	-0.154	-0.332	-0.266	-0.247	-0.058
	p	0.091	0.171	0.003	0.017	0.026	0.607
Turbidity	rho	-0.131	-0.172	-0.263	0.027	0.027	-0.302
	p	0.304	0.177	0.038	0.834	0.837	0.016
Dissolved Oxygen ($mg\ L^{-1}$)	rho	-0.088	-0.049	0.202	-0.086	0.022	0.144
	p	0.432	0.666	0.071	0.444	0.847	0.2
Temperature (°C)	rho	0.016	0.134	-0.116	0.061	0.029	-0.14
	p	0.887	0.233	0.303	0.59	0.798	0.212

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APPENDICES

Appendix 1. Detailed results of PRIMER analyses

Appendix 1.1. SIMPER similarity output for all epifauna species abundance. Analysis was performed on transformed data.

Group Sep2017_Restored
Average similarity: 64.77

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeus herbstii	3.85	22.43	4.44	33.92	33.92
Gobiosoma bosc	3.19	21.17	5.69	32.00	65.92
Palaemonetes vulgaris	1.75	8.77	3.39	13.26	79.18
Petrolisthes armatus	1.29	8.09	7.08	12.23	91.41

Group Year1_Reference
Average similarity: 66.50

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeus herbstii	5.51	23.74	5.89	35.70	35.70
Eurypanopeus depressus	4.55	21.36	4.50	32.13	67.83
Petrolisthes armatus	3.13	9.85	1.64	14.81	82.63
Gobiosoma bosc	1.68	5.39	1.18	8.11	90.74

Group Year1_Restored
Average similarity: 71.51

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Eurypanopeus depressus	5.43	24.27	5.04	33.94	33.94
Panopeus herbstii	4.73	20.28	5.40	28.36	62.30
Gobiosoma bosc	2.73	10.94	2.84	15.29	77.59
Petrolisthes armatus	1.91	6.34	1.42	8.86	86.46
Alpheus heterochaelis	1.00	3.49	1.04	4.88	91.33

Group Year2_Reference
Average similarity: 74.19

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes armatus	8.51	26.47	8.62	35.67	35.67
Panopeus herbstii	4.76	14.42	6.88	19.44	55.11
Ischadium recurvum	3.85	10.85	4.22	14.62	69.73
Eurypanopeus depressus	2.79	8.17	5.51	11.01	80.75
Boonea impressa	2.40	4.96	1.26	6.68	87.43
Menippe adina	1.36	3.05	1.31	4.12	91.55

Group Year2_Restored
Average similarity: 72.90

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes armatus	7.06	14.65	5.08	20.09	20.09
Eurypanopeus depressus	6.14	14.51	4.57	19.90	40.00
Ischadium recurvum	6.54	11.95	3.34	16.39	56.38
Panopeus herbstii	5.20	11.68	5.90	16.03	72.41
Boonea impressa	5.22	7.09	1.21	9.73	82.14
Gobiosoma bosc	2.57	5.81	5.09	7.97	90.11

Appendix 1.2. SIMPER similarity output for epifauna species abundance without *A. probatocephalus* (n-3). Analysis was performed on transformed data.

Group Sep2017_Restored
Average similarity: 66.14

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeus herbstii	3.85	22.43	4.44	33.92	33.92
Gobiosoma bosc	3.19	21.17	5.69	32.00	65.92
Palaemonetes vulgaris	1.75	8.77	3.39	13.26	79.18
Petrolisthes armatus	1.29	8.09	7.08	12.23	91.41

Group Year1_Reference
Average similarity: 66.50

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Panopeus herbstii	5.51	23.74	5.89	35.70	35.70
Eurypanopeus depressus	4.55	21.36	4.50	32.13	67.83
Petrolisthes armatus	3.13	9.85	1.64	14.81	82.63
Gobiosoma bosc	1.68	5.39	1.18	8.11	90.74

Group Year1_Restored
Average similarity: 71.51

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Eurypanopeus depressus	5.43	24.27	5.04	33.94	33.94
Panopeus herbstii	4.73	20.28	5.40	28.36	62.30
Gobiosoma bosc	2.73	10.94	2.84	15.29	77.59
Petrolisthes armatus	1.91	6.34	1.42	8.86	86.46
Alpheus heterochaelis	1.00	3.49	1.04	4.88	91.33

Group Year2_Reference
Average similarity: 74.69

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes armatus	8.51	26.70	8.66	35.75	35.75
Panopeus herbstii	4.76	14.55	6.82	19.48	55.23
Ischadium recurvum	3.85	10.96	4.14	14.67	69.90
Eurypanopeus depressus	2.79	8.25	5.32	11.05	80.95
Boonea impressa	2.40	4.98	1.26	6.67	87.62
Menippe adina	1.36	3.09	1.31	4.14	91.75

Group Year2_Restored
Average similarity: 72.90

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes armatus	7.06	14.65	5.08	20.09	20.09
Eurypanopeus depressus	6.14	14.51	4.57	19.90	40.00
Ischadium recurvum	6.54	11.95	3.34	16.39	56.38
Panopeus herbstii	5.20	11.68	5.90	16.03	72.41
Boonea impressa	5.22	7.09	1.21	9.73	82.14
Gobiosoma bosc	2.57	5.81	5.09	7.97	90.11

Appendix 1.3. Detailed results of BEST BIO-ENV procedure correlating modified water quality variables to epifauna abundance. Analysis performed on data averaged by Habitat-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 Temp
3 DO_mgl
5 Sal
6 pH
7 Turb

Global Test
Sample statistic (Rho): 0.271
Significance level of sample statistic: 14%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 13

Best results

No.Vars	Corr.	Selections
2	0.271	3,5
3	0.261	1,3,5
2	0.223	1,5
1	0.223	3
4	0.202	1,3,5,6
3	0.177	3,5,6
2	0.163	1,3
3	0.148	1,5,6
4	0.139	1,3,5,7
5	0.115	1,3,5-7

Appendix 1.4. SIMPER similarity output for epifauna species biomass without *A. probatocephalus* (n-3). Analysis was performed on transformed data.

Group Sep2017_Restored
Average similarity: 59.43

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Gobiosoma bosc	0.57	24.49	5.48	41.21	41.21
Panopeus herbstii	0.55	16.47	2.71	27.72	68.93
Palaemonetes vulgaris	0.30	9.07	3.89	15.26	84.18
Panopeidae	0.46	6.68	0.41	11.24	95.42

Group Group Remainder_Restored_Reference
Average similarity: 56.87

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Eurypanopeus depressus	2.22	24.34	2.80	42.81	42.81
Panopeus herbstii	1.18	12.15	2.55	21.37	64.18
Petrolisthes armatus	1.08	8.68	1.37	15.27	79.45
Gobiosoma bosc	0.46	4.79	1.28	8.42	87.87
Palaemonetes vulgaris	0.26	1.44	0.75	2.52	90.40

Appendix 1.5. SIMPER similarity output for all epifauna species biomass. Analysis was performed on transformed data.

Group Sep2017_Restored
Average similarity: 59.43

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Gobiosoma bosc	0.57	24.49	5.48	41.21	41.21
Panopeus herbstii	0.55	16.47	2.71	27.72	68.93
Palaemonetes vulgaris	0.30	9.07	3.89	15.26	84.18
Panopeidae	0.46	6.68	0.41	11.24	95.42

Group Group Remainder_Restored
Average similarity: 63.08

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Eurypanopeus depressus	2.57	29.31	3.28	46.47	46.47
Panopeus herbstii	0.81	10.14	3.00	16.08	62.54
Gobiosoma bosc	0.60	7.59	2.14	12.03	74.58
Petrolisthes armatus	0.86	6.80	1.46	10.78	85.35
Alpheus heterochaelis	0.32	2.86	0.93	4.54	89.89
Gobiesox strumosus	0.37	2.06	0.70	3.27	93.16

Group Year1_Reference
Average similarity: 61.45

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Eurypanopeus depressus	2.08	27.45	4.25	44.67	44.67
Panopeus herbstii	1.45	17.49	3.00	28.46	73.13
Petrolisthes armatus	0.82	7.39	1.22	12.02	85.15
Gobiosoma bosc	0.39	3.85	1.13	6.27	91.41

Group Year2_Reference
Average similarity: 55.55

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Petrolisthes armatus	2.02	19.14	3.17	34.46	34.46
Eurypanopeus depressus	1.61	11.78	4.17	21.20	55.66
Panopeus herbstii	1.60	10.87	2.69	19.56	75.22
Menippe adina	0.88	4.13	0.82	7.43	82.65
Ischadium recurvum	0.61	3.57	1.30	6.42	89.06
Gobiosoma bosc	0.29	1.47	0.84	2.65	91.71

Appendix 1.6. Detailed results of BEST BIO-ENV procedure correlating modified water quality variables to epifauna biomass. Analysis performed on data averaged by Habitat-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 Temp
3 DO_mgl
5 Sal
6 pH
7 Turb

Global Test
Sample statistic (Rho): 0.185
Significance level of sample statistic: 61%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 60

Best results

No.Vars	Corr.	Selections
2	0.185	1,5
3	0.164	1,3,5
3	0.156	1,5,6
4	0.154	1,3,5,6
1	0.146	3
2	0.131	1,3
2	0.121	3,5
3	0.116	3,5,6
1	0.112	1
3	0.109	1,5,7

Appendix 1.7. SIMPER similarity output for infauna species abundance. Analysis was performed on transformed data.

Group Spring_Summer
Average similarity: 50.09

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mediomastus spp.	3.23	21.70	2.70	43.33	43.33
Leptochelia rapax	3.04	19.74	2.52	39.40	82.73
Ampeliscidae	1.21	3.28	0.56	6.55	89.28
Capitella capitata	0.57	1.00	0.36	2.00	91.29

Group Fall
Average similarity: 49.06

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Streblospio benedicti	1.96	19.32	1.40	39.38	39.38
Mediomastus spp.	1.85	16.98	1.37	34.61	73.98
Leptochelia rapax	1.22	9.17	0.95	18.70	92.68

Group Winter
Average similarity: 60.47

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Leptochelia rapax	3.00	16.68	3.29	27.59	27.59
Mediomastus spp.	*2.50*	*12.65*	*1.66*	*20.91*	*48.50*
Streblospio benedicti	2.03	10.06	1.83	16.64	65.14
Ampeliscidae	1.56	7.85	1.59	12.98	78.12
Aoridae	1.18	5.35	1.14	8.84	86.96
Nemertea	0.65	2.45	0.68	4.06	91.02

Group Aug2018
Average similarity: 60.32

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Streblospio benedicti	3.68	26.31	2.88	43.62	43.62
Leptochelia rapax	2.51	17.50	2.85	29.02	72.64
Mediomastus spp.	2.00	12.43	2.02	20.61	93.25

Appendix 1.8. SIMPER similarity output for infauna species biomass. Analysis was performed on transformed data.

Group Spring_Summer_Pre-Restoration
Average similarity: 31.85

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mediomastus spp.	0.55	13.06	1.50	41.02	41.02
Leptochelia rapax	0.42	10.01	1.85	31.43	72.45
Haploscoloplos foliosus	0.68	2.39	0.30	7.49	79.94
Parandalia fauveli	0.23	1.46	0.31	4.60	84.54
Laeonereis culveri	0.46	1.35	0.24	4.24	88.78
Scolelepis squamata	0.20	1.09	0.28	3.44	92.21

Group Spring_Post_Restoration
Average similarity: 33.66

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Mediomastus spp.	0.71	13.85	1.91	41.14	41.14
Leptochelia rapax	0.48	7.81	1.39	23.19	64.33
Ampeliscidae	0.40	5.34	1.05	15.86	80.20
Capitella capitata	0.19	1.69	0.54	5.02	85.21
Parandalia fauveli	0.37	1.61	0.34	4.77	89.99
Nemertea	0.18	0.81	0.30	2.40	92.38

Group Summer_Fall_Post-Restoration
Average similarity: 38.04

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Streblospio benedicti	0.34	13.48	1.23	35.43	35.43
Mediomastus spp.	0.37	12.88	1.17	33.86	69.29
Leptochelia rapax	0.25	6.99	0.95	18.37	87.66
Parandalia fauveli	0.26	2.75	0.34	7.22	94.87

Group Winter_Post-Restoration
Average similarity: 47.38

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Leptochelia rapax	0.78	12.41	2.38	26.19	26.19
Ampeliscidae	0.62	9.44	1.50	19.93	46.12
Mediomastus spp.	0.54	7.31	1.44	15.44	61.56
Aoridae	0.41	5.16	1.03	10.89	72.45
Streblospio benedicti	0.35	4.83	1.52	10.19	82.64
Nemertea	0.33	3.00	0.57	6.33	88.96
Parandalia fauveli	0.39	2.56	0.50	5.40	94.36

Appendix 1.9. Detailed results of BEST BIO-ENV procedure correlating modified water quality variables to infauna 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:
Analyze between: Samples
Resemblance measure: D1 Euclidean distance

Variables
1 Temp
3 DO_mgl
5 Sal
6 pH
7 Turb

Global Test
Sample statistic (Rho): 0.435
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	0.435	5,7
1	0.389	5
3	0.388	5-7
2	0.307	5,6
3	0.277	3,5,7
3	0.257	1,5,7
4	0.253	3,5-7
4	0.252	1,5-7
1	0.244	7
2	0.225	1,5

Appendix 1.10. Detailed results of BEST BIO-ENV procedure correlating modified water quality variables to infauna 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 Temp
3 DO_mgl
5 Sal
6 pH
7 Turb

Global Test
Sample statistic (Rho): 0.448
Significance level of sample statistic: 3%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 2

Best results

No.Vars	Corr.	Selections
2	0.448	5,7
3	0.342	5-7
1	0.319	7
1	0.317	5
3	0.304	1,5,7
3	0.253	3,5,7
2	0.240	1,5
4	0.237	1,5-7
2	0.198	5,6
4	0.176	3,5-7

Appendix 2. Output of statistical analyses

Appendix 2.1. Kruskal-Wallis output of date, habitat, and the combined factor date-habitat effect on water quality variables salinity, temperature (°C), dissolved oxygen (mg L^{-1}), pH, and turbidity (NTU).

Kruskal-Wallis Rank Sum Test	**Salinity**	**Temperature**	**Dissolved Oxygen**	**pH**	**Turbidity**
Date	**2.20E-16**	**2.20E-16**	**2.48E-16**	0.0002983	**5.77E-07**
Chi-squared	108.24	112.03	99.283	34.511	46.1
df	13	11	11	11	9
Habitat	0.2281	0.2987	0.028	**8.40E-07**	0.05749
Chi-squared	1.4525	1.0799	4.8283	24.265	3.6083
df	1	1	1	1	1
Date.Habitat	**4.06E-15**	**2.03E-15**	**2.02E-14**	**6.15E-08**	**1.07E-05**
Chi-squared	115.87	113.21	107.81	71.05	52.054
df	21	19	19	19	16

Appendix 2.2. P-value from ANOVA tests on oyster density. Significant results ($p < 0.05$) are bolded.

	Density ($\sqrt{}$ n m^{-2})
date	**0.0012**
habitat	0.5291
date*habitat	**0.0016**
Main Effects ANOVA	
date.habitat	**3.721e-09**

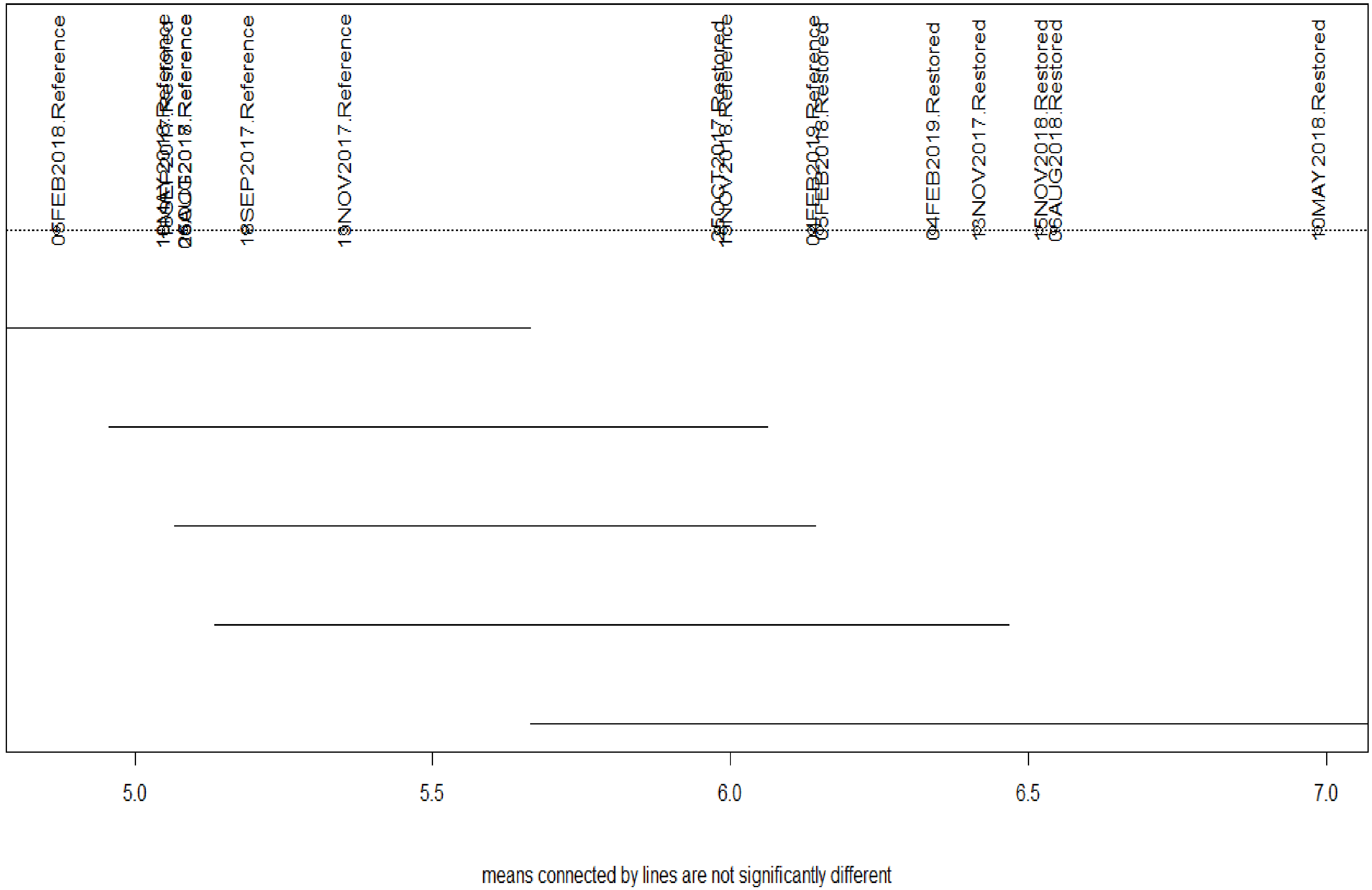
Appendix 2.2a. ANOVA output of date, habitat, and date*habitat effect on oyster density ((Log (n m^{-2})).

	numDF	denDF	F-value	p-value
(Intercept)	1	46	737.38	<.0001
date	7	46	4.2090	**0.0012**
habitat	1	46	0.4023	0.5291
date:habitat	7	46	4.0354	**0.0016**

Appendix 2.2b. ANOVA output of combined factor date.habitat effect on oyster density (Log (n m^{-2})).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date.hab	15	27.3946	1.82631	8.9448	**3.721e-09*****
Residuals	46	9.3921	0.20418		

Appendix 2.2c. Tukey groupings of combined factor date.habitat effect on oyster density (Log (n m^{-2})).



Appendix 2.3. P-values from ANOVA tests on epifauna metrics. Significant results ($p < 0.05$) are bolded.

	Density (√ n m-2)	Biomass (Log (g m^{-2}))	Hill's N1 Diversity
date	**<.0001**	**0.008**	**0.0054**
habitat	0.8850	**0.005**	0.8511
date*habitat	**0.0125**	**<.0001**	**0.0006**
Main Effects ANOVA			
date.hab	**6.617e-06**	**3.799e-09**	**7.622e-08**

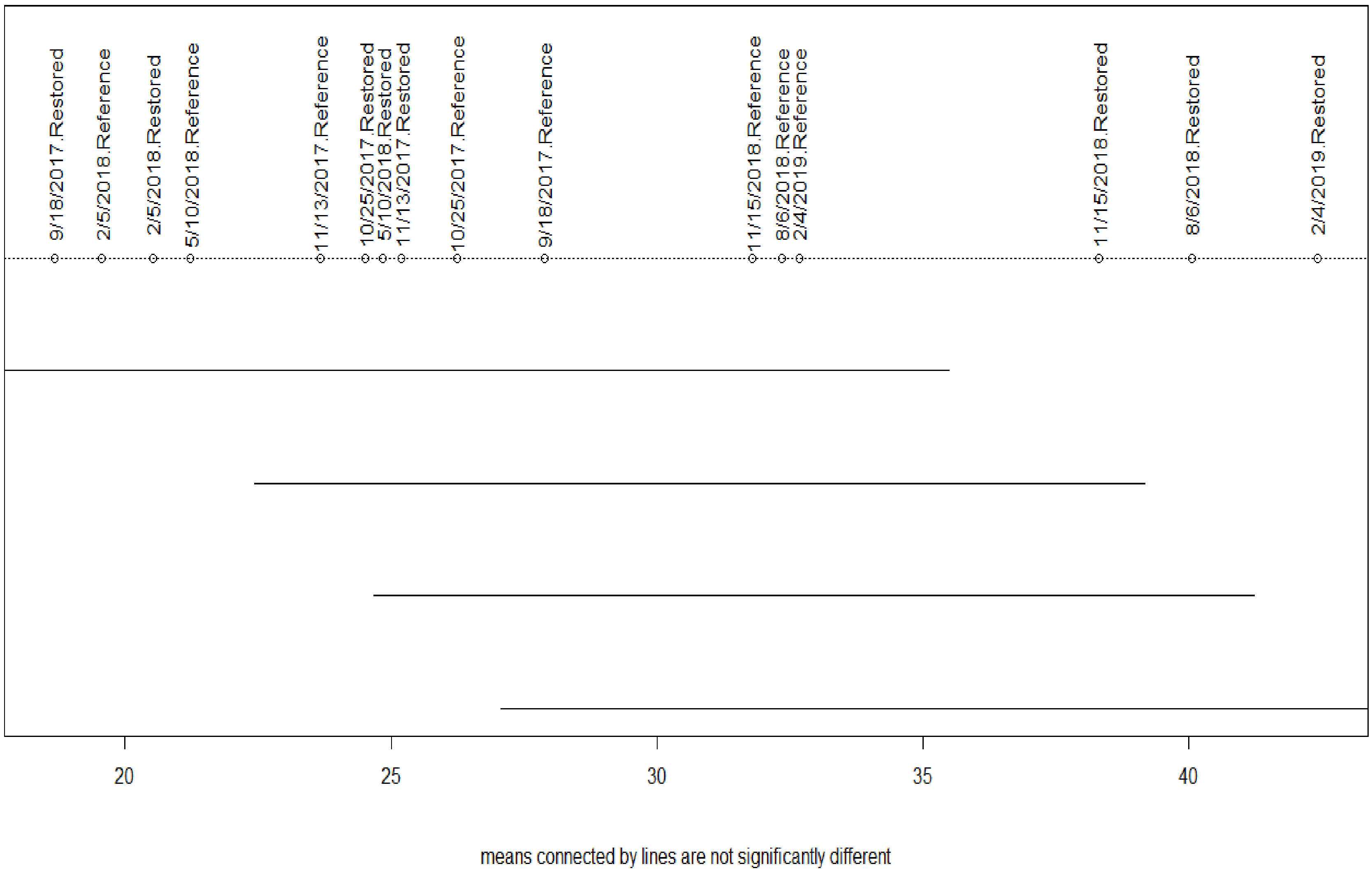
Appendix 2.3a. ANOVA output of date, habitat, and date*habitat effect on epifauna density (√ n m^{-2}).

	numDF	denDF	F-value	p-value
(Intercept)	1	40	127.21718	<.0001
date	7	40	6.62208	**<.0001**
habitat	1	8	0.02228	0.8850
date:habitat	7	40	3.00046	**0.0125**

Appendix 2.3b. ANOVA output of combined factor date.habitat effect on epifauna density (√ n m^{-2}).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date.hab	15	3301.2	220.077	5.145	6.617e-06 ***
Residuals	48	2053.2	42.775		

Appendix 2.3c. Tukey groupings of combined factor date.habitat effect on epifauna density (√ n m^{-2}).



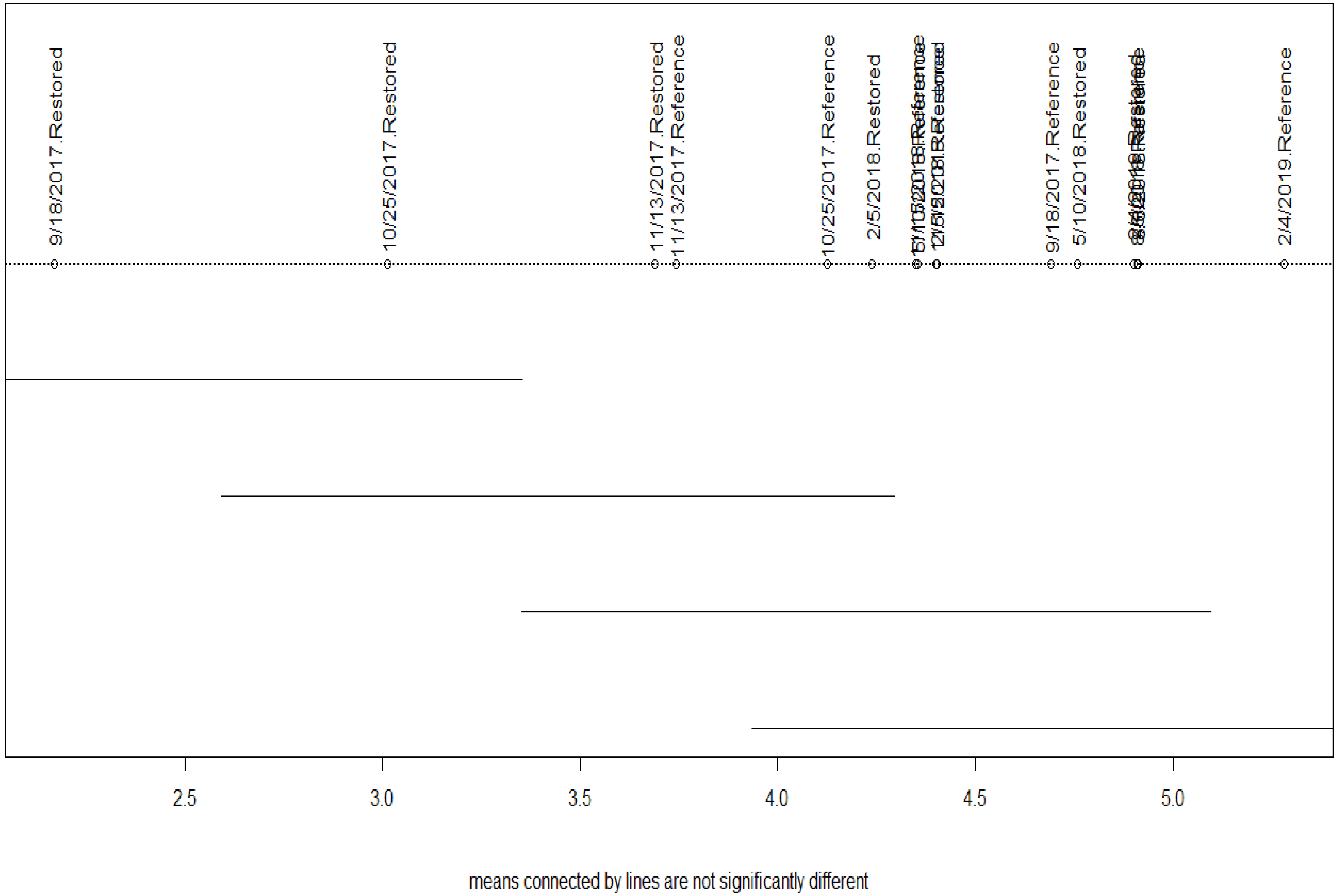
Appendix 2.3d. ANOVA output of date, habitat, and date*habitat effect on epifauna biomass ((Log (g m^{-2})).

	numDF	F-value	p-value
(Intercept)	1	238.19304	<.0001
date	7	3.15227	**0.008**
habitat	1	8.65701	**0.005**
date:habitat	7	6.15301	**<.0001**

Appendix 2.3e. ANOVA output of combined factor date.habitat effect on epifauna biomass ((Log (g m^{-2})).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date.hab	15	37.253	2.48356	8.6901	**3.799e-09** ***
Residuals	48	13.718	0.28579		

Appendix 2.3f. Tukey groupings of combined factor date.habitat effect on epifauna biomass ((Log (g m^{-2})).



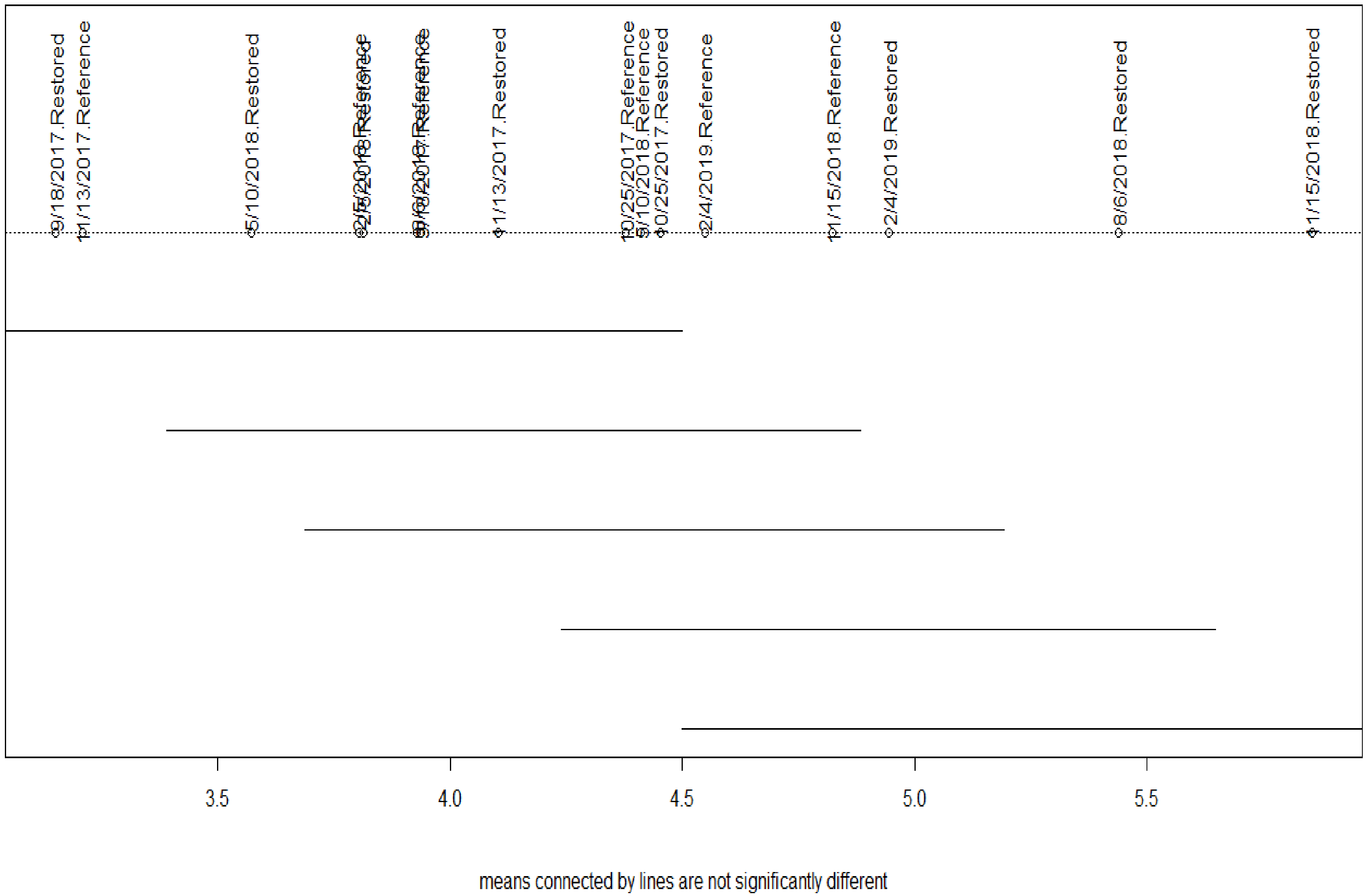
Appendix 2.3g. ANOVA output of date, habitat, and date*habitat effect on epifauna diversity (Hill's N1).

	numDF	F-value	p-value
(Intercept)	1	246.32893	**<.0001**
date	7	3.36185	**0.0054**
habitat	1	0.03561	0.8511
date:habitat	7	4.57294	**0.0006**

Appendix 2.3h. ANOVA output of combined factor date.habitat effect on epifauna diversity (Hill's N1).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date.hab	15	33.352	2.22345	7.1433	**7.622e-08** ***
Residuals	48	14.941	0.31126		

Appendix 2.3i. Tukey groupings of combined factor date.habitat effect on epifauna diversity (Hill's N1).



Appendix 2.4. P-values from 2-Way ANOVA tests on infauna metrics. Significant results ($p < 0.05$) are bolded.

	Biomass (Log (g m^{-2}))	Hill's N1 Diversity
treatment	0.4734	0.7951
date	**<.0001**	**<.0001**
treatment*date	0.4685	0.3900
Main Effects ANOVA		
trt.date	**1.171e-15**	**1.624e-13**

Appendix 2.4a. Kruskal-Wallis output of treatment, date, and combined factor date-treatment effect on infauna density (n m^{-2}).

Kruskal-Wallis Rank Sum Test	Density
Treatment	0.362
chi-squared	0.83103
df	1
Date	**4.19E-14**
chi-squared	82.946
df	9
Date.Trt	**5.26E-11**
chi-squared	88.867
df	19

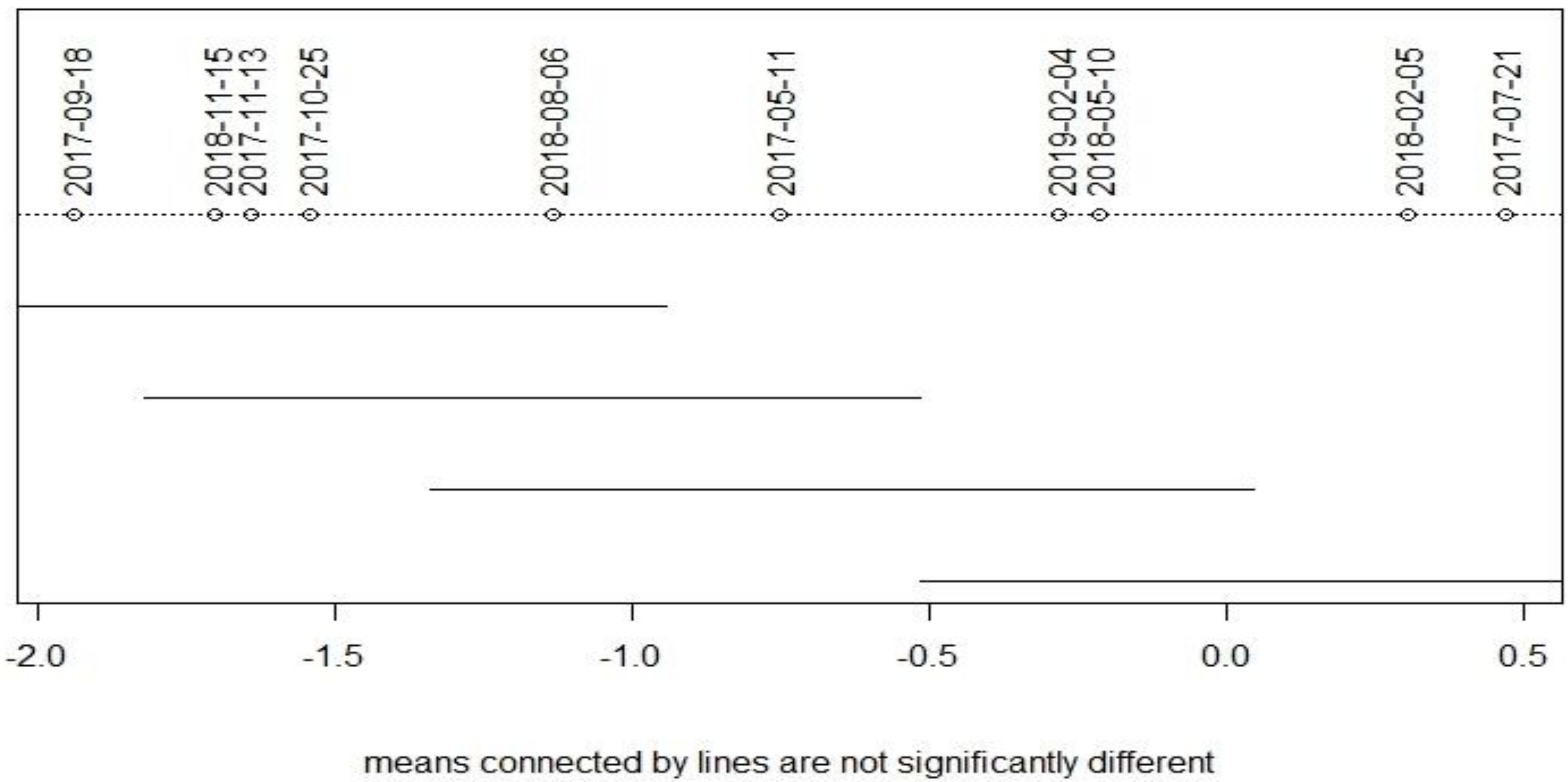
Appendix 2.4b. 2-Way ANOVA output of date, treatment, and treatment*date effect on infauna biomass (Log (g m^{-2})).

	numDF	F-value	p-value
(Intercept)	1	7.272792	**0.0078**
treatment	1	0.516486	0.4734
date	9	9.508182	**<.0001**
trt.date	9	0.968086	0.4685

Appendix 2.4c. ANOVA output of date effect on infauna biomass (Log (g m^{-2})).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date	9	124.14	13.7930	12.989	**1.171e-15** ***
Residuals	170	180.52	1.0619		

Appendix 2.4d. Tukey grouping of date effect on infauna biomass (Log (g m^{-2})).



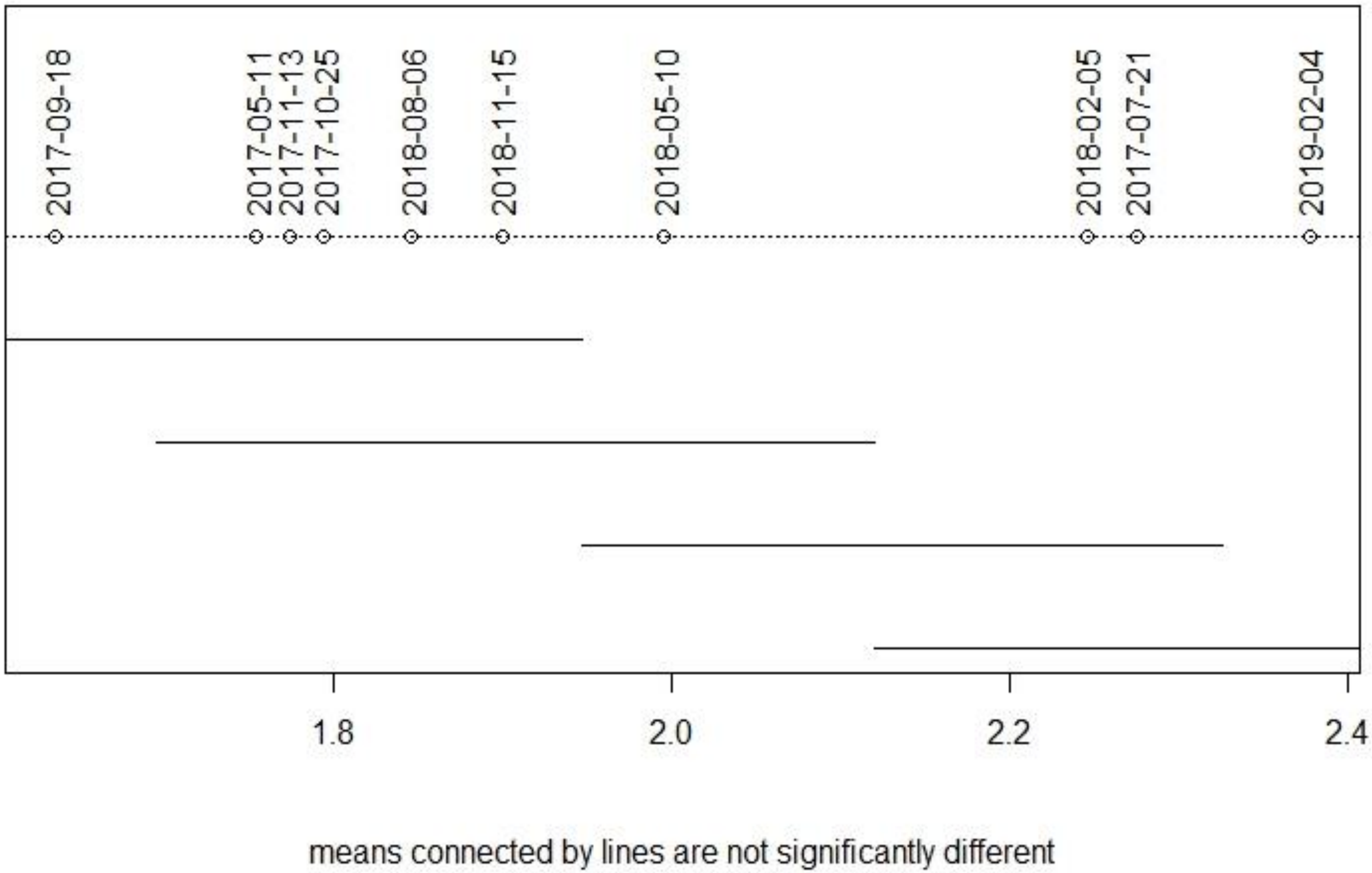
Appendix 2.4e. 2-Way ANOVA output of date, treatment, and treatment*date effect on infauna diversity (√ Hill's N1).

	numDF	F-value	p-value
(Intercept)	1	2.6879966	**<.0001**
treatment	1	0.06764	0.7951
date	9	8.09611	**<.0001**
trt.date	9	1.06703	0.3900

Appendix 2.4f. ANOVA output of date effect on infauna diversity (√ Hill's N1).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
date	9	10.486	1.16505	11.076	**1.624e-13*****
Residuals	170	17.882	0.1051		

Appendix 2.4g. Tukey grouping of date effect on infauna diversity (√ Hill's N1).



Appendix 3. Supplementary tables

Appendix 3.1. Number of oysters assessed for *Perkinsus marinus*, along with temperature and salinity mean ± SE, shell height (SH) range and mean ± SE, mean oyster condition ± SE, number of oysters infected, mean dermo intensity ± SE, and overall prevalence and weighted prevalence of dermo from August 2017 to February 2019 found in oysters at the reference reef; February 2018 to February 2019 for oysters found at the restored reef.

Date	Habitat	# Assessed	Mean Temp. (°C)	Mean Salinity	SH Range (mm)	SH (mm)	Cond.	# Infected	Intensity	Prevalence (%)	Weighted Prevalence
8-Aug-17	Reference	20	30.4	24.4	55-103	78.10 ± 2.91	2.75 ± 0.38	20	1.58 ± 0.19	100	1.58
18-Sep-17	Reference	20	29.5	9.07	54 -101	74.15 ± 3.06	1.95 ± 0.11	14	0.88 ± 0.16	70	0.62
25-Oct-17	Reference	20	21.8	12.7	54-124	81.20 ± 3.92	2.15 ± 0.17	15	1.16 ± 0.18	75	0.87
13-Nov-17	Reference	20	21.4	15.0	57-107	75.45 ± 2.80	2.45 ± 0.15	16	1.21 ± 0.15	80	0.97
5-Feb-18	Reference	20	16.7	22.3	45-99	75.35 ± 3.79	2.35 ± 0.15	12	0.47 ± 0.07	60	0.28
10-May-18	Reference	20	26.8	25.6	40-97	67.60 ± 4.73	2.20 ± 0.14	8	0.67 ± 0.09	40	0.27
6-Aug-18	Reference	20	29.2	30.02	48-99	72.35 ± 3.87	2.70 ± 0.21	14	1.43 ± 0.16	70	1.00
15-Nov-18	Reference	20	11.2	8.89	36-103	73.50 ± 4.00	1.75 ± 0.16	5	0.80 ± 0.12	25	0.20
4-Feb-19	Reference	20	17.6	11.06	44-98	74.40 ± 3.54	1.35 ± 0.13	1	0.67 ± 0.03	5	0.03
5-Feb-18	Restored	10	16.7	20.21	31-70	47.50 ± 3.89	3.00 ± 0.26	1	0.33 ± 0.03	10	0.03
10-May-18	Restored	20	24.35	25.22	40-93	70.15 ± 3.02	2.45 ± 0.14	0	0.00	0	0.00
6-Aug-18	Restored	20	29.1	19.94	53-94	72.85 ± 2.79	2.80 ± 0.17	0	0.00	0	0.00
15-Nov-18	Restored	20	9.7	7.43	52-95	71.15 ± 2.61	1.85 ± 0.15	0	0.00	0	0.00
4-Feb-19	Restored	20	17.4	10.32	47-111	79.85 ± 3.99	2.30 ± 0.22	0	0.00	0	0.00

Appendix 3.2. Mean shell heights of live oysters and spat counts and heights found in station trays at both oyster reefs for all sampling dates.

Reference					Restored				
Date	**Station**	**SH**	**Spat**	**Spat height**	**Date**	**Statio**	**SH**	**Spat**	**Spat height**
18-Sep-17	SCF11	64	—	—	18-Sep-17	SCIB	11		—
18-Sep-17	SCF6	61	—	—	18-Sep-17	SCID	11	—	—
25-Oct-17	SCF10	55	1	—	18-Sep-17	SCIF	16	—	—
25-Oct-17	SCF11	49	0	—	18-Sep-17	SCIG	10	—	—
25-Oct-17	SCF6	26	12	—	25-Oct-17	SCIB	25	6	—
25-Oct-17	SCF9	39	4	—	25-Oct-17	SCID	26	8	—
13-Nov-17	SCF10	48	3	—	25-Oct-17	SCIF	29	10	—
13-Nov-17	SCF11	58	1	—	25-Oct-17	SCIG	30	4	—
13-Nov-17	SCF6	57	8	—	13-Nov-	SCIB	36	5	—
13-Nov-17	SCF9	42	0	—	13-Nov-	SCID	39	3	—
5-Feb-18	SCF10	57	0	—	13-Nov-	SCIF	35	4	—
5-Feb-18	SCF11	50	0	—	13-Nov-	SCIG	30	5	—
5-Feb-18	SCF6	69	0	—	5-Feb-18	SCIB	46	0	—
5-Feb-18	SCF9	49	1	21	5-Feb-18	SCID	43	0	—
10-May-18	SCF10	45	1	5	5-Feb-18	SCIF	44	1	20
10-May-18	SCF11	43	1	5	5-Feb-18	SCIG	41	2	25
10-May-18	SCF6	38	2	5	10-May-	SCIB	40	4	19
10-May-18	SCF9	43	2	6	10-May-	SCID	42	2	22
6-Aug-18	SCF10	39	4	14	10-May-	SCIF	47	0	—
6-Aug-18	SCF11	58	1	24	10-May-	SCIG	46	2	18
6-Aug-18	SCF6	35	8	20	6-Aug-18	SCIB	48	0	—
6-Aug-18	SCF9	35	4	12	6-Aug-18	SCID	54	0	—
15-Nov-18	SCF10	30	6	15	6-Aug-18	SCIF	47	1	19
15-Nov-18	SCF11	50	1	25	6-Aug-18	SCIG	37	4	17
15-Nov-18	SCF6	48	0	—	15-Nov-	SCIB	33	4	16
15-Nov-18	SCF9	35	3	22	15-Nov-	SCID	41	0	—
4-Feb-19	SCF10	36	2	16	15-Nov-	SCIF	39	4	19

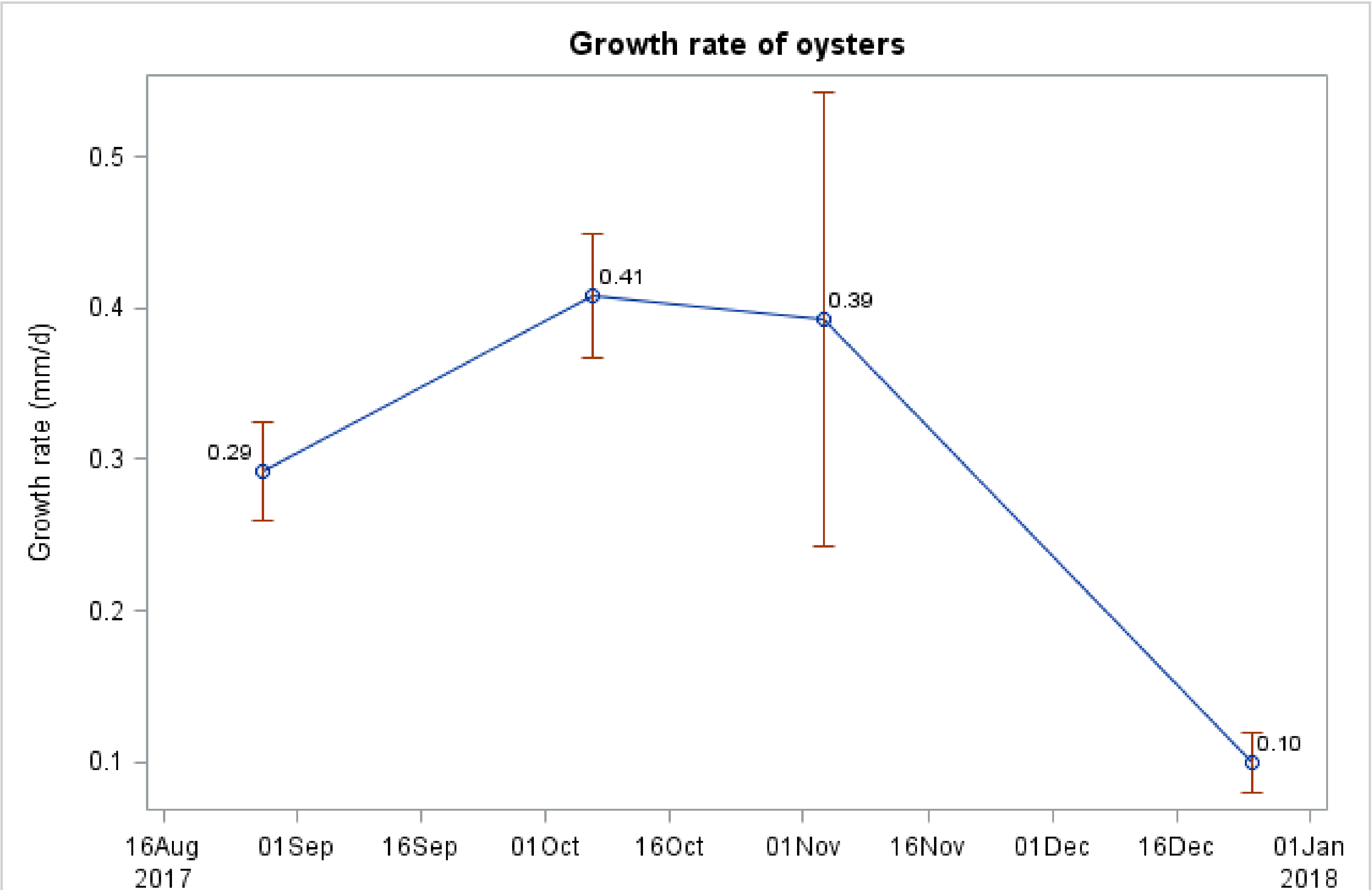
4-Feb-19	SCF11	57	0	—	15-Nov-	SCIG	41	1	20
4-Feb-19	SCF6	55	0	—	4-Feb-19	SCIB	36	3	11
4-Feb-19	SCF9	37	1	11	4-Feb-19	SCID	46	1	13
					4-Feb-19	SCIF	59	1	23
					4-Feb-19	SCIG	55	0	—

Appendix 3.3. Salinity, temperature, dissolved oxygen, pH, turbidity (mean ± SE) during sampling events from May 2017 to February 2019.

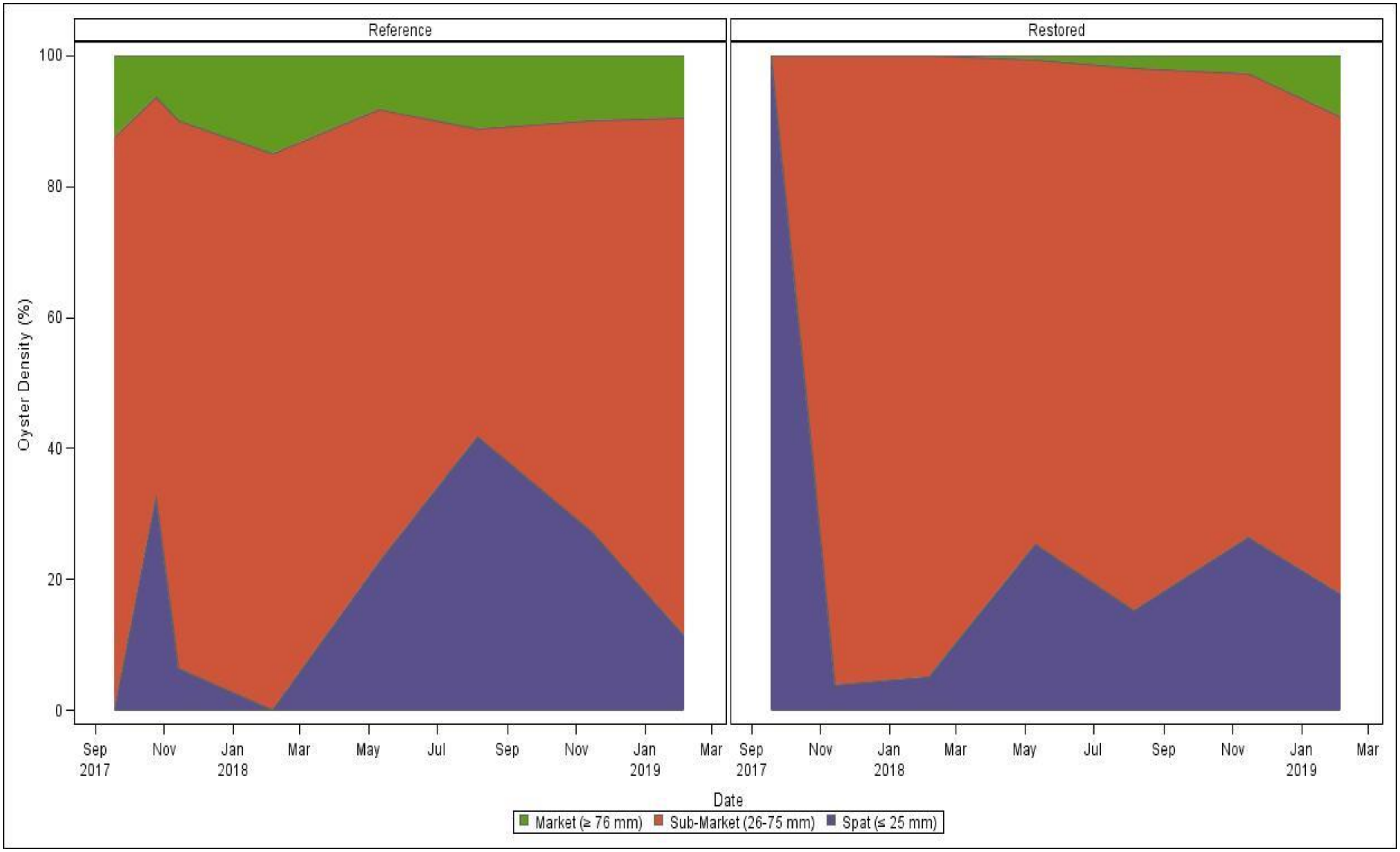
Date	Habitat	Salinity (mean ± SE)	Temperature (°C) (mean ± SE)	Dissolved Oxygen (mg L^{-1}) (mean ± SE)	pH (mean ± SE)	Turbidity (NTU) (mean ± SE)
11-May-17	Reference	—	—	—	—	—
11-May-17	Restored	20.42 ± 0.00	—	—	—	—
19-May-17	Restored	24.395 ± 0.02	27.4 ± 0.00	6.90 ± 0.01	8.00 ± 0.01	48.20 ± 4.10
21-Jul-17	Restored	21.38 ± 0.05	29.68 ± 0.07	6.02 ± 0.03	8.03 ± 0.02	—
07-Aug-17	Restored	24.94 ± 0.26	29.45 ± 0.09	6.21 ± 0.07	8.095 ± 0.01	22.10 ± 5.20
08-Aug-17	Reference	23.82 ± 0.03	30.08 ± 0.19	5.94 ± 0.28	8.135 ± 0.01	11.43 ± 1.63
08-Sep-17	Restored	5.95 ± 0.00	—	—	—	—
18-Sep-17	Reference	9.27 ± 0.02	29.47 ± 0.12	6.56 ± 0.15	8.17 ± 0.01	55.88 ± 6.57
18-Sep-17	Restored	8.29 ± 0.04	29.00 ± 0.06	4.90 ± 0.17	8.03 ± 0.03	27.34 ± 5.93
25-Oct-17	Reference	12.66 ± 0.27	21.82 ± 0.13	8.76 ± 0.12	8.28 ± 0.01	—
25-Oct-17	Restored	11.57 ± 0.11	20.89 ± 0.21	7.66 ± 0.34	8.10 ± 0.07	—
13-Nov-17	Reference	15.01 ± 0.08	21.43 ± 0.13	8.57 ± 0.07	8.21 ± 0.02	10.08 ± 0.93
13-Nov-17	Restored	12.03 ± 0.04	20.99 ± 0.05	7.17 ± 0.15	8.14 ± 0.01	6.69 ± 0.77
05-Feb-18	Reference	22.32± 0.03	16.66 ± 0.02	8.71 ± 0.06	8.32 ± 0.002	13.24 ± 5.58
05-Feb-18	Restored	20.22 ± 0.06	16.68 ± 0.04	7.98 ± 0.15	8.08 ± 0.05	11.39 ± 3.41
10-May-18	Reference	25.65 ± 0.07	26.88 ± 0.08	7.15 ± 0.03	8.07± 0.01	28.80 ± 11.24
10-May-18	Restored	25.22 ± 0.03	24.35 ± 0.02	6.31 ± 0.22	8.01 ± 0.03	23.49 ± 5.45
06-Aug-18	Reference	30.02 ± 0.28	29.18 ± 0.03	5.51 ± 0.08	8.00 ± 0.01	10.95 ± 0.97
06-Aug-18	Restored	19.94 ± 0.21	29.13 ± 0.11	4.49 ± 0.42	8.07 ± 0.02	10.10 ± 5.24
15-Nov-18	Reference	7.83 ± 0.71	11.13 ± 0.14	10.93 ± 0.04	8.06 ± 0.04	9.78 ± 2.74
15-Nov-18	Restored	7.41 ± 0.08	9.94 ± 0.32	10.85 ± 0.11	8.13 ± 0.03	15.70 ± 6.72
04-Feb-19	Reference	10.70 ± 0.27	17.75 ± 0.13	9.48 ± 0.02	8.18 ± 0.01	9.38 ± 2.80
04-Feb-19	Restored	10.06 ± 0.11	17.55 ± 0.08	8.79 ± 0.09	8.04 ± 0.03	5.55 ± 0.72

Appendix 4. Supplementary Figures

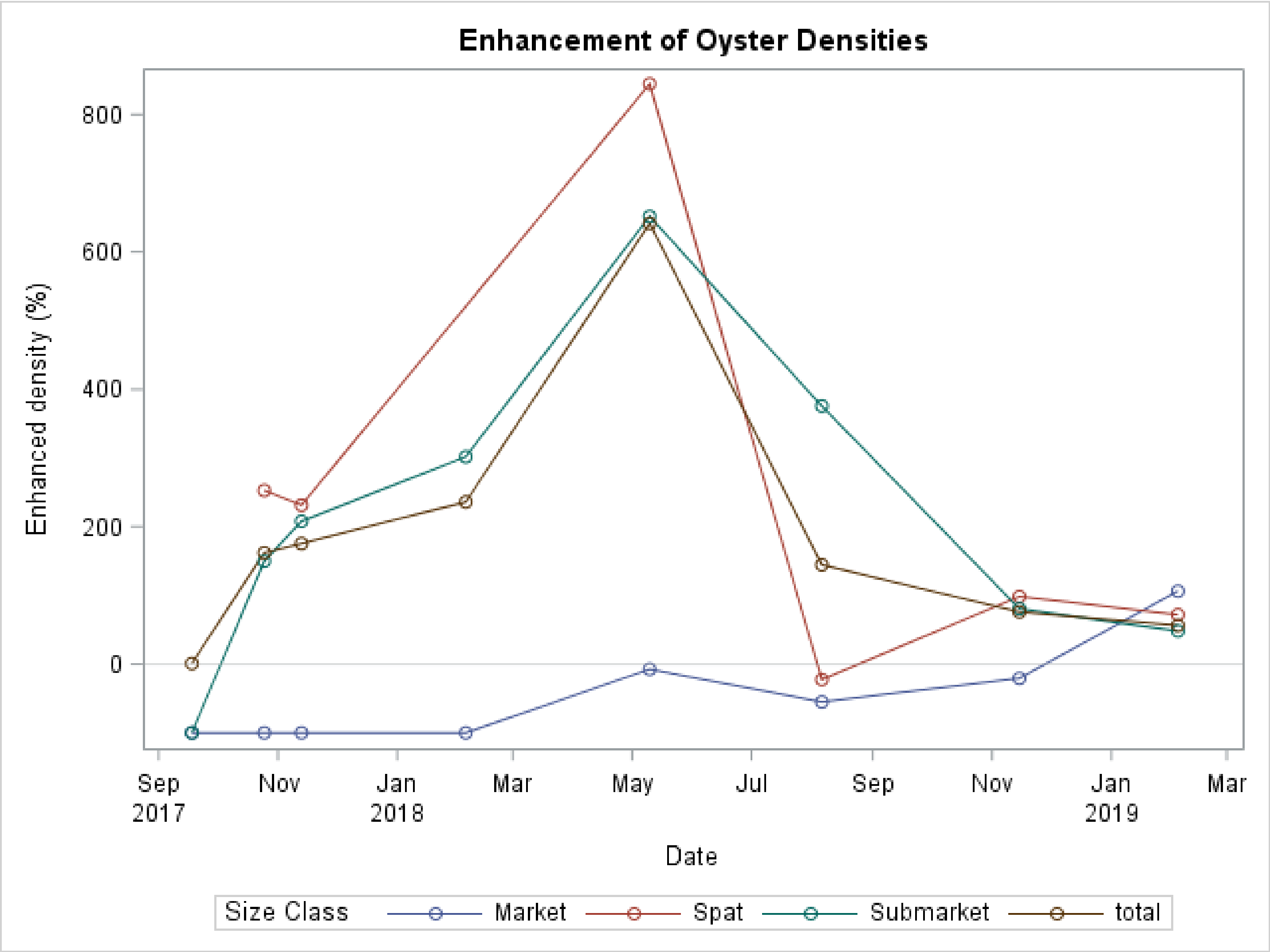
Appendix 4.1. Growth rates (mm d^{-1}) of oysters per day at the restored reef from August to December 2017. Mid-dates are the average number of days between sampling dates.



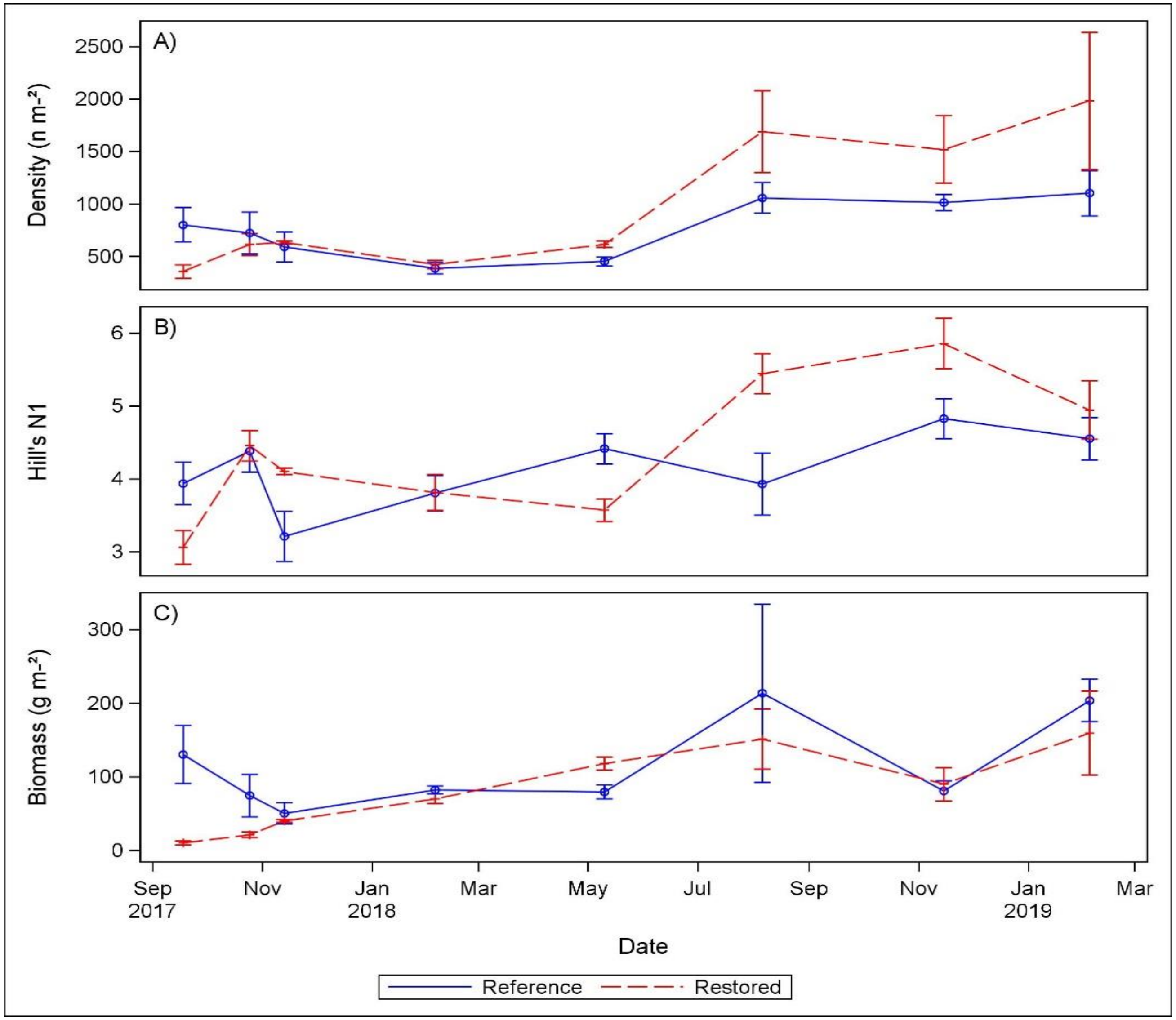
Appendix 4.2. Mean shell height (mm) of sub-market (26-75) and market-sized oysters (≥76) from reference and restored reefs. Market-sized oysters were first observed on the restored reef in May 2018. Error bars represent standard error.



Appendix 4.3. Enhanced oyster densities (% enhanced = ($n_{restored}$ – $n_{reference}$)/ $n_{reference}$) of the restored oyster reef relative to the reference reef per size class for the total number of oysters. Positive value = % more in the restored than the reference (enhanced) and a negative value = % less than the reference (not enhanced).

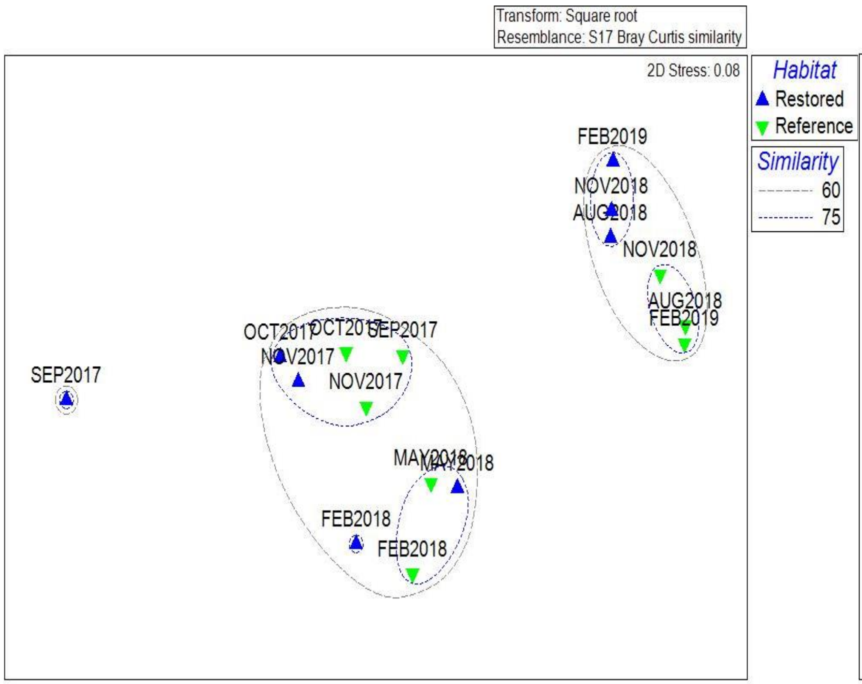


Appendix 4.4. Mean density, biomass, and diversity (Hill's N1) of epifauna communities from August 2017 to February 2019 at restored and reference reefs (including *A. probatocephalus* (3)). Error bars represent standard error.

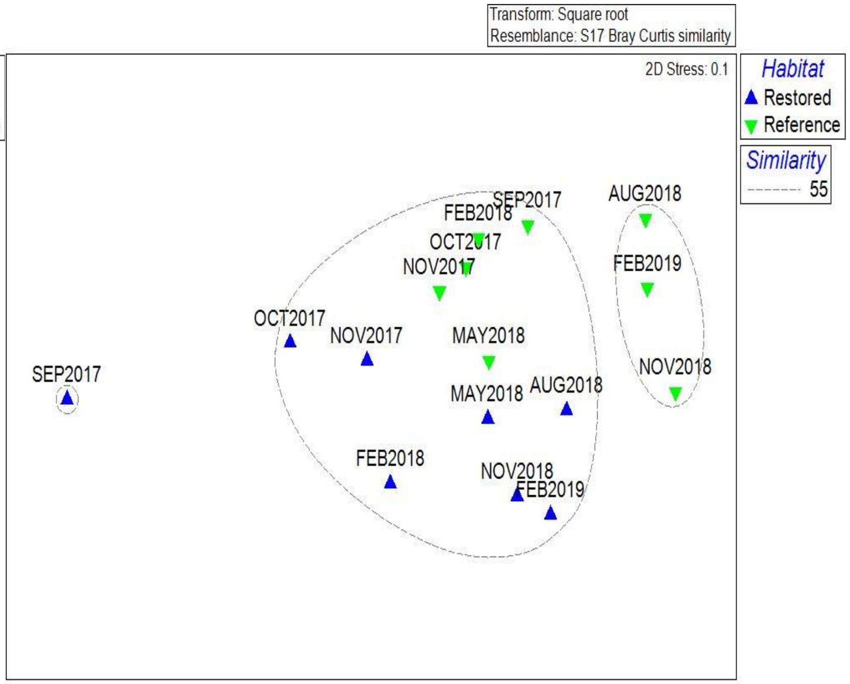


Appendix 4.5. Nonmetric multidimensional scaling (nMDS) for epifauna community structure communities (including *Archosargus probatocephalus* (3)) averaged by Treatment-Habitat including. A) Abundance. B) Biomass.

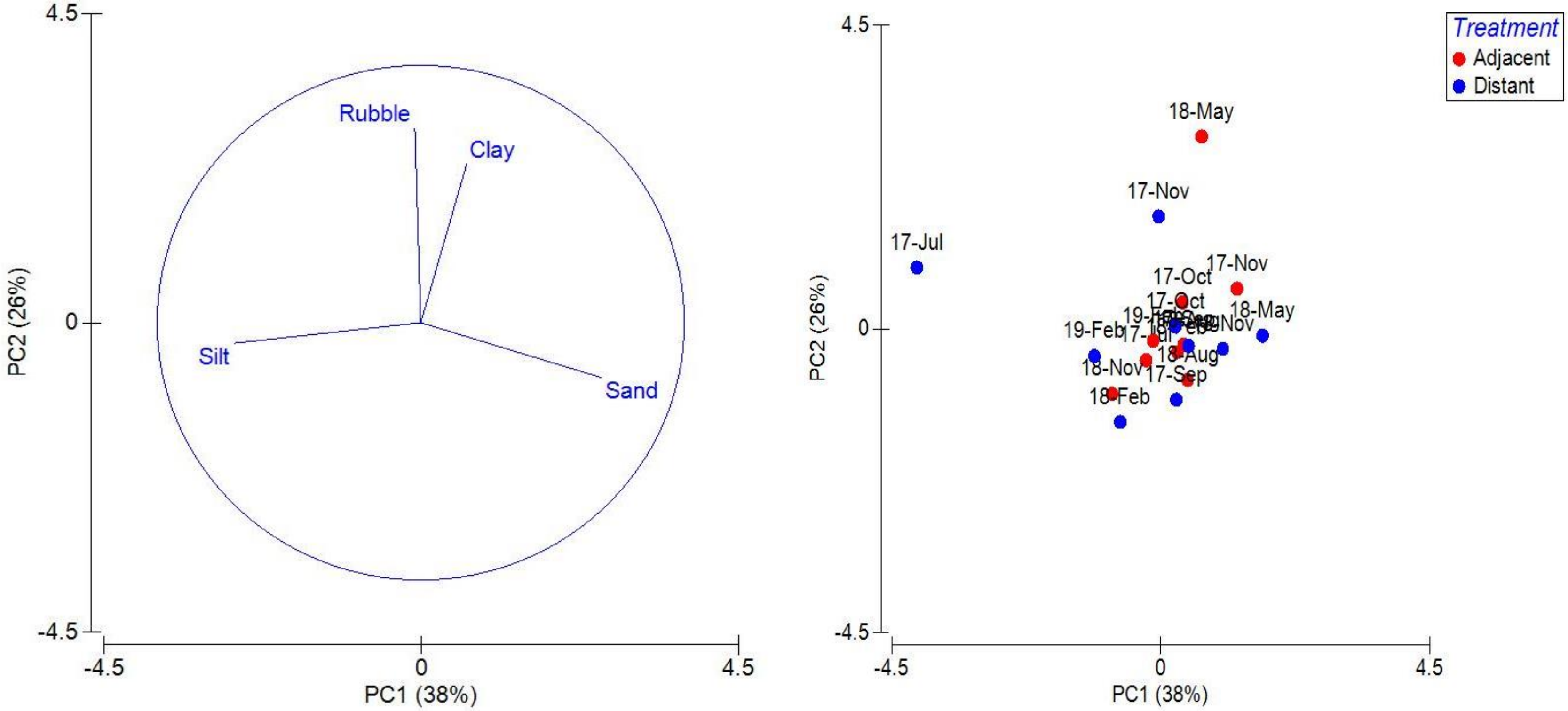
A)



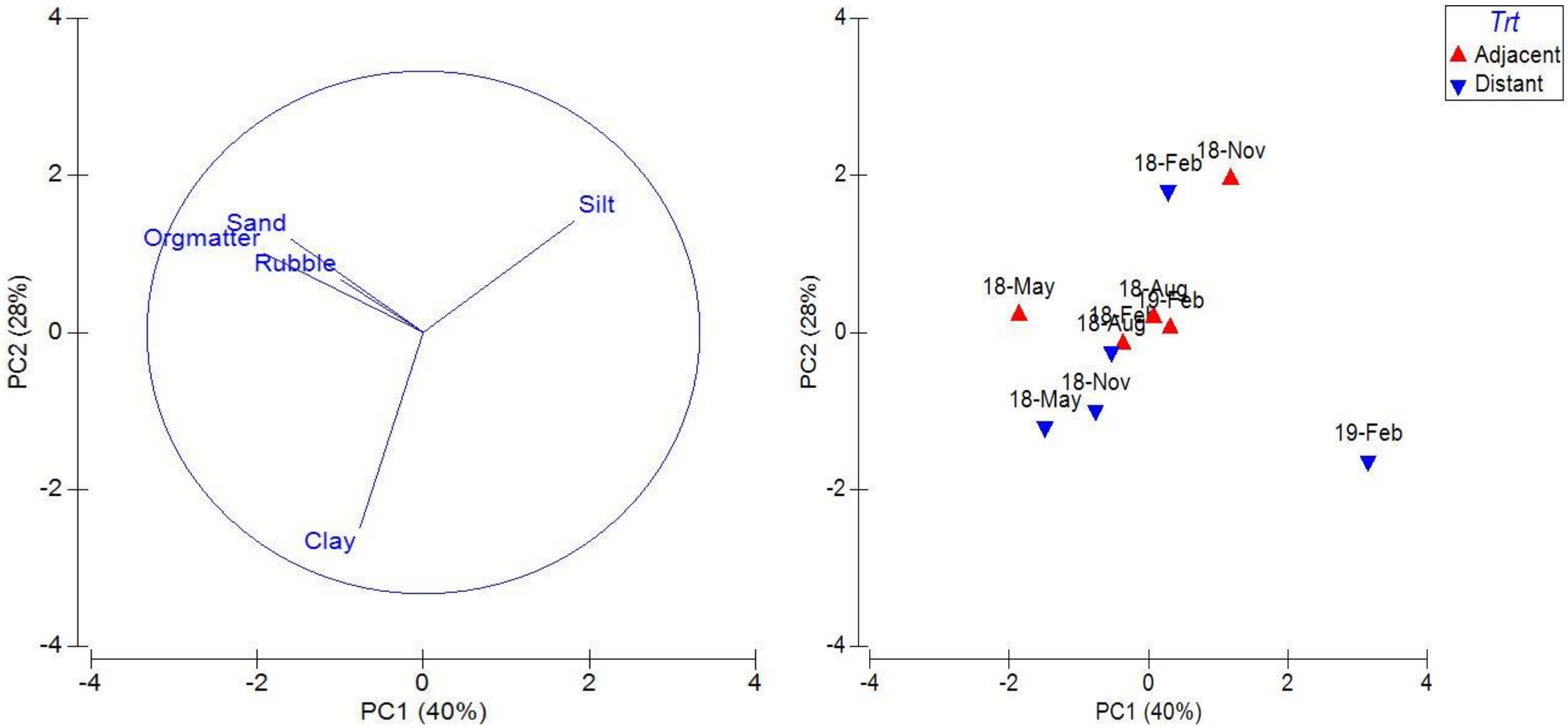
B)



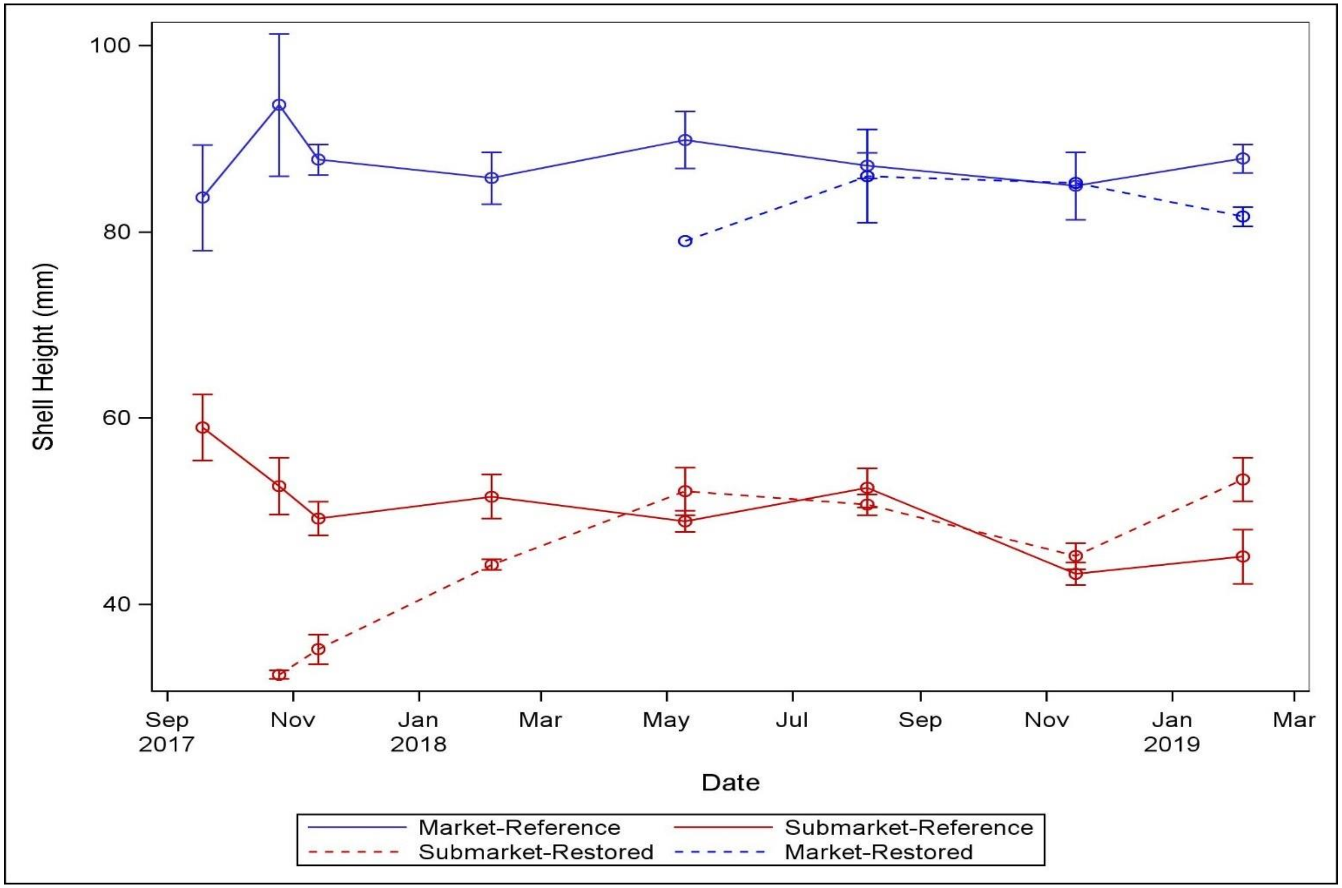
Appendix 4.6. Principal Components Analysis (PCA) for sediment grain size analyses from May 2017 to February 2019 at adjacent and distant sites for the restored reef.



Appendix 4.7. Principal Components Analysis (PCA) for sediment grain size analyses and organic content from February 2018 to February 2019 at adjacent and distant sites for the restored reef.



Appendix 4.8. Mean shell height (mm) of sub-market (26-75) and market-sized oysters (≥76) from reference and restored reefs. Market-sized oysters were first observed on the restored reef in May 2018. Error bars represent standard error.



Appendix 4.9. Growth rates (mm wk^{-1}) of oysters per week at the restored reef from August to December 2017. Mid-dates are the average number of days between sampling dates. Error bars represent standard error.