Guana Tolomato Matanzas National Estuarine Research Reserve
2014 – 2016 Oyster Monitoring Summary

Pam Marcum, Biologist
Nikki Dix, Research Director
Matt Monroe, Biologist
June 8, 2018

INTRODUCTION

Oysters provide many valuable services in estuaries and coastal communities. As suspension feeding bivalves, oysters remove large quantities of particulate carbon from waters and prevent phase shifts of estuarine communities to those dominated by planktonic and microbial organisms (Baird et al. 2004, Newell 1988). By removing suspended particles from the water column, oysters increase light penetration which in turn benefits the growth of submerged aquatic vegetation such as seagrass (Newell & Koch 2004). Suspension feeding causes oysters to integrate water quality conditions, also making them useful as bioindicators. Eastern oysters (*Crassostrea virginica*) have been used to test for the presence of certain metals and for terrestrially sourced nitrogen in U.S. waters (Daskalakis 1996, Fertig et al. 2009, Kimbrough et al. 2008). Oysters also help to mediate eutrophication caused by nitrogen loading of estuarine waters by enhancing denitrification rates (Kellogg et al. 2014, Newell et al. 2002). Oyster reefs can reduce erosion to other estuarine habitats such as salt marsh and can be used as natural breakwaters to mitigate shoreline loss (Meyer et al. 1997, Scyphers et al. 2011, Stricklin et al. 2009). The structures created by oyster reefs also provide shelter as well as productive ecosystems for foraging and consequently host many birds, fish, and invertebrates, some of which are commercially and recreationally important species such as blue crabs, red drum, and snapper (Coen et al. 1999, Coen & Grizzle 2007, Tolley & Volety 2005).

Unfortunately, the importance of oysters and their functions has been highlighted by losses in oyster populations. Nearly 85% of oysters have been lost globally and the density of market sized oysters have declined across the U.S. (Beck et al. 2011, zu Ermgassen et al. 2012). Population declines can be attributed to a combination of centuries of fishing pressure, habitat degradation, and parasitic diseases such as Dermo and MSX (Beck et al. 2011, Ford 1996, Kirby 2004, MacKenzie 2007, Rothschild et al. 1994, Wilbur et al. 2012). Given these declines, monitoring and assessments of existing oyster populations are being carried out across the U.S. to establish baselines for management and restoration (Bergquist et al. 2006, Louisiana Department of Wildlife and Fisheries 2011, Luckenbach et al. 2005, Mann et al. 2009, Nevins et al. 2014, Powers et al. 2009, Ross & Luckenbach 2009, Volety & Haynes 2012).

The eastern oyster is a keystone species in northeast Florida estuaries, including the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR), where intertidal reefs are extensive. Yet local oyster harvesters, other citizen stakeholders, and the regional management and scientific communities have voiced concern that oyster population sustainability in GTMNERR is poorly understood, and requires assessment. The concern is that oyster populations may be threatened by overharvesting and/or other human or environmental factors. A series of re-classifications of harvest areas within the GTMNERR have reduced legal harvest acreages by ~70% from 1985 to 2007 (Dietz 2015), thus raising concerns that intensified harvesting on the remaining oyster reefs may threaten their sustainability. A recent period of heavy predation by

crown conch, *Melongena corona*, in the Matanzas River (Garland & Kimbro 2015) and the possibility that parasitic diseases (e.g. *Perkinsus marinus*, *Haplosporidium nelsoni*) are causing oyster mortality or growth inhibition, reinforce concerns about long-term persistence.

Pilot monitoring of oyster reefs within the GTMNERR and surrounding waters was initiated in 2014. The main objectives were to evaluate the status of oyster populations in the area; provide abundance and size estimates to inform the quantification of ecosystem services provided by oysters; provide baseline estimates of reef, population, and community structure metrics for future assessments; and evaluate methods for long-term monitoring.

A regional approach was adopted for this pilot monitoring program based on perceived differences in water quality, food availability, hydrodynamics, harvesting, and management to determine if the GTM estuary should be spatially stratified in a long-term monitoring program. Regions were created based on the major waterways: Tolomato River, Guana River, Salt Run, Matanzas River, and Pellicer Flats (Figure 1). The Matanzas River was further subdivided into Saint Augustine-the northern portion of the river outside of the GTM boundary; Butler Beach- from the start of the GTM boundary to the start of the South St. Johns harvest area; and Fort Matanzas- bounded north and south by the South St. Johns shellfish harvest area. The Pellicer Flats region included the southern stretch of Matanzas river from the southern boundary of the shellfish harvest area to the southern boundary of the GTMNERR.

In addition to the regional approach, the study also aimed to identify any seasonal patterns in metrics. Finally, the status of local oyster populations was assessed by comparing live oyster densities to data from other studies of intertidal oysters in the southeastern United States.
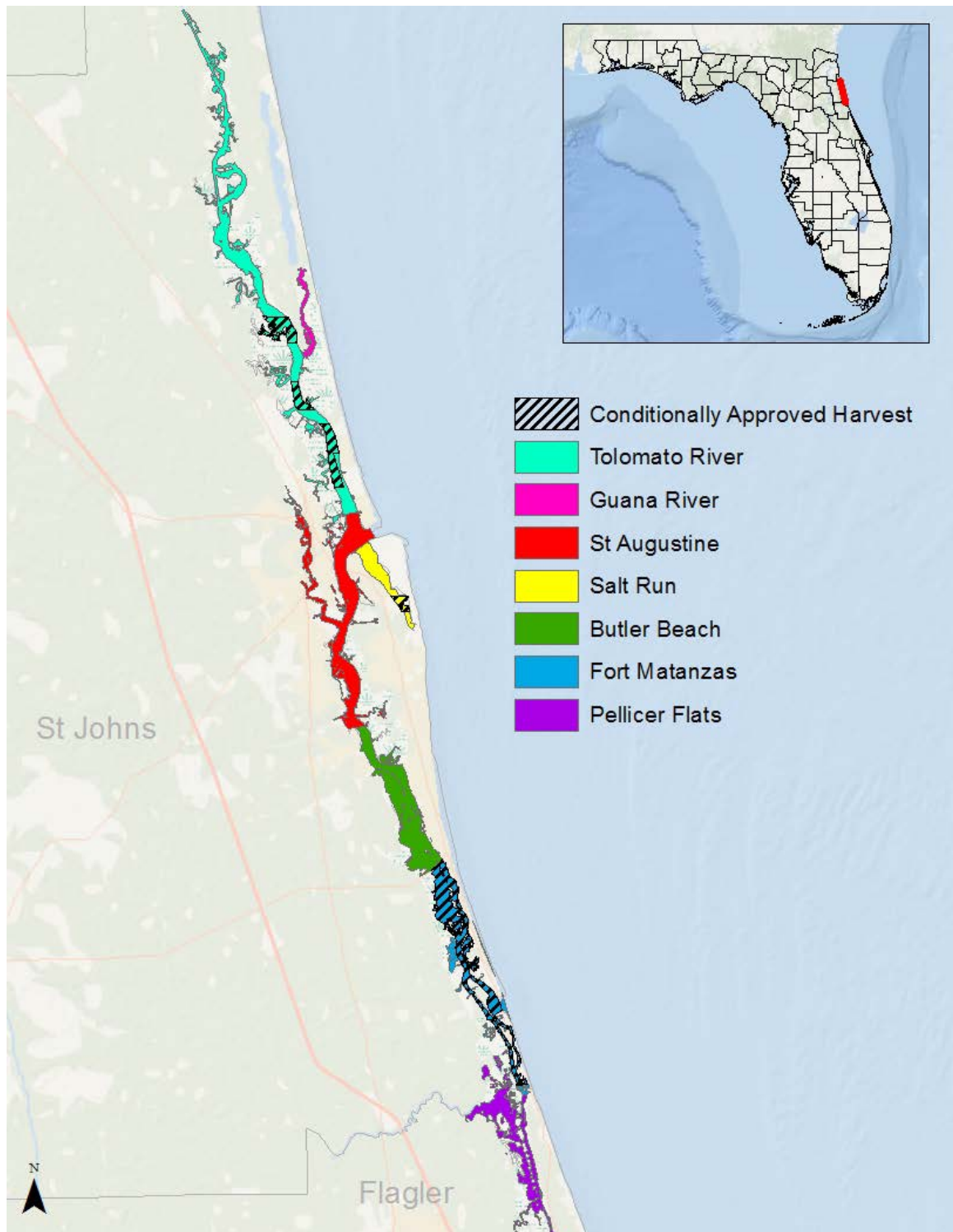
Figure 1. Map of oyster monitoring regions and conditionally approved shellfish harvest areas
(http://www.freshfromflorida.com/Business-Services/Aquaculture/Shellfish-Harvesting-Area-Classification).

METHODS

Oyster reefs were sampled in the winter (Jan-Mar) and summer (Jul-Sep) during 2014 – 2016 (summer only in 2014). Reef metrics can be characterized as those describing reef structure, oyster population structure, and community structure (Table 1).

Reef Structure	Oyster Population Structure	Community Structure
reef height	oyster density	mussel density and size
reef slope	size class frequencies	barnacle density
percent cover of live and dead oysters		crown conch density
percent cover of sediment		other gastropod presence/absence
oyster cluster density		clam density and size

Table 1. Oyster reef metrics

Site Selection

Reefs were selected using a stratified random sampling design. In 2014, three reefs from a 2008 study (Dix 2010) were revisited and the remainder were selected using a random point generator. Beginning summer 2015, a list of reefs was acquired from the St. Johns River Water Management District 2015 Northern Coastal Basin oyster map (http://data-floridaswater.opendata.arcgis.com/datasets/7779f2353b644d6cb513fe2649e4d74b_0). The list was sorted into the regions and a random number table was used to randomly select reefs for sampling. The random reefs were imported into Google Earth to determine if they met the minimum length of six meters and were accessible by land or water. Any reefs that did not meet these two requirements were removed from the list. Morphological classifications of reefs (i.e. isolated patch, fringing, etc.) were not taken into consideration. The final list of reefs was mapped and reefs were grouped by proximity to each other for sampling efficiency.

Overall, 210 reefs were sampled across the seven regions (Table 2a). Sampling within each region was attempted during each season to attain an even distribution throughout the regions and seasons. Of those 210 reefs, 158 were not resampled throughout the three years of sampling (Table 2b). Initial sampling occurred in summer 2014, however, the methods and regions were not yet formally established and fewer samples and metrics were collected than in subsequent years. In 2015, 26 reefs were sampled in both winter and summer to assess temporal variation.

Table 2a Total # reefs sampled						
	S14	W15	S15	W16	S16	**Total**
Tolomato River	3	1	10	4	2	20
Guana River	3	8	8	6	23	48
St Augustine	5	9	11	6	18	49
Salt Run	0	5	7	2	14	28
Butler Beach	2	2	4	0	0	8
Fort Matanzas	4	5	7	16	11	43
Pellicer Flats	0	0	5	5	4	14
Total	17	30	52	39	72	210

Table 2b # Non-Repeated reefs sampled						
	S14	W15	S15	W16	S16	**Total**
Tolomato River	3	1	10	4	2	20
Guana River	3	8	1	6	23	41
St Augustine	5	9	2	6	18	40
Salt Run	0	5	4	2	14	25
Butler Beach	2	2	2	0	0	6
Fort Matanzas	4	5	2	16	11	38
Pellicer Flats	0	0	5	5	4	14
Total	17	30	26	39	72	184

Table 2. Number of reefs sampled per region and season broken down by 2a) total reefs sampled and 2b) unique reefs sampled throughout the 2014-16 monitoring period. W = winter (Jan-Mar) and S = summer (Jul-Sep), followed by the two-digit abbreviated year.

Reef Structure

Reef structure was characterized by the following metrics: overall reef height and slope, quadrat percent cover, and quadrat cluster density. Overall reef metrics were collected from the entirety of the reef. For quadrat estimates and collections, a transect was laid parallel to shore adjacent to the densest portion of each reef. Total length of the transect was recorded. Transect lengths varied but were minimum six meters and maximum of 100 meters. Sampling occurred along the dense side of the transect. The decision was made to focus on the perceived densest portion of each reef to minimize the effect of within-reef variability on regional and seasonal comparisons.

Reef height was determined by measuring the vertical distance between the highest point on the reef and the edge of the reef (Bergquist et al 2006). The edge of the reef was defined as where live oysters or shell were < 10% cover. A string was held in place at the highest point and stretched tightly across to a marked stadia rod at the edge point. A hanging level was attached to the string and the end of the string at the rod was slid up and down until the string read level when held taught. The height on the stadia rod where the string hit was recorded. The distance between the highest point and the stadia rod was also recorded to determine reef slope (reef height ÷ distance).

Percent cover and cluster density were recorded at six random points along the transect (random points taken from an unsorted random number table). A 1-m^2 quadrat was constructed with parallel rows and columns of nylon string to create 100 evenly divided intersecting points (including intersections of string and PVC). The quadrat was laid so that the frame rested along the transect tape. Percent cover for each reef was determined using a point-intercept method modified from Bergquist et al. (2006). The point directly underneath each intersection (determined using a flag pin slid directly down from the intersection) was inspected and categorized as live oyster, dead oyster shell, sediment, or "other" using tallies on the field data sheet. "Other" was defined in the field notes. The total number of intersections for each category was recorded, yielding a percent cover for each quadrat (e.g., # live = % live oyster cover).

Cluster density was determined by counting the total number of oyster clusters that occurred within a 1-m^2 quadrat. A cluster was defined as an independent group of five or more oysters adhered together. To verify independence, clusters were gently rocked to visually determine if any surrounding clusters moved, indicating they were connected. Clusters that were only partially located inside the quadrat were included in the counts.

Population and Community Structure

The number of live crown conch (*Melongena corona*) and crown conch shells with other organisms living in them were recorded within the 1-m^2 quadrats used for percent cover. Any other associated marine gastropods were noted but not quantified.

Oysters and associated fauna were collected from a 0.25-m x 0.25-m subplot located at the first three unsorted points from the random number table. Subplots were designated by a PVC quadrat placed along the transect tape covering the .0 to .25 marks of the meter being sampled. Subplots were excavated up to 15 cm in depth (Rodriguez et al. 2014) and stored in buckets for later processing. For clusters of oysters that extended outside of the quadrat, only the portion of the cluster that fell within the quadrat was collected. The portion that was outside of the quadrat was broken off to ensure that it was not quantified. Most interstitial fauna was retained, but motile species were generally not collected.

Samples were brought back to the lab to be cleaned and processed. Clusters were broken apart to ensure all individual live oysters were included in counts and measurements. Shell height was measured for all live oysters and mussels, and shell length was measured for all live clams, recorded in millimeters to the nearest tenth. Oyster shell height was measured from the beak to the distal end of the largest shell (Figure 2; Baggett et al. 2014). Mussel height was measured from the hinge to the distal edge. Clam shell length was measured along the widest axis. All live barnacles were counted but not measured. The presence or absence of gastropods was also recorded.
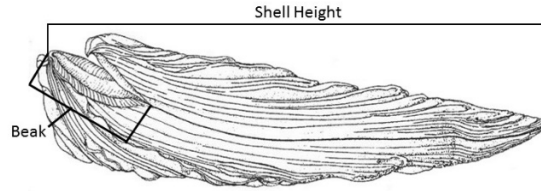
Figure 2. Diagram of shell height measurement (Galtsoff 1964)

Analysis of 2014 data indicated that 50 oysters was a sufficient sample size to determine mean shell height (Figure 3). Measuring only the first random 50 oysters is also recommended by Baggett et al. (2014). Therefore, in 2015, oyster shell height was only measured for the first 50 oysters. All additional live oysters in excess of 50 were counted to determine total oyster density. However, measuring the first 50 oysters, while saving time, does not allow for quantification of oyster densities in specific size classes. Density estimates specific to fishery and spat size classes can be used to test for effects of management-related actions (e.g., harvest, restoration). Therefore, starting in 2016, all collected oysters were measured.

After processing, live samples were returned to the reef or body of water from which they were collected. In the case that samples could not be immediately processed, samples were stored in the freezer. After processing, frozen samples were disposed of at a local shell recycling center.

Larval settlement (spat) patterns were monitored following Florida Fish and Wildlife Research Institute protocols (Parker 2015). Samples were collected using PVC T-shaped structures with cleaned oyster shell suspended from each side of the crossbar (Figure 4). Shells of 5-10 cm shell height were collected from a local shell recycling center, soaked in bleach water for a minimum of 48 hours, and scrubbed with a wire brush to remove any remnants of algae or other attached organisms prior to use. Six cleaned oyster shells were strung on galvanized wire, oriented with the inner surface facing down, and attached with a cable tie to the tree, one on each side of the cross-bar. Trees were deployed on three reefs in each of five regions sampled and placed on the perceived densest portion of the reef inserted until the bottommost shell was approximately five centimeters above the reef. Shells were collected and replaced monthly. Removed shells were placed into labeled bags with a tag containing deployment and reef information and frozen until processing. During processing, each shell was given numerical IDs associated with their physical location on the string, so that "1" was identified as the topmost shell on the string and "6" as the bottommost shell. Shells 1 and 6 were discarded and shells 2 through 5 were observed under a magnifying glass. Larval settlement was determined by counting the number of oyster spat on the bottom/inside of each shell. Spat data from the Fort Matanzas region includes reefs from both Fort Matanzas and Butler Beach regions. Spat was not collected in the Pellicer Creek region.

Figure 4. Spat tree deployed on reef

All sampling was conducted under Florida Fish and Wildlife Conservation Commission Special Activity License SAL-14-1305-SR.

Data Analysis

For this report, sizes of all measured oysters (including the first 50 from 2014-2015 and all oysters from 2016) were used to calculate proportions of oysters in the various size classes (spat = < 25 mm shell height; fishery = ≥ 76 mm shell height). Sampling methods for the summer 2014 sampling season were somewhat different from those listed above (e.g., two collection quadrats instead of three). Those data were only used to evaluate metric correlations.

Correlation analysis was used to evaluate relationships among metrics for the full data set. Since cover and cluster data were recorded at six random locations on the reef while faunal metrics were taken from collected samples at three of those locations, only data from transect locations that included both cover/cluster data and faunal metrics (i.e. collected samples) were included. A non-parametric Spearman correlation test with Holm's p-values was used due to the variety of data types (counts, measures, proportions).

Metrics from the non-repeated reef data set, excluding 2014, were plotted as notched boxplots to evaluate regional and seasonal differences. The notched area provides a 95% confidence interval for differences between group medians, thus boxplots with non-overlapping notches are strong evidence that the medians differ (Chambers et al. 1983).

A repeated measures Analysis of Variance (ANOVA) was used to evaluate oyster density seasonality on the 26 repeated reefs sampled in 2015. A Shapiro-Wilk test for normality and Levene's test of equal variance by season (center = median method) were performed on oyster density averaged to the reef level. There was significant evidence that oyster density did not come from a normal distribution (W=0.88103, p-value= < 0.0001) and the variance in oyster density was

not equal among seasons (F(1)= 7.0668, p-value = 0.008687). Therefore, oyster density was square-root transformed for analysis.

RESULTS

Reef Structure

Reefs were tallest in the Tolomato and Guana Rivers (Figure 5a). Pellicer Flats had the lowest median reef heights of all regions followed by Salt Run, St Augustine, and Fort Matanzas, respectively. Reef slopes were steeper in Tolomato River, Guana River, and St Augustine compared to those in Salt Run, Fort Matanzas, and Pellicer Flats (Figure 5b). The density of oyster clusters was lowest in Salt Run, but there was no evidence that cluster density differed among other regions (Figure 5c). Reef structure metrics did not differ by season (Figure 6).

Guana River reefs had the highest cover of live oysters and Pellicer Flats had the lowest (Figure 7a). Dead shell cover was lowest in St Augustine and higher in Pellicer Flats than Guana River, Salt Run, and St Augustine regions (Figure 7b). Sediment cover was lowest in Pellicer Flats and highest in St Augustine. Median sediment cover was higher in St Augustine than all other regions except Salt Run and Butler Beach (Figure 7c). Live oyster and shell cover were higher in winter; sediment cover was higher in the summer (Figure 8).

Oyster Population Structure

Overall, an average of 1,621 oysters m^{-2} was observed in this study (Table 3). Oyster density was lowest in Salt Run and highest in Pellicer Flats (Figure 9a). The proportion of fishery-sized oysters was highest in Guana River, Salt Run, St Augustine and Fort Matanzas (Figure 9b). Reefs in Pellicer Flats had no fishery-sized oysters and the highest proportion of spat (Figure 9c). In 2015, total oyster density on resampled reefs was significantly lower in summer than in winter (Figure 10, Table 4). On all reefs, the proportion of spat-sized oysters was higher in summer than winter, but there was no evidence of a seasonal difference for fishery-sized oysters (Figure 11a and 11b, respectively).

Size frequency distributions were mostly skewed to the right (Figure 12). For most regions, the highest proportions of spat were observed in summer 2014, winter 2016, and summer 2016. Size distributions in St. Augustine were nearly identical for winter and summer 2016. The Tolomato River region had the highest proportion of spat in summer 2016 than any other region and season.

Primary spat settlement occurred in the late spring/early summer in all regions during 2015-2016 (Figure 13). Smaller settlement events occurred in each region throughout the summer-fall. Unfortunately, Hurricane Matthew prevented retrieval and redeployment of spat collectors during fall 2016. Densities of spat on shell were highest in the Guana River and Ft. Matanzas regions (Figure 13).

Community Structure

Associated fauna observed on oyster reefs throughout this study include annelid worms (*Polydora* spp.), quahog/hard clams (*Mercenaria campechiensis*), oyster drills (*Urosalpinx cinera*), white/striped barnacles (*Balanus amphitrite*), ribbed mussels (*Geukensia demissa*), mahogany date mussels (*Lithophaga bisculata*), crown conch (*Melongena corona*), boring sponges (*Cliona* spp.), slippersnails (*Crepidula* spp.), porcelain crabs (*Petrolisthes armatus*), stone crabs (*Menippe mercenaria*), swimming crabs (*Callinectes* spp.), other xanthid crabs (Family *Panopeidae*), and hermit crabs. Other known faunal associates in the region include: pink barnacles (*Megabalanus cocopoma*), green mussels (*Perna viridis*), black mussel (*Brachidontes exustus*), black smooth mussels (*Mytella charuanna*), and solitary and colonial ascidians (Class Ascidiacea) (Shirley et al. 2016).

Mussel densities were highest on Pellicer Flats reefs. Mussel densities in Tolomato River, Salt Run, and Butler Beach were lower than those in Guana River, St Augustine, and Fort Matanzas (Figure 14a). Barnacle densities were similar throughout the study area; however, values were lowest in St Augustine (Figure 14b). Clam densities were similar throughout the study area, but sample sizes were insufficient to make regional comparisons (Figure 14c). Live crown conch were only found on reefs in Pellicer Flats (Figure 14d). The median value of barnacle density was higher in winter than in summer (Figure 15a). There was no evidence that mussel and clam densities differed among seasons (Figure 15b, c).

Relationships Among Metrics

Reef height was positively correlated with reef slope (Table 5). Reef slope was inversely correlated with shell cover. Oyster cluster density was positively correlated with live oyster cover and densities of oysters, barnacles, mussels, and clams. Live oyster cover was positively correlated with densities of oysters, oyster clusters, barnacles, mussels and clams; and inversely correlated with sediment cover.

Oyster shell cover was positively correlated with percent spat-sized oysters and densities of clams and conch, and inversely correlated with sediment cover, percent fishery-sized oysters, and reef slope (Table 5). Sediment cover was positively correlated with percent fishery-sized oysters and inversely correlated with densities of oysters, mussels, clams, and conch. The proportion of fishery-size oysters was inversely correlated with the proportion of spat-size oysters, shell cover, and densities of oysters, clams, and conch. The proportion of spat-size oysters was positively correlated with densities of oysters, mussels, and clams.

Oyster density was correlated with densities of all associated fauna (Table 6). The strongest relationships were with other bivalves (clams and mussels).

Regional Comparisons

Oyster densities in the GTMNERR and surrounding area were similar to those in studies conducted in the southeastern United States, although incredibly high densities were reported for Ace Basin, South Carolina and Skidaway Island, Georgia. The proportion of oyster recruits (spat) was similar

to other reefs in northeast Florida, six times higher than the proportion reported in North Carolina, and almost half the value reported for the Suwannee River (Florida) estuary. The proportions of fishery-size oysters in the GTMNERR were similar to those reported in other studies but lower than the proportion reported in North Carolina (Table 6).

DISCUSSION

The primary goals of this pilot monitoring were to collect baseline information and evaluate the status of oyster populations in northeast Florida. Given the lack of historical data, trends are challenging to assess. In comparison to intertidal reefs in other regions, densities of oysters in northeast Florida appear to be lower than those in the heart of the South Atlantic Bight but similar to or higher than oyster reefs in west Florida and North Carolina. It is important to consider that densities observed in this study were higher than the average density on reefs overall in the area because reefs were sampled at the perceived densest areas to minimize within-reef variation.

Temporal comparisons to assess oyster population status are available for the three reefs in the Fort Matanzas region sampled in 2008 (Dix 2009, 2010) and 2014-2015 (this study). Mean oyster density on the reefs in 2014-15 was approximately half the observed density in 2008 (92 and 190 0.25 m^{-2}, respectively), suggesting at least a local decline over the past 6-7 years. Since reefs in this region are conditionally approved for shellfish harvest, this finding warrants further study of harvest impacts on local oyster populations.

Size frequency distributions are an indicator of the age structure of a population (Baggett et al. 2014). Distributions heavily skewed to the right indicate mortality at sub-adult stages while flatter distributions indicate survival of multiple recruitment events. Distributions skewed to the right, as observed in this study, are common for intertidal oysters in the southeastern United States (Bahr & Lanier 1981, Coen & Luckenbach 2000, Volety & Savarese 2001). Understanding implications for the oyster fishery and long-term population sustainability will require estimation of growth and mortality rates and population modeling (Dame 2011, Mann et al. 2009, Roegner & Mann 1995). The observed temporal patterns in oyster larvae settlement (i.e., spat peaks in spring) differed slightly from other studies in the southeastern United States which found peaks in both spring and late summer (Arnold et al. 2008, O'Beirn et al. 1996, Parker 2015, Volety & Savarese 2001, Wilson et al. 2005). Further investigation of environmental conditions (e.g., water quality, flow rates) and predation could identify factors limiting late summer/fall settlement.

Observed regional and seasonal differences in oyster reef, population, and community structure may be explained by differences in harvest pressure or predation and other biological, physical, and chemical properties of their surrounding waterbodies. For example, studies have shown flow rates have an effect on spat recruitment (Knights and Walters 2010) and mean growth rates (Lenihan 1999). Reefs were generally tallest in the northern reaches of the study area and flattest to the south, similar to findings by Shirley et al. (2016). Reef height is thought to be influenced by tidal range and depth of inundation, which both increase toward the heart of the South Atlantic Bight (Bartol et al. 1999, Byers et al. 2015, Fodrie et al. 2014, Rodriguez et al. 2014). However, some of the flattest reefs were in Salt Run, in the middle of the study area.

Salt Run is a popular, easily-accessible oyster harvest area, yet the harvestable area is relatively small, resulting in high harvest pressure compared to other areas in northeast Florida. Local harvesting practice is to cull the reefs by hand, knocking off the small oysters and taking only fishery-size oysters. Salt Run reefs were among the lowest for reef height, number of clusters, and oyster density but had one of the highest proportions of fishery-sized oysters. Harvest activities may keep the reef profiles, clusters, and numbers low but the harvest pressure and techniques could be contributing to faster growth rates of oysters in this region. Alternatively, like Pellicer Flats, which also had low reef heights, shallow water may be a limiting factor in vertical growth (Bartol et al. 1999). Oyster growth rates may also be relatively high in Salt Run due to environmental conditions such as high salinity and food availability.

Oyster densities in Pellicer Flats were highest on average, but that pattern was driven by an abundance of spat. Pellicer Flats had the highest proportion of spat of all regions and no fishery-sized oysters. A high density of small oysters indicates sub-adult mortality, which may be a result of disease, toxicity, hydrology, and/or predation. Harvest is not permitted in Pellicer Flats. Predatory crown conchs were only found on reefs in the Pellicer region, consistent with a previous study by Garland & Kimbro (2015) in the same region. Mean crown conch density was higher in this study (3.8 m^{-2} compared to 1.5 m^{-2} found in Garland & Kimbro, 2015), but it is difficult to assess whether the difference is significant. Garland & Kimbro (2015) attributed a sudden increase in crown conchs noted by locals to drought conditions and elevated salinity. On the other hand, the Pellicer Flats region surrounds the mouth of a freshwater tributary (Pellicer Creek) and oyster growth rates tend to decline in lower salinities (Volety & Savarese 2001, Wang et al. 2008). Thus, the lack of large oysters in this region may be a long-term consequence of freshwater discharge and associated factors.

The amount and composition of sediment on reefs may be influenced by geological features, hydrology, and surrounding emergent vegetation. Biological activity and the physical structure of oyster reefs can also affect the amount and composition of reef sediments through benthic-pelagic coupling (Dame et al. 1989). The finding that Pellicer Flats reefs exhibited the lowest sediment cover of all the regions as well as the highest proportion of small oysters suggests a lower level of biological activity compared to other regions. Similarly, higher sediment cover observed in summer compared to winter throughout the study area may be the result of increased biological activity during warmer months and sediment deposition patterns. Haven and Morales-Alamo (1966) saw significantly higher bio-deposits from both oysters and reef-associated filter feeders in summer months. Regionally, sediment cover was highest in Salt Run, St Augustine, and Butler Beach. It's possible that higher nutrient loads in that area fueled production (Dix et al. 2013), resulting in more biological deposits. Future studies could compare sediments on and off oyster reefs to discern the influence of biological activity.

The higher percentage of live oyster cover and shell cover during the winter compared to summer may be a combination of higher bio-deposits in summer, a lag effect of new recruits and higher growth rates in the summer (Manley et al. 2009, Byers 2015), and high-energy nor'easter storms shifting sediments in winter (Defne et al. 2009, Stevenson et al. 1988). The 26 re-sampled reefs in 2015 also exhibited higher total oyster densities in winter than summer. In contrast, in 2008, Dix (2009, 2010) found live oyster cover and oyster densities (of all size classes) more abundant in the summer than the winter. Size frequency plots showed a peak in the proportion of spat-sized oysters

in the winter of 2016. Winter water temperatures during both 2015 and 2016 were above average (data summaries from http://swmprats.net/) which may have supported spawning, although data from spat collectors did not show winter settlement. Predation rates and disease intensity may also have been lowered by milder winters. Seasonal anomalies in water quality and weather parameters may play a strong role in reef cover and oyster population patterns, exemplifying the need for environmental parameters to be included in monitoring.

Data collected during 2014-2016 provided an opportunity to assess methods and develop recommendations for a long-term oyster monitoring program. Correlations were used to identify the methods that provide the most information as quickly as possible. The correlations between oyster clusters, oyster densities and mussel and clam densities suggests that oyster clusters and density could be used as indicators of habitat and filtration functions. The correlation between live cover and oyster density indicates that cover could be used to estimate oyster density (and relative quantities of the ecosystem services they provide). The finding that cluster densities were lowest in the region with the strongest harvest pressure (Salt Run) suggests that cluster density could be an indicator of harvest pressure. The ease and relative quickness of measuring percent cover and clusters would facilitate increased sample sizes and spatial coverage in a non-destructive manner to better assess reef function and services provided on intertidal reefs.

The significant seasonal differences in oyster densities suggest that seasonal sampling should continue. The lack of regional differences in oyster density, with exception of Pellicer Flats, suggests that for large-scale population structure estimates, sampling evenly distributed throughout the reserve might be appropriate and would save resources for more targeted, hypothesis-driven studies. However, Pellicer Flats reefs stood out in many of the metrics and should be sampled separately. While crown conchs were of particular interest during these pilot surveys, all snails and other potential predators need to be considered to quantify potential impacts of predation on oyster populations in the future.

There are some additional concepts that should be considered in long-term oyster monitoring. Differentiating between morphological classifications of reefs (fringe, bar/patch, etc.) may better explain patterns in structure. Fringing reefs are generally sparser with individual oyster clusters rather than the ubiquitous cover found on isolated patch/bar reefs (personal observation). The use of an oyster map for site selection in this study created a bias toward larger isolated reefs, missing many of the marsh/mangrove fringing reefs found in this region. Additional methods need to be tested to assess oyster population and community structure on other structures such as docks, bridges, and seawalls (Drexler et al 2014). The northward migration of mangroves (Cavanaugh et al 2013) should also be considered as oysters colonize red mangrove prop roots.
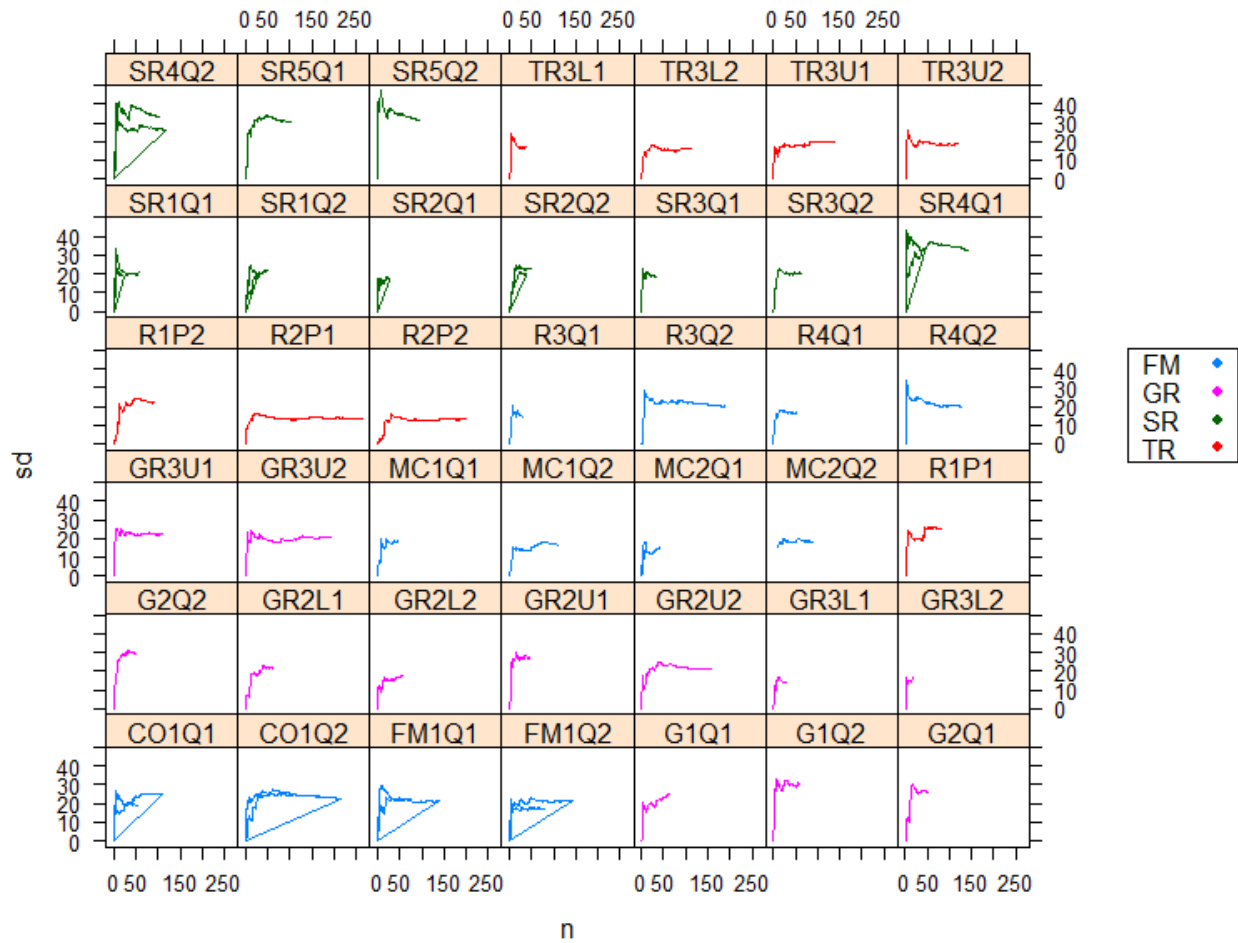
Figure 3. Plot of oyster shell height standard deviation with increasing sample size for reefs sampled in Summer 2014. Reefs are color coded by region FM = Fort Matanzas, GR = Guana River, SR = Salt Run, TR = Tolomato River.

	Tolomato River	Guana River	St Augustine	Salt Run	Butler Beach	Fort Matanzas	Pellicer Flats	Total
	n = 20	n = 41	n = 40	n = 25	n = 6	n = 38	n = 14	n = 184
Reef Height (m)	0.875 ± 0.04* (0.27)	0.861 ± 0.02* (0.29)	0.662 ± 0.02* (0.23)	0.549 ± 0.02* (0.33)	0.777 ± 0.04* (0.32)	0.770 ± 0.02* (0.25)	0.485 ± 0.02* (0.23)	0.717 ± 0.26* (0.34)
Reef Slope	0.213 ± 0.02* (0.44)	0.185 ± 0.01* (0.34)	0.180 ± 0.01* (0.50)	0.165 ± 0.03* (1.47)	0.130 ± 0.01* (0.46)	0.150 ± 0.02* (1.02)	0.121 ± 0.01* (0.36)	0.167 ± 0.14* (0.85)
Oyster Clusters (m^{-2})	14.3 ± 2.0 (0.56)	14.8 ± 0.8 (0.37)	16.2 ± 1.0 (0.32)	10.7 ± 0.9 (0.59)	16.4 ± 4.2 (0.62)	14.3 ± 1.0 (0.40)	15.9 ± 2.7 (0.64)	14.0 ± 0.49 (0.48)
% Cover Live	27.1 ± 3.1 (0.46)	28.8 ± 1.5 (0.34)	26.2 ± 1.5 (0.30)	25.9 ± 1.7 (0.44)	26.2 ± 2.2 (0.21)	28.0 ± 1.6 (0.36)	24.3 ± 4.3 (0.67)	27.0 ± 0.78 (0.39)
% Cover Shell	50.3 ± 5.6 (0.27)	44.4 ± 3.1 (0.38)	34.9 ± 4.7 (0.54)	44.7 ± 2.8 (0.31)		48.7 ± 3.3 (0.35)	68.4 ± 5.2 (0.23)	46.4 ± 1.7 (0.38)
% Cover Sediment	15.1 ± 1.2 (0.20)	24.0 ± 3.3 (0.74)	34.6 ± 5.4 (0.59)	27.7 ± 3.4 (0.61)		21.7 ± 4.1 (0.98)	3.2 ± 1.7 (1.54)	23.8 ± 1.8 (0.82)
Oyster Density (m^{-2})	1477.7 ± 228.4 (0.62)	1565.6 ± 155.6 (0.66)	1687.6 ± 188.7 (0.57)	1309.6 ± 144.3 (0.73)	1642.2 ± 260.7 (0.39)	1675.2 ± 166.6 (0.62)	2648.8 ± 546.0 (0.77)	1620.6 ± 81.8 (0.69)
% Fishery-Sized Oysters	5.7 ± 1.2 (0.81)	12.4 ± 1.6 (0.94)	8.3 ± 1.1 (0.67)	9.6 ± 1.4 (0.96)	2.7 ± 0.8 (0.72)	4.6 ± 0.5 (0.69)	0.04 ± 0.02 (2.34)	7.8 ± 0.6 (1.09)
% Spat-Sized Oysters	44.8 ± 4.1 (0.36)	36.0 ± 2.7 (0.49)	39.8 ± 2.3 (0.29)	37.7 ± 2.8 (0.50)	37.5 ± 5.6 (0.36)	38.3 ± 1.6 (0.26	51.4 ± 3.0 (0.22	38.6 ± 0.7 (0.47)
Barnacles (m^{-2})	196.9 ± 59.9 (2.28)	179.9 ± 20.9 (1. 40)	102.8 ± 28.2 (2.49)	345.4 ± 54.3 (1.91)	157.3 ± 24.7 (1.09)	157.0 ± 29.5 (1.90)	139.6 ± 141.0 (2.08)	222.6 ± 19.0 (2.13)
Mussels (m^{-2})	91.4 ± 12.5 (1.02)	220.7 ± 24.3 (1.33)	271.4 ± 46.5 (1.55)	141.6 ± 17.5 (1.49)	81.3 ± 13.9 (1.19)	267.8 ± 33.5 (1.26)	443.4 ± 66.9 (0.98)	209.3 ± 12.3 (1.47)
Clams (m^{-2})	34.5 ± 10.5 (2.17)	36.0 ± 8.0 (2.38)	36.7 ± 7.0 (1.60)	25.2 ± 5.0 (2.00)	31.6 ± 8.0 (1.60)	39.3 ± 9.3 (2.09)	116.6 ± 36.2 (2.01)	40.6 ± 4.4 (2.40)
Conch (m^{-2})	0	0	0	0	0	0	3.8 ± 1.4 (1.07)	0.3 ± 0.14 (4.92)

Table 3. Mean ± standard error and (coefficient of variation) for each metric by region and for total study area. *standard deviation; 2014-16 non-repeated reefs.
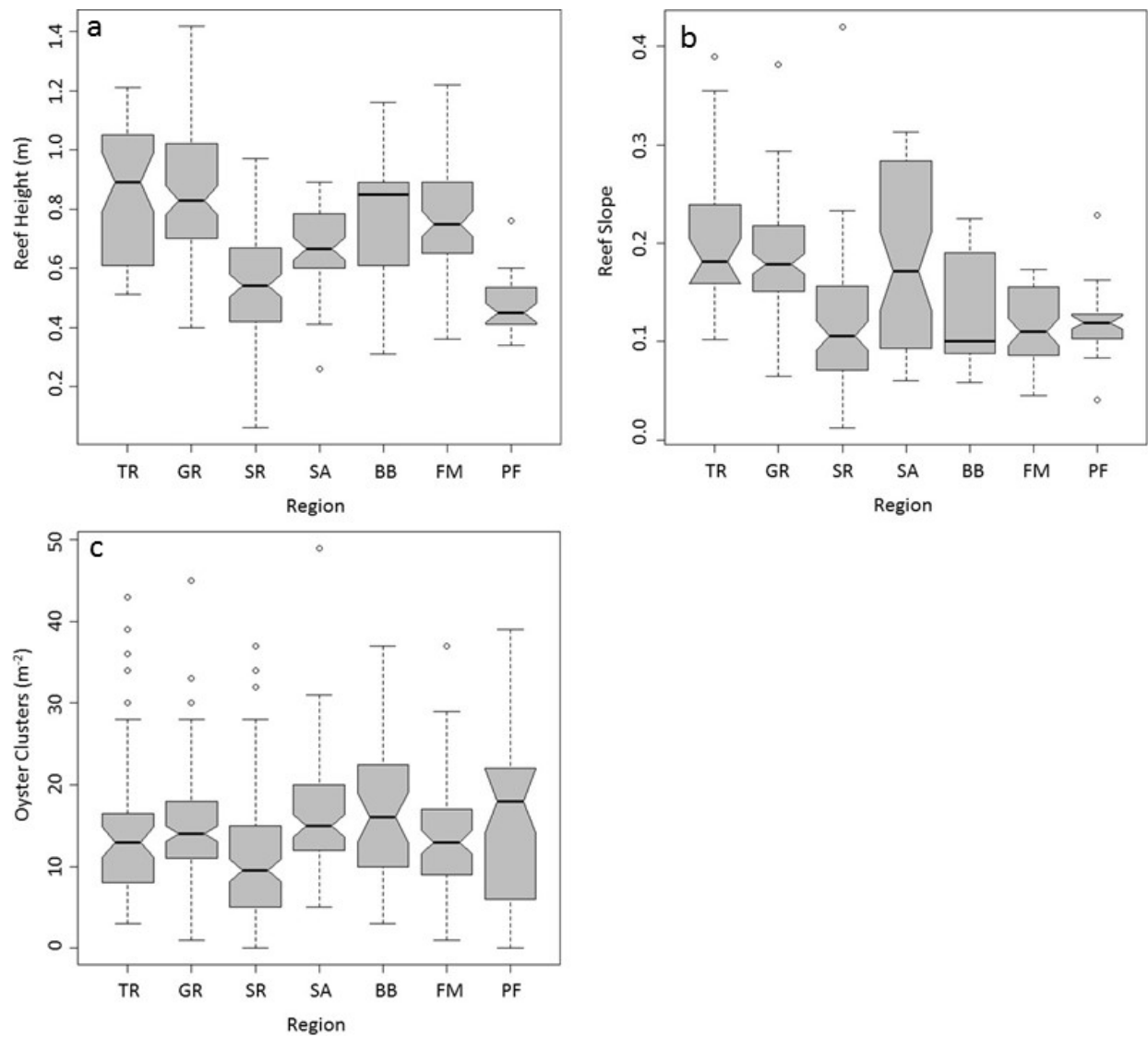
Figure 5. Notched boxplot of a) reef height, b) reef slope, and c) oyster clusters by region (2015-16 non-repeated reefs). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th – 25th percentiles), circles = potential outliers, black bar = median value, TR = Tolomato River (n = 17), GR = Guana River (n = 38), SR = Salt Run (n = 25), SA = St Augustine (n = 35), BB = Butler Beach (n = 4), FM = Fort Matanzas (n = 34), PF = Pellicer Flats (n = 14).
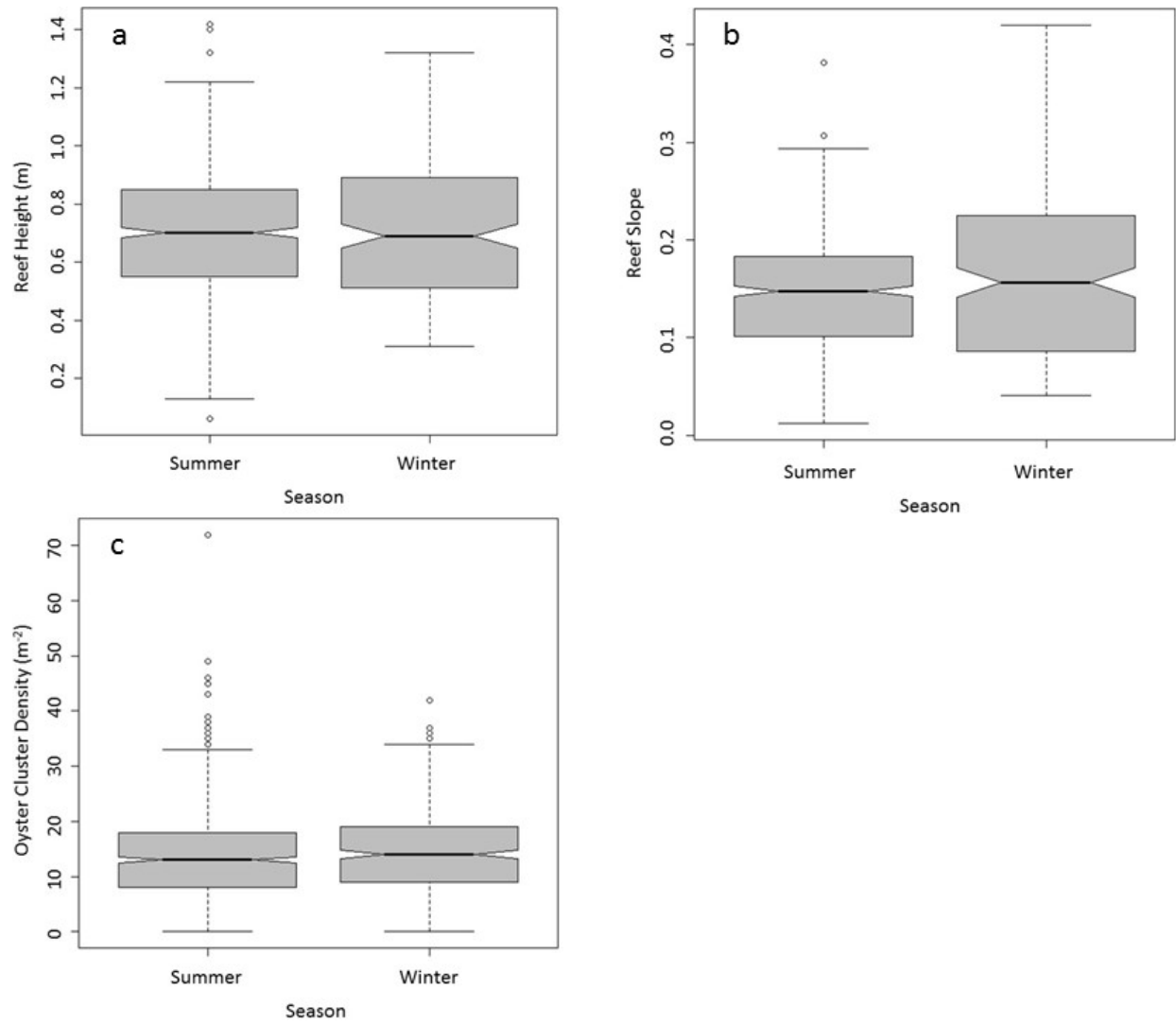
Figure 6. Notched boxplots for a) reef height, b) reef slope, and c) oyster clusters by season (2015-16 non-repeated reefs; Summer n = 98, Winter n = 69). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile value), circles = potential outliers, black bar = median value.
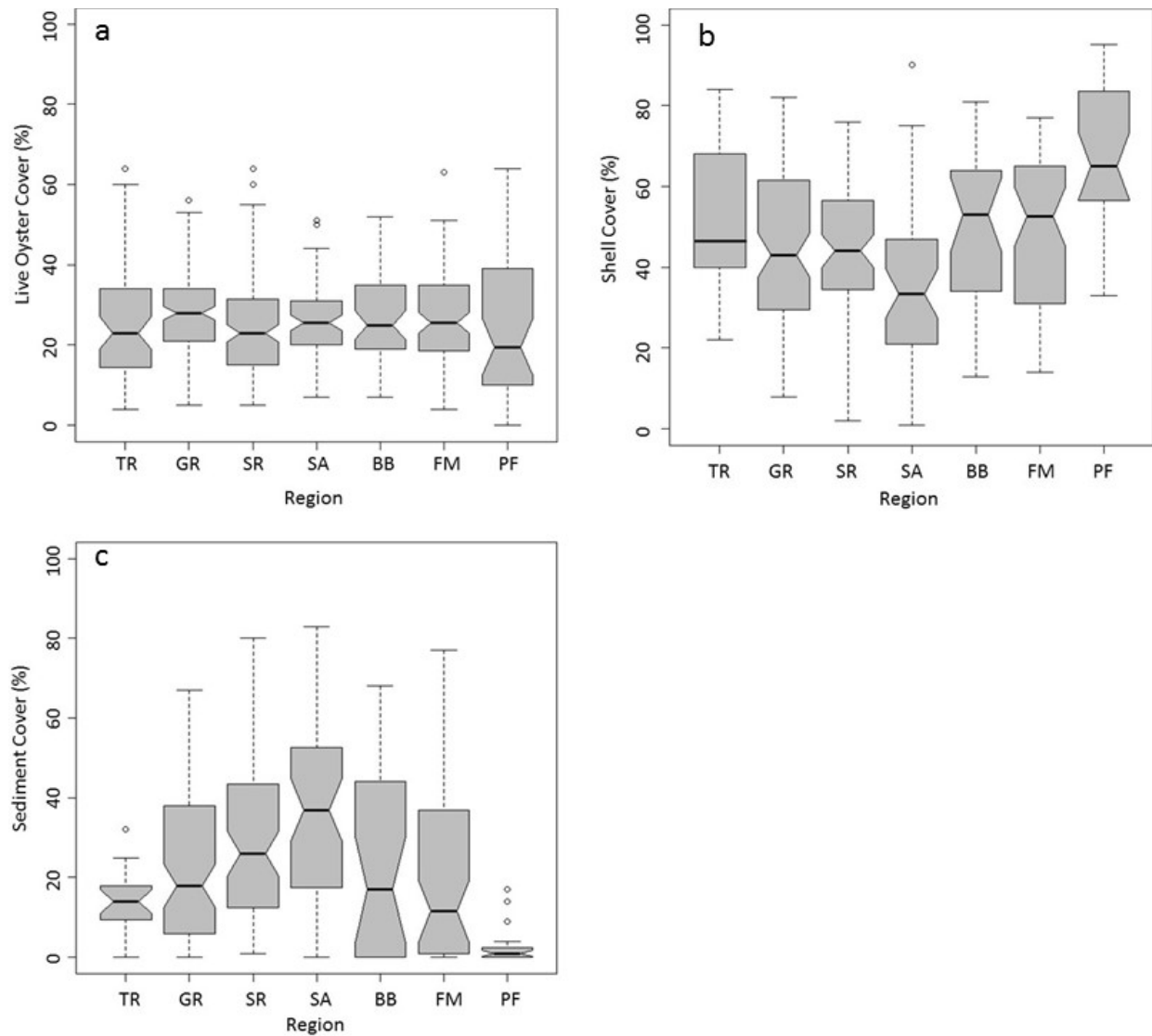
Figure 7. Notched boxplot of a) percent live oyster cover, b) percent shell cover, and c) percent sediment cover split by region (2015-16 non-repeated reefs). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th – 25th percentiles), circles = potential outliers, black bar = median value, TR = Tolomato River (n = 17), GR = Guana River (n = 38), SR = Salt Run (n = 25), SA = St Augustine (n = 35), BB = Butler Beach (n = 4), FM = Fort Matanzas (n = 34), PF = Pellicer Flats (n = 14).
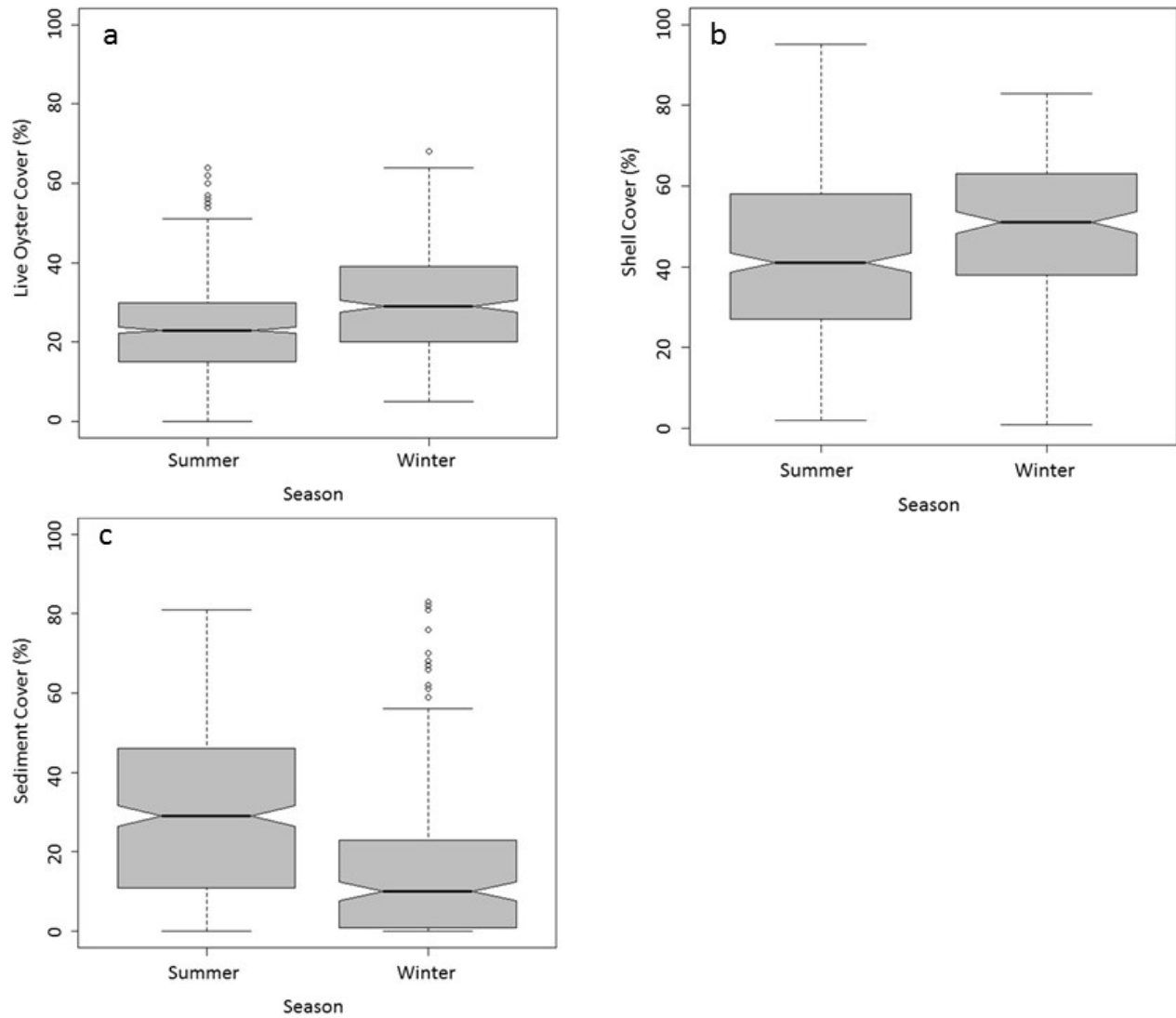
Figure 8. Notched boxplots of percent cover for a) live oysters, b) shell, and c) sediment by season (2015-16 non-repeated reefs; Summer n = 98, Winter n = 69). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile value), circles = potential outliers, black bar = median value.
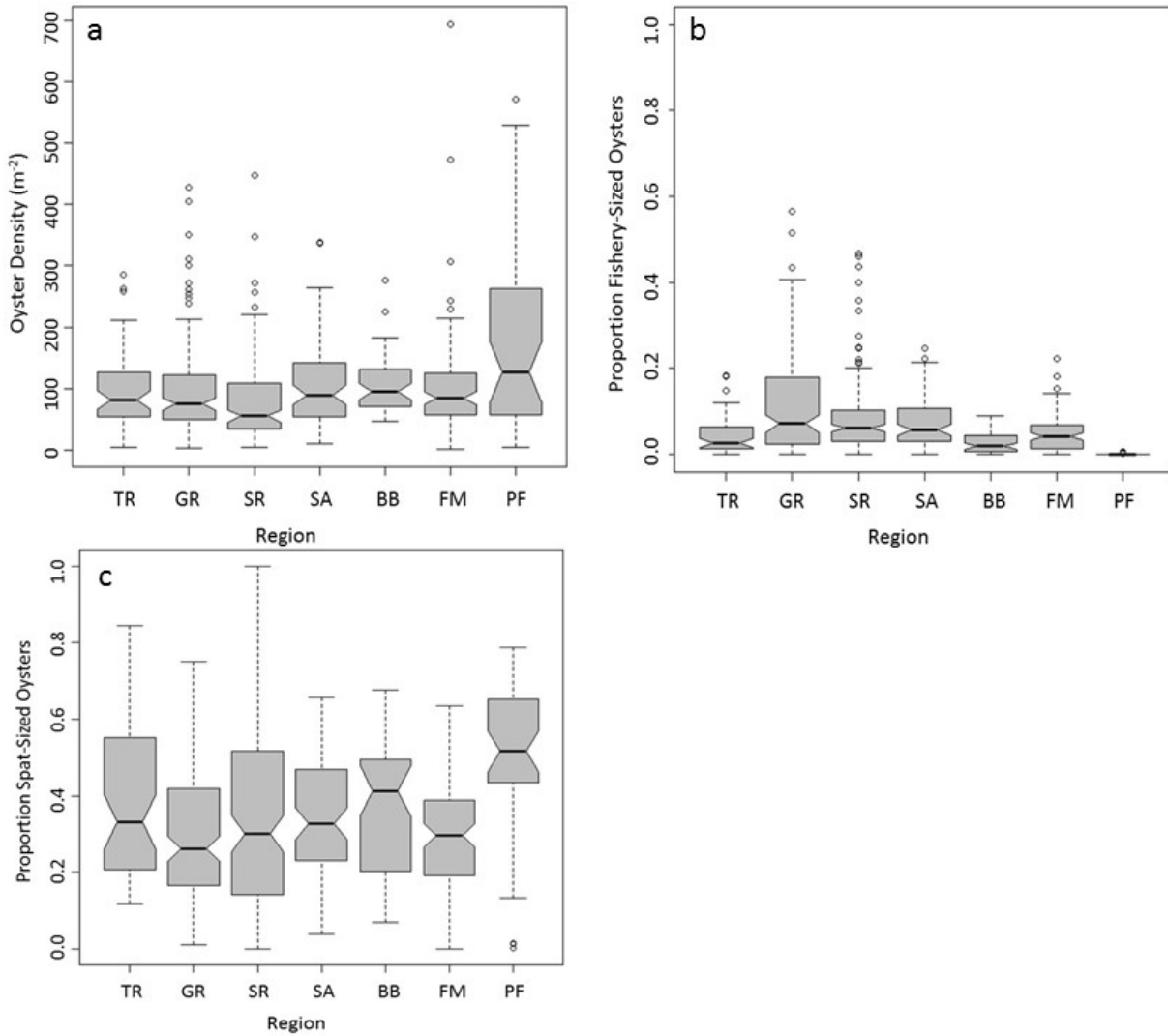
Figure 9. Notched boxplot of a) oyster density, b) proportion of fishery-sized oysters, and c) proportion of spat-sized oysters split by region (2015-16 non-repeated reefs). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th – 25th percentiles), circles = potential outliers, black bar = median value, TR = Tolomato River (n = 17), GR = Guana River (n = 38), SR = Salt Run (n = 25), SA = St Augustine (n = 35), BB = Butler Beach (n = 4), FM = Fort Matanzas (n = 34), PF = Pellicer Flats (n = 14).
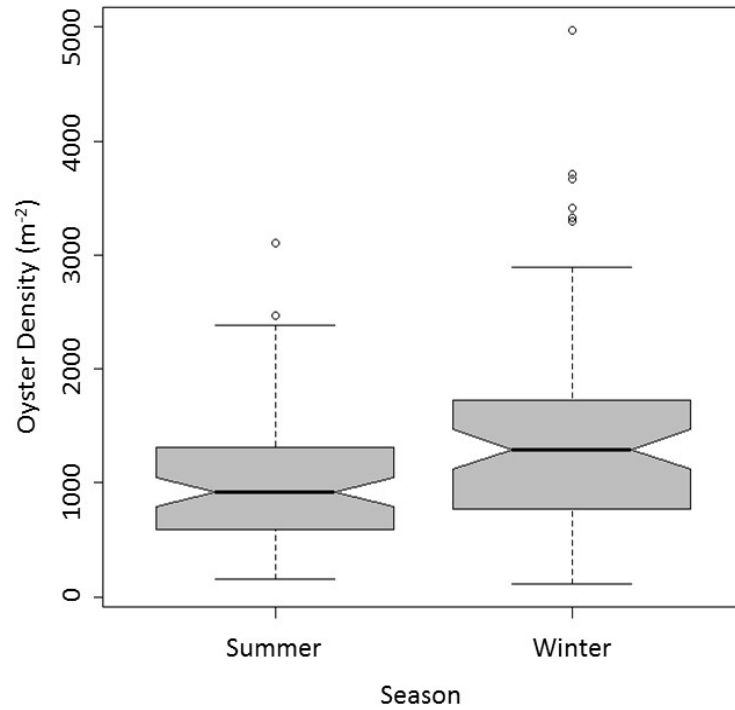
Figure 10. Boxplot oyster density on resampled reefs by season during 2015 (n = 26). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile value), circles = potential outliers, black bar = median value.

Test	Variable	Df	F-value	p-value
Repeated Measures ANOVA	(Intercept)	1/25	138.1671	< 0.001
	Season	1/25	7.4883	0.01126

Table 4. Repeated Measures ANOVA on oyster density on resampled reefs by season during 2015 (n = 26).
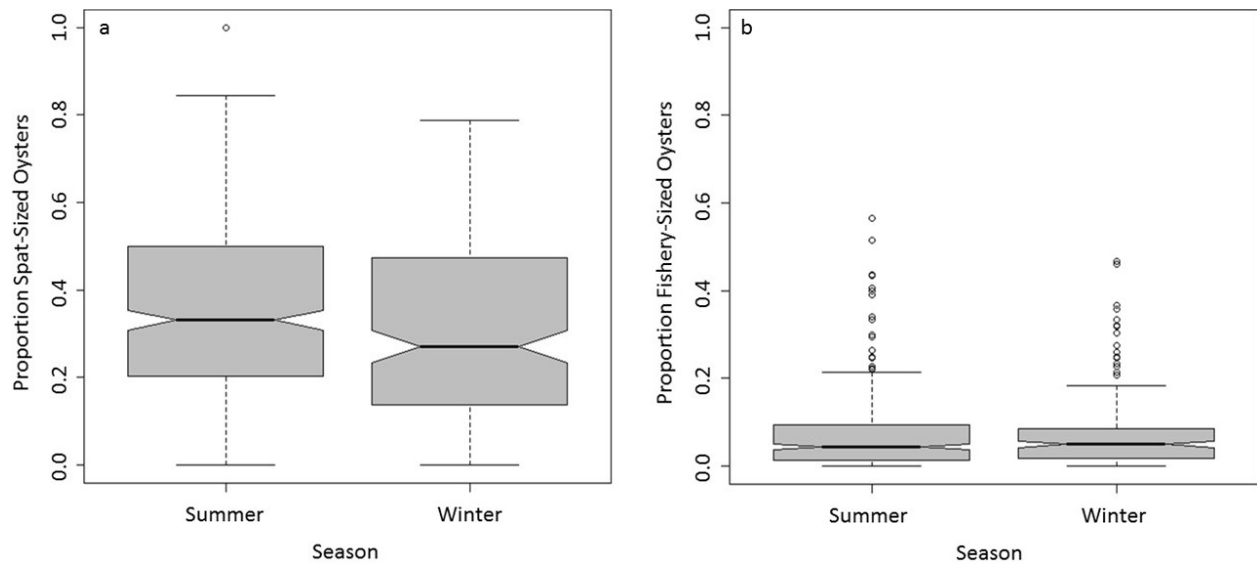
Figure 11. Notched boxplots of proportions of a) spat-sized oysters and b) fishery-sized oysters split by season (for repeated reefs, n = 26). Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile value), circles = potential outliers, black bar = median value.

Figure 12. Oyster size class frequencies by region and season for full data set.
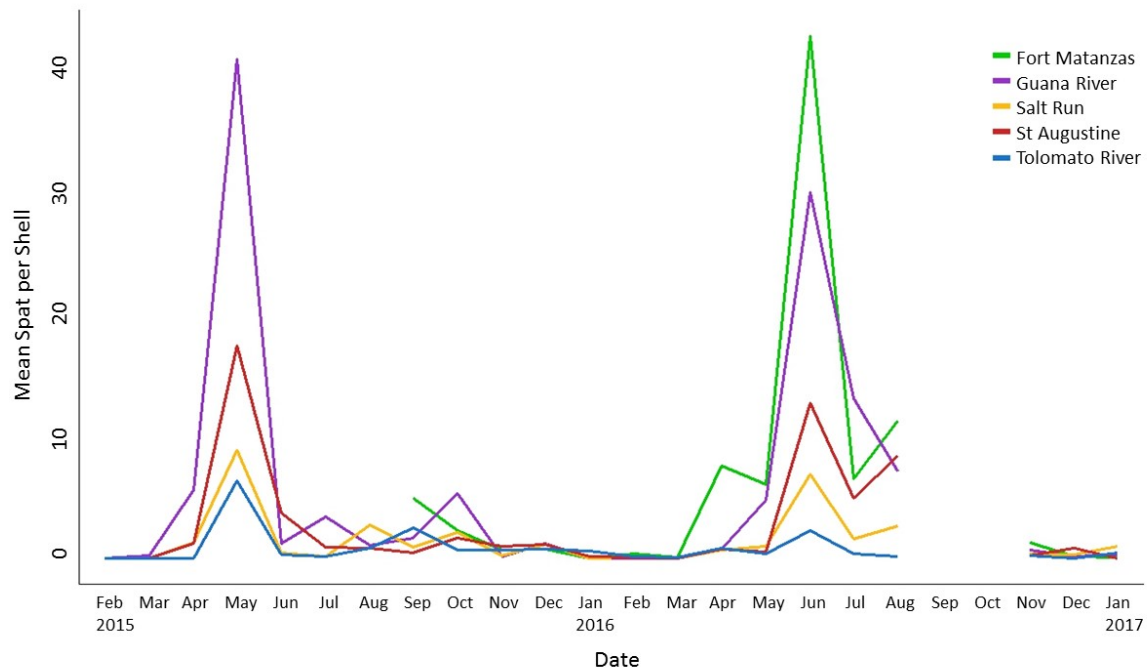
Figure 13. Spat settlement (mean # spat/shell) by region
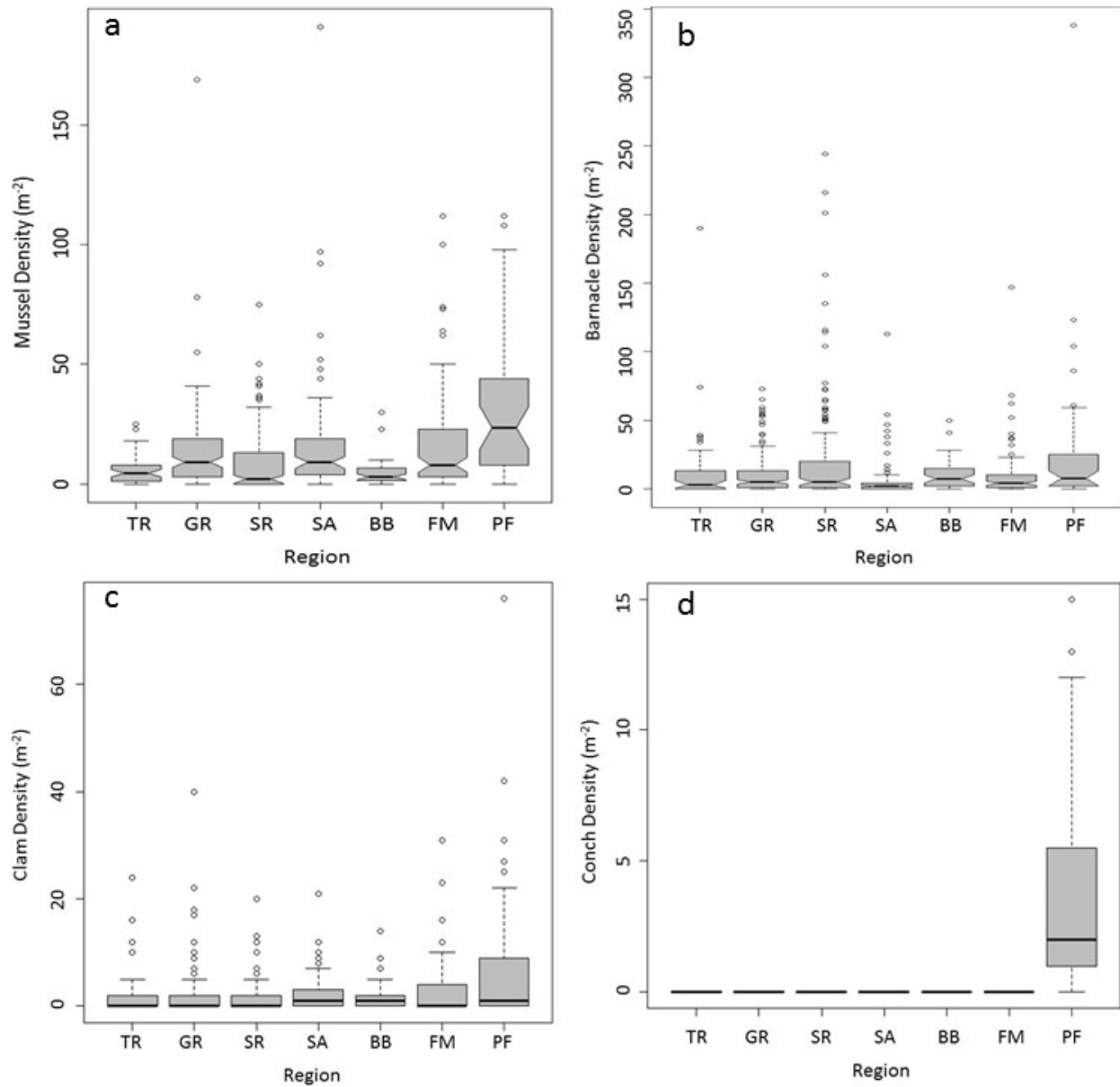
Figure 14. Notched boxplot of a) barnacle density, b) mussel density, and boxplots of c) clam density, and d) conch density all split by region. Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile va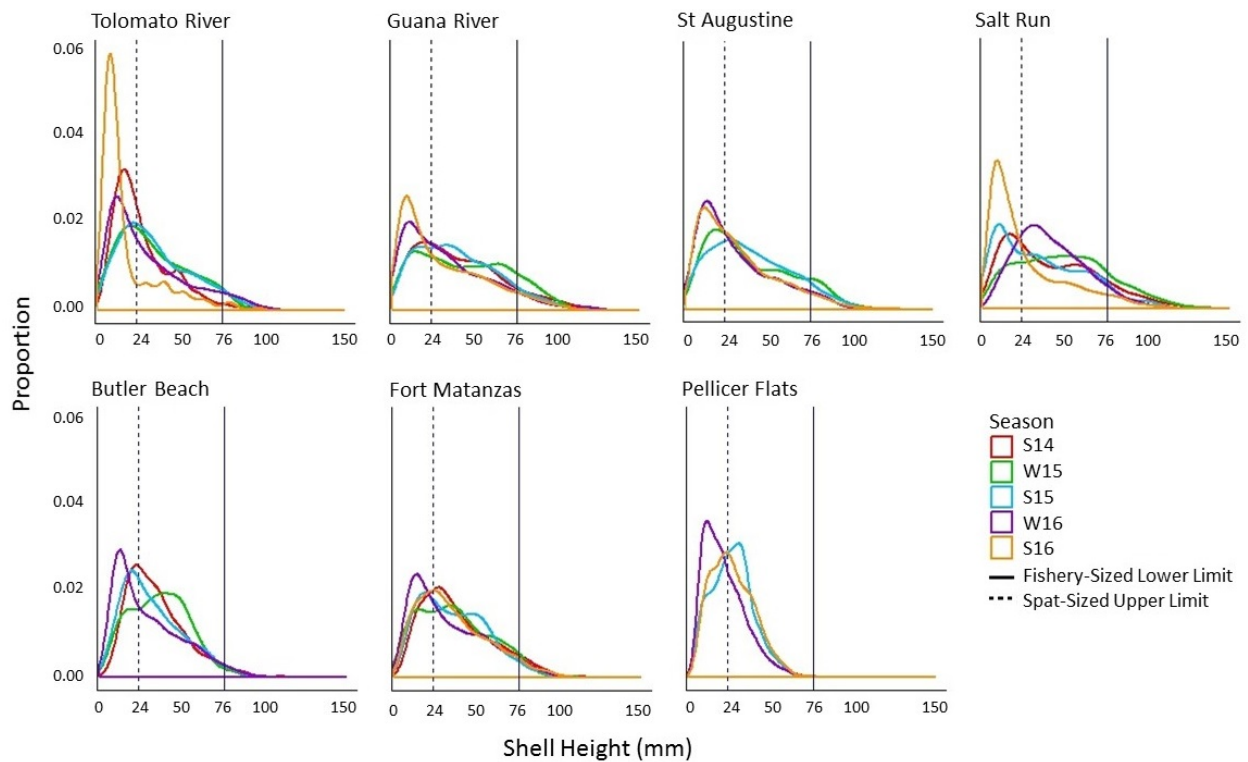lue), circles = potential outliers, black bar = median value, Regions at bottom are TR = Tolomato River, GR = Guana River, SR = Salt Run, SA = St Augustine, BB = Butler Beach, FM = Fort Matanzas, PF = Pellicer Flats.

Figure 15. Notched boxplots of density m^{-2} for a) barnacles, b) mussels, and c) clams by season. Gray box is 25th-75th percentile, whiskers are 1.5x Inter-Quartile Range (IQR = 75th percentile value – 25th percentile value), circles = potential outliers, black bar = median value.
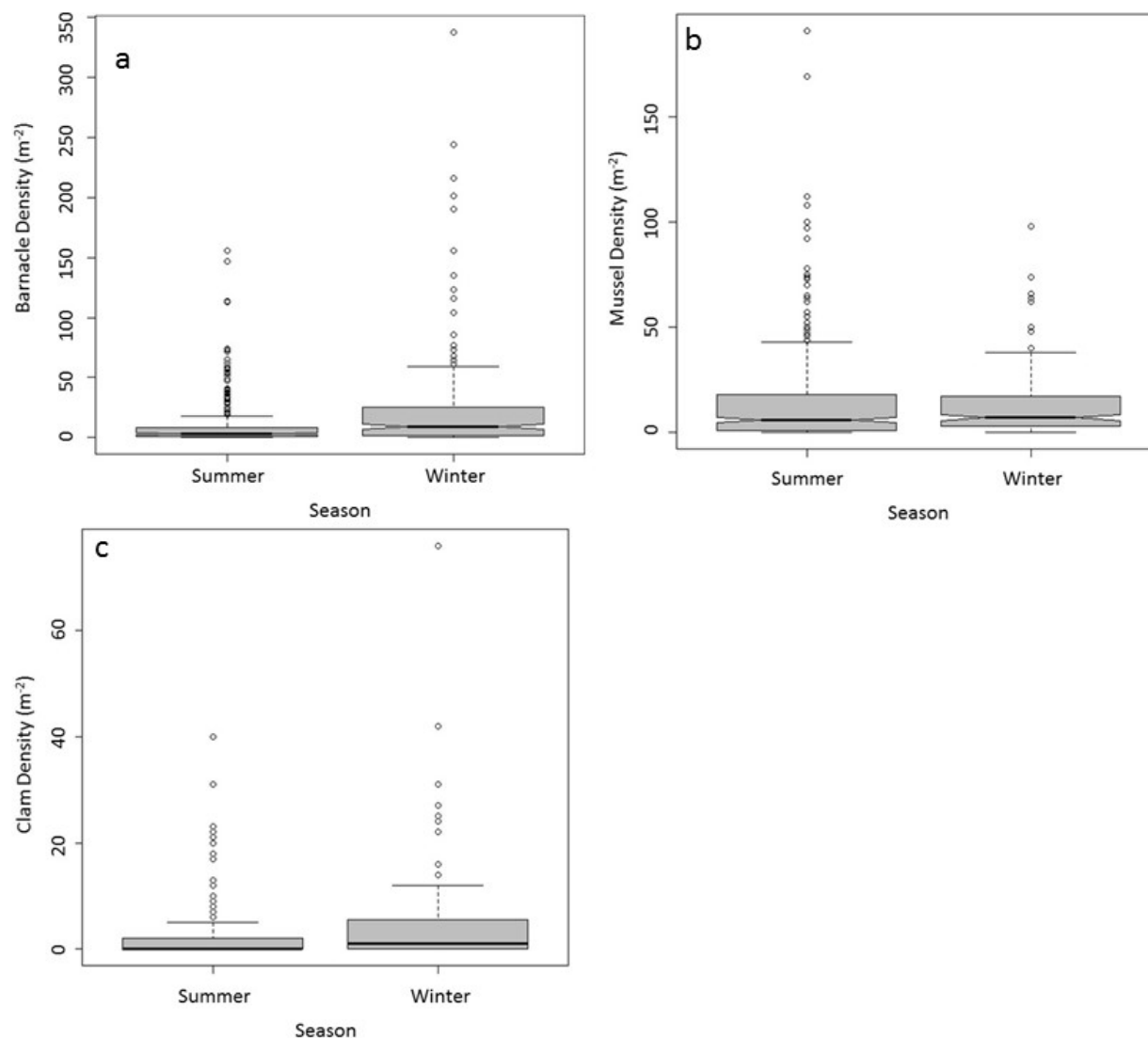
	Reef Height	Reef Slope	Oyster Clusters	% Cover Live	% Cover Dead	% Cover Sediment	Total Oysters	% Fishery-Sized Oysters	% Spat-Sized Oysters	Barnacles	Mussels	Clams	Crown Conch
Reef Height	1	<.0001	0.2998	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	<.0001
Reef Slope	**0.5340**	1	1.0000	0.9591	0.0072	0.2280	1.0000	0.0933	1.0000	1.0000	1.0000	1.0000	1.0000
Oyster Clusters	0.1437	0.1104	1	<.0001	0.1907	0.2583	<.0001	1.0000	0.5153	0.2280	<.0001	0.0005	0.9591
% Cover Live	0.1100	0.1188	**0.5066**	1	0.1249	<.0001	<.0001	0.2583	1.0000	0.0001	<.0001	<.0001	1.0000
% Cover Dead	-0.0505	**-0.2075**	-0.1546	-0.1632	1	<.0001	1.0000	<.0001	<.0001	0.9591	1.0000	0.0103	<.0001
% Cover Sediment	-0.0080	0.1505	-0.1476	**-0.3397**	**-0.8213**	1	<.0001	<.0001	0.0007	1.0000	0.0012	<.0001	<.0001
Total Oysters	0.0871	0.0794	**0.4890**	**0.4612**	0.0729	**-0.3084**	1	0.0005	<.0001	<.0001	<.0001	<.0001	0.0128
% Fishery-Sized Oysters	0.0906	0.1685	0.0365	0.1476	**-0.4519**	**0.3754**	**-0.2421**	1	<.0001	1.0000	1.0000	<.0001	<.0001
% Spat-Sized Oysters	0.0338	-0.0592	0.1326	-0.0001	**0.2784**	**-0.2372**	**0.5553**	**-0.5085**	1	1.0000	<.0001	<.0001	0.1390
Barnacles	0.0370	0.0401	0.1509	**0.2576**	-0.1181	-0.0524	**0.2866**	-0.0252	0.0989	1	1.0000	1.0000	0.1362
Mussels	0.0676	0.0572	**0.3994**	**0.3316**	0.0329	**-0.2304**	**0.6886**	-0.1139	**0.2984**	0.1013	1	<.0001	<.0001
Clams	0.0507	-0.0739	**0.2427**	**0.2764**	**0.2024**	**-0.3558**	**0.5563**	**-0.2862**	**0.5355**	0.0784	**0.5203**	1	0.0425
Crown Conch	**-0.2824**	-0.0895	0.1187	-0.0121	**0.2741**	**-0.3428**	**0.1991**	**-0.3872**	0.1605	0.1613	**0.2727**	0.1813	1
Bold values are significant at α = 0.05													

Table 5. Correlation matrix. Spearman Rank values on bottom diagonal and Holm's p-values on top diagonal.

Location	Mean Oyster Density (m⁻²)	Spat-Sized	Fishery-Sized	Reference
Eastern Shore, Virginia	477-1364		5%	Ross & Luckenbach 2009
Middle Marsh, NC	~1600			Byers et al. 2015
Bird Shoals, NC	371	5.1%	38.3%	Powers et al. 2009
Virginia Creek, NC	~200			Byers et al. 2015
Masonboro Island, NC	~1600			Byers et al. 2015
Lockwoods Folly, NC	~1600			Byers et al. 2015
North Inlet, SC	~1600			Byers et al. 2015
Inlet Creek, Charleston Harbor, SC	861-1646		<10%	Luckenbach et al. 2005
Ace Basin, SC	~8000			Byers et al. 2015
Skidaway Island, GA	~4000			Byers et al. 2015
Sapelo Island, GA	~3000			Byers et al. 2015
Jacksonville, FL	~1600			Byers et al. 2015
St. Augustine, FL	~2000			Byers et al. 2015
Northeast Florida	1520	43.3%	6.8%	Shirley et al. 2016
GTMNERR & St Augustine	1281-2787	34.2%	7.1%	this study
St Augustine & Matanzas River	737			Dix 2009
Suwannee River Estuary	668	61.4%	5.9%	Bergquist et al. 2006
Caloosahatchee Estuary	1440-1620			Volety & Haynes 2012

Table 6. Regional summaries of mean oyster density (m⁻²), percent of new recruits (< 25 mm shell height), and percent of fishery-sized oysters (≥ 76 mm shell height). Data from Byers et al. (2015) were visually estimated from the published graph. Data from Powers et al. (2009) were estimated based on densities reported for size classes.

LITERATURE CITED

Arnold, W. S., M. L. Parker, & S. P. Stephenson. 2008. Oyster monitoring in the northern estuaries. *Final report to the South Florida Water Management District, Grant Number CP040614. FWRI reports F2483-04-F*.

Baggett, L.P., S.P. Powers, R. Brumbaugh, L.D. Coen, B. DeAngelis, J. Greene, B. Hancock & S. Morlock. 2014. *Oyster habitat restoration monitoring and assessment handbook*. Arlington, VA: The Nature Conservancy. 96pp.

Bahr, L.M., & W. P. Lanier. 1981. *The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile* (No. 81/15). US Fish and Wildlife Service.

Baird, D., R. R. Christian, C. H. Peterson & G. A. Johnson. 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. *Ecological Applications* 14:805-822.

Bartol, I. K., R. Mann, & M. Luckenbach. 1999. Growth and mortality of oysters (Crassostrea virginica) on constructed intertidal reefs: effects of tidal height and substrate level. *Journal of Experimental Marine Biology and Ecology* 237(2):157-184.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, A. Carranza, L. D. Coen, C. Crawford, O. Defeo, G. J. Edgar, B. Hancock, M. C. Kay, H. S. Lenihan, M. W. Luckenbach, C. L. Toropova, G. F. Zhang & X. M. Guo. 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61:107-116.

Bergquist, D. C., J. A. Hale, P. Baker & S. M. Baker. 2006. Development of ecosystem indicators for the Suwanee river estuary: oyster reef habitat quality along a salinity gradient. *Estuaries and Coasts* 29:353-360.

Byers, J. E., J. H. Grabowski, M. F. Piehler, A. R. Hughes, H. W. Weiskel, J. C. Malek & D. L. Kimbro. 2015. Geographic variation in intertidal oyster reef properties and the influence of tidal prism. *Limnology and Oceanography* 60:1051-1063.

Cavanaugh K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez & I. C. Feller. 2013. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events and supporting information *PNAS*: www.pnas.org/cgi/doi/10.1073/pnas.1315800111.

Chambers, J. M., W. S. Cleveland, B. Kleiner, B. & P. A. Tukey. 1983. *Graphical methods for data analysis* (Vol. 5, No. 1). Belmont, CA: Wadsworth.

Coen, L. D. & R. Grizzle. 2007. The importance of habitat created by molluscan shellfish to managed species along the Atlantic Coast of the United States. In: J. Thomas & J. Nygard, editors. *The importance of habitat created by molluscan shellfish to managed species along the*

Atlantic Coast of the United States. Washington, D.C.: Atlantic States Marine Fisheries Commission. Commission ASMF habitat management series 8. pp. 16–108.

Coen, L. D., M. W. Luckenbach & D. L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: L. R. Benaka, editor. Fish habitat: essential fish habitat, and rehabilitation. American Fisheries Society, symposium 22. Bethesda, MD: American Fisheries Society. pp. 438–454.

Coen, L. D. & M. W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? *Ecological Engineering* 15:323-343.

Dame, R. F., J. D. Spurrier & T. G. Wolaver. 1989. Carbon, nitrogen and phosphorus processing by an oyster reef. *Marine Ecology Progress Series* 54:249-256.

Dame, R. F. 2011. *Ecology of marine bivalves: an ecosystem approach*. CRC press.

Daskalakis, K. D. 1996. Variability of metal concentrations in oyster tissue and implications to biomonitoring. *Marine Pollution Bulletin* 32:794-801.

Defne, Z., K. A. Haas, & H. M. Fritz. 2009. Wave power potential along the Atlantic coast of the southeastern USA. *Renewable Energy* 34(10):2197-2205.

Dietz, K. 2015. Water quality and oyster sustainability within the Guana Tolomato Mantanzas National Estuarine Research Reserve. Technical Report. Ponte Vedra Beach, Florida: GTMNERR.

Dix, N. G. 2009. How Estuaries Respond to Nutrient Load: the Guana Tolomato Matanzas National Estuarine Research Reserve as a Model Case. National Estuarine Research Reserve Graduate Research Fellowship Final Report. NOAA Award Number: NA06NOS4200054

Dix, N. G. 2010. Nutrient, phytoplankton, and oyster dynamics in a highly flushed subtropical lagoon, northeast Florida. Dissertation. Gainesville, FL: University of Florida.

Dix, N., E. Phlips, & P. Suscy. 2013. Factors controlling phytoplankton biomass in a subtropical coastal lagoon: relative scales of influence. *Estuaries and coasts* 36(5):981-996.

Drexler, M., M. L. Parker, S. P. Geiger, W. S. Arnold & P. Hallock. 2014. Biological assessment of eastern oysters (*Crassostrea virginica*) inhabiting reef, mangrove, seawall, and restoration substrates. *Estuaries and coasts* 37(4): 962-972.

Fertig, B., T. J. B. Carruthers, W. C. Dennison, A. B. Jones, F. Pantus & B. Longstaff. 2009. Oyster and macroalgae bioindicators detect elevated δ15N in Maryland's coastal bays. *Estuaries and Coasts* 32:773-786.

Fodrie, F. J., A. B. Rodriguez, C. J. Baillie, M. C. Brodeur, S. E. Coleman, R. K. Gittman, ... & E. J. Theuerkauf. 2014. Classic paradigms in a novel environment: inserting food web and

productivity lessons from rocky shores and saltmarshes into biogenic reef restoration. *Journal of applied ecology* 51(5):1314-1325.

Ford, S. E. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *Journal of Shellfish Research* 15:45-56.

Galtsoff, P. S. 1964. The American Oyster *Crassostrea virginica* Gmelin. *Fisheries Bulletin* 64:421-425.

Garland, H. G. & D. L. Kimbro. 2015. Drought increases consumer pressure on oyster reefs in Florida, USA. *PloS one* 10(8), e0125095.

Haven, D. S. & R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnology and Oceanography* 11(4):487-498.

Kellogg, M. L., A. R. Smyth, M. W. Luckenbach, R. H. Carmichael, B. L. Brown, J. C. Cornwell, M. F. Piehler, M. S. Owens, D. J. Dalrymple & C. B. Higgins. 2014. Use of oysters to mitigate eutrophication in coastal waters. *Estuarine, Coastal and Shelf Science* 151:156-168.

Kimbrough, K. L., W. E. Johnson, G. G. Lauenstein, J. D. Christensen & D. A. Apeti. 2008. An assessment of two decades of contaminant monitoring in the nation's coastal zone. Silver Spring, MD: NOAA Technical Memorandum NOS NCCOS 74. 105 pp.

Kirby, M. X. 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences USA* 101:13096–13099.

Louisiana Department of Wildlife and Fisheries, Office of Fisheries. 2011. Oyster stock assessment report of the public oyster areas in Louisiana seed grounds and seed reservations. Oyster Data Report Series, No. 17.

Luckenbach, M. W., L. D. Coen, P. G. Ross Jr & J. A. Stephen. 2005. Oyster reef habitat restoration: relationships between oyster abundance and community development bases on two studies in Virginia and South Carolina. *Journal of Coastal Research* 40:64-78.

MacKenzie, C. L. Jr. 2007. Causes underlying the historical decline in eastern oyster (*Crassostrea virginica* Gmelin, 1791) landings. *Journal of Shellfish Research* 26:927-938.

Manley, J., A. Power, & R. Walker. 2009. Effect of submergence depth on the eastern oyster, Crassostrea virginica (Gmelin, 1791), growth, shell morphology, shell characteristics, Perkinsus marinus infection, and mortality in oysters cultured intertidally off-bottom in Georgia. *Occasional Papers of the University of Georgia Marine Extension Service*, 5, 21.

Mann, R., M. Southworth, J. M. Harding & J. A. Wesson. 2009. Population studies of the native eastern oyster, *Crassostrea virginica*, (Gmelin, 1791) in the James River, Virginia, USA. *Journal of Shellfish Research* 28:193-220.

Meyer, D. L., E. C. Townsend & G. W. Thayer. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology* 5:93-99.

Nevins, J. A., J. B. Pollack & G. W. Stunz. 2014. Characterizing nekton use of the largest unfished oyster reef in the United States compared with adjacent estuarine habitats. *Journal of Shellfish Research* 33:227-238.

Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, Crassostrea virginica? In: M. P. Lynch & E. C. Krome, editors. *Understanding the estuary: advances in Chesapeake Bay research*. Gloucester Point, VA: Chesapeake Research Consortium publication 129. pp. 536–546.

Newell, R. I. E., J. C. Cornwell & M. S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. *Limnology and Oceanography* 47:1367-1379.

Newell, R. I. E. & E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793-806.

O'Beirn, F. X., P. B. Heffernan, R. L. Walker & M. L. Jansen. 1996. Young-of-the-year oyster, *Crassostrea virginica*, reproduction in coastal Georgia. *Estuaries* 19:651-658.

Parker, M. L. 2015. Oyster monitoring in the northern estuaries on the Southeast coast of Florida: Final Report (2005-2014). *Florida Fish and Wildlife Research Institute*.

Powers, S. P., C. H. Peterson, J. H. Grabowski & H. S. Lenihan. 2009. Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. *Marine Ecology Progress Series* 389:159–170.

Rodriguez, A. B., F. J. Fodrie, J. T. Ridge, N. L. Lindquist, E. J. Theuerkauf, S. E. Coleman, S. E., ... & M. D. Kenworthy. 2014. Oyster reefs can outpace sea-level rise. *Nature Climate Change* 4(6):493.

Roegner, G. C. & R. Mann, R. 1995. Early recruitment and growth of the American oyster *Crassostrea virginica* (Bivalvia: Ostreidae) with respect to tidal zonation and season. *Marine ecology progress series. Oldendorf* 117(1):91-101.

Ross, P. G. & M. W. Luckenbach. 2009. Population assessment of eastern oysters (*Crassostrea virginica*) in the seaside coastal bays. Coastal Zone Management Program, Virginia Department of Environmental Quality.

Rothschild, B. J., S.J. Ault, P. Goulletquer, & M. Heral. 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Marine Ecology Progress Series* 111:29-39.

Scyphers, S. B., S. P. Powers, K. L. Heck Jr & D. Byron. 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PLoS ONE* 6(8): e22396.

Shirley, M., A. Noel, & N. Dix. 2016. Oyster Condition Assessment Final Project Report. DEP agreement No. CM409. Florida Coastal Management Program.

Stevenson, J. C., L. G. Ward, & M. S. Kearney. 1988. Sediment transport and trapping in marsh systems: implications of tidal flux studies. *Marine Geology* 80(1-2), 37-59.

Stricklin A. G., M. S. Peterson, J. D. Lopez, C. A. May, C. F. Mohrman & M. S. Woodrey. 2009. Do small, patchy, constructed intertidal oyster reefs reduce salt marsh erosion as well as natural reefs? *Gulf and Caribbean Research* 22:21-27.

Tolley, G. & A. K. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *Journal of Shellfish Research* 24:1007-1012.

Volety, A. K., & M. Savarese. 2001. Oysters as indicators of ecosystem health: determining the impacts of watershed alterations and implications for restoration. *Final Report submitted to National life Foundation, South Florida Water Management District (Big Cypress Basin), and Florida Gulf Coast University Foundation*.

Volety, A. K. & L. Haynes. 2012. Oyster monitoring in the Caloosahatchee river and estuary annual report 2012. South Florida Water Management District.

Wang, H., W. Huang, M. A. Harwell, L. Edmiston, E. Johnson, P. Hsieh, ... & X. Liu. 2008. Modeling oyster growth rate by coupling oyster population and hydrodynamic models for Apalachicola Bay, Florida, USA. *ecological modelling* 211(1), 77-89.

Wilbur, A. E., S. E. Ford, J. D. Gauthier & M. Gomez-Chiarri. 2012. Quantitative PCR assay to determine prevalence and intensity of MSX *(Haplosporidium nelsoni)* in North Carolina and Rhode Island oysters *Crassostrea virginica. Diseases of Aquatic Organisms* 102:107-118.

Wilson, C., L. Scotto, J. Scarpa, A. Volety, S. Laramore, & D. Haunert. 2005. Survey of water quality, oyster reproduction and oyster health status in the St. Lucie Estuary. *Journal of Shellfish Research* 24(1), 157-165.

zu Ermgassen, P. S. E., M. D. Spalding, B. Blake, L. D. Coen, B. Dumbauld, S. Geiger, J.H. Grabowski, R. Grizzle, M. Luckenbach, K. McGraw, W. Rodney, J. L. Ruesink, S. P. Powers & R. Brumbaugh. 2012. Historical ecology with real numbers: past and present extent and biomass of an imperiled estuarine habitat. *Proceedings of the Royal Society B* 279: 3393-3400.