Collapsed oyster populations in large Florida estuaries appear resistant to restoration using traditional cultching methods — insights from ongoing efforts in multiple systems

*#Authorship to be determined*

*Data contributions: Jonathan Brucker and Matt Davis*

*Analytical and writing: Jennifer Moore, Fred Johnson, Ed Camp, Steve Geiger, Jonathan Brucker, Ryan Gandy, Tara Miller-Stewart, Andrew Shantz*

*Request review from J Harper*

Abstract

Depressed oyster populations in the northern Gulf of Mexico have been the target of numerous post-*Deepwater Horizon* restoration projects, which have primarily focused on replacing oyster cultch (substrate) to promote spat settlement and increase recruitment. This study assessed oyster populations at the sites of six such projects, which used different cultch types and densities and were carried out in 2015–2021 in three estuaries on the Florida panhandle coast (Pensacola, St. Andrew, and Apalachicola bays). It also explored the durability of the new cultch and the potential effect of freshwater discharge on oyster spat counts. It found that oyster populations did not achieve a persistent increase in counts (controlling for effort) following the restoration efforts, regardless of cultch type or density used in the restoration. The biomass of cultch introduced by the projects also declined over time at rates from 45% to 60% from first to the last period. In the absence of thorough, consistent, and effective experimental project design it is impossible with the available data to say with certainty what is hindering restoration success. However, restoration design deficiencies including uncertainty in the materials used and very small vertical relief of restored reefs post construction are likely contributors to lack of project success. These deficiencies could be addressed by developing a staircase-style restoration program, where replicate treatments (different material types, vertical relief, or both) are staggered in time, in an adaptive management framework that includes explicit high-resolution monitoring of other possible factors driving oyster population recovery across different estuaries.

Introduction

Eastern oyster populations in the northern Gulf of Mexico are depressed from historical levels for poorly understood reasons. Since 2010, the states of Florida, Alabama, Mississippi, Louisiana, and Texas have declared state- or federal-level oyster fishery disasters, with several of these states implementing fishery closures in response to the depressed status of oyster stocks (Mobile Bay in Alabama, Apalachicola Bay in Florida, Galveston Bay in Texas). To date, only one of these stocks (Mobile Bay) has reopened to harvest. The potential reasons for regional oyster declines include prolonged drought, extreme rain events, freshwater releases from water management structures, environmental degradation, overharvesting, harvest management, and insufficient cultching (Petes et al. 2012; Pine et al. 2015; Gledhill et al. 2020; Du et al. 2021; Coastal Alabama Comprehensive Oyster Restoration Plan Marine Resources Division and the National Oceanic and Atmospheric Administration Published by the Deepwater Horizon Alabama Trustee Implementation Group 2021). In 2014, Florida filed suit against Georgia in the US Supreme Court over water management in the Apalachicola River (<https://www.ca10.uscourts.gov/special-master-docket/001>), arguing that excessive water use in the Georgia portion of the Apalachicola-Chattahoochee-Flint river basin contributed to the 2012 oyster population collapse in Apalachicola Bay (Kelly 2019).

Additionally, the sinking of the *Deepwater Horizon* and subsequent oil spill damaged oyster populations in the Gulf of Mexico (Deepwater Horizon Natural Resources Damage Assessment Trustees 2016). *Deepwater Horizon* settlements, resulting from legal proceedings and regulatory fines, have created substantial funding opportunities (more than US$199 million) for oyster restoration in the Gulf. The dollars allocated for restoration exceeded the annual value of oyster landings (Pine et al. 2022), and the ecosystem services of oysters may far exceed their fishery value, estimated between $5,500 and 99,000 per year per hectare (Grabowski 2012). .

Many proposed, ongoing, and historical oyster restoration efforts focus on protecting or adding substrate to replace oyster cultch, a matrix of living and dead material, that was removed or displaced by fishing practices, to create sites for oyster spat settlement (Swift 1897; Swift 1898; Lenihan and Peterson 1998; Pine et al. 2015; Lenihan and Micheli 2000; Howie and Bishop 2021). These restoration efforts attempt to shift oyster reefs from an observed low, but resilient, state to a more desired productive state (Pine et al. 2022). This desired state can vary by location, type of oyster bar (intertidal vs. subtidal), and management goals, but all restoration efforts are expected to provide and promote ecosystem services and create opportunities for oyster harvest through fishery recovery.

Despite the importance of cultch for supporting oyster settlement (Frederick et al. 2016), it remains unknown whether restoration-sourced materials function the same as biologically natural cultch (Graham et al. 2017; Goelz et al. 2020). Many of the current restoration programs are long term (10 years), and information on what has and has not worked in them is lacking. Such information is critical for informing restoration and management in similar systems (Moore and Pine 2021; Pine et al. 2022). To address knowledge gaps and improve restoration performance, the US National Academy of Sciences (NAS) has identified adaptive management as the guiding framework to use within these large restoration programs—to increase their likelihood of success and facilitate learning, and to inform allocation of time and funds for corrective changes during the project lifespan if necessary (NAS 2017, 2022; Pine et al. 2022).

Florida has received or will receive substantial funding from the *Deepwater Horizon* settlements and penalties, including planned payments of at least $680 million in damages, $392 million in civil penalties, and $356 million in criminal penalties (University of New Hampshire and NOAA Coastal Response Research Center 2017). Some of these funds (with more planned) have been directed to oyster reef restoration projects with multiple objectives including ecosystem services and restoration of fisheries.

We assessed ongoing and recently completed oyster restoration efforts in three large estuaries in the Florida panhandle (Pensacola, St. Andrew, and Apalachicola bays) to assess the following questions:

1. How do temporal trends in oyster counts vary among the three depressed sites?
2. In a focal site (Apalachicola Bay), how do oyster temporal trends vary among separate restoration projects?
3. Are oyster spat counts in Apalachicola Bay associated with freshwater discharge, cultch material, or cultch density?
4. How well do different types and densities of restoration-sourced cultch persist following deployment?

We found that these large restoration programs are not having the desired outcome of increasing live oyster populations. This may be because these systems are trapped in a resilient but low-oyster-production state (Johnson et al. 2022) that is resistant to restoration, or that the restoration programs as designed were not effective, or both. Our work suggests substantial uncertainty persists in how to successfully restore oyster populations at large scales in Florida. Addressing these uncertainties will require strong leadership from agency, academic, and industry leaders to conduct restoration projects in frameworks that allow for better learning to increase the likelihood of success.

# Study sites

We assessed oyster population trends in three estuaries in the Florida panhandle that have ongoing or recently completed oyster restoration projects: Pensacola Bay, St. Andrew Bay, and Apalachicola Bay (Figure 1). Pensacola Bay in northwest Florida (Santa Rosa and Escambia counties) is the fourth largest estuary in Florida, with a surface area of approximately 50,990 ha. Reported oyster landings, trips, and catch-per-unit-effort (CPUE) for Pensacola Bay have declined since the current mandatory trip-ticket program was fully implemented in 1986 (Figure 2). The East Bay arm of St. Andrew Bay, near Panama City (Okaloosa and Walton counties), has a total surface area of approximately 176,847 ha (Comp and Seaman 1988). Oyster landings and trips for East Bay are not available, but they have declined in surrounding counties, and harvest in recent years has been near zero. Apalachicola Bay is a 348,029 ha estuary in Franklin County that supported the largest oyster fishery in Florida before collapsing in fall 2012 (Pine et al. 2015). Apalachicola Bay was closed to commercial harvest from December 2020 through December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

## Management actions

Cultch material was deposited in each bay in phases by state management agencies as part of multiple projects led by the state of Florida with funds from the *Deepwater Horizon* oil spill settlement. Reef construction methods across projects were similar and designed to minimize costs and maximize the area over which materials were deployed. Reef materials were either quarried shell, crushed granite, or a Kentucky limestone of graded size (often #4, 25–64 mm) transported on barges via inland and coastal waterway and then “planted” at specific locations (Table 1).

Site selection was based on local knowledge of historical or extant reef locations. Most of the work was carried out from 2015 to 2017, with one project taking place in summer 2021. Two state agencies, FWC and the Florida Department of Environmental Protection (FDEP), managed the projects under the sponsorship of the Natural Resource Damage Assessment (NRDA), and Gulf Environmental Benefit Fund (GEBF) administered by National Fish and Wildlife Foundation (NFWF). One project each took place in Pensacola and St. Andrew bays, and four in Apalachicola Bay. The work carried out under these projects is summarized in Table 1. Across all projects, the area and density (thickness or depth) of cultch material deployed varied from the planned application due to construction challenges and storm events that occurred during the studies.

As a simple description of watershed-scale discharge characteristics in recent decades, we summarized river discharge for primary rivers entering Pensacola and Apalachicola bays as a proxy for salinity and nutrient inputs before, during, and after restoration efforts by plotting the percent deviation in mean river discharge (cubic feet per second [CFS] by convention) from the mean period of instrument records by month and year. St. Andrew Bay has no significant freshwater inputs (Crowe et al. 2008). We began this time series in 2005, 10 years prior to the start of the restoration projects covered by this study, to capture antecedent river discharge conditions. Pensacola Bay has three tributaries (Escambia, Blackwater, and Yellow rivers), and we used data from USGS gauge 02375500 on the Escambia River because this is the largest (by discharge). For Apalachicola Bay, we summarized river discharge information from USGS gauge 02358000 on the Apalachicola River at Chattahoochee.

# Methods

## Field collections

Similar methods were followed across projects to count live oysters and mass of cultch material, based on techniques used in Florida since the 1980s (Florida Fish and Wildlife Research Institute 2021). Divers randomly placed ¼ m2 (0.5 m on each side) quadrats at selected sites, removed all oysters and cultch material to wrist depth, and placed the material in bags. Once bags were returned to the vessel, they were either processed on location or returned to the lab, where counts of live and dead oysters, measurements of shell height, weight of cultch material, and study-specific metrics (e.g., identification of other benthic species) were recorded.

## Fisheries-dependent data

For each bay, using publicly available FWC (2022) data, the annual landings (meat pounds) and trips were summed for each county bordering the bay, and CPUE was calculated as landings/trips.

## Data analysis

Methods for analyzing oyster count data followed Moore et al. (2020). We conducted two separate analyses. The first assessed how oyster counts responded to restoration efforts (i.e., how they changed following restoration) in all three bays (Pensacola, St. Andrew, and Apalachicola). The second analysis explored additional questions—whether oyster spat counts were influenced by freshwater discharge and how they differed over time, cultch material, and cultch density; it focused on four projects in a single bay, Apalachicola (Table 1).

The dependent variables in both analyses were the number of spat, seed, or legal-size oysters. The independent variables were as follows.

* + Period, a continuous variable considered in both analyses, combined sampling months into common blocks of time—winters (October–March), represented by even numbers, and summers (April–September), represented by odd numbers.
  + Bay (Pensacola, St. Andrew, or Apalachicola) was included as a categorical variable in the first analysis, comparing restoration responses by bay.
  + Type and density of cultch material, considered only in the second analysis (which focused on Apalachicola Bay), were represented as a single categorical variable by the name of the project, as each of the four Apalachicola Bay projects used a different cultch material, density, and start time.
  + River discharge, measured as the number of recent days in which discharge fell below certain specified levels was also considered in the second study. This is discussed in more detail below.

For both analyses, we used site (a named oyster reef) as a random effect to account for correlation among quadrat samples at each site.

The two analyses followed these general steps:

1. Counts of live oysters in each bay and for each restoration site and period (a common time factor) were summed into three size classes (the dependent variables): spat (<26 mm shell height), seed (larger than spat but too small to harvest legally, 26–75 mm shell height), and legal to harvest (>75 mm shell height). Separate analyses were completed for each size class. For the restoration projects NRDA 4044 and GEBF 5007, counts per size class were totaled in the field. For projects NFWF-1 and NFWF-2021, count totals (all sizes combined) were converted to counts per size class by calculating the proportion of oysters within each size class from concurrent oyster shell-height samples and multiplying the totals by these proportions. The results were then rounded to convert the numbers of oysters per size class to integers to match the NRDA 4044 and GEBF 5007 data.
2. The count data distribution was assessed by examining the ratio between the count mean and variance for each study site.
3. Generalized linear models (GLMs; Bolker et al. 2009) with a negative binomial distribution were used to assess how oyster counts in all three size classes varied over different independent variables, using the R package glmmTMB (Brooks et al. 2017).
4. We assumed that the total oyster counts per site would be related to the number of quadrats collected. We included the number of quadrats as an effort offset (log link function; Zuur et al. 2009; Zuur et al. 2013). Based on this, we changed the model from modeling counts to modeling a rate measured as count/quadrat. Because the quadrats were the same size for each study site, the total area sampled in each period only changed as a function of the number of quadrats. Using counts and accounting for effort, as opposed to converting the counts to CPUE based on area sampled, has two main advantages. First, it maintains the response as an integer, allowing the use of a negative binomial distribution (appropriate for oyster count data; Moore et al. 2020); and second, fitted values and confidence intervals do not contain negative values (Zuur et al. 2009).
5. The model fit to each data set was assessed visually by comparing data and a predicted line fitted to these data with 95% confidence intervals.
6. Comparisons were made between models with different combinations of independent variables using the Akaike information criterion (AIC), where the lowest AIC value represents the best fit of the models tested (Burnham and Anderson 2002).
7. Models were fit to data using the glmmTMB package (Brooks et al. 2017), and predicted values (marginal means) were made from the best fit model using the ggeffects package (Lüdecke 2018) in R (R Core Team 2021).

The first analysis looked broadly at oyster population responses to restoration in three bays (Apalachicola, Pensacola, and St. Andrew.) The dependent variables were the number of oysters in the spat, seed, and legal-size categories. The independent variables (main effects) were period (continuous) or Bay (categorical). We fit five models to the data: Model 1 was an intercept only model, Models 2, 3, and 4 included Bay, Period, or both Bay and Period as main effects. Model 5 included the interaction between Period and Bay. The relative fit of these models was then compared by AIC and models were ranked from lowest (best fitting) to highest based on AIC score. If two models were within two AIC units of each other, a likelihood ratio test was used to assess whether these two models differed significantly. For the best fitting model autocorrelation in the residuals was assessed by using the DHARMa package (Hartig 2022) in R by simulating new response data from the specified model and then using qq plots to check for deviations from the expected distribution graphically, a KS test to test whether observed and expected distributions differed, and a Durbin-Watson test to check for temporal autocorrelation. Significance of each test assumed a p<0.05 level. The second analysis considered a more complex set of factors and focused on Apalachicola Bay, the only bay in the study with data available from multiple projects in a single ecosystem. This analysis assessed the independent variables of cultch material and density (which varied by project) and freshwater discharge (which varied over time). As in the first analysis, the dependent variables were the number of oysters in the spat, seed, and legal-size categories. The independent variables were period, project (as a proxy for cultch type and density), and river discharge.

We explored how the different cultch materials and densities used persisted over time. We summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, site, and period. Total cultch weights for Apalachicola Bay were made integers by rounding to the nearest whole kilogram. Data were summarized by project, and calculations of mean and variance by project suggested the data were over-dispersed (variance > mean). We then fit similar GLMs assuming a negative binomial distribution for oyster count data to the observed cultch biomass. To create a comparative framework across substrates, we predicted the amount of cultch per ¼ m2 in period 14, the last monitoring period.

River discharge was measured as the number of days in a given period or the prior period (as a measure of antecedent discharge) when the Apalachicola River discharge was below 12,000 or below 6,000 CFS measured at Jim Woodruff gage (USGS 02358000). The 12,000 CFS reference point is important because the adjacent floodplain becomes inundated at discharge near this level (Light et al. 1998; Fisch and Pine 2016). The exact point of inundation may have changed over time due to riverbed degradation (S. Leitman, personal communication). Regardless, we used this reference point as an indicator of low freshwater inputs. A discharge level of <6,000 CFS indicates extreme low river discharge, because it approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam. Data and all code used for the analyses are available from the following Git repository: <https://github.com/billpine/AB_DEP.git>.

# Results

## River discharge patterns

Apalachicola River discharge deviated significantly (50–100% below the average for the period of instrument records) for three or more months in 2006, 2007, and 2008, with extreme drought in 2011 (9 of 12 months), 2012 (12 of 12 months), 2016 (6 of 12 months), and 2017 (4 of 12 months). Escambia River discharge patterns were generally similar, reflecting the regional effects of drought (Figure 9). Regional river discharge patterns for 2019–2021 were generally average to above average for most months.

## Trends in fisheries-dependent data

Trends in FWC fisheries-dependent data since 1986 show the Apalachicola Bay commercial fishery was larger (trips and landings) than those of Pensacola and St. Andrew bays combined. Apalachicola trips and landings increased sharply during the early 2000s, peaking just before the fishery collapsed in 2012 (Figure 2). Apalachicola Bay was closed to oyster harvest by FWC in December 2020, with a reopening scheduled for December 2025. Pensacola, St. Andrew, and Apalachicola bays show similar trends of increasing trips and landings in the mid-1980s and again in 2005–2010. Since 2010–2012, trips and landings have declined in all three bays, with declining (Apalachicola) or minimal (Pensacola and St. Andrew) levels of commercial fishing activity since 2015, when the regional oyster restoration programs assessed in this analysis began.

## Trends in oyster counts following restoration

Apalachicola Bay restoration efforts took place across four different projects in periods 2, 6, and 13 and oysters were sampled in periods 2-10, and 12-15. Pensacola Bay restoration took place in Period 2 and sampling was conducted in periods 5-7, 10, and 15. St. Andrew restoration also took place in Period 2 and sampling took place in period 5, 7, and 10.

Observed patterns in oyster spat CPUE for Apalachicola Bay show a decline in oyster spat from about 300 per quadrat in Period 2 to near zero in Period 10 across all locations (mat plot of sites, seed\_study2). No sampling was conducted in Period 11. Beginning in Period 13 observed oyster spat per quadrat ranged from near 0 to more than 750 depending on the location within Apalachicola Bay. A similar pattern was observed in Period 14 with spat per quadrat again ranging from near zero to more than 1000 per quadrat. This was not observed in Period 15 as spat per quadrat declined to less than 125 per quadrat across all locations. In Pensacola Bay oyster spat per quadrat were less than 50 spat per quadrat in all time periods sampling took place (Periods 5-7, 10) declining to near zero in Period 15. St. Andrews Bay observed oyster spat per quadrat of between 0 and about 125 in Periods 5 and 7 and for most sites in Period 10, but one site in Period 10 was observed to have more than 500 spat per quadrat (Figure x mat plot).

From the GLM model, the dispersion parameter from the negative binomial distribution (“nbinom2” family formulation) was <1 for all models, suggesting extreme over-dispersion. The best fitting model (lowest AIC value, highest AIC weight) was the Bay \* Period model (Table 2). No autocorrelation in residuals was detected (K-S test p= 0.66; D-W test p = 0.08). The significant interaction term suggests the temporal patterns in oyster counts are unique within each Bay. For the bay \* period model, Apalachicola Bay live spat counts per quadrat declined (beta = −0.06, SE =0.05) but this trend was not significant (p = 0.18). Pensacola and St. Andrew bays show different trends in oyster spat counts and uncertainty in beta estimates was greater than Apalachicola (Pensacola Bay, beta = -0.41, SE beta = 0.11, p = 0.001; St. Andrew Bay, beta = 0.21, SE beta = 0.18, p = 0.13). The small beta value suggests a median change of less than one oyster spat per quadrat for each period. We predicted mean (marginal mean) live oyster spat counts (95% CI) for the last sampling period (15) for a single ¼ m2 quadrat for comparison between studies. These predicted values were Apalachicola = 12.98 (5.77–29.18, 95% CI), Pensacola = 0.60 (0.15–2.39, 95% CI), and St. Andrew = 220.99 (13.03–3,747.87, 95% CI).

Fitting the same bay \* period model to counts of seed or legal-sized oysters revealed a similar pattern as seen in oyster spat. The observed pattern in counts of seed oysters in Apalachicola Bay shows a decline in counts beginning in period 2 with increases at some sites near the end of the time series in period 15. Pensacola Bay seed oyster counts were low and erratic and the lowest observed counts were at the end of the time series in Period 15. St. Andrew Bay seed and legal oyster counts were also low.

## Apalachicola Bay oyster spat response to restoration

Observed counts of oyster spat in Apalachicola Bay ranged from 0 to more than 1,000 per ¼ m2 depending on restoration project, site and period (Figures 4, 7-9). We compared the simplest model with no main effects to a model that included Period as a main effect. These models were not seperable from an AIC (delta AIC = 0.8) or likelihood-ratio test (p=0.10). However, visual assessments of oyster spat CPUE by Period and Project suggest different patterns in oyster spat over time by Project (Figure 7). We then fit five additional models (Table 3) including main effects of Period, Project, Period + Project, Period + Dry days, and Period + lag(Dry days) and the interactive term of Project\*Period.

The best fitting negative binomial GLM model with site as a random effect and log of the number of quadrats as an offset to control for sampling effort included project \* period terms (Table 3). The statistical significance of period varied by project. Period was not significant for project GEBF-5007 (beta = -0.10, SE = 0.09, p = 0.27), NFWF-2021 (beta = -1.01, SE = 0.66, p = 0.1), NRDA-4044 (beta = -0.03, SE = 0.1, p = 0.07) but was for NFWF-1 (beta = -0.61, SE = 0.1, p = 0.01). Beta values across all four studies in Apalachicola Bay, and regardless of cultch material or cultch density, counts of oyster spat declined over time following restoration. The predicted median number of oyster spat per ¼ m2 transect in period 14 was 7.1 (4.8–10.6), much lower than in period 1 (102.2, 58.6–178.3; Figure 6).

Including the number of days river discharge was below 12,000 CFS in our model did not improve model fit (delta AIC 59; Table 3). This model does estimate both period (beta = −0.21, SE = 0.04, p < 0.001) and the low-days term (beta = −0.006, SE = 0.003, p = 0.07) being statistically significant in the model; for each additional day discharge was below 12,000 CFS, the median number of oyster spat declined by about one per ¼ m2 quadrat. Similar results were not seen for a model that included a one-period lag on the number of days discharge was below 12,000 CFS, suggesting that the number of low days in the prior period did not influence the number of spat in the current period (p = 0.27). Modifying the river discharge threshold to 6,000 CFS resulted in a nonsignificant river discharge term (p = 0.21).

Comparisons of the performance of individual projects as restoration actions designed to increase spat production are difficult because of variation in the timing of the start of monitoring for each project. For example, one project did not start monitoring oyster populations until nearly two years after construction. Other projects started monitoring the same year. This matters if the response of oyster spat numbers to cultch addition is different immediately after the restoration action than it is in the following years. However, the goal of the restoration is to enable colonization and persistence of multiple cohorts of oysters (all size classes) and accretion of cultch material over multiple years. Therefore, if the restoration is successful, the oyster count response should persist over multiple years. This is why we did not address the age of the restored reef in our analyses.

To create a comparative framework across studies with different materials and starting points, we predicted the mean number of oyster spat per ¼ m2 in period 14, the last monitoring period in Apalachicola Bay. In this comparison, three projects (NFWF-1, NRDA 4044, and NRDA 5007) completed construction three to five years before the last period of data, and one (project FWC-2021) less than two years before. If the materials, amount, or time since construction was completed significantly influenced oyster reef restoration performance, the predicted values for each project in the common period should differ.

For the NFWF-1 project (quarried shell cultch), we predicted in period 14 a mean number of live oyster spat of about 0.82 (0.11–6.22, 95% CI) per ¼ m2 quadrat. The NRDA 4044 project also used quarried shell cultch, and the mean predicted number of live spat in period 14 was higher at about 4.5 (2.3–9.1, 95% CI). The predicted mean number of live oyster spat per ¼ m2 quadrat for the rock cultch projects varied. For project GEBF 5007 the mean predicted live oyster spat count per ¼ m2 quadrat was about 18.3 (8.6–39.0, 95% CI), and for project NFWF-2021 it was 15.8 (8.9–28.3, 95% CI). In project NFWF-1, a shell cultch project, live oyster spat counts immediately after restoration were more than 100× greater those in any other project (Figure 5). These high initial spat counts did not result in higher counts in legal-size oysters in subsequent periods, however, nor were these high spat counts observed again.

## Persistence of cultch material in Apalachicola Bay

From an AIC perspective, models that included period + substrate or that examined the period \* substrate interaction (with the log of the number of transects as an offset to control for effort) were not distinguishable (delta AIC between top models = 1.5; Table 2). From a management perspective, the interaction term is of interest to help understand how the biomass of either rock or shell changes over time. For rock substrate, the change in biomass over time was significant (beta = −0.08, SE = 0.03, p = 0.01), but the change was not significant for shell (beta = −0.05, SE = 0.04, p = 0.5).

However, more important than the statistical significance is whether the material persisted. The slope is negative for both substrates, indicating declines over time. The predicted biomass of rock per ¼ m2 quadrat changed over time (Figure 7) from about 5.07 kg per ¼ m2 quadrat (2.5–10.2, 95% CI) in period 2 to about 2.0 kg per ¼ m2 quadrat (1.4–2.9, 95% CI). The shell biomass changed from about 1.7 kg per ¼ m2 quadrat (1.1–2.7, 95% CI) to about 0.93 (0.6–1.5, 95% CI). Because the shell is less dense than rock, the differences in biomass per quadrat are not surprising. These results suggest a biomass decline of about 60% for the shell material and about 45% for the rock material by the end of period 14.

These are measures of mass, not surface area, and the extent of oyster spat settlement depends on the surface area. However, if we assume a loss in area proportional to the loss in mass, then shell degraded faster than rock material. The relationship between cultch area, persistence, and settlement suitability are all areas of future work with important implications for restoration efforts.

Graphical assessment of the mass of cultch material and the number of live oyster spat in Apalachicola Bay

Finally, we assessed the relationships between cultch mass and the number of live oyster spat from each quadrat. We graphically examined the relationship between the weight of cultch and the number of spat per quadrat across projects in Apalachicola Bay and found no clear pattern (Figure 8). This relationship is important because it suggests that the number of live spat observed can vary widely for a given biomass of cultch, or at least across the range in cultch biomass observed in Apalachicola. The relationships between the biomass of cultch that persists on reefs, and how this relates to the biomass of cultch when oyster populations were higher and supported a commercial fishery, are unknown.

# Discussion

There are two key takeaways from this analysis.

1. Oyster populations in Pensacola, St. Andrew, and Apalachicola bays do not appear to have responded to restoration efforts designed to promote spat settlement and accelerate population recovery. This lack of response has occurred in bays within different watersheds and projects using different restoration materials. This suggests there may be fundamental flaws in the design of oyster restoration projects, ecosystem changes that limit oyster population response, or both.
2. The lack of oyster population response has occurred at a time when river discharges ranged from moderate drought to normal for the instrument period of recorded river discharge. This suggests that salinity, and other river-related ecosystem drivers such as nutrients, have also been near normal. River discharge is considered a significant driver of salinity in Florida panhandle estuaries. Salinity in Apalachicola Bay was identified as a driver of oyster survival in Florida’s 2014 lawsuit against Georgia (Florida v Georgia , No 142 Original, 2014), but observed oyster population responses to variation in freshwater discharge and resulting salinity in the bay are variable (Buzan et al. 2009; Fisch and Pine 2015; Gledhill et al. 2020; Moore et al. 2020). This lack of response has also happened while commercial fisheries have been closed (Apalachicola Bay) or have had extremely low landings (Pensacola and St. Andrew bays).

Based on these empirical results, and on previous modeling efforts for Apalachicola Bay oysters (Pine et al. 2015) and oyster populations in general (Johnson et al. 2022), we are concerned that the Pensacola, St. Andrew, and Apalachicola bay oyster populations are degraded to a point that no restoration or management action may be effective in restoring them. Pine et al. (2015) highlighted the risk of a catastrophic and persistent collapse in the Apalachicola oyster fishery if oyster recruitment levels remained below the average reported in the independent fisheries monitoring data (1990–2013) used in their analysis. Johnson et al. (2022) further demonstrated the risk of a transition to a stable, resilient, low population state for oysters and the difficulty in reversing this to a more desired state in a generalized oyster population model.

The lack of results until now, possible reasons for it, and potential next steps are discussed in more detail below.

## Disappointing restoration results

Adaptive management as part of ecosystem restoration requires ongoing exploration of data to assess whether restoration efforts are effective (or at least trending toward a desired state) and then adapting accordingly. We assessed completed and ongoing oyster restoration efforts in three bays with depressed oyster stocks. Our results suggest that restoration and management efforts in Pensacola, St. Andrew, and Apalachicola bays have not had the intended response of shifting oyster populations from a resilient, low-abundance state to a more desired, high-abundance state. This conclusion is supported by data from different watersheds with restoration efforts using similar materials, construction designs, and monitoring programs.

Restoration efforts in all three bays were guided by previous actions in Apalachicola Bay, where irregular cultching has been part of oyster management efforts since at least 1949 (Whitfield and Beaumariage 1977). Hurricane Elena in 1985 reduced oyster populations in Apalachicola Bay by as much as 95% (Berrigan 1988, 1990; Livingston 2015). However, a rapid population recovery was observed (Berrigan 1988, 1990), for reasons that may or may not be solely related to restoration (Fisch and Pine 2016). The observed changes both in the physical (Edmiston et al. 2008) and biological (Berrigan 1988; Edmiston et al. 2008; Livingston 2015) aspects of Apalachicola Bay post – Hurricane Elena led to intensive oyster management and restoration efforts (Berrigan 1990).

Berrigan (1990) noted that 156 ha of oyster reef received 472 m3 of *Rangia* clamshell per ha as part of the intensive restoration. Livingston et al. (1999) described a major wild oyster spat recruitment event in the fall of 1985 on remaining oyster reefs in Apalachicola Bay. Within 18 months, restored oyster bars (monitored as part of restoration; Berrigan 1990) supported 587 oysters/m2. Apalachicola Bay met oyster population benchmarks to support harvest (Berrigan 1990), leading to the reopening of the oyster fishery with a new management system that included on-water check stations and excise taxes to support monitoring. The state of Florida recovered the costs of these restoration and monitoring efforts within a few years (Berrigan 1990), and this management system was later dropped (Pine et al. 2015). If a previous restoration effort was successful, why has a similar response to current restoration efforts not been observed?

## Reasons restoration may not be working

The cultch density used by Berrigan (1990; shell cultch) of about 472 cubic meters per acre was similar to the density used in the largest (rock cultch; project NRDA 5007) and most recent (rock cultch; project FWC 2021) restoration efforts, and similar to the highest treatment level of recent shell cultch projects (project NFWF-1) for Apalachicola Bay (Table 1). Pine et al. (2015) used a model fit to historic Apalachicola fisheries-dependent and -independent data to demonstrate how an intensive cultching program of about 50 ha per year could reduce the risk of an irreversible oyster fishery collapse in Apalachicola Bay. This cultching area is slightly larger than the average area cultched each year between the restoration efforts following Hurricane Elena in 1985 (Berrigan 1990; Pine et al. 2015) and the beginning of regional restoration efforts in 2015. What is unknown and could not be included in the Pine et al. (2015) simulations is what density of cultching material (amount per area) was required.

Kimbro et al. (2020) conducted similar restoration experiments in Apalachicola Bay using quarried oyster shells on reefs 0.4 ha in size at shelling densities of zero, 153 m3, and 306 m3. They observed a positive response to oyster reef restoration 10 months post-restoration during the same time frame as high oyster spat counts occurred on the NFWF-1 project reefs covered by this study (Figure 6). They also observed higher oyster counts (defined as juveniles <25 mm and adults ≥25 mm) on reefs with increased reef mass. Follow-up assessments beyond 10 months are unavailable for the reefs discussed in Kimbro et al. (2020). Our work followed reefs that were similarly restored (materials, densities, and starting time) several years post-construction and found that the initial oyster population response to restoration as measured by counts did not persist (Figure 6).

These recommended or observed cultching levels are area estimates (e.g., 50 ha recommended from simulation, about 40 ha restored on average in Apalachicola since the mid-1980s; Pine et al. 2015) that describe the surface area of cultch available for spat to settle. The volume of cultch material (cubic meters) and the size of individual cultch pieces determine the vertical relief added to the extant reef. For example, ¼ m3 of small cobble placed as cultch in a tidal system is likely to rapidly slough, flatten (decline in vertical relief), and expand in the footprint area due to currents moving the small mass of each cobble piece. On the other hand, a ¼ m3 boulder is likely to be more resistant to movement and flattening because of its higher mass and would provide more vertical relief. This vertical relief difference may be necessary for elevating the cultch material into suitable water quality or hydrodynamic conditions. Colden et al. (2017) found that oyster reefs with height > 0.3 m in the Chesapeake Bay region had higher oyster survival, density, and overall complexity than oyster reefs < 0.3 m, and higher-elevation reefs were more likely to persist. In 2017 the NAS highlighted the NFWF-1 project assessed in this study as an example of a restoration project designed to experimentally evaluate oyster population responses to different cultch density treatments (NAS 2017). However, our results show this project did not answer the questions as proposed, perhaps because of construction challenges and design errors leading to limited contrast in elevation among the different cultch treatments.

Side-scan sonar mapping is used as a performance assessment metric on a subset of restored reefs in Pensacola, St. Andrew, and Apalachicola bays, including measurements of vertical relief. The elevation of restored reefs in these systems is variable but generally low (about 0.05 m). Because the material used for restoration efforts is either small and dense (#4 limestone 19–38 mm in diameter) or larger and less dense (quarried oyster shell 50–75 mm in diameter), it is likely susceptible to being transported away from the intended restoration site, buried in sediment, or sculpted by currents to a low-relief structure (about 0.05 m). This low-relief structure is likely interrupted across its surface by subtle waves of higher-density material (volumetrically), resulting in slightly higher vertical relief (about 0.1 m) in some areas. Regardless, cultch material in various forms at different original mass levels has persisted on these restored reefs at low mass levels (Figure 8), and relief and critically, oyster spat settlement on this material has been very low, for reasons that are not known.

Smith et al. (2021), as part of a 15-year assessment of the performance of an oyster reef restoration project in the Chesapeake Bay, found that restored reefs were like unrestored reference reefs based on a variety of metrics within six years following restoration. For some metrics, such as shell height, the restored and reference reefs were similar within three years, and as the restored reefs aged, they became more stable and possibly more resilient. In Florida, the restoration of the Lone Cabbage Reef in Suwannee Sound demonstrated oyster spat settlement and persistence on the restored reef within six months following construction. Oysters have persisted and successfully settled on the reef in the four years since construction, and oyster densities on the restored and nearby reference reefs are now similar (W.E. Pine, *unpublished information*). Increase in oyster reef elevation from the Smith et al. (2021) restoration project in the Chesapeake Bay was about 0.14 m (see online supplemental information in Smith et al. 2021), and for the Lone Cabbage project in Florida it was about 0.36 m (Pine et al. 2022). Combined with the results from Colden et al.’s project (2017; 0.4 m), elevation changes on restored reefs that persisted over time had about 3–8× the elevation contrast observed on restored sites in Apalachicola, Pensacola, and St. Andrew bays.

Materials used for reef construction and other oyster restoration efforts vary widely (Bersoza Hernandez 2018; Goelz et al. 2020). In Florida, oyster restoration materials include multiple types of limestone, quarried oyster shells, recycled clam shells, crushed granite, and artificial materials. Florida state law reserves part of the shells from the commercial oyster trade for restoration and cultching.

(23) OYSTER AND CLAM SHELLS PROPERTY OF DEPARTMENT

(a) Except for oysters used directly in the half-shell trade, 50 percent of all shells from oysters and clams shucked commercially in the state shall be and remain the property of the department when such shells are needed and required for rehabilitation projects and planting operations, in cooperation with the Fish and Wildlife Conservation Commission, when sufficient resources and facilities exist for handling and planting such shell, and when the collection and handling of such shell is practicable and useful, except that bona fide holders of leases and grants may retain 75 percent of such shell as they produce for aquacultural purposes.

— Florida Statute 597.010

Critically, the half-shell trade, which (as indicated above) is exempt from this requirement, is the market for the majority of oysters harvested in Florida waters.

The Berrigan (1990) restoration project in Apalachicola Bay, which is considered successful, used clam shells dredged from Lake Pontchartrain, Louisiana, as cultch material. Smith et al. (2021) describe a successful long-term oyster restoration project that also used dredged shell in Chesapeake Bay, Virginia. Limestone used in the restoration projects covered by this study was mined in Kentucky and made of calcite, dolomite, and quartz. It is denser (structure and mass) and older (geologic age) than the limestone used successfully (measured by counts and persistence of oysters) for intertidal reef restoration in Suwannee Sound, Florida (J. Yeager, University of Florida Department of Geological Sciences, personal communication; Pine et al. 2022). Whether the chemical composition and physical characteristics of the limestone used in the projects in Florida may influence its effectiveness as cultch is unknown.

Cultching efforts in Apalachicola Bay have been identified as contributing to the long-term sustainability of harvest in the bay prior to 2010 (Zu Ermgassen et al. 2012). But this observation is called into doubt by the observed oyster fishery collapse in 2012 and by a combination of modeling (Pine et al. 2015; Johnson et al. 2022) and empirical assessments (this work). Efforts are underway (J. Casteel, University of Florida, Department of Wildlife Ecology and Conservation, personal communication) to reconstruct shell biomass (volume) removed by harvest for the major oyster fisheries in Florida, and preliminary results suggest that shell material removals far exceed material replaced by recent restoration efforts. Understanding the magnitude of cultch removals can likely inform the scale of restoration required to shift degraded oyster populations from undesired to desired status (Johnson et al. 2022).

## Future directions

The repeated and ongoing cultching efforts in Florida estuaries to reverse observed declines in oyster populations are a test of a single hypothesis—that oyster populations have declined because of limitations in cultch. Cultch limitations have been tested explicitly for intertidal oyster reefs in one location in Florida (Lone Cabbage Reef, Suwannee Sound; Frederick et al. 2016; Pine et al. 2022). Other hypotheses related to oyster population and reef decline—including cascading predatory responses (Kimbro et al. 2017), recruitment overfishing, persistent and virulent disease (known or unknown), the effects of fishing, or some combination of these—are more difficult to assess for Pensacola, St. Andrew, and Apalachicola bays because of inadequate monitoring program design, including short and inconsistent time series in available data. This lack of data could be addressed by developing a staircase-style restoration program, where replicate treatments (different material types, vertical relief, or both) are staggered in time, in an adaptive management framework that includes explicit high-resolution monitoring of other possible factors driving oyster population recovery across different estuaries (Walters et al. 1988; Pine et al. 2022).

# Conclusions

Oyster populations in Apalachicola, Pensacola, and St. Andrew bays appear resistant to restoration and recovery at this time, despite legal actions (Apalachicola Bay), large restoration efforts, very low levels of reported harvest (Pensacola and St. Andrew bays), and two years of a five-year harvest moratorium (2020–2025) in Apalachicola Bay. Unfortunately, a combination of experimental design deficiencies (e.g., absence of controls, lack of strong treatment contrasts, no experimentation in materials) and inadequate monitoring make it difficult to determine which of the factors that have been previously hypothesized to drive oyster population dynamics (e.g., degraded reefs and low cultch availability, river discharge, fishing effects) are responsible. For example, a persistent uncertainty in oyster restoration and management is how oyster fishing practices impact oyster vital rates and oyster reef architecture, yet in Apalachicola Bay where the largest oyster restoration efforts have taken place, oyster harvest was permitted in areas where restoration was ongoing until 2020. Regrettably, many of the same restoration and management uncertainties identified in this assessment have persisted for decades or even centuries in Florida (Swift 1897; Swift 1898; Camp et al. 2015; Pine et al. 2015). This suggests an absence of learning.

These deficiencies also make it impossible to identify the necessary components of successful restoration (i.e., fishing effects, reef material, area, or height). Without the ability to evaluate these factors from the available data, we must rely on comparisons with restoration and management projects that appear to have met their goals. These include examples from the Chesapeake Bay region (e.g., Colden et al. 2017; Smith et al. 2022) and Florida (Pine et al. 2022), which document the use of naturally occurring materials to construct reefs with 0.3–0.4 m relief from the bottom. In Delaware Bay (Haskin Shellfish Research Lab 2022) a recently implemented system of spatial management in Mobile Bay provide examples for management of wild oyster fisheries that appear to be sustainable through highly regulated, carefully monitored, and adaptively managed harvest.

Resistance to learning to inform restoration is a widespread problem in ongoing restoration efforts in the Gulf of Mexico (NAS 2022) and has been a challenge to large-scale restoration and management efforts for decades (Walters 1986; Gunderson 1999; Walters 2007; Pine et al. 2022). Gunderson (1999), in a classic assessment of learning and barriers to learning in adaptive ecosystem assessment and management, suggested:

A central tenet of AEAM [adaptive ecosystem assessment and management] is learning, yet learning seems to be intertwined with cycles of policy success and failure. If policies are working (or appear to be working), there is little or no emphasis on learning. It is when policy fails, either dramatically or chronically, that learning is deemed necessary and a priority. The challenge to develop a capacity for learning continues to be problematic among most resource institutions. Yet, when needed, that capacity seems to come by focusing on understanding (not efficiency) and by networking with those who practice learning.

Understanding why these systems have not responded to restoration efforts so far is critical to informing future restoration efforts, including nearly $20 million in additional restoration funding currently being considered for Apalachicola Bay. More decisive agency, academic, and community leadership, emphasizing a commitment to learning through rigorous experimental design and monitoring, is needed to guide these restoration programs to achieve their stated goals of restoring oyster populations to support ecosystem services and viable fisheries for the benefit of the people of Florida and the Gulf of Mexico region.

# Acknowledgments

We recognize the assistance of many FDEP, FDACS, FWC, FSU, and other staff in completing field and lab efforts to collect and process these samples. We thank A. Morgan for editorial assistance. Erica Levine with FWC-FWRI kindly created the map in Figure 1.

# References

Berrigan, M. E. 1988. Management of oyster resources in Apalachicola Bay following Hurricane Elena. Journal of Shellfish Research 7:281–288.

Berrigan, M. E. 1990. Biological and economical assessment of an oyster resource development project in Apalachicola Bay, Florida. Journal of Shellfish Research 9:149–158.

Bersoza Hernández, A., R. D. Brumbaugh, P. Frederick, R. Grizzle, M. W. Luckenbach, C. H. Peterson, and C. Angelini. 2018. Restoring the eastern oyster: how much progress has been made in 53 years? Frontiers in Ecology and the Environment 16:463–471.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9(2):378–400. <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>.

Buzan, D., W. Lee, J. Culbertson, N. Kuhn, and L. Robinson. 2009. Positive relationship between freshwater inflow and oyster abundance in Galveston Bay, Texas. Estuaries and Coasts 32:206–212.Camp, E. V., W. E. Pine III, K. Havens, A. S. Kane, C. J. Walters, T. Irani, A. B. Lindsey, and J. G. Morris. 2015. Collapse of a historic oyster fishery: diagnosing causes and identifying paths toward increased resilience. Ecology and Society 20(3).

Coastal Alabama Comprehensive Oyster Restoration Plan Marine Resources Division and the National Oceanic and Atmospheric Administration published by the Deepwater Horizon Alabama Trustee Implementation Group. 2021. Retrieved from https://www.gulfspillrestoration.noaa.gov/sites/default/files/2021-12%20AL%20Final%20Coastal%20Alabama%20Comprehensive%20Oyster%20Restoration%20Strategy\_508.pdf

Comp and Seaman. 1988. Estuarine habitat and fishery resources in Florida. Pages 337–435 in W. Seaman Jr., editor. Florida aquatic habitat and fishery resources. FL AFS, Eustis.

Colden, A.M., Latour, R.J. and Lipcius, R.N., 2017. Reef height drives threshold dynamics of restored oyster reefs. Marine Ecology Progress Series 582:1-13.

Crowe, J. B., W. Huang, F. G. Lewis. 2008. Assessment of freshwater inflows to North Bay from the Deer Point Watershed of the St. Andrew Bay system. Water resources assessment 08-01, Northwest Florida Water Management District, Havana, Florida. Available here under supporting documents <https://nwfwater.com/Water-Resources/Surface-Water-Improvement-and-Management/St.-Andrew-Bay>.

Deepwater Horizon Natural Resource Damage Assessment Trustees. 2016. Deepwater Horizon oil spill: final programmatic damage assessment and restoration plan and final programmatic environmental impact statement. Website maintained by the National Oceanographic and Atmospheric Administration, Washington, DC. Chapters of plan available <http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan>.

Du, J., K. Park, C. Jensen, T. M. Dellapenna, W. G. Zhang, and Y. Shi. 2021. Massive oyster kill in Galveston Bay caused by prolonged low-salinity exposure after Hurricane Harvey. Science of the Total Environment 774:145132.

Edmiston, H. L., S. A. Fahrny, M. S. Lamb, L. K. Levi, J. M. Wanat,J. S. Avant, K. Wren and N. C. Selly. 2008. Tropical storm and hurricane impacts on a Gulf Coast estuary: Apalachicola Bay, Florida. Journal of Coastal Research 55:38–49.

Fisch, N. C., and W. E. Pine. 2016. A complex relationship between freshwater discharge and oyster fishery catch per unit effort in Apalachicola Bay, Florida: an evaluation from 1960 to 2013. Journal of Shellfish Research 35:809–825.

Florida Fish and Wildlife Commission. 2021. Commercial Fisheries Landings in Florida. online

<https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/>

Fish and Wildlife Research Institute. 2021. Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute Oyster Monitoring Procedures. Chapter 11 *in* Radabaugh K.R., Moyer R.P., Geiger S.P. (editors) Oyster Integrated Mapping and Monitoring Program Report for the State of Florida. St. Petersburg, FL: Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission. FWRI Technical Report 22, Version 2

Florida v Georgia, No 142 Original. 2014. Files related to this case are maintained by the Special Master of the US Supreme Court here https://www.ca10.uscourts.gov/special-master-142.

Frederick, P., N. Vitale, B. Pine, J. Seavey, and L. Sturmer. 2016. Reversing a rapid decline in oyster reefs: effects of durable substrate on oyster populations, elevations, and aquatic bird community composition. Journal of Shellfish Research 35(2):359–367.

Gledhill, J. H., A. F. Barnett, M. Slattery, K. L. Willett, G. L. Easson, S. S. Otts, and D. J. Gochfeld. 2020. Mass mortality of the Eastern Oyster *Crassostrea virginica* in the western Mississippi Sound following unprecedented Mississippi River flooding in 2019. Journal of Shellfish Research 39:235–244.

Goelz, T., B. Vogt, and T. Hartley. 2020. Alternative substrates used for oyster reef restoration: a review. Journal of Shellfish Research 39(1):1–12.

Graham, P. M., T. A. Palmer, and J. Beseres Pollack. 2017. Oyster reef restoration: substrate suitability may depend on specific restoration goals. Restoration Ecology 25(3):459–470.

Gunderson, L. 1999. Resilience, flexibility and adaptive management––antidotes for spurious certitude? Conservation Ecology 3(1).

Hartig, F. 2022. DHARMa: Residual Diagonstics for Hierarchical (Multi-level/mixed) Regression Models. https://CRAN.R-project.org/package=DHARMa

Haskin Shellfish Research Lab. 2022. Stock Assessment Workshop New Jersey Delaware Bay Oyster Beds(24th SAW). J. Morson, D. Bushek, and J. Giushttps editors. online: https://hsrl.rutgers.edu/SAWreports/SAW2022.pdf

Howie, A.H. and Bishop, M.J., 2021. Contemporary oyster reef restoration: responding to a changing world. Frontiers in Ecology and Evolution. p.518.

Johnson, F.J., W. E. Pine, III, and E. V. Camp. 2022. A Cautionary Tale: Management Implications of Critical Transitions in Oyster Fisheries. Canadian Journal of Fisheries and Aquatic Sciences. https://cdnsciencepub.com/doi/pdf/10.1139/cjfas-2021-0133

Kaplan, D. A., M. Olabarrieta, P. Frederick, and A. Valle-Levinson. 2016. Freshwater detention by oyster reefs: quantifying a keystone ecosystem service. PLoS ONE 11(12).

Kimbro, D. L., J. W. White, H. Tillotson, N. Cox, M. Christopher, O. Stokes-Cawley, S. Yuan, T. J. Pusack, C. D. Stallings. 2017. Local and regional stressors interact to drive a salinization-induced outbreak of predators on oyster reefs. Ecosphere 8:e01992.

Kimbro, D.L., Stallings, C.D. and White, J.W., 2020. Diminishing returns in habitat restoration by adding biogenic materials: a test using estuarine oysters and recycled oyster shell. Restoration Ecology 28: 1633-1642.

Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecological Applications 8:128–140.

Lenihan, H. S., and F. Micheli. 2000. Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict by ecological experimentation. Fishery Bulletin 98:86–95.

Light, H. M., M. R. Darst, and J. W. Grubbs. 1998. Aquatic habitats in relation to river flow in the Apalachicola River floodplain, Florida. US Geological Survey professional paper 1594. US Government Printing Office, Washington, DC.

Livingston, R. J. 2015. Climate change and coastal ecosystems: long-term effects of climate and nutrient loading on trophic organization. CRC, Boca Raton, Florida, USA.

Lüdecke, D. 2018. ggeffects: tidy data frames of marginal effects from regression models. Journal of Open Source Software 3(26):772.

Moore, J. F., W. E. Pine, P. C. Frederick, S. Beck, M. Moreno, M. J. Dodrill, M. Boone, L. Sturmer, and S. Yurek. 2020. Trends in oyster populations in the northeastern Gulf of Mexico: an assessment of river discharge and fishing effects over time and space. Marine and Coastal Fisheries 12:191–204.

Moore, J. F., and W. E. Pine. 2021. Bootstrap methods can help evaluate monitoring program performance to inform restoration as part of an adaptive management program. PeerJ 9(May 4):e11378.

NAS (National Academies of Sciences, Engineering, and Medicine). 2017. Effective monitoring to evaluate ecological restoration in the Gulf of Mexico. National Academies Press, Washington, DC.

NAS (National Academies of Sciences, Engineering, and Medicine). 2022. An approach for assessing US gulf coast ecosystem restoration: A Gulf Research Program environmental monitoring report. National Academies Press, Washington, DC, <https://nap.nationalacademies.org/catalog/26335/an-approach-for-assessing-us-gulf-coast-ecosystem-restoration-a>.

Petes, L. E., A. J. Brown, and C. R. Knight. 2012. Impacts of upstream drought and water withdrawals on the health and survival of downstream estuarine oyster populations. Ecology and Evolution 2:1712–1724.

Pine, W. E., F. A. Johnson, P. C. Frederick, and L. G. Coggins. 2022. Adaptive management in practice and the problem of application at multiple scales—insights from oyster reef restoration on Florida’s gulf coast. Marine and Coastal Fisheries 14(1):e10192.

Pine, W. E., C. J. Walters, E. V. Camp, R. Bouchillon, R. Ahrens, L. Sturmer, and M. E. Berrigan. 2015. The curious case of Eastern Oyster *Crassostrea virginica* stock status in Apalachicola Bay, Florida. Ecology and Society 20(3).

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, [https://www.R-project.org/](https://www.r-project.org/).

Smith, R.S., Lusk, B. and Castorani, M.C., 2022. Restored oyster reefs match multiple functions of natural reefs within a decade. Conservation Letters, p.e12883.

Swift, F. 1897. Survey of the oyster regions of St. Vincent Sound, Apalachicola Bay, and St. George Sound, Florida. U.S. Commission of Fishes and Fisheries, Extracted from Report of Commissioner for 1896. U.S. Commission of Fishes and Fisheries, Washington, D.C., USA.

Swift, F. 1898. The oyster-grounds of the west Florida coast: their extent, conditions, and peculiarities. Pages 185-187 in Proceedings and Papers of the National Fishery Congress, Tampa, Florida, January 19-24, 1898. U.S. Commission of Fish and Fisheries, Washington, D.C., USA.

University of New Hampshire and NOAA Coastal Response Research Center. 2017. Online <https://crrc.unh.edu/sites/crrc.unh.edu/files/media/docs/Workshops/dwh_eddm_2017/funding_diagram._final.pdf>

Walters, C.J., 1986. Adaptive management of renewable resources. Macmillan Publishers Ltd.

Walters, C.J., 2007. Is adaptive management helping to solve fisheries problems?. AMBIO: A Journal of the Human Environment. 36: 304-307.

Walters, C. J., J. S. Collie, and T. Webb. 1988. Experimental designs for estimating transient responses to management disturbances. Canadian Journal of Fisheries and Aquatic Sciences 45:530–538.

Whitfield, W. K., Jr., and D. S. Beaumariage. 1977. Shellfish management in Apalachicola Bay: past-present-future. Pages 130-140 *in* R. J. Livingston and E. A. Joyce, Jr., editors. Proceedings of the Conference on the Apalachicola Drainage System. Florida Marine Resource Publication No. 26. Florida Department of Natural Resources, Tallahassee, Florida, USA.

Zu Ermgassen, P., M. D. Spalding, B. Blake, L. D. Coen, B. Dumbauld, S. Geiger, J. H. Grabowski, R. Grizzle, M. Luckenbach, K. McGraw, and W. Rodney. 2012. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. Proceedings of the Royal Society B: Biological Sciences 279:3393–3400.

Zuur, A. F., J. M. Hilbe, and E. N. Leno. 2013. A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics, Newburgh, UK.

Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Table 0.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Bay | Period | Year | Month | Project | Site | Number quadrants |
| Apalachicola | 2 | 2015 | 10 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 2 | 2015 | 10 | NFWF-1 | Dry Bar | 74 |
| Apalachicola | 2 | 2015 | 10 | NFWF-1 | Hotel Bar | 74 |
| Apalachicola | 2 | 2016 | 1 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 2 | 2016 | 2 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 2 | 2016 | 2 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 3 | 2016 | 4 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 3 | 2016 | 5 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 3 | 2016 | 5 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 3 | 2016 | 6 | NRDA-4044 | Dry Bar | 5 |
| Apalachicola | 3 | 2016 | 7 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 3 | 2016 | 7 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 3 | 2016 | 8 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 4 | 2016 | 10 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 4 | 2016 | 10 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 4 | 2016 | 10 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 4 | 2017 | 1 | NFWF-1 | Bulkhead | 74 |
| Apalachicola | 4 | 2017 | 1 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 4 | 2017 | 1 | NFWF-1 | Hotel Bar | 74 |
| Apalachicola | 4 | 2017 | 2 | NFWF-1 | Bulkhead | 1 |
| Apalachicola | 4 | 2017 | 2 | NFWF-1 | Hotel Bar | 1 |
| Apalachicola | 5 | 2017 | 4 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 5 | 2017 | 4 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 5 | 2017 | 4 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 5 | 2017 | 4 | NRDA-4044 | Cat Point | 30 |
| Apalachicola | 5 | 2017 | 4 | NRDA-4044 | Eleven Mile | 30 |
| Apalachicola | 5 | 2017 | 4 | NRDA-4044 | Hotel Bar | 45 |
| Apalachicola | 5 | 2017 | 4 | NRDA-4044 | Normans Bar | 15 |
| Apalachicola | 5 | 2017 | 5 | NRDA-4044 | Green Point | 15 |
| Apalachicola | 5 | 2017 | 5 | NRDA-4044 | Normans Bar | 30 |
| Apalachicola | 5 | 2017 | 5 | NRDA-4044 | North Spur | 15 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Cabbage Lumps | 15 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Cabbage Top | 30 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Dry Bar | 55 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Lighthouse Bar | 30 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Little Gully | 30 |
| Apalachicola | 5 | 2017 | 6 | NRDA-4044 | Normans Bar | 15 |
| Apalachicola | 5 | 2017 | 7 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 5 | 2017 | 7 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 5 | 2017 | 7 | NRDA-4044 | Bayou Flats | 15 |
| Apalachicola | 5 | 2017 | 7 | NRDA-4044 | Redfish Creek | 45 |
| Apalachicola | 5 | 2017 | 8 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 6 | 2017 | 10 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 6 | 2017 | 10 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 6 | 2017 | 11 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 6 | 2017 | 11 | NRDA-4044 | Cat Point | 30 |
| Apalachicola | 6 | 2017 | 11 | NRDA-4044 | Hotel Bar | 15 |
| Apalachicola | 6 | 2017 | 12 | NRDA-4044 | Cabbage Lumps | 15 |
| Apalachicola | 6 | 2017 | 12 | NRDA-4044 | Green Point | 15 |
| Apalachicola | 6 | 2017 | 12 | NRDA-4044 | North Spur | 15 |
| Apalachicola | 6 | 2018 | 1 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 6 | 2018 | 2 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 6 | 2018 | 2 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 6 | 2018 | 2 | NRDA-4044 | Dry Bar | 45 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Bayou Flats | 15 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Eleven Mile | 30 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Hotel Bar | 30 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Lighthouse Bar | 30 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Normans Bar | 60 |
| Apalachicola | 6 | 2018 | 3 | NRDA-4044 | Redfish Creek | 45 |
| Apalachicola | 7 | 2018 | 4 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 7 | 2018 | 4 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 7 | 2018 | 4 | NRDA-4044 | Cabbage Top | 30 |
| Apalachicola | 7 | 2018 | 4 | NRDA-4044 | Dry Bar | 15 |
| Apalachicola | 7 | 2018 | 4 | NRDA-4044 | Little Gully | 30 |
| Apalachicola | 7 | 2018 | 5 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | 8 Mile | 30 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | 9 Mile B | 5 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | Cabbage Top | 15 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | Hotel Bar | 45 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | King 9 Mile | 15 |
| Apalachicola | 7 | 2018 | 6 | GEBF-5007 | North Spur | 30 |
| Apalachicola | 7 | 2018 | 7 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 7 | 2018 | 7 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 7 | 2018 | 8 | GEBF-5007 | Cat Point | 45 |
| Apalachicola | 7 | 2018 | 8 | GEBF-5007 | Cat Point Spur | 30 |
| Apalachicola | 7 | 2018 | 8 | GEBF-5007 | East Hole | 30 |
| Apalachicola | 7 | 2018 | 8 | GEBF-5007 | Monkeys Elbow | 30 |
| Apalachicola | 7 | 2018 | 8 | GEBF-5007 | Peanut Ridge | 30 |
| Apalachicola | 7 | 2018 | 8 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 7 | 2018 | 9 | GEBF-5007 | Bulkhead | 15 |
| Apalachicola | 7 | 2018 | 9 | GEBF-5007 | East Hole | 60 |
| Apalachicola | 8 | 2018 | 11 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 8 | 2018 | 11 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 8 | 2018 | 12 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 8 | 2019 | 1 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 8 | 2019 | 1 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 8 | 2019 | 1 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 9 | 2019 | 4 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 9 | 2019 | 4 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 9 | 2019 | 5 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 9 | 2019 | 6 | GEBF-5007 | 9 Mile B | 10 |
| Apalachicola | 9 | 2019 | 6 | GEBF-5007 | Bulkhead | 15 |
| Apalachicola | 9 | 2019 | 6 | GEBF-5007 | East Hole | 30 |
| Apalachicola | 9 | 2019 | 6 | GEBF-5007 | Hotel Bar | 45 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | 8 Mile | 30 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | 9 Mile B | 15 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | Cabbage Top | 15 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | East Hole | 60 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | King 9 Mile | 15 |
| Apalachicola | 9 | 2019 | 7 | GEBF-5007 | North Spur | 30 |
| Apalachicola | 9 | 2019 | 8 | GEBF-5007 | Cat Point | 45 |
| Apalachicola | 9 | 2019 | 8 | GEBF-5007 | Cat Point Spur | 30 |
| Apalachicola | 9 | 2019 | 8 | GEBF-5007 | Monkeys Elbow | 30 |
| Apalachicola | 9 | 2019 | 8 | GEBF-5007 | Peanut Ridge | 30 |
| Apalachicola | 9 | 2019 | 8 | NFWF-1 | Hotel Bar | 75 |
| Apalachicola | 9 | 2019 | 9 | NFWF-1 | Bulkhead | 75 |
| Apalachicola | 9 | 2019 | 9 | NFWF-1 | Dry Bar | 75 |
| Apalachicola | 9 | 2019 | 9 | NRDA-4044 | Cabbage Lumps | 15 |
| Apalachicola | 9 | 2019 | 9 | NRDA-4044 | Cabbage Top | 30 |
| Apalachicola | 9 | 2019 | 9 | NRDA-4044 | Green Point | 15 |
| Apalachicola | 9 | 2019 | 9 | NRDA-4044 | North Spur | 15 |
| Apalachicola | 10 | 2019 | 10 | NRDA-4044 | Dry Bar | 60 |
| Apalachicola | 10 | 2019 | 10 | NRDA-4044 | Hotel Bar | 45 |
| Apalachicola | 10 | 2019 | 10 | NRDA-4044 | Redfish Creek | 15 |
| Apalachicola | 10 | 2019 | 11 | NRDA-4044 | Bayou Flats | 15 |
| Apalachicola | 10 | 2019 | 11 | NRDA-4044 | Eleven Mile | 30 |
| Apalachicola | 10 | 2019 | 11 | NRDA-4044 | Lighthouse Bar | 30 |
| Apalachicola | 10 | 2019 | 11 | NRDA-4044 | Normans Bar | 60 |
| Apalachicola | 10 | 2019 | 11 | NRDA-4044 | Redfish Creek | 30 |
| Apalachicola | 10 | 2019 | 12 | NRDA-4044 | Cat Point | 30 |
| Apalachicola | 10 | 2019 | 12 | NRDA-4044 | Little Gully | 30 |
| Apalachicola | 12 | 2020 | 12 | GEBF-5007 | Cabbage Top | 15 |
| Apalachicola | 12 | 2020 | 12 | GEBF-5007 | North Spur | 30 |
| Apalachicola | 12 | 2021 | 1 | GEBF-5007 | Hotel Bar | 45 |
| Apalachicola | 13 | 2021 | 4 | GEBF-5007 | 8 Mile | 30 |
| Apalachicola | 13 | 2021 | 4 | GEBF-5007 | 9 Mile B | 15 |
| Apalachicola | 13 | 2021 | 4 | GEBF-5007 | Cat Point | 45 |
| Apalachicola | 13 | 2021 | 4 | GEBF-5007 | East Hole | 30 |
| Apalachicola | 13 | 2021 | 4 | GEBF-5007 | King 9 Mile | 15 |
| Apalachicola | 13 | 2021 | 6 | GEBF-5007 | Bulkhead | 15 |
| Apalachicola | 13 | 2021 | 6 | GEBF-5007 | Cat Point Spur | 30 |
| Apalachicola | 13 | 2021 | 6 | GEBF-5007 | East Hole | 60 |
| Apalachicola | 13 | 2021 | 6 | GEBF-5007 | Monkeys Elbow | 30 |
| Apalachicola | 13 | 2021 | 6 | GEBF-5007 | Peanut Ridge | 30 |
| Apalachicola | 13 | 2021 | 7 | NRDA-4044 | Bayou Flats | 15 |
| Apalachicola | 13 | 2021 | 7 | NRDA-4044 | Cabbage Lumps | 15 |
| Apalachicola | 13 | 2021 | 7 | NRDA-4044 | Eleven Mile | 30 |
| Apalachicola | 13 | 2021 | 7 | NRDA-4044 | Redfish Creek | 45 |
| Apalachicola | 13 | 2021 | 8 | FWC-2021 | Cat Point | 30 |
| Apalachicola | 13 | 2021 | 8 | FWC-2021 | East Lumps | 30 |
| Apalachicola | 13 | 2021 | 8 | FWC-2021 | Lighthouse Bar | 30 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Cabbage Top | 30 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Dry Bar | 45 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Green Point | 15 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Hotel Bar | 45 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Lighthouse Bar | 30 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | Little Gully | 30 |
| Apalachicola | 13 | 2021 | 9 | NRDA-4044 | North Spur | 15 |
| Apalachicola | 14 | 2021 | 10 | FWC-2021 | Cat Point | 15 |
| Apalachicola | 14 | 2021 | 10 | FWC-2021 | East Lumps | 15 |
| Apalachicola | 14 | 2021 | 11 | FWC-2021 | Lighthouse Bar | 15 |
| Apalachicola | 14 | 2021 | 12 | NRDA-4044 | Cat Point | 30 |
| Apalachicola | 14 | 2021 | 12 | NRDA-4044 | Dry Bar | 15 |
| Apalachicola | 14 | 2021 | 12 | NRDA-4044 | Normans Bar | 60 |
| Apalachicola | 14 | 2022 | 1 | FWC-2021 | Cat Point | 15 |
| Apalachicola | 14 | 2022 | 1 | FWC-2021 | East Lumps | 15 |
| Apalachicola | 14 | 2022 | 2 | FWC-2021 | Lighthouse Bar | 15 |
| Apalachicola | 15 | 2022 | 5 | FWC-2021 | Cat Point | 15 |
| Apalachicola | 15 | 2022 | 5 | FWC-2021 | East Lumps | 15 |
| Apalachicola | 15 | 2022 | 5 | FWC-2021 | Lighthouse Bar | 15 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | Boathouse Lumps | 30 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | Escribano Point | 30 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | Mussel Beds | 15 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | No Name Bar | 15 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | Point No Point Bar | 15 |
| Pensacola | 5 | 2017 | 9 | NRDA-4044 | Trout Bayou | 45 |
| Pensacola | 6 | 2017 | 10 | NRDA-4044 | Big John Bar | 15 |
| Pensacola | 6 | 2017 | 10 | NRDA-4044 | East River | 60 |
| Pensacola | 6 | 2017 | 10 | NRDA-4044 | Half Moon Bar | 15 |
| Pensacola | 6 | 2017 | 10 | NRDA-4044 | Square Bar | 15 |
| Pensacola | 6 | 2017 | 10 | NRDA-4044 | White Point Bar | 30 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Big John Bar | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Boathouse Lumps | 30 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | East River | 60 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Escribano Point | 30 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Half Moon Bar | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Mussel Beds | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | No Name Bar | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Point No Point Bar | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Square Bar | 15 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | Trout Bayou | 45 |
| Pensacola | 7 | 2018 | 7 | NRDA-4044 | White Point Bar | 30 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Big John Bar | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Boathouse Lumps | 30 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | East River | 60 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Escribano Point | 30 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Half Moon Bar | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Mussel Beds | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | No Name Bar | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Point No Point Bar | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Square Bar | 15 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | Trout Bayou | 45 |
| Pensacola | 10 | 2019 | 11 | NRDA-4044 | White Point Bar | 30 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | Boathouse Lumps | 30 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | Escribano Point | 30 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | Mussel Beds | 15 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | No Name Bar | 15 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | Point No Point Bar | 15 |
| Pensacola | 15 | 2022 | 6 | NRDA-4044 | Trout Bayou | 45 |
| Pensacola | 15 | 2022 | 7 | NRDA-4044 | Big John Bar | 15 |
| Pensacola | 15 | 2022 | 7 | NRDA-4044 | East River | 60 |
| Pensacola | 15 | 2022 | 7 | NRDA-4044 | Half Moon Bar | 15 |
| Pensacola | 15 | 2022 | 7 | NRDA-4044 | Square Bar | 15 |
| Pensacola | 15 | 2022 | 7 | NRDA-4044 | White Point Bar | 30 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Crooked Creek Point | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Doyle Bayou | 30 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | East Power Lines | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Goose Point | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Little Oyster Bar Point | 12 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Newman Bayou Bar | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | Off Little Oyster Bar Ridge | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | South Channel Ridge | 15 |
| St. Andrew | 5 | 2017 | 8 | NRDA-4044 | West Bay Point | 30 |
| St. Andrew | 7 | 2018 | 4 | NRDA-4044 | East Power Lines | 15 |
| St. Andrew | 7 | 2018 | 4 | NRDA-4044 | Newman Bayou Bar | 15 |
| St. Andrew | 7 | 2018 | 4 | NRDA-4044 | West Bay Point | 30 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | Crooked Creek Point | 15 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | Doyle Bayou | 30 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | Goose Point | 15 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | Little Oyster Bar Point | 15 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | Off Little Oyster Bar Ridge | 15 |
| St. Andrew | 7 | 2018 | 5 | NRDA-4044 | South Channel Ridge | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | Crooked Creek Point | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | Doyle Bayou | 30 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | Goose Point | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | Little Oyster Bar Point | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | Off Little Oyster Bar Ridge | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | South Channel Ridge | 15 |
| St. Andrew | 10 | 2019 | 12 | NRDA-4044 | West Bay Point | 30 |
| St. Andrew | 10 | 2020 | 1 | NRDA-4044 | East Power Lines | 15 |
| St. Andrew | 10 | 2020 | 1 | NRDA-4044 | Newman Bayou Bar | 15 |

Table 1. Key characteristics of the six oyster restoration projects reviewed for this study.

| Bay | Project name | Agencya | Construction time frame | Material | Amount (cubic meters) | Sites | Average density (cubic meters per acre) |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Pensacola | NRDA 4044 | FDEP | Fall 2016 | Limestone aggregate | 15,270 | 17 | 174 |
| St. Andrew | NRDA 4044 | FDEP | Summer 2016 | Crushed granite | 12,997 | 9 | 153 |
| Apalachicola | NRDA 4044 | FDEP | Fall 2015 | Quarried shell | 18,992 | 16 | 153 |
| Apalachicola | GEBF 5007 | FDEP | Fall 2017 | Limerock aggregate | 73,015 | 14 | 229 |
| Apalachicola | NFWF-1 | FWC | Summer/Fall 2015 | Quarried shell | 7,340 | 3 | 76, 153, 229, 306 |
| Apalachicola | NFWF-2021 | FWC | Summer 2021 | Limerock aggregate | 7,340 | 3 | 229 |

a FDEP = Florida Department of Environmental Protection; FWC = Florida Fish and Wildlife Conservation Commission.

Table 2. Model selection table for the GLM of oyster count data from subtidal reefs in three bays in the Florida panhandle. The predicted response is number of spat per ¼ m2 quadrat. AIC and delta AIC are provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); bay = Pensacola, East (St. Andrew), or Apalachicola bay.

| Model | Degrees of freedom | AIC | Delta AIC | AIC Weight |
| --- | --- | --- | --- | --- |
| Period \* bay + offset(log(number of quadrats)) | 8 | 2,658.09 | 0.0 | 0.98 |
| Period + bay + offset(log(number of quadrats)) | 6 | 2,666.65 | 8.56 | 0.01 |
| Period + offset(log(number of quadrats)) | 4 | 2,668.68 | 10.59 | 0.00 |
| Bay + offset(log(number of quadrats)) | 5 | 2670.01 | 11.92 | 0.00 |
| offset(log(number of quadrats)) | 3 | 2672.18 | 14.09 | 0.00 |

Table 3. Model selection table for the GLM of oyster count data from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay. The predicted response is number of spat per ¼ m2 quadrat. AIC and delta AIC provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; low days = the number of days river discharge was below 12,000 CFS; site = the location where the sampling occurred.

| Model | Degrees of freedom | AIC | Delta AIC | AIC Weight |
| --- | --- | --- | --- | --- |
| Period \* project + 1|site + offset(log(number of quadrats)) | 10 | 1876.40 | 0 | 1.0 |
| Period \* project + 1|site + offset(log(number of quadrats)) | 7 | 1890.79 | 14.39 | 0 |
| Project + 1|site | 6 | 1896.42 | 20.02 | 0 |
| Period + low days + 1|site + offset(log(number of quadrats)) | 5 | 1925.68 | 49.27 | 0 |
| Period + 1|site + offset(log(number of quadrats)) | 4 | 1940.32 | 63.92 | 0 |
| 1|site + offset(log(number of quadrats)) | 3 | 1941.08 | 64.68 | 0 |
| Period + (low days previous period) + 1|site + offset(log(number of quadrats)) | 5 | 1941.58 | 65.17 | 0 |

![Diagram

Description automatically generated]()

Figure 1. Location of Pensacola, St. Andrew, and Apalachicola bays in the Florida panhandle.



Figure 2. Publicly available fisheries-dependent data from the Florida Fish and Wildlife Conservation Commission (https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/), 1986–present. Each row represents a different bay, and each column represents a different data category. The y axes differ because of the large differences in landings and trips between bays.

Chart

Description automatically generated

Figure 3. A schematic demonstrating the placement and persistence of cultch material by project (y axis, red line) over time (x axis) and the sampling events (grey circles) that collected oyster count data from each project. Project AB NRDA-4044 only collected samples from one site in Period 3 (open circle) and sampling did not begin on other sites until Period 5. Even number periods include the months October-March beginning in 2015 and odd-number periods are summers months April-September beginning in 2016.

Text, table

Description automatically generated

Figure 4. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for Apalachicola Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note each plot has a different y-axis.

Calendar

Description automatically generated

Figure 5. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for Pensacola Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note each plot has a different y-axis.

Calendar

Description automatically generated

Figure 6. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for St. Andrew Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note each plot has a different y-axis.



Figure 7. Oyster spat count per quadrat (CPUE) by site within Apalachicola Bay (each panel) and period (x-axis). Dots represent counts over time for each project defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note: the first counts for projects NRDA-4044 were taken in one period after restoration for Dry Bar only and Period 5 for other sites. Project GEBF-5007 were taken one period after the restoration action. Projects NFWF-1 and NFWF-2021 began count monitoring in the same period as the restoration (see Figure 3).



Figure 8. Oyster spat count per quadrat (CPUE) for two sites within Apalachicola Bay (East Lumps left panel, Lighthouse Bar right panel) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. For East Lumps site (left panel) the cultch material was placed in Apalachicola Bay and monitoring begin in Period 13, and oyster spat were recorded during monitoring efforts in Period 13 and 14, and oyster spat counts declined drastically in Period 15. For Lighthouse Bar (right panel) the NRDA-4044 project had material placed in Apalachicola Bay in Period 2, but sampling in Period 3 only occurred at one site and did not begin at other sites until Period 5. Note the large difference in counts in Period 13 between project NRDA-4044 (shell cultch about five years old) and NFWF-2021 (recent rock cultch) as indicated by the arrow.

Chart, scatter chart

Description automatically generated

Figure 9. Oyster spat count per quadrat (CPUE; left panels) and seed count per quadrat (right panels) for two sites within Apalachicola Bay (East Lumps top row, Lighthouse Bar bottom row) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. The arrows highlight the change in count from spat to seed size oyster from period t to period t+1 and the ellipses highlight the drastic change by a factor of 3 -5 in the y axis between the spat and seed counts. Critically these changes occur between Period 14 (winter) and Period 15 (summer).

Chart, histogram

Description automatically generated

Figure 4. Predicted count of live spat by period for a single ¼ m2 quadrat from each of the three study systems. The black line represents the line of best fit for each period, and the grey area represents the 95% confidence interval. Even-number periods are winters (November–April) beginning in 2015; odd-number periods are summers (April–September) beginning in 2016. Predictions are made for a single quadrat because of the large differences in the average number of quadrats completed in each bay. The y axes differ because of the large differences between bays.

Figure 5. Live oyster spat CPUE per ¼ m2 quadrat, by period, from each of the four projects in Apalachicola Bay. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April–September) beginning in 2016.

Chart, scatter chart

Description automatically generated

Figure 6. Example plot to demonstrate the fit of the negative binomial GLM. Dots on the plot represent the sum of the rounded weights of cultch from the NFWF-1 project. The model in R is written as Roundwt ~ Period + offset(log(Num\_quads)) and is fit to a subset of the data consisting of only the results of the NFWF-1 project. The solid black line represents the predicted total rounded weight of cultch for an average number of quadrats (150) predicted for every period; the grey area represents its 95% confidence interval.

Chart, histogram

Description automatically generated

Alternate Figure 6. Example plot to demonstrate the fit of the negative binomial GLM. The model in R is written as Sum\_spat ~ Period \* Project + offset(log(Num\_quads)), which is an interactive model allowing for a unique slope for each project across periods. Dots on the plot represent the total number of live spat for each period and site from the NFWF-1 project. The solid black line represents the rounded weight of cultch for an average number of quadrats (150) predicted for every period; the grey area represents its 95% confidence interval. The y axis is large because this is the amount of material that would come from 150 quadrats.

Graphical user interface, chart, histogram

Description automatically generated

Alternate Figure 6. Live oyster counts for a single ¼ m2 quadrat by period, predicted using an nbGLM model in R, generally written as Sum\_spat ~ Period \* Project + offset(log(Num\_quads)). This is an interactive model allowing for a unique slope for each project. The solid black line represents the predicted number of live spat; the grey area represents its 95% confidence interval. All study sites had more than one quadrat sampled, and no study site was sampled in all periods. Predicted values are shown for all periods and for a single quadrat to demonstrate the difference in predicted number of live oyster spat for a common level of sampling effort, and to demonstrate the variability in predicted counts and population trajectory over time as a representation of live oyster spat trends for each study site. The utility of this plot is up for discussion.

Graphical user interface

Description automatically generated

Figure 7. Predicted change in cultch biomass from the four Apalachicola Bay study sites. The model in R is written as Roundwt ~ Period + offset(log(Num\_quads)) and is fit individually to subsets of the data which represent the different projects. The solid black line represents the predicted total rounded weight of cultch for a single quadrat for every period; the grey area represents its 95% confidence interval. All study sites had more than one quadrat sampled, and no study site was sampled in all periods. Predictions are only made for the periods that were sampled. The utility of this plot is up for discussion.

Chart, scatter chart

Description automatically generated

Figure 8. Live oyster spat and weight of cultch (kg) for each quadrat by period for the four Apalachicola Bay studies. The NFWF-1 and NRDA 4044 projects used shell cultch, and the NRDA 5007 and FWC 2021 projects used limestone cultch.

A screenshot of a computer

Description automatically generated with low confidence

Figure 9. Deviations in river discharge from the period of instrument records for the Escambia and Apalachicola rivers. Darker colors equate to larger deviations, with colors in the blue spectrum representing higher river discharge and colors in the red spectrum representing lower river discharge. White or near-white represents values within +/− 10% of the period of instrument records.

Chart, scatter chart, box and whisker chart

Description automatically generated

Figure 10. Live oyster spat CPUE for all Apalachicola Bay study sites and number of days Apalachicola River discharge (measured at the Chattahoochee gauge) was below 12,000 CFS (below which inundation of floodplain is limited). UPDATED SEPT 6 2022