Abstract

Depressed oyster *Crassostrea virginica* populations in the northern Gulf of Mexico have been the target of numerous post-*Deepwater Horizon* restoration projects. These projects primarily focus on replacing oyster cultch (substrate) to promote spat settlement, increase recruitment, and bolster adult oyster populations. This study assesses oyster populations at the sites of six such efforts, which used different cultch types and densities between 2015–2022 in three estuaries in the Florida panhandle (Pensacola, St. Andrew, and Apalachicola bays). Total restoration costs for these projects were more than $14M. Counts of different size classes of oysters did not persistently increase following restoration, regardless of cultch type or density used. Positive responses to restoration efforts were irregular, short-lived, and seemed only to occur for spat-size oysters immediately after restoration. None of the restoration efforts significantly improved abundance of oysters of any size class in any of the three estuaries throughout the study. It is unclear what is hindering restoration success because of monitoring program shortcomings. However, restoration design and implementation deficiencies, including materials used and minimal vertical relief of restored reefs post-construction, likely contribute to the lack of project success. These shortcomings must be addressed through fundamental changes in oyster restoration and monitoring efforts in Florida to foster learning, improve restoration strategies, and ultimately recover oyster populations.

Introduction

Eastern oyster populations in the northern Gulf of Mexico are depressed from historical levels for widely speculated but 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). As of the end of 2022, only one of these stocks (Mobile Bay) has reopened to harvest. The proposed reasons for regional oyster declines include prolonged drought, extreme rain events, freshwater releases from water management structures, environmental degradation, overharvesting, oil spill, and insufficient cultching (Petes et al. 2012; Pine et al. 2015; Deepwater Horizon Natural Resources Damage Assessment Trustees 2016; Kelly 2019; 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).

Many proposed, ongoing, and historical oyster restoration efforts in the US Gulf of Mexico 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 1898; Lenihan and Peterson 1998; Lenihan and Micheli 2000; Howie and Bishop 2021). These restoration efforts attempt to shift oyster reefs from an observed low but possibly resilient state to a more desired productive state (Pine et al. 2022). While the restoration objective can vary by location, type of oyster bar (intertidal vs. subtidal), and management goals, restoration efforts are expected to persistently increase oyster populations so that they will provide and promote ecosystem services (Smith et al. 2022), and support fishery recovery.

Despite the importance of cultch for supporting oyster settlement (Lenihan and Peterson 1998; Frederick et al. 2016; Solinger et al. 2022), the amount, height, and type of cultch that are likely to perform best in different restorations are poorly understood (Graham et al. 2017; Goelz et al. 2020). Some current restoration programs in the Florida panhandle are long-term (10 years), and information on what has and has not worked is lacking. Such information is critical for guiding current and future restoration and management in an adaptive framework in similar systems (Pine et al. 2022).

We assessed ongoing and recently completed oyster restoration efforts in three large estuaries in the Florida panhandle to evaluate the following questions:

(1) How do temporal trends in oyster counts vary among the three depressed bays where restoration has occurred (Pensacola, St. Andrew, and Apalachicola bays)?

(2) In a focal site (Apalachicola Bay), how do trends in oyster spat (the life stage hypothesized to respond first to restoration) vary among separate restoration projects?

(3) Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?

(4) How do oyster spat densities compare across projects and cultch densities in Apalachicola Bay?

(5) How well do different types and densities of cultch used in restoration persist in Pensacola, St. Andrew, and Apalachicola bays?

We show that large restoration programs are not having the desired outcome of increasing live oyster populations of any size class. Lack of response 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 ineffective at shifting populations from the low-production state. Our work suggests that substantial uncertainty persists in how to restore oyster populations at large scales in Florida successfully. Addressing these uncertainties will require treating restoration projects as experiments to promote learning and increase the likelihood of successfully restoring oyster populations.

# 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 mandatory trip-ticket program was fully implemented in 1986 (Figure 2). Most oyster landings from St. Andrew Bay are from the East Bay arm, which 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 landings have declined to near zero in surrounding counties in recent years. Apalachicola Bay is a 348,029-ha estuary in Franklin County that supported the largest oyster fishery in Florida before collapsing in the fall of 2012 (Pine et al. 2015). Apalachicola Bay was closed to commercial harvest from December 2020 - December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

## Restoration 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 to previous cultching efforts since the 1970s (Berrigan 1988; 1990; GSMFC 2010) designed to maximize area of material covered. Reef materials were either quarried shells, crushed granite, or a Kentucky-sourced limestone of graded size (often #4, 25–64 mm) transported on barges and "planted" at specific locations (Table 1; FDACS 2015; 2016a, b; 2017).

Site selection was based on local knowledge of historical or extant reef locations. Three state agencies, FWC, Florida Department of Agriculture and Consumer Services, Division of Aquaculture (FDACS), 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 the National Fish and Wildlife Foundation (NFWF). Four projects took place in Apalachicola Bay, one each in Pensacola and St. Andrew bays (Figure 3; Table 1). Across all projects, the realized area and density of cultch material deployed varied from the planned application due to construction challenges and storm events. These challenges resulted in uncertainty in the restored reefs' actual area and cultch density.

The relationship between freshwater discharge from the Apalachicola River and oyster populations in Apalachicola Bay is of significant management concern and a focal aspect of a US Supreme Court Case (Florida v Georgia, No 142 Original. 2014). Because Apalachicola Bay is the only one of these three bays where upstream reservoir operations can influence freshwater inputs (Leitman et al. 2015), we summarized river discharge for the Apalachicola River as a proxy for salinity and nutrient inputs before, during, and after restoration efforts. We did this by plotting the percent deviation in mean river discharge (cubic feet per second [CFS] by convention; USGS gauge 02358000) from the mean Period of instrument records by month and year. To capture antecedent river discharge conditions, we began this time series in 2002, 10 years before the oyster fishery collapse and 13 years before the restoration projects covered by this study.

# Methods

## Field collections

Similar oyster monitoring methods were followed across projects to count live oysters and measure the mass of cultch material (Florida Fish and Wildlife Research Institute 2021). Divers randomly placed ¼ m2 (0.5 m on each side) quadrats at restoration sites, removed all oysters and cultch material to wrist depth, and placed the cultch and oysters in bags. Bags were returned to the vessel, processed on location, or returned to the lab. Oysters were counted, heights measured, and cultch biomass was recorded. Restoration and monitoring efforts occurred at different times depending on bay and Project. To simplify analyses, we created a time variable "period", a continuous variable that combined sampling months into common blocks of time with winter (October–March), represented by even numbers, and summer (April–September), represented by odd numbers).

## Fisheries-dependent data

Annual oyster landings (meat pounds; FWC 2022) and trips were summed for each county bordering each bay, and catch-per-unit-effort (CPUE) was calculated as landings/trips.

## Data analysis

We conducted five related analyses. For Question 1, we assessed how oyster counts changed following restoration in all three bays (Pensacola, St. Andrew, and Apalachicola) while controlling for differences in sampling effort. Questions 2 and 3 explored whether oyster spat counts in Apalachicola Bay were influenced by freshwater discharge and how counts differed over time, cultch material, and cultch density. This cultch type analysis is only possible for Apalachicola Bay because multiple studies were conducted in this bay (Table 1). For Question 4, we assessed trends in oyster cultch biomass across materials (Apalachicola only) and bay (Question 5). For Questions 4 and 5 we summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, site, and Period (defined below). This sum would include the cultch material placed on the reef during restoration and any cultch material (living or dead) accumulated on the substrate. Total cultch weights were made integers by rounding to the nearest whole kilogram. We used methods following Moore et al. (2020), and the dependent variables were the number of spat (<26mm shell height), seed (26-75mm shell height), or legal-size oysters (>75mm shell height) depending on the question. The independent variables were as follows.

* + Period, a continuous variable for time considered, which combined sampling months into blocks of time—winters (October–March), represented by even numbers, and summers (April–September), represented by odd numbers. (Questions 1-5)
  + Bay (Pensacola, St. Andrew, or Apalachicola) was a categorical variable, comparing restoration responses by bay. (Questions 1 and 5)
  + Type and density of cultch material were represented as a single categorical variable by the project name, as each of the four Apalachicola Bay projects used a different cultch material, density, and start time. (Questions 3, 4)
  + River discharge metrics based on the number of days discharge was below specified levels. (Question 3)

We used the restoration site (a named oyster reef) as a random effect (uniquely named for each site and bay or site and Project combination) to account for correlation among quadrat samples at each site (Questions 1-5).

The analyses followed these general steps:

1. Counts of live oysters in each bay and for each restoration site and Period were summed into three size classes (the dependent variables): spat (<26 mm shell height), seed (larger than spat but below minimum legal harvest size, 26–75 mm shell height), and legal to harvest (>75 mm shell height). 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 classes 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 rounded to convert the numbers of oysters per size class to integers to match the NRDA-4044 and GEBF-5007 data.
2. 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 separately varied over different independent variables (Question 1), using the R package glmmTMB (Brooks et al. 2017).
3. We assumed that the total oyster counts per site would be related to the sampling effort (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). This change effectively caused our models to predict the rate measured as count/quadrat while maintaining the dependent variable as an integer of counts. 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 as the dependent variable and offsetting for effort, instead of converting the counts to CPUE based on the area sampled, has two main advantages. First, it maintains the response as an integer, allowing a negative binomial distribution (appropriate for oyster count data; Moore et al. 2020); second, fitted values and confidence intervals do not contain negative values (Zuur et al. 2009).
4. Comparisons were made between models with different combinations of independent variables using the Akaike information criterion (AICc). The lowest AICc value represents the best fit of the models tested (Burnham and Anderson 2002).
5. Autocorrelation in the residuals for the top model was assessed by using the DHARMa package (Hartig 2022) in R (R Core Team 2022). This approach simulates new response data from the specified model, 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 was assumed at a p<0.05 level.
6. 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 emmeans (Lenth 2022) and ggeffects packages (Lüdecke 2018) in R (R Core Team 2022).

*Question 1: Oyster restoration response across Pensacola, St. Andrew, and Apalachicola bays*

We first looked broadly at oyster population responses to restoration across three bays (Apalachicola, Pensacola, and St. Andrew, Question 1). The dependent variables were the number of oysters in the spat, seed, or legal-size categories (separate analyses for each category). The independent variables (main effects) were Period (continuous) or Bay (categorical). We fit five models to the data: Model 0 was intercept-only, Models 1, 2, and 3 included Bay, Period, or both Bay and Period as main effects, respectively. Model 4 included the interaction between Period and Bay. Model 5 allowed trends in oyster counts to vary across site in each Bay (site nested within Bay). Model 6 was the same as model 5 but also allowed different dispersion parameters for the negative binomial model for each Bay. We used the default glmmTMB optimizer (nlminb) for fitting all models, and no convergence issues were identified.

*Question 2: How do oyster trends vary among restoration projects in Apalachicola Bay?*

Restoration efforts in Apalachicola Bay differ from Pensacola and St. Andrew bays because there have been at least four restoration efforts since 2015 in Apalachicola Bay using different materials and starting at different times (Table 1), and only one restoration effort in the other bays. We hence focus here on only Apalachicola Bay. For Question 2 (change in oyster counts across projects) and Question 3 (spat count association with freshwater discharge), we assessed the independent variables of cultch material and density (which varied by Project) and freshwater discharge (which varied over time). As in Question 1, 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. For Question 2, we fit eight different models to the data (Table 3). We checked model convergence using the default glmmTMB optimizer nlminb and the BFGS. Models that converged using both estimators had similar results, but only the BFGS converged for all models, so model comparisons were made based on results using BFGS and models compared with AICc. The autocorrelation of the residuals was checked with the DHARMa package (Hartig 2022). 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 NFWF-2021) less than two years before. If the materials, amount, or time since construction completion significantly influenced oyster reef restoration performance, the predicted values for each Project in the common Period should differ.

*Question 3: Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?*

We then compared the best-fitting model from Question 2 (Table 3) to four additional models which included different Apalachicola River discharge metrics, to see if model fit improved (Table 4). River discharge metrics were the number of days in each Period or the prior Period (as a measure of antecedent discharge) when 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. Regardless, we used this reference point to indicate low freshwater inputs. A discharge level of <6,000 CFS indicates extremely low river discharge because it approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam.

*Question 4: Is cultch biomass related to the number of live oysters in Apalachicola Bay?*

To assess relationships between oyster spat densities and cultch densities we summarized biomass of cultch per quadrat and treated cultch biomass as the response variable in the same negative-binomial GLMM models used to assess the response of oyster spat counts in Question 2 (Table 2). We fit ten different models to the data, to assess the relationship between cultch mass and Period, Project, SP (random effect; a variable combining site and project name). We also included the sum of spat in each quadrat as a factor (Spat sum) and the interaction between Spat sum and Project (Spat sum:project) to see if the relationship between live oyster spat and cultch mass differed by Project (Appendix 2). Some of these models were overfitted thus, comparisons were made with eight simpler models (Table 5; Appendix 2).

*Question 5: How does cultch material persist in all three bays?*

To explore how cultch material persisted in different Bays (Table 6) and by Project within Apalachicola Bay (Table 7), we used negative binomial GLM models to assess how the sum of cultch weights changed over time in each bay (all projects). In Apalachicola Bay we assessed persistence of cultch material by Project (because of different materials and restoration time frames). Data were summarized by Project, and calculations of mean and variance by Project suggested the data were over-dispersed (variance > mean) supporting the use of a negative binomial distribution. To create a comparative framework across substrates, we predicted the amount of cultch per ¼ m2 in the last monitoring period for each study (Figure 3).

Data and all code used for the analyses are available from the following Git repository: https://github.com/billpine/panhandle\_oyster\_response.git.

# Results

## River discharge patterns

Apalachicola River discharge deviated significantly (50–100% below the average for the Period of instrument records; Figure 4) for three or more months in 2002, 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). Regional river discharge patterns for 2013–2022 were generally closer to average than 2002-2012.

## Trends in fisheries-dependent data

Trends in FWC fisheries-dependent data since 1986 show that the Apalachicola Bay commercial fishery (trips and landings) was larger than those of Pensacola and St. Andrew bays combined. Apalachicola trips and landings increased sharply during the early 2000s, peaking before the fishery collapse 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. 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.

## Question 1: Oyster restoration response across Pensacola, St. Andrew, and Apalachicola bays

Plots of the raw CPUE for spat, seed, and legal-size oysters in all three bays show values near zero for all size classes (Figures 5-7). The best fitting GLM (Table 2; Appendix 2) suggests that oyster restoration responses over time in each bay were different, but none of the predicted responses suggest a positive response in counts of live oysters after restoration. For live spat in Apalachicola and St. Andrew bays, we found the coefficient of the slope describing trends in live oyster spat per quadrat over Period did not differ from zero (p=0.96 and p=0.23). But the slope coefficient did differ from zero for Pensacola (p=0.0006) and this slope coefficient was estimated to be negative (beta coefficient = -0.39) and highly uncertain (SE = 0.11, 95% CI = -0.61 – 0.17). Predicted live oyster spat (marginal means) per quadrat for Apalachicola was 14.08 live spat (95% CI 5.29-37.45), Pensacola was 0.70 live spat (95% CI 0.16 – 3.14), and St. Andrew Bay predicted live oyster spat was 226 (95% CI 13.79 – 3703.89).

A similar pattern was observed for seed-size oysters across bays, with the slope coefficient not differing from zero for Apalachicola Bay (p=0.99) and St. Andrew Bay (p=0.68) but differing from zero for Pensacola Bay (p=0.02) with a decline in seed size oysters over time (beta = -0.34, SE = 0.14, 95% CI = -0.61 – -0.06). Counts of legal-size oysters were near zero in all bays (Figure 5), creating model convergence issues limiting further analyses of legal-size oysters (Appendix 2). These results suggest a positive response to restoration (increase in counts) was not observed for any size class of oysters in Apalachicola, St. Andrew, or Pensacola bays.

## Question 2 How do oyster spat temporal trends vary among separate restoration projects in Apalachicola Bay?

Trends in oyster spat CPUE by Project over time in Apalachicola Bay (Figure 8) suggest an initial increase in oyster spat immediately following restoration for projects where monitoring data were available (NFWF-1 and NFWF-2021) but as with the NRDA-4044 and GEBF-5007 projects within 3-4 periods following restoration spat numbers are near zero or extremely low (Figure 8). When high counts of spat were observed, these spat did not persist to seed or legal size (Figures 9-10). To examine trends in Apalachicola Bay oyster spat by Project, we created a new variable (SP) which combined the site and project name. This allowed us to fit models to the data which nested site within Project and allowed Period to vary across Project (Appendix 2). We fit eight different models to the data (Table 2; Appendix 2). Of the eight models fit to the data (Table 2, Appendix 2), the model which included terms for Period, Project, a nested period by SP term, and an interaction term between Period and Project while controlling for effort was the best fitting (Table 2). For three of the projects, GEBF-5007, NRDA-4044, and NFWF-2021 the coefficient of the slope of live oyster spat counts over time (Period) did not differ from zero (p = 0.51, p= 0.51, p= 0.09) and for the NFWF-1 project the slope did differ from zero (p<0.0001) and this trend was negative (slope coefficient beta = -0.64, SE = 0.15, 95% CI = -0.94 – -0.35). These results demonstrate that none of the restoration projects in Apalachicola Bay have had the desired positive response over time to restoration.

We then predicted the marginal means of oyster spat from a single ¼-m2 quadrat in the last Period of sampling for comparison purposes between each Project using the best fitting model from Table 3. For the projects that used limestone rock, predicted live oyster spat for GEBF-5077 in period 12 was 15.73 live spat per quadrat (95% CI 8.45 – 29.27) and for project NFWF-2021 in period 15 we predicted 119.03 (95% CI 30.88 – 458.82). For the projects that used shell cultch, for NRDA-4044 in period 13 we predicted 5.14 live oysters (95% CI 3.06 – 8.63), and for NFWF-1 we predicted in period 9 there were 5.39 live oyster spat (95% CI 1.20 – 24.26).

Question 3 Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?

We added coefficients describing different river discharge metrics to the best fitting model comparing live spat counts across Project and time in Apalachicola Bay to see whether including river discharge information would improve mode fit (Table 3). These river discharge metrics include the number of days river discharge was below 12,000 CFS, days below 12,000 CFS lagged by 1 period, number of days river discharge was below 6,000 CFS and days below 6,000 CFS lagged by 1 period. Including these river discharge metrics did not improve model fit (Table 3) suggesting that the observed lack of positive response in live oyster spat was not influenced by river discharge metrics assessed (Figure 11).

Question 4: Is cultch biomass related to the number of live oysters?

Simple plots of mean cultch weight (kg, x-axis) and total live spat (y-axis) per quadrat suggests that for the two studies monitored immediately following cultching (NFWF-1 and NFWF-2021) as the number of live spat increases, so does cultch biomass, but only for one or two periods (Figures 13 and 14) before the number of spat collapses and retracts toward the origin, even for the same biomass of cultch (Figure 14).

Efforts to predict cultch biomass had little success (Appendix 2). Diagnostic assessments of model fitting to cultch biomass data suggested most models were overparameterized (Appendix 2). The best fitting model (lowest AICc and highest model weight) did not include oyster spat as a parameter (Table 5).

Question 5: How does cultch material persist?

The best fitting model comparing trends in oyster cultch biomass over Period across all three bays included an interaction term between Period and Bay, suggesting a different response on oyster cultch biomass over time in each Bay. St. Andrew and Pensacola bays only received a single cultching treatment, compared to multiple cultching treatments over time for Apalachicola Bay. For St. Andrew Bay the slope did not differ from zero (p=0.23) suggesting a non-significant trend in cultch biomass over time. In Pensacola Bay the slope did differ from zero (p=0.02) and the sign of the slope coefficient was negative (beta = - 0.03) suggesting cultch biomass decreased over time.

Because Apalachicola Bay received multiple cultching treatments, we examined trends in cultch biomass in this bay using models like Question 2, which allowed for unique responses by Project over time. The NFWF-2021 Project did not have a significant slope parameter (p=0.44), but for the other three projects the slope parameter did differ from zero (GEBF-5007 p=0.02; NFWF-1 p<0.0001; NRDA-4044 p=0.0002) and the slope was positive for GEBF-5007 but negative for NFWF-1 and NRDA-4044 (Appendix 2). Cultch persistence thus varied by Project over time.

We then predicted the marginal means of oyster cultch biomass from a single ¼-m2 quadrat in the last Period of sampling for each Project for comparison purposes between projects in Apalachicola Bay. Predicted oyster cultch biomass for the NFWF-2021 (limestone cultch) Project was 8.58 kg per ¼-m2 quadrat (Period 15, 95% CI 4.03–18.30); GEBF-5077 (limestone cultch) was 4.29 kg per ¼-m2 quadrat (Period 12, 95% CI 2.94 – 6.27); the NFWF-1 (quarried shell) was 0.97 kg per ¼-m2 quadrat (Period 9, 95% CI 0.47 – 2.02); and NRDA 4044 (shell cultch) predicted cultch biomass was 1.45 kg per ¼-m2 quadrat (Period 13, 95% CI 1.01 –2.09).

*Discussion*

Restoration efforts in the Gulf of Mexico region are widespread owing both to the large need, and substantial funding resources available related to the *Deepwater Horizon* oil spill. The performance of these restoration efforts, conducted on behalf of the public, must be assessed frequently and rigorously to ascertain whether they are successful or whether new approaches are necessary. We examined oyster restoration projects across three different bays in the Florida panhandle, and evaluated how recruitment of spat, seed, and legal-size oysters responded to the deployment of varying cultch types and densities – an often-used restoration approach. We found the oyster populations did not respond as expected to the restoration actions. Our results suggest three key points

(1) Oyster populations in Pensacola, St. Andrew, and Apalachicola bays do not appear to have responded as designed 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 result suggests there may be fundamental flaws in the design of oyster restoration projects, that there have been ecosystem changes that now limit oyster population response, or both.

(2) The lack of oyster population response to restoration actions is not readily explained by environmental or fishery conditions. The analyses cover a time when river discharges ranged from moderate drought to normal for the instrument period of recorded river discharge. This observed river discharge pattern and concurrent lack of oyster response suggest that salinity, and other river-related ecosystem drivers, such as nutrients, were near average when oyster populations failed to respond positively to restoration. This lack of response has also happened while commercial fisheries have declined sharply (Apalachicola Bay) or have had extremely low landings and trips (Pensacola and St. Andrew bays). The singular, additive, or interacting effects of environmental and fishery forces on oyster population resilience, recovery, and management is a persistent uncertainty in Florida and across the species' range.

(3) Some restoration efforts have not triggered any positive response as measured by oyster spat across the range of cultch material deployed from < 1 kg per quadrat to more than 12 kg of cultch per quadrat using either shell or rock material (NRDA-4044 and GEBF-5007; Figures 13 and 14). This result suggests that even when cultch material is present, oyster spat may exist for only one or two periods before collapsing as demonstrated for projects NFWF-1 and potentially NFWF-2021. The relationships between counts of spat and 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.

Interestingly, the loss of oyster spat is much faster than the loss of cultch biomass on the same reefs. This rapid oyster spat loss also occurs on unrestored reefs from similar monitoring efforts in Apalachicola Bay (Johnson et al. in-review). Figures 13 and 14 suggest that observed oyster spat losses may be occurring during winter months (October-March). While this is possibly an artifact of the irregular sampling necessitating the use of combined months of time in our analyses, winter is most likely when abiotic stressors (high temperatures, low dissolved oxygen) are lower, thus spat survival is potentially higher in winter. We recommend that counts of oyster spat take place in winter periods when spat settlement (new recruits) is not actively occurring. Winter spat counts may be more useful in informing relative year-class strength and recruitment to legal size than summer spat counts when high losses are expected to occur simply as a function of oysters having a type-III survival curve.

A final hypothesis based on these empirical and previous modeling for Apalachicola Bay oysters (Pine et al. 2015; Johnson et al. in-review) and generalized oyster population modeling efforts (Johnson et al. 2022), is that Pensacola, St. Andrew, and Apalachicola bay oyster populations may be degraded to the point that current restoration actions are ineffective in reversing the observed oyster population collapse. Pine et al. (2015) highlighted the risk of a catastrophic and persistent failure in the Apalachicola oyster fishery if oyster recruitment levels remained below the average reported in the available independent fisheries monitoring data (1990–2013). Johnson et al. (in-review), using the same fisheries independent data as Pine et al. (2015) but updated through 2021, found very high spat mortality rates following the 2012 Apalachicola fishery collapse. 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 scale of restoration or some sort of natural perturbation necessary to shift this system from a resilient, but undesired state to a desired, more productive state, is unknown (Pine et al. 2022). But the reversal of the collapse is likely many orders of magnitude larger than restoration efforts that have been attempted so far (Johnson et al. 2022). Even if these massive restoration efforts were completed, the likelihood of their success is unknown because as designed restoration is a test of a single hypothesis – lack of substrate is limiting oyster population recovery.

## Disappointing restoration results

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 to a desired, high-abundance state. This conclusion is supported by data from different watersheds with restoration efforts using similar materials, construction designs, and monitoring programs.

In Apalachicola Bay, project NFWF-1, a shell cultch project, and NFWF-2021, a rock cultch project, live oyster spat counts immediately after restoration were several orders of magnitude greater than those in any other project or Period (Figures 8-10). In projects GEBF-5007 and NRDA-4044 no increases in spat settlement were recorded in response to restoration. However, these projects did not begin monitoring oyster response until 6-18 months post-construction, meaning any potential restoration responses immediately after restoration were not observed. Potentially these projects also saw large increases in spat and then rapid declines immediately after restoration like NFWF-1 and NFWF-2021, but because of the lag between completion of restoration and monitoring this is not known (Figures 5, 8-10). Critically for Project NFWF-1 these high initial spat counts did not result in higher counts in seed or legal-size oysters in subsequent periods (Figures 5), nor were these high spat counts observed again for this Project (Figure 5).

The reasons for observed higher spat counts immediately following restoration in Apalachicola Bay (projects NFWF-1 and NFWF-2021) yet a lack of observed spat counts in similar magnitude even with similar cultch biomass levels in other projects (Figures 13 and 14) is unknown. Though the mean predicted live oyster spat values tended to be lower for shell substrate compared to rock, different starting times for projects, limit this conclusion. However, confidence intervals in estimated live oyster spat do generally overlap across projects with different substrates in Apalachicola and patterns of either no response (NRDA-4044 and GEBF-5077 for Apalachicola, Pensacola, and St. Andrew bays), or positive response followed by rapid declines in spat (NFWF-1; Apalachicola bay only) is consistent.

The relationship between the weight of cultch and the number of spat per quadrat across projects (color dots) and sites (individual plots) in Apalachicola Bay (the only bay where multiple materials and projects were used) is complicated (Figures 13-14). We found no clear pattern across sites in Apalachicola between cultch weight and total number of spat and Project (Figure 13). For projects GEBF-5007 (rock) and NRDA-4044 (shell), spat counts were near zero across a range of cultch biomass levels. Importantly, oyster spat response to restoration was not monitored for either Project immediately after restoration was complete (Figure 3). For other projects, NFWF-1 (light blue dots, shell cultch) and NFWF-2021 (red dots, rock cultch) show a general pattern of increasing spat in quadrats with more cultch biomass (Figure 13).

Plotting mean cultch weight and total spat by Project and Period in Apalachicola Bay suggests that total spat in each quadrat increases as cultch weight increases per quadrat, but only for one or two periods (Figures 13 and 14). Statistical analyses of these patterns was difficult (Appendix 2) but there is some suggestion that including the number of live spat as a parameter did not improve on our model assessing patterns in cultch biomass over time (Table 5; Appendix 2). The available data show that for two studies the total number of spat per quadrat increases initially post-restoration, but then the number of oyster spat rapidly declines (even for the same biomass of cultch; Figure 14). Ultimately the pattern observed in these data suggests that the observed total number of spat and cultch biomass per quadrat collapses and retracts toward the origin over time, as seen in projects NFWF-1 and NFWF-2021 (Figure 14); although Period 15 is informed only from samples in May (Appendix 1). This is an important result because it shows that the live oyster spat counts do not always persist even when apparently (perhaps minimally) sufficient levels of cultch are available.

Has restoration worked previously?

While the current restoration efforts appear to have failed to restore oysters, similar actions are reported to be successful in Florida in the past over relatively short time periods (Berrigan 1988; 1990). Restoration efforts in Pensacola, St. Andrew, and Apalachicola 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) which may or may not have contributed to rapid oyster fishery recovery as measured by trips and landings during the late 1980's – 2010's for Apalachicola whereas St. Andrew and Pensacola bay fisheries dependent data suggests only fishery declines to very low trips or landings within the first 10 years of available data. Irregular cultching efforts have taken place in St. Andrews and Pensacola Bays since the 1970's, however, these restoration efforts have not been assessed, and based on fisheries dependent data the fisheries do not appear to have responded positively to restoration efforts.

A more recent restoration effort in Apalachicola Bay is documented in Kimbro et al. (2020) who conducted similar restoration experiments to Berrigan (1988) using quarried oyster shells on reefs 0.4 ha in size at shelling densities of zero, 153 m3, and 306 m3 (over a 0.4 ha area). Kimbro et al. (2020) observed a positive response to oyster reef restoration ten 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). Kimbro et al. (2020) also observed higher oyster counts (defined as juveniles <25 mm and adults ≥25 mm) on reefs with increased reef mass. Thus, for the Kimbro et al. (2020) work and two of the projects assessed here (NFWF-1 and NFWF-2021), short-term spat responses were evident following the placement of cultch material. Critically, follow-up assessments beyond 10 months are unavailable for the reefs discussed in Kimbro et al. (2020), but our analysis of reefs that were restored around the same time with similar materials and cultch densities during NFWF-1 several years post-construction and found that the initial oyster population response to restoration as measured by spat counts did not persist through time (Figures 5; 9-10). The reason this spat response was only observed immediately following cultching and not in subsequent periods, nor did the spat that were observed persist to seed or legal sizes, is a critical uncertainty that must be addressed to inform current and future restoration efforts in Apalachicola Bay and elsewhere.

## Reasons restoration may not be working

One possible explanation for the observed lack of positive oyster population response observed in Pensacola, St. Andrew, and Apalachicola bays is that the restoration actions were inappropriate—e.g., inappropriate material, density/height, or total area. The cultch density used following the 1985 oyster fishery collapse and closure in Apalachicola Bay (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). Regarding the total area necessary for restoration, Pine et al. (2015) suggested 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 assessed by Pine et al. (2015) is the characteristics of cultching material, such as density (amount per area, and whether that material persisted on the area or was dispersed, which drives restoration height), material type (shell vs. rock, or different sizes of material), that would be required to prevent collapse.

Because the shell used in cultching is less dense than rock used in cultching, the differences observed in biomass per quadrat across studies in Apalachicola Bay are not surprising. These results suggest a biomass decline of about 50-80% for the shell material and an increase of about 15-50% in cultch biomass for the rock material predicted by the end of monitoring. Critically, these are measures of mass, not surface area, and the extent of oyster spat settlement on substrate depends on the surface area. The relationship between cultch area, persistence, and settlement suitability are all areas of future work with important implications for restoration efforts (Hemeon et al. 2020).

Another possible explanation for our observed restoration failure is that the elevation of the restored reefs was too low. Previous oyster restoration work has emphasized the importance of reef elevation as a critical factor (Colden et al. 2017; Smith et al. 2021). 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.

The importance of elevation has been confirmed in several recent oyster restoration projects. Smith et al. (2021, 2022), 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 elevation, 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. Oyster densities on the restored Lone Cabbage and nearby reference reefs are now similar (W.E. Pine, *unpublished information*). The 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 (about 0.05 m; R. Gandy FWRI). In the restoration projects examined in this study, the material used is either small and dense (#4 limestone 19–38 mm in diameter) or larger, and less dense (quarried oyster shell 37–75 mm in diameter) and likely susceptible to being transported away from the intended restoration site, buried in sediment, or sculpted by currents to a low-relief structure. 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 12). Critically, oyster spat settlement has been very low for unknown reasons and it is possible that restoration efforts do not recreate the ecology of the pre-collapsed system.

A final possible explanation for why the recent restorations failed is that the materials used were not conducive for oyster spat settling and surviving. 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. Previous restoration projects in Apalachicola Bay (Berrigan 1988; 1990) used clam shells dredged from Lake Pontchartrain, Louisiana as cultch material or quarried oyster shell (Kimbro et al. 2020). Smith et al. (2021) describes a successful long-term oyster restoration project using dredged shells in Chesapeake Bay, Virginia. The limestone used in this study's restoration projects is 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 before 2010 (Zu Ermgassen et al. 2012). 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 the NFWF-1 Project did not answer the questions as proposed, and whether cultching in Apalachicola Bay in previous years has contributed meaningfully to the sustainability of harvests is doubtful based on the observed oyster fishery collapse in 2012. Project NFWF-2021 (the only Project begun after Apalachicola Bay fishery closure) also observed a large increase in spat post-construction, and seed oysters were present in subsequent samples (Figure 10). Continued monitoring of this Project will be important to understand whether these seed oysters survive to legal size, but design deficiencies including lack of spatial replication and paired unrestored control sites will create challenges in drawing strong conclusions related to the role of the fishery closure. These and other experimental design issues should be addressed in future restoration experiments (Pine et al. 2022).

## Future directions

The repeated and ongoing cultching efforts in Florida estuaries to reverse observed declines in oyster populations test a single hypothesis—that oyster populations have declined because of limitations in cultch. The ways these restorations have been designed, implemented, and monitored make it difficult to sufficiently evaluate more detailed hypotheses about the characteristics of cultch that are necessary. For example, differences in the monitoring timing make it challenging to differentiate the failure of oyster spat to successfully settle on restored material, from failure to survive past some critical size or life history stage. Further, the restoration projects, though they differ in materials, are similar in that they all created low elevation restored refs, which is in part related to them all consisting of smaller-sized materials. While these approaches to restoration may be understandable given their similarity to past restoration efforts (Berrigan 1990), the lack of experimental relief has likely hampered learning as to whether cultch material is limiting oyster populations in the Florida panhandle. Alternative hypotheses related to oyster population decline—include cascading predatory responses (Kimbro et al. 2017), recruitment overfishing, discard mortality, virulent disease (known or unknown), or some combination of these remain largely unassessed and impossible to address with available data.

*Conclusions*

Oyster populations in Apalachicola, Pensacola, and St. Andrew bays appear resistant to current restoration approaches and recovery at this time, despite legal actions designed to force equitable water allocation to reduce salinity (Apalachicola Bay; Barnett 2021), large restoration efforts (totaling more than $14,200,000; Table 1), low levels of reported harvest and effort (Pensacola and St. Andrew bays), and two years of a five-year harvest moratorium (2020–2025) in Apalachicola Bay. Regrettably, many of the same restoration and management uncertainties identified in this assessment have persisted for decades or centuries in Florida (Swift 1897; Swift 1898; Camp et al. 2015; Pine et al. 2015).

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). This may be because many restoration efforts have not been designed with resolving uncertainty as the major goal because of a belief that what should be done was strongly influenced by past success (even if past restoration was never assessed). But this approach does not consider that the system states may not be the same. In a classic assessment of barriers to learning in adaptive ecosystem assessment and management, Gunderson (1999) 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 is critical to informing future restoration efforts, including nearly $20 million in additional restoration funding currently being considered for Apalachicola Bay. Decisive agency, academic, and community leadership emphasizing a commitment to learning to improve restoration and management is needed successfully restore oyster populations to support ecosystem services and viable fisheries for the benefit of the people of the Gulf of Mexico region.

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# References

Barnett, C. 2021. Why America's water waters are futile. Tampa Bay Times. April 9, 2021. https://www.tampabay.com/opinion/2021/04/09/why-americas-water-wars-are-futile-column/

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, G. and Seaman W. 1988. Estuarine habitat and fishery resources in Florida. Pages 337–435 in W. Seaman Jr., editor. Florida aquatic habitat and fishery resources. Florida Chapter, American Fisheries Society, Eustis, Florida.

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.

Florida Department of Agriculture and Consumer Services. 2015. Natural Resource Damage Assessment oyster reef restoration in Apalachicola Bay purchase and placement of oyster cultch material. Tallahassee, Florida. 37 pp.

Florida Department of Agriculture and Consumer Services. 2016a. Natural Resource Damage Assessment (NRDA) oyster reef restoration in the Pensacola Bay system oyster cultch deposition.Tallahassee, Florida. 23 pp.

Florida Department of Agriculture and Consumer Services. 2016b. Natural Resource Damage Assessment (NRDA) oyster reef restoration in the St. Andrews [sic] Bay system oyster cultch deposition. Tallahassee, Florida. Cultching Report 25 pp.

Florida Department of Agriculture and Consumer Services. 2017. Gulf coast ecosystem restoration council grant oyster reef resotration [sic] in the Apalachicola Bay sustem oyster cultch deposition DEP greement RES01.Tallahassee, Florida. 35 pp.

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

Hemeon, K. M., Ashton-Alcox, K. A., Powell, E. N., Pace, S. M., Poussard, L. M., Solinger, L. K., & Soniat, T. M. 2020. Novel shell stock–recruitment models for Crassostrea virginica as a function of regional shell effective surface area, a missing link for sustainable management. Journal of Shellfish Research 39: 633-654.

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.

Lenth R. 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package

version 1.8.1-1, https://CRAN.R-project.org/package=emmeans.

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.

Smith, R.S., Cheng, S.L. and Castorani, M.C., Meta‐analysis of ecosystem services associated with oyster restoration. Conservation Biology. https://doi.org/10.1111/cobi.13966

Swift, F. 1897. Survey of the oyster regions of St. Vincent Sound, Apalachicola Bay, and St. George Sound, Florida. US Commission of Fishes and Fisheries, Extracted from Report of Commissioner for 1896. US Commission of Fishes and Fisheries, Washington, DC, 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. US Commission of Fish and Fisheries, Washington, DC, 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.