# 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 have focused on replacing oyster cultch (substrate) to promote spat settlement, increase recruitment, and bolster adult oyster populations. This study assessed outcomes of six such efforts, which used different cultch types and densities between 2015 and 2022 in three estuaries in the Florida panhandle (Pensacola, St. Andrew, and Apalachicola bays). Total restoration costs for these projects were more than $14 million. Oyster counts did not persistently increase following restoration, regardless of cultch type or density. Positive responses to restoration efforts were irregular and 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 study estuaries. Contributing elements are likely to include design and implementation factors such as materials used and the height of the restored reefs. However, monitoring programs have not been able to deliver a clear picture of what is hindering restoration success. For oyster restoration efforts to succeed, changes are needed both in their implementation and in the way they are monitored, in order to promote continuous learning and improvement.

# Introduction

Eastern oyster (*Crassostrea virginica*) populations in the northern Gulf of Mexico are depressed from historical levels. Since 2010, Florida, Alabama, Mississippi, Louisiana, and Texas have declared state- or federal-level oyster fishery disasters, and at least three states have implemented fishery closures (in Mobile Bay in Alabama, Apalachicola Bay in Florida, and Galveston Bay in Texas). As of the end of 2022, only one of these stocks (Mobile Bay) had reopened to harvest.

The reasons for regional oyster declines are widely speculated but poorly understood. Proposed reasons include prolonged drought, extreme rain events, freshwater releases from water management structures, environmental degradation, overharvesting, the *Deepwater Horizon* oil spill, and insufficient cultching (Petes et al. 2012; Pine et al. 2015; DHNRDA Trustees 2016; Kelly 2019; Gledhill et al. 2020; Du et al. 2021; MRD and NOAA 2021).

Many oyster restoration efforts in the Gulf of Mexico have focused on adding substrate to replace cultch, a matrix of living and dead material that oyster spat need in order to settle and grow, which was removed or displaced during fishing (Lenihan and Peterson 1998; Swift 1898; Lenihan and Micheli 2000; Howie and Bishop 2021). These restoration efforts attempt to convert 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, many restoration efforts are expected to persistently increase oyster populations so that they will provide and promote ecosystem services (Smith et al. 2022 a,b) 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 an evaluation of what has and has not worked is lacking. Such information is critical for guiding current and future restoration and management (Pine et al. 2022).

This study assessed ongoing and recently completed oyster restoration efforts in three large estuaries in the Florida panhandle where oyster populations are depressed and restoration efforts have taken place: Pensacola, St. Andrew, and Apalachicola bays. Assessing restoration across three separate estuaries with different watersheds reduced the likelihood of estuary-specific factors (such as water quality, predation, or disease) limiting the effectiveness of restoration. Much of our analysis focused on Apalachicola Bay, the only one of the three for which data are available from multiple projects using different cultch densities, and the only one with regulated river (freshwater) inputs.

We explored the following questions:

1. How have oyster counts varied over time in these bays?
2. In Apalachicola Bay, how have trends in oyster spat (the life stage hypothesized to respond first to restoration) varied over time across different restoration projects?
3. Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?
4. How do counts of live oyster spat compare across different cultch densities in Apalachicola Bay?
5. How well does cultch used in restoration persist in Pensacola, St. Andrew, and Apalachicola bays?

We found that large restoration programs in the Florida panhandle are not having the desired outcome of increasing live oyster populations of any size class. This may be due to project design flaws, environmental factors, or fishery effects, or a tipping point may have been crossed trapping oyster populations in a low-production state that is resistant to restoration (Johnson et al. 2022).

For restoration efforts to succeed, they must be frequently and vigorously assessed and adjusted as needed (Pine et al. 2022). Our work suggests that substantial uncertainty persists about how to restore oyster populations at large scales in Florida. This uncertainty can best be managed by using an adaptive management approach (Walters 1986; Walters et al. 1988) that treats restoration projects as ongoing experiments—promoting continuous learning and improvement and thus increasing the projects’ likelihood of success.

# Study sites

The study focused on three Florida panhandle bays (Figure 1):

* **Pensacola Bay** is the fourth largest estuary in Florida, with a surface area of approximately 50,990 ha. Reported oyster landings, trips, and catch per unit of effort (CPUE) for Pensacola Bay have declined since the mandatory trip-ticket program was fully implemented in 1986 (Figure 2).
* **St. Andrew Bay’s** oyster landings are mostly from the East Bay arm, which has a surface area of approximately 27,715 ha (Brim and Handley 2006). Oyster landings and trips for East Bay are not available, but landings have declined to near zero in surrounding counties in recent years (Figure 2).
* **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). It was closed to commercial harvest from December 2020 to December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

Restoration and monitoring efforts in these bays were led by three state agencies, under the sponsorship of the Natural Resource Damage Assessment and Gulf Environmental Benefit Fund), with funds from the *Deepwater Horizon* oil spill settlement (Table 1). Reef construction methods across projects were similar to other cultching efforts that have been carried out since the 1970s (Berrigan 1988; 1990; VanderKooy 2012), 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 designated locations (Table 1; FDACS 2015; 2016a, b; 2017). Site selection for restoration efforts was based on local knowledge of historical or extant reef locations. Four projects took place in Apalachicola Bay and one each in Pensacola and St. Andrew bays (Figure 3).

In all projects, the area and density of cultch that was deposited differed from that originally planned due to construction challenges and storm events. These challenges also resulted in uncertainty about the restored reefs’ actual area, cultch density, and vertical relief. All monitoring efforts were conducted on the same sites where restoration took place.

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 recent US Supreme Court Case (Florida v Georgia, No 142 Original, 2014). This case evaluated whether Georgia’s upstream water use altered salinities in Apalachicola Bay leading to the 2012 collapse of oyster populations (Kelly 2019). The US Supreme Court found that Florida failed to demonstrate that Georgia’s water use was the sole cause or a major contributing factor to the oyster population collapse and dismissed the case (Barrett 2021).

Apalachicola Bay is the only one of the study bays where upstream reservoir operations can influence freshwater inputs (Leitman et al. 2016) and freshwater inputs are what create estuarine conditions in all three bays. Continuous data on salinity and nutrient inputs before, during, and after restoration efforts are not available for the restoration sites in any of the three bays and region-wide water quality monitoring networks are lacking (Dale et al. 2021). Because of the management interest in Apalachicola Bay related to water inputs, we summarized Apalachicola River discharge as a proxy for salinity and nutrients (factors widely discussed to influence oyster populations; Fisch and Pine 2016) 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. We noted the frequency of months where discharge was below reference points related to floodplain inundation because of the management interest in the relationship between low-discharge periods and negative impacts on oyster populations. 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 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 and processed on location or returned to the lab. Oysters were counted, heights were measured, and cultch mass was recorded. Restoration and monitoring efforts occurred at different times depending on bay and project.

## Fisheries-dependent data

Annual oyster landings (meat pounds; Florida Fish and Wildlife Conservation Commission 2022) and trips were summed for each county bordering each bay, and CPUE was calculated as landings/trips.

## Data analysis

We conducted five related analyses, some targeting all three bays and some focused on Apalachicola Bay (for which we had the most detailed information from multiple restoration efforts). These analyses focused on how oyster counts changed at restoration sites (question 1); how they differed over time, cultch material, and cultch density (question 2); whether they were influenced by freshwater discharge (question 3) or cultch mass (question 4); and how cultch mass changed over time (question 5). The five research questions are discussed in more detail below.

The dependent variables used in this analysis were the number of spat (<26mm shell height), seed (26–75mm shell height), or legal-size (>75mm shell height) oysters; different size classes were relevant to different questions with most assessments focusing on counts of spat.

The independent variables were as follows:

* + **Period,** a continuous variable, combined sampling months into blocks of time in order to simplify analysis. Winters (October–March) were represented by even numbers, and summers (April–September) by odd numbers. (This variable was relevant to all five research questions.)
  + **Bay,** a categorical variable, compared restoration responses by bay—Pensacola, St. Andrew, or Apalachicola. (This variable was relevant to questions 1 and 5.)
  + **Project,** a categorical variable, represented both type and density of cultch material, as each of the four Apalachicola Bay projects used a different cultch material and density and had a different start time. (This variable was relevant to questions 3 and 4.)
  + **River (freshwater) discharge,** measured as the number of days discharge was below specified levels, served as a proxy for salinity and nutrient inputs. (This variable was relevant to question 3.)

We used the restoration site (a named oyster reef) as a random effect (uniquely named for each site + bay or site + project combination) to account for correlation among quadrat samples at each site. (This was relevant to all five questions.)

The analyses followed these general steps:

1. Counts of live oysters in each bay and for each restoration site and period were summed into the three size classes that served as our dependent variables: spat, seed, and legal to harvest. 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), which varied across sites. To control for this, 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).

1. 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).
2. Autocorrelation in the residuals for the top model was assessed using the DHARMa package (Hartig 2022) in R (R Core Team 2021). This approach simulates new response data from the specified model, qq plots to check for deviations from the expected distribution graphically, a K‑S test to see 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.
3. 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 (Lüdecke 2018) packages in R (R Core Team 2021).

These steps were applied to our five research questions as described below.

Question 1: How have oyster counts responded to restoration efforts across Pensacola, St. Andrew, and Apalachicola bays?

We first looked broadly at oyster population responses to restoration across all three bays. The dependent variables were the number of oysters in the spat, seed, or legal-size categories (separate analyses were conducted for each category). The independent variables (main effects) were period (continuous) or bay (categorical).

Mulitple models describing differenty hypothesis were fit 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 sites 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 have oyster spat trends varied over time across different restoration projects in Apalachicola Bay?

Apalachicola Bay has undergone more restoration efforts than Pensacola and St. Andrew bays in the last decade—at least four since 2015, using different materials and starting at different times, compared to only one each in the other bays (Table 1). This question hence focused on Apalachicola Bay. Both for this question and for question 3 (spat count association with freshwater discharge), also Apalachicola Bay–specific, we assessed the independent variables of project, which represented cultch material and density, and river discharge (which varied over time). The focus in these two questions was on spat counts because spat is the life stage hypothesized to respond first to restoration. 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 (NFWF-2021) less than two years before. If the materials, amount, or time since construction completion influenced oyster reef restoration performance (as measured by different numbers of oysters per sampling unit), the predicted cultch mass 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). Of the bays under study, only Apalachicola Bay has regulated river inputs (Apalachicola River).

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 CFS 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. One-year lags were also included to account for antecedent conditions and possible oyster population responses (Wilber 1992; Fisch and Pine 2016).

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

To assess relationships between oyster spat densities and cultch densities, we summarized mass of cultch per quadrat by site and period and treated cultch mass as the response variable in the same negative-binomial GLM models used to assess the response of oyster spat counts in question 2 (Table 2). We fit 10 different models to the data, to assess the relationship between cultch mass and period, project, and site (again a random effect). 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 well 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 (across 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 and 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 were generally closer to average for 2013–2022 than for 2002–2012.

## Trends in fisheries-dependent data

FWC 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.

## Response of oyster counts to restoration efforts (all three 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 to 0.17). Predicted live oyster spat (marginal means) per ¼ m2 for Apalachicola was 14.08 (95% CI 5.29 to 37.45), for Pensacola 0.70 (95% CI 0.16 to 3.14), and for St. Andrew Bay 226 (95% CI 13.79 to 3,703.89).

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 to −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). A positive response to restoration (increase in counts) was not observed for any size class of oysters in Apalachicola, St. Andrew, or Pensacola bays.

## Oyster spat trends across restoration projects (Apalachicola Bay)

Trends in oyster spat CPUE by project over time in Apalachicola Bay (the only study bay with data available from multiple projects) suggest an initial increase in oyster spat (the life stage believed to respond first to restoration) 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 18-24 months following restoration, spat numbers were 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 used the variable “site” as a random effect. 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 these eight models, the model which included terms for period, project, a nested period by site 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). 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 to −0.35).

These results demonstrate that none of the restoration projects in Apalachicola Bay have had the desired sustained increase in oyster spat following 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 per ¼ m2 (95% CI 8.45 to 29.27). We do not know the depth of material excavated, so if we assume only the top layer of cultch is removed we can convert to oysters/m2 by dividing the predicted number of quadrat by 0.25. This results in 62.9 oysters/m2 (95% CI 33.8 to 117.1). For project NFWF-2021 in period 15 we predicted 119.03 (95% CI 30.88 to 458.82) oysters per ¼ m2 or 476 oysters/m2 (95% CI 123.5 to 1835.3).

For the projects that used shell cultch, for NRDA-4044 in period 13 we predicted 5.14 live oyster spat (95% CI 3.06 to 8.63) per ¼ m2 (20.6 oysters/m2; 95% CI 12.2 to 34.5), and for NFWF-1 in period 9 we predicted 5.39 (95% CI 1.20 to 24.26) per ¼ m2 (21.5 oysters/m2; 95% CI 4.8 to 97.0).

## Effect of freshwater discharge on oyster spat counts (Apalachicola Bay)

We added coefficients describing different river discharge metrics to the best-fitting model comparing live spat counts across project and period in Apalachicola Bay (the only study bay with regulated river inputs) to see whether including river discharge information would improve model fit (Table 3). These river discharge metrics include the number of days discharge was below 12,000 CFS, days below 12,000 CFS lagged by 1 period, days 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 the river discharge metrics assessed (Figure 11).

## Effect of cultch mass on oyster counts (all three bays)

Simple plots of mean cultch weight and total live spat per quadrat suggest that, for the two studies monitored immediately following cultching (NFWF-1 and NFWF-2021), as the cultch mass increases so does the number of live spat—but only for one or two periods (6-12 months of time; 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 mass had little success (Appendix 2). Diagnostic assessments of model fitting to cultch mass 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).

## Persistence of cultch material (all three bays)

The best-fitting model comparing trends in oyster cultch mass over time across all three bays included an interaction term between period and bay, suggesting a different response on oyster cultch mass 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 nonsignificant trend in cultch mass 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 mass decreased over time.

Because Apalachicola Bay received multiple cultching treatments, we examined trends in cultch mass 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 mass from a single ¼ m2 quadrat in the last period of sampling for each project, for comparison purposes between projects in Apalachicola Bay. Again we do not know the depth of material excavated, so if we assume only the top layer of cultch is removed we can convert to kg/m2 by dividing the predicted oyster cultch by quadrat by 0.25. Predicted oyster cultch mass for the NFWF-2021 (limestone cultch) project was 8.58 kg per ¼ m2 (period 15, 95% CI 4.03 to 18.30 [ 8.58 kg/m2; 95% CI 16.1 to 73.2]); for GEBF-5077 (limestone cultch) it was 4.29 kg per ¼ m2 period 12, 95% CI 2.94 to 6.27; [ 17.16.58 kg/m2; 95% CI 11.76 to 25.08]); for NFWF-1 (quarried shell) it was 0.97 kg per ¼ m2 (period 9, 95% CI 0.47 to 2.02; [ 3.88 kg/m2; 95% CI 1.88 to 8.08]); and for NRDA-4044 (shell cultch) it was 1.45 kg per ¼ m2 (period 13, 95% CI 1.01 to 2.09; [5.80 kg/m2; 95% CI 4.04 to 8.36]).

# Discussion

Cultching efforts in Florida estuaries to reverse observed declines in oyster populations test a single hypothesis—that oyster populations have declined because of insufficient cultch. The ways the restoration efforts reviewed in this article have been designed, implemented, and monitored make it difficult to sufficiently evaluate more detailed hypotheses about the characteristics of cultch that are necessary to restore oyster populations—or whether cultch limitation is the actual reason for the collapse.

For example, differences in the timing of monitoring make it challenging to differentiate between the failure of oyster spat to successfully settle on restored material and their failure to survive past some critical size or life stage. Further, the restoration projects, though they used different materials, all created low-elevation restored reefs from relatively small materials. While this approach may be understandable given its similarity to past restoration efforts (Berrigan 1990), the lack of experimental contrasts in relief has likely made it difficult to determine whether cultch material is limiting oyster populations in the Florida panhandle.

Alternative hypotheses related to oyster population decline—including cascading predatory responses (Kimbro et al. 2017), recruitment overfishing, discard mortality, virulent disease (known or unknown), freshwater inflow, climate change and some combination of these—remain largely unassessed and impossible to address with available data. The reasons for the 2012 collapse and the decade-plus period of low oyster abundance are uncertain (Camp et al. 2015; Kimbro et al. 2017; Pusack et al. 2018; F et al. 2019; Johnson et al. in-press) and have been debated as far as the US Supreme Court (Kelly 2019; Barnett 2021).

We found that, after restoration efforts, oyster populations did not show a sustained increase, and cultch material persistence was variable. This has been the case in different bays within different watersheds, which reduces the likelihood of bay-specific abiotic or biotic conditions limiting restoration success. This suggests there may be a variety of factors inhibiting population recovery, including flaws in the design of oyster restoration projects, regional ecosystem changes that now limit oyster population response to restoration, or legacy environmental or fishery management effects that have resulted in the systems being trapped in a persistent low-population state (Johnson et al. 2022; Pine et al. 2022). The singular, additive, or interacting effects of environmental, ecological, and fishery forces on oyster population resilience, recovery, and management form a persistent uncertainty in Florida and across the species’ range.

For the restoration projects in Pensacola, St. Andrew, and Apalachicola bays, information which may have helped determine the proximal causes of restoration failure, and informed upcoming restoration efforts in these same systems—such as salinity, disease, oyster predators, and design aspects of the restored reef (including cultch type, area, and vertical changes in relief over time)—was either not collected or only collected after restoration. This uncertainty does not, however, have to be a barrier to improved restoration outcomes. Uncertainty can be addressed effectively using the adaptive management framework (Holling 1978; Walters 1986; Pine et al. 2022)—an approach for improving natural resource management by systematically learning from management outcomes. Adaptive management approaches to restoration have been recommended by the *Deepwater Horizon* Natural Resource Damage Assessment trustees (2017) and National Academies of Sciences, Engineering, and Medicine (NAS 2017, 2022), but these recommendations have so far not been widely implemented for oyster restoration (Pine et al. 2022). Greater commitment to adaptive management can improve learning and ultimately restoration outcomes (Pine et al. 2022).

## Spat responses to different cultch materials in Apalachicola Bay

Trends in oyster spat counts in the restoration data (Figures 13 and 14) suggest that observed oyster spat losses are occurring from October to March. The timing of these losses is surprising: winter is when abiotic stressors, such as high temperatures and low dissolved oxygen, are less likely to occur, thus increasing the potential for spat survival. However, average wind speeds from October to March are some of the highest of the year, and wind direction during this time is predominantly from the east and northeast; thus, stronger waves and currents during these months, destabilizing oyster reefs made from small materials and causing spat mortality. This is an area for future work.

In Apalachicola Bay, in projects NFWF-1 (shell cultch) and NFWF-2021 (rock cultch), 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 NRDA-4044 (shell cultch) and GEBF-5007 (rock cultch), 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 restoration responses immediately after restoration were not observed. These projects may also have seen 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 (Figure 5), nor were such high spat counts observed again for this project (Figure 5).

The reasons for the higher spat counts observed immediately after restoration in Apalachicola Bay for some projects but not others (Figures 13 and 14), even with similar cultch mass levels, are unknown. The mean predicted live oyster spat values tended to be lower for shell substrate than for rock; but different starting times for projects limit the reliability of this conclusion. 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) are consistent.

The relationship between cultch mass and the number of spat per quadrat across projects and sites (individual plots) in Apalachicola Bay (the only bay with multiple projects using multiple material types) is complicated (Figures 13–14). We found no clear pattern across sites in Apalachicola between cultch mass and total number of spat (Figure 13). For projects GEBF-5007 (rock) and NRDA-4044 (shell), spat counts were near zero across a range of cultch mass 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 (shell cultch) and NFWF-2021 (rock cultch) show a general pattern of increasing spat in quadrats with more cultch mass (Figure 13).

Plotting mean cultch mass and total spat by project and period in Apalachicola Bay suggests that total spat in each ¼-m2 quadrat as cultch mass increases, but only for one or two periods (Figures 13 and 14). Statistical analysis of these patterns was difficult (Appendix 2), but including the number of live spat as a parameter did not improve our model’s assessment of patterns in cultch mass over time (Table 5; Appendix 2). Ultimately the pattern observed in these data show total spat and cultch mass per quadrat both collapse and retract toward the origin over time, as seen in projects NFWF-1 and NFWF-2021 (Figure 14) and a pattern that should be carefully assessed in future sampling for colonization by spat and possible reversal in count and biomass trends. This is an important result because it shows that the live oyster spat counts do not always persist even when apparently (perhaps minimally) levels of cultch are available.

## Limited success of past restoration efforts

Recent restoration efforts in Pensacola, St. Andrew, and Apalachicola bays were guided by previous projects 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 1980s to 2010s for Apalachicola. In contrast, St. Andrew and Pensacola bay fisheries-dependent data indicate very low trips and landings for this same time period. Irregular cultching efforts have taken place in St. Andrews and Pensacola bays since the 1970s. 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 has been documented by 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). They observed a positive response to oyster reef restoration 10 months post-restoration (Kimbro et al. 2020 defined two size classes of oysters; juveniles <25 mm and adults ≥25 mm) during the same time frame as high oyster spat (< 25 mm) counts occurred on the NFWF‑1 project reefs covered by this study (Figure 6). Kimbro et al. (2020) also observed higher oyster counts on reefs with increased reef mass. Thus, for their work and for 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 (NFWF-1), found that, several years post-construction, the initial oyster population response to restoration, as measured by spat counts, did not persist (Figures 5 and 9–10). Spat count increases were only observed immediately following cultching and not in subsequent periods, nor did the spat that were observed persist to seed or legal sizes. The reason for this is unknown. This is a critical uncertainty that must be addressed in Apalachicola Bay and elsewhere.

## Potential reasons for limited success

One possible explanation for the apparent lack of restoration success is that the restoration actions were ineffective—for example, in their choice of material, density/height, or total area. The cultch density used following the 1985 oyster fishery collapse and closure in Apalachicola Bay, about 472 m3 per acre of shell cultch (Berrigan 1990), was similar to the density used in the largest and most recent restoration efforts (NRDA-5007 and FWC-2021, respectively), both using rock cultch, and similar to the highest treatment level of recent shell cultch projects for Apalachicola Bay (NFWF‑1; Table 1).

Regarding the total area necessary for restoration, Pine et al. (2015) recommended an intensive cultching program of about 50 ha per year—slightly more than the average area cultched each year between the 1985 post–Hurricane Elena restoration efforts and the beginning of regional restoration efforts in 2015 (Berrigan 1990). Aside from area, other optimum characteristics of cultching material—such as density (amount per area, and whether that material remains or is dispersed, which drives restoration height), type (shell vs. rock), and size—remain unknown.

Because the shell used in cultching is less dense than the rock used in cultching, the differences observed in cultch mass per quadrat across studies in Apalachicola Bay are not surprising. These results predict a decline of about 50–80% for shell cultch mass and an increase of about 15–50% in rock cultch mass 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 the apparent lack of restoration success is that the elevation of the restored reefs was too low. Previous oyster restoration work has emphasized the importance of reef elevation (Colden et al. 2017; Smith et al. 2022b). Additional elevation may be necessary to raise the cultch material into suitable water quality, hydrodynamic conditions, or avoid predators (Johnson and Smee 2014). Colden et al. (2017) found that oyster reefs with height > 0.3 m in two Virginia sub-estuaries within the Chesapeake Bay 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. (2022a, 2022b), as part of a 15-year assessment of the performance of an oyster reef restoration project in Virginia waters of the Chesapeake Bay, found that restored reefs were similar to unrestored reference reefs in 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 one Chesapeake Bay restoration project discussed above was about 0.14 m (Smith et al. 2022b, supplemental information); for another it was 0.4 m (Colden et al. 2017); and for the Lone Cabbage project in Florida it was about 0.36 m (Pine et al. 2022). These 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 Florida Fish and Wildlife Research Institute). We are not suggesting there is a uniform elevation requirement or even a minimum required elevation but are highlighting these successful restoration efforts as having contrasting elevation to adjacent areas without restoration. The relationships among elevation, inundation, wave action, oyster settlement, and persistence are complicated (Breitburg et al. 1995; Soniat et al. 2004; Morris et al. 2021).

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 to be 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.

Cultch material in various forms at different original mass levels has persisted on these restored reefs only at low mass levels (Figure 12), and it is possible that one reason for the low oyster spat settlement in this area is that restoration efforts may not have re-created the ecology that existed before the collapse – if this is possible.

A final possible explanation for the oyster population’s failure to respond as hoped to restoration efforts is that the materials used were not conducive to oyster spat settling and surviving. Materials used in oyster restoration efforts vary widely (Bersoza Hernandez et al. 2018; Goelz et al. 2020). In Florida, they include multiple types of limestone, quarried oyster shells, recycled clam shells, crushed granite, and artificial materials. Previous restoration projects in Apalachicola Bay used clam shells dredged from Lake Pontchartrain, Louisiana (Berrigan 1988, 1990), or quarried oyster shell (Kimbro et al. 2020). One successful long-term oyster restoration project in Chesapeake Bay used dredged shells (Smith et al. 2022b).

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, as 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 limestone 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). But whether cultching alone has contributed meaningfully to the sustainability of harvests overall is doubtful, based on the observed oyster fishery collapse in 2012 and lack of response to cultch additions examined here. The National Academies of Sciences, Engineering, and Medicine 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). Because of deviations in the original experimental design (described in NAS 2017), the different cultch treatments cannot be assessed from available data. Project NFWF-2021 (the only project begun after the 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 the lack of spatial replication and paired unrestored control sites will make it difficult to draw strong conclusions about the effects of the restoration or fishery closure.

Johnson et al. (2022) demonstrated the risk of a transition to a stable, resilient, low population state for oysters and the difficulty of reversing this to a more desired state in a generalized oyster population model. The scale of restoration, or 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 a reversal of the collapse is likely to require many orders of magnitude more effort than has been attempted so far (Johnson et al. 2022).

Even if such massive restoration efforts were completed, the likelihood of their success is unknown because, as currently designed, they test only a single hypothesis—that more and better substrate is the key to oyster population recovery. In order to better understand success factors and more confidently predict project outcomes, more research is needed to assess cultching efforts and while at the same time explore other factors that may affect oyster population recovery and persistance.

# Conclusions

Recent efforts to restore oyster populations in Apalachicola, Pensacola, and St. Andrew bays have cost more than $14,200,000 (Table 1). At time of writing, Apalachicola Bay is two years into a five-year harvest moratorium (2020–2025), and the oyster harvest in Pensacola and St. Andrew bays has been low for decades.

Many restoration efforts, in the Gulf of Mexico and elsewhere, have not had the desired outcome (LaPeyre et al. 2022; NAS 2022). Uncertainty about how to restore and manage oyster populations has persisted for decades or even centuries in Florida (Swift 1897, 1898; Pine et al. 2015), and there has long been a call to incorporate more learning into restoration and management programs (Walters 1986; Gunderson 1999; Walters 2007; Bouwes et al. 2016; NAS 2022; Pine et al. 2022). The adaptive management framework offers a systematic way to do this (Holling 1978). It can help such programs identify critical uncertainties and guide them toward actions that increase the likelihood of success (Bouwes et al. 2016; Friberg et al. 2016; Pine et al. 2022).

In the past, this type of learning may not have been a goal of restoration programs because uncertainty was not perceived as an issue and action choices were strongly influenced by perceived past success (even if outcomes had not been systematically assessed). Even if past efforts did succeed, such a prescriptive approach (Williams 2010) does not consider that system states may change, and when they do, restoration strategies and scale often need to change too (Johnson et al. 2022). Adaptive management can contribute dramatically to a project’s success. Yet it has been difficult to incorporate into ecosystem management. As Gunderson (1999) noted:

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.

A greater incorporation of learning in oyster restoration and management efforts can substantially increase the chances for oyster population recovery, which would in turn support ecosystem services and viable fisheries for the benefit of people in the Gulf of Mexico region.

# Acknowledgments

We recognize the assistance of many staff members at the Florida Department of Environmental Protection, Florida Department of Agriculture and Consumer Services, Florida Fish and Wildlife Conservation Commission, Florida State University, and other agencies in completing field and lab efforts to collect and process the samples that informed our analysis. We are very appreciative of the analytical assistance provided by B. Bolker. The paper was greatly improved by comments and support from F. Johnson, E. Camp, B. Healy, J. Isbell, C. Walters, J. Trexler, R. Ahrens, P. Hood, M. Allen, and S. Larkin. We thank A. Morgan for editorial work. E. Levine with the Florida Fish and Wildlife Conservation Commission and Research Institute kindly created the map in Figure 1.

# References

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

Barrett, A. C. 2021. On Exceptions to Second Report of Special Master. Supreme Court of the United States No 142. Original. Available https://www.supremecourt.gov/opinions/20pdf/22o142\_m648.pdf

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.

Bouwes, N., S. N. Bennett, and J. M. Wheaton. 2016. Adapting adaptive management for testing the effectiveness of stream restoration: an intensively monitored watershed example. Fisheries 41:84–91.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Breitburg, D.L., M. A. Palmer, and T. Loher. 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. Marine Ecology Progress Series 125:45-60.

Brim, M. S., and L. R. Handley. 2021. St. Andrew Bay. Seagrass status and trends in the northern Gulf of Mexico: 1940-2002, 155-169. United States Geologic Survey https://pubs.usgs.gov/sir/2006/5287/pdf/St.AndrewBay.pdf

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.

Burnham, K. P. and D.R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer. Berlin.

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).

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

Dale, L.L., J. Patrick Cronin, V.L. Brink, B. Tirpak, J. M. Tirpak and W. E. Pine III. 2021. Identifying Information Gaps in Predicting Winter Foraging Habitat for Juvenile Gulf Sturgeon. Transactions of the American Fisheries Society 150:222-241.

DHNRDA (Deepwater Horizon Natural Resource Damage Assessment) Trustees. 2017. 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 at <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.

FDACS (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. FDACS, Tallahassee, Florida.

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

FDACS (Florida Department of Agriculture and Consumer Services). 2016b. Natural Resource Damage Assessment (NRDA) oyster reef restoration in the St. Andrew Bay system oyster cultch deposition. Cultching Report. FDACS, Tallahassee, Florida.

FDACS (Florida Department of Agriculture and Consumer Services). 2017. Gulf coast ecosystem restoration council grant oyster reef restoration in the Apalachicola Bay system oyster cultch deposition DEP agreement RES01. FDACS, Tallahassee, Florida.

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 Conservation Commission. 2022. Commercial Fisheries Landings in Florida. https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/.

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

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

Friberg, N., N. V. Angelopoulos, A. D. Buijse, I. G. Cowx, J. Kail, T. F. Moe, H. Moir, M. T. O’Hare, P. F. Verdonschot, and C. Wolter. 2016. Effective river restoration in the 21st century: from trial and error to novel evidence-based approaches. Advances in Ecological Research 55:535–611.

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 diagnostics for hierarchical (multi-level/mixed) regression models. https://CRAN.R-project.org/package=DHARMa.

Hemeon, K. M., K. A. Ashton-Alcox, E. N. Powell, S. M. Pace, L. M. Poussard, L. K. Solinger, and T. M. Soniat. 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.

Holling, C. S., editor. 1978. Adaptive environmental assessment and management. Wiley, New York.

Howie, A. H., and M. J. Bishop, 2021. Contemporary oyster reef restoration: responding to a changing world. Frontiers in Ecology and Evolution 9. DOI 10.3389/fevo.2021.689915

Johnson, K.D. and D. L. Smee. 2014. Predators influence the tidal distribution of oysters (Crassostrea virginica). Marine Biology 161:1557-1564.

Johnson, F. A., 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.

Johnson, F. A., E. V. Camp, R. Gandy, and W. E. Pine III. In-Press. Demography of oystesr pre- an dpost collapse in Apalachicola Bay, Florida, using stage-based counts. Marine and Coastal Fisheries.

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).

Kelly, P. K. Jr. 2019. Report of the Special Master December 11, 2019. Number 142 Original In the Supreme Court of the United States. Available https://www.ca10.uscourts.gov/sites/ca10/files/SM142/670.pdf

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

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

La Peyre, M. K., D. A. Marshall, S. C. L. Buie, A. Hijuelos, and G. D. Steyer. 2022. Are

we falling short on restoring oysters at a regional scale? Environmental Management 70:581–592.

Leitman, S., W. E. Pine III, and G. Kiker. 2016. Management options during the 2011–2012 drought on the Apalachicola River: a systems dynamic model evaluation. Environmental Management 58:193-207.

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.

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.

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.

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

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.

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.

Morris, R. L., M. K. La Peyre, B. M. Webb, D. A. Marshall, D. M. Bilkovic, J. Cebrian, G. McClenachan, K. M. Kibler, L. J. Walters, D. Bushek and E. L. Sparks. 2021. Large‐scale variation in wave attenuation of oyster reef living shorelines and the influence of inundation duration. Ecological Applications 31, p.e02382.

Morson, J., D. Bushek, and J. Giushttps, editors. 2022. Stock Assessment Workshop New Jersey Delaware Bay Oyster Beds (24th SAW). Haskin Shellfish Research Lab. Commercial Township, New Jersey. https://hsrl.rutgers.edu/?s=saw+reports

MRD (Marine Resources Division, Alabama Department of Conservation and Natural Resources) and NOAA (National Oceanic and Atmospheric Administration). 2021. Coastal Alabama Comprehensive Oyster Restoration Plan. Published by the Deepwater Horizon Alabama Trustee Implementation Group. https://www.gulfspillrestoration.noaa.gov/sites/default/files/2021-12%20AL%20Final%20Coastal%20Alabama%20Comprehensive%20Oyster%20Restoration%20Strategy\_508.pdf.

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).

Pusack, T.J., D.L. Kimbro, J. W. White and C. D. Stallings. 2019. Predation on oysters is inhibited by intense or chronically mild, low salinity events. Limnology and Oceanography 64:81-92.

Pusack, T.J., J. W.White, H. G. Tillotson, D. L. Kimbro and C. D. Stallings. 2018. Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters. Journal of Experimental Marine Biology and Ecology 501:74-82.

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

Smith, R. S., S. L. Cheng, and M. C. Castorani. 2022a. Meta‐analysis of ecosystem services associated with oyster restoration. Conservation Biology. https://doi.org/10.1111/cobi.13966.

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

Solinger, L. K., K. A. Ashton-Alcox, E. N. Powell, K. M. Hemeon, S. M. Pace, T. M.

Soniat, and L. M. Poussard. 2022. Oysters beget shell and vice versa: generating management goals for live oysters and the associated reef to promote maximum sustainable yield of *Crassostrea virginica*. Canadian Journal of Fisheries and Aquatic Sciences:1–14.

Soniat, T.M., C. M. Finelli, and J. T. Ruiz. 2004. Vertical structure and predator refuge mediate

oyster reef development and community dynamics. Journal of Experimental Marine Biology and Ecology 310:163-182.

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

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.

VanderKooy, S. 2012. The Oyster Fishery of the Gulf of Mexico, United States: A Regional Management Plan – 2012 Revision. Publication No. 202, Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan.New York.

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.

Wilber, D.H., 1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuarine, Coastal and Shelf Science 35:179-190.

Williams, B. 2010. Passive and active adaptive management: approaches and an example. Journal of Environmental Management 92:1371–1378.

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. R. Springer, New York.