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

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Abstract

Depressed oyster *Crassostrea virginica* populations in the northern Gulf of Mexico have been the target of numerous post-*Deepwater Horizon* restoration projects, which primarily focus on replacing oyster cultch (substrate) to promote spat settlement, increase recruitment, and bolster adult oyster populations. This study assessed oyster populations at the sites of six such efforts, which used different cultch types and densities and were carried out in 2015–2022 in three estuaries on the Florida panhandle coast (Pensacola, St. Andrew, and Apalachicola bays). Total restoration costs were more than $14M. It also explored the durability of the new cultch and the potential effect of freshwater discharge on oyster spat counts. It found that counts of oysters of different size classes did not persistently increase following restoration (while controlling for sampling effort), regardless of cultch type or density used in the restoration. Positive responses to restoration efforts were short-lived, generally < 6 months, and seemed only to occur for spat-size oysters immediately after restoration. The biomass of cultch introduced by the projects also changed over time depending on cultch material used. With the available data, it is impossible to say with certainty what is hindering restoration success because of monitoring program shortcomings. However, restoration design deficiencies, including uncertainty in the materials used and minimal vertical relief of restored reefs post-construction, likely contribute to the lack of project success. These deficiencies must be addressed through fundamental, programmatic design changes in oyster restoration and monitoring efforts used 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 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). Only one of these stocks (Mobile Bay) has reopened to harvest. The potential reasons for regional oyster declines include prolonged drought, extreme rain events, freshwater releases from water management structures, environmental degradation, overharvesting, harvest management, 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 focus on protecting or adding substrate to replace oyster cultch, a matrix of living and dead material that was removed or displaced by fishing practices, to create sites for oyster spat settlement (Swift 1897; Swift 1898; Lenihan and Peterson 1998; Pine et al. 2015; Lenihan and Micheli 2000; Howie and Bishop 2021). These restoration efforts attempt to shift oyster reefs from an observed low but resilient state to a more desired productive state (Pine et al. 2022). This desired state can vary by location, type of oyster bar (intertidal vs. subtidal), and management goals, but all restoration efforts are expected to persistently increase oyster populations that will provide and promote ecosystem services (Smith et al. 2022), as well as support fishery recovery.

Despite the importance of cultch for supporting oyster settlement (Frederick et al. 2016), the amount, height, and type of cultch that are likely to perform best in different restorations are not well understood (Graham et al. 2017; Goelz et al. 2020). Some of the current restoration programs in the Florida panhandle are long-term (10 years), and information on what has and has not worked in them is lacking. Such information is critical for informing restoration and management in similar systems (Moore and Pine 2021; Pine et al. 2022).

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

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

(2) In a focal site (Apalachicola Bay), how do oyster temporal trends vary among separate restoration projects?

(3) Are oyster spat counts in Apalachicola Bay associated with freshwater discharge, cultch material, or cultch density? How do oyster spat densities compare across project and cultch density?

(4) How well do different types and densities of restoration-sourced cultch persist following deployment?

We found that large restoration programs are not having the desired outcome of increasing live oyster populations. This may be because these systems are trapped in a resilient but low-oyster-production state (Johnson et al. 2022) that is resistant to restoration, or the restoration programs as designed were ineffective. Our work suggests substantial uncertainty persists in how to restore oyster populations at large scales in Florida successfully. Addressing these uncertainties will require strong leadership from agency, academic, and industry leaders to conduct restoration projects in frameworks that allow for better learning to increase the likelihood of 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 current mandatory trip-ticket program was fully implemented in 1986 (Figure 2). The East Bay arm of St. Andrew Bay, near Panama City (Okaloosa and Walton counties), has a total surface area of approximately 176,847 ha (Comp and Seaman 1988). Oyster landings and trips for East Bay are not available, but they have declined in surrounding counties, and harvest in recent years has been near zero. Apalachicola Bay is a 348,029-ha estuary in Franklin County that supported the largest oyster fishery in Florida before collapsing in the fall of 2012 (Pine et al. 2015). Apalachicola Bay was closed to commercial harvest from December 2020 through December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

## Management actions

Cultch material was deposited in each bay in phases by state management agencies as part of multiple projects led by the state of Florida with funds from the *Deepwater Horizon* oil spill settlement. Reef construction methods across projects were similar and designed to minimize costs and maximize the area over which materials were deployed like previous cultching efforts in the 1980s (Berrigan 1988; 1990). Reef materials were either quarried shells, crushed granite, or a Kentucky limestone of graded size (often #4, 25–64 mm) transported on barges via inland and coastal waterway and then "planted" at specific locations (Table 1; FDACS 2015; 2016a, b; 2017).

Site selection was based on local knowledge of historical or extant reef locations. Most of the work was carried out from 2015 to 2017, with one project taking place in the summer of 2021 (Figure 3). Three state agencies, FWC, 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). One project each took place in Pensacola and St. Andrew bays, and four in Apalachicola Bay. The work carried out under these projects is summarized in Table 1. Across all projects, the area and density (thickness or depth) of cultch material deployed varied from the planned application due to construction challenges and storm events during the studies. These challenges resulted in uncertainty in the actual area and height of the restored reefs constructed.

Because Apalachicola Bay is the only one of these three bays where upstream reservoir operations can influence freshwater inputs, 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. We began this time series in 2005, 10 years before the start of the restoration projects covered by this study, to capture antecedent river discharge conditions.

# Methods

## Field collections

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

## Fisheries-dependent data

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

## Data analysis

We conducted four related analyses. For Question 1, we assessed how oyster counts responded to restoration efforts (i.e., how they changed following restoration) in all three bays (Pensacola, St. Andrew, and Apalachicola). We then focused on Apalachicola Bay for more detailed analyses because Apalachicola Bay is the only bay where freshwater inputs can be influenced via upstream dam operations and where multiple restoration projects using different materials and staring points in time have been conducted. Questions 2 and 3 explored whether oyster spat counts were influenced by freshwater discharge and how they differed over time, cultch material, and cultch density within a single bay, Apalachicola (Table 1). For Question 4, we assessed oyster trends across restoration projects using different cultch materials at different times for all bays, and then at greater detail within Apalachicola Bay because restoration efforts used different materials and different starting times. For all questions, 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 in both analyses, which combined sampling months into common blocks of time—winters (October–March), represented by even numbers, and summers (April–September), represented by odd numbers. (Questions 1-4)
  + Bay (Pensacola, St. Andrew, or Apalachicola) was included as a categorical variable in the first analysis, comparing restoration responses by bay. (Question 1 and 4)
  + Type and density of cultch material were represented as a single categorical variable by the name of the project, as each of the four Apalachicola Bay projects used a different cultch material, density, and start time. (Question 3, 4)
  + River discharge measured as the number of recent days in which discharge fell below certain specified levels. (Question 3)

We used 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 1-4).

The analyses followed these general steps:

1. Counts of live oysters in each bay and for each restoration site and period (a common time factor) were summed into three size classes (the dependent variables): spat (<26 mm shell height), seed (larger than spat but too small to harvest legally, 26–75 mm shell height), and legal to harvest (>75 mm shell height). 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 the use of 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), where the lowest AICc value represents the best fit of the models tested (Burnham and Anderson 2002). If two models were within two AICc units of each other, a likelihood ratio test was used to assess whether these two models differed significantly.
5. Model autocorrelation in the residuals for the top model was assessed by using the DHARMa package (Hartig 2022) in R by simulating new response data from the specified model and then using qq plots to check for deviations from the expected distribution graphically, a KS test to test whether observed and expected distributions differed, and a Durbin-Watson test to check for temporal autocorrelation. Significance 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) and all analyses were done in R (R Core Team 2021).

*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. 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 6 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. Models were ranked from lowest (best fitting) to highest based on AICcc score. We then used the emtrends package (Lenth 2022) to estimate the marginal means of the predicted beta values and uncertainty for the top model as well as test whether the parameters differ from zero.

*Question 2 how do oyster trends vary among restoration projects in Apalachicola Bay and Question 3 are oyster spat counts in Apalachicola Bay associated with freshwater discharge, cultch material or cultch density?*

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. Apalachicola Bay is also the only bay where freshwater inputs can be influenced via upstream releases from reservoirs (Leitman et al. 2015). For Question 2 (change in oyster counts across projects) and Question 3 (spat count association with freshwater discharge, cultch material and density) 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 both 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. The relative fit of these models was again compared by AICc and if the top models were within two AICc units, a likelihood ratio test was used to assess whether these two models differed significantly. To create a comparative framework across studies with different materials and starting points, we predicted the mean number of oyster spat per ¼ m2 in the last monitoring period (period 15). In this comparison, three projects (NFWF-1, NRDA 4044, and NRDA 5007) completed construction three to five years before the last period of data, and one (project FWC-2021) less than two years before. If the materials, amount, or time since construction was completed significantly influenced oyster reef restoration performance, the predicted values for each project in the common period should differ.

We then compared the best fitting model of the eight models described in Table 3 to four additional models which describe different Apalachicola River discharge metrics to see if model fit improved with the addition of river discharge information (Table 4). River discharge was measured as the number of days in each period or the prior period (as a measure of antecedent discharge) when the Apalachicola River discharge was below 12,000 or below 6,000 CFS measured at Jim Woodruff gage (USGS 02358000). The 12,000 CFS reference point is important because the adjacent floodplain becomes inundated at discharge near this level (Light et al. 1998; Fisch and Pine 2016). The exact point of inundation may have changed over time due to riverbed degradation. Regardless, we used this reference point as an indicator of low freshwater inputs. A discharge level of <6,000 CFS indicates extreme low river discharge, because it approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam.

*Question 4: Examining the persistence of cultch material*

To explore how cultch material and cultch density in different projects persisted over time, we again used negative binomial GLM models to assess how the sum of the weight of cultch collected by divers during oyster surveys persisted over time in each bay (all projects) and then in Apalachicola Bay we assessed persistence of cultch material by project (because of different materials and restoration time frames). We first summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, site, and period. This sum would include both the cultch material placed on the reef during restoration as well as any cultch material (living or dead) that had accumulated on the substrate. Total cultch weights for Apalachicola Bay were made integers by rounding to the nearest whole kilogram. Data were summarized by project, and calculations of mean and variance by project suggested the data were over-dispersed (variance > mean). To create a comparative framework across substrates, we predicted the amount of cultch per ¼ m2 in the last monitoring period.

Data and all code used for the analyses are available from the following Git repository: <https://github.com/billpine/AB_DEP.git>.

# Results

## River discharge patterns

Apalachicola River discharge deviated significantly (50–100% below the average for the period of instrument records) for three or more months in 2006, 2007, and 2008, with extreme drought in 2011 (9 of 12 months), 2012 (12 of 12 months), 2016 (6 of 12 months), and 2017 (4 of 12 months). Regional river discharge patterns for 2017–2022 were generally closer to average than 2011-2016.

## Trends in fisheries-dependent data

Trends in FWC fisheries-dependent data since 1986 show the Apalachicola Bay commercial fishery was larger (trips and landings) than those of Pensacola and St. Andrew bays combined. Apalachicola trips and landings increased sharply during the early 2000s, peaking prior to fishery collapse in 2012 (Figure 3). Apalachicola Bay was closed to oyster harvest by FWC in December 2020, with a reopening scheduled for December 2025. Pensacola, St. Andrew, and Apalachicola bays show similar trends of increasing trips and landings in the mid-1980s and again in 2005–2010. Since 2010–2012, trips and landings have declined in all three bays, with declining (Apalachicola) or minimal (Pensacola and St. Andrew) levels of commercial fishing activity since 2015, when the regional oyster restoration programs assessed in this analysis began.

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

Apalachicola Bay restoration efforts took place across four different projects in periods 2, 6, and 13. Divers sampled oysters to track response to restoration in periods 2-10 and 12-15, depending on Project (Figure 4). Pensacola Bay restoration took place in Period 2 and oyster sampling was conducted in periods 5-7, 10, and 15. St. Andrew restoration also took place in Period 2 and oyster sampling took place in period 5, 7, and 10 (Figure 4).

From the GLM models, the dispersion parameter from the negative binomial distribution ("nbinom2" family formulation) was <1 for all models, suggesting extreme over-dispersion. The best fitting model for oyster spat (lowest AICcC value, highest AICcC weight) was the Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) (Table 2). Because site is uniquely coded this model allows different responses by site over time in each bay. No autocorrelation in residuals was detected (K-S test p= 0.41; D-W test p = 0.18). The significant interaction term suggests that each bay's temporal patterns in oyster counts are unique. Apalachicola Bay live spat counts per quadrat declined (beta of the slope = -0.004, SE = 0.07, 95% CI = -0.15-0.14) and this trend was not significantly different from zero (p = 0.96). Pensacola and St. Andrew bays show uncertain trends in oyster spat counts. Pensacola beta values for the slope of oyster spat counts over time were larger than Apalachicola (beta = -0.39, SE = 0.11, 95% CI = -0.61-0.17) and this slope did differ from zero (p=0.0006). For St. Andrew Bay, the slope was highly uncertain (beta = 0.21, SE = 0.18, 95% CI = -0.14-0.57) and this slope did not differ from zero (p=0.23). We then predicted the marginal means of oyster spat from a single ¼-m2 quadrat in Period 15 for comparison purposes between each bay. Predicted live oyster spat for Apalachicola was 14.08 live spat per quadrat (95% CI 5.29-37.45), Pensacola was 0.70 live spat per quadrat (95% CI 0.16-3.14), and St. Andrew Bay predicted live oyster spat was 226 (95% CI 13.79-3703.89).

Fitting the same Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) model to counts of seed or legal-sized oysters revealed a similar pattern as seen in oyster spat. The observed pattern in counts of seed oysters in Apalachicola Bay shows a decline in counts (beta = -0.002, SE = 0.091, 95% CI = -0.18-0.18) and this slope did not differ from zero (p=0.99). For Pensacola Bay the trend in seed count also showed a decline over time overall (beta = -0.34, SE = 0.14, 95% CI = -0.61 - -0.06 and this slope did differ from zero (p=0.02). The trend for St. Andrew Bay for seed count was positive over time overall (beta = 0.01, SE = 0.24, 95% CI = -0.38 - 0.57 and this slope did not differ from zero (p=0.68). Counts of legal-size oysters were consistently low (Figure 5) creating model convergence issues even after fitting attempts with multiple optimizers for the Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) model. No further analyses of legal counts across bay were done.

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

To examine trends in Apalachicola Bay oyster spat by project, we fit eight different models to the data (Table 2). To simplify nesting of site within project in our model structure (which would allow period to vary by site across project), we created a new variable (SP) which combined the site and project name. The best fitting model for oyster spat (lowest AICcC value, highest AICcC weight) was the Period + Project + (Period | SP) + Period:Project + offset(log(Num\_quads)) (Table 3). Because site is uniquely coded this model allows for temporal trends to vary across site. Autocorrelation in residual results were mixed as the K-S test was not significant (K-S test p= 0.21) but the Durbin-Watson test was (D-W test p = 0.03) likely due to different sites sampled with each project. No adjustment was made. We estimated unique temporal patterns for each project. The trend in live oyster spat counts per quadrat over time did not differ from zero for projects GEBF-5007 (beta of the slope = -0.06, SE = 0.10, 95% CI = -0.26-0.13, p = 0.51), NRDA-4044 (beta of the slope = 0.04, SE = 0.07, 95% CI = -0.09-0.18, p = 0.51) or NFWF-2021 (beta of the slope = -1.04, SE = 0.60, 95% CI = -2.24-0.15, p = 0.09). For project NFWF-1, the trend in live oyster spat per quadrat was significantly different from zero (p<0.0001) and this trend was negative (beta of the slope = -0.64, SE = 0.15, 95% CI = -0.94 - -0.35.

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

We then fit four additional models (Table 4) that compared the best fit model from Question 2, to the same model with terms describing 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 (Table 3). Including these river discharge metrics did not improve model fit (Table 3).

*Question 3 continued how do oyster spat densities compare across project and cultch density?*

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. 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 FWC-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).

We assessed the relationships between cultch mass and the number of live oyster spat from each quadrat for each project in Apalachicola Bay. We fit ten different models (Table 5) to the data, to assess the relationship between cultch mass and Period, Project, SP (random effect) and 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. Four models all had similar AICc values (within three AICc units) and the model with the highest weight (0.55) was the most complicated model Roundwt ~ (1 | SP) + Spat\_sum + Period + Project + (0 + Period | SP) + Period:Project + offset(log(Num\_quads)) which also allowed for a unique negative binomial dispersion parameter. Diagnostic assessments of model fitting for these models suggests that several may be overparameterized. We examined simpler models to assess whether including the number of live spat did not improve model fit (Table 5). For example, a comparison of a model that included Spat sum as a parameter (Roundwt ~ Spat\_sum + Period + Project + (Period | SP) + Period:Project + offset(log(Num\_quads))) to a model without Spat sum (Roundwt ~ Period + Project + (Period | SP) + Period:Project + offset(log(Num\_quads)) the delta AICc value between the two models is 1.8, which suggests including spat sum does not improve model fit and the Spat sum parameter was not significant in the model (p=0.64).

## *Question 4: Examining the persistence of cultch material*

We plotted the weight per quadrat (kg) by bay and project over period to assess patterns (Figure 12). For Pensacola and St. Andrew, the cultch material used for project NRDA-4044 was limestone or granite (Table 1). Plotting the biomass of this material per quadrat over time (Figure 13) demonstrated a wide spread in the amount of material collected over time but no strong indication of an increase or decline. Because Apalachicola Bay is the only system where multiple materials (rock and shell) have been used for different projects, we were able to examine Apalachicola Bay for more insight into cultch persistence by project (Figure 13-14). We fit the same GLM models described previously first to compare all bays (Question 1) and to compare projects within Apalachicola Bay (Question 2). The Roundwt ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) model did not converge with either the default or the BFGS optimizer. From an AICcC perspective, the Roundwt ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) and the Roundwt ~ (1 | Site) + Bay + offset(log(Num\_quads)) were the top two models separable by 2.5 AICc units.

The significant interaction term suggests that each bay's temporal patterns in oyster cultch biomass are unique. Apalachicola Bay cultch biomass per quadrat had a positive slope (beta of the slope = 0.04, SE = 0.02, 95% CI = 0.008-0.07) and this trend was significantly different from zero (p = 0.02). Pensacola beta values for the slope of oyster spat counts over time were negative (beta = -0.03, SE = 0.03, 95% CI = -0.08-0.03) and this slope did differ from zero (p=0.02). For St. Andrew Bay, the slope was highly uncertain (beta = -0.07, SE = 0.05, 95% CI = -0.20-0.05) and this slope did not differ from zero (p=0.23). We then predicted the marginal means of oyster spat from a single ¼-m2 quadrat in Period 15 for comparison purposes between each bay. Predicted live oyster spat for Apalachicola was 3.76 kg cultch per quadrat (95% CI 2.54-5.56), Pensacola was 1.71 kg cultch per quadrat (95% CI 0.99-2.94), and St. Andrew Bay predicted cultch per quadrat was 1.34 kg (95% CI 0.46-37-3.85).

The same general GLM models fit to the counts of live oyster spat with Apalachicola Bay (Question2) were then fit to the four projects for Apalachicola Bay. The top 3 models (delta AICC< 3) were the Roundwt ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) followed by the Round\_wt ~ Period + Project + (Period | Site) + Period:Project + offset(log(Num\_quads)) and Round\_wt ~ (1 | SP) + Period + Project + (0 + Period | SP) + Period:Project + offset(log(Num\_quads)) models. AICc weights were 0.45, 0.24, and 0.23 respectively.

The significant interaction term suggests that each project's temporal patterns in oyster cultch biomass are unique. The FWC-2021 project cultch biomass per quadrat had a positive slope over time (beta of the slope = 0.09, SE = 0.11, 95% CI = -0.14-0.31) and this trend was not significantly different from zero (p = 0.44). The GEBF-5007 project beta values for the slope of oyster spat counts over time were positive (beta = 0.05, SE = 0.02, 95% CI = 0.01-0.09) and this slope did differ from zero (p=0.02). For the NFWF-1 project, the slope was negative (beta = -0.14, SE = 0.02, 95% CI = -0.19- -0.09) and this slope did differ from zero (p<0.0001). Finally the NRDA-4044 project, the slope was negative (beta = -0.05, SE = 0.01, 95% CI = -0.07- -0.02) and this slope did differ from zero (p=0.0002).

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. Predicted oyster cultch biomass for the NFWF-2021 project was 8.58 kg per ¼-m2 quadrat (Period 15, 95% CI 4.03-18.30); GEBF-5077 was 4.29 kg per ¼-m2 quadrat (Period 12, 95% CI 2.94-6.27); the NFWF-1 was 0.97 kg per ¼-m2 quadrat (Period 9, 95% CI .47-2.02); and finally the NRDA 4044 predicted cultch biomass was 1.45 kg per ¼-m2 quadrat (Period 13, 95% CI 1.01-2.09).

# Discussion

The 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 been closed for part of the time series (Apalachicola Bay) or have had extremely low landings and trips (Pensacola and St. Andrew bays).

(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 than12 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. 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 show that our observed oyster spat losses are occurring during winter months (October-March). Winter is most likely when disease prevalence (Petes et al. 2012) and abiotic stress (high temperatures, low dissolved oxygen) are likely much lower than in summer. Thus, survival spat survival during winter is potentially higher. The relationships between 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.

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), 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 these same fisheries independent data 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.

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

In project NFWF-1, a shell cultch project, and NFWF-2021, a rock cultch project, live oyster spat counts immediately after restoration was several orders of magnitude greater than those in any other project or period (Figures 8-10). However, the GEBF-5007 and NRDA-4044 did not begin monitoring oyster response for 6-18 months post-construction, meaning any potential restoration responses do not inform these models immediately after restoration. Potentially these projects also saw large increases in spat and then rapid declines immediately after restoration similar to NFWF-1 and NFWF-2021, but because of the lag between completion of restoration and monitoring this is not known (Figures 4, 8-10). Critically for projects NFWF-1 and NFWF-2021, these high initial spat counts did not result in higher counts in seed or legal-size oysters in subsequent periods (Figure 5, 8-10), nor were these high spat counts observed again (Figure 5). Though the mean predicted values tended to be lower for shell compared to rock, overlapping confidence intervals for all by one project in one period (NFWF-1, Period 2) limit this conclusion. However, for all projects, mean predicted values for the last period of monitoring are small.

The relationship between the weight of cultch (kg, x-axis) and the number of spat (y-axis) per quadrat across projects (color dots) and sites (individual plots) in Apalachicola Bay 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), cultch levels 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 FWC-2021 (red dots, rock cultch) show a general pattern of increasing spat in quadrats with more cultch biomass (Figure 13).

When cultch weight (kg, x-axis) and total spat (y-axis) is plotted by project (colored dots), over period (individual plots), a pattern is evident (Figure 14). This pattern suggests total spat in each quadrat increases as cultch weight increases per quadrat, but only for one or two periods. 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 observed in period 2). Ultimately the observed total number of spat and cultch biomass per quadrat collapses and retracts toward the origin. A similar but not as dramatic pattern is also apparent with project NFWF-2021 (red dots, rock cultch material; Figure 14) in periods 13-15.

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

## Reasons restoration may not be working

One possible explanation for the observed lack of positive response is that the restoration actions were inappropriate—e.g., inappropriate material, density/height, or total area. The cultch density used following the 1985 collapse/decline 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, which implies restoration height), material type (shell vs. rock, or different sizes of material), that would be required to prevent collapse.

Because the shell is less dense than rock, the differences observed in biomass per quadrat 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).

Kimbro et al. (2020) conducted similar restoration experiments in Apalachicola Bay using quarried oyster shells on reefs 0.4 ha in size at shelling densities of zero, 153 m3, and 306 m3. They observed a positive response to oyster reef restoration 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). They 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, 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). Our work followed reefs that were similarly restored (materials, densities, and starting time) several years post-construction and found that the initial oyster population response to restoration as measured by counts did not persist (Figure 5). The reason this cultch was only observed immediately following cultching and not in subsequent periods, nor did the cultch that were observed continue, is a critical uncertainty to be addressed to inform Apalachicola Bay oyster restoration.

One 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). Still, oyster spat settlement has been very low for unknown reasons.

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. A the previous restoration project in Apalachicola Bay (Berrigan 1988; 1990) used clam shells dredged from Lake Pontchartrain, Louisiana as cultch material. 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.

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

| Bay | Project name | Agencya | Construction time frame | Material | Amount (cubic meters) | Sites | Average density (cubic meters per acre) | Project coste |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Pensacola | NRDA 4044 | FDEP | Fall 2016 | Limestone aggregate | 15,270 | 17 | 174 | $5,370,596b |
| St. Andrew | NRDA 4044 | FDEP | Summer 2016 | Crushed granite | 12,997 | 9 | 153 | Part of b |
| Apalachicola | NRDA 4044 | FDEP | Fall 2015 | Quarried shell | 18,992 | 16 | 153 | Part of b |
| Apalachicola | GEBF 5007 | FDEP | Fall 2017 | Limerock aggregate | 73,015 | 14 | 229 | $4,680,000c |
| Apalachicola | NFWF-1 | FWC | Summer/Fall 2015 | Quarried shell | 7,340 | 3 | 76, 153, 229, 306 | $4,189,400d |
| Apalachicola | NFWF-2021 | FWC | Summer 2021 | Limerock aggregate | 7,340 | 3 | 229 | Part of d |

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

b Fact sheet: https://www.gulfspillrestoration.noaa.gov/sites/default/files/wp-content/uploads/FL-Regional-Projects-2014.pdf

c Fact sheet: https://www.restorethegulf.gov/sites/default/files/FPL\_FactSheet\_20160909\_FL\_Apa\_Oyster.pdf

d Fact sheet: https://www.nfwf.org/sites/default/files/gulf/Documents/fl-apalachicola-bay.pdf

e Total restoration costs $14,239,996

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

| Model | Degrees of freedom | AICcc | Delta AICcc | AICcc Weight |
| --- | --- | --- | --- | --- |
| tmb 5: Sum\_spat ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) | 10 | 2651.60 | 0.00 | 0.85 |
| tmb 6: Sum\_spat ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) with unique NB dispersion ~Bay | 12 | 2655.43 | 3.83 | 0.13 |
| tmb 3: Sum\_spat ~ (1 | Site) + Period + Bay + Period:Bay + offset(log(Num\_quads)) | 8 | 2658.94 | 7.33 | 0.02 |
| tmb 2: Sum\_spat ~ (1 | Site) + Period + Bay + offset(log(Num\_quads)) | 6 | 2667.14 | 15.54 | 0.00 |
| tmb 1: Sum\_spat ~ (1 | Site) + Period + offset(log(Num\_quads)) | 4 | 2668.91 | 17.31 | 0.00 |
| tmb 4: Sum\_spat ~ (1 | Site) + Bay + offset(log(Num\_quads)) | 5 | 2670.36 | 18.75 | 0.00 |
| tmb0: Sum\_spat ~ (1 | Site) + offset(log(Num\_quads)) | 3 | 2672.32 | 20.72 | 0.00 |

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

| Model | k | AICc | Delta AICc | AICc Weight |
| --- | --- | --- | --- | --- |
|  |  |  |  |  |
| tmb 5: Sum\_spat ~ Period + Project + (Period | Site) + Period:Project + offset(log(Num\_quads)) | 12 | 1875.69 | 0.00 | 0.65 |
| tmb 6: Sum\_spat ~ Period + Project + (Period | SP) + Period:Project + offset(log(Num\_quads)) includes unique dispersion parameter for each Project | 15 | 1877.45 | 1.76 | 0.27 |
| tmb7: Sum\_spat ~ (1 | SP) + Period + Project + (0 + Period | SP) + Period:Project + offset(log(Num\_quads)) | 14 | 1881.26 | 5.57 | 0.04 |
| tmb 3: Sum\_spat ~ (1 | Site) + Period + Project + Period:Project + offset(log(Num\_quads)) | 10 | 1881.68 | 5.99 | 0.03 |
| tmb 2: Sum\_spat ~ (1 | Site) + Period + Project + offset(log(Num\_quads)) | 7 | 1895.31 | 19.62 | 0.00 |
| tmb 4: Sum\_spat ~ (1 | Site) + Project + offset(log(Num\_quads)) | 6 | 1900.31 | 24.62 | 0.00 |
| tmb 1: Sum\_spat ~ (1 | Site) + Period + offset(log(Num\_quads)) | 4 | 1921.95 | 46.26 | 0.00 |
| tmb0: Sum\_spat ~ (1 | Site) + offset(log(Num\_quads)) | 3 | 1923.32 | 47.63 | 0.00 |
|  |  |  |  |  |
|  |  |  |  |  |

Table 4. Model selection table comparing the best fit GLM of oyster count data from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay (Table 3) to the same model with additional terms describing river discharge metrics for the Apalachicola River. The predicted response is number of spat per ¼ m2 quadrat. AICcc and delta AICcc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; low days12 = the number of days river discharge was below 12,000 CFS; 12k\_lag = the number of days river discharge was below 12,000 CFS lagged by 1 period (to test antecedent conditions); low days6 = the number of days river discharge was below 6,000 CFS; 6k\_lag = the number of days river discharge was below 6,000 CFS lagged by 1 period (to test antecedent conditions); site = the location where the sampling occurred.

| Model | k | AICc | Delta AICc | AICc Weight |
| --- | --- | --- | --- | --- |
|  |  |  |  |  |
| tmb 5: Sum\_spat ~ Period + Project + (Period | Site) + Period:Project + offset(log(Num\_quads)) | 12 | 1875.69 | 0.00 | 0.40 |
| tmb 5.12k\_lag: Sum\_spat ~ Period + Project + (Period | Site) + 12k\_lag + Period:Project + offset(log(Num\_quads)) | 13 | 1877.19 | 1.50 | 0.19 |
| tmb 5.12k\_lag: Sum\_spat ~ Period + Project + (Period | Site) + 6k\_lag + Period:Project + offset(log(Num\_quads)) | 13 | 1877.53 | 1.84 | 0.16 |
| tmb 5.12k\_lag: Sum\_spat ~ Period + Project + (Period | Site) + 12k + Period:Project + offset(log(Num\_quads)) | 13 | 1878.01 | 2.32 | 0.13 |
| tmb 5.12k\_lag: Sum\_spat ~ Period + Project + (Period | Site) + 6k + Period:Project + offset(log(Num\_quads)) | 13 | 1878.08 | 2.39 | 0.12 |
|  |  |  |  |  |
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Table 5. Model selection table for the GLM assessing trends in oyster cultch mass from subtidal reefs restored using different materials, at different densities, over time, and with different levels of live oyster spat in Apalachicola Bay. The predicted response is mass of cultch per ¼ m2 quadrat. AICc and delta AICc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; low days = the number of days river discharge was below 12,000 CFS; site = the location where the sampling occurred.

| Model | Degrees of freedom | AICc | Delta AICc | AICc Weight |
| --- | --- | --- | --- | --- |
| Period \* project + 1|site + offset(log(number of quadrats)) | 10 | 1,278.78 | 0 | 1.0 |
| Period + project + 1|site + offset(log(number of quadrats)) | 7 | 1,297.58 | 18.78 | 0 |
| Project + 1|site | 6 | 1,304.39 | 25.59 | 0 |
| Period + 1|site + offset(log(number of quadrats)) | 5 | 1,389.67 | 110.87 | 0 |
| 1|site + offset(log(number of quadrats)) | 4 | 1,394.95 | 116.15 | 0 |

Table 6. Model selection table for the GLM assessing patterns in oyster cultch biomass from subtidal reefs in three bays in the Florida panhandle. The predicted response is biomass of cultch (kg) per ¼ m2 quadrat. AICcc and delta AICcc are provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); bay = Pensacola, East (St. Andrew), or Apalachicola bay.

| Model | Degrees of freedom | AICcc | Delta AICcc | AICcc Weight |
| --- | --- | --- | --- | --- |
| tmb 5: Round\_wt ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num\_quads)) | 10 | 2053.0 | 0.00 | 0.66 |
| tmb 3: Round\_wt ~ (1 | Site) + Period + Bay + Period:Bay + offset(log(Num\_quads)) | 8 | 2055.4 | 2.49 | 0.19 |
| tmb 2: Round\_wt ~ (1 | Site) + Period + Bay + offset(log(Num\_quads)) | 6 | 2058.54 | 5.59 | 0.04 |
| tmb 1: Round\_wt ~ (1 | Site) + Period + offset(log(Num\_quads)) | 4 | 2058.54 | 5.59 | 0.04 |
| tmb0: Round\_wt ~ (1 | Site) + offset(log(Num\_quads)) | 3 | 2058.66 | 5.70 | 0.04 |
| tmb 4: Round\_wt ~ (1 | Site) + Bay + offset(log(Num\_quads)) | 5 | 2058.90 | 5.95 | 0.03 |
| tmb 6: Round\_wt ~ Period + Bay + (Period | SP) + Period:Bay + offset(log(Num\_quads)) includes unique dispersion parameter for each Bay | Did not converge |  |  |  |
|  |  |  |  |  |
|  |  |  |  |  |

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| --- | --- | --- | --- | --- |
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Table 7. Model selection table for the GLM of oyster cultch biomass from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay. The predicted response is number of spat per ¼ m2 quadrat. AICcc and delta AICcc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; site = the location where the sampling occurred.

| Model | k | AICc | Delta AICc | AICc Weight |
| --- | --- | --- | --- | --- |
| tmb 3: Round\_wt ~ (1 | Site) + Period + Project + Period:Project + offset(log(Num\_quads)) | 10 | 1274.09 | 0.00 | 0.45 |
| tmb 5: Round\_wt ~ Period + Project + (Period | Site) + Period:Project + offset(log(Num\_quads)) | 12 | 1275.32 | 1.23 | 0.24 |
| tmb7: Round\_wt ~ (1 | SP) + Period + Project + (0 + Period | SP) + Period:Project + offset(log(Num\_quads)) | 14 | 1275.41 | 1.32 | 0.23 |
| tmb 6: Round\_wt ~ Period + Project + (Period | SP) + Period:Project + offset(log(Num\_quads)) includes unique dispersion parameter for each Project | 15 | 1277.49 | 3.40 | 0.08 |
| tmb 2: Round\_wt ~ (1 | Site) + Period + Project + offset(log(Num\_quads)) | 7 | 1296.24 | 22.14 | 0.00 |
| tmb 4: Round\_wt ~ (1 | Site) + Project + offset(log(Num\_quads)) | 6 | 1303.75 | 29.66 | 0.00 |
| tmb 1: Round\_wt ~ (1 | Site) + Period + offset(log(Num\_quads)) | 4 | 1306.45 | 32.36 | 0.00 |
| tmb0: Round\_wt ~ (1 | Site) + offset(log(Num\_quads)) | 3 | 1311.33 | 37.24 | 0.00 |
|  |  |  |  |  |
|  |  |  |  |  |

![Diagram

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

Chart

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Figure 2. Deviations in river discharge from the period of instrument records for the Escambia (top panel) and Apalachicola rivers (bottom panel). Darker colors equate to larger deviations, with colors in the blue spectrum representing higher river discharge and colors in the red spectrum representing lower river discharge. White or near-white represents values within +/− 10% of the period of instrument records.



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

Chart

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Figure 4. A schematic demonstrating the placement and persistence of cultch material by project (y-axis, red line) over time (x-axis) and the sampling events (grey circles) that collected oyster count data from each project. Project AB (Apalachicola Bay) NRDA-4044 only collected samples from one site in Period 3 (open circle) and sampling did not begin on other sites until Period 5. Even number periods include the months October-March beginning in 2015 and odd-number periods are summers months April-September beginning in 2016.

Text, table

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

Calendar

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

Calendar

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Figure 7. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for St. Andrew Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note each plot for each oyster size class has a different y-axis.



Figure 8. Oyster spat count per quadrat (CPUE) by site within Apalachicola Bay (each panel) and period (x-axis). Dots represent counts over time for each project defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-Septemer) beginning in 2016. Note: the first counts for projects NRDA-4044 were taken in one period after restoration for Dry Bar only and Period 5 for other sites. Project GEBF-5007 were taken one period after the restoration action. Projects NFWF-1 and NFWF-2021 began count monitoring in the same period as the restoration (see Figure 3).



Figure 9. Oyster spat count per quadrat (CPUE) for two sites within Apalachicola Bay (East Lumps left panel, Lighthouse Bar right panel) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. For East Lumps site (left panel) the cultch material was placed in Apalachicola Bay and monitoring begin in Period 13, and oyster spat were recorded during monitoring efforts in Period 13 and 14, and oyster spat counts declined drastically in Period 15. For Lighthouse Bar (right panel) the NRDA-4044 project had material placed in Apalachicola Bay in Period 2, but sampling in Period 3 only occurred at one site and did not begin at other sites until Period 5. Note the large difference in counts in Period 13 between project NRDA-4044 (shell cultch about five years old) and NFWF-2021 (recent rock cultch) as indicated by the arrow.

Chart, scatter chart

Description automatically generated

Figure 10. Oyster spat count per quadrat (CPUE; left panels) and seed count per quadrat (right panels) for two sites within Apalachicola Bay (East Lumps top row, Lighthouse Bar bottom row) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. The arrows highlight the change in count from spat to seed size oyster from period t to period t+1 and the ellipses highlight the drastic change by a factor of 3 -5 in the y axis between the spat and seed counts. Critically these changes occur between Period 14 (winter) and Period 15 (summer).

Chart, scatter chart, box and whisker chart

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Figure 11. Live oyster spat CPUE for all Apalachicola Bay study sites and number of days Apalachicola River discharge (measured at the Chattahoochee gauge) was below 12,000 CFS (below which inundation of floodplain is limited).



Figure 12. Oyster cultch biomass per quadrat (y-axis, kg) over time (x-axis, period) for Apalachicola, Pensacola, and St. Andrew bays (each panel). Projects (Table 1) are defined by color. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016.

A picture containing text, indoor

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Figure 13. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay sites (each individual panels) and project (colored dots).

Diagram

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Figure 14. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay periods (each individual panels) and project (colored dots). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016.

Appendix 1

Table A1. Summary of the number of quadrant samples in each Bay, Period, Year, Month, Project, and Site used in this analyses.

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

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Chart, histogram

Description automatically generated

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

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

Chart, scatter chart

Description automatically generated

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

Chart, histogram

Description automatically generated

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

Graphical user interface, chart, histogram

Description automatically generated

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

Graphical user interface

Description automatically generated

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