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

# Introduction

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

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

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

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

Florida has or will receive substantial funding from the DWH settlements and penaltiies including planned payments of at least $680M for damages, $392M from civil penalties, and $356M in criminal penalties (https://crrc.unh.edu/sites/crrc.unh.edu/files/media/docs/Workshops/dwh\_eddm\_2017/funding\_diagram.\_final.pdf). Some of these funds (with more planned) have been directed to oyster reef restoration projects with multiple objectives including ecosystem services and restoration of fisheries. We assessed ongoing and recently completed oyster restoration efforts in three large estuaries in the Florida panhandle (Pensacola, St. Andrew, and Apalachicola bays) to assess (1) How do temporal trends in oyster counts vary among the three depressed sites?; (2) In a focal site (Apalachicola Bay), how do oyster temporal trends vary among separate restoration projects?; (3) Are oyster counts in Apalachicola Bay associated with freshwater discharge, cultch material, or cultch density?; and 4) How well do different types and densities of restoration-sourced cultch persist following deployment? We found that these large restoration programs are not having the desired outcome of increasing live oyster populations. This may be because these systems are trapped in a resilient, but low-oyster production state (Johnson et al. 2022) that are resistent to restoration, the restoration programs as designed (amount, type, architechture, and location of restoration materials) were not effective, or both. Our work suggests substantial uncertainties persists in how to successfully restore oyster populations at large scales in Florida and 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 likelihood of success.

# Methods

## 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 126,000 acres. Reported oyster landings, trips, and 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 (Figure 1), near Panama City, Florida (Okaloosa and Walton counties), has a total surface area of approximately 437,000 acres (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 (Figure 2). Apalachicola Bay is a 860,000 acre estuary in Franklin County that supported the largest oyster fishery in Florida before collapsing in 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).

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

## Management actions

Cultch material was deposited in each bay in phases by state management agencies (Florida Department of Environmental Protection [FWC] and Florida Department of Agriculture and Consumer Services) as part of multiple projects led by the state of Florida with funds from the *Deepwater Horizon* oil spill settlement (Table 1). Reef construction methods across studies were similar and designed to minimize costs and maximize the area over which materials were deployed. Reef materials were either quarried shell or a Kentucky limestone of graded size (often #4, 38–76 mm) transported on barges via inland and coastal waterway and then “planted” at specific locations.

Site selection was based on local knowledge of historical or extant reef locations. In Pensacola Bay, approximately 20,103 cubic yards of limerock aggregate were distributed at 17 different sites (XXX acres) at an approximate density of 228 cubic yards per acre (FDACS 2016a) during September and October 2016 (NRDA 4044 project). In St. Andrew Bay, approximately 17,000 cubic yards of crushed granite were distributed on nine oyster reefs (XXX acres) at a density of about 200 cubic yards per acre (FDACS 2016b) in June 2016 (NRDA 4044 project). In Apalachicola Bay, four different restoration efforts with similar objectives and methodologies occurred during this time. As part of the NRDA 4044 project, approximately 24,840 cubic yards of quarried shell material was deployed on 16 different sites at an average cultch density of 200 cubic yards per acre. In the GEBF-5007 project, approximately 95,500 cubic yards of limerock aggregate was deployed on 14 different oyster reef sites. The average density of cultch material was 300 cubic yards per acre. The third project within Apalachicola (project NFWF-1) deployed 9,600 cubic yards of shell material in sites 2 acres in size at densities of 100, 200, 300, or 400 cubic yards per acre. The fourth project deployed 9,600 cubic yards (project NFWF-2021) of limestone at a density of 300 cubic yards per acre at three different stations. Across all studies, the actual area and density (thickness or depth) of cultch material deployed varied due to construction challenges and storm events that occurred during the study.

## Field collections

Similar methods were followed across projects to estimate live oyster counts and mass of cultch material, based on techniques used in Florida since the 1980s (FWC 2021 https://myfwc.com/media/27745/oimmp-v2-ch11.pdf). Divers randomly placed ¼ m2 (0.5 m on each side) quadrats at selected sites, removed all oysters and cultch material to a wrist-deep depth, and placed material in bags. Once bags were returned to the vessel, they were either processed on location or returned to the lab, where counts of live and dead oysters, measurements of shell height, weight of cultch material, and study-specific metrics (e.g., idenfitication of other benthic species) were recorded.

## Fisheries-dependent data

For each bay, using publicly available FWC data (https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/), the annual landings (meat pounds) and trips were summed for each county bordering the bay, and CPUE calculated as landings/trips.

## Data analysis

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

1. Counts of live oysters in each bay (Pensacola, St. Andrew, Apalachicola) and at each restoration site and period (a common time factor) were summed into three size classes: spat (<26 mm shell height), sub-legal (locally termed “seed” oysters, 26–75 mm shell height), and legal to harvest (>76 mm shell height). Separate analyses were completed for each size class. For the restoration projects NRDA 4044 and GEBF 5008, counts per size class were totaled in the field. For projects NFWF-1 and NFWF-2021, count totals (all sizes combined) were converted to counts per size class by calculating the proportion of oysters within each size class from concurrent oyster shell-height samples and multiplying the totals by these proportions. The results were then rounded to convert the numbers of oysters per size class to integers to match the NRDA 4044 and GEBF 5008 data.
2. The count data distribution was assessed by examining the ratio between the count mean and variance for each study (Table 1).
3. Generalized linear models (GLMs; Bolker et al. 2009) with a negative binomial distribution were used to assess how oyster counts (three dependent variables based on size class—spat, seed, and legal) varied over different independent variables, using the R package glmmTMB (Brooks et al. 2017). The independent variables were as follows. Period—a variable representing continuous time, used to combine sampling months into common blocks of time. These were defined as October–March are odd number periods and April–September are even number periods and these time blocks served as continues independent variable in both analyses. Bay (Pensacola, St. Andrew, or Apalachicola) was included as a categorical independent variable for the first analysis comparing restoration response by bay. Additional independent variables considered in the second analysis focusing on Apalachicola Bay were the type and density of cultch material (represented as a categorical variable by the name of the study, as each study used different cultch material, density, and starting periods) and the number of recent days when discharge fell below certain specified levels. For both analyses, we used site (a named oyster reef) as a random effect to account for correlation among quadrat samples at each site.
4. We assumed that the total oyster counts per site would be related to the number of quadrats collected. We included the number of quadrats as an effort offset (log link function; Zuur et al. 2009, 2013). Based on this, we changed the model from modeling counts to modeling a rate measured as the count/quadrat as the response variable. Because the quadrats were the same size in each study, the total area sampled in each period only changed as a function of the number of quadrats. Using counts and accounting for effort, as opposed to converting the counts to CPUE based on area sampled, has two main advantages. First, it maintains the response as an integer, allowing the use of a negative binomial distribution (appropriate for oyster count data; Moore et al. 2020), and second, fitted values and confidence intervals do not contain negative values (Zuur et al. 2009).
5. The model fit to each data set was assessed visually by comparing data and a predicted line fitted to these data with 95% confidence intervals.
6. Comparisons were made between models with different combinations of independent variables using the Akaike information criterion (AIC), where the lowest AIC value represents the best fit of the models tested (Burnham and Anderson 2002).
7. Models were fit to data using the glmm.TMB package (Brooks et al. 2017), and predicted values (marginal means) were made from the best fit model using the ggeffects package (Lüdecke 2018) in R (R Core Team 2021).

We completed a second separate analysis for Apalachicola Bay, because only this system had data available from multiple projects in a single system to assess the independent variables of different cultch materials and density (described by the “study” variable) and freshwater discharge. The dependent variables were the number of oysters in the spat, seed, or legal-size categories. The independent variables included period, study (Table 1), and a variable which represented the number of days in a given period or the prior period (as a measure of antecedent discharge) when the Apalachicola River discharge was below 12,000 or below 6,000 CFS measured at Jim Woodruff gage (USGS 02358000).

The 12,000 CFS reference point is important because the adjacent floodplain becomes inundated at discharge near this level (Light et al. 1998, Fisch and Pine 2016). The exact point of inundation may have changed over time due to riverbed degradation (S. Leitman, personal communication). Regardless, we used the discharge level of <12,000 CFS as an indicator of low freshwater inputs. Similarly, 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.

We explored how the different cultch materials and densities used (see Table 1) persisted over time. We summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, site, and period. Total cultch weights for Apalachicola Bay were made integers by rounding to the nearest whole kilogram. Data were summarized by project, and calculations of mean and variance by project suggested the data were over-dispersed (variance > mean). We then fit similar GLM models assuming a negative binomial distribution for oyster count data to the observed cultch biomass. To create a comparative framework across substrates, we predicted the amount of cultch per ¼ m2 in period 13, the last monitoring period. Because Apalachicola was the only bay where both rock and shell cultch were used, we focused analyses on comparing substrates in this bay only.

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

## 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 Pensacola and St. Andrew bays combined (Figure 2). Apalachicola trips and landings increased sharply during the early 2000s, peaking in 2012 when the fishery collapsed (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 a similar trend of increasing trips and landings in the mid-1980s and again in 2005–2010. Since 2010–2012, trips and landings have declined in all three bays, with declining (Apalachicola) or minimal (Pensacola and St. Andrew) levels of commercial fishing activity since 2015, when the regional oyster restoration programs assessed in this analysis began.

## Trends in oyster counts in Apalachicola, Pensacola, and St. Andrew bays following restoration

The dispersion parameter from the negative binomial distribution (“nbinom2” family formulation) was <1 for all models, suggesting extreme over-dispersion (Figure 3). We were most interested in the bay \* period interaction as a framework to assess trends in oyster counts over time for each bay. This interaction effect reveals whether bays have similar patterns in oyster counts, or whether temporal patterns are unique within each location. In addition to being the model of greatest management interest, the model including bay \* period also had the lowest AIC value (delta AIC between lowest AIC and model with second-lowest AIC = 3.3; Table 2). For the bay \* period model, Apalachicola Bay live spat counts per quadrat declined (beta = −0.17, SE beta = 0.04, p < 0.0001). Pensacola and St. Andrew bays showed different trends in oyster spat counts compared to Apalachicola, but uncertainty in beta estimates was greater (Pensacola Bay, beta = 0.07, SE beta = 0.15, p = 0.10; St. Andrew Bay, beta = 0.25, SE beta = 0.20, p = 0.03). Even though the estimated slope is positive for Pensacola and St. Andrew bays, this trend is uncertain (high standard error on beta terms). The low value suggests a median increase of about one oyster spat per quadrat for each period. This increase contrasts with Apalachicola Bay, which was declining at a median level of about 0.8 live oyster spat per quadrat per period. Predicted mean (marginal mean) live oyster spat counts (95% CI) for the last period of the time series (period 14) for a single ¼ m2 quadrat are Apalachicola = 6.7 (4.4–10.0, 95% CI), Pensacola = 15.3 (1.5–160.8, 95% CI), and St. Andrew = 570.5 (33.0–9,864.0, 95% CI).

Fitting the same bay \* period model to counts of seed or legal-sized oysters revealed a similar pattern as seen in oyster spat. The observed and predicted results show declines in seed oysters over time in Apalachicola Bay, relatively constant values in Pensacola Bay, and increasing but low counts in St. Andrew Bay. St. Andrew Bay was the only system to have at least one live oyster per quadrat predicted (1.6 live legal oysters [0.41–6.20, 95% CI]), whereas the other bays are predicted to have less than one live legal oyster per quadrat (Apalachicola 0.65 [0.31–1.38, 95% CI], Pensacola 0.14 [0.04–0.50, 95% CI]).

The fishery closure in Apalachicola Bay occurred in period 12, and the last period of data for this bay is period 13. Predicted oyster counts for seed, spat, and legal-size oysters for these periods did not increase between periods 12 and 13, and observed counts for spat and seed was similar to prior periods. However, observed counts for legal-size oysters was higher in periods 12 and 13 than in earlier periods. It is unknown whether this was directly related to the fishery closure during period 12.

## Apalachicola Bay oyster spat response to restoration

Observed counts of oyster spat in Apalachicola Bay range from 0 to more than 80,000 per ¼ m2 depending on restoration project and period (Table 1, Figure 5), with oyster counts across the study diminishing over time (Figure 5).

Results from the negative binomial GLM model with site as a random effect and log of the number of quadrats as an offset to control for sampling effort found period was significant (beta = −0.17, SE = 0.04, p < 0.001), suggesting that across all four studies, and regardless of cultch material or cultch density, counts of oyster spat declined over time following restoration. The predicted median number of oyster spat per ¼ m2 transect in period 14 was 7.1 (4.8–10.6), much lower than period 1 (102.2, 58.6–178.3; Figure 6).

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

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

To create a comparative framework across studies with different materials and starting points, we predicted the mean number of oyster spat per ¼ m2 in period 13, the last monitoring period in Apalachicola Bay. In this comparison, three studies (projects NFWF-1, NRDA 4044, and NRDA 5007) completed construction three to five years before the last period of data, and one (project FWC-2021) less than two years before. If the materials, amount, or time since construction was completed significantly influenced oyster reef restoration performance, the predicted values for each project in the common period should differ.

For the NFWF-1 project (quarried shell cultch), we predicted in period 13 a mean number of live oyster spat of about 0.82 (0.11–6.22, 95% CI) per ¼ m2 quadrat. The NRDA 4044 project also used quarried shell cultch, and the mean predicted number of live spat in period 13 was higher at about 4.5 (2.3–9.1, 95% CI). The predicted mean number of live oyster spat per ¼ m2 quadrat for the rock cultch projects varied. For project GEBF 5007 the mean predicted live oyster spat count per ¼ m2 quadrat was about 18.3 (8.6–39.0, 95% CI), and for project NFWF-2021 it was 15.8 (8.9–28.3, 95% CI). In project NFWF-1, a shell cultch project, live oyster spat counts immediately after restoration were more than 100× greater those in any other project (Figure 5). These high initial spat counts did not result in higher counts in legal-size oysters in subsequent periods, nor were these high spat counts observed again.

## Persistence of cultch material in Apalachicola Bay

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

However, more important than the statistical significance is whether the material persisted. The slope is negative for both substrates, indicating declines over time. The predicted biomass of rock per ¼ m2 quadrat changed over time (Figure 7) from about 5.07 kg per ¼ m2 quadrat (2.5–10.2, 95% CI) in period 2 to about 2.0 kg per ¼ m2 quadrat (1.4–2.9, 95% CI). The shell biomass changed from about 1.7 kg per ¼ m2 quadrat (1.1–2.7, 95% CI) to about 0.93 (0.6–1.5, 95% CI). Because the shell is less dense than rock, the differences in biomass per quadrat are not surprising. These results suggest a biomass decline of about 60% for the shell material and about 45% for the rock material by the end of period 13.

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

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

# Discussion

There are two key takeaways from this analysis.

1. Oyster populations in Pensacola, St. Andrew, and Apalachicola bays do not appear to have responded to restoration efforts designed to promote spat settlement and accelerate population recovery. This lack of response occurs in bays within different watersheds and with different restoration materials. This suggests there may be fundamental flaws in the design of oyster restoration projects, ecosystem changes that limit oyster population response, or both.
2. The lack of oyster population response has occurred in a period of time with river discharges ranging from moderate drought to generally normal for the study period. This suggests that salinity, and other river-related ecosystem drivers such as nutrients, have also been near normal. River discharge is considered a significant driver of salinity in Florida panhandle estuaries. Salinity in Apalachicola Bay has been identified as a driver of oyster survival in legal proceedings (FL v GA 2014), but observed oyster population responses to variation in freshwater discharge and resulting salinity in the bay are variable (Buzan et al. 2009; Fisch and Pine 2015; Gledhill et al. 2020; Moore et al. 2021). This lack of response has also happened while commercial fisheries have been closed (Apalachicola Bay) or have had extremely low landings (Pensacola and St. Andrew bays).

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

## Disappointing restoration results

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

Restoration efforts in all three bays were guided by previous actions in Apalachicola Bay, where irregular cultching has been part of oyster management efforts since at least 1949 (Whitfield and Beaumariage 1977). Hurricane Elena in 1985 reduced oyster populations in Apalachicola Bay (Berrigan 1988, 1990) by as much as 95% (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 management and restoration efforts for oyster populations (Berrigan 1990).

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

## Reasons restoration may not be working

The cultch density used by Berrigan (1990) of about 617 cubic yards per acre was about twice the density used in the most significant (rock cultch; project NRDA 5007) and most recent (rock cultch; project FWC 2021) restoration efforts and about 50% more than the highest treatment level of recent shell cultch projects (project NFWF 1) for Apalachicola Bay. Pine et al. (2015) used a model fit to historic Apalachicola fisheries-dependent and -independent data to demonstrate how an intensive cultching program of about 50-ha per year could reduce the risk of an irreversible oyster fishery collapse in Apalachicola Bay. This cultching area is slightly larger than the average area cultched each year between the restoration efforts following Hurricane Elena (Berrigan 1990; Pine et al. 2015) and the beginning of regional restoration efforts in 2015. What is unknown and could not be included in the Pine et al. (2015) simulations is what density of cultching material (amount per area) was required (see below).

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. Kimbro et al. (2020) observed a positive response to oyster reef restoration 10 months post-restoration during the same period as high oyster spat counts occurred on the NFWF-1 project reefs in this study (Figure 6). Kimbro et al. (2020) also observed higher oyster counts (defined as juveniles < 25 mm and adults ≥ 25 mm) on reefs with increased reef mass. Follow-up assessments beyond 10 months are unavailable for the reefs in Kimbro et al. (2020). Our work followed similarly restored reefs (materials, densities, and starting time) several years post-construction and found that the initial oyster population response to restoration as measured by counts did not persist (Figure 6).

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

Side-scan sonar mapping is used as an assessment metric on a subset of restored reefs in Pensacola, St. Andrew, and Apalachicola bays, including measurements of vertical relief. The elevation of restored reefs in these systems is variable but generally low (about 0.05 m). Because the material used for restoration efforts is either small and dense (#4 limestone 5–25 mm in diameter) or larger and less dense (quarried oyster shell 50–75 mm in diameter), it is likely susceptible to being transported away from the intended restoration site, buried in sediment, or sculpted by currents to a low-relief structure (about 0.05 m). This low-relief structure is likely interrupted across its surface by subtle waves of higher-density material (volumetrically), resulting in slightly higher vertical relief (about 0.1 m) in some areas. Regardless, cultch material in various forms at different mass levels has persisted on these restored reefs at low mass levels (Figure 8), and relief (FWC side scan report) and critically, oyster spat settlement on this material has been very low for reasons that are not known.

Smith et al. (2021), as part of a 15-year assessment of the performance of an oyster reef restoration project in the Chesapeake Bay, found that restored reefs were like unrestored reference reefs based on a variety of metrics within six years following restoration. For some metrics, such as shell height, the restored and reference reefs were similar within three years, and as the restored reefs aged, they became more stable and possibly more resilient. In Florida, the restoration of the Lone Cabbage Reef in Suwannee Sound demonstrated oyster spat settlement and persistence on the restored reef within six months following construction. Oysters have persisted and successfully settled on the reef in the four years since construction, and oyster densities on the restored and nearby reference reefs are now similar (W.E. Pine, personal communication). 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 within 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 associated with restored reefs that persisted over time were about 3–8× the elevation contrast observed on restored sites in Apalachicola, Pensacola, and St. Andrew bays.

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

(23) OYSTER AND CLAM SHELLS PROPERTY OF DEPARTMENT

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

— Florida Statute 597.010

Crtitically, oysters sold as half-shell trade, which is the market for the majority of oysters harvested, are exempt from this requirement. The Berrigan (1990) restoration project, identified as a successful project in Apalachicola Bay, used clam shells dredged from Lake Pontchartrain, LA, as cultch material. Smith et al. (2021) describe a successful long-term oyster restoration project that also used dredged shell in Chesapeake Bay, VA. Limestone used in the restoration projects in Table 1 is mined in Kentucky and is denser (structure and mass), older (geologic age), and made of calcite, dolomite, and quartz (J. Yeager, UF Geology, personal communication) than limestone used successfully (measured by counts and persistence of oysters) for intertidal reef restoration in Suwannee Sound, Florida (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 (Zu Ermgassen et al. 2012). But this observation is called into doubt by the observed oyster fishery collapse in 2012 and by a combination of modeling (Pine et al. 2015; Johnson et al. 2022) and empirical assessments (this work). Efforts are underway (J. Casteel, University of Florida) to reconstruct shell biomass (volume) removed by harvest for the major oyster fisheries in Florida, and preliminary results suggest that shell material removals far exceed material replaced by recent restoration efforts. Understanding the magnitude of cultch removals can likely inform the scale of restoration required to shift degraded oyster populations from undesired to desired status (Johnson et al. 2022).

*Future direction*

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

# Conclusions

Oyster populations in Apalachicola, Pensacola, and St. Andrew bays appear resistant to restoration and recovery, despite legal actions (Apalachicola Bay), large restoration efforts, very low levels of reported harvest (Pensacola and St. Andrew bays), and two years of a five-year harvest moratorium (2020–2025) in Apalachicola Bay. Unfortunately, a combination of experimental design deficiencies (e.g., absence of controls, lack of strong treatment contrasts, no experimentation in materials) and inadequate monitoring make it difficult to determine which of the factors that have been previously hypothesized to drive oyster population dynamics (e.g., river discharge, fishing effects) are responsible. Regrettably, many of the same restoration and management uncertainties identified in this assessment have persisted for long periods in Florida (decades to centuries; Swift 1897, Pine et al. 2015, Camp et al. 2015). This suggests an absence of learning.

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

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

A central tenet of AEAM [adaptive ecosystem assessment and management] is learning, yet learning seems to be intertwined with cycles of policy success and failure (Westley 1995). If policies are working (or appear to be working), there is little or no emphasis on learning. It is when policy fails, either dramatically or chronically, that learning is deemed necessary and a priority. The challenge to develop a capacity for learning continues to be problematic among most resource institutions. Yet, when needed, that capacity seems to come by focusing on understanding (not efficiency) and by networking with those who practice learning.

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

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Table 1. Summary of deployment date, location, common name, coordinating State of Florida agency, cultch material, amount of material, number of sites material deployed, and average material density as designed for oyster restoration projects in three Florida panhandle estuaries. FDEP = Florida Department of Environmental Protection, FWC = Florida Fish and Wildlife Conservation Commission.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Construction season and year | Bay | Project name | Agency | Material | Amount (yds3 by convention) | Sites | Average material density (yds3 per acre by convention |
| Fall 2016 | Pensacola | NRDA 4044 | FDEP | Limerock aggregate | 20,103 | 17 | 228 |
| Summer 2016 | St. Andrew | NRDA 4044 | FDEP | Crushed granite | 17,000 | 9 | 200 |
| Fall 2016 | Apalachicola | NRDA 4044 | FDEP | Quarried shell | 24,840 | 16 | 200 |
| Fall 2017 | Apalachicola | GEBF 5007 | FDEP | Limerock aggregate | 95,500 | 14 | 300 |
| Summer 2015 | Apalachicola | NFWF-1 | FWC | Quarried shell | 9,600 | 3 | 100,200,300,400 |
| Summer 2021 | Apalachicola | NFWF-2021 | FWC | Limerock aggregate | 9,600 | 3 | 300 |

Table 2. Model selection table for the GLM model of oyster count data from subtidal reefs from three bays in the Florida panhandle (Pensacola, East, and Apalachicola). The predicted response is number of spat per ¼ m2 quadrat. Akaike information criteria (AIC), and delta AIC are provided to inform comparisons of the model statistical fit to the data.

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Degrees of freedom | AIC | Delta AIC |
| Period \* Bay + offset(log(number of quadrats)) | 8 | 2711.5 | 0.0 |
| Period + Bay + offset(log(number of quadrats)) | 6 | 2714.8 | 3.3 |
| Period + offset(log(number of quadrats)) | 4 | 2717.8 | 6.3 |

Table 3. Model selection table for the GLM model of oyster count data from subtidal reefs from three estuaries in the Florida panhandle. The predicted response is number of spat per ¼ m2 quadrat. Akaike information criteria (AIC), and delta AIC provided to inform comparisons of the model statistical fit to the data. Period is a continuous variable which describes time. Project is a categorical variable identifying which project carried out a specific restoration (Table 1), Low Days is the number of days river discharge was below 12,000 CFS and Site is the location in space the sampling occurred.

|  |  |  |  |
| --- | --- | --- | --- |
| Model | Degrees of freedom | AIC | Delta AIC |
| Period\*Project + 1|Site + offset(log(number of quadrats)) | 10 | 2078.8 | 0 |
| Period + Low days + 1|Site + offset(log(number of quadrats)) | 5 | 2138.3 | 59.5 |
| Period + 1|Site | 4 | 2139.4 | 60.6 |
| Period + 1|Site + offset(log(number of quadrats)) | 4 | 2139.4 | 60.6 |
| Period + (Low days Previous Period) + 1|Site + offset(log(number of quadrats)) | 5 | 2140.2 | 61.4 |
| Low days + 1|Site + offset(log(number of quadrats)) | 4 | 2158.6 | 79.8 |

#####################

*Figures*

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###This will be a really great map of the panhandle with the FL inset

Figure 1. Pensacola, St. Andrew, and Apalachicola bays…

A picture containing calendar

Description automatically generated

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/>). Each row represents a different bay (Apalachicola panels A-C, Pensacola panels D-F, St. Andrew panel G-I) and each column represents a different metric with the commercial trips in the first column, middle column as CPUE (catch-per-unit-effort), and last column as the landings (by convention in pounds). Note the y-axis are different on most panels by row because of the large differences in observations for each Bay.

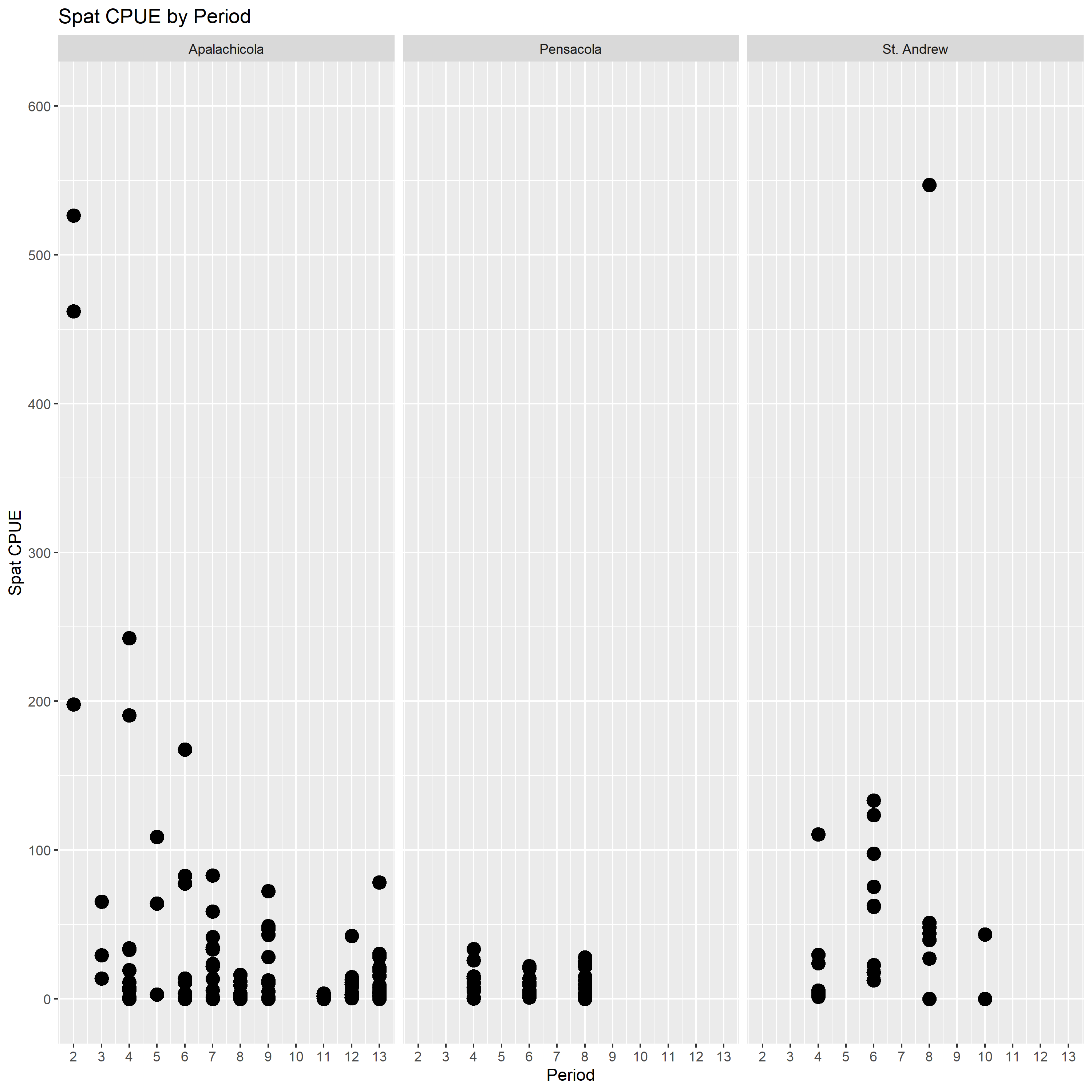


Figure 3. Period of time (x-axis) and spat CPUE (y-axis) per quadrat in each of the three study systems (Apalachicola, Pensacola, St. Andrew bays). Even number Periods are winter (November-April) beginning in 2015 while odd number Periods are summer (May-October) beginning in 2016.

Chart, histogram

Description automatically generated

Figure 4. Predicted count of live spat (y-axis) by Period of time (x-axis) for a single ¼ m2 quadrat from each of the three study systems (Apalachicola, Pensacola, St. Andrew). The black line is the best predicted values for each Period and the grey ribbon represent the 95% confidence intervals around this line of best fit. Even number Periods are winter (November-April) beginning in 2015 while odd number Periods are summer (May-October) 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. Predicting for a single quadrat allows for comparisons of the predicted count, for a standardized unit of effort in each Bay, as a measure of abundance and population trajectory over time. Note the large differences in the y-axis for each plot.

Chart, scatter chart

Description automatically generated

Figure 5 Version 1. Apalachicola Bay live oyster spat CPUE (y-axis, counts per ¼ m2 quadrat) from each of the four studies in Apalachicola Bay over time (Period, x-axis). Each panel is a different study completed by FDEP or FWC (Table 1). Even number Periods are winter (November-April) beginning in 2015 while odd number Periods are summer (May-October) beginning in 2016.

Chart, scatter chart

Description automatically generated

Figure 6 Preamble. This is an example plot to demonstrate fit of the nbGLM from TMB. These data (dots on the plot) are the sum of the rounded weights of cultch from the NFWF\_1 study. The model in R is written as Roundwt ~ Period + offset(log(Num\_quads) and is fit to a subset of the data which is only the NFWF\_1 study. This is just a simple approach of sub-setting the data compared to fitting the interactive model, but both will fit and the values are nearly identical. I did both approaches to explore model performance. The predicted value (solid black line) is the predicted total (sum) rounded weight of cultch for an average number of quadrats (150) predicted for every Period. The ribbon is the 95% confidence interval around the predicted value. The y-axis is large because this is the amount of material that would come from 150 quadrats. This plot is just inserted to demonstrate visually the performance of the nbGLM using TMB predicted values compared to the data. This same type of model will be used for live spat counts and cultch biomass.

Chart, histogram

Description automatically generated

Figure 6 Preamble. This is an example plot to demonstrate fit of the nbGLM from TMB. 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. These data (dots on the plot) are the total number of live spat for each Period and Site from the NFWF\_1 study. The predicted value (solid black line) is the predicted rounded weight of cultch for an average number of quadrats (150) predicted for every Period. The ribbon is the 95% confidence interval around the predicted value. The y-axis is large because this is the amount of material that would come from 150 quadrats. This plot is just inserted to demonstrate visually the performance of the nbGLM using TMB predicted values compared to the data. This same type of model will be used for live spat counts and cultch biomass.

Graphical user interface, chart, histogram

Description automatically generated

Figure 6. These are the predicted live oyster count for a single ¼ m2 quadrat predicted using a nbGLM model in R generally 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. The predicted value (solid black line) is the predicted number of live spat for a single quadrat for every Period. The ribbon is the 95% confidence interval around the predicted value. All studies had more than one quadrat sampled, and no study sampled in all periods. I have predicted over 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 (a single quadrat) to demonstrate both the variability in predicted counts and population trajectory over time as a representation of live oyster spat trends for each study. This utility of this plot is up for discussion.

Graphical user interface

Description automatically generated

Figure 7. Predicted change in cultch biomass from the four different studies in Apalachicola. 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 studies. The predicted value (solid black line) is the predicted total (sum) rounded weight of cultch for a single quadrat for every Period summed across sites. The ribbon is the 95% confidence interval around the predicted value. All studies had more than one quadrat sampled, and no study sampled in all periods. Predictions are only made for the periods that were sampled. The utility of this plot is up for discussion.

Chart, histogram

Description automatically generated

Alternate Figure 7. Predicted change in cultch biomass from a single study (NFWF 2021) in Apalachicola. The model in R is written as Roundwt ~ Period + offset(log(Num\_quads) and is fit individually to data from a single study. The predicted value (solid black line) is the predicted total (sum) rounded weight of cultch for a single quadrat for every Period summed across sites. The ribbon is the 95% confidence interval around the predicted value. I can force the prediction and plotting for periods that were not sampled (as above, no sampling for FWC 2021 in Periods 2-11. But I don't like predicting over a period of time when there are no data. The utility of this plot is up for discussion.

Chart, scatter chart

Description automatically generated

Figure 8 Alternate. Live oyster spat (y-axis) and weight of cultch (x-axis, kg) for each quadrat across Period in Apalachicola Bay by study. The y-axis limited to a value of 1000 because of the high values of live counts observed in Period 2. For Apalachicola Bay the NFWF\_1 and NRDA\_4044 studies are shell cultch and the NRDA\_5007 and FWC\_2021 are limestone cultch.

A screenshot of a computer

Description automatically generated with low confidence

Figure 9. Deviations in river discharge from the instrument period of record from the Escambia and Apalachicola rivers. Darker colors equate to larger deviations from Period of record with colors in the blue spectrum representing positive deviations (higher river discharge) and colors in the red spectrum representing negative deviations (lower river discharge). White, or near white colors represent values equal to the Period of record or within +/- 10%.

Chart, scatter chart

Description automatically generated

Figure 10. Live oyster spat CPUE across study and Site from Apalachicola Bay (y-axis) and number of days Apalachicola River discharge (Chattahoochee gauge) is below 12,000 CFS (x-axis). The 12,000 CFS threshold is generally considered the point in which the river begins to inundate the floodplain. The more days the river is below 12,000 are periods of time discharge is low.