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

*#Authorship to be determined*

*Data contributions: Jonathan Brucker and Matt Davis*

*Analytical and writing: Jennifer Moore, Fred Johnson, Ed Camp, Steve Geiger*

*Request review from J Harper*

*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, citing reasons including prolonged drought, extreme rain events, or freshwater releases from water management structures (Petes et al. 2012; Pine et al. 2015; Gledhill et al. 2020; Du et al. 2021; Herrmann ABCD). Several of these states have implemented fishery closures in response to the depressed status of oyster stocks (i.e., Mobile Bay in Alabama, Apalachicola Bay in Florida, Galveston Bay in Texas). Still, only one of these stocks (Mobile Bay) has reopened to harvest. 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). In this suit, Florida argues that 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). 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). Subsequent settlements resulting from legal proceedings and regulatory fines created substantial funding opportunities (more than $199M US) for oyster restoration in the Gulf of Mexico. The dollars allocated for restoration exceeded the annual value of oyster landings (Pine et al. 2022).

Many proposed, ongoing, and historical oyster restoration efforts focus on adding various materials for oyster spat (larvae) to settle and grow (Howie and Bishop 2021). Adding this material to the substrate is often an effort to promote a positive oyster shell budget because harvest removes shell stock (Pine et al. 2015). Naturally produced shell also degrades over time and shell may be displaced from the oyster reef when harvesters cull undersized oysters and cultch material away from the reef (Swift 1897; Lenihan et al. 2000; Pine et al. 2015). Restoration sources material outside the management interest system to replace natural oyster cultch, a complex matrix of living and dead material where oyster larvae settle and grow. 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). However, uncertainty persists about the type of restoration materials to use and whether these materials function the same biologically as natural cultch material (Graham et al. 2017; Goelz et al. 2020).

We used data from ongoing and recently completed efforts to shift oyster populations from undesired to desired states through restoration and fishery closure projects in estuaries in Florida waters of the northern Gulf of Mexico. Many of the large restoration programs that are currently funding these efforts are long-term (10-year) projects. Still, information describing what did and did not work in the current restoration efforts is needed to inform other proposed restoration and management projects in similar systems (Moore and Pine 2021; Pine et al. 2022). To increase the likelihood of the restoration achieving its stated goals and facilitating learning under an adaptive management framework (National Academy of Science [NAS] 2017; Pine et al. 2022), assessments of these long-term restoration efforts should be ongoing. Doing so allocates time and funds for corrective changes to achieve the restoration objective of shifting the oyster population from an undesired state to a more desirable one. This desired state can vary by location, type of oyster bar (intertidal vs. subtidal), and management goals. Still, these restoration efforts are expected to provide and promote ecosystem services and create opportunities for oyster harvest through fishery recovery.

Site description – We assessed oyster population trends in three estuaries in the Florida panhandle that currently have ongoing or recently completed oyster restoration projects. Pensacola Bay (Figure 1) in northwest Florida (Santa Rosa and Escambia counties) is the fourth largest estuary in Florida, with a surface area of approximately 126,000 total acres. Reported oyster landings, trips, and CPUE for Pensacola Bay in recent decades have declined (Figure 2) since the current mandatory TRIP ticket program was fully implemented in 1986. The East Bay (Figure 1) arm of St. Andrew Bay, near Panama City, Florida (Okaloosa and Walton Counties), is one region of St. Andrew Bay that has a total surface area of approximately 437,000 acres (Comp and Seaman 1988). Reported oyster landings and trips for East Bay are not available. Still, they are available for the counties surrounding St. Andrew Bay where oyster trips and landings have declined and harvest in recent years is near zero (Figure 2). Apalachicola Bay is a large estuary of 860,000 acres in Franklin County, which historically supported the largest oyster fishery in Florida before collapsing in fall of 2012 (Pine et al. 2015) and was closed to commercial harvest in December 2020 through December 2025 by the Florida Fish and Wildlife Conservation Commission.

Management actions – Cultch material was deposited in each Bay in phases by individual state management agencies (Florida Department of Environmental Protection, DEP; Florida Fish and Wildlife Conservation Commission, FWC; Florida Department of Agriculture and Consumer Services, FDACS) as part of three different projects led by the State of Florida with funds made available following the *Deepwater Horizon* oil spill. In Pensacola Bay, approximately 20,103 cubic yards of limerock aggregate were distributed at 17 different sites at an approximate density of 228 cubic yards per acre (FDACS 2016a) during September and October 2016. In St. Andrew Bay, approximately 17,000 cubic yards of crushed granite were distributed on nine oyster reefs at a density of about 200 cubic yards per acre (FDACS 2016b) in June 2016. In Apalachicola Bay, four different restoration projects with similar objectives and methodologies occurred during this time. In the first (NRDA), approximately 24,840 cubic yards of fossil shell material was deployed on 16 different sites at an average cultch density of 200 cubic yards per acre. In the second project (FDEP), approximately 95,500 cubic yards of limerock aggregate was deployed as part of an FDEP project on fourteen different oyster reef sites. The average density of cultch material was 300 cubic yards per acre. The third project (FWC) deployed 9600 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 XYZ (FWC NFWF 2) cubic yards of limestone at a density of ABC at Z 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.

*Methods*

Fisheries dependent data – For each Bay, using FWC public data (https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/), the landings and trips were summed by county surrounding the Bay, and the calculated catch-per-unit effort (CPUE) as annual landings/ trips.

Reef construction – Reef construction methods across studies were similar and designed to minimize costs and maximize the amount of material 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.

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 haphazardly place ¼-m2 (0.5-m on each side) quadrats at selected sites, remove all oysters and cultch material to a "wrist-deep" depth, and place material in bags. Once bags are returned to the vessel, they are 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 recorded.

Data Analyses – Methods for analyzing oyster count data followed Moore et al. (2020). We conducted two separate analyses to address specific questions of management interest. The first analysis assessed how oyster counts of each size class varied over time and between the three different bays (Pensacola, St. Andrew, and Apalachicola bays). The second analysis focused on specific management questions that could only be addressed using data from Apalachicola Bay. These questions include whether oyster counts of each size class were influenced by freshwater discharge into Apalachicola Bay and how oyster counts differed over time, cultch material, and cultch density used in the four projects (Table 1) that are ongoing within Apalachicola Bay.

The general approach for the two analyses followed these steps:

(1) Counts of live oysters in each Bay (Pensacola, East, Apalachicola) and at each restoration site and Period were summed into three size classes, spat (<26-mm shell height), sub-legal (locally termed "seed" oyster; 26-75-mm shell height), and legal harvest (>76-mm shell height). For some studies, counts were totaled in these categories in the field. For other studies, total counts (all sizes) were converted to counts per size class by calculating the proportion of oysters within each size class from concurrent oyster shell height samples.

(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 (dependent variable) varied over different independent variables. The dependent variable was the number of oysters in each size class (spat, seed, legal). The independent variables include Period, a variable representing continuous-time used to combine sampling months into winter (November-April) or summer (May-October). Bay (Pensacola, St. Andrew, and Apalachicola bays) was included as a categorical independent variable for the first analysis. For both analyses, we used Site 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). Using effort as an offset, we change 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).

(4) 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.

(5) Comparisons were made between models with different combinations of independent variables using AIC.

(6) 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).

As a visual assessment of watershed-scale discharge characteristics, 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 (CFS by convention) from the Period of instrument record by month and year beginning in 2005. We started the time series about ten 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 larger (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 at Chattahoochee).

We completed a second separate analysis for Apalachicola Bay because several independent variables of management interest only apply to this system. Analyzing available data and understanding Apalachicola Bay oyster response to restoration actions is complicated because of variability in the construction methods and monitoring program site names used as part of ongoing restoration efforts. In Apalachicola Bay, FWC and FDACS used multiple restoration materials (limestone or quarried shell) at different cultching densities (Table 1). Monitoring efforts to track oyster population response have been similar across studies. The initiation of monitoring post-construction has varied from monitoring beginning within weeks of cultch planted to beginning 1-2 years following cultch placement because of Covid-19-related delays. The dependent variables for these analyses were the same as the first analysis, the number of oysters in the spat, seed, or legal-size categories (separate analyses for each dependent variable). The independent variables included Period, Study (studies described in Table 1), and a variable which represents the number of days in a Period Apalachicola River discharge was below 12,000 or 6,000 CFS (by convention) measured at the Jim Woodruff gage (USGS 02358000). How river discharge may relate to oyster population dynamics is a key management interest in the river basin (FL v GA 2015). This 12,000 CFS reference point is important because the adjacent floodplain becomes inundated at discharge levels 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 use the number of days per Period Apalachicola River discharge was < 12,000 CFS as an indicator of low freshwater inputs. Similarly, the number of days Apalachicola River discharge was < 6,000 CFS indicates extreme low river discharge periods because this river level approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam.

We explored how the different cultch materials and densities used in Table 1 persist over time. We summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, Site, and Period. We then used a similar generalized linear model framework as the live oyster count data to assess patterns in cultch material persistence across projects and Period.

Data and all code used for analyses is available from the following Git repository https://github.com/billpine/AB\_DEP.git .

*Results*

Trends in fisheries-dependent data

Trends in fisheries-dependent data from FWC 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 2000's peaking in 2012 when the fishery collapsed (Figure 2). Apalachicola Bay was closed to oyster harvest by FWC in December 2020, with a scheduled reopening in 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 trips and landings have declined in all three bays, with minimal levels of commercial fishing activity since 2015, when the current regional oyster restoration programs assessed in this analysis began.

Trends in oyster counts across Apalachicola, Pensacola, and St. Andrew Bays across reefs following restoration

The dispersion parameter from the negative binomial distribution ("binom2" family formulation) was <1 for all models, suggesting extreme overdispersion (Figure 3). We were most interested in the Bay \* Period mode as a framework to assess trends in oyster counts over time for each Bay. In addition to being the model of greatest management interest, this model also had the lowest AIC value (delta AIC between lowest AIC and model with second-lowest AIC = 3.3; Table X). For the Bay \* Period model Apalachicola Bay live spat counts declined (beta = -0.17, SE beta = 0.04, p<0.0001). Pensacola and St. Andrew bays show 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 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 about a median level of 0.8 live oysters 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 – 9864.0 95% CI). Only St. Andrew Bay is predicted (although highly uncertain) to increase since the beginning of the time series (Figure 4).

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 how 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 is Period 13. Predicted oyster counts for seed, spat, and legal size oysters for these periods do not increase between Periods 12 and 13 and observed CPUE for spat and seed are similar for prior periods. However, CPUE for legal-size oysters is higher in Periods 12 and 13 than observed in earlier periods. It is unknown whether this is directly related to the fishery closure during Period 12.

Apalachicola Bay oyster spat response to restoration from multiple studies

Observed counts of oyster spat in Apalachicola Bay by restoration Project (Table 1) range from 0 to more than 80,000 per ¼-m2 depending on project and Period (Figure 5), with oyster counts across study trending closer to zero from the early to most recent Periods (Figure 5).

We created a single data frame that integrated all survey efforts across Projects and standardized site names. We then fit GLM models assuming a negative binomial distribution to these data to describe the number of oysters of each size class over time (Period) with Site as a random effect and the log of the number of quadrats as an offset to control for differences in sampling effort. Results from this model found Period was significant (beta = -0.17, SE = 0.04, p < 0.001), suggesting that over time across the study, cultch material, cultch density used, counts of oyster spat declined over time following restoration. The predicted median number of oyster spat per ¼-m2 transect in Period 14 was 7.1 (4.8 – 10.6), much lower than in Period 1 (102.2, 58.6 – 178.3; Figure 6). We again fit a negative binomial model including terms for Period and a parameter describing the number of days river discharge was below 12,000 CFS. 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) are important in the model, suggesting that for each day increase in the number of days discharge is below 12,000 CFS the median number of oyster spat declines by about 1 oyster spat per ¼-m2 quadrat. The same model, but with a one-Period lag on the number of days discharge was below 12,000 CFS (as a measure of the potential influence of antecedent flow conditions), suggested 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).

Examining the different projects does not provide clear patterns into how counts of oyster spat change over time. We fit a GLM model assuming a negative binomial distribution that included Period and Project (four different projects, two using rock and two using shell; Table 1) to the observed oyster spat per quadrat counts. Comparisons of the performance of individual projects as a restoration action designed to increase spat production are difficult because of variations in the timing of when the monitoring began on each Project. For example, one project monitoring did not start until nearly two years following construction. If the response of cultch to restoration is different two years following restoration than immediately after restoration, then this would not be clear. However, 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. 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 this comparison, three studies completed their construction efforts 3-5 years before the last Period of data (NFWF-1, NRDA 4044, NRDA 5007), and FWC-2021 would be < 2 years since construction. If the time since construction significantly influenced, the predicted values for each study in the common Period should differ.

For the NFWF-1 Project (quarried shell cultch), we predict in Period 13 a mean number of live oyster spat of about 0.82 (95% CI 0.11 – 6.22) 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 lower at about 4.5 (95% CI 2.3 - 9.1). The predicted mean number of live oyster spat per ¼-m2 quadrat for the rock cultch projects varies. For Project NRDA 5007 mean predicted live oyster spat count per ¼-m2 quadrat was about 18.3 (95% CI 8.6 – 39.0), and project FWC-2021 mean predicted = 15.8 (95% CI 8.9 - 28.3). Project NFWF-1, a shell cultch project, had very high initial (soon after restoration) observed live oyster spat counts more than 100x those of any other projects (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

Total cultch weights for Apalachicola Bay were made integers by rounding to the nearest whole kilogram. Data were then subset for each 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 14, the last monitoring Period. Because Apalachicola was the only Bay where both rock and shell cultch were used, we focused analyses on comparing substrates on this Bay only. From an AIC perspective, models that included Period + Substrate or that examined the interaction between Period\*Substrate (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 (95% CI 2.5 – 10.2) in Period 2 to about 2.0 kg per ¼-m2 quadrat (95% CI 1.4 – 2.9). The shell biomass changed from about 1.7 kg per ¼-m2 quadrat (95% CI 1.1 – 2.7) to about 0.93 (95% CI 0.6 – 1.5). 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. The critical point is that 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 the area to the loss in mass, then shell mass and similar area degraded faster than rock material. 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.

River discharge as a proxy for salinity and nutrient patterns

Apalachicola River discharge deviated significantly (i.e., 50-100% below Period of 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 in 2019-2021 have generally been average to above average for most months (Figure 9).

*Discussion*

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 oyster state to a more desired, high oyster state. This conclusion is supported by data from three different bays in different watersheds restored with similar materials, construction designs, and monitoring programs. Restoration efforts in all three bays are guided by previous actions in Apalachicola Bay, where irregular clutching has been part of oyster management efforts since at least 1949 (Whitfield and Beaumariage 1977). Hurricane Elena in 1985 impacted oyster populations in Apalachicola Bay (Berrigan 1988, 1990), reducing oyster populations by as much as 95% (Livingston 2015). However, a rapid population recovery was observed in Apalachicola Bay following Hurricane Elena (Berrigan 1990) for reasons that may or may not be singularly 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 effort for oyster populations (Berrigan 1990). Berrigan (1990) identify that 156 ha of oyster reef received 472 m3 of *Rangia* clamshell per ha as part of the intensive restoration. Livingston et al. (1999) describe a major wild oyster spat 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). The oyster fishery reopened 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 is a similar response not observed from ongoing restoration efforts?

*Cultch density, volume, area, and material*

The cultch density used by Berrigan (1990) of about 617 yds3 per acre is about twice the density used in the most significant (rock cultch; NRDA 5007) and most recent (rock cultch; FWC 2021) restoration efforts and about 50% more than the highest treatment level of recent shell cultch projects (NFWF 1; Table 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 clutching program over about 400 ac per year could reduce the risk of an irreversible oyster fishery collapse in Apalachicola Bay. This clutching area is about four times the average area cultched each year between restorations following Hurricane Elena (Berrigan 1990; Pine et al. 2015) and the beginning of the most recent regional restoration efforts in 2015. 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 ten months post-restoration during the same Periods high oyster spat counts occurred on the NFWF-1 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 (kg). Follow-up assessments beyond ten months are unavailable for the reefs in Kimbro et al. (2020). Our work follows 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., 400 ac recommended from simulation, 100 ac restored on average since the mid-1980s) which describe the surface area of cultch available for spat to settle. Critically, the volume of cultch material (cubic meters of material) and the material's size determine the vertical relief added to the extant reef. For example, a 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. A cubic meter boulder is likely more resistant to movement because of its higher mass and would provide more vertical relief by not being flattened. This vertical relief difference (the height from the bottom) may be necessary for elevating the cultch material into suitable water quality or hydrodynamic conditions. Colden et al. (2017) found that oyster reefs > 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 Science (NAS) highlighted the NFWF 1 project assessed in this study as an example 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 sub-set of restored reefs in Pensacola, St. Andrew, and Apalachicola bays, including measurements of vertical relief (elevation). 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 4-10 mm in size) or larger and less dense (quarried oyster shell 50-75 mm in size) 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 (Figure 8), at low relief, and critically oyster spat settlement on this material has been very low for reasons that are not known.

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

Materials used for reef construction and various 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 (OIMMP). State of Florida statutes include language that is relevant to these restoration efforts, where statute 597.010

(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.

From this statute, Florida requires 50% of the shell material removed from harvest to be available for public use, including planting (cultching). These statutes exempt shell material from this requirement for oysters used in the half-shell market. Thus, oysters sold as half-shell (a national market), 50% of their shells are not required for re-use within Florida. 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 may not have been accurate, as supported by the observed oyster fishery collapse in 2012 and 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).

*Resistant to restoration?*

There are at least six 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. Critically, this lack of response occurs in bays within different watersheds and 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 measured population response has occurred when river discharge ranged from moderate drought to generally normal river discharge for the Period of instrument record. This would suggest that salinity (and other river-related ecosystem drivers such as nutrients) have been near normal (based on the instrument period of record) since 2015. This lack of response has also happened while commercial fisheries have been closed (Apalachicola Bay) or extremely low based on commercial fisheries landings information (Pensacola and St. Andrew bays). 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 responses in Apalachicola (and elsewhere) are more variable (Buzan et al. 2009; Fisch and Pine 2015; Gledhill et al. 2020; Moore et al. 2021).

(3) The restoration efforts assessed here (Table 1) focus on subtidal oyster reefs. Assessing whether restoration practices used on intertidal reefs can be extended to subtidal is an essential next step.

(4) The type and size of cultch material used in restoration should be re-assessed in Florida for ongoing restoration efforts. 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) also used dredged clam shell in the Chesapeake Bay. Oyster shell material is cited as one of the most effective shell restoration materials (Frederick et al. 2016). Limestone used in restoration projects in Pensacola, St. Andrew, and Apalachicola bays (Table 1) is mined in Kentucky and is denser (structure and mass), older (geologic age), and made of calcite, dolomite, and quartz (Jon Yeager, UF Geology, *personal communication*). Whether the chemical composition and physical characteristics of the limestone used in the different projects in Florida may influence the effectiveness of this material as cultch is unknown.

(5) The repeated and ongoing cultching efforts in Florida estuaries to reverse observed declines in oyster populations are a test of a single factor – that oyster populations have declined because of limitations in cultch. Other hypotheses, including the higher abundance of oyster predators (Kimbro et al. 2017), persistent disease (known or unknown), the effects of fishing, or some combination of all of these are more difficult to assess because of in adequate monitoring program design including short and inconsistent time series in available data. This could be addressed through development of a stair-case style restoration program in an adaptive management framework across different estuaries (Walters et al. 1988; Pine et al. 2022).

(6) 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 observed in the available fisheries independent monitoring data (1990-2013) used in their analyses. 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. There is significant concern 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 altering current conditions.

*Conclusions*

Low recruitment levels have persisted despite restoration efforts and management actions based on an empirical assessment of oyster recruits, seed, and legal-size oysters for Pensacola, St. Andrew, and Apalachicola Bay. These systems may have transitioned to a low productivity state that has proven resistant to restoration at the scales undertaken (Table 1), management actions (Apalachicola fishery closure), or environmental conditions (generally normal river discharge levels). Unfortunately, a combination of experimental design deficiencies (e.g., absence of controls, lack of strong treatment contrasts, no experimentation in materials) make it difficult to determine which factors that have been previously hypothesized to drive oyster population dynamics (i.e., river discharge, fishing effects). These deficiencies also make it impossible to identify the necessary components of successful restoration (reef material, area, or height) to learn. In absence of an ability to evaluate these factors from the available data, we are left with comparative assessments to restoration and management efforts projects that appear to have met their goals. This includes examples from the Chesapeake Bay region (e.g., Colden et al. 2017; Smith et al. 2022) or Florida (Pine et al. 2022) which document the use of naturally occuring materials constructed at elevations that are 0.3-0.4 m relief from the bottom. Of the management of a wild oyster fishery that is highly regulated, carefully monitored, and adaptively managed that appears sustainable Delaware Bay (<https://hsrl.rutgers.edu/SAWreports/index.htm>) or a recetly implemented innovative system of spatial management in Mobile Bay, Alabama. Unfortunately, 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). 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 (AEAM) suggests

A central tenet of AEAM 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.

Oyster populations in Apalachicola, Pensacola, and St. Andrew bays also appear resistant to changing from an undesired to desired population state despite large restoration efforts totaling tens of millions of dollars and very low levels of reported harvest in Pensacola and St. Andrew bays and a five year harvest moratorium (2020-2025) in Apalachicola Bay. Understanding why these systems have not responded to restoration efforts so far is critical to informing future restoration efforts, including nearly $20M in additional restoration dollars 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. DEP = 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 | DEP | Limestone | 20,103 | 17 | 228 |
| Summer 2016 | St. Andrew | NRDA 4044 | DEP | Crushed granite | 17,000 | 9 | 200 |
| Fall 2016 | Apalachicola | NRDA 4044 | DEP | Quarried shell | 24,840 | 16 | 200 |
| Fall 2017 | Apalachicola | GEBF 5007 | DEP | 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 |  | 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.

Chart, scatter chart

Description automatically generated

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

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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. Live oyster spat CPUE (y-axis, counts per ¼ m2 quadrat) from each study in Apalachicola Bay over time (Period, x-axis). Each panel is a different study completed by DEP or FWC. Even number Periods are winter (November-April) beginning in 2015 while odd number Periods are summer (May-October) beginning in 2016. The NFWF\_1 study uses shell cultch and the other studies use rock cultch.

Chart, scatter chart

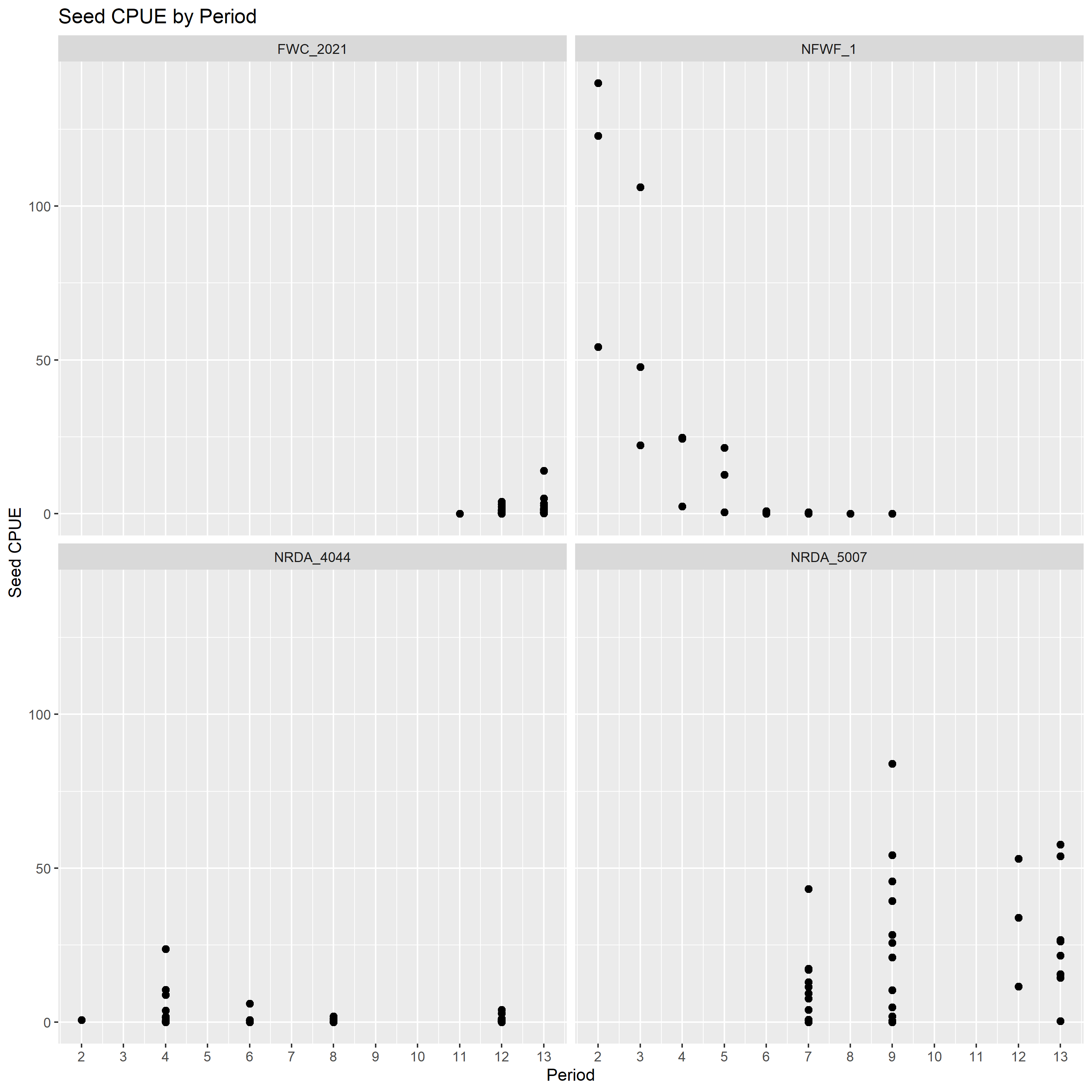
Description automatically generated

Figure 5 Version 2. Total live oyster spat (y-axis) from each study over time (Period, x-axis). This figure will probably go away because it isn't standardized, but it is just an example of what the different projects are counting in Apalachicola. Even number Periods are winter (November-April) beginning in 2015 while odd number Periods are summer (May-October) beginning in 2016.

Chart

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Seed CPUE by study



Legal cpue by study

Chart, scatter chart

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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

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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.