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 historic levels for poorly understood reasons. Since 2010, the states of Florida, Alabama, Mississippi, Louisiana, and Texas have all declared state or federal level oyster fishery disasters, citing reasons including prolonged drought, extreme rain events, or freshwater releases from water management structures (refs). 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 U.S. Supreme Court over water management in the Apalachicola River. In this suit, Florida argues that water use in the Georgia portion of the Apalachicola-Chattahoochee-Flint river basin may have contributed to the 2012 oyster population collapse in Apalachicola Bay (ref). Oyster populations in the Gulf of Mexico were damaged by the sinking of the *Deepwater Horizon* and subsequent oil spill (Deepwater Horizon Natural Resources Damage Assessment Trustees, 2016). Subsequent settlements resulting from legal proceedings and regulatory fines created substantial funding opportunities (more than $199M U.S.) 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 oyster harvesters cull undersized oysters and cultch material away from the reef (Swift 1897; 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 (ref).

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 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, in general, these restoration efforts are expected to provide and promote ecosystem services and create opportunities for oyster harvest through fishery recovery.

Site description – Oyster population trends were assessed 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 implemented in 1985. 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 which 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, but are available for the counties comprising St. Andrew Bay where oyster trips and landings in recent decades 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. Andrews Bay approximately 17,000 cubic yards of crushed granite was distributed on nine different 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 cards 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. 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 of cultch material deployed varied due to construction challenges and storm events that occurred during the study.

Table 1. Summary of deployment date, location, and project description.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| 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 |
| June 2016 | St. Andrews | NRDA 4044 | DEP | Crushed granite | 17,000 | 9 | 200 |
| November 2016 ?? | Apalachicola | NRDA 4044 | DEP | Quarried shell | 24,840 | 16 | 200 |
| November 2017 | Apalachicola | GEBF 5007 | DEP | Limerock aggregate | 95,500 | 14 | 300 |
| August 2015 | Apalachicola | NFWF-1 | FWC | Quarried shell | 9,600 | 3 | 100,200,300,400 |
| July 2021 | Apalachicola | NFWF-2021 | FWC | Limerock aggregate | 9,600 |  | 300 |

*Methods*

*Methods*

Fisheries dependent data – Commercial fisheries landings data for each of the three bays from Florida Fish and Wildlife Conservation Commission public database were summarized. For each bay the landings and trips were summed by county surrounding the bay, and the calculated catch-per-unit effort (CPUE) as annual landings/annual trips.

Reef construction – Reef construction methods across studies were similar and were designed to minimize costs and maximize amount of material deployed. Sites were selected for cultch placement based on local knowledge of historic or extant reef locations. Cultch material was deployed on site from barges by washing material from barge deck using high pressure hoses at a prescribed density. Reef materials were either quarried shell or a “Kentucky” limestone of graded size (often #4, 1.5-3 inches in size) transported on barges via inland and coastal waterway and then “planted” at specific locations.

Field collections – Similar methods were followed for all projects to estimate live oyster counts and mass of cultch material based on methods used in Florida since the 1980s (FWC 2021 <https://myfwc.com/media/27745/oimmp-v2-ch11.pdf>) where divers haphazardly place ¼-m2 (0.5-m on each side) quadrats at selected sites and 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 site or returned to the lab where counts of live and dead oysters, measurements of shell height, weight of cultch material, and other metrics depending on study were recorded.

Data Analyses – Methods for analyzing oyster count data followed Moore et al. (2020) modified based on how data were collected in the field. We conducted two separate analyses to address specific questions of mangement interest. The first analyses 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 analyses focused on a series of specific management questions that could only be addressed using data from Apalachicola Bay including how oyster counts of each size class were influenced by freshwater discharge into Apalachicola Bay and how oyster counts differed over time and cultch material and cultch density used in the four different projects that are ongoing within Apalachicola Bay.

The general approach for the two analyses followed these steps:

(1) Counts of live oysters at each restoration site and period were summed into three size classes, spat (<26-mm shell height), sublegal (locally termed “seed” oyster; 26-75-mm shell height), and legal harvest (>76-mm shell height). For some studies, counts were totaled in this way in the field and 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 to the sample of total oysters.

(2) The distribution of the count data was assessed by examining the ratio between the count mean and variance at each site.

(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 variabiles include Period a variable representing continuous time used to combine sampling months into winter (November-April) or summer (May-October). For analyses one, Bay (Pensacola, St. Andrew, and Apalachicola bays) was also used as a categorical independent variable. 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 at each site, so we included the number of quadrats as an offset of effort (log link function; Zuur et al. 2009, 2013). By using effort as an offset in this way 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 across study, the area sampled 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 density 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). We.

(4) Model fit was assessed visually by comparing data and a predicted line fitted to these data with 95% confidence intervals.

(5) Model comparison between independent variables was made using AICc.

(6) Models were fit to data using the glmm.TMB package (Brooks et al. 2017) and predicted values were made from the best fit model using the ggeffects package (Lüdecke 2018) in R (R Core Team 2021).

We then summarized river discharge for primary rivers entering each bay as a proxy for salinity and nutrient inputs prior, during, and after restoration efforts in each Bay 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 began the time series about 10 years prior to restoration efforts to capture antecedent river discharge conditions prior to restoration beginning. Pensacola Bay has three rivers that enter the bay (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. Andrews Bay is unusual in that it has no major freshwater inputs (Crowe et al. 2008) thus no summary of freshwater inputs was made. For Apalachicola Bay we summarized river discharge information from USGS gauge 02358000 (Apalachicola at Chattahoochee).

A second set of analyses were conducted 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 and monitoring programs used as part of ongoing restoration efforts. In Apalachicola Bay, multiple restoration materials (limestone or quarried shell) cultch has been used in Apalachicola Bay at different densities (Table 1). Because of construction challenges, some sites may have received both limestone and shell. 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 monitoring beginning 1-2 years following cultch placement because of Covid-19 related delays. For these analyses the dependent variables were the same as above, the number of oysters in either 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 describes the number of days in a Period Apalachicola River discharge was below 12,000 CFS (by convention) measured at the Jim Woodruff gage (USGS 02358000). This river discharge metric, and how this may relate to oyster population dynamics, is a key management interest in the system (FL v GA 2015). This reference point is important because at discharge levels of about 12,000 CFS the adjacent floodplain becomes inundated (Light et al. 1998, Fisch and Pine 2016) although the exact point of inundation may have changed over time due to river bed 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.

Additionally, because the projects in Table 1 use different cultch materials and densities, and there is uncertainty related to how this cultch material persists 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.

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 several orders of magnitude larger (trips and landings) than Pensacola and St. Andrews 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. Andrews, and Apalachicola bays show a similar pattern of increasing trips and landings in the mid-1980's and again in the 2005-2010 period. Since 2010 trips and landings have declined in all three bays, with extremely low levels of commercial fishing (trips and landings) since 2015 when the curent regional oyster restoration programs assessed in this analysis began.

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

The dispersion parameter from the negative binomial distribution (binom2 family formulation) was <1 for all models, suggesting extreme overdispersion (example 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 AICc 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. Andrews 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. Andrews beta = 0.25, SE beta = 0.20, p=0.03). Even though the estimated slope is positive for Pensacola and St. Andrews bays, this trend is uncertain (high standard error on beta terms). The value is low suggesting a median increase of about one oyster spat per quadrat for each time period (example back transformation exp0.25 = 1.3). This contrasts with Apalachicola Bay which was declining at about a median level of 0.8 live oysters per quadrat per Period (exp-0.18 = 0.8). Predicted 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), Pensacola = 15.3 (1.5 - 160.8), and St. Andrews = 570.5 (33.0 – 9864.0) with only St. Andrews having a predicted (and highly uncertain response measured in the betas) increase since the beginning of the time series (Figure 4).

Table 3. 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 |
|  |  |  |  |

Fitting the same Bay \* Period model to counts of seed or legal sized oysters revealed a similar pattern as seen in oyster spat – observed and predicted declines in seed oysters over time in Apalachicola Bay, relatively constant values in Pensacola Bay, and increasing, but low counts in St. Andrews Bay. St. Andrews 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]; Pensacola 0.14, [0.04 – 0.50]).

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, S.E. = 0.04, p < 0.001) suggesting that over time for each Period and across study and cultch material used, and density of cultch material deployed, counts of oyster spat did not respond positively to restoration action. Predicted 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 slightly (exp-0.006) by about 1 oyster spat per ¼-m2 quadrat. The same model, but with a one-Period lag on the number days discharge was below 12,000 CFS (as a measure of 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).

Table 4. 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.

|  |  |  |  |
| --- | --- | --- | --- |
| 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 |

An examination of the different projects, which were deployed in different Periods and monitoring begin in different Periods, 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 counts of oyster spat per quadrat. Comparisons of the performance of project in producing oyster spat are difficult because of variations in the timing of when the monitoring began on each project. As an example, for one project monitoring did not begin 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 intent of the restoration is to provide substrate in a way that will allow colonization and accretion of material over many years. If the restoration is successful, the count response should persist over multiple years. To create a comparative framework across studies with different materials and starting points, we predicted the number of oyster spat per ¼-m2 in period 14, the last Period of monitoring. In this comparison three studies would have completed their construction efforts 3-5 years prior to the last Period of data (NFWF-1, NRDA 4044, NRDA 5007) and FWC-2021 would be < 2 years since construction. If time since construction were a major influence, then the predicted values for each study in the common Period should differ. For the NFWF-1 project which used quarried shell cultch, we predict in Period 14 a median number of live oyster spat of about 26.2 (95% CI 8.6 - 79.4) per ¼-m2 quadrat. The NRDA 4044 project also used quarried shell cultch and the median predicted number of live spat in Period 14 was lower at about 3.5 (95% CI 1.7 - 7.1). For the projects that used rock cultch the predicted median number of live oyster spat per ¼-m2 quadrat vary. For project NRDA 5007 median predicted live oyster spat count per ¼-m2 quadrat was about 15.4 (95% 8.3 – 28.3), and project FWC-2021 median predicted = 7.0 (4.5 - 10.9). An interesting result is that the most recent (existing fewest number of years) constructed reef project FWC-2021 had predicted counts that was lower than the older rock cultch project NRDA 5007. Project NFWF-1, a shell cultch project, had very high initial (soon after restoration) observed live oyster spat counts that were more than 100x those any of the other projects (Figure 5). The extreme dispersion observed for this project (Figure 5, observed counts) resulted in poor model fit.

Persistance of cultch material in Apalachicola Bay

Total cultch weights for Apalachicola Bay were made integers by rounding to 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 as described 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 Period of monitoring. Because Apalachicola was the only bay where both rock and shell were used, we focused analyses to compare substrates on this bay only. From an AIC perspective, models that included Period + Substrate or models that examined the interaction between Period\*Substrate (both with 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, what is more important than the statistical significance is whether the material persisted over time – 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 (1.4 – 2.9), whereas the biomass of shell changed from about 1.7 kg per ¼-m2 quadrat (1.1 – 2.7) to about 0.93 (0.6 – 1.5). Because shell is less dense than rock, the differences in biomass per quadrat are not surprising - these results suggest a decline of about 60% biomass for the shell material by the end of period 13 and about 45% of the rock material. A 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 supporting 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, 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 generally been average to above average for most months (Figure 9).

*Discussion*

Our results suggest restoration and management efforts in Pensacola, St. Andrews, 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 based on data from three different bays in different watersheds but with common restoration materials, techniques, 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 to 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 an intensive management and restoration effort for oyster populations (Berrigan 1990). Efforts detailed in 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 set occurring 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), and 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. Comparative data on historic clutching efforts for Pensacola and St. Andrews bays are not available. 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) conducting 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, observed a positive response to oyster reef restoration ten months post-restoration during the same time Periods high oyster spat counts were observed 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 not available for the reefs in Kimbro et al. (2020). Our work does follow similarly restored reefs (materials, densities, and starting time) over several years post-construction and found that the initial oyster population response to restoration as measured by counts did not persist (Figure 6).

Notably, 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. Pine et al. (2015) identified a key uncertainty to address in determining the volume to cultch to use in these efforts. 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 (i.e., tidal, storm, etc.) moving the small mass of each individual cobble piece. A cubic meter boulder is likely more resistant to movement from currents 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 higher than 0.3 m in the Chesapeake Bay region had higher oyster survival, density, and overall complexity than oyster reefs < 0.3 m, and these 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, that experiment does not appear to have answered the questions as designed, perhaps because of construction challenges 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. Andrews, 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 0.04-0.08 m in size) or larger and less dense (quarried oyster shell X-Y" 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) interrupted by subtle waves of higher-density of material (volumetrically) which results in slightly higher vertical relief (about 0.1 m). Regardless, cultch material in various forms at different mass levels has persisted on these restored reefs (Figure 8), 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 Lone Cabbage Reef in Suwannee Sound demonstrated oyster spat settlement and persistence on the restored reef within six months following construction and oysters have persisted and successfully settled on the reef in each of 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 the results from 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. Andrews 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 for 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 suggests 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 five key takeaways from this analysis:

(1) Oyster populations in Pensacola, St. Andrews, 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.

(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. River discharge is thought to be a major driver of salinity, and salinity a major driver of oyster survival (demonstrated by the State of Florida position in FL v GA). This would suggest that salinity (and other river-related ecosystem drivers such as nutrients) have been near normal (based on 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. Andrews bays).

(3) The restoration efforts assessed here (Table 1) focus on subtidal oyster reefs. The Lone Cabbage Reef restoration project has shown a positive response to restoration, but that project has focused on the restoration of intertidal oyster reefs. Assessing whether restoration practices used at Lone Cabbage Reef can be extended to subtidal habitats is an important 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 which is 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). The Lone Cabbage Reef project used a soft limestone of a geologic formation that is part of the exposed Florida platform within Suwannee Sound. The limestone was quarried from within the Suwannee River basin (near Branford, Florida). This soft limestone is primarily dolomite, likely from the "Avon Park" formation, a relatively young age (thousands of years). Limestone used in restoration projects in Pensacola, St. Andrews, 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*). How 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 higher abundance of oyster predators (Kimbro et al. 2017) or persistent disease (known or unknown) are more difficult to assess because of short time series in available data such as counts of predators on restored reefs.

(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. Andrews, and especially Apalachicola Bay oyster populations are in such a degraded state that no restoration or management action considered may be effective in altering current conditions.

*Conclusions*

Based on the empirical assessment of oyster recruits, seed, and legal-size oysters for Pensacola, St. Andrews, and Apalachicola Bay, low recruitment levels have persisted, and 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) make it difficult to determine which factors that have been previously hypothesized to drive oyster population dynamics (i.e., river discharge, fishing effects) or are necessary components of successful restoration (reef material, area, or height) to learn going forward. In absence of an ability to evaluate these factors from the available data, we are left with a comparative assessment to restoration projects that have proven successful from the Chesapeake Bay region (e.g., Colden et al. 2017; Smith et al. 2022) or Florida (Pine et al. 2022) or an example wild oyster fishery that is highly regulated, carefully monitored, and adaptively managed that appears sustainable (Delaware Bay; https://hsrl.rutgers.edu/SAWreports/index.htm). 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). This 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. Andrews bays also appear resistant to changing from an undesired to desired population state despite large restoration efforts totaling tens of millions of dollars and ver;y low levels of reported harvest in Pensacola and St. Andrews 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. Stronger leadership and a commitment to learning may be needed to guide these restoration and management efforts 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.

*Acknowledgments*

*References*

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*Figures*

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###This will be a really great map of the panhandle with the F.L. inset

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

A picture containing scatter chart

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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 top row, Pensacola middle row, St. Andrews bottom row) 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

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Figure 3. Period of time (x-axis) and spat CPUE (y-axis) per quadrat in each of the three study systems (Apalachicola, Pensacola, St. Andrews 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. Andrews). 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

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Figure 5 Version 1. Live oyster spat CPUE (y-axis, counts per ¼ m2 quadrat) from each study 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

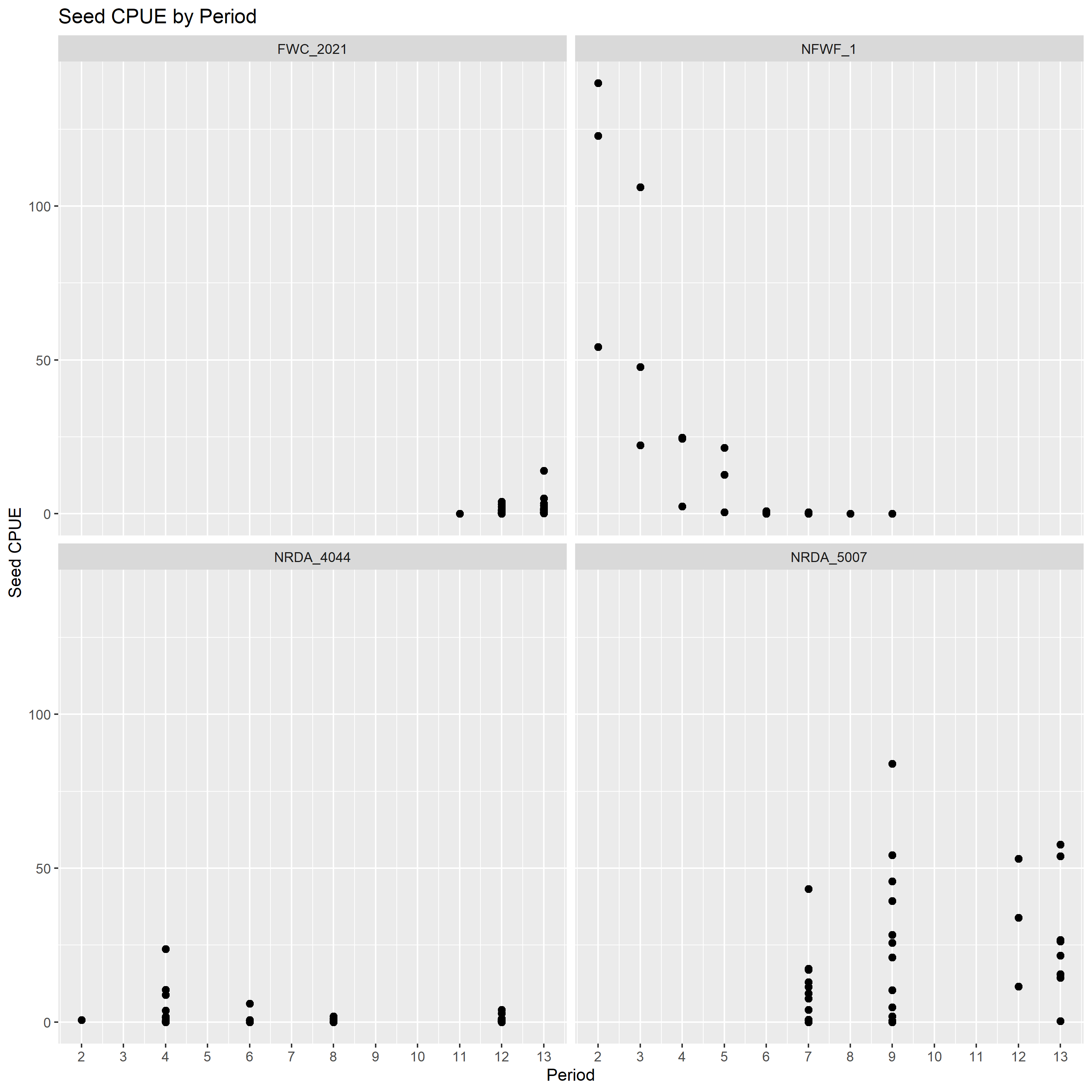
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Figure 5 Version 2. Total live oyster spat (y-axis) from each study over time (Period, x-axis). This figure will probably go away because it isn't standardized, but it is just an example of what the different projects are counting in Apalachicola. 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

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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

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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

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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

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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

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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.

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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

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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.