

**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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1 Abstract

2 Depressed oyster *Crassostrea virginica* populations in the northern Gulf of Mexico have been
3 the target of numerous post-*Deepwater Horizon* restoration projects, which primarily focus on
4 replacing oyster cultch (substrate) to promote spat settlement, increase recruitment, and
5 bolster adult oyster populations. This study assesses oyster populations at the sites of six such
6 efforts, which used different cultch types and densities and were carried out in 2015–2022 in
7 three estuaries on the Florida panhandle coast (Pensacola, St. Andrew, and Apalachicola bays).
8 Total restoration costs were more than \$14M. The durability of the new cultch and the
9 potential effect of freshwater discharge on oyster spat counts were also explored. Counts of
10 oysters of different size classes did not persistently increase following restoration (while
11 controlling for sampling effort), regardless of cultch type or density used in the restoration.
12 Positive responses to restoration efforts were irregular, short-lived, generally < 6 months, and
13 seemed only to occur for spat-size oysters immediately after restoration. None of the
14 restoration efforts significantly improved abundance of oysters of any size class in any of the
15 three estuaries. With the available data, it is not possible to say with certainty what is hindering
16 restoration success because of monitoring program shortcomings. However, restoration design
17 and implementation deficiencies, including uncertainty in the materials used and minimal
18 vertical relief of restored reefs post-construction, likely contribute to the lack of project
19 success. These short comings must be addressed through fundamental changes in oyster
20 restoration and monitoring efforts used in Florida to foster learning, improve restoration
21 strategies, and ultimately recover oyster populations.

22

23 Introduction

24 Eastern oyster populations in the northern Gulf of Mexico are depressed from historical levels
25 for widely speculated but poorly understood reasons. Since 2010, the states of Florida,
26 Alabama, Mississippi, Louisiana, and Texas have declared state- or federal-level oyster fishery
27 disasters, with several of these states implementing fishery closures in response to the
28 depressed status of oyster stocks (Mobile Bay in Alabama, Apalachicola Bay in Florida,
29 Galveston Bay in Texas). Only one of these stocks (Mobile Bay) has reopened to harvest. The
30 potential reasons for regional oyster declines include prolonged drought, extreme rain events,
31 freshwater releases from water management structures, environmental degradation,
32 overharvesting, oil spill, and insufficient cultching (Petes et al. 2012; Pine et al. 2015;
33 Deepwater Horizon Natural Resources Damage Assessment Trustees 2016; Kelly 2019; Gledhill
34 et al. 2020; Du et al. 2021; Coastal Alabama Comprehensive Oyster Restoration Plan Marine
35 Resources Division and the National Oceanic and Atmospheric Administration Published by the
36 Deepwater Horizon Alabama Trustee Implementation Group 2021).

37 Many proposed, ongoing, and historical oyster restoration efforts focus on protecting or
38 adding substrate to replace oyster cultch, a matrix of living and dead material that was
39 removed or displaced by fishing practices, to create sites for oyster spat settlement (Swift 1897;
40 Swift 1898; Lenihan and Peterson 1998; Pine et al. 2015; Lenihan and Micheli 2000; Howie and
41 Bishop 2021). These restoration efforts attempt to shift oyster reefs from an observed low but
42 apparently resilient state to a more desired productive state (Pine et al. 2022). While the
43 desired state can vary by location, type of oyster bar (intertidal vs. subtidal), and management
44 goals, all restoration efforts are expected to persistently increase oyster populations so that

they will provide and promote ecosystem services (Smith et al. 2022), and support fishery recovery.

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

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

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

(2) In a focal site (Apalachicola Bay), how do trends in oyster spat (the life stage hypothesized to respond first to restoration) vary among separate restoration projects?

(3) Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?

(4) How do oyster spat densities compare across projects and cultch densities in Apalachicola Bay?

(5) How well do different types and densities of restoration-sourced cultch persist following deployment in Pensacola, St. Andrew, and Apalachicola bays?

We show that large restoration programs are not having the desired outcome of increasing live oyster populations of any size class. This may be because these systems are trapped in a resilient but low-oyster-production state (Johnson et al. 2022) that is resistant to restoration, or that the restoration programs (as designed) were ineffective at shifting populations from the low production state. Our work suggests that substantial uncertainty persists in how to restore oyster populations at large scales in Florida successfully. Addressing these uncertainties will require strong leadership from agency, academic, and industry leaders to conduct restoration projects in frameworks that allow for better learning to increase the likelihood of successfully restoring oyster populations.

Study sites

We assessed oyster population trends in three estuaries in the Florida panhandle that have ongoing or recently completed oyster restoration projects: Pensacola Bay, St. Andrew Bay, and Apalachicola Bay (Figure 1). Pensacola Bay in northwest Florida (Santa Rosa and Escambia counties) is the fourth largest estuary in Florida, with a surface area of approximately 50,990 ha. Reported oyster landings, trips, and catch-per-unit-effort (CPUE) for Pensacola Bay have declined since the current mandatory trip-ticket program was fully implemented in 1986 (Figure 2). Most oyster landings from St. Andrew Bay are taken from the East Bay arm which has a total surface area of approximately 176,847 ha (Comp and Seaman 1988). Oyster landings and trips for East Bay are not available, but they have declined in surrounding counties, and harvest in recent years has been near zero. Apalachicola Bay is a 348,029-ha estuary in Franklin County that supported the largest oyster fishery in Florida before collapsing in the fall of 2012 (Pine et

al. 2015). Apalachicola Bay was closed to commercial harvest from December 2020 through December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

Restoration actions

Cultch material was deposited in each bay in phases by state management agencies as part of multiple projects led by the state of Florida with funds from the *Deepwater Horizon* oil spill settlement. Reef construction methods across projects were similar and designed to minimize costs and maximize the area over which materials were deployed like previous cultching efforts since the 1970s (Berrigan 1988; 1990; GSMFC 2010). Reef materials were either quarried shells, crushed granite, or a Kentucky sourced limestone of graded size (often #4, 25–64 mm) transported on barges and then "planted" at specific locations (Table 1; FDACS 2015; 2016a, b; 2017).

Site selection was based on local knowledge of historical or extant reef locations. Most of the work was carried out from 2015 to 2017, with one project taking place in the summer of 2021 (Figure 3). Three state agencies, FWC, Florida Department of Agriculture and Consumer Services, Division of Aquaculture (FDACS), and the Florida Department of Environmental Protection (FDEP), managed the projects under the sponsorship of the Natural Resource Damage Assessment (NRDA) and Gulf Environmental Benefit Fund (GEBF), administered by the National Fish and Wildlife Foundation (NFWF). One project took place in each of Pensacola and St. Andrew bays, and four in Apalachicola Bay. The work carried out under these projects is summarized in Table 1. Across all projects, the realized area and density (thickness or depth) of cultch material deployed varied from the planned application due to construction challenges

and storm events during the studies. These challenges resulted in uncertainty in the actual area and height of the restored reefs constructed.

The relationship between freshwater discharge from the Apalachicola River and oyster populations in Apalachicola Bay is of significant management concern at a focal aspect of a recent US Supreme Court Case (Florida v Georgia, No 142 Original. 2014). Because Apalachicola Bay is the only one of these three bays where upstream reservoir operations can influence freshwater inputs (Leitman et al. 2015), we summarized river discharge for the Apalachicola River as a proxy for salinity and nutrient inputs before, during, and after restoration efforts. We did this by plotting the percent deviation in mean river discharge (cubic feet per second [CFS] by convention; USGS gauge 02358000) from the mean period of instrument records by month and year. We began this time series in 2002, 10 years prior to oyster fishery collapse and 13 years before the start of the restoration projects covered by this study, to capture antecedent river discharge conditions.

Methods

Field collections

Similar oyster monitoring methods were followed across projects to count live oysters and mass of cultch material, based on techniques used in Florida since the 1980s (Florida Fish and Wildlife Research Institute 2021). Divers randomly placed $\frac{1}{4}$ m² (0.5 m on each side) quadrats at selected sites, removed all oysters and cultch material to wrist depth, and placed the cultch and oysters in bags. Once bags were returned to the vessel, they were either processed on location or returned to the lab. There counts of live and dead oysters,

measurements of shell height, weight of cultch material, and study-specific metrics (e.g., identification of other benthic species) were recorded.

Apalachicola Bay restoration efforts took place across four different projects in periods (a continuous variable for time which combined sampling months into common blocks of time) 2, 6, and 13. Divers sampled oysters to track response to restoration in periods 2-10 and 12-15, depending on Project (Figure 3). Pensacola Bay restoration took place in Period 2 and oyster sampling was conducted in periods 5-7, 10, and 15. St. Andrew restoration also took place in Period 2 and oyster sampling took place in period 5, 7, and 10 (Figure 3; Appendix 1).

Fisheries-dependent data

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

Data analysis

We conducted five related analyses. For Question 1, we assessed how oyster counts responded to restoration efforts (i.e., how counts changed following restoration) in all three bays (Pensacola, St. Andrew, and Apalachicola) while controlling for differences in sampling effort. We then focused on Apalachicola Bay for more detailed analyses because Apalachicola Bay is the only bay where multiple restoration projects using different materials and starting points in time have been conducted. Questions 2 and 3 explored whether oyster spat counts were influenced by freshwater discharge and how they differed over time, cultch material, and cultch density within a single bay, Apalachicola (Table 1). For Questions 4 and 5, we assessed trends in oyster cultch across restoration projects using different cultch materials at different

times for Apalachicola in detail (Question 4; Apalachicola Bay is the only one of the three where multiple materials and projects have been completed), and across all three bays in Question 5. For Questions 4 and 5 we summed the weight of cultch collected by divers conducting the oyster surveys by cultch material, site, and period (a continuous variable for time which combined sampling months into common blocks of time—winters (October–March), represented by even numbers, and summers (April–September), represented by odd numbers). This sum would include both the cultch material placed on the reef during restoration as well as any cultch material (living or dead) that had accumulated on the substrate. Total cultch weights were made integers by rounding to the nearest whole kilogram. We used methods following Moore et al. (2020), and the dependent variables were the number of spat (<26mm shell height), seed (26-75mm shell height), or legal-size oysters (>75mm shell height) depending on the question. The independent variables were as follows.

- Period, a continuous variable for time considered in both analyses, which combined sampling months into common blocks of time—winters (October–March), represented by even numbers, and summers (April–September), represented by odd numbers. (Questions 1-5)
- Bay (Pensacola, St. Andrew, or Apalachicola) was included as a categorical variable in the first analysis, comparing restoration responses by bay. (Question 1 and 5)
- Type and density of cultch material were represented as a single categorical variable by the name of the project, as each of the four Apalachicola Bay projects used a different cultch material, density, and start time. (Question 3, 4)

- River discharge measured as the number of recent days in which discharge fell below certain specified levels. (Question 3)

We used restoration site (a named oyster reef) as a random effect (uniquely named for each site and bay or site and project combination) to account for correlation among quadrat samples at each site (Questions 1-5).

The analyses followed these general steps:

- (1) Counts of live oysters in each bay and for each restoration site and period (a common time factor) were summed into three size classes (the dependent variables): spat (<26 mm shell height), seed (larger than spat but below minimum legal harvest size, 26–75 mm shell height), and legal to harvest (>75 mm shell height). For the restoration projects NRDA-4044 and GEBF-5007, counts per size class were totaled in the field. For projects NFWF-1 and NFWF-2021, count totals (all sizes combined) were converted to counts per size classes by calculating the proportion of oysters within each size class from concurrent oyster shell-height samples and multiplying the totals by these proportions. The results were rounded to convert the numbers of oysters per size class to integers to match the NRDA-4044 and GEBF-5007 data.
- (2) Generalized linear models (GLMs; Bolker et al. 2009) with a negative binomial distribution were used to assess how oyster counts in all three size classes separately varied over different independent variables (Question 1), using the R package glmmTMB (Brooks et al. 2017).
- (3) We assumed that the total oyster counts per site would be related to the sampling effort (number of quadrats collected). We included the number of quadrats as an effort

offset (log link function; Zuur et al. 2009; Zuur et al. 2013). This change effectively caused our models to predict the rate measured as count/quadrat while maintaining the dependent variable as an integer of counts. Because the quadrats were the same size for each study site, the total area sampled in each period only changed as a function of the number of quadrats. Using counts as the dependent variable and offsetting for effort, instead of converting the counts to CPUE based on the area sampled, has two main advantages. First, it maintains the response as an integer, allowing the use of a negative binomial distribution (appropriate for oyster count data; Moore et al. 2020); second, fitted values and confidence intervals do not contain negative values (Zuur et al. 2009).

(4) Comparisons were made between models with different combinations of independent variables using the Akaike information criterion (AICc), where the lowest AICc value represents the best fit of the models tested (Burnham and Anderson 2002).

(5) Model autocorrelation in the residuals for the top model was assessed by using the DHARMA package (Hartig 2022) in R by simulating new response data from the specified model and then using qq plots to check for deviations from the expected distribution graphically, a KS test to test whether observed and expected distributions differed, and a Durbin-Watson test to check for temporal autocorrelation. Significance was assumed at a $p < 0.05$ level.

(6) Models were fit to data using the glmmTMB package (Brooks et al. 2017) and predicted values (marginal means) were made from the best fit model using the emmeans (Lenth

2022) and ggeffects packages (Lüdecke 2018) and all analyses were done in R (R Core Team 2021).

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

We first looked broadly at oyster population responses to restoration across three bays (Apalachicola, Pensacola, and St. Andrew, Question 1). The dependent variables were the number of oysters in the spat, seed, or legal-size categories (separate analyses for each category). The independent variables (main effects) were Period (continuous) or Bay (categorical). We fit five models to the data: Model 0 was intercept-only, Models 1, 2, and 3 included Bay, Period, or both Bay and Period as main effects, respectively. Model 4 included the interaction between Period and Bay. Model 5 allowed trends in oyster counts to vary across site in each Bay (site nested within Bay). Model 6 was the same as model 5 but also allowed different dispersion parameters for the negative binomial model for each Bay. We used the default glmmTMB optimizer (nlminb) for fitting all models and no convergence issues were identified.

Question 2: How do oyster trends vary among restoration projects in Apalachicola Bay?

Restoration efforts in Apalachicola Bay differ from Pensacola and St. Andrew bays because there have been at least four restoration efforts since 2015 in Apalachicola Bay using different materials and starting at different times (Table 1), and only one restoration effort in the other bays. We hence focus here on only Apalachicola Bay. For Question 2 (change in oyster counts across projects) and Question 3 (spat count association with freshwater discharge) we assessed the independent variables of cultch material and density (which varied by project) and freshwater discharge (which varied over time). As in Question 1, the dependent variables were

the number of oysters in the spat, seed, and legal-size categories. The independent variables were period, project (as a proxy for cultch type and density), and river discharge. For Question 2 we fit eight different models to the data (Table 3). We checked model convergence using both the default glmmTMB optimizer nlminb and the BFGS. Models that converged using both estimators had similar results, but only the BFGS converged for all models so model comparisons were made based on results using BFGS. The relative fit of these models was again compared by AICc. Autocorrelation of the residuals was checked with the DHARMA package (Hartig 2022). In this comparison, three projects (NFWF-1, NRDA 4044, and NRDA 5007) completed construction three to five years before the last period of data, and one (project NFWF-2021) less than two years before. If the materials, amount, or time since construction was completed significantly influenced oyster reef restoration performance, the predicted values for each project in the common period should differ.

Question 3: Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?

We then compared the best fitting model of the eight models assessed in question 2 (Table 3) to four additional models which describe different Apalachicola River discharge metrics (using the same fitting routine and model checks) to see if model fit improved with the addition of river discharge information (Table 4). River discharge was measured as the number of days in each period or the prior period (as a measure of antecedent discharge) when the Apalachicola River discharge was below 12,000 or below 6,000 CFS measured at Jim Woodruff gage (USGS 02358000). The 12,000 CFS reference point is important because the adjacent floodplain becomes inundated at discharge near this level (Light et al. 1998; Fisch and Pine 2016). The exact point of inundation may have changed over time due to riverbed degradation.

Regardless, we used this reference point as an indicator of low freshwater inputs. A discharge level of <6,000 CFS indicates extreme low river discharge, because it approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam.

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

To assess relationships between oyster spat densities and cultch densities we summarized biomass of cultch per quadrat and treated cultch biomass as the response variable in the same negative-binomial GLMM models used to assess response of oyster spat counts in Question 2 (Table 2). We fit ten different models to the data, to assess the relationship between cultch mass and Period, Project, SP (random effect; a variable combining site and project name) and we also included the sum of spat in each quadrat as a factor (Spat sum) and the interaction between Spat sum and Project (Spat sum:project) to see if the relationship between live oyster spat and cultch mass differed by project (Appendix 2). Some of these models were overfitted thus comparisons were made with eight simpler models (Table 5; Appendix 2).

Question 5: How does cultch material persist in all three bays?

To explore how cultch material persisted in different Bays (Pensacola, St. Andrew, and Apalachicola; Table 6) and by project within Apalachicola Bay (Table 7), we again used negative binomial GLM models to assess how the sum of the weight of cultch collected by divers during oyster surveys changed over time in each bay (all projects). In Apalachicola Bay we assessed persistence of cultch material by project (because of different materials and restoration time frames; similar approaches as with live oyster spat counts in Questions 2 and 3 above). Data were summarized by project, and calculations of mean and variance by project suggested the

data were over-dispersed (variance > mean). To create a comparative framework across substrates, we predicted the amount of cultch per $\frac{1}{4}$ m² in the last monitoring period for each study (Figure 3).

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

Results

River discharge patterns

Apalachicola River discharge deviated significantly (50–100% below the average for the period of instrument records; Figure 4) for three or more months in 2002, 2006, 2007, and 2008, with extreme drought in 2011 (9 of 12 months), 2012 (12 of 12 months), 2016 (6 of 12 months), and 2017 (4 of 12 months). Regional river discharge patterns for 2013–2022 were generally closer to average than 2002–2012.

Trends in fisheries-dependent data

Trends in FWC fisheries-dependent data since 1986 show the Apalachicola Bay commercial fishery was larger (trips and landings) than those of Pensacola and St. Andrew bays combined. Apalachicola trips and landings increased sharply during the early 2000s, peaking prior to fishery collapse in 2012 (Figure 2). Apalachicola Bay was closed to oyster harvest by FWC in December 2020, with a reopening scheduled for December 2025. Pensacola, St. Andrew, and Apalachicola bays show similar trends of increasing trips and landings in the mid-1980s and again in 2005–2010. Trips and landings have declined in all three bays, with declining

(Apalachicola) or minimal (Pensacola and St. Andrew) levels of commercial fishing activity since 2015, when the regional oyster restoration programs assessed in this analysis began.

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

Plots of the raw CPUE for spat, seed, and legal size oysters in all three bays show values near zero for all size classes (Figures 5-7). The best fitting GLM (Table 2; Appendix 2) suggests that oyster restoration responses over time in each bay were different but none of the predicted responses suggest a positive response in counts of live oysters after restoration. For live spat in Apalachicola and St. Andrew bays, we found the coefficient of the slope describing trends in live oyster spat per quadrat over period did not differ from zero ($p=0.96$ and $p=0.23$) but the slope coefficient did differ from zero for Pensacola ($p=0.0006$) and this slope coefficient was estimated to be negative (beta coefficient = -0.39) and highly uncertain ($SE = 0.11$, $95\% CI = -0.61 - 0.17$). Predicted live oyster spat (marginal means) per quadrat for Apalachicola was 14.08 live spat ($95\% CI 5.29-37.45$), Pensacola was 0.70 live spat ($95\% CI 0.16 - 3.14$), and St. Andrew Bay predicted live oyster spat was 226 ($95\% CI 13.79 - 3703.89$).

A similar pattern was observed for seed size oysters across bays with the slope coefficient not differing from zero for Apalachicola Bay ($p=0.99$) and St. Andrew Bay ($p=0.68$) but the slope coefficient did differ from zero for Pensacola Bay ($p=0.02$) and the slope suggested a decline in seed size oysters over time (beta = -0.34 , $SE = 0.14$, $95\% CI = -0.61 - -0.06$). Counts of legal-size oysters were near zero in all bays (Figure 5) creating model convergence issues limiting further analyses of legal-size oysters (Appendix 2). These results suggest that a positive response to restoration (increase in counts) has not been observed for any size class of oysters in Apalachicola, St. Andrew, or Pensacola bays.

Question 2 How do oyster spat temporal trends vary among separate restoration projects in Apalachicola Bay?

Trends in oyster spat CPUE by project over time in Apalachicola Bay (Figure 8) suggest an initial increase in oyster spat immediately following restoration for projects where monitoring data were available (NFWF-1 and NFWF-2021) but as with the NRDA-4044 and GEBF-5007 projects within 3-4 periods following restoration spat numbers are near zero or extremely low (Figure 8). When high counts of spat were observed, these spat did not persist to seed or legal size (Figures 9-10). To examine trends in Apalachicola Bay oyster spat by project, we created a new variable (SP) which combined the site and project name. This allowed us to fit models to the data which nested site within project and allowed period to vary across project (Appendix 2). We fit eight different models to the data (Table 2; Appendix 2). Of the eight models fit to the data (Table 2, Appendix 2), the model which included terms for Period, Project, a nested period by SP term, and an interaction term between Period and Project while controlling for effort was the best fitting (Table 2). For three of the projects, GEBF-5007, NRDA-4044, and NFWF-2021 the coefficient of the slope of live oyster spat counts over time (Period) did not differ from zero ($p = 0.51$, $p = 0.51$, $p = 0.09$) and for the NFWF-1 project the slope did differ from zero ($p < 0.0001$) and this trend was negative (slope coefficient $\beta = -0.64$, $SE = 0.15$, $95\% CI = -0.94 - -0.35$). These results demonstrate that none of the restoration projects in Apalachicola Bay have had the desired positive response over time to restoration.

We then predicted the marginal means of oyster spat from a single $\frac{1}{4}$ -m² quadrat in the last period of sampling for comparison purposes between each project using the best fitting model from Table 3. For the projects that used limestone rock, predicted live oyster spat for

345 GEBF-5077 in period 12 was 15.73 live spat per quadrat (95% CI 8.45 – 29.27) and for project
346 NFWF-2021 in period 15 we predicted 119.03 (95% CI 30.88 – 458.82). For the projects that
347 used shell cultch, for NRDA-4044 in period 13 we predicted 5.14 live oysters (95% CI 3.06 –
348 8.63), and for NFWF-1 we predicted in period 9 there were 5.39 live oyster spat (95% CI 1.20 –
349 24.26).

350 Question 3 Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?

351 We added coefficients describing different river discharge metrics to the best fitting
352 model comparing live spat counts across project and time in Apalachicola Bay to see whether
353 including river discharge information would improve model fit (Table 3). These river discharge
354 metrics include the number of days river discharge was below 12,000 CFS, days below 12,000
355 CFS lagged by 1 period, number of days river discharge was below 6,000 CFS and days below
356 6,000 CFS lagged by 1 period. Including these river discharge metrics did not improve model fit
357 (Table 3) suggesting that the observed lack of positive response in live oyster spat was not
358 influenced by river discharge metrics assessed (Figure 11).

359 Question 4: Is cultch biomass related to the number of live oysters?

360 Simple plots of mean cultch weight (kg, x-axis) and total live spat (y-axis) per quadrat
361 suggests that for the two studies monitored immediately following cultching (NFWF-1 and
362 NFWF-2021) as the number of live spat increases, so does cultch biomass, but only for one or
363 two periods (Figures 13 and 14) before the number of spat collapses and retracts toward the
364 origin, even for the same biomass of cultch (Figure 14).

365 Efforts to predict cultch biomass had little success (Appendix 2). Diagnostic assessments
366 of model fitting to cultch biomass data suggested most models were overparameterized

(Appendix 2). The best fitting model (lowest AICc and highest model weight) did not include oyster spat as a parameter (Table 5).

Question 5: How does cultch material persist?

The best fitting model comparing trends in oyster cultch biomass over Period across all three bays included an interaction term between Period and Bay, suggesting a different response on oyster cultch biomass over time in each Bay. St. Andrew and Pensacola bays only received a single cultching treatment, compared to multiple cultching treatments over time for Apalachicola Bay. For St. Andrew Bay the slope did not differ from zero ($p=0.23$) suggesting a non-significant trend in cultch biomass over time. In Pensacola Bay the slope did differ from zero ($p=0.02$) and the sign of the slope coefficient was negative ($\beta = -0.03$) suggesting cultch biomass decreased over time.

Because Apalachicola Bay received multiple cultching treatments, we examined trends in cultch biomass in this bay using models like Question 2, which allowed for unique responses by Project over time. The NFWF-2021 project did not have a significant slope parameter ($p=0.44$), but for the other three projects the slope parameter did differ from zero (GEBF-5007 $p=0.02$; NFWF-1 $p<0.0001$; NRDA-4044 $p=0.0002$) and the slope was positive for GEBF-5007 but negative for NFWF-1 and NRDA-4044 (Appendix 2). Cultch persistence thus varied by project over time.

We then predicted the marginal means of oyster cultch biomass from a single $\frac{1}{4}\text{-m}^2$ quadrat in the last period of sampling for each project for comparison purposes between projects in Apalachicola Bay. Predicted oyster cultch biomass for the NFWF-2021 (limestone cultch) project was 8.58 kg per $\frac{1}{4}\text{-m}^2$ quadrat (Period 15, 95% CI 4.03–18.30); GEBF-5077

(limestone cultch) was 4.29 kg per $\frac{1}{4}$ -m² quadrat (Period 12, 95% CI 2.94 – 6.27); the NFWF-1 (quarried shell) was 0.97 kg per $\frac{1}{4}$ -m² quadrat (Period 9, 95% CI 0.47 – 2.02); and NRDA 4044 (shell cultch) predicted cultch biomass was 1.45 kg per $\frac{1}{4}$ -m² quadrat (Period 13, 95% CI 1.01 – 2.09).

Discussion

Restoration efforts in the Gulf of Mexico region are widespread owing both to the large need, and substantial funding resources available related to the *Deepwater Horizon* oil spill. The performance of these restoration efforts, conducted on behalf of the public, must be assessed frequently and rigorously to ascertain whether they are successful or whether new approaches are necessary. We examined oyster restoration projects across three different bays in the Florida panhandle, and evaluated how recruitment of spat, seed, and legal-size oysters responded to the deployment of varying cultch types and densities – an often-used restoration approach. We found the oyster populations did not respond as expected to the restoration actions. Our results suggest three key points

- (1) Oyster populations in Pensacola, St. Andrew, and Apalachicola bays do not appear to have responded as designed to restoration efforts designed to promote spat settlement and accelerate population recovery. This lack of response has occurred in bays within different watersheds and projects using different restoration materials. This result suggests there may be fundamental flaws in the design of oyster restoration projects, that there have been ecosystem changes that now limit oyster population response, or both.
- (2) The lack of oyster population response to restoration actions is not readily explained by environmental or fishery conditions. The analyses cover a time when river discharges ranged

from moderate drought to normal for the instrument period of recorded river discharge. This observed river discharge pattern and concurrent lack of oyster response suggest that salinity, and other river-related ecosystem drivers, such as nutrients, were near average when oyster populations failed to respond positively to restoration. This lack of response has also happened while commercial fisheries have declined sharply (Apalachicola Bay) or have had extremely low landings and trips (Pensacola and St. Andrew bays). The singular, additive, or interacting effects of environmental and fishery forces on oyster population resilience, recovery, and management is a persistent uncertainty in Florida and across the species' range.

(3) Some restoration efforts have not triggered any positive response as measured by oyster spat across the range of cultch material deployed from < 1 kg per quadrat to more than 12 kg of cultch per quadrat using either shell or rock material (NRDA-4044 and GEBF-5007; Figures 13 and 14). This result suggests that even when cultch material is present, oyster spat may exist for only one or two periods before collapsing as demonstrated for projects NFWF-1 and potentially NFWF-2021. The relationships between counts of spat and the biomass of cultch that persists on reefs, and how this relates to the biomass of cultch when oyster populations were higher and supported a commercial fishery are unknown.

Interestingly, the loss of oyster spat is much faster than the loss of cultch biomass on the same reefs. This rapid oyster spat loss also occurs on unrestored reefs from similar monitoring efforts in Apalachicola Bay (Johnson et al. in-review). Figures 13 and 14 suggest that observed oyster spat losses may be occurring during winter months (October-March). While this is possibly an artifact of the irregular sampling necessitating the use of combined months of time in our analyses, winter is most likely when abiotic stressors (high temperatures, low

dissolved oxygen) are lower, thus spat survival is potentially higher in winter. We recommend that counts of oyster spat take place in winter periods when spat settlement (new recruits) is not actively occurring. Winter spat counts may be more useful in informing relative year-class strength and recruitment to legal size than summer spat counts when high losses are expected to occur simply as a function of oysters having a type-III survival curve.

A final hypothesis based on these empirical and previous modeling for Apalachicola Bay oysters (Pine et al. 2015; Johnson et al. in-review) and generalized oyster population modeling efforts (Johnson et al. 2022), is that Pensacola, St. Andrew, and Apalachicola bay oyster populations may be degraded to the point that current restoration actions are ineffective in reversing the observed oyster population collapse. Pine et al. (2015) highlighted the risk of a catastrophic and persistent failure in the Apalachicola oyster fishery if oyster recruitment levels remained below the average reported in the available independent fisheries monitoring data (1990–2013). Johnson et al. (in-review), using the same fisheries independent data as Pine et al. (2015) but updated through 2021, found very high spat mortality rates following the 2012 Apalachicola fishery collapse. Johnson et al. (2022) further demonstrated the risk of a transition to a stable, resilient, low population state for oysters and the difficulty in reversing this to a more desired state in a generalized oyster population model. The scale of restoration or some sort of natural perturbation necessary to shift this system from a resilient, but undesired state to a desired, more productive state, is unknown (Pine et al. 2022). But the reversal of the collapse is likely many orders of magnitude larger than restoration efforts that have been attempted so far (Johnson et al. 2022). Even if these massive restoration efforts were

completed, the likelihood of their success is unknown because as designed restoration is a test of a single hypothesis – lack of substrate is limiting oyster population recovery.

Disappointing restoration results

Our results suggest that restoration and management efforts in Pensacola, St. Andrew, and Apalachicola bays have not had the intended response of shifting oyster populations to a desired, high-abundance state. This conclusion is supported by data from different watersheds with restoration efforts using similar materials, construction designs, and monitoring programs.

In Apalachicola Bay, project NFWF-1, a shell cultch project, and NFWF-2021, a rock cultch project, live oyster spat counts immediately after restoration were several orders of magnitude greater than those in any other project or period (Figures 8-10). In projects GEBF-5007 and NRDA-4044 no increases in spat settlement were recorded in response to restoration. However, these projects did not begin monitoring oyster response until 6-18 months post-construction, meaning any potential restoration responses immediately after restoration were not observed. Potentially these projects also saw large increases in spat and then rapid declines immediately after restoration like NFWF-1 and NFWF-2021, but because of the lag between completion of restoration and monitoring this is not known (Figures 5, 8-10). Critically for project NFWF-1 these high initial spat counts did not result in higher counts in seed or legal-size oysters in subsequent periods (Figures 5), nor were these high spat counts observed again for this project (Figure 5).

The reasons for observed higher spat counts immediately following restoration in Apalachicola Bay (projects NFWF-1 and NFWF-2021) yet a lack of observed spat counts in similar magnitude even with similar cultch biomass levels in other projects (Figures 13 and 14)

is unknown. Though the mean predicted live oyster spat values tended to be lower for shell substrate compared to rock, different starting times for projects, limit this conclusion. However, confidence intervals in estimated live oyster spat do generally overlap across projects with different substrates in Apalachicola and patterns of either no response (NRDA-4044 and GEBF-5077 for Apalachicola, Pensacola, and St. Andrew bays), or positive response followed by rapid declines in spat (NFWF-1; Apalachicola bay only) is consistent.

The relationship between the weight of cultch and the number of spat per quadrat across projects (color dots) and sites (individual plots) in Apalachicola Bay (the only bay where multiple materials and projects were used) is complicated (Figures 13-14). We found no clear pattern across sites in Apalachicola between cultch weight and total number of spat and project (Figure 13). For projects GEBF-5007 (rock) and NRDA-4044 (shell), spat counts were near zero across a range of cultch biomass levels. Importantly, oyster spat response to restoration was not monitored for either project immediately after restoration was complete (Figure 3). For other projects, NFWF-1 (light blue dots, shell cultch) and NFWF-2021 (red dots, rock cultch) show a general pattern of increasing spat in quadrats with more cultch biomass (Figure 13).

Plotting mean cultch weight and total spat by project and period in Apalachicola Bay suggests that total spat in each quadrat increases as cultch weight increases per quadrat, but only for one or two periods (Figures 13 and 14). Statistical analyses of these patterns was difficult (Appendix 2) but there is some suggestion that including the number of live spat as a parameter did not improve on our model assessing patterns in cultch biomass over time (Table 5; Appendix 2). The available data show that for two studies the total number of spat per quadrat increases initially post-restoration, but then the number of oyster spat rapidly declines

(even for the same biomass of cultch; Figure 14). Ultimately the pattern observed in these data suggests that the observed total number of spat and cultch biomass per quadrat collapses and retracts toward the origin over time, as seen in projects NFWF-1 and NFWF-2021 (Figure 14); although Period 15 is informed only from samples in May (Appendix 1). This is an important result because it shows that the live oyster spat counts do not always persist even when apparently (perhaps minimally) sufficient levels of cultch are available.

Has restoration worked previously?

While the current restoration efforts appear to have failed to restore oysters, similar actions are reported to be successful in Florida in the past over relatively short time periods (Berrigan 1988; 1990). Restoration efforts in Pensacola, St. Andrew, and Apalachicola bays were guided by previous actions in Apalachicola Bay, where irregular cultching has been part of oyster management efforts since at least 1949 (Whitfield and Beaumariage 1977). Hurricane Elena in 1985 reduced oyster populations in Apalachicola Bay by as much as 95% (Berrigan 1988, 1990; Livingston 2015). However, a rapid population recovery was observed (Berrigan 1988, 1990), for reasons that may or may not be solely related to restoration (Fisch and Pine 2016). The observed changes both in the physical (Edmiston et al. 2008) and biological (Berrigan 1988; Edmiston et al. 2008; Livingston 2015) aspects of Apalachicola Bay post-Hurricane Elena led to intensive oyster management and restoration efforts (Berrigan 1990) which may or may not have contributed to rapid oyster fishery recovery as measured by trips and landings during the late 1980's – 2010's for Apalachicola whereas St. Andrew and Pensacola bay fisheries dependent data suggests only fishery declines to very low trips or landings within the first 10 years of available data. Irregular cultching efforts have taken place in St. Andrews

and Pensacola Bays since the 1970's, however, these restoration efforts have not been assessed, and based on fisheries dependent data the fisheries do not appear to have responded positively to restoration efforts.

A more recent restoration effort in Apalachicola Bay is documented in Kimbro et al. (2020) who conducted similar restoration experiments to Berrigan (1988) using quarried oyster shells on reefs 0.4 ha in size at shelling densities of zero, 153 m³, and 306 m³ (over a 0.4 ha area). Kimbro et al. (2020) observed a positive response to oyster reef restoration ten months post-restoration during the same time frame as high oyster spat counts occurred on the NFWF-1 project reefs covered by this study (Figure 6). Kimbro et al. (2020) also observed higher oyster counts (defined as juveniles <25 mm and adults ≥25 mm) on reefs with increased reef mass. Thus, for the Kimbro et al. (2020) work and two of the projects assessed here (NFWF-1 and NFWF-2021), short-term spat responses were evident following the placement of cultch material. Critically, follow-up assessments beyond 10 months are unavailable for the reefs discussed in Kimbro et al. (2020), but our analysis of reefs that were restored around the same time with similar materials and cultch densities during NFWF-1 several years post-construction and found that the initial oyster population response to restoration as measured by spat counts did not persist through time (Figures 5; 9-10). The reason this spat response was only observed immediately following cultching and not in subsequent periods, nor did the spat that were observed persist to seed or legal sizes, is a critical uncertainty that must be addressed to inform current and future restoration efforts in Apalachicola Bay and elsewhere.

Reasons restoration may not be working

One possible explanation for the observed lack of positive oyster population response observed in Pensacola, St. Andrew, and Apalachicola bays is that the restoration actions were inappropriate—e.g., inappropriate material, density/height, or total area. The cultch density used following the 1985 oyster fishery collapse and closure in Apalachicola Bay (Berrigan 1990; shell cultch) of about 472 cubic meters per acre was similar to the density used in the largest (rock cultch; project NRDA 5007) and most recent (rock cultch; project FWC 2021) restoration efforts, and similar to the highest treatment level of recent shell cultch projects (project NFWF-1) for Apalachicola Bay (Table 1). Regarding the total area necessary for restoration, Pine et al. (2015) suggested an intensive cultching program of about 50 ha per year could reduce the risk of an irreversible oyster fishery collapse in Apalachicola Bay. This cultching area is slightly larger than the average area cultched each year between the restoration efforts following Hurricane Elena in 1985 (Berrigan 1990; Pine et al. 2015) and the beginning of regional restoration efforts in 2015. What is unknown and could not be assessed by Pine et al. (2015) is the characteristics of cultching material, such as density (amount per area, and whether that material persisted on the area or was dispersed, which drives restoration height), material type (shell vs. rock, or different sizes of material), that would be required to prevent collapse.

Because the shell used in cultching is less dense than rock used in cultching, the differences observed in biomass per quadrat across studies in Apalachicola Bay are not surprising. These results suggest a biomass decline of about 50-80% for the shell material and an increase of about 15-50% in cultch biomass for the rock material predicted by the end of monitoring. Critically, these are measures of mass, not surface area, and the extent of oyster

spat settlement on substrate depends on the surface area. The relationship between cultch area, persistence, and settlement suitability are all areas of future work with important implications for restoration efforts (Hemeon et al. 2020).

Another possible explanation for our observed restoration failure is that the elevation of the restored reefs was too low. Previous oyster restoration work has emphasized the importance of reef elevation as a critical factor (Colden et al. 2017; Smith et al. 2021). This vertical relief difference may be necessary for elevating the cultch material into suitable water quality or hydrodynamic conditions. Colden et al. (2017) found that oyster reefs with height > 0.3 m in the Chesapeake Bay region had higher oyster survival, density, and overall complexity than oyster reefs < 0.3 m, and higher-elevation reefs were more likely to persist.

The importance of elevation has been confirmed in several recent oyster restoration projects. Smith et al. (2021, 2022), as part of a 15-year assessment of the performance of an oyster reef restoration project in the Chesapeake Bay, found that restored reefs were like unrestored reference reefs based on a variety of metrics within six years following restoration. For some metrics, such as elevation, the restored and reference reefs were similar within three years, and as the restored reefs aged, they became more stable and possibly more resilient. In Florida, the restoration of the Lone Cabbage Reef in Suwannee Sound demonstrated oyster spat settlement and persistence on the restored reef within six months following construction. Oysters have persisted and successfully settled on the reef in the four years since construction. Oyster densities on the restored Lone Cabbage and nearby reference reefs are now similar (W.E. Pine, *unpublished information*). The increase in oyster reef elevation from the Smith et al. (2021) restoration project in the Chesapeake Bay was about 0.14 m (see online supplemental

information in Smith et al. 2021), and for the Lone Cabbage project in Florida it was about 0.36 m (Pine et al. 2022). Combined with the results from Colden et al.'s project (2017; 0.4 m), elevation changes on restored reefs that persisted over time had about 3–8× the elevation contrast observed on restored sites in Apalachicola, Pensacola, and St. Andrew bays (about 0.05 m; R. Gandy FWRI). In the restoration projects examined in this study, the material used is either small and dense (#4 limestone 19–38 mm in diameter) or larger, and less dense (quarried oyster shell 37–75 mm in diameter) and likely susceptible to being transported away from the intended restoration site, buried in sediment, or sculpted by currents to a low-relief structure. This low-relief structure is likely interrupted across its surface by subtle waves of higher-density material (volumetrically), resulting in slightly higher vertical relief (about 0.1 m) in some areas. Regardless, cultch material in various forms at different original mass levels has persisted on these restored reefs at low mass levels (Figure 12). Critically, oyster spat settlement has been very low for unknown reasons and it is possible that restoration efforts do not recreate the ecology of the pre-collapsed system.

A final possible explanation for why the recent restorations failed is that the materials used were not conducive for oyster spat settling and surviving. Materials used for reef construction and other oyster restoration efforts vary widely (Bersosa 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. Previous restoration projects in Apalachicola Bay (Berrigan 1988; 1990) used clam shells dredged from Lake Pontchartrain, Louisiana as cultch material or quarried oyster shell (Kimbrow et al. 2020). Smith et al. (2021) describes a successful long-term oyster restoration project using dredged

606 shells in Chesapeake Bay, Virginia. The limestone used in this study's restoration projects is
607 made of calcite, dolomite, and quartz. It is denser (structure and mass) and older (geologic age)
608 than the limestone used successfully (measured by counts and persistence of oysters) for
609 intertidal reef restoration in Suwannee Sound, Florida (J. Yeager, University of Florida
610 Department of Geological Sciences, personal communication; Pine et al. 2022). Whether the
611 chemical composition and physical characteristics of the limestone used in the projects in
612 Florida may influence its effectiveness as cultch is unknown.

613 Cultching efforts in Apalachicola Bay have been identified as contributing to the long-
614 term sustainability of harvest in the bay before 2010 (Zu Ermgassen et al. 2012). In 2017 the
615 NAS highlighted the NFWF-1 project assessed in this study as an example of a restoration
616 project designed to experimentally evaluate oyster population responses to different cultch
617 density treatments (NAS 2017). However, our results show the NFWF-1 project did not answer
618 the questions as proposed, and whether cultching in Apalachicola Bay in previous years has
619 contributed meaningfully to the sustainability of harvests is doubtful based on the observed
620 oyster fishery collapse in 2012. Project NFWF-2021 (the only project begun after Apalachicola
621 Bay fishery closure) also observed a large increase in spat post-construction, and seed oysters
622 were present in subsequent samples (Figure 10). Continued monitoring of this project will be
623 important to understand whether these seed oysters survive to legal size, but design
624 deficiencies including lack of spatial replication and paired unrestored control sites will create
625 challenges in drawing strong conclusions related to the role of the fishery closure. These and
626 other experimental design issues should be addressed in future restoration experiments (Pine
627 et al. 2022).

628 Future directions

629 The repeated and ongoing cultching efforts in Florida estuaries to reverse observed declines in
630 oyster populations test a single hypothesis—that oyster populations have declined because of
631 limitations in cultch. The ways these restorations have been designed, implemented, and
632 monitored make it difficult to sufficiently evaluate more detailed hypotheses about the
633 characteristics of cultch that are necessary. For example, differences in the monitoring timing
634 make it challenging to differentiate the failure of oyster spat to successfully settle on restored
635 material, from failure to survive past some critical size or life history stage. Further, the
636 restoration projects, though they differ in materials, are similar in that they all created low
637 elevation restored refs, which is in part related to them all consisting of smaller-sized materials.
638 While these approaches to restoration may be understandable given their similarity to past
639 restoration efforts (Berrigan 1990), the lack of experimental relief has likely hampered learning
640 as to whether cultch material is limiting oyster populations in the Florida panhandle. *Alternative*
641 hypotheses related to oyster population decline—include cascading predatory responses
642 (Kimbrow et al. 2017), recruitment overfishing, discard mortality, virulent disease (known or
643 unknown), or some combination of these remain largely unassessed and impossible to address
644 with available data.

645 *Conclusions*

646 Oyster populations in Apalachicola, Pensacola, and St. Andrew bays appear resistant to current
647 restoration approaches and recovery at this time, despite legal actions designed to force
648 equitable water allocation to reduce salinity (Apalachicola Bay; Barnett 2021), large restoration
649 efforts (totaling more than \$14,200,000; Table 1), low levels of reported harvest and effort

(Pensacola and St. Andrew bays), and two years of a five-year harvest moratorium (2020–2025) in Apalachicola Bay. Regrettably, many of the same restoration and management uncertainties identified in this assessment have persisted for decades or centuries in Florida (Swift 1897; Swift 1898; Camp et al. 2015; Pine et al. 2015).

Resistance to learning to inform restoration is a widespread problem in ongoing restoration efforts in the Gulf of Mexico (NAS 2022) and has been a challenge to large-scale restoration and management efforts for decades (Walters 1986; Gunderson 1999; Walters 2007; Pine et al. 2022). This may be because many restoration efforts have not been designed with resolving uncertainty as the major goal because of a belief that what should be done was strongly influenced by past success (even if past restoration was never assessed). But this approach does not consider that the system states may not be the same. In a classic assessment of barriers to learning in adaptive ecosystem assessment and management, Gunderson (1999) suggested:

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

Understanding why these systems have not responded to restoration efforts is critical to informing future restoration efforts, including nearly \$20 million in additional restoration funding currently being considered for Apalachicola Bay. Decisive agency, academic, and community leadership emphasizing a commitment to learning to improve restoration and management is needed successfully restore oyster populations to support ecosystem services and viable fisheries for the benefit of the people of the Gulf of Mexico region.

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

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

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

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

^c Fact sheet: https://www.restorethegulf.gov/sites/default/files/FPL_FactSheet_20160909_FL_Apa_Oyster.pdf

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

^e Total restoration costs \$14,239,996

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

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

Table 3. Model selection table for the GLM of oyster count data from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay. The predicted response is number of spat per $\frac{1}{4}$ m² quadrat. AICcc and delta AICcc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; site = the location where the sampling occurred.

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

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

Model	k	AICc	Delta AICc	AICc Weight
tmb 5: Sum_spat ~ Period + Project + (Period Site) + Period:Project + offset(log(Num_quads))	12	1875.69	0.00	0.40
tmb 5.12k_lag: Sum_spat ~ Period + Project + (Period Site) + 12k_lag + Period:Project + offset(log(Num_quads))	13	1877.19	1.50	0.19
tmb 5.12k_lag: Sum_spat ~ Period + Project + (Period Site) + 6k_lag + Period:Project + offset(log(Num_quads))	13	1877.53	1.84	0.16
tmb 5.12k_lag: Sum_spat ~ Period + Project + (Period Site) + 12k + Period:Project + offset(log(Num_quads))	13	1878.01	2.32	0.13
tmb 5.12k_lag: Sum_spat ~ Period + Project + (Period Site) + 6k + Period:Project + offset(log(Num_quads))	13	1878.08	2.39	0.12

Table 5. Model selection table for the GLM assessing trends in oyster cultch mass from subtidal reefs restored using different materials, at different densities, over time, and with different levels of live oyster spat in Apalachicola Bay. The predicted response is mass of cultch per $\frac{1}{4}$ m² quadrat. AICc and delta AICc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; site = the location where the sampling occurred.

Model	Degrees of freedom	AICc	Delta AICc	AICc Weight
Tmb5.nospat: Roundwt ~ Period + Project + (Period SP) + Period:Project + offset(log(Num_quads))	12	1277.18	0.00	0.44
tmb3 Roundwt ~ (1 SP) + Spat_sum + Period + Project + Period:Project + offset(log(Num_quads))	11	1278.26	1.08	0.26
tmb5: Roundwt ~ Spat_sum + Period + Project + (Period SP) + Period:Project + offset(log(Num_quads))	13	1279.48	2.30	0.14
tmb6: Roundwt ~ Spat_sum + Period + Project + (Period SP) + Period:Project + offset(log(Num_quads)) includes unique dispersion parameter for each project	16	1280.20	3.02	0.10
tmb5x: Roundwt ~ Period + Project + (Period SP) + Period:Project + Spat_sum:Project + offset(log(Num_quads))	16	1280.98	3.80	0.07
tmb4: Roundwt ~ (1 SP) + Project + offset(log(Num_quads))	6	1304.35	27.16	0.00
tmb1: Roundwt ~ (1 SP) + Spat_sum + Period + offset(log(Num_quads))	5	1307.31	30.13	0.00
tmb00: Roundwt ~ (1 SP) + Spat_sum + offset(log(Num_quads))	4	1309.96	32.78	0.00
tmb0: Roundwt ~ (1 SP) + offset(log(Num_quads))	3	1312.55	35.37	0.00

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

Model	Degrees of freedom	AICcc	Delta AICcc	AICcc Weight
tmb 3: Round_wt ~ (1 Site) + Period + Bay + Period:Bay + offset(log(Num_quads))	8	2055.4	0.00	0.56
tmb 2: Round_wt ~ (1 Site) + Period + Bay + offset(log(Num_quads))	6	2058.54	3.11	0.12
tmb 1: Round_wt ~ (1 Site) + Period + offset(log(Num_quads))	4	2058.54	3.11	0.12
tmb0: Round_wt ~ (1 Site) + offset(log(Num_quads))	3	2058.66	3.22	0.11
tmb 4: Round_wt ~ (1 Site) + Bay + offset(log(Num_quads))	5	2058.90	3.46	0.10
tmb 5: Round_wt ~ Period + Bay + (Period Site) + Period:Bay + offset(log(Num_quads))	Did not converge			
tmb 6: Round_wt ~ Period + Bay + (Period SP) + Period:Bay + offset(log(Num_quads)) includes unique dispersion parameter for each Bay	Did not converge			

Table 7. Model selection table for the GLM of oyster cultch biomass from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay. The predicted response is number of spat per $\frac{1}{4}$ m² quadrat. AICcc and delta AICcc provided to inform comparisons of the model statistical fit to the data. Period = a continuous variable which describes time (one-half year, summer or winter); project = a categorical variable identifying type and density of cultch; site = the location where the sampling occurred.

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

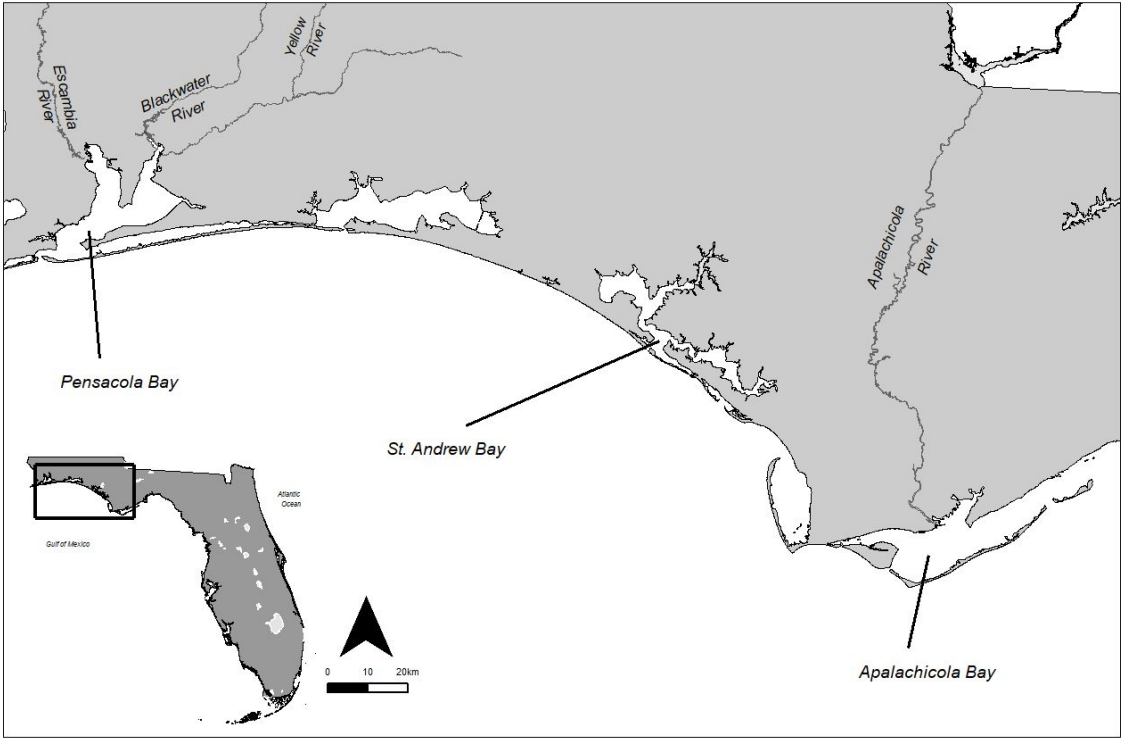


Figure 1. Location of Pensacola, St. Andrew, and Apalachicola bays in the Florida panhandle.

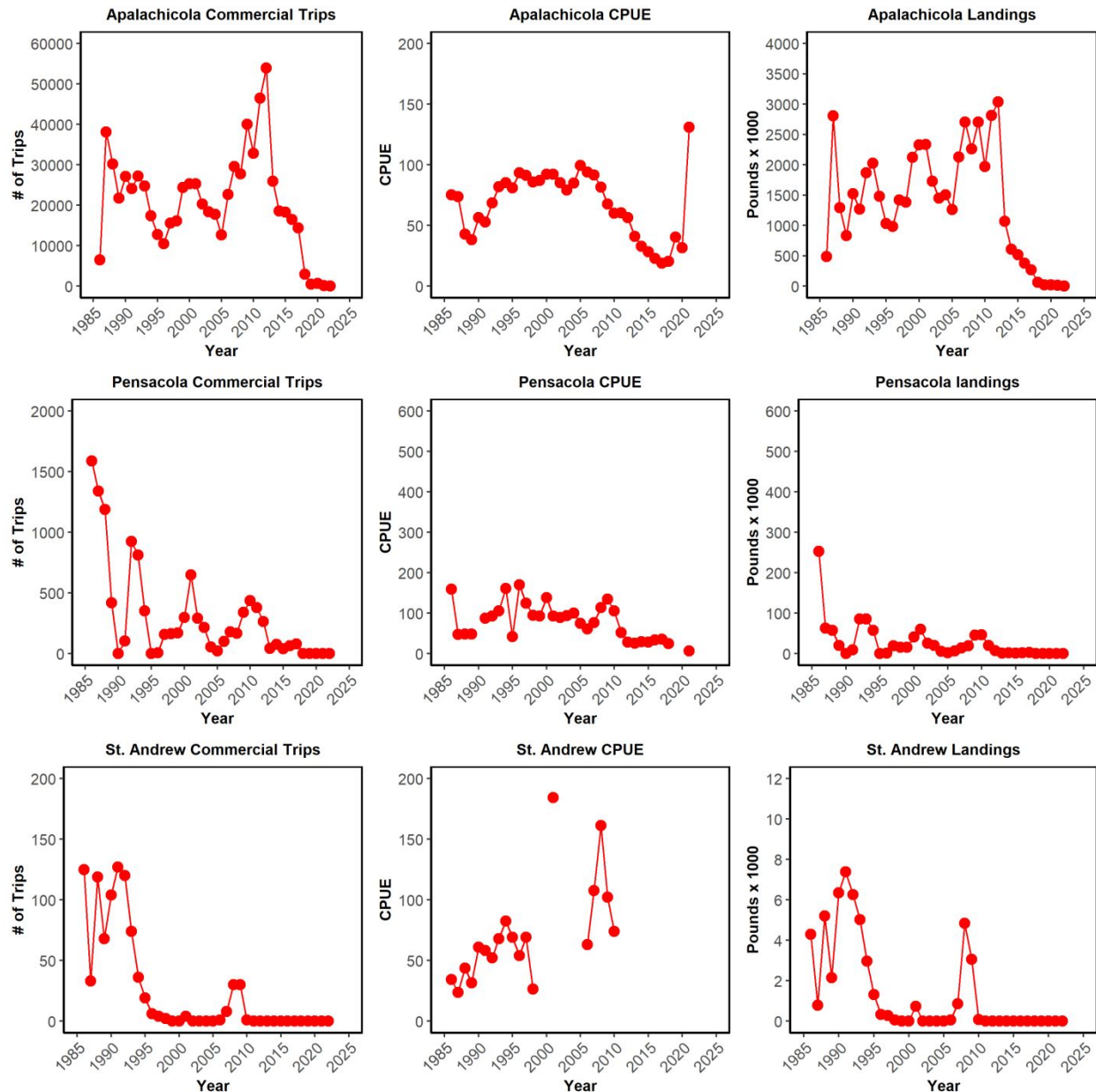


Figure 2. Publicly available fisheries-dependent data from the Florida Fish and Wildlife Conservation Commission (<https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/>), 1986–present. Each row represents a different bay, and each column represents a different data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

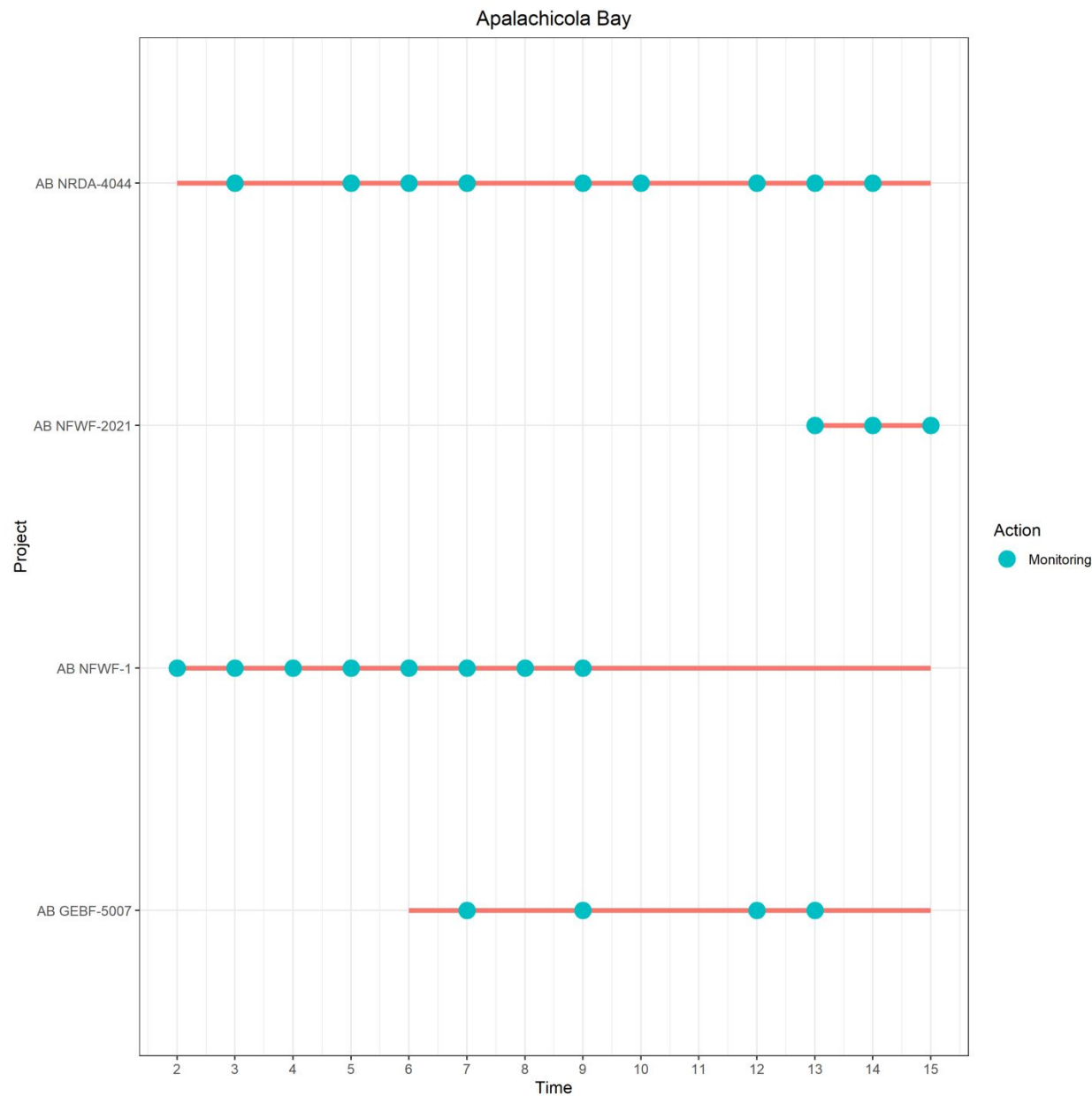


Figure 3. A schematic demonstrating the placement and persistence of cultch material by project (y-axis, red line) over time (x-axis) and the sampling events (grey circles) that collected oyster count data from each project. Project AB (Apalachicola Bay) NRDA-4044 only collected samples from one site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

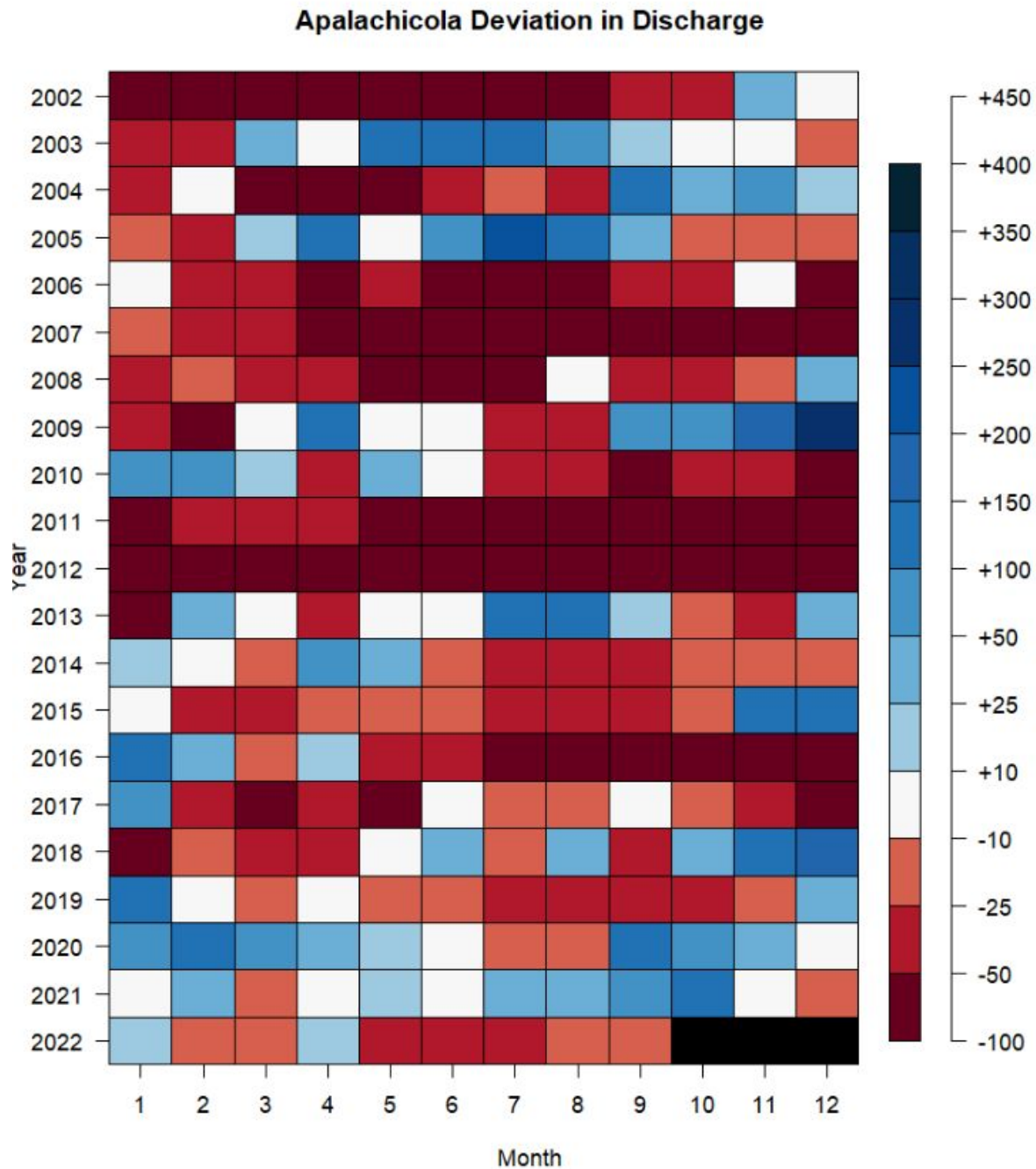


Figure 4. Deviations in river discharge from the period of instrument records for the Apalachicola River. Darker colors equate to larger deviations, with colors in the blue spectrum representing higher river discharge and colors in the red spectrum representing lower river discharge. White or near-white represents values within $\pm 10\%$ of the period of instrument records.



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

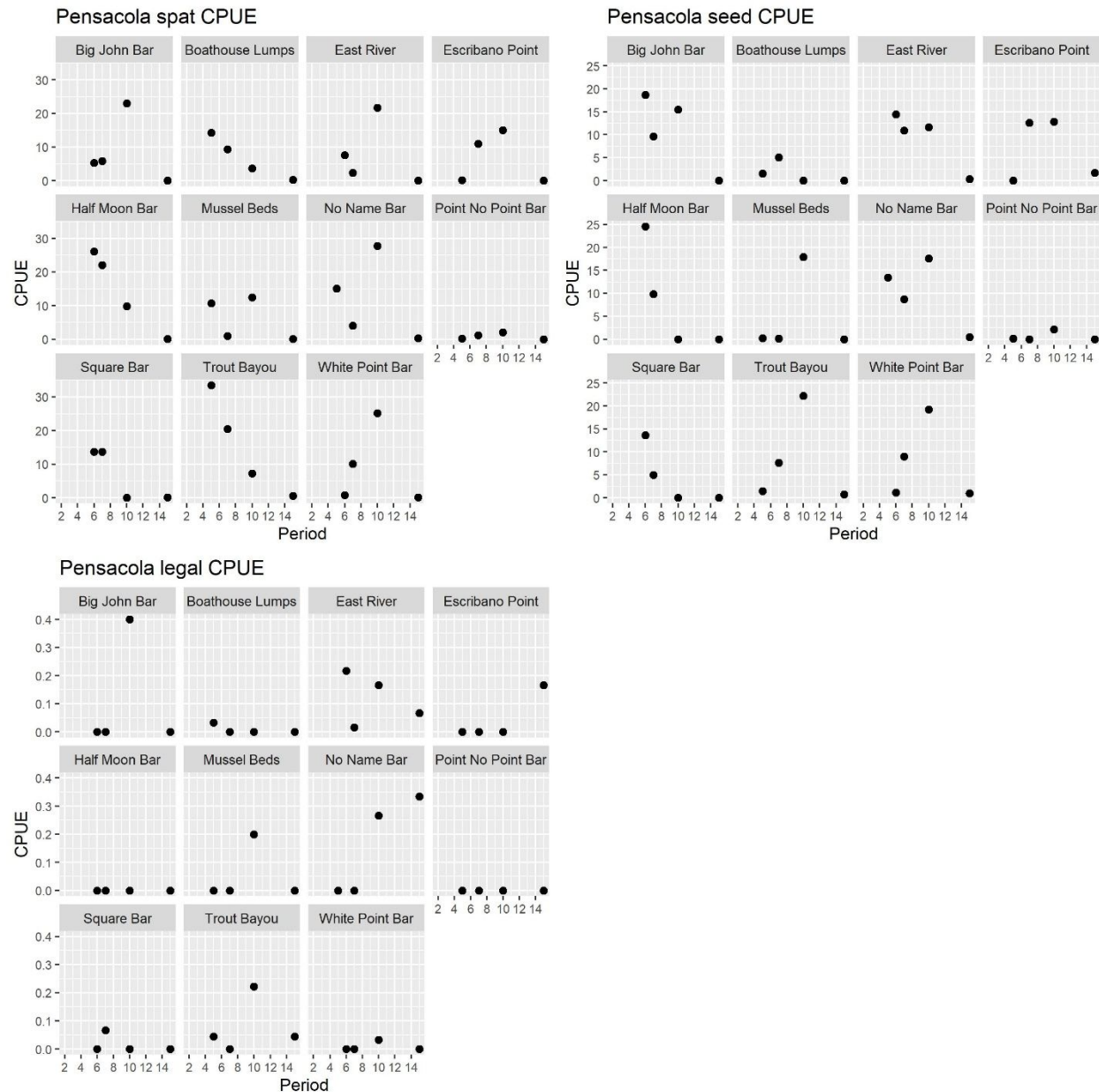


Figure 6. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for Pensacola Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. Note each plot for each oyster size class has a different y-axis.

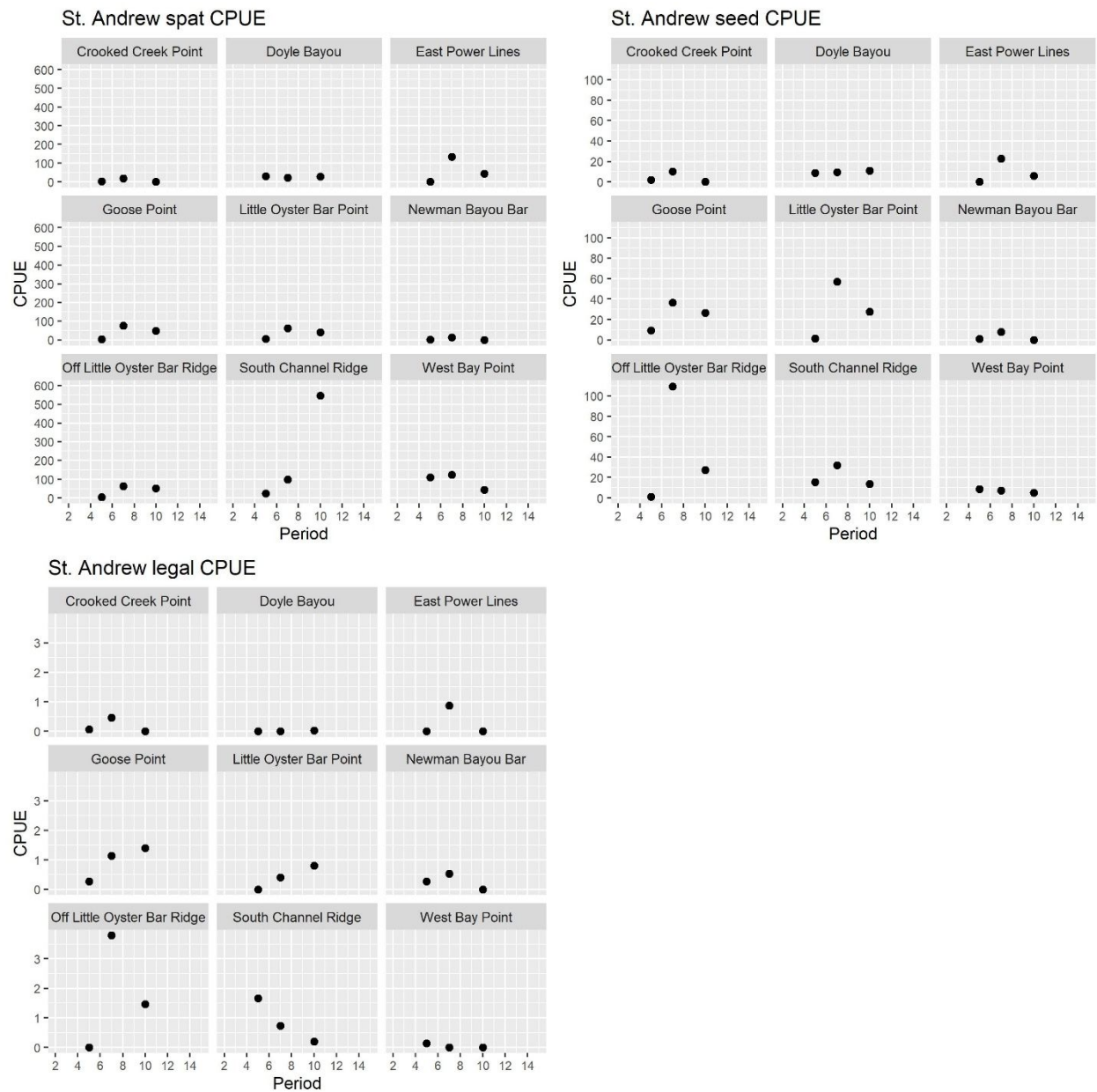


Figure 7. Spat, seed, and legal size oyster count per quadrat (CPUE) by period for St. Andrew Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. Note each plot for each oyster size class has a different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

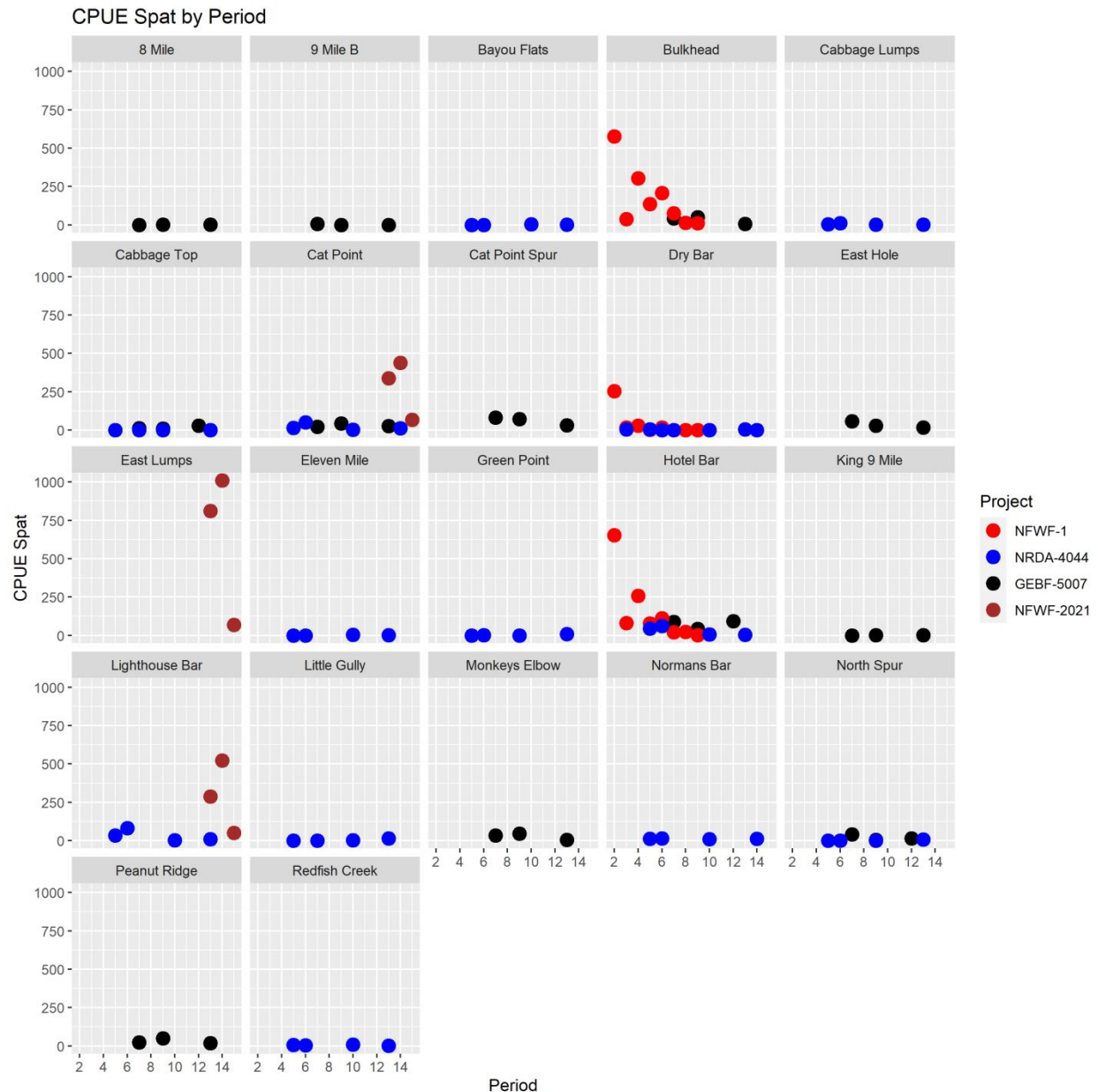


Figure 8. Oyster spat count per quadrat (CPUE) by site within Apalachicola Bay (each panel) and period (x-axis). Dots represent counts over time for each project defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September)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

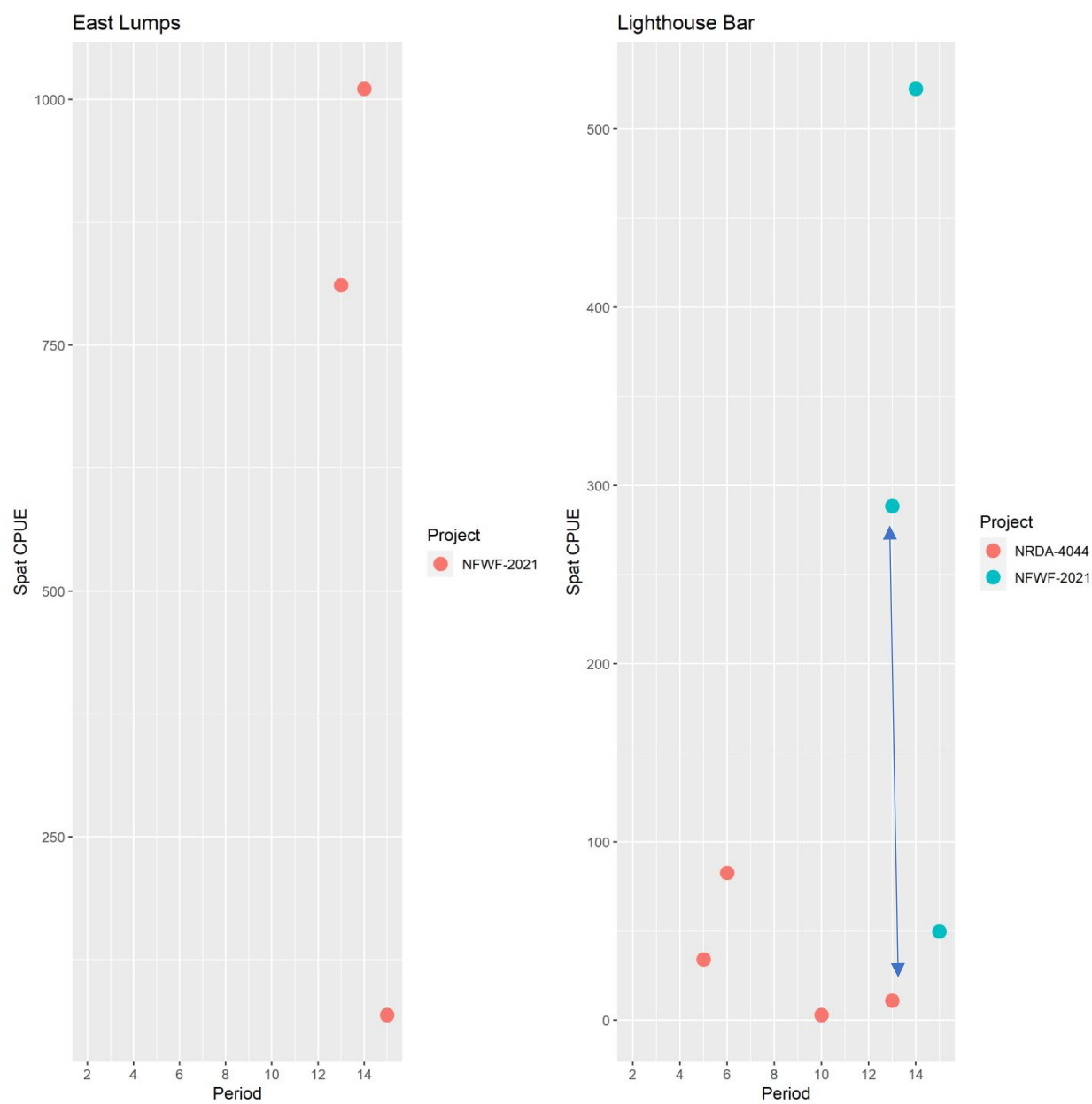


Figure 9. Oyster spat count per quadrat (CPUE) for two sites within Apalachicola Bay (East Lumps left panel, Lighthouse Bar right panel) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods are winters (October-March) beginning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

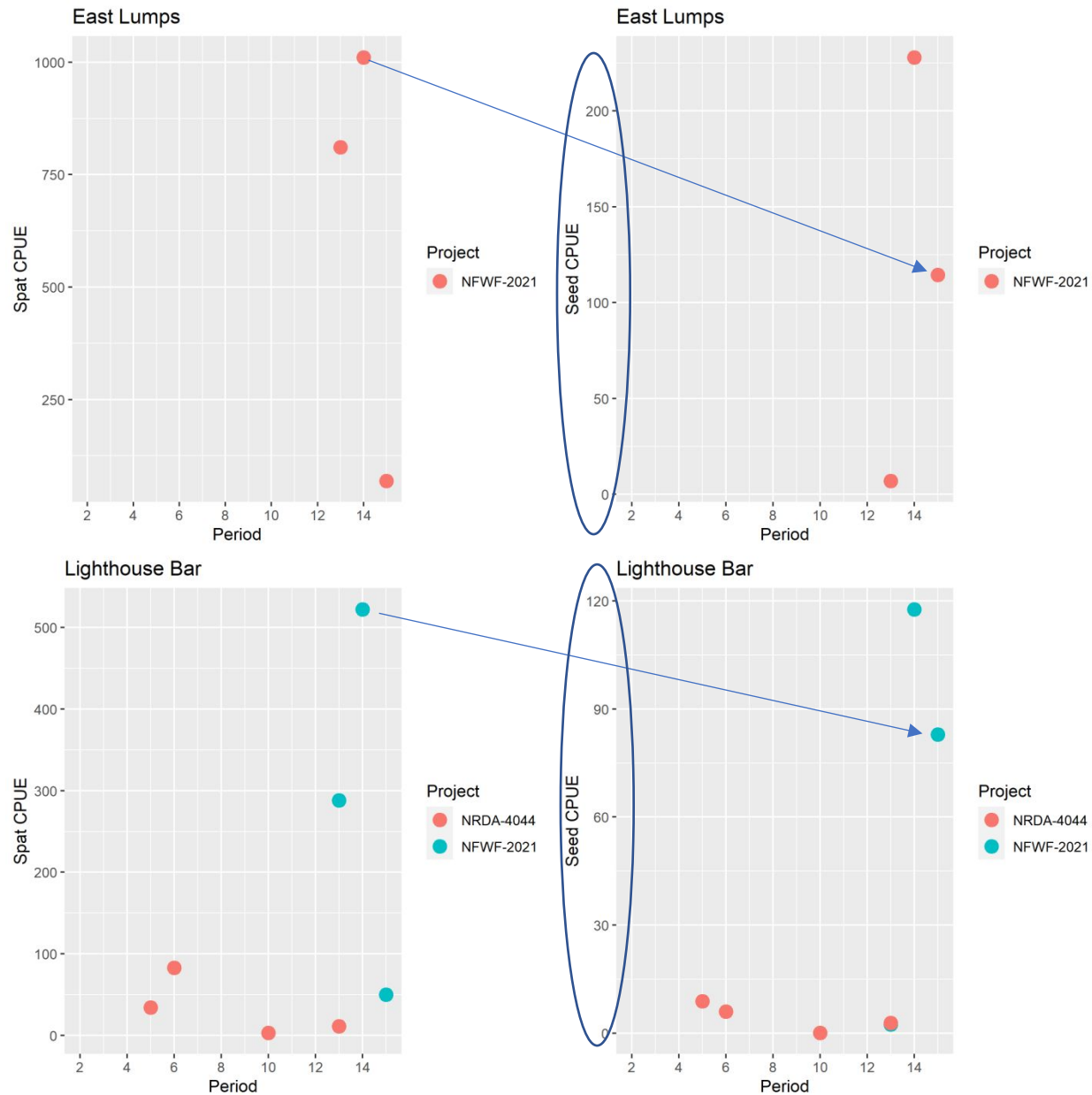


Figure 10. Oyster spat count per quadrat (CPUE; left panels) and seed count per quadrat (right panels) for two sites within Apalachicola Bay (East Lumps top row, Lighthouse Bar bottom row) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number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

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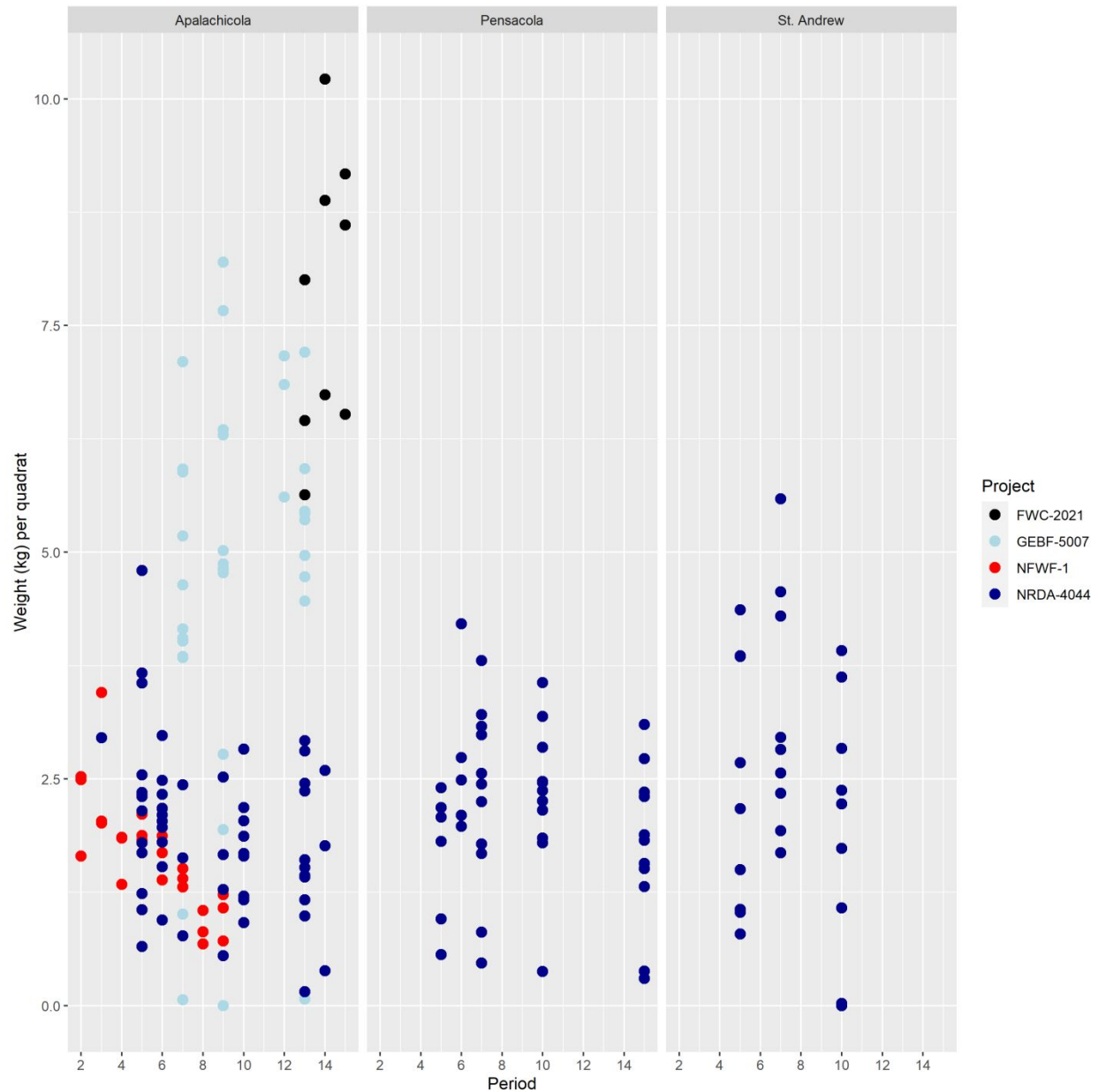


Figure 12. Oyster cultch biomass per quadrat (y-axis, kg) over time (x-axis, period) for Apalachicola, Pensacola, and St. Andrew bays (each panel). Projects (Table 1) are defined by color. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September)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

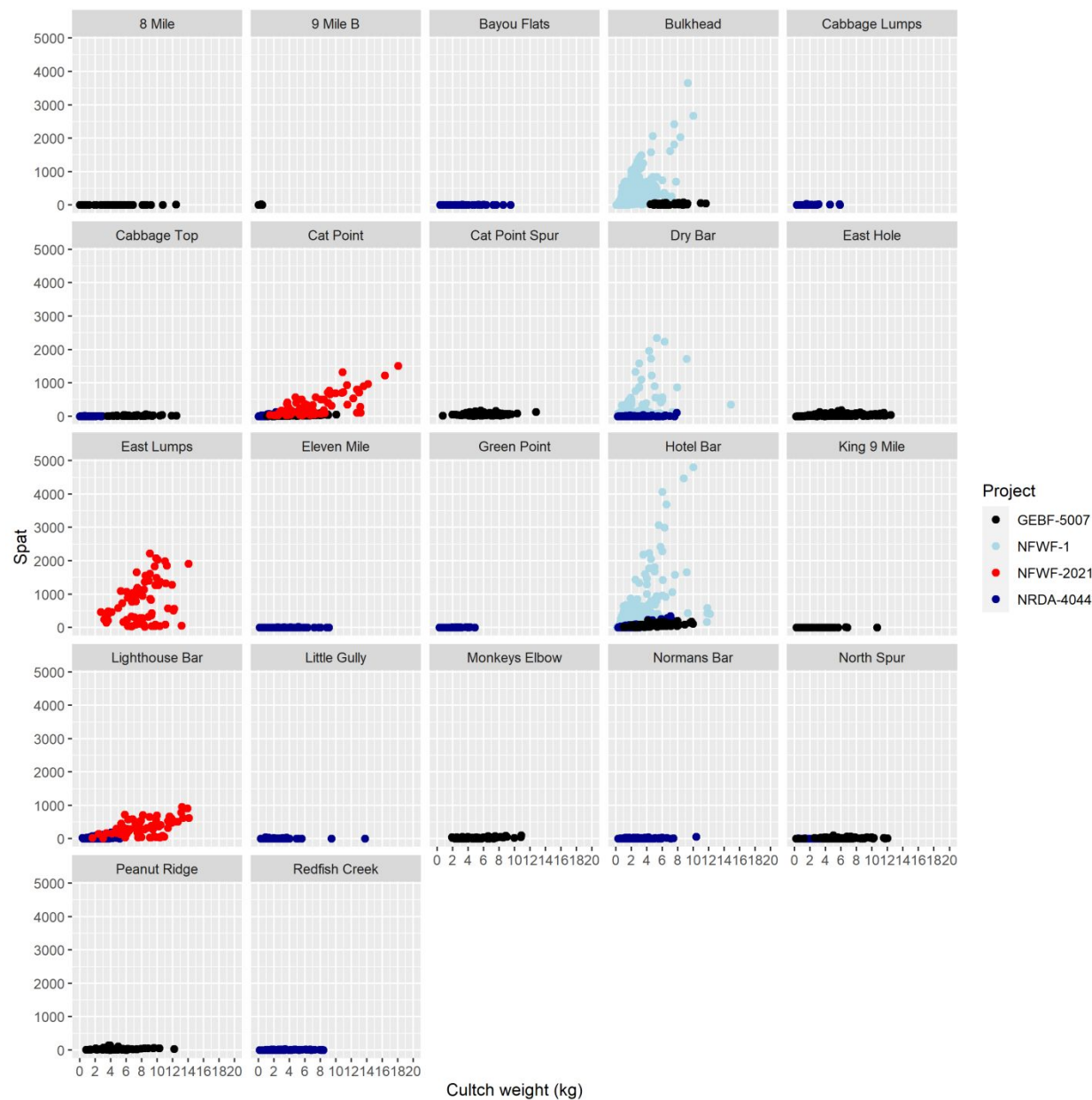


Figure 13. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay sites (each individual panels) and project (colored dots).

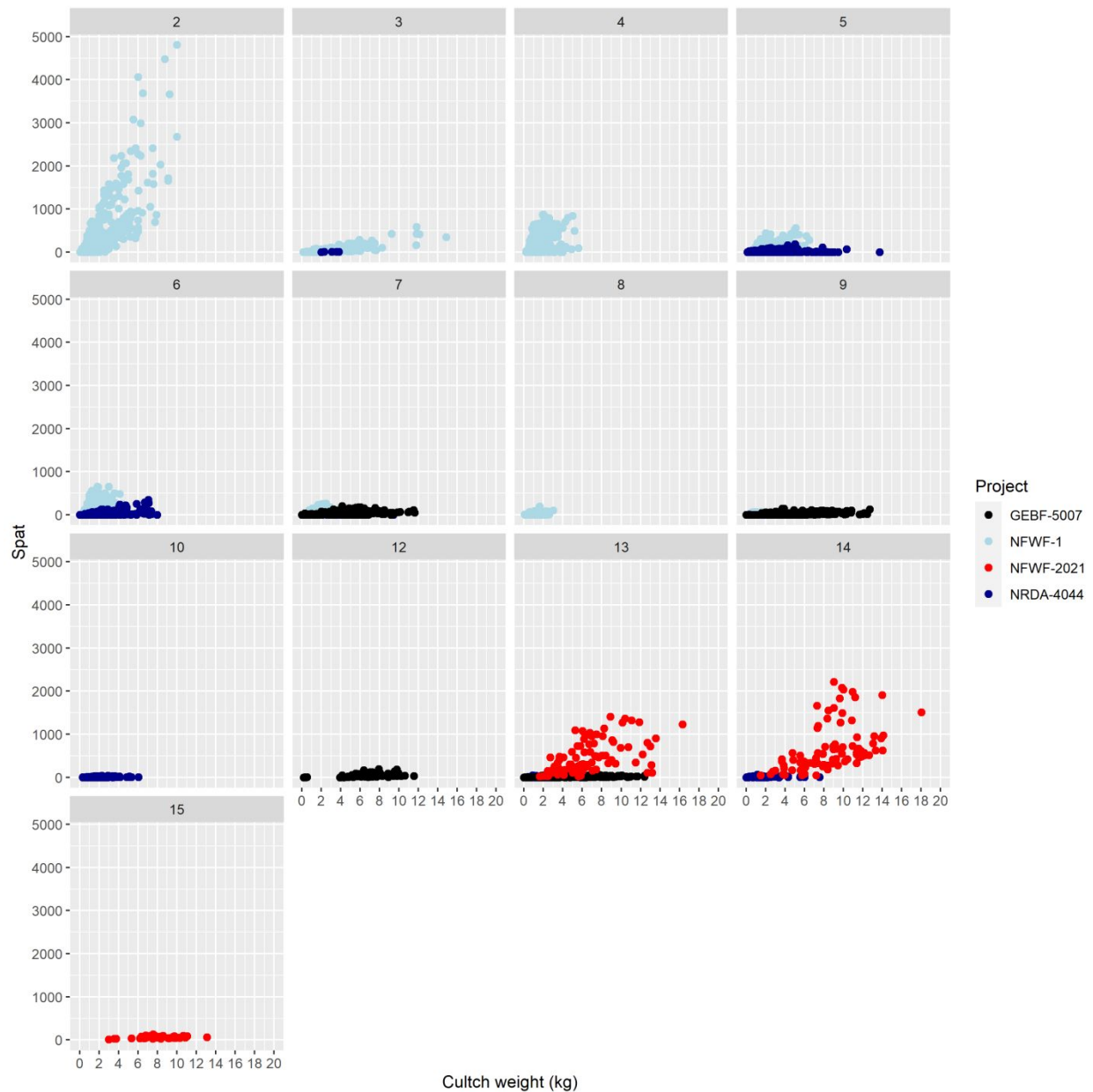


Figure 14. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay periods (each individual panels) and project (colored dots). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in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

Appendix 1

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

Bay	Period	Year	Month	Project	Site	Number quadrants
Apalachicola	2	2015	10	NFWF-1	Bulkhead	75
Apalachicola	2	2015	10	NFWF-1	Dry Bar	74
Apalachicola	2	2015	10	NFWF-1	Hotel Bar	74
Apalachicola	2	2016	1	NFWF-1	Bulkhead	75
Apalachicola	2	2016	2	NFWF-1	Dry Bar	75
Apalachicola	2	2016	2	NFWF-1	Hotel Bar	75
Apalachicola	3	2016	4	NFWF-1	Bulkhead	75
Apalachicola	3	2016	5	NFWF-1	Dry Bar	75
Apalachicola	3	2016	5	NFWF-1	Hotel Bar	75
Apalachicola	3	2016	6	NRDA-4044	Dry Bar	5
Apalachicola	3	2016	7	NFWF-1	Bulkhead	75
Apalachicola	3	2016	7	NFWF-1	Dry Bar	75
Apalachicola	3	2016	8	NFWF-1	Hotel Bar	75
Apalachicola	4	2016	10	NFWF-1	Bulkhead	75
Apalachicola	4	2016	10	NFWF-1	Dry Bar	75
Apalachicola	4	2016	10	NFWF-1	Hotel Bar	75
Apalachicola	4	2017	1	NFWF-1	Bulkhead	74
Apalachicola	4	2017	1	NFWF-1	Dry Bar	75
Apalachicola	4	2017	1	NFWF-1	Hotel Bar	74
Apalachicola	4	2017	2	NFWF-1	Bulkhead	1
Apalachicola	4	2017	2	NFWF-1	Hotel Bar	1
Apalachicola	5	2017	4	NFWF-1	Bulkhead	75
Apalachicola	5	2017	4	NFWF-1	Dry Bar	75
Apalachicola	5	2017	4	NFWF-1	Hotel Bar	75
Apalachicola	5	2017	4	NRDA-4044	Cat Point	30
Apalachicola	5	2017	4	NRDA-4044	Eleven Mile	30
Apalachicola	5	2017	4	NRDA-4044	Hotel Bar	45
Apalachicola	5	2017	4	NRDA-4044	Normans Bar	15
Apalachicola	5	2017	5	NRDA-4044	Green Point	15
Apalachicola	5	2017	5	NRDA-4044	Normans Bar	30
Apalachicola	5	2017	5	NRDA-4044	North Spur	15
Apalachicola	5	2017	6	NRDA-4044	Cabbage Lumps	15
Apalachicola	5	2017	6	NRDA-4044	Cabbage Top	30
Apalachicola	5	2017	6	NRDA-4044	Dry Bar	55
Apalachicola	5	2017	6	NRDA-4044	Lighthouse Bar	30
Apalachicola	5	2017	6	NRDA-4044	Little Gully	30
Apalachicola	5	2017	6	NRDA-4044	Normans Bar	15
Apalachicola	5	2017	7	NFWF-1	Bulkhead	75
Apalachicola	5	2017	7	NFWF-1	Hotel Bar	75
Apalachicola	5	2017	7	NRDA-4044	Bayou Flats	15
Apalachicola	5	2017	7	NRDA-4044	Redfish Creek	45
Apalachicola	5	2017	8	NFWF-1	Dry Bar	75
Apalachicola	6	2017	10	NFWF-1	Bulkhead	75

Apalachicola	6	2017	10	NFWF-1	Hotel Bar	75
Apalachicola	6	2017	11	NFWF-1	Dry Bar	75
Apalachicola	6	2017	11	NRDA-4044	Cat Point	30
Apalachicola	6	2017	11	NRDA-4044	Hotel Bar	15
Apalachicola	6	2017	12	NRDA-4044	Cabbage Lumps	15
Apalachicola	6	2017	12	NRDA-4044	Green Point	15
Apalachicola	6	2017	12	NRDA-4044	North Spur	15
Apalachicola	6	2018	1	NFWF-1	Bulkhead	75
Apalachicola	6	2018	2	NFWF-1	Dry Bar	75
Apalachicola	6	2018	2	NFWF-1	Hotel Bar	75
Apalachicola	6	2018	2	NRDA-4044	Dry Bar	45
Apalachicola	6	2018	3	NRDA-4044	Bayou Flats	15
Apalachicola	6	2018	3	NRDA-4044	Eleven Mile	30
Apalachicola	6	2018	3	NRDA-4044	Hotel Bar	30
Apalachicola	6	2018	3	NRDA-4044	Lighthouse Bar	30
Apalachicola	6	2018	3	NRDA-4044	Normans Bar	60
Apalachicola	6	2018	3	NRDA-4044	Redfish Creek	45
Apalachicola	7	2018	4	NFWF-1	Dry Bar	75
Apalachicola	7	2018	4	NFWF-1	Hotel Bar	75
Apalachicola	7	2018	4	NRDA-4044	Cabbage Top	30
Apalachicola	7	2018	4	NRDA-4044	Dry Bar	15
Apalachicola	7	2018	4	NRDA-4044	Little Gully	30
Apalachicola	7	2018	5	NFWF-1	Bulkhead	75
Apalachicola	7	2018	6	GEBF-5007	8 Mile	30
Apalachicola	7	2018	6	GEBF-5007	9 Mile B	5
Apalachicola	7	2018	6	GEBF-5007	Cabbage Top	15
Apalachicola	7	2018	6	GEBF-5007	Hotel Bar	45
Apalachicola	7	2018	6	GEBF-5007	King 9 Mile	15
Apalachicola	7	2018	6	GEBF-5007	North Spur	30
Apalachicola	7	2018	7	NFWF-1	Bulkhead	75
Apalachicola	7	2018	7	NFWF-1	Hotel Bar	75
Apalachicola	7	2018	8	GEBF-5007	Cat Point	45
Apalachicola	7	2018	8	GEBF-5007	Cat Point Spur	30
Apalachicola	7	2018	8	GEBF-5007	East Hole	30
Apalachicola	7	2018	8	GEBF-5007	Monkeys Elbow	30
Apalachicola	7	2018	8	GEBF-5007	Peanut Ridge	30
Apalachicola	7	2018	8	NFWF-1	Dry Bar	75
Apalachicola	7	2018	9	GEBF-5007	Bulkhead	15
Apalachicola	7	2018	9	GEBF-5007	East Hole	60
Apalachicola	8	2018	11	NFWF-1	Dry Bar	75
Apalachicola	8	2018	11	NFWF-1	Hotel Bar	75
Apalachicola	8	2018	12	NFWF-1	Bulkhead	75
Apalachicola	8	2019	1	NFWF-1	Bulkhead	75
Apalachicola	8	2019	1	NFWF-1	Dry Bar	75
Apalachicola	8	2019	1	NFWF-1	Hotel Bar	75
Apalachicola	9	2019	4	NFWF-1	Dry Bar	75
Apalachicola	9	2019	4	NFWF-1	Hotel Bar	75
Apalachicola	9	2019	5	NFWF-1	Bulkhead	75
Apalachicola	9	2019	6	GEBF-5007	9 Mile B	10
Apalachicola	9	2019	6	GEBF-5007	Bulkhead	15

Apalachicola	9	2019	6	GEBF-5007	East Hole	30
Apalachicola	9	2019	6	GEBF-5007	Hotel Bar	45
Apalachicola	9	2019	7	GEBF-5007	8 Mile	30
Apalachicola	9	2019	7	GEBF-5007	9 Mile B	15
Apalachicola	9	2019	7	GEBF-5007	Cabbage Top	15
Apalachicola	9	2019	7	GEBF-5007	East Hole	60
Apalachicola	9	2019	7	GEBF-5007	King 9 Mile	15
Apalachicola	9	2019	7	GEBF-5007	North Spur	30
Apalachicola	9	2019	8	GEBF-5007	Cat Point	45
Apalachicola	9	2019	8	GEBF-5007	Cat Point Spur	30
Apalachicola	9	2019	8	GEBF-5007	Monkeys Elbow	30
Apalachicola	9	2019	8	GEBF-5007	Peanut Ridge	30
Apalachicola	9	2019	8	NFWF-1	Hotel Bar	75
Apalachicola	9	2019	9	NFWF-1	Bulkhead	75
Apalachicola	9	2019	9	NFWF-1	Dry Bar	75
Apalachicola	9	2019	9	NRDA-4044	Cabbage Lumps	15
Apalachicola	9	2019	9	NRDA-4044	Cabbage Top	30
Apalachicola	9	2019	9	NRDA-4044	Green Point	15
Apalachicola	9	2019	9	NRDA-4044	North Spur	15
Apalachicola	10	2019	10	NRDA-4044	Dry Bar	60
Apalachicola	10	2019	10	NRDA-4044	Hotel Bar	45
Apalachicola	10	2019	10	NRDA-4044	Redfish Creek	15
Apalachicola	10	2019	11	NRDA-4044	Bayou Flats	15
Apalachicola	10	2019	11	NRDA-4044	Eleven Mile	30
Apalachicola	10	2019	11	NRDA-4044	Lighthouse Bar	30
Apalachicola	10	2019	11	NRDA-4044	Normans Bar	60
Apalachicola	10	2019	11	NRDA-4044	Redfish Creek	30
Apalachicola	10	2019	12	NRDA-4044	Cat Point	30
Apalachicola	10	2019	12	NRDA-4044	Little Gully	30
Apalachicola	12	2020	12	GEBF-5007	Cabbage Top	15
Apalachicola	12	2020	12	GEBF-5007	North Spur	30
Apalachicola	12	2021	1	GEBF-5007	Hotel Bar	45
Apalachicola	13	2021	4	GEBF-5007	8 Mile	30
Apalachicola	13	2021	4	GEBF-5007	9 Mile B	15
Apalachicola	13	2021	4	GEBF-5007	Cat Point	45
Apalachicola	13	2021	4	GEBF-5007	East Hole	30
Apalachicola	13	2021	4	GEBF-5007	King 9 Mile	15
Apalachicola	13	2021	6	GEBF-5007	Bulkhead	15
Apalachicola	13	2021	6	GEBF-5007	Cat Point Spur	30
Apalachicola	13	2021	6	GEBF-5007	East Hole	60
Apalachicola	13	2021	6	GEBF-5007	Monkeys Elbow	30
Apalachicola	13	2021	6	GEBF-5007	Peanut Ridge	30
Apalachicola	13	2021	7	NRDA-4044	Bayou Flats	15
Apalachicola	13	2021	7	NRDA-4044	Cabbage Lumps	15
Apalachicola	13	2021	7	NRDA-4044	Eleven Mile	30
Apalachicola	13	2021	7	NRDA-4044	Redfish Creek	45
Apalachicola	13	2021	8	FWC-2021	Cat Point	30
Apalachicola	13	2021	8	FWC-2021	East Lumps	30
Apalachicola	13	2021	8	FWC-2021	Lighthouse Bar	30
Apalachicola	13	2021	9	NRDA-4044	Cabbage Top	30

Apalachicola	13	2021	9	NRDA-4044	Dry Bar	45
Apalachicola	13	2021	9	NRDA-4044	Green Point	15
Apalachicola	13	2021	9	NRDA-4044	Hotel Bar	45
Apalachicola	13	2021	9	NRDA-4044	Lighthouse Bar	30
Apalachicola	13	2021	9	NRDA-4044	Little Gully	30
Apalachicola	13	2021	9	NRDA-4044	North Spur	15
Apalachicola	14	2021	10	FWC-2021	Cat Point	15
Apalachicola	14	2021	10	FWC-2021	East Lumps	15
Apalachicola	14	2021	11	FWC-2021	Lighthouse Bar	15
Apalachicola	14	2021	12	NRDA-4044	Cat Point	30
Apalachicola	14	2021	12	NRDA-4044	Dry Bar	15
Apalachicola	14	2021	12	NRDA-4044	Normans Bar	60
Apalachicola	14	2022	1	FWC-2021	Cat Point	15
Apalachicola	14	2022	1	FWC-2021	East Lumps	15
Apalachicola	14	2022	2	FWC-2021	Lighthouse Bar	15
Apalachicola	15	2022	5	FWC-2021	Cat Point	15
Apalachicola	15	2022	5	FWC-2021	East Lumps	15
Apalachicola	15	2022	5	FWC-2021	Lighthouse Bar	15
Pensacola	5	2017	9	NRDA-4044	Boathouse Lumps	30
Pensacola	5	2017	9	NRDA-4044	Escribano Point	30
Pensacola	5	2017	9	NRDA-4044	Mussel Beds	15
Pensacola	5	2017	9	NRDA-4044	No Name Bar	15
Pensacola	5	2017	9	NRDA-4044	Point No Point Bar	15
Pensacola	5	2017	9	NRDA-4044	Trout Bayou	45
Pensacola	6	2017	10	NRDA-4044	Big John Bar	15
Pensacola	6	2017	10	NRDA-4044	East River	60
Pensacola	6	2017	10	NRDA-4044	Half Moon Bar	15
Pensacola	6	2017	10	NRDA-4044	Square Bar	15
Pensacola	6	2017	10	NRDA-4044	White Point Bar	30
Pensacola	7	2018	7	NRDA-4044	Big John Bar	15
Pensacola	7	2018	7	NRDA-4044	Boathouse Lumps	30
Pensacola	7	2018	7	NRDA-4044	East River	60
Pensacola	7	2018	7	NRDA-4044	Escribano Point	30
Pensacola	7	2018	7	NRDA-4044	Half Moon Bar	15
Pensacola	7	2018	7	NRDA-4044	Mussel Beds	15
Pensacola	7	2018	7	NRDA-4044	No Name Bar	15
Pensacola	7	2018	7	NRDA-4044	Point No Point Bar	15
Pensacola	7	2018	7	NRDA-4044	Square Bar	15
Pensacola	7	2018	7	NRDA-4044	Trout Bayou	45
Pensacola	7	2018	7	NRDA-4044	White Point Bar	30
Pensacola	10	2019	11	NRDA-4044	Big John Bar	15
Pensacola	10	2019	11	NRDA-4044	Boathouse Lumps	30
Pensacola	10	2019	11	NRDA-4044	East River	60
Pensacola	10	2019	11	NRDA-4044	Escribano Point	30
Pensacola	10	2019	11	NRDA-4044	Half Moon Bar	15
Pensacola	10	2019	11	NRDA-4044	Mussel Beds	15
Pensacola	10	2019	11	NRDA-4044	No Name Bar	15
Pensacola	10	2019	11	NRDA-4044	Point No Point Bar	15
Pensacola	10	2019	11	NRDA-4044	Square Bar	15
Pensacola	10	2019	11	NRDA-4044	Trout Bayou	45

Pensacola	10	2019	11	NRDA-4044	White Point Bar	30
Pensacola	15	2022	6	NRDA-4044	Boathouse Lumps	30
Pensacola	15	2022	6	NRDA-4044	Escribano Point	30
Pensacola	15	2022	6	NRDA-4044	Mussel Beds	15
Pensacola	15	2022	6	NRDA-4044	No Name Bar	15
Pensacola	15	2022	6	NRDA-4044	Point No Point Bar	15
Pensacola	15	2022	6	NRDA-4044	Trout Bayou	45
Pensacola	15	2022	7	NRDA-4044	Big John Bar	15
Pensacola	15	2022	7	NRDA-4044	East River	60
Pensacola	15	2022	7	NRDA-4044	Half Moon Bar	15
Pensacola	15	2022	7	NRDA-4044	Square Bar	15
Pensacola	15	2022	7	NRDA-4044	White Point Bar	30
St. Andrew	5	2017	8	NRDA-4044	Crooked Creek Point	15
St. Andrew	5	2017	8	NRDA-4044	Doyle Bayou	30
St. Andrew	5	2017	8	NRDA-4044	East Power Lines	15
St. Andrew	5	2017	8	NRDA-4044	Goose Point	15
St. Andrew	5	2017	8	NRDA-4044	Little Oyster Bar Point	12
St. Andrew	5	2017	8	NRDA-4044	Newman Bayou Bar	15
St. Andrew	5	2017	8	NRDA-4044	Off Little Oyster Bar Ridge	15
St. Andrew	5	2017	8	NRDA-4044	South Channel Ridge	15
St. Andrew	5	2017	8	NRDA-4044	West Bay Point	30
St. Andrew	7	2018	4	NRDA-4044	East Power Lines	15
St. Andrew	7	2018	4	NRDA-4044	Newman Bayou Bar	15
St. Andrew	7	2018	4	NRDA-4044	West Bay Point	30
St. Andrew	7	2018	5	NRDA-4044	Crooked Creek Point	15
St. Andrew	7	2018	5	NRDA-4044	Doyle Bayou	30
St. Andrew	7	2018	5	NRDA-4044	Goose Point	15
St. Andrew	7	2018	5	NRDA-4044	Little Oyster Bar Point	15
St. Andrew	7	2018	5	NRDA-4044	Off Little Oyster Bar Ridge	15
St. Andrew	7	2018	5	NRDA-4044	South Channel Ridge	15
St. Andrew	10	2019	12	NRDA-4044	Crooked Creek Point	15
St. Andrew	10	2019	12	NRDA-4044	Doyle Bayou	30
St. Andrew	10	2019	12	NRDA-4044	Goose Point	15
St. Andrew	10	2019	12	NRDA-4044	Little Oyster Bar Point	15
St. Andrew	10	2019	12	NRDA-4044	Off Little Oyster Bar Ridge	15
St. Andrew	10	2019	12	NRDA-4044	South Channel Ridge	15
St. Andrew	10	2019	12	NRDA-4044	West Bay Point	30
St. Andrew	10	2020	1	NRDA-4044	East Power Lines	15
St. Andrew	10	2020	1	NRDA-4044	Newman Bayou Bar	15

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1 *Appendix 2 Detailed descriptions of all models fit to data for each question.*

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

3 From the GLM models, the dispersion parameter from the negative binomial
 4 distribution ("nbinom2" family formulation) was <1 for all models, suggesting over-dispersion.
 5 The best fitting model for oyster spat (lowest AICcC value, highest AICcC weight) was the Period
 6 + Bay + (Period | Site) + Period:Bay + offset(log(Num_quads)) (Table 2). Because site is uniquely
 7 coded, this model allows different responses by site over time in each bay. No autocorrelation
 8 in residuals was detected (K-S test $p = 0.40$; D-W test $p = 0.18$). The significant interaction term
 9 suggests that each bay's temporal patterns in oyster counts are unique. Apalachicola Bay live
 10 spat counts per quadrat declined (beta of the slope = -0.004 , SE = 0.07 , 95% CI = $-0.15 - 0.14$)
 11 and this trend was not significantly different from zero ($p = 0.96$). Pensacola and St. Andrew
 12 bays show uncertain trends in oyster spat counts. Pensacola coefficient values for the slope of
 13 oyster spat counts over time were larger than Apalachicola (beta = -0.39 , SE = 0.11 , 95% CI = $-$
 14 $0.61 - 0.17$) and this slope coefficient did differ from zero ($p=0.0006$). For St. Andrew Bay, the
 15 slope coefficient was highly uncertain (beta = 0.21 , SE = 0.18 , 95% CI = $-0.14 - 0.57$) and this
 16 slope did not differ from zero ($p=0.23$).

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

19 To examine trends in Apalachicola Bay oyster spat by project, we fit eight different
 20 models to the data (Table 2). To simplify nesting of site within project in our model structure
 21 (which would allow period to vary by site across project), we created a new variable (SP) which
 22 combined the site and project name. Creating the variable SP allows different responses by site

over time in each project. The best fitting model for oyster spat (lowest AICcC value, highest AICcC weight) was the Period + Project + (Period | SP) + Period:Project + offset(log(Num_quads)) (Table 3). Autocorrelation in residual results were mixed as the K-S test was not significant (K-S test $p = 0.21$) but the Durbin-Watson test was (D-W test $p = 0.03$) likely due to different numbers of sites sampled with each project. No adjustment was made. The trend in live oyster spat counts per quadrat over time did not differ from zero for projects GEBF-5007 (slope coefficient $\beta = -0.06$, SE = 0.10, 95% CI = -0.26 – 0.13, $p = 0.51$), NRDA-4044 (slope coefficient $\beta = 0.04$, SE = 0.07, 95% CI = -0.09 – 0.18, $p = 0.51$) or NFWF-2021 (slope coefficient $\beta = -1.04$, SE = 0.60, 95% CI = -2.24 – 0.15, $p = 0.09$). For project NFWF-1, the trend in live oyster spat per quadrat was significantly different from zero ($p < 0.0001$) and this trend was negative (slope coefficient $\beta = -0.64$, SE = 0.15, 95% CI = -0.94 – -0.35).

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

We then fit four additional models (Table 4) that compared the best fit model from Question 2 (Table 3) to models with terms describing the number of days river discharge was below 12,000 CFS, days below 12,000 CFS lagged by 1 period, number of days river discharge was below 6,000 CFS and days below 6,000 CFS lagged by 1 period (Table 3). Including these river discharge metrics did not improve model fit (Table 3).

Question 4: Is cultch biomass related to the number of live oysters?

Four models all had similar AICc values (within three AICc units) and the model with the highest weight (0.38) was the most complicated model $\text{Roundwt} \sim (1 | \text{SP}) + \text{Spat_sum} + \text{Period} + \text{Project} + (0 + \text{Period} | \text{SP}) + \text{Period:Project} + \text{offset}(\log(\text{Num_quads}))$ which also allowed for a unique negative binomial dispersion parameter. Diagnostic assessments of model fitting for

these models suggests that several may be overparameterized. We examined nine simpler models to assess whether including the number of live spat did not improve model fit (Table 5). For these simpler models, model fit was not improved by including oyster spat counts as a main effect (across all projects) or as an interaction term for each project (Table 5). The lowest AICc and highest model weight was for a model that did not include information on oyster spat (Table 5). This suggests live oyster spat did not influence oyster cultch biomass.

Question 5: How does cultch material persist?

We plotted the weight per quadrat (kg) by bay and project over period to assess patterns (Figure 12). For Pensacola and St. Andrew, the cultch material used for project NRDA-4044 was limestone or granite (Table 1). Plotting the biomass of this material per quadrat over time (Figure 13) demonstrated a widespread in the amount of material collected over time but no strong indication of an increase or decline. Because Apalachicola Bay is the only system where multiple materials (rock and shell) have been used for different projects, we were able to examine Apalachicola Bay for more insight into cultch persistence by project (Figures 13-14). We fit the same GLM models described previously first to compare all bays (Question 1) and to compare projects within Apalachicola Bay (Question 2).

In comparing the persistence of cultch material across the three bays, the Roundwt ~ Period + Bay + (Period | Site) + Period:Bay + offset(log(Num_quads)) model did not converge with either the default or the BFGS optimizer. From an AICcC perspective a simpler models the Roundwt ~ Period + Bay + (1 | Site) + Period:Bay + offset(log(Num_quads)) was the top model (lowest AICc value and AICc Weight = 0.56; Table 5).

Apalachicola Bay cultch biomass per quadrat had a positive slope (beta of the slope = 0.04, SE = 0.02, 95% CI = 0.008 – 0.07) and this trend was significantly different from zero ($p = 0.02$). Pensacola beta values for the slope of oyster spat counts over time were negative (beta = -0.03, SE = 0.03, 95% CI = -0.08 – 0.03) and this slope did differ from zero ($p=0.02$). For St. Andrew Bay, the slope was highly uncertain (beta = -0.07, SE = 0.05, 95% CI = -0.20 – 0.05) and this slope did not differ from zero ($p=0.23$). We then predicted the marginal means of oyster biomass from a single $\frac{1}{4}$ -m² quadrat in Period 15 for comparison purposes between each bay. Predicted live oyster spat for Apalachicola was 3.76 kg cultch per quadrat (95% CI 2.54 – 5.56), Pensacola was 1.71 kg cultch per quadrat (95% CI 0.99 – 2.94), and St. Andrew Bay predicted cultch per quadrat was 1.34 kg (95% CI 0.46 – 3.85).

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

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

88 this slope did differ from zero ($p=0.02$). For the NFWF-1 project, the slope was negative ($\beta =$
89 -0.14 , $SE = 0.02$, $95\% \text{ CI} = -0.19 - -0.09$) and this slope did differ from zero ($p<0.0001$). Finally,
90 for the NRDA-4044 project the slope was negative ($\beta = -0.05$, $SE = 0.01$, $95\% \text{ CI} = -0.07 - -$
91 0.02) and this slope did differ from zero ($p=0.0002$).

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