

**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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Dear Marine and Coastal Fisheries Editorial Team:

We have extensively revised the manuscript "Collapsed oyster populations in large Florida estuaries appear resistant to restoration using traditional cultching methods — insights from ongoing efforts in multiple systems" following guidance from the Editor, AE, and two reviewers. Below we provide the original comment in italics and follow with our response.

*The reviews suggest that, subject to major revisions, your paper could be suitable for publication. All of the reviewers, including the AE and myself, commented that the text was overly long, sometimes confusing, and "preachy" in some cases. All of these lead to the key messages that are supported by the data being lost. All also though the manuscript addresses a very important topic and has important things to say.*

*Therefore, I invite you to respond to the reviewer(s)' comments and revise your manuscript. The revisions should address the comments and also involve a major rewrite and tightening.*

Thank you for the supportive comments. With the assistance of a professional copy editor, we have extensively revised the manuscript to better focus on the key results, improve clarity, and reduce "preachy-ness" of the manuscript. We also eliminated one analyses within the paper that simplifies the paper through a reduction in text and tables.

Reviewer: 1

Comments to the Author

*The work conducted here is an important contribution to the literature. In my review, I see three substantial issues.*

*1. As written, the manuscript is written with a great deal of jargon and coding and this obscures the work and the important findings. For example, for the sake of the modeling, time was divided into periods which seems appropriate. But then the authors keep that convention in the text and the figures, forcing a reader to decode odd and even numbers and do some math to figure out what year each period is in. Is there any reason that this can't be done?*

We appreciate the positive response to our manuscript. In revisions we have worked to reduce the jargon of the manuscript and simplify the language. For example, throughout we have revised the units of the assessment of oyster counts and cultch mass from a per quadrat framework to a per  $\frac{1}{4}$  m<sup>2</sup> (the size of the quadrat). We have also provided the conversion to the m<sup>2</sup> unit requested by the reviewer where appropriate. We do caution on expansion of the mean values of these estimates because of the high dispersion and frequency of zeros. We have kept the analyses in terms of time periods because this provides analytical improvements by allowing for multiple samples to be considered in the same time step. This also allows for simple graphical comparisons of observed, standardized oyster spat counts on different substrate at the same time window. We have added additional information throughout to better identify the Period by year. This is explained in the figure captions and is described in detail

including which months and samples are in each Period in Appendix 1. We attempted to add a second y axis with these labels, but were not successful in making this visually appealing.

*2. There is surprisingly little reference to work done in other areas. For example, there is virtually no mention of the work done in Mobile Bay by researchers based at the Dauphin Island Sea Lab specifically about reef height, location, etc. There is mention of work in Chesapeake Bay but the context for this work could be more inclusive of the substantial work done in oyster restoration.*

We have expanded references throughout the paper. However, if the reviewer is aware of specific articles from work in Mobile Bay by DISL staff, please provide the reference. We are aware of oyster restoration and management efforts in Alabama and are in regular communication with Alabama Marine Resources staff. We have also cited their ongoing restoration efforts in this manuscript.

*3. Inadequate attention is paid to alternative explanations for the observed data beyond issues with the cultching. For example, the question of larval supply is skimmed over in lines 640-644. Will putting cultch down work if we change how we do it, or have there been changes that may mean that putting cultch down may not work as a single solution? As noted, large sums of money and effort are put into these projects and it's not clear that these projects are working. (Lines 595-597 caught my attention.)*

All of these restoration projects are a test of a single hypothesis—that oyster populations have declined because of insufficient cultch. In the revised manuscript (lines 393-398) we begin the discussion by pointing out this simple fact and then follow this in subsequent paragraphs (lines 409-440) with discussions of alternative possible explanations. We have also provided references to detailed assessments of the oyster population collapse observed in Apalachicola Bay in 2012 (line 409-415). We highlight that what we are assessing in this paper is response to restoration in three different estuaries (lines 417-419) which reduces the likelihood of bay-specific abiotic or biotic conditions limiting restoration success unless the limiting factor is an unknown regional limitation.

A recent newspaper series documented similar lack of response to restoration using similar methods in Mississippi waters

(<https://www.propublica.org/article/mississippi-spent-millions-failed-to-save-oyster-reefs>)

*lines 37-39 Awkward phrasing*

Revised as requested.

*Line 58 and throughout: 'Bays' should be capitalized, I believe, as those are all proper names of bays (Pensacola Bay, St. Andrew Bay, etc.)*

We are using the correct capitalization when referring to multiple bays based on the journal style manual and other publishing standards.

*Line 111. Should 'at' be 'and'?*

Revised as suggested.

*Line 125. What number of quadrants per site? Minimum number? Range?*

This information is included in the Supplemental Files, Appendix 1.

*Line 146: 'Staring' should be 'starting'*

Thank you, corrected.

*Line 281: over-dispersed was used as a term earlier but explained here. Might move that section in parentheses to the first mention of over-dispersed*

Revised as suggested.

*Line 404: Suggest 'intended' (or 'hoped') instead of 'designed'*

Revised as suggested.

*Acknowledgements need updated project numbers for the current placeholders 'YYYY-YYY'*

Revised as suggested.

We appreciate the detailed review by Reviewer 1.

*Reviewer: 2*

#### *Comments to the Author*

*Overall, I think that this is a very important study and one that should be reviewed and considered both by funding agencies and restoration practitioners. As is always the case with large scale environmental restoration efforts, it would be ideal for there to be more data available on project performance and environmental (both physical and biotic) conditions that can help explain the patterns observed. However, investments in these data are rare at the scale/level of resolution needed to be valuable. So, I think the authors are doing their best with a limited data set. At times, I think that the study verges on preaching to the restoration community and perhaps criticizing them with a tone that may not be conducive to provoking the changes that the authors recommend. Thus, I suggest a strong review of such statements and consideration of reframing them to be less confrontational and more, directly forward-looking. I am not an expert in the statistics so was not able to comment on their validity. However, I also did not see any particularly glaring issues with how the data were analyzed. I am favorable towards the study being published if the revisions suggested below are made.*

Thank you for the encouraging comments.

#### *Suggested revisions*

*L 19: shortcomings not short comings*

We have corrected.

*L36: some of these citations seem improperly formatted*

We have corrected.

*L 41: What is meant by a 'low but apparently resilient state' - resilient to evolving back into a more robust, living reef?*

We have removed this term.

*L 44: I this this phrasing is statement is not correct - "all restorations are expected to persistently increase... ". It is my perception that investments in restoration are made with the goal of locally enhancing oyster populations. But, there is not necessary the expectation that all project expect persistent increases in population size.*

We have revised this sentence (lines 35-38) to state "...many restoration efforts attempt to..."

*Research Questions:*

*It is unclear in Q1 whether these are oyster counts in the bays in general or on the restoration project specifically.*

We have clarified in the methods that all data are from restoration sites (lines 122-123).

*Q2 and 3: why only Apalachicola was investigated for these questions is unclear. I encourage you to provide some justification to support understanding by the reader.*

We have clarified that Apalachicola is the only system where different projects within one bay can be compared over time because none of the other systems have data available from multiple projects. We also clarified that Apalachicola Bay is the only estuary with regulated river inputs thus the only system where freshwater input can be modified via management (lines 103-118).

*Q3: In the framing of the paper in the earlier parts of the introduction, there is not really any motivation for understanding project to project differences... so this question comes out of nowhere.*

We have explained the reason for assessing freshwater inputs in revision (lines 103-118).

*Is there some reason to expect the projects to differ based on their design, placement, timing of deployment?*

Yes, the different projects use different materials. The different timing of deployment would potentially represent different abiotic and biotic conditions in the bays when the cultch material is placed.

*L72: the redundant use of leadership and leaders is a bit clunky*

This has been removed in revision.

*L73: There seems to be some underlying blame being suggested in this statement to those conducting restoration that they are not learning from prior projects. I think that this phrasing may act to repel such entities from wanting to read/engage with this work so suggest some rephrasing here.*

This has been removed in revision.

*L84-85: is there at lease a personal communication to cite about this statement?*

This information is included in Figure 2 and a reference to that figure has been added.

*L287: were none of the months or years significantly higher than average?*

This information is included in Figure 4.

*L.311-312: can you scale these estimates of spat per quadrat to be the number per meter square so they are more meaningful/interpretable?*

The units have been revised throughout to change the reference from a per quadrat unit to per  $\frac{1}{4}$  m<sup>2</sup>. Scaling to m<sup>2</sup> is also presented, and we have added a note to caution the user in expansion of reported estimates to larger spatial units given the overdispersion in the observed counts at the  $\frac{1}{4}$  m<sup>2</sup> scale. Lines 305-313 as an example.

*Ln 335: I do not know what the SP term is*

This has been removed and clarified in revision. This is just the term for the random effect.

*Ln 350-358: What is the justification for using these river discharge values and the single period lags? Is there a connection between these discharge values and the salinity observed in Apalachicola? Is there a connection between this lag period and the ecology of oysters? I think these details would be helpful in the methods.*

This is discussed in detail lines 245-261.

*Ln 362: Isn't this statement written incorrectly - it seems that the driver is predicted to be cultch biomass and response live spat, so I recommend reorganizing the statement.*

Thank you, this has been revised.

*Lb 403: Multiple use of 'designed' in this sentence is a clunky*

Thank you, this has been revised.

*Discussion;*

*Overall I appreciate the interpretation of the data in the discussion and find the conclusions drawn to be fair and appropriate based on the study's findings and the literature. The one topic that the authors do not give much/any attention to is whether the broader food webs in these bays are now no longer conducive to supporting spat survivorship (i.e there are too many predators of spat that suppress their success) - this is just very briefly alluded to in the Future Directions section.*

Thank you for the encouraging comments. In revision we have expanded on "other topics" (lines 409-415; 416-440)

*Editor's Comments to Author:**Associate Editor**Comments to Author:*

*The manuscript reports on important findings of major interest. Nevertheless, I find the manuscript as submitted almost bafflingly over-long, repetitive, and difficult to follow. Presentations of data and statistics are difficult to interpret. There is a simple message in this paper: deploying cultch in these estuaries did not stimulate the restoration of oyster populations. It is not clear to me why this message should require nearly 80 pages.*

We have worked with a professional copy editor to revise the manuscript to focus the writing and to highlight the key messages. We have removed the formal analyses assessing relationships between live oyster spat and cultch mass. This was a complicated analyses which simplifies the message while providing the same information by simply referring the reader to plots of the data. Overall, the AE provides limited detail to address their concerns. We will discuss with the Editor.

*The discussion of reasons for failure barely acknowledges the most likely causes: predation on spat and early juvenile oysters, and possibly disease, especially Dermo. For both of these factors, salinity regimes are crucial, yet no salinity data are offered, only the proxy variable river discharge, which is far less informative. How could there be no salinity data available for these sites?*

In revision we have highlighted how continuous salinity data are not available in two of the three bays in this study and, in the one bay where it is available, it is not available to the restoration sites (lines 110-114). This lack of region-wide water quality monitoring has been highlighted in a previous paper (Dale et al. 2021). Apalachicola River discharge as a proxy for salinity, nutrients, and other factors and we have provided references to key documents that synthesize this information and recent debates (Kelly 2019 for example).

We appreciate the AE proposing additional factors including predation and disease. There is no ongoing oyster disease monitoring program in these systems. There is not a long-term monitoring program for oyster predators, and the role of oyster predators on the Apalachicola Bay oyster collapse in 2012 (and other factors) is widely debated as we identify in lines 409-415 in revision.

*The term "cultch biomass" is used throughout to express the amount of cultch material deployed. The term should be just "mass." Biomass on cultch, including oysters and all else, would be interesting, but is not mentioned.*

We have revised to only refer to this as cultch mass.

*Reef restoration, even without oysters, can be ecologically beneficial. I am also curious why some effort was not made to quantify cultch in terms of surface area rather than mass. It would be a more relevant variable, and computable from mass with some simple algorithms.*

We are unaware of these algorithms for irregular objects. We only have mass data available for analyses and introducing the uncertainty around a conversion to area would further complicate analyses.

Thank you for the opportunity to revise this manuscript. We look forward to publishing the paper with MCF soon.

Regards,

Bill Pine

For co-authors.

For Peer Review Only



## 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. These projects primarily  
4 have focused on replacing oyster cultch (substrate) to promote spat settlement, increase  
5 recruitment, and bolster adult oyster populations. This study assessed outcomes of six such  
6 efforts, which used different cultch types and densities between 2015 and 2022 in three  
7 estuaries in the Florida panhandle (Pensacola, St. Andrew, and Apalachicola bays). Total  
8 restoration costs for these projects were more than \$14 million. Oyster counts did not  
9 persistently increase following restoration, regardless of cultch type or density. Positive  
10 responses to restoration efforts were irregular and short-lived, and seemed only to occur for  
11 spat-size oysters immediately after restoration. None of the restoration efforts significantly  
12 improved abundance of oysters of any size class in any of the study estuaries. Factors  
13 contributing to these results likely include design and implementation elements such as  
14 materials used and the height of the restored reefs. However, monitoring programs have not  
15 been able to deliver a clear picture of what is hindering restoration success. For oyster  
16 restoration efforts to succeed, changes are needed both in their implementation and in the way  
17 they are monitored, in order to promote continuous learning and improvement.

## 18 **Introduction**

19 Eastern oyster (*Crassostrea virginica*) populations in the northern Gulf of Mexico are depressed  
20 from historical levels. Since 2010, Florida, Alabama, Mississippi, Louisiana, and Texas have  
21 declared state- or federal-level oyster fishery disasters, and at least three states have

implemented fishery closures (Mobile Bay in Alabama, Apalachicola Bay in Florida, and Galveston Bay in Texas). As of the end of 2022, only one of these stocks (Mobile Bay) had reopened to harvest.

The reasons for regional oyster declines are widely speculated but poorly understood. Proposed reasons include prolonged drought, extreme rain events, freshwater releases from water management structures, environmental degradation, overharvesting, the *Deepwater Horizon* oil spill, and insufficient cultching (Petes et al. 2012; Pine et al. 2015; DHNRDA Trustees 2016; Kelly 2019; Gledhill et al. 2020; Du et al. 2021; MRD and NOAA 2021).

Many oyster restoration efforts in the Gulf of Mexico have focused on adding substrate to replace cultch, a matrix of living and dead material that oyster spat need in order to settle and grow, which was removed or displaced during fishing (Lenihan and Peterson 1998; Swift 1898; Lenihan and Micheli 2000; Howie and Bishop 2021). These restoration efforts attempt to convert oyster reefs from an observed low but possibly resilient state to a more desired productive state (Pine et al. 2022). While restoration objectives can vary by location, type of oyster bar (intertidal vs. subtidal), and management goals, many restoration efforts attempt to increase oyster populations so that they will provide and promote ecosystem services (Smith et al. 2022 a,b) and support fishery recovery.

Despite the importance of cultch for supporting oyster settlement (Lenihan and Peterson 1998; Frederick et al. 2016; Solinger et al. 2022), the amount, height, and type of cultch that are likely to perform best in different restorations are poorly understood (Graham et al. 2017; Goelz et al. 2020). Some current restoration programs in the Florida panhandle are long-term (10 years), and an evaluation of what has and has not worked is lacking. Such

information is critical for guiding current and future restoration and management (Pine et al. 2022).

This study assessed ongoing and recently completed oyster restoration efforts in three large estuaries in the Florida panhandle where oyster populations are depressed and restoration efforts have taken place: Pensacola, St. Andrew, and Apalachicola bays. Assessing restoration across three separate estuaries with different watersheds reduced the likelihood of estuary-specific factors (such as water quality, predation, or disease) limiting the effectiveness of restoration. Much of our analysis focused on Apalachicola Bay, the only one of the three for which data are available from multiple projects using different cultch densities, and the only one with regulated river (freshwater) inputs.

We explored the following questions:

- (1) How have oyster counts varied over time in these bays?
- (2) In Apalachicola Bay, how have trends in oyster spat (the life stage hypothesized to respond first to restoration) varied over time across different restoration projects?
- (3) Are oyster spat counts in Apalachicola Bay associated with freshwater discharge?
- (4) How do counts of live oyster spat compare across different cultch densities in Apalachicola Bay?
- (5) How well does cultch used in restoration persist in Pensacola, St. Andrew, and Apalachicola bays?

We found that large restoration programs in the Florida panhandle are not having the desired outcome of increasing live oyster populations of any size class. This may be due to project design flaws, unknown environmental factors, fishery effects, or a tipping point may

have been crossed trapping oyster populations in a low-production state that is resistant to restoration (Johnson et al. 2022).

For restoration efforts to succeed, they must be frequently and vigorously assessed and adjusted as needed (Pine et al. 2022). Our work suggests that substantial uncertainty persists about how to restore oyster populations at large scales in Florida. This uncertainty can best be managed by using an adaptive management approach (Walters 1986; Walters et al. 1988) that treats restoration projects as ongoing experiments—promoting continuous learning and improvement and thus increasing the projects' likelihood of success.

#### **Study sites**

The study focused on three Florida panhandle bays (Figure 1):

- **Pensacola Bay** is the fourth largest estuary in Florida, with a surface area of approximately 50,990 ha. Reported oyster landings, trips, and catch per unit of effort (CPUE) for Pensacola Bay have declined since the mandatory trip-ticket program was fully implemented in 1986 (Figure 2).
- **St. Andrew Bay** has a surface area of approximately 27,715 ha (Brim and Handley 2006) and oyster landings are mostly from the East Bay arm of the bay. Oyster landings and trips for East Bay specifically are not available, but landings have declined to near zero in the counties surrounding St. Andrew Bay in recent years (Figure 2).
- **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). It was

closed to commercial harvest from December 2020 to December 2025 by the Florida Fish and Wildlife Conservation Commission (FWC).

Restoration and monitoring efforts in these bays were led by three state agencies, under the sponsorship of the Natural Resource Damage Assessment and Gulf Environmental Benefit Fund), with funds from the *Deepwater Horizon* oil spill settlement (Table 1). Reef construction methods across projects were similar to other cultching efforts that have been carried out since the 1970s (Berrigan 1988; 1990; VanderKooy 2012), designed to maximize area of material covered.

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 “planted” at designated locations (Table 1; FDACS 2015; 2016a, b; 2017). Site selection for restoration efforts was based on local knowledge of historical or extant reef locations. Four projects took place in Apalachicola Bay and one each in Pensacola and St. Andrew bays (Figure 3).

In all projects, the area and density of cultch that was deposited differed from that originally planned due to construction challenges and storm events. These challenges also resulted in uncertainty about the restored reefs’ actual area, cultch density, and vertical relief. All monitoring efforts were conducted on the same sites where restoration took place.

The relationship between freshwater discharge from the Apalachicola River and oyster populations in Apalachicola Bay is of significant management concern and a focal aspect of a recent US Supreme Court Case (Florida v Georgia, No 142 Original, 2014). This case evaluated whether Georgia’s upstream water use altered salinities in Apalachicola Bay leading to the 2012 collapse of oyster populations (Kelly 2019). The US Supreme Court found that Florida failed to

demonstrate that Georgia's water use was the sole cause or a major contributing factor to the oyster population collapse and dismissed the case (Barrett 2021).

Apalachicola Bay is the only one of the study bays where upstream reservoir operations can influence freshwater inputs (Leitman et al. 2016) and freshwater inputs are what create estuarine conditions in all three bays. Continuous data on salinity and nutrient inputs before, during, and after restoration efforts are not available for the restoration sites in any of the three bays and region-wide water quality monitoring networks are lacking (Dale et al. 2021). Because of the management interest in Apalachicola Bay related to water inputs, we summarized Apalachicola River discharge as a proxy for salinity and nutrient input (factors widely discussed to influence oyster populations; Fisch and Pine 2016; Gledhill et al. 2020) inputs before, during, and after restoration efforts.

## **Methods**

### Field collections

Similar methods were followed across projects to count live oysters and measure the mass of cultch material (Florida Fish and Wildlife Research Institute 2021). Divers randomly placed  $\frac{1}{4}$  m<sup>2</sup> (0.5 m on each side) quadrats at restoration sites, removed all oysters and cultch material to wrist depth, and placed the cultch and oysters in bags. Bags were returned to the vessel and processed on location or returned to the lab. Oysters were counted, heights were measured, and cultch mass was recorded. Restoration and monitoring efforts occurred at different times depending on bay and project.

## 128 Fisheries-dependent data

129 Annual oyster landings (meat pounds; Florida Fish and Wildlife Conservation Commission 2022)  
130 and trips were summed for each county bordering each bay, and CPUE was calculated as  
131 landings/trips.

## 132 Data analysis

133 The five questions were assessed via corresponding analyses. Some analyses considered all  
134 three bays and some focused on Apalachicola Bay (for which we had the most detailed  
135 information from multiple restoration efforts). These analyses focused on how oyster counts  
136 changed at restoration sites (question 1); how they differed over time, cultch material, and  
137 cultch density (question 2); whether they were influenced by freshwater discharge (question 3)  
138 or cultch mass (question 4); and how cultch mass changed over time (question 5). Though each  
139 analysis was performed separately, they share both common elements (dependent variables  
140 and some independent variables) and general steps, each of which are described below.  
141 However, these variables and steps were developed into multiple alternative models for each  
142 analysis and question, and the construction of each model is described below to aide  
143 reproducibility (see also Appendix 1 and 2).

144 The dependent variables used in these analyses were the number of spat (<26mm shell  
145 height), seed (26–75mm shell height), or legal-size (>75mm shell height) oysters counted from  
146 monitoring; different size classes were relevant to different questions with most assessments  
147 focusing on counts of spat because of low numbers of other size classes.

148 The independent variables used in some combination for each of the analyses were as  
149 follows:

- **Period**, an integer modeled as a continuous variable, combined sampling months into blocks of time in order to simplify analysis. Winters (October–March) were represented by even numbers, and summers (April–September) by odd numbers. (This variable was relevant to all five research questions.)
- **Bay**, a categorical variable, compared restoration responses by bay—Pensacola, St. Andrew, or Apalachicola. (This variable was relevant to questions 1 and 5.)
- **Project**, a categorical variable, represented both type and density of cultch material, as each of the four Apalachicola Bay projects used a different cultch material and density and had a different start time. (This variable was relevant to questions 3 and 4.)
- **River (freshwater) discharge**, a continuous variable that measured the number of days discharge was below specified levels, served as a proxy for salinity and nutrient inputs. (This variable was relevant to question 3.)

We used the restoration site (a named oyster reef) as a random effect (uniquely named for each site + bay or site + project combination) to account for correlation among quadrat samples at each site. (This was relevant to all questions.)

The analyses followed these general steps:

- (1) Counts of live oysters in each bay and for each restoration site and period were summed into the three size classes that served as our dependent variables: spat, seed, and legal to harvest. 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 a sub-sample of oysters that were measured and



172 multiplying the totals by these proportions. The results were rounded to convert the  
173 numbers of oysters per size class to integers to match the NRDA-4044 and GEBF-5007  
174 data.

175 (2) Generalized linear models (GLMs; Bolker et al. 2009) with a negative binomial  
176 distribution were used to assess how oyster counts in all three size classes separately  
177 varied over different independent variables (question 1), using the R package glmmTMB  
178 (Brooks et al. 2017).

179 (3) We assumed that the total oyster counts per site would be related to the sampling  
180 effort (number of quadrats collected), which varied across sites. To control for this, we  
181 included the number of quadrats as an effort offset (log link function; Zuur et al. 2009;  
182 Zuur et al. 2013). This change effectively caused our models to predict the rate  
183 measured as count/quadrat while maintaining the dependent variable as an integer of  
184 counts. Because the quadrats were the same size for each study site, the total area  
185 sampled in each period only changed as a function of the number of quadrats.  
186 Using counts as the dependent variable and offsetting for effort, instead of converting  
187 the counts to CPUE based on the area sampled, has two main advantages. First, it  
188 maintains the response as an integer, allowing a negative binomial distribution  
189 (appropriate for oyster count data; Moore et al. 2020). Second, fitted values and  
190 confidence intervals do not contain negative values (Zuur et al. 2009).

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

(5) Autocorrelation in the residuals for the top model was assessed using the DHARMA package (Hartig 2022) in R (R Core Team 2021). This approach simulates new response data from the specified model, qq plots to check for deviations from the expected distribution graphically, a K-S test to see 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 (Lüdtke 2018) packages in R (R Core Team 2021).

These steps were applied to our research questions as described below.

*Question 1: How have oyster counts responded to restoration efforts across Pensacola, St. Andrew, and Apalachicola bays?*

We first looked broadly at oyster population responses to restoration across all three bays. The dependent variables were the number of oysters in the spat, seed, or legal-size categories (separate analyses were conducted for each category). The independent variables (main effects) were period (continuous) and bay (categorical).

Multiple models describing different hypothesis were fit 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 sites 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 have oyster spat trends varied over time across different restoration projects in Apalachicola Bay?*

Apalachicola Bay has undergone more restoration efforts than Pensacola and St. Andrew bays in the last decade—at least four since 2015, using different materials and starting at different times, compared to only one each in the other bays (Table 1). This question hence focused on Apalachicola Bay. Both for this question and for question 3 (spat count association with freshwater discharge), also Apalachicola Bay-specific, we assessed the independent variables of project, which represented cultch material and density, and river discharge (which varied over time). The focus in these two questions was on spat counts because spat is the life stage hypothesized to respond first to restoration. 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 the default glmmTMB optimizer nlminb and the alternative 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 and models compared with AICc. The 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 (NFWF-2021) less than two years before. If the materials, amount, or time since construction completion influenced

oyster reef restoration performance (as measured by different numbers of oysters per sampling unit), the predicted cultch mass 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 from question 2 (Table 3) to four additional models which included different Apalachicola River discharge metrics, to see if model fit improved (Table 4). Of the bays under study, only Apalachicola Bay has regulated river inputs (Apalachicola River).

River discharge metrics were the number of days in each period or the prior period (as a measure of antecedent discharge) when Apalachicola River discharge was below 12,000 CFS 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 to indicate low freshwater inputs. A discharge level of <6,000 CFS indicates extremely low river discharge because it approaches the minimum required water release of 5,000 CFS at Jim Woodruff Dam. One-year lags were also included to account for antecedent conditions and possible oyster population responses (Wilber 1992; Fisch and Pine 2016). We also visually assessed discharge patterns by plotting the percent deviation in mean river discharge (cubic feet per second [CFS] by convention) from the mean period of instrument records by month and year. We noted the frequency of months where discharge was below reference points related to floodplain inundation because of the management interest in the relationship between low-discharge periods and negative impacts on oyster populations. To capture antecedent river discharge

conditions, we began this time series in 2002, 10 years before the oyster fishery collapse and 13 years before the restoration projects covered by this study.

*Question 4: Cultch mass relationships to live oyster counts (Apalachicola)*

To assess relationships between cultch mass and oyster spat densities, we summarized mass of cultch per quadrat by site, project, and period in simple plots. This was only done for Apalachicola Bay because this is the only bay with multiple projects. Simple graphical assessments were used to examine these relationships.

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

To explore how cultch material persisted in different bays (Table 5), and by project within Apalachicola Bay (Table 6), we used negative binomial GLM models to assess how the sum of cultch weights changed over time in each bay (across all projects). In Apalachicola Bay we assessed persistence of cultch material by project (because of different materials and restoration time frames). Data were summarized by project, and calculations of mean and variance by project suggested the data were over-dispersed (variance > mean), supporting the use of a negative binomial distribution. To create a comparative framework across substrates, we predicted the amount of cultch per  $\frac{1}{4} \text{ m}^2$  (Figure 3) and  $\text{m}^2$  in the last monitoring period for each study.

Data and all code used for the analyses are available from the following Git repository:

[https://github.com/billpine/panhandle\\_oyster\\_response.git](https://github.com/billpine/panhandle_oyster_response.git).

## 279 **Results**

### 280 River discharge patterns

281 Apalachicola River discharge deviated significantly (50–100% below the average for the period  
282 of instrument records; Figure 4) for three or more months in 2002, 2006, 2007, and 2008, with  
283 extreme drought in 2011 (9 of 12 months), 2012 (12 of 12 months), 2016 (6 of 12 months), and  
284 2017 (4 of 12 months). Regional river discharge patterns were generally closer to average for  
285 2013–2022 than for 2002–2012.

### 286 Trends in fisheries-dependent data

287 FWC data since 1986 show that the Apalachicola Bay commercial fishery (trips and landings)  
288 was larger than those of Pensacola and St. Andrew bays combined. Apalachicola trips and  
289 landings increased sharply during the early 2000s, peaking the year of the fishery collapse in  
290 2012 (Figure 2). Apalachicola Bay was closed to oyster harvest by FWC in December 2020, with  
291 a reopening scheduled for December 2025. Pensacola, St. Andrew, and Apalachicola bays show  
292 similar trends of increasing trips and landings in the mid-1980s and again in 2005–2010. Trips  
293 and landings have declined in all three bays, with declining (Apalachicola) or minimal (Pensacola  
294 and St. Andrew) levels of commercial fishing activity since 2015, when the regional oyster  
295 restoration programs assessed in this analysis began.

### 296 Question 1: Response of oyster counts to restoration efforts (all three bays)

297 Plots of the raw CPUE for spat, seed, and legal-size oysters in all three bays show values  
298 near zero for all size classes (Figures 5–7). The best fitting GLM (Table 2; Appendix 2) suggests  
299 that oyster restoration responses over time in each bay were different, but none of the  
300 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  $\frac{1}{4}$  m<sup>2</sup> through periods (time) 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  $-0.61$  to  $0.17$ ). We do not know the depth of material excavated, so if we assume only the top layer of cultch is removed we can convert to oysters/m<sup>2</sup> by dividing the predicted number of oysters by quadrat by  $0.25$ . Caution should be taken with scaling estimates from the  $\frac{1}{4}$  m<sup>2</sup> unit of sampling because of the extreme dispersion in the observed counts. Predicted live oyster spat (marginal means) per  $\frac{1}{4}$  m<sup>2</sup> for Apalachicola was  $14.08$  (95% CI  $5.29$  to  $37.45$ ) or  $56.32$  oyster spat /m<sup>2</sup> ( 95% CI  $21.16$  to  $149.80$ ). For Pensacola  $0.70$  (95% CI  $0.16$  to  $3.14$ ) live oyster spat per  $\frac{1}{4}$  m<sup>2</sup> were predicted ( $2.80$  oyster spat/m<sup>2</sup> 95% CI  $0.64$  to  $12.56$ ). In St. Andrew Bay estimates were highly uncertain  $226$  (95% CI  $13.79$  to  $3,703.89$ ) live oyster spat per  $\frac{1}{4}$  m<sup>2</sup> were predicted ( $904$  oyster spat/m<sup>2</sup> 95% CI  $55.16$  to  $14,815.56$ ).

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 differing from zero for Pensacola Bay ( $p = 0.02$ ) with a decline in seed-size oysters over time (beta =  $-0.34$ , SE =  $0.14$ , 95% CI  $-0.61$  to  $-0.06$ ). 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). A positive response to restoration (increase in counts) was not observed for any size class of oysters in Apalachicola, St. Andrew, or Pensacola bays.

## Question 2: Oyster spat trends across restoration projects (Apalachicola Bay)

Trends in oyster spat CPUE by project over time in Apalachicola Bay (the only study bay with data available from multiple projects) suggest an initial increase in oyster spat (the life stage believed to respond first to restoration) 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 18-24 months following restoration, spat numbers were 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 fit eight different models to the data (Table 2; Appendix 2). Of these eight models, the model which included terms for period, project, a nested period by site term, and an interaction term between period and project, while controlling for effort, was the best fitting (Table 2). For three of the separate Apalachicola Bay 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 ( $p = 0.51$ ,  $p = 0.51$ ,  $p = 0.09$ ). 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  $-0.94$  to  $-0.35$ ). These results demonstrate that none of the restoration projects in Apalachicola Bay have had the desired sustained increase in oyster spat following restoration.

Comparisons of the best-fitting-model (Table 3) predicted the marginal means of oyster spat from a single  $\frac{1}{4}$  m<sup>2</sup> quadrat in the last period of sampling showed differences between projects. For the projects that used limestone rock, predicted live oyster spat for GEBF-5077 in period 12 was 15.73 per  $\frac{1}{4}$  m<sup>2</sup> (95% CI 8.45 to 29.27) or 62.9 oyster spat/m<sup>2</sup> (95% CI 33.8 to



117.1). For project NFWF-2021 in period 15 we predicted 119.03 (95% CI 30.88 to 458.82) oysters per  $\frac{1}{4}$  m<sup>2</sup> or 476 oyster spat /m<sup>2</sup> (95% CI 123.5 to 1835.3). For the projects that used shell cultch, for NRDA-4044 in period 13 we predicted 5.14 live oyster spat (95% CI 3.06 to 8.63) per  $\frac{1}{4}$  m<sup>2</sup> (20.6 oyster spat /m<sup>2</sup>; 95% CI 12.2 to 34.5), and for NFWF-1 in period 9 we predicted 5.39 (95% CI 1.20 to 24.26) per  $\frac{1}{4}$  m<sup>2</sup> (21.5 oyster spat /m<sup>2</sup>; 95% CI 4.8 to 97.0).

### Question 3: Effect of freshwater discharge on oyster spat counts (Apalachicola Bay)

We added coefficients describing different river discharge metrics to the best-fitting model comparing live spat counts across project and period in Apalachicola Bay (the only study bay with regulated river inputs) to see whether including river discharge information would improve model fit (Table 3). These river discharge metrics include the number of days discharge was below 12,000 CFS, days below 12,000 CFS lagged by 1 period (6 months), days below 6,000 CFS, and days below 6,000 CFS lagged by 1 period. Including these river discharge metrics did not improve model fit (Table 3), suggesting that the observed lack of positive response in live oyster spat was not influenced by the river discharge metrics assessed (Figure 11).

### Question 4: Cultch mass relationships to live oyster counts (Apalachicola)

Simple plots of mean cultch weight and total live spat per  $\frac{1}{4}$  m<sup>2</sup> suggest that, for the two studies in Apalachicola Bay monitored immediately following cultching (NFWF-1 and NFWF-2021), as the cultch mass increases so does the number of live spat—but only for one or two periods (6-12 months of time; Figures 13 and 14) before the number of spat collapses and retracts toward the origin, even for the same biomass of cultch (Figure 14). The other two studies were not monitored immediately after cultching and the same patterns are not observed.

Question 5: Persistence of cultch material (all three bays)

The best-fitting model comparing trends in oyster cultch mass over time across all three bays included an interaction term between period and bay, suggesting a different response on oyster cultch mass 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 nonsignificant trend in cultch mass 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 mass decreased over time.

Because Apalachicola Bay received multiple cultching treatments, we examined trends in cultch mass 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 mass from a single  $\frac{1}{4}$  m<sup>2</sup> quadrat in the last period of sampling for each project, for comparison purposes between projects in Apalachicola Bay. Again we do not know the depth of material excavated, so if we assume only the top layer of cultch is removed we can convert to kg/m<sup>2</sup> by dividing the predicted oyster cultch by quadrat by 0.25 but we urge caution in these types of expansions because of heterogeneity across the surface of the reef. Predicted oyster cultch mass for the NFWF-2021

(limestone cultch) project was 8.58 kg per  $\frac{1}{4}$  m<sup>2</sup> (period 15, 95% CI 4.03 to 18.30 [ 8.58 kg/m<sup>2</sup>; 95% CI 16.1 to 73.2]); for GEBF-5077 (limestone cultch) it was 4.29 kg per  $\frac{1}{4}$  m<sup>2</sup> period 12, 95% CI 2.94 to 6.27; [ 17.16.58 kg/m<sup>2</sup>; 95% CI 11.76 to 25.08]); for NFWF-1 (quarried shell) it was 0.97 kg per  $\frac{1}{4}$  m<sup>2</sup> (period 9, 95% CI 0.47 to 2.02; [ 3.88 kg/m<sup>2</sup>; 95% CI 1.88 to 8.08]); and for NRDA-4044 (shell cultch) it was 1.45 kg per  $\frac{1}{4}$  m<sup>2</sup> (period 13, 95% CI 1.01 to 2.09; [5.80 kg/m<sup>2</sup>; 95% CI 4.04 to 8.36]).

## Discussion

Decisions to add cultch material in Florida estuaries to reverse observed declines in oyster populations imply and thus essentially test a single hypothesis—that oyster populations have declined because of insufficient cultch. However, the ways the restoration efforts reviewed in this article have been designed, implemented, and monitored make it difficult to sufficiently evaluate this simple hypothesis, as well as more detailed hypotheses about the characteristics of cultch that are necessary to restore oyster populations—or whether cultch limitation is the actual reason for the collapse.

For example, differences in the timing of monitoring make it challenging to differentiate between the failure of oyster spat to successfully settle on restored material and their failure to survive past some critical size or life stage. Further, the restoration projects, though they used different materials, all created low-elevation restored reefs from relatively small materials. While this approach may be understandable given its similarity to past restoration efforts (with uncertain outcomes; Berrigan 1990), the lack of experimental contrasts in relief has likely made it difficult to determine whether cultch material is limiting oyster populations in the Florida panhandle.

Alternative hypotheses related to oyster population decline—including cascading predatory responses (Kimbrow et al. 2017), recruitment overfishing, discard mortality, virulent disease (known or unknown), freshwater inflow, climate change and some combination of these—remain largely unassessed and impossible to address with available data. The reasons for the 2012 collapse and the decade-plus period of low oyster abundance are uncertain (Camp et al. 2015; Kimbro et al. 2017; Pusack et al. 2018; Johnson et al. in-press) and have been debated as far as the US Supreme Court (Kelly 2019; Barnett 2021).

We found that, after restoration efforts, oyster populations did not show a sustained increase, and cultch material persistence was variable. This has been the case in different bays within different watersheds, which reduces the likelihood of bay-specific abiotic or biotic conditions limiting restoration success. This suggests there may be a variety of factors inhibiting population recovery, including flaws in the design of oyster restoration projects, regional ecosystem changes that now limit oyster population response to restoration, or legacy environmental or fishery management effects that have resulted in the systems being trapped in a persistent low-population state (Johnson et al. 2022; Pine et al. 2022). The singular, additive, or interacting effects of environmental, ecological, and fishery forces on oyster population resilience, recovery, and management form a persistent uncertainty in Florida and across the species' range.

For the restoration projects in Pensacola, St. Andrew, and Apalachicola bays, information which may have helped determine the proximal causes of restoration failure, and informed upcoming restoration efforts in these same systems—such as salinity, disease, oyster predators, and design aspects of the restored reef (including cultch type, area, and vertical

changes in relief over time)—was either not collected or only collected after restoration. This uncertainty does not, however, have to be a barrier to improved restoration outcomes. Uncertainty can be addressed effectively using the adaptive management framework (Holling 1978; Walters 1986; Pine et al. 2022)—an approach for improving natural resource management by systematically learning from management outcomes. Adaptive management approaches to restoration have been recommended by the *Deepwater Horizon* Natural Resource Damage Assessment trustees (2017) and National Academies of Sciences, Engineering, and Medicine (NAS 2017, 2022), but these recommendations have so far not been widely implemented for oyster restoration (Pine et al. 2022). Greater commitment to adaptive management can improve learning and ultimately restoration outcomes (Pine et al. 2022).

#### Spat responses to different cultch materials in Apalachicola Bay

Trends in oyster spat counts in the restoration data (Figures 13 and 14) suggest that observed oyster spat losses are occurring from October to March. The timing of these losses is surprising: winter is when abiotic stressors, such as high temperatures and low dissolved oxygen, are less likely to occur, thus increasing the potential for spat survival. However, average wind speeds from October to March are some of the highest of the year, and wind direction during this time is predominantly from the east and northeast; thus, stronger waves and currents during these months could be destabilizing oyster reefs made from small materials and causing spat mortality. This is an area for future work.

In Apalachicola Bay, in projects NFWF-1 (shell cultch) and NFWF-2021 (rock cultch), 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 NRDA-4044 (shell cultch) and

GEBF-5007 (rock cultch), no increases in spat settlement were recorded in response to restoration. However, these projects (NRDA-4044 and GEBF-5007) did not begin monitoring oyster response until 6–18 months post-construction, meaning any restoration responses immediately after restoration were not observed. These projects may also have seen 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 (Figure 5), nor were such high spat counts observed again for this project (Figure 5).

The reasons for the higher spat counts observed immediately after restoration in Apalachicola Bay for some projects but not others (Figures 13 and 14), even with similar cultch mass levels, are unknown. The mean predicted live oyster spat values tended to be lower for shell substrate than for rock; but different starting times for projects limit the reliability of this conclusion. 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) are consistent.

The relationship between cultch mass and the number of spat per quadrat across projects and sites (individual plots) in Apalachicola Bay (the only bay with multiple projects using multiple material types) is complicated (Figures 13–14). We found no clear pattern across sites in Apalachicola between cultch mass and total number of spat (Figure 13). For projects GEBF-5007 (rock) and NRDA-4044 (shell), spat counts were near zero across a range of cultch

mass 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 (shell cultch) and NFWF-2021 (rock cultch) show a general pattern of increasing spat in quadrats with more cultch mass (Figure 13; red dots for example).

Plotting mean cultch mass and total spat by project and period in Apalachicola Bay suggests that total spat increases with cultch mass, but only for one or two periods (Figures 13 and 14). Ultimately the pattern observed in these data show total spat and cultch mass per quadrat both collapse and retract toward the origin over time, as seen in projects NFWF-1 and NFWF-2021 (Figure 14) and a pattern that should be carefully assessed in future sampling for colonization by spat and possible reversal in count and biomass trends. This is an important result because it shows that the live oyster spat counts do not always persist even when apparently (perhaps minimal) levels of cultch are available.

#### Limited success of past restoration efforts

Recent restoration efforts in Pensacola, St. Andrew, and Apalachicola bays were guided by previous projects 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 1980s to 2010s for Apalachicola. In contrast, St. Andrew and Pensacola bay fisheries-dependent data indicate very low trips and landings for this same time period. Irregular cultching efforts have taken place in St. Andrews and Pensacola bays since the 1970s. 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 has been documented by 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 m<sup>3</sup>, and 306 m<sup>3</sup> (over a 0.4 ha area). They observed a positive response to oyster reef restoration 10 months post-restoration (Kimbrow et al. 2020 defined two size classes of oysters; juveniles <25 mm and adults ≥25 mm) during the same time frame as high oyster spat (< 25 mm) counts occurred on the NFWF-1 project reefs assessed by this study (Figure 6). Kimbro et al. (2020) also observed higher oyster counts on reefs with increased reef mass. Thus, for their work (Kimbrow et al. 2020) and for 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 (NFWF-1), found that, several years post-construction, the initial oyster population response to restoration, as measured by spat counts, did not persist (Figures 5 and 9–10). Spat count increases were only observed immediately following cultching and not in subsequent periods, nor did the spat that were observed persist



to seed or legal sizes. The reason for this is unknown. This is a critical uncertainty that must be addressed in Apalachicola Bay and elsewhere.

#### Potential reasons for limited success

One possible explanation for the apparent lack of restoration success is that the restoration actions were ineffective—for example, in their choice of material, density/height, or total area. The cultch density used following the 1985 oyster fishery collapse and closure in Apalachicola Bay, about 472 m<sup>3</sup> per acre of shell cultch (Berrigan 1990), was similar to the density used in the largest and most recent restoration efforts (NRDA-5007 and FWC-2021, respectively), both using rock cultch, and similar to the highest treatment level of recent shell cultch projects for Apalachicola Bay (NFWF-1; Table 1).

Regarding the total area necessary for restoration, Pine et al. (2015) recommended an intensive cultching program of about 50 ha per year—slightly more than the average area cultched each year between the 1985 post-Hurricane Elena restoration efforts and the beginning of regional restoration efforts in 2015 (Berrigan 1990). Aside from area, other optimum characteristics of cultching material—such as density (amount per area, and whether that material remains or is dispersed, which drives restoration height), type (shell vs. rock), and size—remain unknown.

Because the shell used in cultching is less dense than the rock used in cultching, the differences observed in cultch mass per quadrat across studies in Apalachicola Bay are not surprising. These results predict a decline of about 50–80% for shell cultch mass and an increase of about 15–50% in rock cultch mass 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 the apparent lack of restoration success is that the elevation of the restored reefs was too low. Previous oyster restoration work has emphasized the importance of reef elevation (Colden et al. 2017; Smith et al. 2022b). Additional elevation may be necessary to raise the cultch material into suitable water quality, hydrodynamic conditions, or avoid predators (Johnson and Smee 2014). Colden et al. (2017) found that oyster reefs with height  $> 0.3$  m in two Virginia sub-estuaries within the Chesapeake Bay 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. (2022a, 2022b), as part of a 15-year assessment of the performance of an oyster reef restoration project in Virginia waters of the Chesapeake Bay, found that restored reefs were similar to unrestored reference reefs in 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, Florida (Pine et al. 2022) demonstrated oyster spat settlement within six months following construction and 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 one Chesapeake Bay restoration project discussed above was about 0.14 m (Smith et al. 2022b, supplemental information); for another it was 0.4 m (Colden et al. 2017); and for the Lone Cabbage project in Florida it was about 0.36 m (Pine et al. 2022). These 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 Florida Fish and Wildlife Research Institute). We are not suggesting there is a uniform elevation requirement or even a minimum required elevation but are highlighting these successful restoration efforts as having contrasting elevation to adjacent areas without restoration. The relationships among elevation, inundation, wave action, oyster settlement, and persistence are complicated (Breitburg et al. 1995; Soniat et al. 2004; Morris et al. 2021).

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 to be 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.

Cultch material in various forms at different original mass levels has persisted on these restored reefs only at low mass levels (Figure 12), and it is possible that one reason for the low oyster spat settlement in this area is that restoration efforts may not have re-created the ecology that existed before the collapse – if this is possible.

A final possible explanation for the oyster population's failure to respond as hoped to restoration efforts is that the materials used were not conducive to oyster spat settling and surviving. Materials used in oyster restoration efforts vary widely (Bersoza Hernandez et al. 2018; Goelz et al. 2020). In Florida, they include multiple types of limestone, quarried oyster shells, recycled clam shells, crushed granite, and artificial materials. Previous restoration projects in Apalachicola Bay used clam shells dredged from Lake Pontchartrain, Louisiana (Berrigan 1988, 1990), or quarried oyster shell (Kimbrow et al. 2020).

The limestone used in this study's largest restoration projects (from Kentucky) is made of calcite, dolomite, and quartz. It is denser (structure and mass) and older (geologic age) than the limestone (from Florida, likely Avon Park formation) used successfully, as measured by counts and persistence of oysters, for intertidal reef restoration in Suwannee Sound, Florida (J. Yeager, University of Florida Department of Geological Sciences, personal communication; Pine et al. 2022). Whether the chemical composition and physical characteristics of different types of limestone may influence its effectiveness as cultch is unknown.

Cultching efforts in Apalachicola Bay have been identified as contributing to the long-term sustainability of harvest in the bay before 2010 (Zu Ermgassen et al. 2012). But whether cultching alone has contributed meaningfully to the sustainability of harvests overall is doubtful, based on the observed oyster fishery collapse in 2012 and lack of response to cultch additions examined here. The National Academies of Sciences, Engineering, and Medicine highlighted the NFWF-1 project, assessed in this study, as an example of a restoration project designed to experimentally evaluate oyster population responses to different cultch density treatments (NAS 2017). Because of deviations in the original experimental design (described in

NAS 2017), the different cultch treatments cannot be assessed from available data. Project NFWF-2021 (the only project begun after the Apalachicola Bay fishery closure) also observed a large increase in spat post-construction, and seed oysters were present in subsequent samples (Figure 10). Continued monitoring of this project will be important to understand whether these seed oysters survive to legal size, but the lack of spatial replication and paired unrestored control sites will make it difficult to draw strong conclusions about the effects of the restoration or fishery closure.

Johnson et al. (2022) demonstrated the risk of a transition to a stable, resilient, low population state for oysters and the difficulty of reversing this to a more desired state in a generalized oyster population model. The scale of restoration, or 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 a reversal of the collapse is likely to require many orders of magnitude more effort than has been attempted so far (Johnson et al. 2022).

Even if such massive restoration efforts were completed, the likelihood of their success is unknown because, as currently designed, they test only a single hypothesis—that more and better substrate is the key to oyster population recovery. In order to understand success factors and more confidently predict project outcomes, more research is needed to assess cultching efforts and while at the same time explore other factors that may affect oyster population recovery and persistence.

## **Conclusions**

Recent efforts to restore oyster populations in Apalachicola, Pensacola, and St. Andrew bays have cost more than \$14,200,000 (Table 1). At time of writing, Apalachicola Bay is two years

into a five-year harvest moratorium (2020–2025), and the oyster harvest in Pensacola and St. Andrew bays has been low for decades.

Many restoration efforts, in the Gulf of Mexico and elsewhere, have not had the desired outcome (LaPeyre et al. 2022; NAS 2022). Uncertainty about how to restore and manage oyster populations has persisted for decades or even centuries in Florida (Swift 1897, 1898; Pine et al. 2015), and there has long been a call to incorporate more learning into restoration and management programs (Walters 1986; Gunderson 1999; Walters 2007; Bouwes et al. 2016; NAS 2022; Pine et al. 2022). The adaptive management framework offers a systematic way to do this (Holling 1978). It can help such programs identify critical uncertainties and guide them toward actions that increase the likelihood of success (Bouwes et al. 2016; Friberg et al. 2016; Pine et al. 2022).

In the past, this type of learning may not have been a goal of restoration programs because uncertainty was not perceived as an issue and action choices were strongly influenced by perceived past success (even if outcomes had not been systematically assessed). Even if past efforts did succeed, such a prescriptive approach (Williams 2010) does not consider that system states may change, and when they do, restoration strategies and scale often need to change too (Johnson et al. 2022). Adaptive management can contribute dramatically to a project's success. Yet it has been difficult to incorporate into ecosystem management. As Gunderson (1999) noted:

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.

A greater incorporation of learning in oyster restoration and management efforts can substantially increase the chances for oyster population recovery, which would in turn support ecosystem services and viable fisheries for the benefit of people in 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 <sup>a</sup>	Construction time frame	Material	Amount (cubic meters)	Sites	Average density (cubic meters per acre)	Project cost <sup>e</sup>
Pensacola	NRDA 4044	FDEP	Fall 2016	Limestone aggregate	15,270	17	174	\$5,370,596 <sup>b</sup>
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 <sup>c</sup>
Apalachicola	NFWF-1	FWC	Summer/Fall 2015	Quarried shell	7,340	3	76, 153, 229, 306	\$4,189,400 <sup>d</sup>
Apalachicola	NFWF-2021	FWC	Summer 2021	Limerock aggregate	7,340	3	229	Part of d

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

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

<sup>c</sup> Fact sheet: [https://www.restorethegulf.gov/sites/default/files/FPL\\_FactSheet\\_20160909\\_FL\\_Apa\\_Oyster.pdf](https://www.restorethegulf.gov/sites/default/files/FPL_FactSheet_20160909_FL_Apa_Oyster.pdf)

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

<sup>e</sup> 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 m<sup>2</sup> 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  $\frac{1}{4}$  m<sup>2</sup> 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 m<sup>2</sup> 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 patterns in oyster cultch biomass from subtidal reefs in three bays in the Florida panhandle. The predicted response is biomass of cultch (kg) per  $\frac{1}{4}$  m<sup>2</sup> 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 6. Model selection table for the GLM of oyster cultch biomass from subtidal reefs restored using different materials, at different densities, and at different times in Apalachicola Bay. The predicted response is number of spat per ¼ m<sup>2</sup> 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



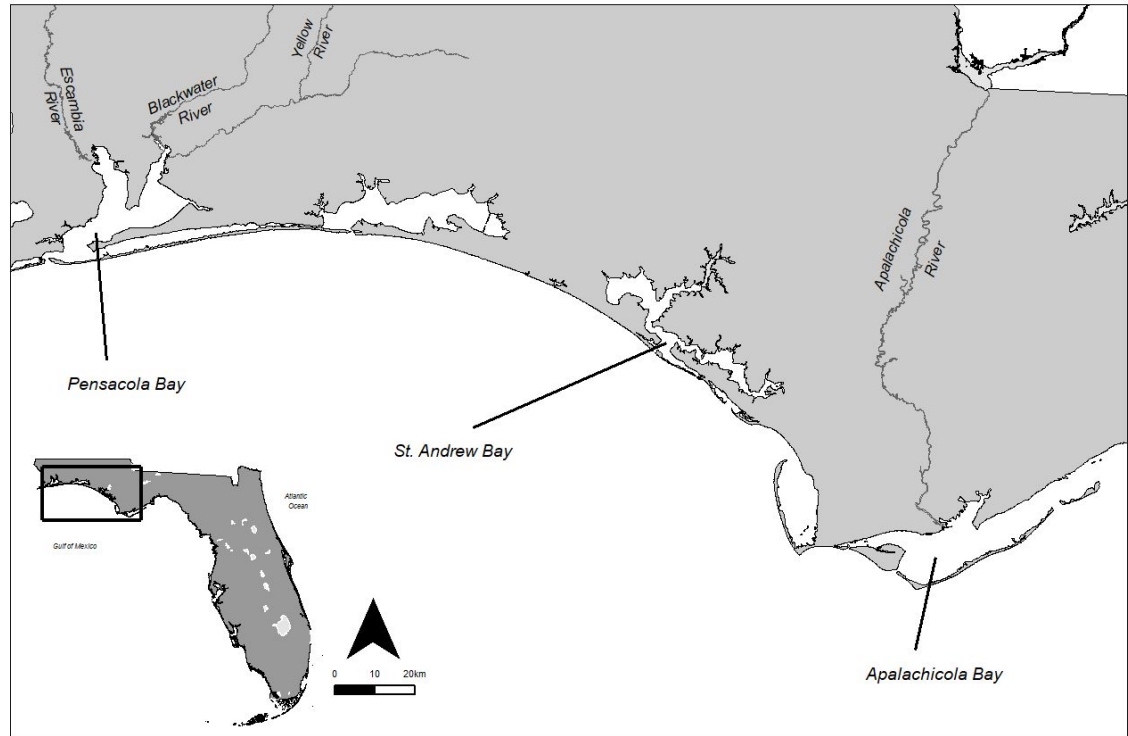


Figure 1. Location of Pensacola, St. Andrew, and Apalachicola bays in the Florida panhandle.

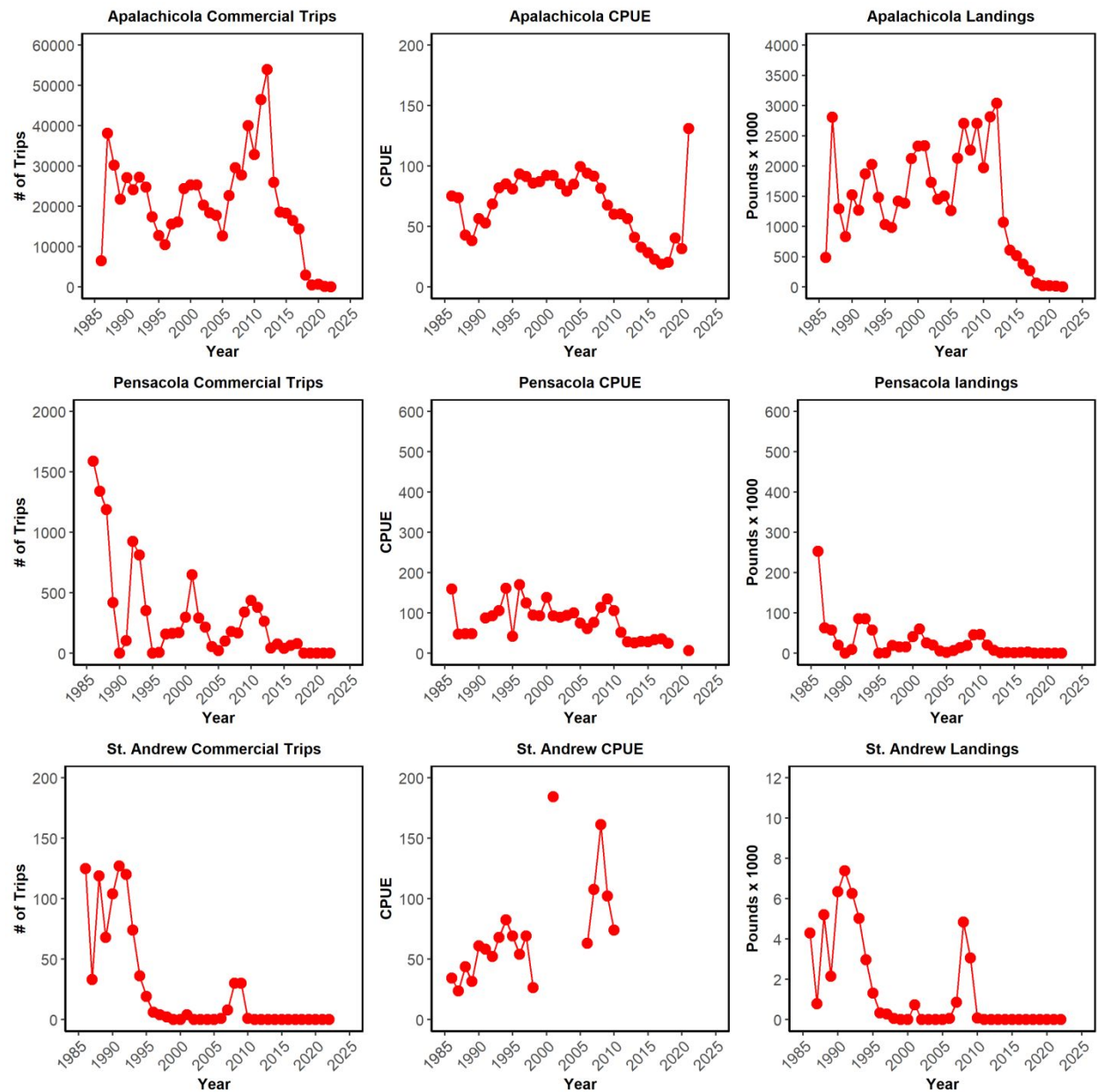


Figure 2. Publicly available fisheries-dependent data from the Florida Fish and Wildlife Conservation Commission (<https://myfwc.com/research/saltwater/fishstats/commercial-fisheries/landings-in-florida/>), 1986–2022. Landings data are provisional for 2022 per agency standards. Each row represents a different bay, and each column represents a different data category. The y-axes differ by row (bay) because of the large differences in landings and trips between bays.

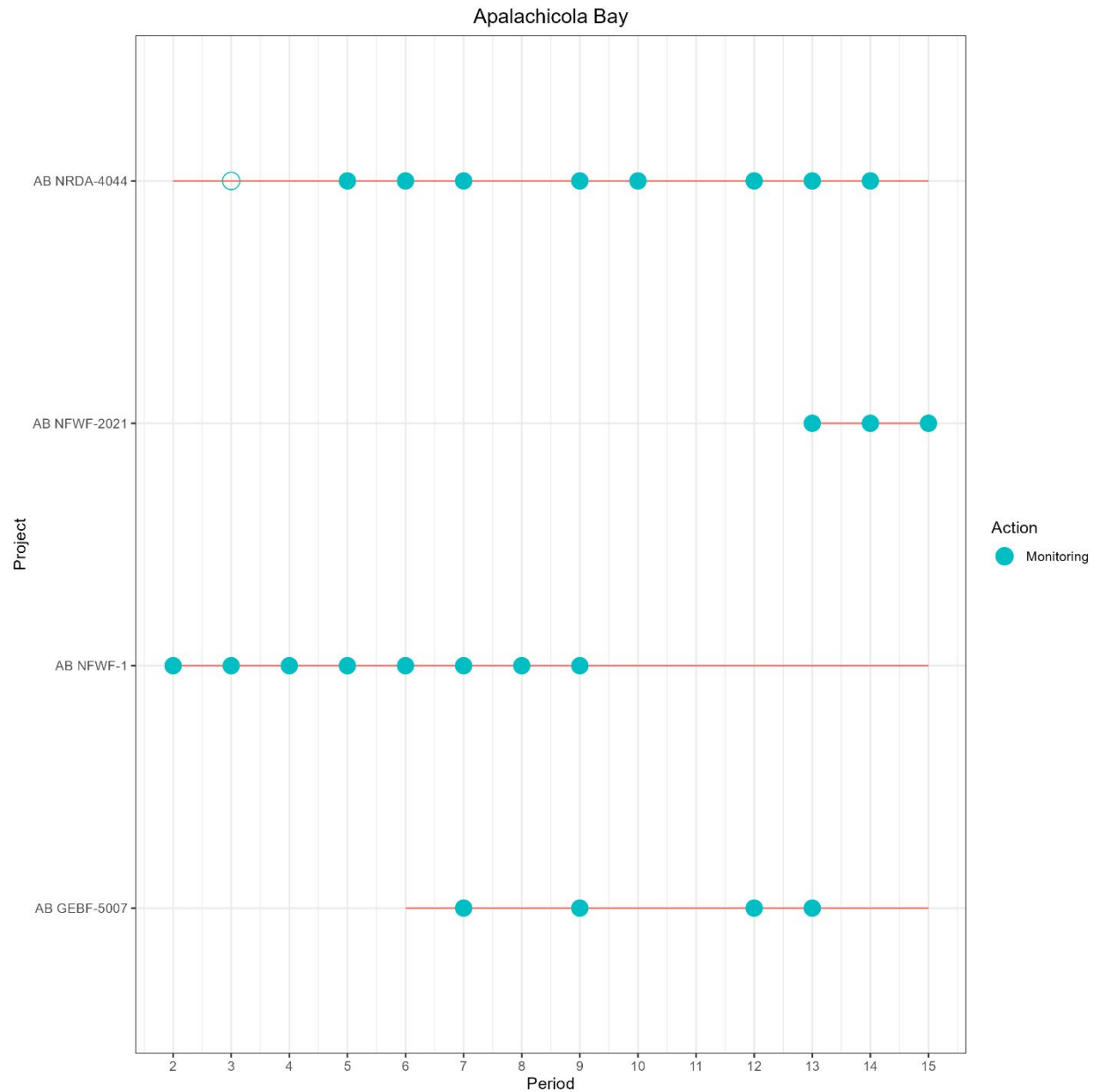


Figure 3. A schematic demonstrating the placement and persistence of cultch material by project (y-axis, red line) over time (x-axis) and the sampling events (grey circles) that collected oyster count data from each project. Project AB (Apalachicola Bay) NRDA-4044 only collected samples from one site 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.

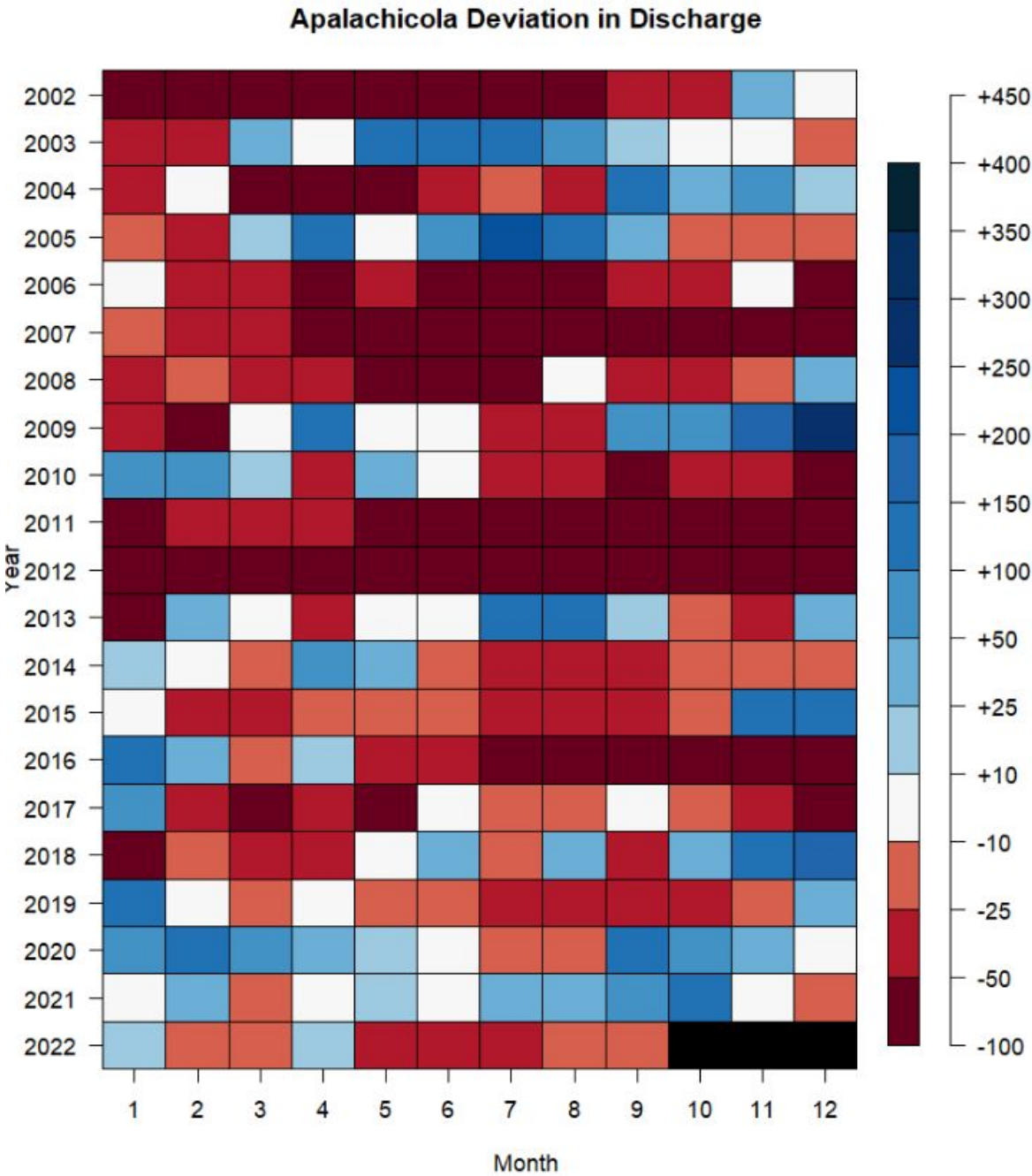


Figure 4. Deviations in river discharge from the period of instrument records for the Apalachicola River. Darker colors equate to larger deviations, with colors in the blue spectrum representing higher river discharge and colors in the red spectrum representing lower river discharge. White or near-white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



Figure 5. Spat, seed, and legal-size oyster count per quadrat (CPUE;  $\frac{1}{4}$  m<sup>2</sup> quadrat) 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.

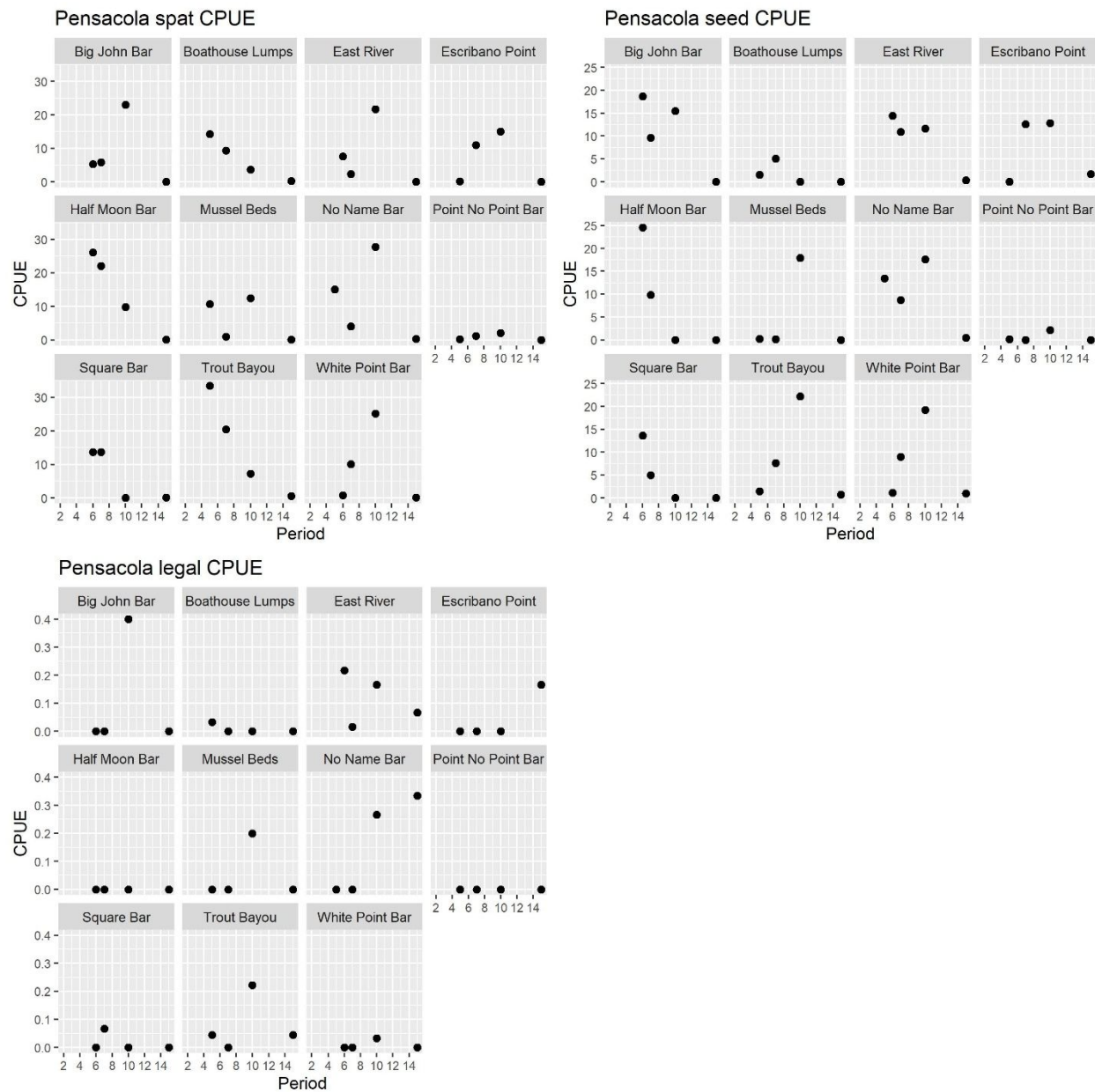


Figure 6. Spat, seed, and legal size oyster count per quadrat (CPUE,  $\frac{1}{4}$  m<sup>2</sup> quadrat) by period for Pensacola Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. Note each plot for each oyster size class has a different y-axis.



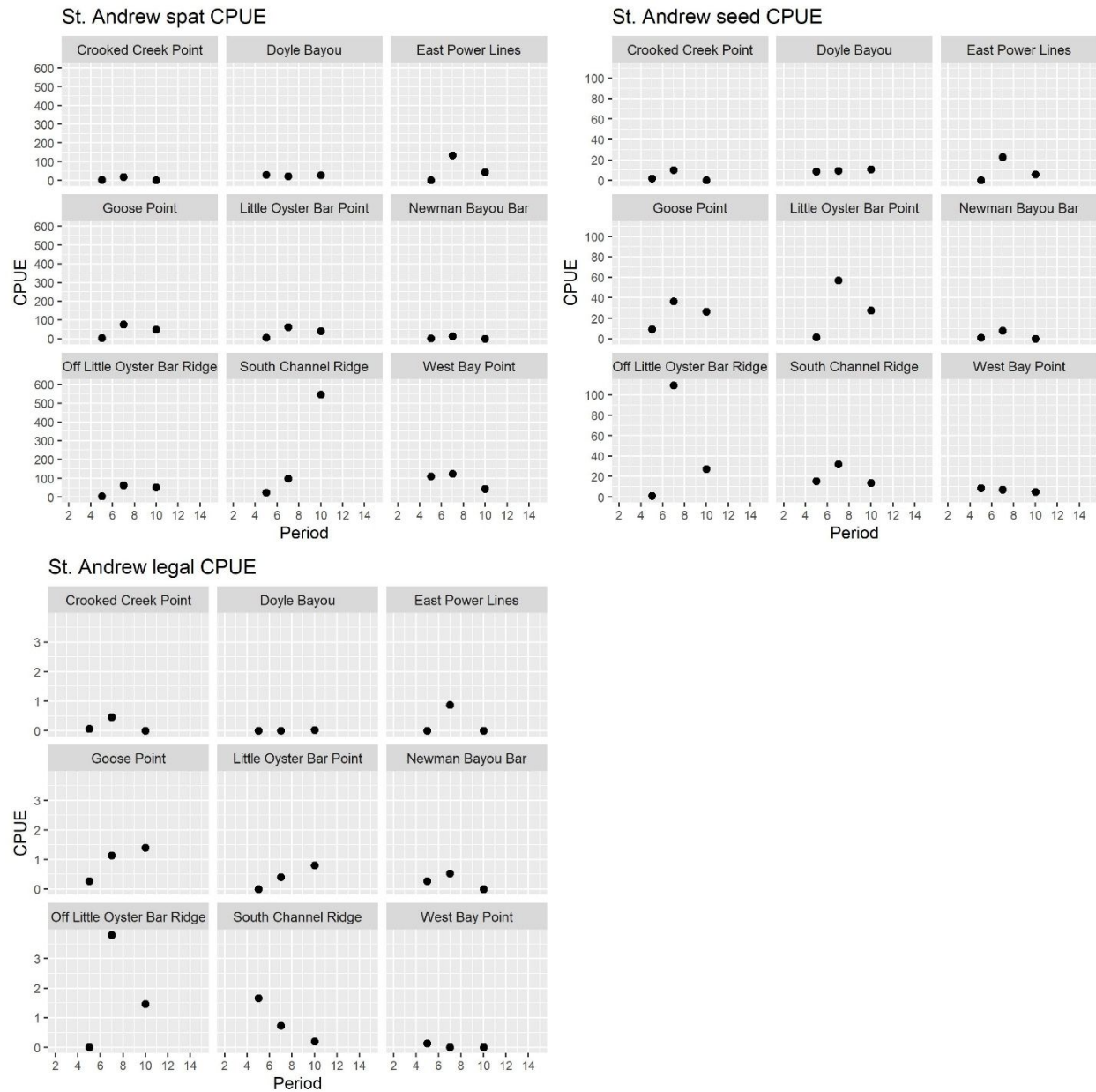


Figure 7. Spat, seed, and legal size oyster count per quadrat (CPUE,  $\frac{1}{4}$  m<sup>2</sup> quadrat) by period for St. Andrew Bay, Florida. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in 2016. Note each plot for each oyster size class has a different y-axis.

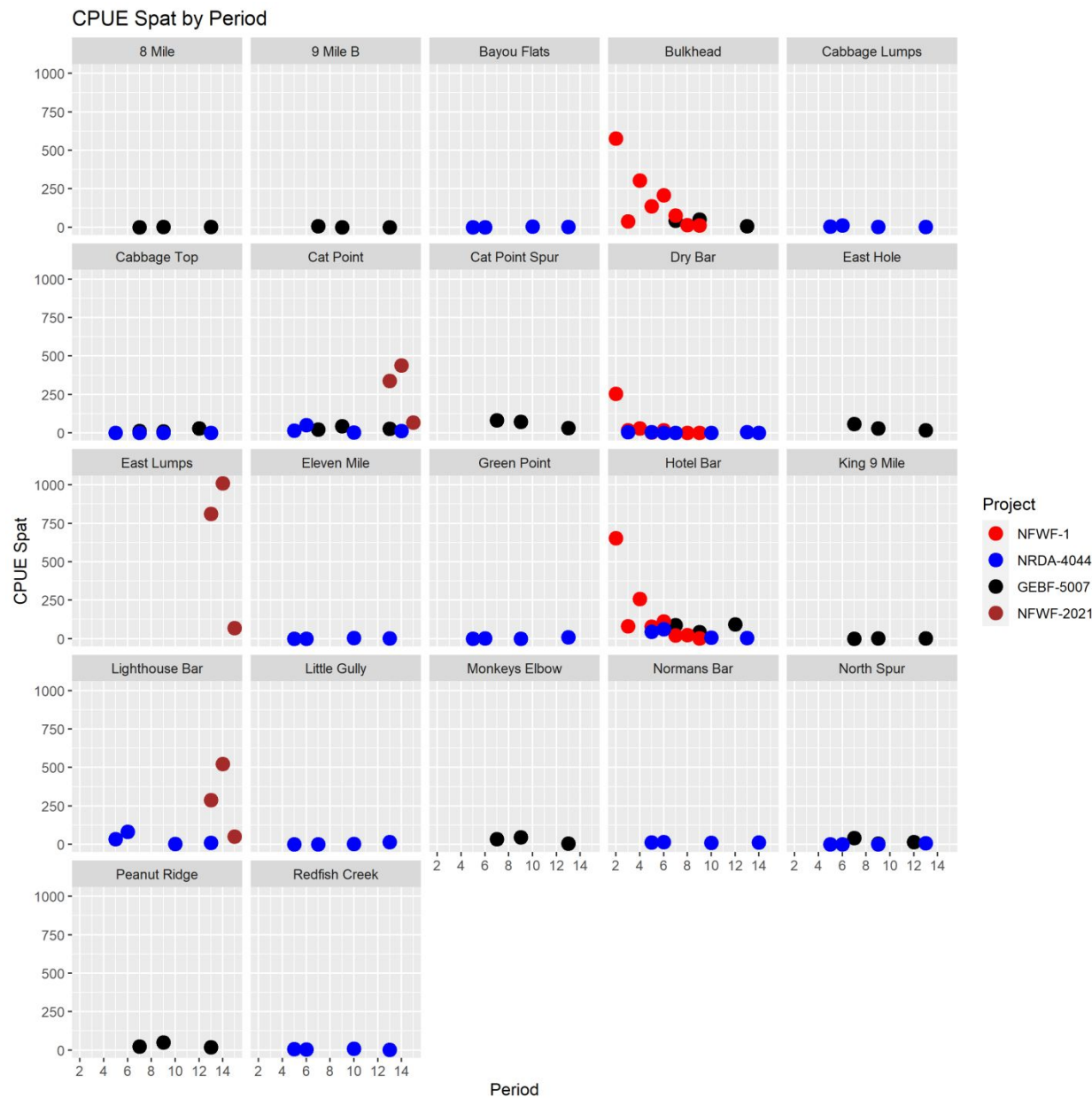


Figure 8. Oyster spat count per quadrat (CPUE,  $\frac{1}{4}$  m<sup>2</sup> quadrat) by site within Apalachicola Bay (each panel) and period (x-axis). Dots represent counts over time for each project defined by color (Table 1). Even-number periods are winters (October-March) beginning in 2015; odd-number 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).



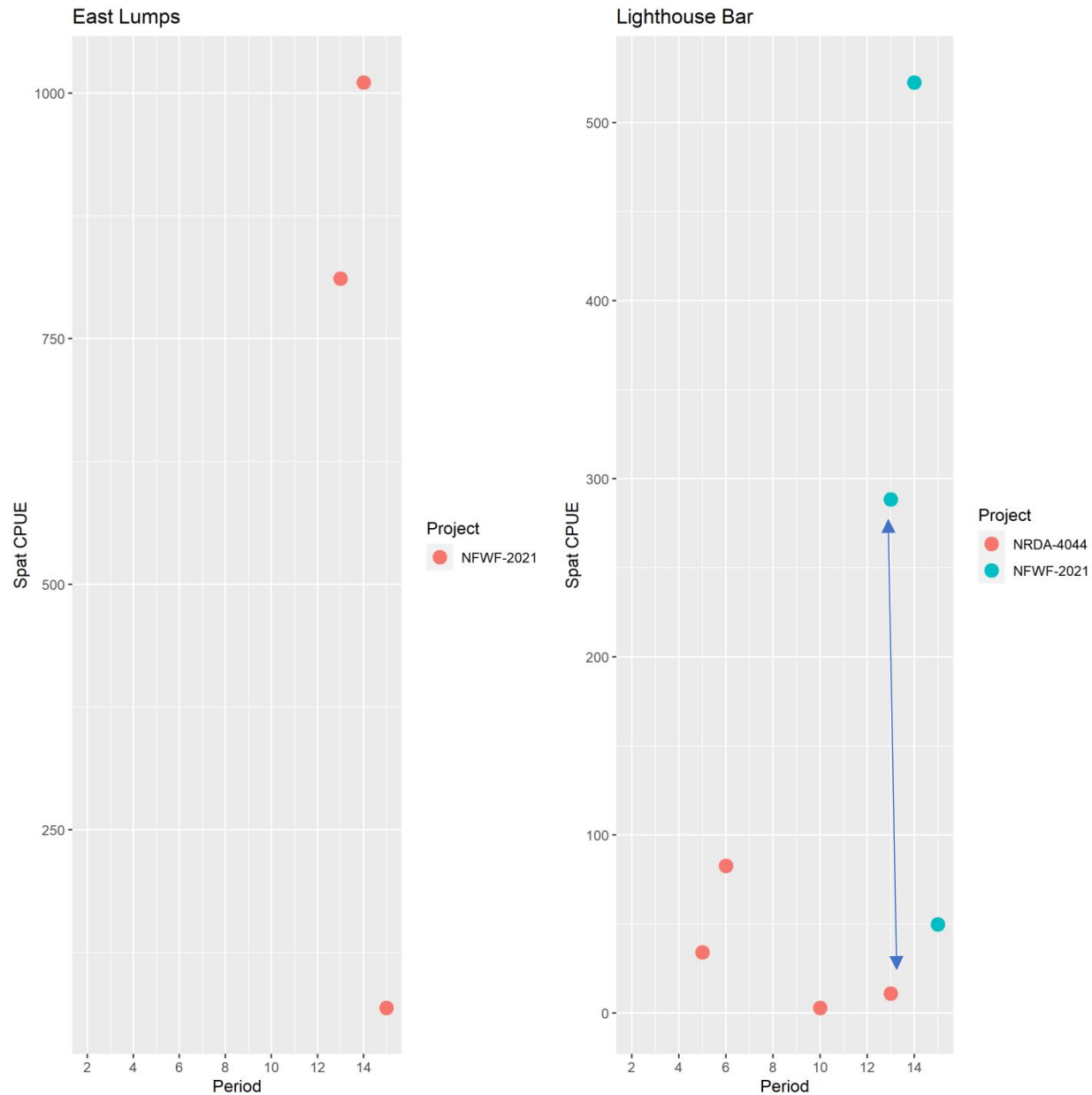


Figure 9. Oyster spat count per quadrat (CPUE;  $\frac{1}{4}$  m<sup>2</sup> quadrat) for two sites within Apalachicola Bay (East Lumps left panel, Lighthouse Bar right panel) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number periods 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 began 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.

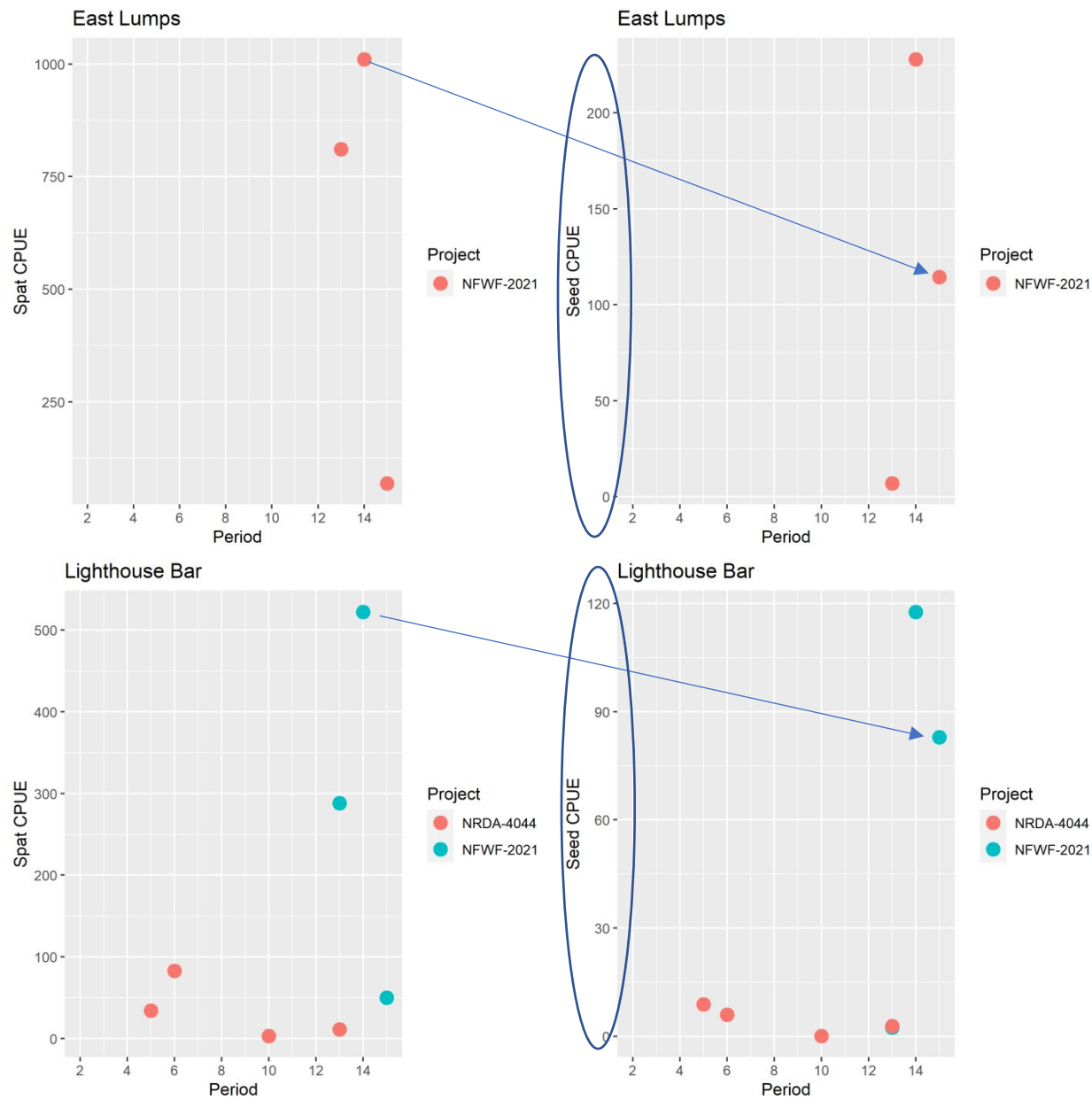


Figure 10. Oyster spat count per quadrat (CPUE; left panels) and seed count per quadrat (right panels) for two sites within Apalachicola Bay (East Lumps top row, Lighthouse Bar bottom row) and Period (x-axis). Dots represent counts over time for two different projects defined by color (Table 1). Even-number 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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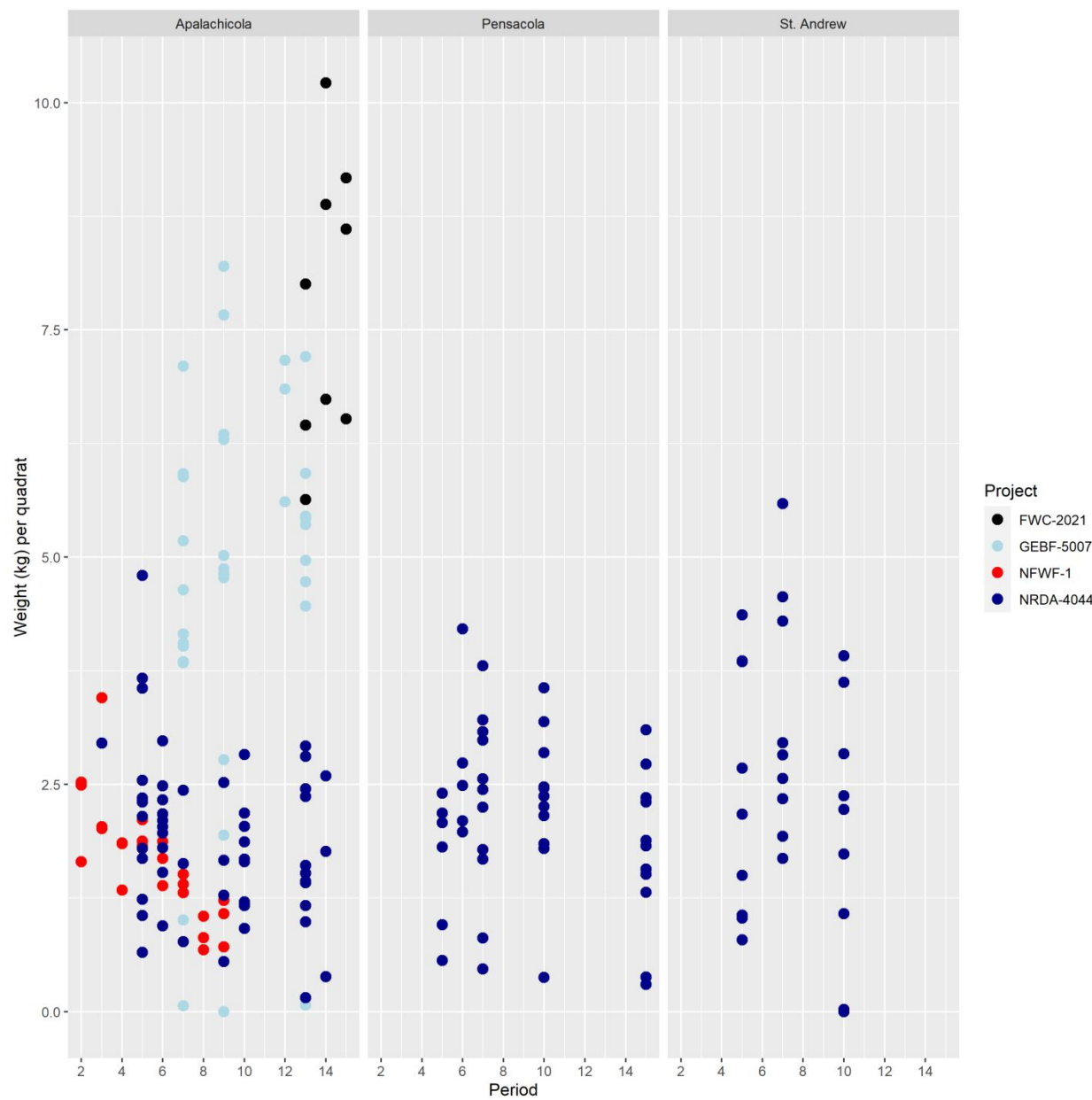


Figure 12. Oyster cultch biomass per quadrat (y-axis, kg) over time (x-axis, period) for Apalachicola, Pensacola, and St. Andrew bays (each panel). Projects (Table 1) are defined by color. Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September)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

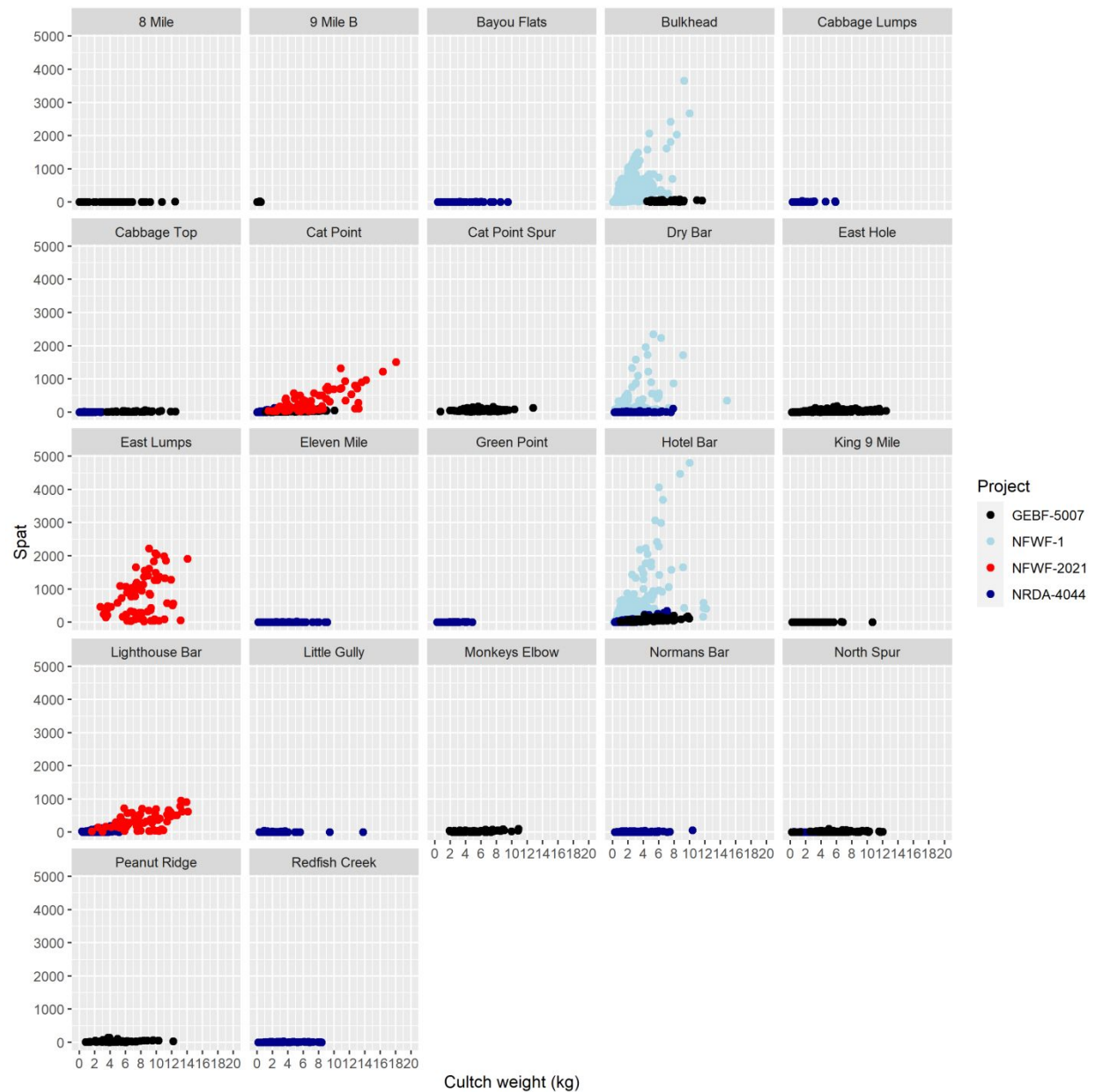


Figure 13. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay sites (each individual panels) and project (colored dots).

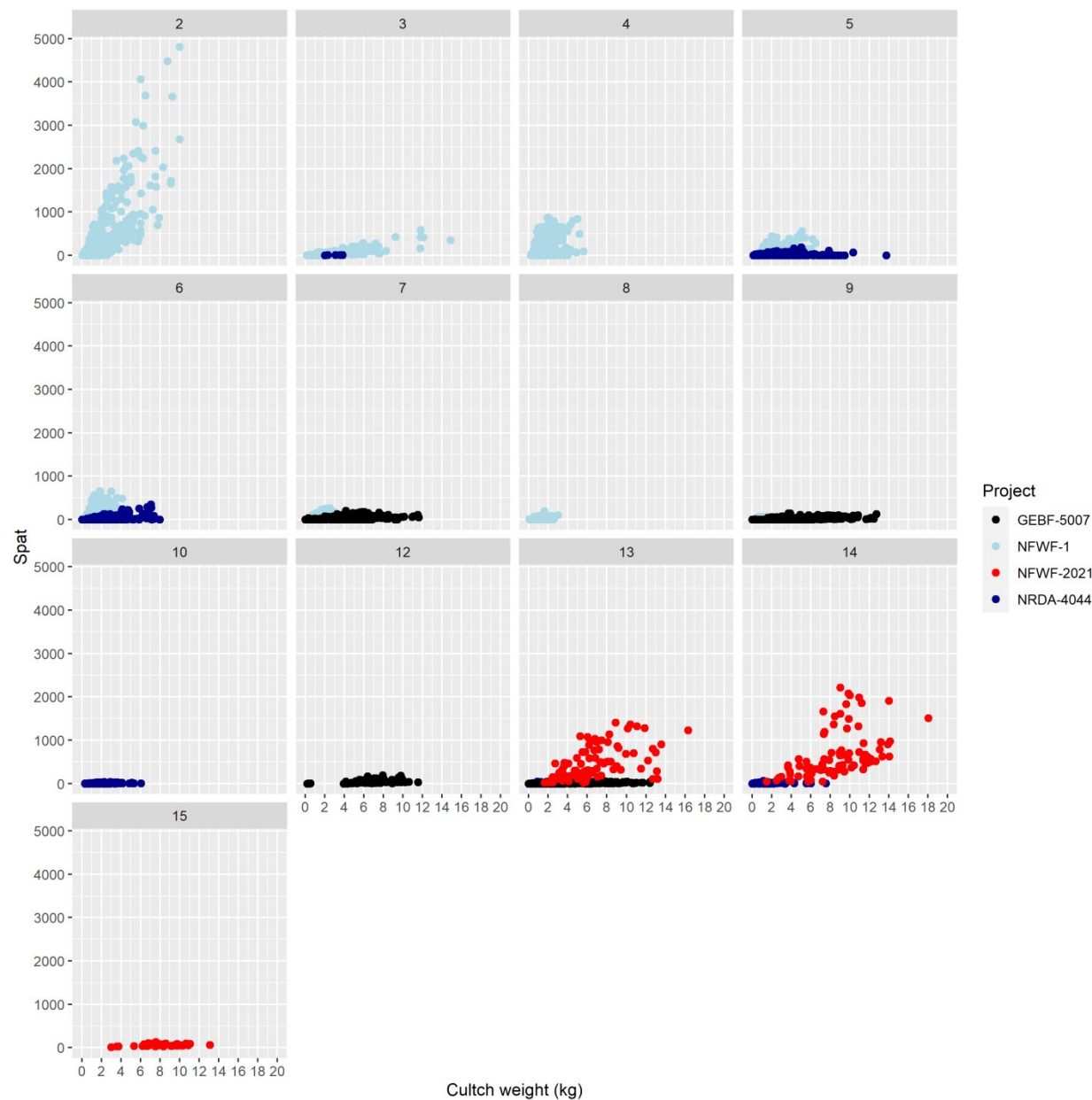


Figure 14. Live oyster spat CPUE (y-axis) and cultch biomass per quadrat (x-axis, kg) for all Apalachicola Bay periods (each individual panels) and project (colored dots). Even-number periods are winters (October-March) beginning in 2015; odd-number periods are summers (April-September) beginning in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

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  $\frac{1}{4}$ -m<sup>2</sup> declined (beta of the slope =  $-0.004$ , SE =  $0.07$ , 95% CI =  $-0.15$  to  $0.14$ ) and  
 11 this trend was not significantly different from zero ( $p = 0.96$ ). Pensacola and St. Andrew bays  
 12 show uncertain trends in oyster spat counts. Pensacola coefficient values for the slope of oyster  
 13 spat counts over time were larger than Apalachicola (beta =  $-0.39$ , SE =  $0.11$ , 95% CI =  $-0.61$  to  
 14  $0.17$ ) and this slope coefficient did differ from zero ( $p=0.0006$ ). For St. Andrew Bay, the slope  
 15 coefficient was highly uncertain (beta =  $0.21$ , SE =  $0.18$ , 95% CI =  $-0.14$  to  $0.57$ ) and this slope  
 16 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 again used the unique site by  
 22 project name as a random effect to allow 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  $\frac{1}{4}$ -m<sup>2</sup> over time did not differ from zero for projects GEBF-5007 (slope coefficient  $\beta = -0.06$ , SE = 0.10, 95% CI = -0.26 to 0.13,  $p = 0.51$ ), NRDA-4044 (slope coefficient  $\beta = 0.04$ , SE = 0.07, 95% CI = -0.09 to 0.18,  $p = 0.51$ ) or NFWF-2021 (slope coefficient  $\beta = -1.04$ , SE = 0.60, 95% CI = -2.24 to 0.15,  $p = 0.09$ ). For project NFWF-1, the trend in live oyster spat per  $\frac{1}{4}$ -m<sup>2</sup> 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 to -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: Cultch mass relationships to live oyster counts (Apalachicola)*

No additional information is needed as this was a graphical assessment.

*Question 5: How does cultch material persist?*

We plotted the weight per  $\frac{1}{4}$ -m<sup>2</sup> (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  $\frac{1}{4}$ -m<sup>2</sup> 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 6).

Apalachicola Bay cultch biomass per  $\frac{1}{4}$ -m<sup>2</sup> had a positive slope (beta of the slope = 0.04, SE = 0.02, 95% CI = 0.008 to 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 to 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 to 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  $\frac{1}{4}$ -m<sup>2</sup> quadrat in Period 15 for comparison purposes between each bay. Predicted live oyster spat for Apalachicola was 3.76 kg cultch per  $\frac{1}{4}$ -m<sup>2</sup> (95% CI 2.54 to 5.56), Pensacola was 1.71 kg cultch per  $\frac{1}{4}$ -m<sup>2</sup> (95% CI 0.99 to 2.94), and St. Andrew Bay predicted cultch per  $\frac{1}{4}$ -m<sup>2</sup> was 1.34 kg (95% CI 0.46 to 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 ( $\Delta AIC < 3$ ) were the  $\text{Roundwt} \sim \text{Period} + \text{Bay} + (\text{Period} | \text{Site}) + \text{Period}:\text{Bay} + \text{offset}(\log(\text{Num\_quads}))$  followed by the  $\text{Round\_wt} \sim \text{Period} + \text{Project} + (\text{Period} | \text{Site}) + \text{Period}:\text{Project} + \text{offset}(\log(\text{Num\_quads}))$  and  $\text{Round\_wt} \sim (1 | \text{SP}) + \text{Period} + \text{Project} + (0 + \text{Period} | \text{SP}) + \text{Period}:\text{Project} + \text{offset}(\log(\text{Num\_quads}))$  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  $\frac{1}{4} \text{ m}^2$  had a positive slope over time (beta of the slope = 0.09, SE = 0.11, 95% CI = -0.14 to 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 to 0.09) and this slope did differ from zero ( $p=0.02$ ). For the NFWF-1 project, the slope was negative (beta = -0.14, SE = 0.02, 95% CI = -0.19 to -0.09) and this slope did differ from zero ( $p<0.0001$ ). Finally, for the NRDA-4044 project the slope was negative (beta = -0.05, SE = 0.01, 95% CI = -0.07 to -0.02) and this slope did differ from zero ( $p=0.0002$ ).