Florida Oyster Recovery Science Guidance Series:

002 - Oyster Habitat Monitoring

2025

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Cover image: Mangroves growing on an intertidal oyster (*Crassostrea virginica*) reef in southern Estero Bay, Lee County, Florida. Credit: Florida Department of Environmental Protection.

Oyster habitat monitoring is a dynamic field with active development of new methods and evaluation of existing ones. This document will receive periodic updates to keep pace with the state of the science and recommended practices. Reader feedback on ways to improve this document's utility to the oyster recovery science community is welcomed. Suggestions or questions regarding this document may be sent to Stephen.Durham@FloridaDEP.gov or Stephen.Geiger@myFWC.com and questions about the Florida Oyster Recovery Science Working Group may be directed to Katie.Konchar@TNC.org.

Summary of the Florida Oyster Recovery Science Working Group

The Florida Oyster Recovery Science (FORS) Working Group was established in 2019 and includes members from an array of federal and state agencies, universities, industry, and non-profit organizations who share a vision for the future of Florida's oyster populations and habitats. The vision of FORS includes oyster habitat that is thriving and providing ecosystem services and oyster fisheries that are sustainable. The vision also includes effective management of oysters through science-based plans that are adaptable to changing conditions and coordinated through partnerships among community stakeholders including natural resource agencies, academic institutions, non-governmental organizations, and businesses.

To attain that vision, the FORS Working Group pursues the following goals: 1) develop and foster a community of practice of natural resource professionals committed to recovering and managing Florida's oyster habitats and fisheries; 2) develop science-based guidance to inform oyster recovery and management of Florida's oyster habitat and fisheries by fostering comparability among metrics, methods and models; 3) support the assessment of status and trends in Florida's oyster habitat and fisheries; 4) identify and overcome barriers and challenges for oyster recovery and management; and 5) share information with the broader community of natural resource managers, researchers, and restoration practitioners working towards Florida's oyster recovery. This document is a step towards goal 2: developing science-based guidance documents.

This document was created to improve comparability and provide technical guidance to researchers, natural resource managers, and contractors involved in designing oyster monitoring programs. The guidance in this document includes consideration of monitoring goals, minimum recommended monitoring metrics, attributes to consider for sampling design, data quality guidelines, and references to existing accepted methods.

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This document was created by the FORS Working Group monitoring subcommittee, which is composed of members from State resource management entities, universities, and non-profit organizations. The subcommittee (authors) and external reviewers are as follows:

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Contents

Executive Summary

Monitoring is a critical component of any oyster habitat management or restoration program. The data gathered through monitoring activities underpin nearly every action that resource managers take and enable the outcomes of those actions to be understood. It is therefore important to design monitoring activities carefully and with the program's objectives in mind.

In this document, we step through design considerations for ground-based monitoring programs for both intertidal and subtidal oyster resources. We frame the decisions in the context of three general categories of program objectives: those that prioritize capturing geographic variability, those that prioritize documenting temporal variability, or programs that focus equally on both temporal and spatial variability. We also mention some of the important tradeoffs to consider with monitoring designs tailored to each category. Our discussion then covers selection of monitoring metrics, as well as when, where, and how frequently to monitor. We also describe the importance of data management and data quality assurance and control procedures to running an effective monitoring program. We suggest that all oyster monitoring programs in Florida should, at minimum, measure: 1) live oyster density, 2) oyster habitat area, 3) live oyster size frequency distribution, and, for intertidal reefs, 4) percent live cover.

Throughout this document, we sought to highlight and bring together the numerous, well-regarded resources already present in the literature rather than create a new protocol. In particular, we focus on the most prominent oyster monitoring documents currently in use in Florida, including the “Oyster Habitat Restoration Monitoring and Assessment Handbook” (Baggett et al. 2014), the “Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute Oyster Monitoring Procedures” (FWRI 2021), the “Oyster Condition Assessment Protocol” (Walters et al. 2016), and the “Guana Tolomato Matanzas National Estuarine Research Reserve Oyster Monitoring Protocol” (Marcum et al. 2023). These documents cover the methods used by some of the key agencies and organizations monitoring Florida's oyster resources, including the Florida Fish and Wildlife Conservation Commission, the Florida Department of Environmental Protection, and The Nature Conservancy, and highlighting them has the added benefit of encouraging inter-comparability of new oyster monitoring data with existing datasets from established monitoring programs.

Finally, the appendix reports on a simulation comparing common quadrat placement methods used in Florida that illustrates the complexity of seemingly straightforward method choices. Although there are statistical reasons to choose one method or another, this exercise suggested that the practical impact of this choice can be dependent on other factors. In particular, the variation in live oyster density across the (hypothetical) reef surface tended to overwhelm most of the methodological differences in performance for all but the largest sample sizes.

We hope that readers find this document to be an accessible, informative, and credible entry to a sprawling topic. As the profile of oyster restoration and management continues to rise nationally and locally, it is increasingly important that oyster habitat monitoring programs use well-designed methods that are suited to their program objective(s) and that, ideally, will produce comparable results to other monitoring efforts. In this way, the significant investments of time and financial resources in individual projects can yield the largest possible collective knowledge benefit for those working to preserve and enhance Florida's oyster resources.

Introduction to Monitoring

Monitoring is integral to science-based management of natural resources. As the ongoing, general decline of oyster fisheries and reef habitat over the last century has become widely recognized (Kirby 2004, Beck et al. 2011), resource management and restoration organizations have increasingly prioritized oyster habitat monitoring to test hypotheses and gain critical knowledge for making decisions. Fisheries-independent monitoring of oysters has a long history in many locations, and a variety of techniques (e.g., quadrat-based sampling, tonging, and drone-based aerial surveys) and study designs have been used (e.g., Paynter et al. 2013; Baggett et al. 2014; Walters et al. 2016; Marcum et al. 2018, 2023; Schulte et al. 2018; FWRI 2021; Willberg et al. 2022; Windle et al. 2022; Espriella et al. 2023). **This document seeks to synthesize key information from a selection of these monitoring protocols, as well as individual research papers and reports, rather than duplicate them. The publications cited here contain thorough explanations of specific monitoring techniques, and practitioners are encouraged to refer to these publications for further detail.** We also note here that this document is intentionally focused on more traditional ground-based monitoring approaches because they are relatively low-cost and have been widely used on both natural and restored, and intertidal and subtidal, oyster reefs in Florida for many years. For information about aerial mapping and monitoring (e.g., drone-based operations, Windle et al. 2022; Espriella et al. 2023) or monitoring and assessment of the ecosystem services provided by oyster habitats (e.g., services described in Grabowski et al. 2012), we refer readers to two other available and forthcoming documents in the Florida Oyster Recovery Science Guidance Series: Anderson et al. (2023) and Camp et al. (*in prep*), respectively.

Monitoring goals

The spatial and temporal scope of oyster monitoring projects will depend on the specific objectives and research questions of the monitoring effort, as well as the resources available, given it is impossible to simultaneously maximize a project's spatial scale, sample density, duration, temporal resolution, and cost-effectiveness. Conceptually, here we split this optimization problem into three general categories of objectives that commonly arise from the resulting tradeoffs in oyster monitoring:

- **Objective 1.** Detect spatial and temporal changes in oyster populations at a regional or estuary level through long-term monitoring (i.e., prioritize generality over specificity for any particular time period or location).

- **Objective 2.** Detect smaller-scale spatial and temporal changes due to local acute impacts (e.g., a coastal development project), restoration (e.g., artificial oyster reef construction), or fishery closures/openings (i.e., prioritize temporal and spatial specificity—high resolution—over generality).

- **Objective 3.** A blend of objectives 1 and 2 that would detect both longer-term changes across a broader region or estuary and shorter temporal changes at specific locations (i.e., balance the need for spatial and temporal specificity with generality—usually at some cost to both).

One of the most common needs for oyster habitat monitoring is the production of baseline data to enable assessment of spatial and temporal changes (Objective 1). This type of monitoring is essential to the missions of government agencies and other organizations that require location-specific, accurate, and long-term data for use in land and resource management planning, making permitting decisions, and other tasks for steering environmental policy. The optimal monitoring program would accurately characterize oyster habitat condition within a given area with acceptable precision, and a cost-effective and efficient investment of staff time and resources that, ideally, could be maintained indefinitely. This monitoring requires a balance between comprehensiveness and statistical power on one hand, and logistical feasibility and sustainability on the other.

Restoration and coastal zone construction (e.g., docks, navigation channels, and living shorelines) may occur at small spatial scales and thus may require finer-scale monitoring to have reasonable probabilities of detecting effects on local oyster populations (Objective 2). Documentation of the causes of local acute or short-term impacts, or of a project's performance trajectory in the case of living shorelines, frequently requires longitudinal (repeated) monitoring of a relatively high density of sampling units and at high (e.g., sub-annual) frequencies that can be impractical for larger-scale monitoring goals, such as understanding the condition of oyster habitat across an estuary.

A combined approach (Objective 3) is likely to be the most useful for many oyster monitoring programs. Meeting Objective 3 involves splitting sampling effort between stratified random selection of sampling units across a larger geographic area and longitudinal sampling of a handful of sampling units. For a given number of sampling units, this strategy allows for a broader geographic perspective than if all sampling units were monitored at every time step, while also not completely losing longitudinal sampling's increased sensitivity to detect temporal change. Mitigating the costs to both spatial and temporal scope with this strategy, however, may require including additional sampling units to achieve comparable statistical power to detect changes (i.e., a greater investment of time and effort in sampling) than strategies that prioritize one or the other exclusively.

After the objective(s) and research question(s) have been decided, designing a baseline monitoring program should begin with a clear identification of the geographic area and time period of interest to guide a search for existing data from other past or present monitoring efforts. Existing data can be very useful for planning monitoring to either extend an existing series of data (i.e., choosing locations, indicators, and methods that would allow datasets to be integrated) or to avoid duplication of efforts and conserve resources (e.g., if another program is already monitoring oyster habitat in a portion of the geographic area of interest). Recent monitoring data, protocol documents, and contacts for many monitoring projects in Florida can be found at the Florida Department of Environmental Protection's Statewide Ecosystem Assessment of Coastal and Aquatic Resources Data Discovery Interface repository[4], and regional summaries of the state's monitoring programs can be found in the Oyster Integrated Mapping and Monitoring Program Report (Radabaugh et al. 2019). Once an understanding of the monitoring objectives and relevant existing information is achieved, program design can proceed to deciding which metrics should be monitored, how to conduct the sampling for them,

[4] https://data.florida-seacar.org/

and what quality assurance and data management procedures must be implemented to ensure the program data are accurate, usable, and accessible. Although not covered in detail in this document, we also emphasize here that measurable performance criteria—and plans for ongoing adaptive management or maintenance in case they are not met—are often critically important for a program's long-term success and may be required for some jurisdictions or applications, e.g., for built-infrastructure projects, such as living shoreline installations, or certain restoration projects.

Monitoring Metrics

Several publications describe a variety of metrics for monitoring intertidal and subtidal oyster populations. These publications include the following:

- The "Oyster Habitat Restoration Monitoring and Assessment Handbook" (Baggett et al. 2014) was developed by representatives from NOAA Restoration Center, The Nature Conservancy, the University of South Alabama, and Florida Atlantic University. The handbook provides a detailed guide on recommended monitoring metrics and techniques applicable to restored, intertidal or subtidal reefs.
- The "Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute Oyster Monitoring Procedures" (FWRI 2021) was compiled from internal standard operating procedures at FWRI. It describes the metrics used by FWRI oyster monitoring and provides instructions on how they are measured on natural subtidal and intertidal reefs across a number of estuaries in Florida.
- The Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) baseline oyster resource assessment (Marcum et al. 2018) outlines the metrics and methods used in a pilot monitoring project. The methods were developed for assessing baseline reef, population, and community structure on intertidal oyster reefs within sub-estuaries of the ~76,000-acre reserve. In 2022, annual long-term monitoring was initiated[5], the protocols (Marcum et al. 2023) and data for which can be found at https://data.florida-seacar.org/programs/details/4000.
- The "Oyster Condition Assessment Protocol" (Walters et al. 2016) was developed by representatives from University of Central Florida, St. Johns River Water Management District, GTMNERR, and Northeast Florida Aquatic Preserves. This protocol describes a suite of metrics used to assess the condition of intertidal oyster reefs in northeast Florida and provides instructions on how to measure them.
- The "Oyster Model Inventory: Identifying Critical Data and Modeling Approaches to Support Restoration of Oyster Reefs in Coastal U.S. Gulf of Mexico Waters" (La Peyre et

[5] Also in 2022, the Florida Department of Environmental Protection Office of Resilience and Coastal Protection completed and adopted oyster monitoring standard operating procedures for its oyster monitoring programs based in part on the protocols developed by GTMNERR staff. That document is available upon request; inquiries may be directed to FloridaCoasts@FloridaDEP.gov.

al. 2021), describes approaches and required metrics for modeling habitat suitability indices, larval transport, reef population, and metapopulations.

- Readers interested in remote monitoring and habitat mapping or monitoring for ecosystem services should refer to other volumes in this *Florida Oyster Recovery Science Guidance Series* (e.g., Anderson et al., 2023 on oyster habitat mapping or Camp et al., *in prep*, about oyster ecosystem services).

The first four resources listed above include a broad variety of metrics and are summarized within Table 1. Baggett et al. (2014) identified universal metrics which should be monitored for every oyster habitat restoration project. These metrics include reef areal dimensions, reef height, oyster density, and oyster size-frequency distribution, which are also a strong foundation for monitoring both intertidal and subtidal natural oyster populations and so appear in some form in all four documents.

Table 1. A comparison of parameters described in monitoring guides. Walters et al. (2016) and Marcum et al. (2023) follow similar methods and thus are included within the same column.

Metric	**FWRI monitoring protocol (FWRI 2021)**	**Northeast Florida Oyster Condition Assessment Protocol (Walters et al. 2016)* and GTMNERR Oyster Monitoring Protocol (Marcum et al. 2023)†**	**Oyster Habitat Restoration Monitoring and Assessment Handbook (Baggett et al. 2014)**
Reef type	Natural, intertidal or subtidal.	Natural, intertidal.	Restored, intertidal or subtidal.
Reef selection	Depends on monitoring objectives; past examples include repeat sampling of 3 reefs at each of 5 sites.	Depends on monitoring objectives; past examples include stratified random sampling.	Before/After Control/Impact (BACI) design: monitor control site (unrestored) and impact site (location of oyster restoration) before and after reef construction.
Quadrat arrangement	15 0.5 x 0.5-m quadrats haphazardly placed on the reef.	5 1 x 1-m quadrats with nested 0.25 x 0.25-m quadrats randomly placed along transect that extends across the densest areas of live oysters on the reef* (6 quadrats used for GTMNERR†).	Quadrats randomly placed by superimposing a numbered grid on an aerial photo/diagram of the reef, then randomly selecting locations.

Density of live oysters	Live and dead oysters (with articulated shells) excavated and counted within 0.5 x 0.5-m quadrats.	Live oysters excavated to 15 cm depth and counted within 0.25 x 0.25-m quadrats (or until the anoxic layer is reached†).	Live oysters excavated and counted within quadrats. Quadrat size depends on oyster density; number of quadrats depends on variance of the metric in question.
Shell height	Measured for 50 live oysters per 0.5 x 0.5-m quadrat.	Measured for 50 live oysters per 0.25 x 0.25-m quadrat*. Measured for all live oysters per 0.25 x 0.25-m quadrat†.	Measured for at least 50 oysters from each quadrat (total of at least 250 oysters measured per reef).
Monitoring frequency	Minimum of twice annually (spring and fall). Years of monitoring depends on funding.	Twice annually (winter and summer)*. Annually in winter (Dec - Mar)†.	Monitor immediately if using seed oysters. Otherwise, monitor annually at the end of the oyster growing season. Monitoring should extend 1-2 years at minimum; preferably 4-6 years.
Water quality	Depth, temperature, salinity, pH, dissolved oxygen, and Secchi depth are monitored.	Not monitored*. Temperature, salinity, dissolved oxygen, depth, pH, turbidity, chlorophyll, nitrogen, phosphorus, bacteria, and more (as listed at http://cdmo.baruch.sc.edu/data/available-data/) are monitored every 15-min and monthly at nearby permanent stations†.	Salinity, dissolved oxygen, and temperature are monitored. Additional monitoring of chlorophyll *a* and seston (total particulates and organic content) can show water quality improvement following reef establishment.
Disease	*Perkinsus marinus* (Dermo) prevalence and intensity determined in 5 oysters per reef.	Not monitored.	*Perkinsus marinus* (Dermo) prevalence and intensity monitoring recommended in 25 oysters per reef. Same oysters can be used for *Haplosporidium nelsoni* (MSX) monitoring.
Reproductive state	Histological examination used to classify the reproductive stage of 5 oysters per reef.	Not monitored.	Histological examination used to classify the reproductive stage of 25 oysters per reef.

Spat settlement	Spat settlement monitored monthly on strings of oyster shells.	Not monitored*. Spat settlement monitored monthly on strings of oyster shells from 2015 - 2020†.	Spat settlement monitored on tiles or shell trays of known area and depth. Monitoring design can include study of temporal and spatial variability in settlement.
Growth and mortality	3 replicates of 30 wild oysters placed in open (and/or closed) cages with shell height and mortality monitored monthly. New oysters are added each month and the surviving oysters are discarded to the reef at the end of the month.	Not monitored*. Not regularly monitored†.	Not monitored.
Percent cover	Not monitored.	Percent cover of live oysters, shell, benthos, and other invertebrates determined by point-intercept method in 1 x 1-m quadrats. “Box” (recently dead) oyster and mangrove categories added in 2022†.	Includes metrics for percent cover in quadrats of marsh or mangrove plants, sponges, or encrusting organisms, but not oysters.
Reef height	Not monitored.	Measured as the vertical distance between the highest point on the reef and the nearest edge of the reef with a string, level, and stadia rod or laser level.	Measured every 1 m along reef crest using RTK GPS or graduated rod and transit for intertidal reefs. For subtidal reefs, side-scan sonar (or sounding pole) used along reef crest to calculate mean reef height compared to surrounding sediment.
Reef area dimensions	Not monitored.	Not monitored.	Project footprint is maximum areal extent of the reef complex; reef area is the summed area of living and non-living oyster shell within the project footprint.
Slope	Not monitored.	Reef slope = reef height ÷ distance. Distance = the lateral distance between the highest point and the corresponding height on the stadia rod used for the reef height measurement.	Change in shoreline slope or elevation of surrounding area can be monitored using RTK GPS and/or laser level and graduated rod; reef slope not mentioned.

Reef thickness	Not monitored.	Thickness (vertical distance from top of oysters to benthos) measured in 5 random locations and in highest location in each 0.25-m x 0.25-m quadrat*. Not monitored†.	Not monitored.
Cluster density	Not monitored.	Number of clusters (groups of > 5 live oysters) recorded in each 1 x 1-m quadrat.	Not monitored.
Burial	Not monitored.	Depth above and below sediment line recorded for all live oysters and oyster clusters in each 0.25 x 0.25-m quadrat*. Not monitored†.	Not monitored.
Associated fauna	Number of live predators (e.g., oyster drills) recorded in 0.5 x 0.5-m quadrats.	Species and lengths of other live mollusks in 1 x 1-m quadrats and sessile invertebrates in 0.25 x 0.25-m quadrats recorded.	Protocols described for monitoring of infaunal invertebrates, finfish, crustaceans, and waterbirds.
Invasive species	Not monitored.	Invasive species collected and preserved for DNA extraction*. Presence of invasive species noted†.	Monitoring of associated fauna can also be used to document invasive species.
Shell budget	All shell and substrate is collected from 0.5 x 0.5-m quadrats. Weight and volume of live oysters, oyster drills, other organisms, oyster shell, planted shell, shell hash, and other substrate are measured individually.	Not monitored.	All substrate is collected from quadrats. Shell volumes of live oysters, boxes, and cultch are measured individually.
Condition index	Analyzed on 5 oysters per reef.	Not monitored.	Analyzed in 25 oysters per sample.
Shell pests	Analyzed on 5 oysters per reef.	Not monitored.	Can be incorporated in other faunal monitoring.

* Northeast Florida Oyster Condition Assessment Protocol only
† GTMNERR Oyster Monitoring Protocol only

Here we suggest that all Florida oyster monitoring programs should minimally measure the following four metrics (three if the reefs are subtidal), regardless of the program goals:

1. live oyster density,
2. oyster habitat area,

3. live oyster size-frequency distribution, and
4. percent live cover (for intertidal oyster reefs only).

Encouraging consistency between monitoring programs in these minimum metrics will be helpful because the particular metrics that are chosen, and how they are measured, frequently vary across monitoring programs. For instance, metrics such as reef slope, reproductive condition, disease intensity, and shell pests (Figure 1) are not included in many protocols because they can be labor-intensive to measure and tend to provide more specialized information that may not be called for, depending on a particular monitoring program's objective(s). Cases arise, however, when known issues with a particular oyster population require additional information to clarify their impacts in order to inform management decisions. For instance, a resource manager facing a decline in live oysters may need answers to questions that cannot always be addressed using live oyster density and size-frequency data alone. Additional monitoring data would need to be collected in order to answer questions such as: Are the oysters maturing and spawning? What are the levels of spat settlement? Is disease high enough to preclude gonad maturation or cause mortality?

Point-intercept percent cover is another example of a metric that can serve specialized

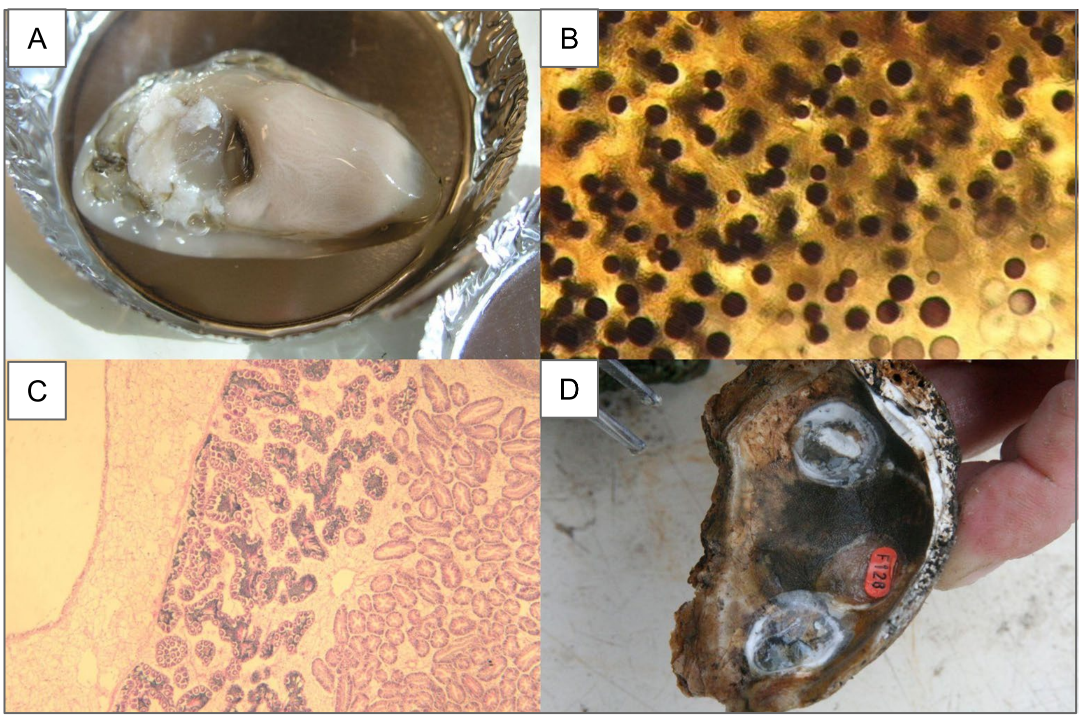

Figure 1. Examples of some other metrics include A) condition index (soft tissue separated from shell), B) disease (microscope image showing heavy infection of *Perkinsus marinus*), C) reproductive studies (microscope image showing oyster male gonads) and D) growth (shell tagged for tracking growth of juvenile oysters). Credit: FWRI.

purposes (Table 1). It tends to be correlated with live oyster density, but the method does not require removal of shells from the reef and can be assessed quickly. The point-intercept method has been used, for example, to compare created reefs (from which shell may not be easily removable) with natural reefs (Walters et al. 2016, Marcum et al. 2018, Safak et al. 2020). It should be noted, however, that this method is generally only feasible on intertidal reefs, where each grid intersection within the quadrat can be easily examined. The percent cover approach may also be useful for rapid reconnaissance in a broad geographic area for estuaries for which there is little or no existing oyster habitat data (Figure 2).

Metric choice is often influenced by resource managers' finite time and resources, which inevitably require a tradeoff between the quantity of data that can be collected and their detail or quality. This choice must be made carefully, however, because it can have significant impacts on later analytical power and/or the dataset's comparability with other monitoring datasets (and consequently, the inferences that can be made from it). In addition to the percent live cover method just discussed, protocols for other oyster monitoring metrics can be modified in various ways to increase their efficiency. For instance, oyster size measurements can be binned and reported as densities by size class. This method can be significantly faster than recording individual measurements for each oyster, but the resulting data are only directly comparable to similarly binned data (i.e., requiring higher-resolution data to be coarsened to make comparisons possible and preventing meaningful comparisons with other binned datasets that used different bin thresholds). For instance, 25-75 and ≥75 mm bins and 10-mm increment bins are two common binning schemes but results are difficult to compare because 25 and 75 are not multiples of 10. The efficiency is inversely related to the resolution of the resulting size distribution, which depends on the number and distribution of bins used. Another common way of making density and size monitoring more manageable is subsampling to generate

Figure 2. A point-intercept quadrat for measuring percent cover on an intertidal oyster reef. Credit: GTMNERR.

representative data from a given sample, but care must be taken to conduct the subsampling in an unbiased manner (e.g., see Figure 22 in Baggett et al. 2014). Finally, new proxies for estimating monitoring metrics like oyster size and density from drone imagery are emerging because of drones' abilities to rapidly gather high-resolution data over a broad geographic area with little or no impact to the reefs (e.g., Windle et al. 2019, 2020; Anderson et al. 2023; Espriella et al. 2023), although currently, the up-front costs for the necessary equipment, software, training, and data storage can be substantial (Anderson et al., 2023).

Some other program objectives or design needs, such as broader questions about ecological structure and function, habitat value or suitability, or ecosystem services, may be best addressed by collecting additional metrics. For instance, many oyster monitoring programs include water quality data collection in their oyster monitoring fieldwork to provide valuable environmental context (e.g., see the "Universal Environmental Variables" recommended by Baggett et al. 2014). Some natural resource managers may also collect counts and/or measurements of associated oyster reef fauna if they have reasons to be concerned about factors such as predation intensity or invasive species (e.g., Marcum et al. 2018, 2023).

These examples illustrate how the program context influences the incorporation of additional metrics into a monitoring program and the methods used to measure the chosen suite of metrics. The next sections go into more detail about many of the relevant factors to consider when making these decisions.

Sampling Design

This section describes the most important considerations for developing a sampling design for oyster monitoring, including selecting the locations, the sample sizes and the timing and frequency of sampling activities. In addition to these technical aspects of sampling design, the structural and population impact of removing oysters during monitoring should also be taken into account. For instance, removal of reef substrate and breaking apart clusters of oysters is usually necessary to achieve an accurate count of the number of live oysters in a sample and for accurate shell height measurements. Generally, the potential injury to a reef from sampling activities is far outweighed by the value of the resulting monitoring information for resource management, but the cost-to-benefit ratio may be higher for programs that repeatedly sample the same reef(s), those where oysters must be removed from the field for processing, and programs that monitor reefs with low oyster densities. To mitigate unnecessary harm to the monitored populations, especially due to substrate loss and oyster mortality, sampled oysters should be rapidly returned to the location of origin on the reef whenever possible. If oysters cannot be removed in the first place—such as while monitoring oysters growing on substrate that is not easily removed (e.g., a created reef with limestone substrate) or a reef whose condition is judged to be too fragile for normal sampling—oysters may be counted and measured *in situ*, but the data should not be considered directly comparable to those collected via removal sampling.

Selection of sampling locations

Most oyster monitoring programs will require defining at least six attributes of sampling location:

1. sampling universe (the spatial extent of the area of interest; e.g., an entire bay or portion of an estuary, or a specific project such as restoration or impact assessment);
2. strata (e.g., inshore vs. offshore, intertidal vs. subtidal, high/moderate/low salinity);
3. sampling unit selection method (e.g., random, stratified random);
4. sampling unit (e.g., oyster reef, transect on a portion of a reef);
5. method for selecting the specific areas of the sampling unit (e.g., randomized quadrats/sample locations, haphazard quadrats/sample locations, belt transects, random or evenly spaced quadrats/sample locations along a transect);
6. temporal consideration of sampling locations (e.g., fixed locations vs. random selection of new locations each year).

Selection of the six attributes above are interrelated. For example, the decision of (4) the sampling unit will also affect (5) the method of sampling, which could be quadrats (Marcum et al. 2023, FWRI 2021; Figure 3), a belt transect (Moore et al. 2020, Moore and Pine 2021), or a tong or dredge with predictable efficiency and bottom area coverage (e.g., Paynter et al. 2013; Schulte et al. 2018; Willberg et al. 2022). Likewise, the sampling unit selection may also be influenced by (1) the sampling universe determination. These decisions may also determine whether statistical weighting of monitoring results or allocation of samples based on sampling unit area or other criteria is required to develop valid inferences about the sampling universe (e.g., Krebs 2014). For example, if the sampling universe is an estuary and the sampling units are individual intertidal reefs, then any of the protocols in Table 1 could apply. If, however, there is also a large range of reef sizes in the estuary (e.g., small reefs are often far more common than large reefs; Figure 4), then the number of samples per reef may need to be varied by reef size to avoid a sampling imbalance (i.e., any given square meter is more likely to be sampled on a small reef than on a large reef). Depending on the range of reef sizes, either a protocol with a larger sample size (i.e., FWRI 2021) to allow the number of samples to vary, or a method that allocates sampling units across the sampling universe without regard to reef boundaries (e.g., Moore et al. 2020, Moore and Pine 2021) may be preferable.

The choice of sampling unit is also driven, in part, by implicit assumptions about the degree of morphological or genetic distinctness of the oyster population between reefs. Although “reef type” often refers simply to the general growing habit category of the reef itself (e.g., patch, string, fringing, etc.), the diversity of reef habitat can be conceptualized in a variety of other dimensions, such as oyster genetic diversity (e.g., driven by local larval dispersal and settlement patterns), oyster morphology (e.g., size), sediment characteristics, reef-associated biodiversity (e.g., macroinvertebrates, grasses, mangroves or other flora), and water depth, to name a few. If variation in one of these or another parameter of interest is similar both within and between reefs, that is another indication that allocating samples strictly by area (e.g., a random transect method) is likely the more straightforward approach. If, however, there is an element of reef type diversity that a program considers meaningful, and that varies more between than within reefs, then two alternatives are to: 1) adjust the strata definitions to include the habitat variable; or 2)

Figure 3. Monitoring percent cover using a quadrat placed along a transect. Credit: GTMNERR.

ensure it is reflected in the choice of sampling unit (note that a third possibility is that the variable is already effectively incorporated into a program's existing stratification scheme because many reef habitat characteristics are likely to be correlated with common stratification variables, such as salinity).

If monitoring is designed to cover a large area, such as the entirety of an estuary, stratified random sampling should be used to ensure representation of the spectrum of reef types and conditions (e.g., salinity gradients) within the estuary. Strata should be representative of the area being monitored and may be determined based upon factors such as water quality or by region of the estuary. The sampling unit should then be randomly selected within each stratum.

The number of sampling units (reefs, transects, etc.) selected for monitoring will depend on the characteristics of the area of interest (e.g., the variance within sampling units vs. variance between sampling units) and the program resources available. If the sampling universe, for instance, contains only a small number of similar intertidal reefs, then fewer sampling units may be needed and any of the protocols in Table 1 could potentially meet the monitoring need, but if there are many reefs spread out over a large area, or they are very different in their characteristics (e.g., shape, size, subtidal/intertidal, local water quality, etc.), then a larger number of sampling units, most likely grouped into strata, may be required to adequately document oyster population conditions across the sampling universe. In this case, the best protocol to use as guidance would depend on how the number of reefs and variability are divided among strata: if the reefs within each strata tend to be similar, then an approach like that of FWRI (2021)—which tends to emphasize selecting a subset of representative reefs for longitudinal monitoring—may work well. Whereas cases with a large number of reefs, or where the reefs within strata vary in size or type, may be better assessed using methods based on

Figure 4. Small oyster reefs are often more numerous than larger reefs, and the range of sizes could have implications for the selection of sampling methods for an oyster monitoring program. Credit: GTMNERR.

random selection of sampling units (e.g., Walters et al., 2016 or Marcum et al., 2018). See Section 3.4 below for further discussion of sample size.

Often researchers assume that variability within reefs is less than variability among reefs. Understanding the within vs. among variance patterns may help make decisions for (4) the sampling unit (oyster reef or transect on a portion of a reef). *A priori* identification of transects across reefs potentially allows for more representative sampling of oyster populations encompassing multiple reefs because all of the oyster habitat area in the sampling universe has an equal chance of being sampled, as well as testing heterogeneity within reefs by allowing multiple transects for larger reefs. This approach has been demonstrated to perform better for mixed long-term and restoration monitoring in recent studies (Moore et al. 2020, Moore and Pine 2021). The location and orientation of the transect, however, can have large influences on the results, such that knowledge of local environmental gradients or patterns on the reef (e.g., elevation/topography) is often needed to appropriately place the transect (see Appendix for a simulated example).

Decisions for (6) temporal considerations of sampling location may include randomly selecting new sampling units each year (repeated cross-sectional sampling), repeatedly monitoring the same sampling units (longitudinal sampling), or a combination of the two. How repeated monitoring over time is handled will depend on the characteristics of the area of interest, the monitoring objective(s), and the program resources available. As mentioned previously, repeated monitoring of the same reefs through time is likely a more powerful approach for detecting change and parsing within-reef versus between-reef components of variation (e.g., well-suited to Before/After Control/Impact, or BACI, monitoring approaches like those described in Baggett et al., 2014), but places a high level of importance on the representativeness of the initial site selection (Butler et al. 2022). Alternatively, randomly selecting new reefs every year may make it more difficult to detect temporal change but will provide a more complete picture of the quality of oyster habitat within the sampling universe. Combining the two approaches (i.e., repeatedly monitoring a subset of reefs as well as randomly selecting a subset each year) offers some benefits of both strategies but is likely to be more costly in staff time and resources than either individual strategy alone (see Butler et al. 2022 for an example from social science research).

Program resources (funds and staff time) are an important consideration as well, because monitoring is both time- and labor-intensive. In particular, programs being designed for a large and/or complex sampling universe may find that representative sampling of the entire area during every sampling season is not logistically feasible. One way to approach this problem is to adopt a rotational approach, wherein certain areas of the sampling universe or subsets of sampling units are the focus in rotating years (e.g., the GTMNERR long-term oyster monitoring program[6] is a current example). This unbalanced approach may restrict the types of statistical comparisons that can be made among rotation areas and may require more seasons to build a time series capable of detecting temporal trends in the rotation areas but is an example of the types of tradeoffs that program managers need to consider.

Site selection for monitoring created reefs or restoration sites generally follows a BACI design (Baggett et al. 2014). Under this framework, monitoring is conducted at one or more control sites (where restoration is absent) and one or more impact sites (the location(s) of oyster restoration) both before and after reef construction. This powerful monitoring design makes it possible to distinguish restoration effects from unrelated changes (e.g., due to environmental variables that affect both the control and impact reefs). For further guidance on site selection on restored reefs, see Coen et al. (2004), Brumbaugh et al. (2006), Brumbaugh and Coen (2009), and Baggett et al. (2014).

Sampling frequency and timing

The timing of sampling for both intertidal and subtidal oyster habitat monitoring should be consistent from year to year because many oyster monitoring metrics exhibit natural variations with seasonal periodicities in both settings. For programs that plan to sample once per year, sampling in January or February is recommended in order to avoid spawning season and to target the end of the growing season (Baggett et al. 2014). If seasonal sampling is feasible, monitoring should be completed during peak spawning and low spawning seasons (often spring-fall and winter, respectively, in many parts of Florida; e.g., FWRI 2021). Targeting peak spawning season enables monitoring of spat settlement, an important indicator to consider when diagnosing low oyster densities, for instance, which may be caused by either recruitment failure (i.e., low spat availability) or juvenile and/or adult mortality. Alternatively, for monitoring programs whose main purpose is to determine the impact of harvest, the beginning and ending dates of each harvest season are likely more important factors for deciding when to sample.

[6] https://data.florida-seacar.org/programs/details/4000

Quadrat placement

Quadrats are commonly used in oyster reef monitoring to select a subset of oysters for counting and measurement. Quadrat area is generally 0.0625 m^2, 0.25 m^2, or 1 m^2. Placement of quadrats is critical to ensure accurate representation of the reef itself, as many oyster reef surfaces exhibit substantial variations in characteristics such as elevation and live-oyster density. Common approaches for quadrat placement on oyster reefs include randomized selection of quadrat locations using a grid (Baggett et al. 2014), blindly tossing the quadrat in a haphazard approach (FWRI 2021), randomly placing quadrats along a transect (Walters et al. 2016, Marcum et al. 2023; Figure 5), using a belt transect (Moore et al. 2020), or regularly spacing a series of quadrats along a transect (Moore et al. 2020). See the Appendix for a simulation comparing the performance of these quadrat placement methods for live oyster density monitoring.

Transect approaches are less commonly used to monitor oyster populations than random or haphazard quadrat placement but transects have long been a preferred sampling approach for monitoring terrestrial plant communities, especially across gradients (Bauer 1943, Ludwig and Cornelius 1987, Buckland et al. 2007, Schweiger et al. 2016). Sampling design considerations for oyster populations are analogous to those for plant communities, in that both are composed

Figure 5. Transect quadrat sampling on an oyster reef in Mosquito Lagoon. Credit: Linda Walters.

of sessile organisms whose characteristics often vary systematically along environmental gradients. Thus, lessons from the scientific literature on sampling design and data analysis approaches for monitoring plants are often also applicable to oysters. For instance, for reefs on which a gradient is evident (e.g., elevation gradients are common), transects should ideally be oriented parallel to the gradient (i.e., from reef edge across the crest in the case of an elevation gradient, which is often perpendicular to the long axis of the reef), and unless mitigating considerations demand otherwise, any quadrats used should be distributed evenly across the transect to have the greatest chance of representatively sampling the gradient[7] (see Appendix). If transects are used, it can be more efficient to identify their placement prior to going out in the field (e.g., using imagery; Moore et al. 2020). A similar approach can be taken with random quadrat placement as well (e.g., Baggett et al. 2014), but the efficiency gains over haphazard placement on reefs are less clear.

Most of the quadrat placement methods described above are impractical for monitoring subtidal reefs due to the difficulty of following a transect or grid pattern while diving in often limited-visibility conditions, so many subtidal oyster monitoring programs utilize oyster tongs (e.g., hand tongs or mechanical or hydraulic patent tongs) or dredges to sample a known area of bottom instead of employing diver quadrat sampling. In either case, sample locations are usually chosen using methods analogous to one or more of the random or haphazard techniques described in, e.g., Baggett et al. (2014), Moore et al. (2020), or Marcum et al. (2023). When quadrats are used, care must be taken to avoid placing all quadrats in a high-density region of a heterogenous reef, so divers should avoid swimming over the reef to visually search for a sampling location (for instance, divers with the Florida Department of Environmental Protection swim out 10 m from either the starboard or port side of their boat before diving to the bottom and placing the quadrat wherever they happen to descend[2]).

Sample size

Optimizing a design framework often relies on prior collection of data that can be used to evaluate homogeneity of sampling units and ideal sample size. The power analytic framework has been the predominant method for planning sample-size and there is extensive literature documenting this approach (Kraemer and Thiemann 1987, Cohen 1988, Lipsey 1990, Murphy and Myors 1998, Bausell and Li 2002, Legendre et al. 2002, Baggett et al. 2014, Krebs 2014, Schweiger et al. 2016). In this context, statistical power can be conceptualized as the probability of correctly rejecting the null hypothesis, or the probability that the 100(1-α) percent confidence interval correctly excludes the value of the null hypothesis, where α is the probability of committing a Type I error. If null hypothesis significance testing is determined to be the primary goal of the monitoring program, then performing a power analysis is strongly recommended. For example, if there is a treatment effect in the population (e.g., restored vs. natural oyster reefs), then it would be imperative for researchers to determine whether any group differences exist and the direction of the effect.

In the power analytic approach, the appropriate sample size is calculated by specifying all of the following variables: (a) the population effect size to detect, (b) the population model error

[7] Note that this guidance differs from Walters et al. (2016) and Marcum et al. (2023), which place transects extending across the densest portion of a reef rather than orienting them to representatively sample the full range of variation.

variance, and (c) the desired probability of a Type I error (α). Baggett et al. (2014) provide instructions for using this approach, illustrated with an example applying this sample size calculation to monitoring oyster densities on a reef. In addition, Cohen (1988) provides tables for the necessary sample sizes to achieve a specified power for comparisons of two groups. Ideally, researchers should also perform a sensitivity analysis by evaluating a range of effect sizes to conceptualize the nonlinear relationship between effect size and sample size for their particular use case.

Although null hypothesis testing alone may be appropriate in some situations, there are many circumstances where an estimate with confidence bounds of the parameter of interest is desired, which requires a different approach to sample size estimation. The goal of the Accuracy in Parameter Estimation (AIPE) approach is to obtain accurate parameter estimates corresponding to the population value by achieving a sufficiently narrow confidence interval. The AIPE approach to sample-size planning is a more recent development than the power analytic approach and does not have as large a body of literature for reference (but see Algina and Olejnik 2000, Bonett and Wright 2000, Darlington 1990, Han and Meeker 1991 chapter 8, Kelley et al. 2003, Kelley 2007a, Kelley 2007b, Kelley and Maxwell 2008, Maxwell et al. 2008, Kelley 2008, Kelley and Rausch 2011, Lai and Kelley 2011, Kelley et al. 2018, Kelley et al. 2019). It is important to note that when the width of the confidence interval decreases, the expected accuracy of the parameter estimate increases. Thus, while the goal of the power analytic approach is to plan sample size so that the confidence interval does not contain the null value, the general goal of AIPE is to plan sample size so that the confidence interval is sufficiently narrow. Narrow confidence intervals provide the same information as null hypothesis significance tests, but additionally provide information about the precision of the estimated parameter. Sample size in the AIPE framework is determined by specifying the desired width of the confidence interval (i.e., the expected precision of the estimate). The required values for sample-size planning under the AIPE approach are the following: (a) the desired confidence interval width or half-width, (b) the confidence level (e.g., 95%), and (c) the population model error variance. One benefit of the AIPE approach to sample-size planning is that the only unknown value required to plan sample size is the population model error variance, whereas the population effect size is also required for the power analytic approach. A sensitivity analysis can be implemented for the AIPE approach by performing a Monte Carlo simulation study in a population where the parameter estimate is set to be the true value, but the sample size used is based on the incorrect value. Methods for the Behavioral, Educational, and Social Sciences (Kelley 2007c) is an R package (R Development Core Team 2021) that implements the AIPE approach to planning sample size. Both R statistical software (R Development Core Team 2021) and the MBESS package (Kelley 2007c) are open source and freely available.

Depending on the objective(s) of the monitoring program, sample size planning may be approached from either the power analytic or the AIPE approach, or through a careful combination of both. An acceptable framework combining both approaches is to plan sample sizes to attain the desired statistical power and to obtain precise estimates for the parameters of interest. The appropriate sample size is likely to differ between the two approaches, in which case it is advisable to use the larger of the two sample size estimates. If the estimated sample sizes given by the two approaches are dramatically different, the program manager must decide which value is the more appropriate sample size given the specific goals of the program and other considerations discussed above, such as logistical and financial feasibility.

Data Quality Assurance and Control

Environmental monitoring programs aimed at informing management decisions should include some level of data quality assurance and control (QA/QC) procedures, as well as sound data management practices. QA strategies include development of written standard operating procedures and field logistics plans, as well as personnel training and certification procedures (Figure 6). QC strategies include calibrating field crew members and evaluating variability among observers on a regular basis to assess the accuracy and precision of field and lab measurements. Data management practices that should be considered include documenting and implementing plans for maintenance of data records and metadata (e.g., procedures for backup and long-term storage of data and documentation), as well as making program data and important related information (e.g., metadata, field and lab protocols, data analysis scripts, etc.) timely, reliable, and accessible to users.

There are numerous resources available for information on best practices for QA/QC and data management. For instance, EPA (2019) provides comprehensive guidance on QA/QC for ecological monitoring and FDEP's Office of Resilience and Coastal Protection recently developed a quality plan for oyster monitoring[8]. The FAIR (Findability, Accessibility,

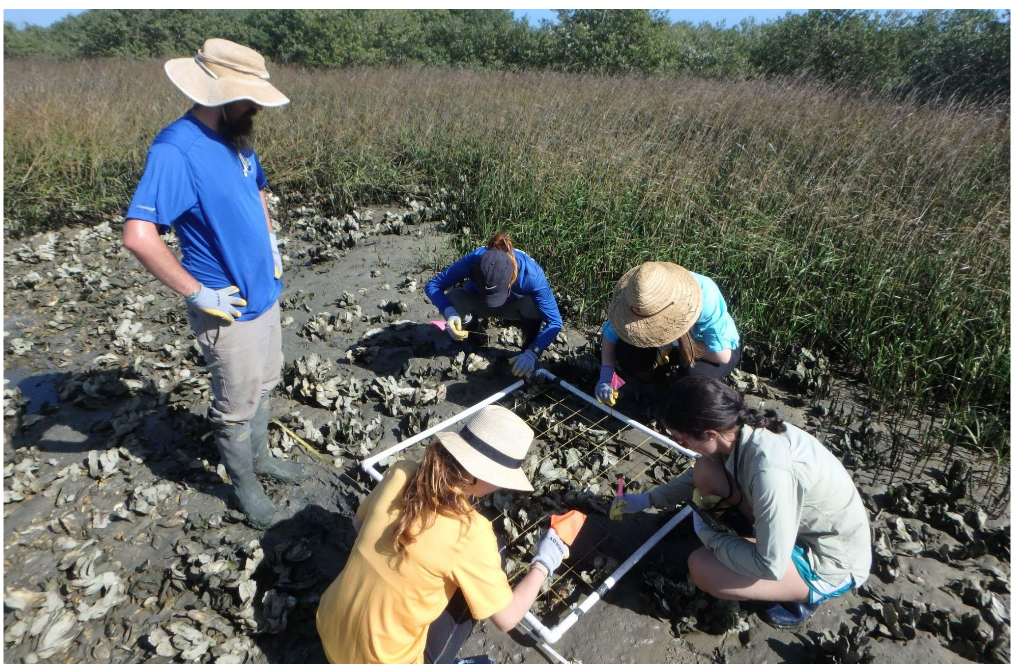

Figure 6. Field training on point-intercept percent cover measurement. Credit: GTMNERR.

[8]http://publicfiles.dep.state.fl.us/DEAR/DEARweb/QA/Plans/2021-2022_QualityPlans/RCPOysterMonitoringQAPlan_Final_2022-06-30_Signed_acc.pdf

Interoperability, Reuse) Principles[9] are also a useful framework for developing data management practices that will help ensure the longevity and maximal usability of monitoring datasets.

The accessibility of monitoring data is particularly important in recognition of the fact that the extensive oyster habitat area in Florida makes the comprehensive, long-term monitoring that is needed impossible for any individual program or organization alone, and in light of public accessibility of project data being an increasingly common condition of funding awards. Many academic institutions, government agencies and granting organizations maintain online portals for their own data products or those they have funded (e.g., Florida State University DigiNole[10], U.S. Geological Survey ScienceBase[11], U.S. National Science Foundation Public Access Repository[12]), but there are a variety of online data repositories available for public sharing of oyster habitat monitoring data that are not institution- or funding-specific, including:

1. Florida-focused:
    a. Florida Geospatial Open Data Portal[13], maintained by the Florida Geographic Information Office
    b. Statewide Ecosystem Assessment of Coastal and Aquatic Resources Data Discovery Interface[14], run by the Florida Department of Environmental Protection
2. Regional:
    a. Gulf of Mexico Research Initiative Information and Data Cooperative[15], run by the Gulf of Mexico Research Initiative
3. National/international:
    a. Dryad[16], an open data repository focused on research datasets from any discipline
    b. Environmental Data Initiative[17], which began as the data repository for the U.S. Long Term Ecological Research Network
    c. Ocean Biodiversity Information System[18], run by the IOC-UNESCO International Oceanographic Data and Information Exchange program
    d. Zenodo[19], a general open science repository maintained by the European Organization for Nuclear Research

[9] https://www.go-fair.org/fair-principles/
[10] www.diginole.lib.fsu.edu/research-repository
[11] www.sciencebase.gov
[12] www.par.nsf.gov
[13] www.geodata.floridagio.gov
[14] www.data.florida-seacar.org
[15] www.data.gulfresearchinitiative.org
[16] www.datadryad.org
[17] www.edirepository.org
[18] www.obis.org
[19] www.zenodo.org

Conclusion

By utilizing available resources, this guidance document encourages practitioners to establish monitoring programs with clearly defined objectives and performance criteria, as appropriate, and to thoughtfully balance the need to maximize information gain with their project's unique logistical constraints when planning and implementing their programs. By clearly defining objectives and performance criteria, the practitioner can make more informed decisions about which metrics to choose, how to develop a sample plan, and how to use the metrics to evaluate testable hypotheses to achieve their program objective(s). The FORS Working Group recommends that all oyster monitoring programs in Florida monitor live oyster density, oyster habitat area, and live oyster size-frequency distribution on all oyster reefs as well as percent live cover on intertidal reefs. This monitoring should be implemented with QA/QC strategies, data management plans, and detailed documentation to encourage data comparability and usability. Specific approaches to site selection, quadrat placement, and other details may vary between monitoring programs, but as long as accuracy and precision are documented, relative change over time in oyster habitat can be assessed and compared, and different monitoring programs can directly benefit from each other's work and collectively improve evidence-based resource protection statewide.

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Appendix

Simulating Quadrat Placement

There are a variety of quadrat placement methods in use by oyster monitoring programs in Florida and their relative performance is not well understood due to the rarity of directly comparable sets of data collected with different protocols. The methods are generally different combinations of random versus fixed spacing and one-dimensional placement along a transect versus two-dimensional placement across the reef surface.

The simulation presented here was designed to examine the impact of quadrat placement on simulated monitoring results for a single reef. In this simulation, a hypothetical oyster reef with three “zones” of varying characteristics are represented by simple concentric ovals (Figure A1). Three straight lines were added through the center of the reef in different directions to represent possible transect orientations. Points representing quadrat sampling locations were then placed in different arrangements to simulate four different methods that are in use by oyster monitoring programs around Florida (Figure A1):

1. randomly across the entire reef footprint (called “Area random” in Figure A1)—analogous to the haphazard sampling method used by the Florida Fish and Wildlife Research Institute (FWRI 2021);
2. randomly from an equally spaced grid of possible sample locations (called “Area grid” in Figure A1)—this is the strategy advocated in the The Nature Conservancy’s Oyster Restoration Monitoring Handbook (Baggett et al. 2014);

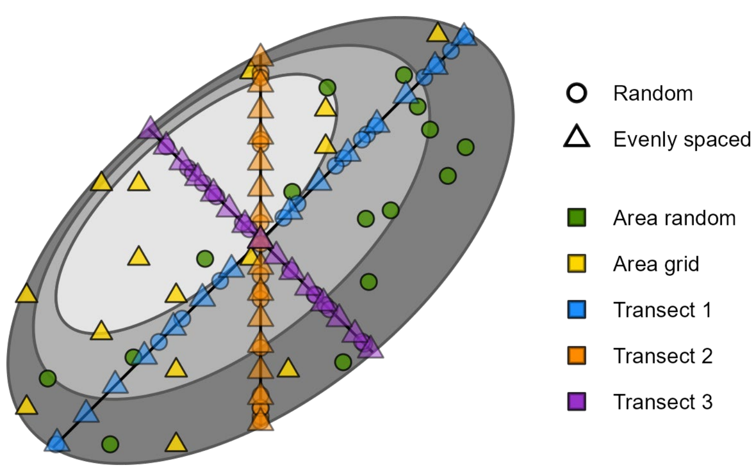

Figure A1. An idealized oyster reef made with three concentric ovals representing “zones” to simulate a gradient for comparing different quadrat placement methods. The plot shows one iteration of the sample location selection (n = 15) using each of four methods.

3. randomly along the length of each transect—this is the strategy used by Guana Tolomato Matanzas NERR (Marcum et al. 2023) and the NE Florida Oyster Condition Assessment Protocol (Walters et al. 2016);

4. evenly spaced along the length of each transect—this is a commonly used method to sample transects in plant ecology and has also been shown to be successful in rocky intertidal habitats (e.g., Miller and Ambrose, 2000).

Three sample sizes were tested (n = 5, 10, and 15), and each sample size was repeated 1000 times. After each iteration, the proportion of sample points falling within each zone was calculated for each method (Figures A3 and A4). The results demonstrate that equally spaced sample locations along a transect (i.e., method 4) parallel with the zone gradient (i.e., transects 2 and 3 in Figure A1) have the highest probability of yielding representative sampling of the

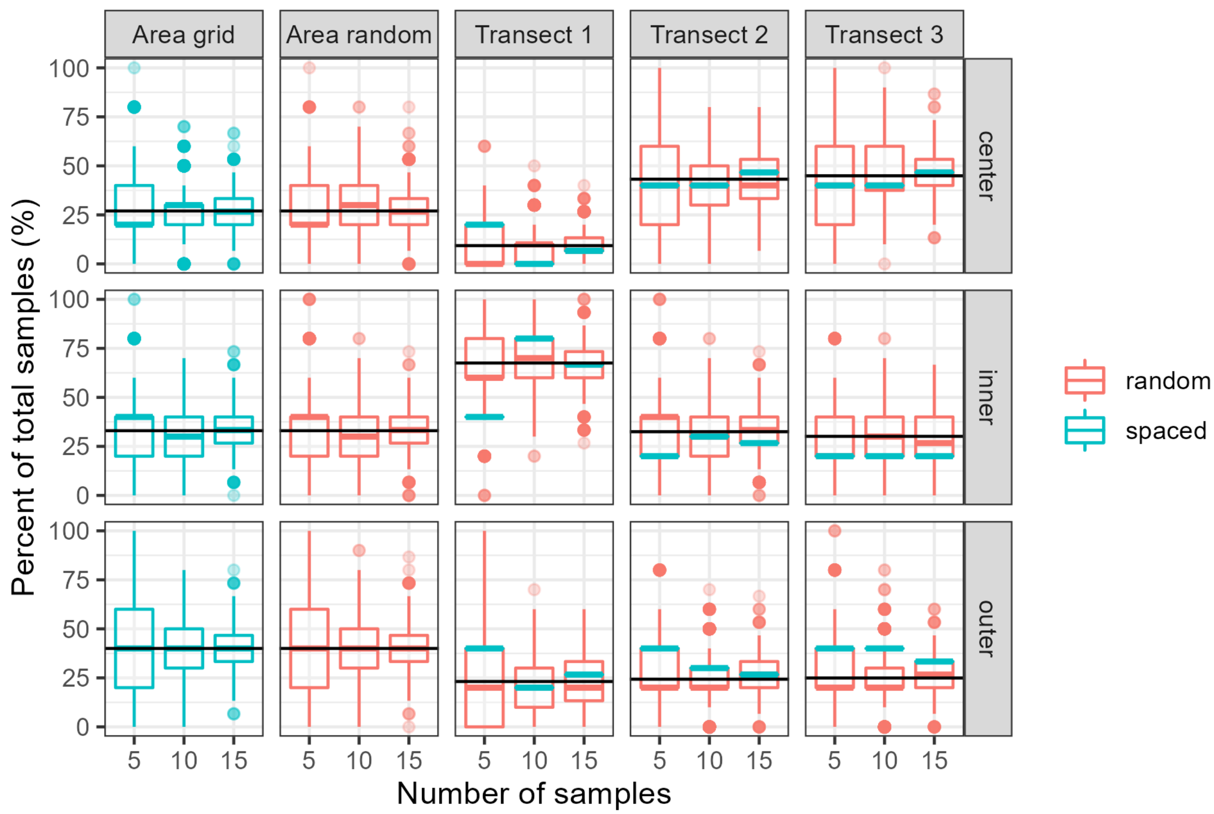

Figure A3. Plots of sample size by percent of samples (i.e., quadrats) in each zone. Each row corresponds with a reef gradient "zone" and each column x color combination corresponds to a sample location selection method. Black horizontal lines show the actual proportion of reef area or transect length in each zone; note that, in contrast to the transect plots, the area proportions represent the true coverage of each zone across the simulated reef.

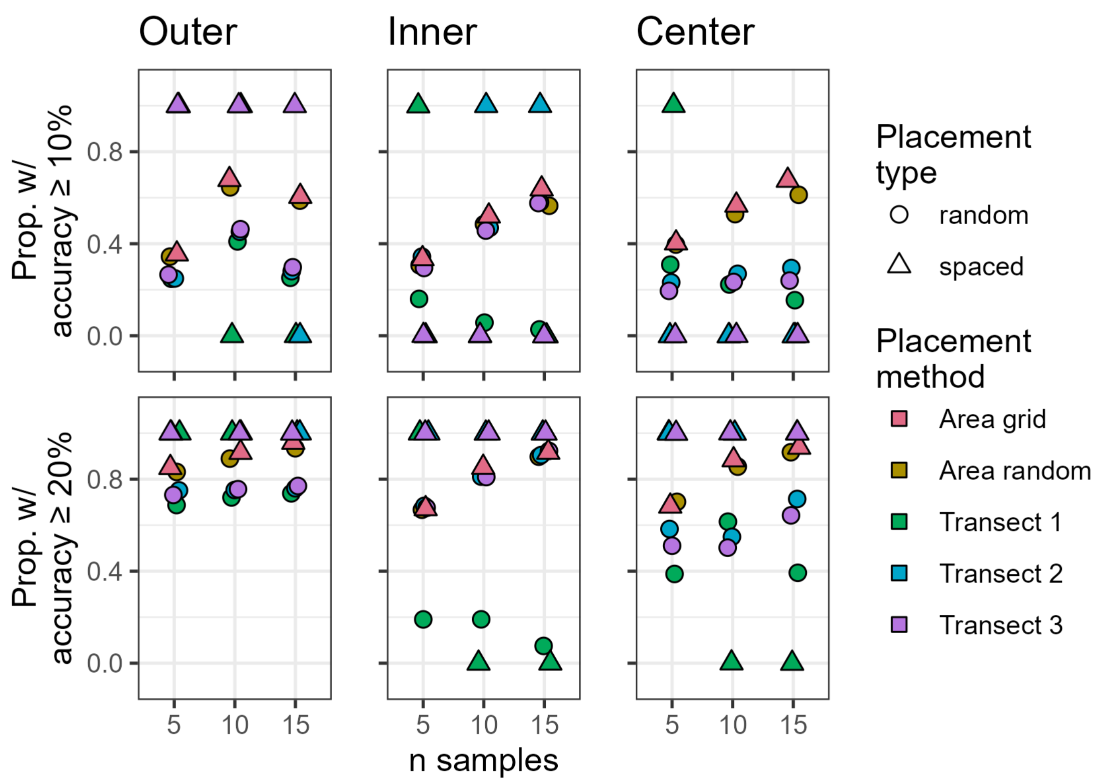

Figure A4. Plots showing the proportion of sample location selection iterations whose results were within 10% (top row) and 20% (bottom row) of the expected value for each "zone". Data points are jittered to prevent complete overlap.

gradient for a given sample size, especially smaller sample sizes, largely because there is only one possible arrangement of the quadrats with this method (Figure A4).

To test the practical impact of the quadrat placement method choice on monitoring results, we also incorporated density values into the simulation by calculating an empirical relationship between oyster density and tidal elevation and assigning depth values to each zone. To generate realistic hypothetical density values we fit a truncated[20] regression model to a set of reef elevation vs. mean density and standard error observations from monitoring of a series of experimental reefs that were constructed at four tidal elevations in North Carolina: -0.5 m, -0.6 m, -0.75 m, and -0.9 m (Figure A5; "large" reefs from Fodrie et al. 2014, Figure 2c). The raw data values were not provided in Fodrie et al. (2014), so mean densities and standard errors were estimated from their Figure 2c using the metaDigitise package in R (Pick et al. 2018) and are shown in Table A1. The regression model was run using the R package brms (Bürkner 2017, 2018) and all plots and analyses were conducted in R using the RStudio integrated development environment (R Core Team 2021, RStudio Team 2021). To apply the reef elevation vs. mean density relationship to our simulation, we arbitrarily assigned the full

[20] Negative response values were not allowed.

Table A1. The mean densities and standard errors by depth for the “large” reefs in Figure 2c from Fodrie et al. (2014). The values were estimated directly from the figure image using the metaDigitize package in R (Pick et al., 2018).

Depth (m)	Mean density (m^{-2})	Standard error
-0.50	1159.4	260.9
-0.60	956.5	202.9
-0.75	956.5	478.3
-0.90	275.4	159.4

depth range to the three “zones” (outer zone = -0.9 m, inner zone = -0.7 m, and center zone = -0.5 m) to maximize the range of possible density values in the simulation. The simulation was then re-run and the model fit was used to predict density values by zone for every sample in each iteration. We then used Kruskal-Wallis tests to compare the simulated density values across methods for each iteration and sample size (Figure A6).

The Kruskal-Wallis test results suggested that, although evenly spacing quadrats along a

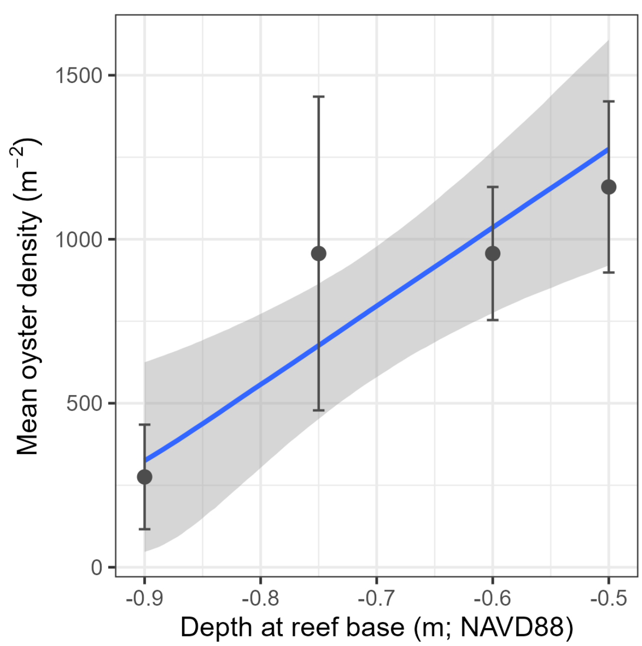

Figure A5. Plot showing the truncated regression model fit to the mean density (± se) values for “large” reefs from Fodrie et al. (2014), Figure 2c.

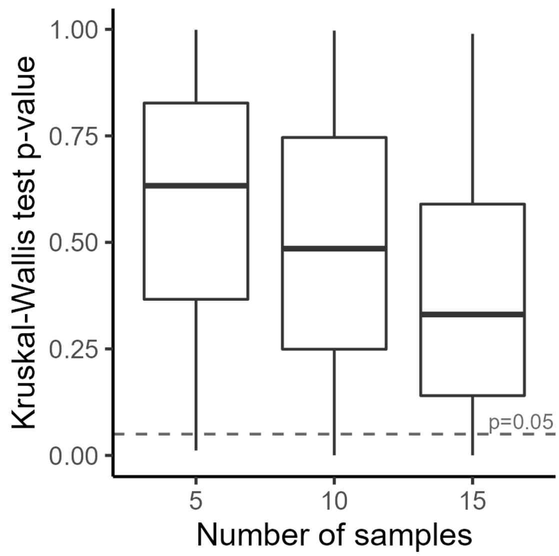

Figure A6. Box plots showing the distribution of p-values from Kruskal-Wallis tests comparing the simulated density values from the different quadrat placement methods for each simulation trial, broken out by sample size. The grey dashed line shows p = 0.05.

transect was the most likely placement method to yield representative samples of the zone gradient (Figure A3), the variation in density estimates between samples and zones was high enough that significant differences between methods were found in only 1%, 5%, and 11% of iterations for sample sizes of five, 10, and 15, respectively (Figure A6). Further, when the distributions of density estimates by placement method and sample size were plotted, the median values for nearly all of the methods were within ±20% of the expected reef-level mean density value (i.e., the sum of the oyster abundance values, estimated from the modeled mean densities, at each depth/zone divided by the total reef area; Figure A7).

Altogether, these results suggest that the practical impact of the quadrat placement method used is likely to be limited, depending on the target effect size of a given monitoring program, although we caution that a more confident statement of the importance of this choice must await more thorough analysis to consider additional factors, such as variations in the number of reefs and their sizes, shapes and topographies. Additional analyses which test the generality of this finding for other oyster monitoring metrics are also needed. Finally, we note that there may be differences in the oyster density vs. depth relationship between the experimental reefs constructed by Fodrie et al. (2014), which were still growing vertically, and natural reefs that may have been accreting for longer periods of time. For instance, the relationship is unlikely to be linear on natural intertidal oyster reefs that have reached the elevation beyond which it is difficult for oysters to survive the duration of emersion at low tide, because the highest oyster densities are likely to be found on the reef flanks in these cases, rather than at the highest elevations.

Readers may also note the counterintuitive finding that density estimates from Transect 1, which crossed the simulated reef perpendicular to the zone gradient, were closer to the expected value than the estimates from Transects 2 and 3, which were nearly parallel with the zone gradient. This result was a spurious consequence of the substantial proportion of Transect 1 that fell within the inner zone which, given the depth assignment (i.e., -0.5 m), had an expected mean density value of ~794 oysters m^{-2}. By chance, this expected value for the inner zone was very close to the reef-level expected mean density value of ~753 oysters m^{-2}. If the arrangement of zones and depth assignments had been different, we think it is unlikely that Transect 1 would have outperformed Transects 2 and 3.

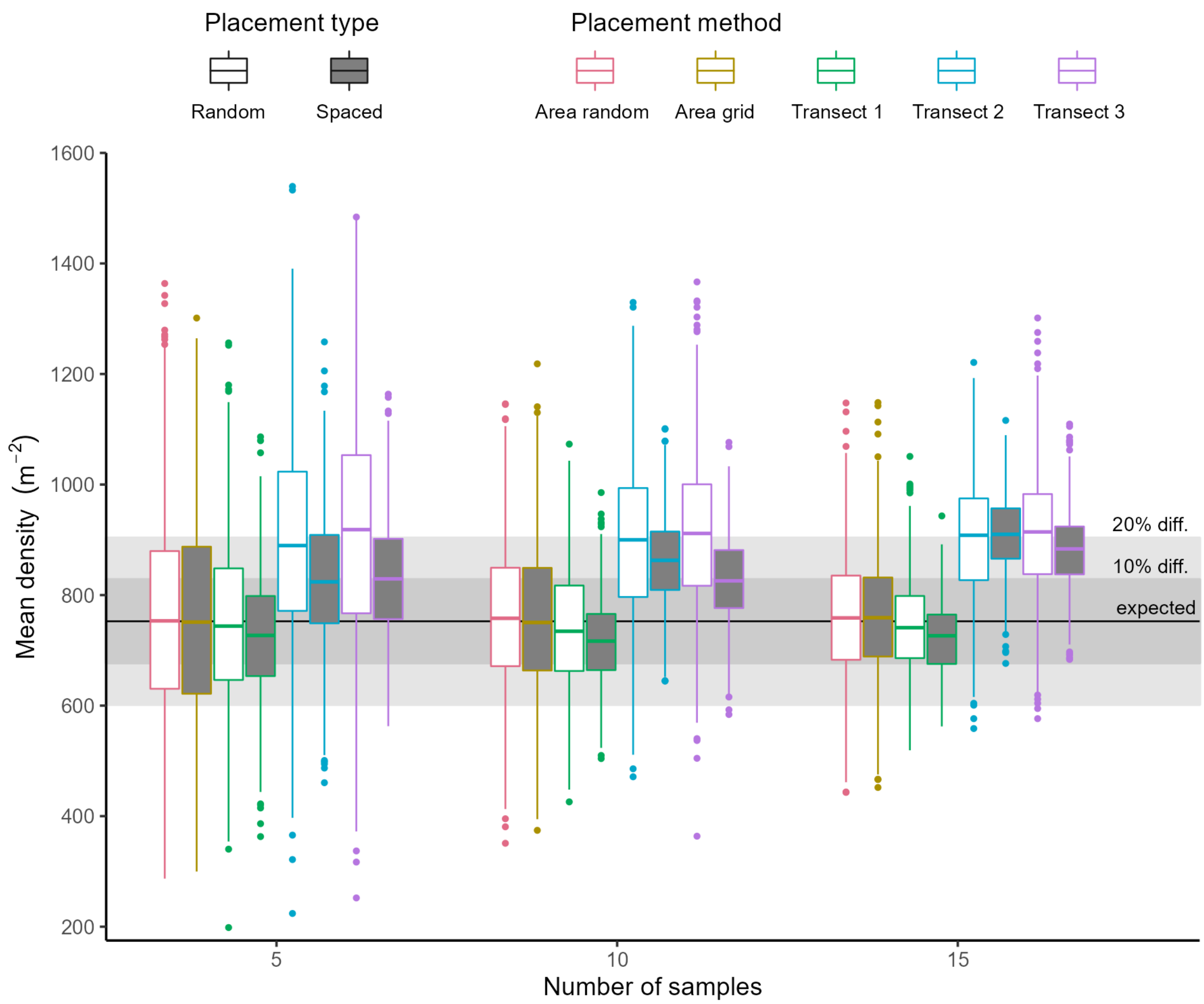

Figure A7. Boxplots showing the distribution of mean density estimates for all iterations of the simulation by sample size and grouped by method. The black horizontal line shows the expected reef-level mean density value and the dark- and light-gray shaded regions show the ranges of density values within ±10% and ±20% of the expected value, respectively.