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Special issue:

# Efficacy of probability surveys for ESA-listed coral species in southern Florida.

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ABSTRACT

As coral populations have declined on coral reefs in the United States, one federal management tool to conserve species is the U.S. Endangered Species Act (ESA). Evaluation of the population status and trends for each species at the ecosystem scale requires periodic surveys, but surveys require a sampling effort sufficient to detect change at high levels of precision over time. Therefore, we assessed the feasibility of diver-based survey data to quantitatively evaluate the seven ESA-listed coral species on Florida's coral reefs. Data are from two complementary monitoring programs constructed from the same probability-based survey design that incorporates stratification created from density mean-variance spatial patterns of abundant target species. The survey design also included along-shore sub-regional gradients and marine spatial planning to tailor the sample frame specifically to the spatial distributions of each threatened species. We evaluated a multi-species design by comparing precision-sample size relationships from two stratification schemes. Results showed that constructing a composite scheme from the habitat use of 4 ESA-listed species resulted in a multi-species design with predicted precision estimates (CV) from 7.5% to 20% for six threatened species. These precision levels enable detection of change in mean density from 15% to 40% (approximately 2 SEs or twice the CV). This level of precision ranked as high as those for many abundant species for four threatened species and somewhat lower for the two rarest species. However, controlling survey precision at the regional scale would likely require sample sizes at least 3 times larger than a typical survey effort for most ESA-listed species.

INTRODUCTION

Coral declines over the last several decades are well-documented (Hughes and Tanner 2000, Gardner et al. 2003, Bruno and Selig 2007, Knowlton and Jackson 2008, Dietzel et al. 2020, Tebbett et al. 2023) and the causes are clear. Global warming causes coral bleaching (Glynn 1993, Hoegh-Guldberg 1999, Hughes et al. 2018), and coral diseases are widespread and increasing in severity (Bruno et al. 2007, Walton et al 2018, Muller et al. 2020). Hurricanes cause damage at local and regional scales (Gardner et al. 2005, Madden et al. 2023). Geography is important in places like Florida where winter cold fronts have caused periodic and large-scale mortality (Lirman et al. 2011). Globally, coral cover has declined from 36±1.4% to 19±0.4% from 1997 to 2018 (47% decline; Tebbett et al. 2023). Depending on the region and habitat type, coral cover in Florida has declined approximately 12-76% from the 1970s to 2021 (Somerfield et al. 2008, Ruzicka et al. 2013, Viehman et al. 2023). In comparison, coral cover on high relief reefs in the US Virgin Islands has declined between 58-63% from 1999 to 2021 (Viehman et al. 2023). These changes in coral cover translate to decreases in colony abundance and changes to the demographic structure of individual coral species (Dietzel et al. 2020). For example, many of the abundant, reef building and ecologically important species in Florida are now considered occasional or rare (Porter and Meier 1992, Ruzicka et al. 2013) and the iconic pillar coral, *Dendrogyra cylindrus*, is regionally extinct (Jones et al. 2021, Neely et al 2021).

In response to the decline in population abundance of corals, assessments of species' extinction risk have been conducted globally for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species and regionally, in the United States, through the U.S. Endangered Species Act listing process with the intention to manage and conserve declining species (Mace et al. 2008, Federal Register 2006, 2014, Gutierrez et al. 2024). The criteria of listing threatened species by both processes contain similar evaluation elements such as the magnitude of population abundance decline and changes in productivity and spatial structure (Brainard et al. 2011, IUCN 2012). However, a majority of the data used in these risk assessments are acquired from surveys designed to evaluate coral community and ecosystem function indicators not coral populations (Mace et al. 2008, Brainard et al. 2011, Gutierrez et al. 2024). For the survey data that are designed to evaluate coral populations, the selected target species are usually not the threatened IUCN Red List and ESA-listed species (NMFS 2022).

Seven reef-building coral species are listed as threatened under the ESA in Florida and the Caribbean – *Acropora cervicornis*, *A. palmata*, *Orbicella annularis*, *O. faveolata*, *O. franksi*, *Dendrogyra cylindrus*, and *Mycetophyllia ferox* (Federal Register 2006, 2014). The recovery documents developed for these listed species identify the biological, conservation, and threat assessments as well as the actions needed to recover the species (NMFS 2015a, b; NMFS 2022). Biological assessment actions include improving the understanding of population demographic structure, genetic structure, and population dynamics and include implementation of monitoring species abundance and distribution over time to evaluate population status (NMFS 2015a, b). For each species, effective monitoring requires periodic surveys to estimate population abundance at the ecosystem scale with a sampling effort sufficient to detect change at high levels of precision over time. While U.S. coral reef jurisdictions conduct repeated, regular ecosystem-scale coral surveys (NOAA CRCP 2021), and Florida has additional monitoring specific to coral stressors (i.e., bleaching; Waddell 2017), neither of these surveys have been specifically designed to provide population estimates for ESA-listed species with low abundance.

A probabilistic sampling approach can provide the underlying framework for a survey design that is specifically tailored to these threatened species. For Florida's coral reefs, two complementary programs (NOAA's National Coral Reef Monitoring Program (NCRMP) and Florida Reef Resiliency Program's Disturbance Response Monitoring (DRM)) use a single survey design that optimizes sampling efficiency to provide high-precision estimates of population metrics at relatively low sample sizes (Miller et al. 2002, Smith et al. 2011a). The stratified random survey design reduces population variance based on two factors. First, coral density varies based on different reef habitat features such as depth, rugosity, and reef type (e.g. hardbottom, spur-and-groove, patch reef). Second, habitats with high density typically also have high variance, while habitats with low density have low variance. Benthic maps of reef habitat features are incorporated into the stratification of the survey area (i.e. domain or sample frame). Stratification partitions the survey domain into sectors of low, moderate, and high variance of coral density. The optimization process allocates sampling (the number of sites to be sampled) by stratum area and the variance of target species density. The survey design of the two Florida programs is optimized for a select number of coral species that are abundant and ecologically important. Both programs, however, include all observed coral species in field surveys. The long-term monitoring data provided by these complementary programs allows for the statistical evaluation of survey design parameters needed to optimize surveys specific to rare ESA-listed species. Even though tailoring a survey design through stratification and optimal allocation is standard practice for rare species (Lohr 2022), there remains the potential of not observing these species when they are actually present in the sample frame (Chao and Lee 1992). Estimation of sample coverage provides a metric to evaluate if rare species are adequately sampled in a survey (Chiu 2023).

Given the need to monitor change in ESA-listed species and the challenge of low density, the goal of this study was to determine which survey design strategy is best suited to obtain precise abundance estimates in a cost-effective manner. The objectives of our study were to: 1) evaluate sampling coverage, 2) evaluate the most effective survey design and obtainable levels of precision of future surveys for selected ESA-listed coral species using density as the design metric, 3) determine the most effective way to tailor the stratification for ESA species, and 4) evaluate survey effort requirements in relation to precision and spatial scale (e.g. domain and region estimates).

## METHODS

### *Study Area*

The study area encompassed reef habitats of Florida's coral reef ecosystem extending for 476 km from Broward County to the Dry Tortugas (Fig. 1), including three main geographic regions – Southeast Florida, Florida Keys, and Dry Tortugas. In the Southeast Florida region, reef habitat types are well-developed linear reef complexes, a series of ridges, patch reefs, and colonized pavement. The Florida Keys and Dry Tortugas regions consist of a semi-continuous series of bank-barrier reefs (i.e. fore reef) and the Florida Keys also includes patch reefs and back reef areas between the fore reef and either land or barrier islands extending from Biscayne National Park through the Florida Keys.

### *Diver Probability Surveys*

This study utilized data from diver-based surveys of stony corals conducted by two ongoing long-term monitoring programs: 1) NOAA's National Coral Reef Monitoring Program (NCRMP), which surveys biennially to evaluate population status and change, and 2) Florida Reef Resiliency Program's Disturbance Response Monitoring (DRM), which surveys corals annually for bleaching and disease. The data in this study included the surveys from 2014 to

2016 for NCRMP and from 2013 to 2016 for DRM. Both programs use methods and stratified random design detailed in Smith et al. (2011a). The survey domain encompassed all mapped live coral habitat area from nearshore to offshore (0-33m depth for NCRMP; 0-20m depth for DRM) between Broward County and the Dry Tortugas. For both programs, stratified random site selection was based on a gridded sample frame consisting of 100 x 100 m grid cells (primary sampling units, PSU) and stratified by cross-shelf zonation (e.g., back reef, fore reef), depth, reef morphology (e.g., patch reefs, spur-groove reefs), and reef complexity. The number, size and relative condition of adult scleractinian coral colonies (maximum diameter ≥ 4 cm) for all coral species were measured in situ along one (NCRMP) or two (DRM) belt transect(s) ($10m^2$ each transect) per PSU (NCCOS 2017, DRM 2017). An individual colony was considered to be a continuous skeletal unit; therefore, a colony that was part of the same skeleton but divided into two or more separate pieces of live tissue was considered to be one colony (Meesters et al. 1996). For each PSU, density was computed as the number of colonies per $m^2$ and occurrence was scored as the presence (1) or absence (0) of a given species within the $10m^2$ belt transect.

Sample coverage was estimated using the abundance-based sample coverage equation in Chiu (2023). Population metrics estimated from diver surveys included mean density ($\overline{D}$, number of colonies per unit area) and proportion occurrence ($\overline{P}$, proportion of PSUs with one or more colony). Estimation of strata- and domain-level population metrics followed standard procedures for stratified random sampling (Cochran 1977, Lohr 2022). Domain-level estimates were computed as the weighted average of stratum-level estimates, illustrated for mean density as

$$\overline{D}_{st} = \sum_h w_h \overline{D}_h \quad , \tag{1}$$

where $\overline{D}_{st}$ is mean colony density for the stratified domain (i.e., spatial sample frame), $\overline{D}_h$ is mean colony density in stratum $h$, and $w_h$ is the stratum weighting factor, the stratum proportion of sample units in the domain. The weighting factor was computed as

$$w_h = \frac{N_h}{\sum_h N_h} \quad , \tag{2}$$

where $N_h$ is the total possible stratum PSUs. In this formulation, the stratum weighting factor equals the stratum proportion of area within the sampling domain. Computation of the variance of domain-wide mean density ($var[\overline{D}_{st}]$) was computed in a similar fashion as the weighted average of strata variances,

$$var[\overline{D}_{st}] = \sum_h w_h^2 \, var[\overline{D}_h] \ , \tag{3}$$

where the variance of mean density in stratum $h$ ($var[\overline{D}_h]$) was,

$$var[\overline{D}_h] = \left(1 - \frac{n_h}{N_h}\right)\frac{s_h^2}{n_h} \ , \tag{4}$$

and the sample variance ($s_h^2$) among PSUs $i$ in stratum $h$ was computed as,

$$s_h^2 = \frac{\sum_i (D_{hi} - \overline{D}_h)^2}{n_h - 1} \ . \tag{5}$$

The quantity $\left(1 - \frac{n_h}{N_h}\right)$ in equation 4 is the finite population correction factor. Survey error, as a measure of precision, was estimated as the coefficient of variation of mean density,

$$CV(\overline{D}_{st}) = \frac{SE(\overline{D}_{st})}{\overline{D}_{st}} \quad , \tag{6}$$

the standard error expressed as a proportion of the mean, where $SE(\overline{D}_{st}) = \sqrt{var(\overline{D}_{st})}$. For the NCRMP and DRM surveys, sampling effort was allocated among strata according to a Neyman strategy (Cochran 1977), taking into account both stratum area (i.e., number of PSUs) and stratum variance of density for a suite of abundant coral species.

*Design Performance Analysis for ESA Species*

The NCRMP/DRM stratification-allocation scheme enabled estimation of domain-wide population metrics for target abundant coral species at substantially higher precision and lower cost (i.e., sample sizes) compared to a simple random design (Smith et al. 2011a). The feasibility of diver surveys to monitor less abundant populations of ESA corals was analyzed with respect to detecting changes over time (i.e., from survey to survey). Precision-sample size relationships were developed as in Smith et al. (2011a) using

$$n^* = \frac{(\sum_h w_h s_h)^2}{V(\bar{D}_{st}) + \frac{1}{N}\sum_h w_h s_h^2} \quad , \qquad (7)$$

where $n^*$ is the number of sampled PSUs required to achieve a specified variance for a future survey, $s_h$ is the standard deviation of density in stratum $h$, $s_h^2$ is the sample variance of density in stratum $h$, $V(\bar{D}_{st})$ is the desired variance for mean density, and $N$ is the total number of possible PSUs in the domain. Estimation of $n^*$ presumes that PSUs will be distributed among strata according to a Neyman allocation scheme,

$$n_h = n\left[\frac{w_h s_h}{\sum_h w_h s_h}\right] \quad , \qquad (8)$$

which accounts for both stratum area ($w_h$) and variance ($s_h$). Desired variance of domain-wide mean density was estimated using a target CV,

$$V(\bar{D}_{st}) = (CV(\bar{D}_{st}) \cdot \bar{D}_{st})^2. \qquad (9)$$

The 95% confidence interval for $\overline{D}_{st}$ is approximately two standard errors; thus, the minimum detectable change in mean density from one survey to the next is approximately twice the CV.

The NCRMP/DRM cross-shelf stratification scheme (Table 1) was based on density mean-variance spatial patterns for abundant coral species. These analysis strata (AS) were the basis for Neyman allocation (eq. 8), and estimation of population metrics (e.g., eq. 1) and associated standard errors. Investigations of stratification schemes more tailored to spatial distributions of ESA species took advantage of an inherent feature of the NCRMP/DRM surveys that incorporated additional factors (along-shore gradients, marine spatial planning) that may impact spatial distributions of corals. For random selection, the allocated PSUs to sample in each AS were first sub-allocated by geographical subregions (Fig. 1) and spatial management zones (marine reserves, fishing zones) proportional to their respective areas within a stratum. This proportional sub-allocation strategy to smaller 'field strata' (FS) was the practical equivalent of simple random sampling within an analysis stratum, and thus did not alter the original AS selection probability of PSUs. This provided flexibility for further dividing AS by subregions and/or management zones to construct more effective stratification schemes for ESA corals without introducing bias into variance estimates (Cochran 1977). Considering colony density as a measure of per unit habitat use (Manly et al. 1993), the building blocks of FS were used to construct habitat use strata (HUS) for ESA species that spatially partitioned mean and variance of density into low, moderate, and high use categories. This procedure entailed comparing individual FS means (e.g., subregions) with the corresponding AS mean (e.g., a habitat-depth category), combining spatially adjacent FS with similar means into larger HUS, and then confirming the new groupings with statistical tests for differences in means and variances.

Design performance was analyzed for ESA coral species as well as two abundant species, *Montastraea cavernosa* and *Siderastrea siderea*, as references. Three stratification schemes were compared: (1) habitat use (HUS), (2) the NCRMP/DRM stratification (AS), and (3) simple random sampling (SRS). Analysis of SRS required a re-weighting of the NCRMP/DRM stratified random observations to meet the assumptions for simple random sampling, namely that sampling was conducted proportional to strata area. In contrast, the AS design employed by NCRMP/DRM used a Neyman scheme that allocated sampling effort according to both strata area and variance of density (eq. 8). The stratum sample size ($n_h$) condition for SRS is

$$\frac{n_{h,SRS}}{n} = \frac{N_h}{N} = w_h \quad , \tag{10}$$

in which $n_{h,SRS}$ is proportional to $N_h$, the total PSUs in a stratum. Computation of $n_{h,SRS}$ was carried out for the survey AS design by

$$n_{h,SRS} = w_h \times n \quad , \tag{11}$$

which was then used to compute the observation weight *t* in stratum *h* for a SRS design,

$$t_{h,SRS} = \frac{n_{h,SRS}}{n_{h,AS}} . \tag{12}$$

Evaluation of precision-sample size relationships for SRS entailed multiplying stratum weights $t_{h,SRS}$ by each observation in the respective analysis stratum *h*, and then computing *n** for a simple random design,

$$n^*(SRS) = \frac{s^2}{V(\bar{D}) + \frac{1}{N}s^2}\,. \qquad (13)$$

All computations were carried out using SAS (SAS Institute, v 9.4) and R (R Core Team, v3.1.3) software packages.

## RESULTS

The 2013-2016 NCRMP/DRM surveys sampled 758 PSUs (Fig. 1, Table 1) and six ESA-listed coral species were observed: *A. cervicornis*, *A. palmata*, *M. ferox*, *O. annularis*, *O. faveolata*, and *O. franksi*). A seventh ESA coral, *Dendrogyra cylindrus*, is known to inhabit Florida's coral reefs, but is present at such low numbers that it was not observed in these surveys. The estimate of sample coverage for the survey was 0.999943. To aid interpretation of design performance analyses, a $CV(\bar{D}_{st})$ of 15% was considered as a general benchmark for survey precision, and the sample size for the 2016 NCRMP/DRM survey of n=451 PSUs served as a reference point for a feasible level of sampling effort in a single survey year in Florida. The AS scheme employed by the NCRMP/DRM surveys was projected to require sample sizes less than 451 to achieve a 15% CV for three ESA species, and greater than 451 for three species (Fig. 2). For all six ESA species, the projected $n^*(15\%)$ for simple random sampling ranged from 3 to 10 times higher compared to the respective $n^*(15\%)$ for the AS design.

Construction of species-specific habitat use strata (HUS) that incorporated components of reef habitats such as cross-shelf zonation (e.g., back reef, fore reef), depth, reef morphology (e.g., patch reefs, spur-groove reefs), substrate complexity-rugosity, along shelf gradients, and marine spatial planning is illustrated for *O. faveolata* for the Florida Keys region using patch reef habitats as the example (Fig. 3). Mean density in patch reef habitats differed by cross-shelf analysis strata (inshore, mid-channel, offshore), and thus the original AS scheme was left unchanged (Fig. 3A). Within the mid-channel patch reef AS, mean density in the lower Keys subregion was similar to the Keys-wide average, mean densities in the adjacent middle and upper Keys subregions were above average, and mean density in the Biscayne subregion was below average (Fig. 3B). The mid-channel patch reef AS was subsequently divided into habitat use strata corresponding to three subregion groupings: lower Keys, middle-upper Keys, and Biscayne. The lower Keys mid-channel patch reefs were further subdivided into smaller HUS by management zone (open to fishing, marine protected areas), based on differences in mean density (Fig. 3C). This procedure resulted in 28 HUS for *O. faveolata* for the southern Florida survey domain (Table 2), compared to the original 30 analysis strata (Table 1). The number of HUS for three additional ESA species (*A. cervicornis*, *O. annularis*, *O. franksi*) ranged from 12 to 26 (Table 2). Comparing precision-cost relationships between the AS and species-specific HUS schemes (Fig. 2), $n^*(15\%)$ was lower for HUS for *A. cervicornis*, slightly higher for *O. franksi*, and similar to AS for *O. annularis* and *O. faveolata*. Two species, *A. palmata* and *M. ferox,* were too rare for habitat use analysis.

To evaluate a multispecies design, combining the HUS schemes for the four ESA species analyzed resulted in 55 unique strata (Table 2). Precision-sample size relationships were compared for this composite species habitat use stratification with the AS scheme for the six ESA species and two abundant coral species (Table 3). For the AS stratification (Table 3A), the expected precision for the benchmark annual survey effort (n=451) ranged from about 4% CV for the most abundant species (*S. siderea*: occupancy rate $\bar{P} \approx 0.85$, $\bar{D} \approx 1.3$ colonies per m$^2$) to about 30% CV for the two rare species (*A. palmata* and *M. ferox*: $\bar{P} \leq 0.01$, $\bar{D} \approx 0.001$).

However, the composite species HUS scheme improved the expected precision for all species (Table 3B): the projected CVs were 5% or less for *M. cavernosa* and *S. siderea* ($\bar{P} > 0.60$), about 7.5% for *O. faveolata* and *O. franksi* ($\bar{P} \approx 0.10$ to 0.30), about 15% for *A. cervicornis* and *O. annularis* ($\bar{P} = 0.04$), and about 20% for the two rare species. Evaluating the composite HUS scheme at the region scale (Dry Tortugas, Florida Keys, Broward-Miami) indicated that projected overall sample sizes would be considerably higher to achieve a precision of 15% for separate surveys in each region compared to a southern Florida survey domain encompassing all three regions (Table 4).

## DISCUSSION

Combined diver probability surveys from NCRMP and DRM in southern Florida had a high sample coverage estimate and therefore provided the foundation to quantitatively evaluate the feasibility of surveys to monitor ESA-listed coral species. These surveys incorporate stratification based on density mean-variance spatial patterns of abundant target species but are structured to include additional factors (along-shore gradients, marine spatial planning) that may impact spatial distributions of corals. These fine-scale elements were the building blocks to tailor the sample frame to spatial distributions of each threatened species. The NCRMP/DRM 2016 survey effort was used as a benchmark of a reasonable sample size for a future ESA-listed species survey. Comparison of precision-sample size relationships from two stratification schemes were conducted for a multi-species design. The results showed that constructing a composite scheme from the habitat use of 4 ESA species resulted in a multi-species design with predicted precision estimates (CV) ranging from 7.5% to 20% for all six species. These precision levels enable detection of change in mean density ranging from 15% to 40% (approximately 2

SEs or twice the CV). This level of precision for four threatened species ranked as high as those for many abundant species and somewhat lower for the two rarest species (Smith et al. 2011a). However, controlling survey precision at the regional scale (Broward-Miami, Florida Keys, and Dry Tortugas separately) would require sample sizes at least 3 times higher than the 2016 NCRMP/DRM survey effort for most ESA-listed species.

A key challenge in designing a survey for rare species is adequately detecting these species when they are actually present. The pooled survey data in this study was optimally allocated for target species that did not include the ESA-listed species which necessitated an estimate of sample coverage. Sample coverage is a metric of sample completeness and is defined as the proportion of individuals of each species in a given sample where values range from 0 to 1 (Chao and Lee 1992, Chiu 2023). Our estimate of sample coverage was close to 1 (0.999943) which signified that we were able to adequately observe the six ESA-listed coral species included in this study. However, the survey did not detect *Dendrogyra cylindrus*. This species has been considered naturally rare on the Florida reef tract (Chan et al. 2019). The number of known *Dendrogyra* colonies in the Florida population (SE Florida, Florida Keys, and Dry Tortugas) was 819 individuals from 2014 to 2020 (Neely et al. 2021). However, after fate tracking all colonies during this time period, the population experienced a 93% loss of colonies and the species was determined to be functionally extinct (Neely et al. 2021).

This study examined both the stratification and allocation components of survey design for ESA-listed coral species by comparing the precision-sample size relationships among stratification schemes. As expected, the two stratified designs (AS and HUS) provided a higher level of precision at much less effort than simple random design for individual species. Given the heterogeneous nature of both habitat and the distribution of abundance, stratification effectively created different subareas of homogeneous abundance and variance. Using a single-species design with the existing NCRMP/DRM stratification scheme (AS) or the species-specific habitat use scheme (HUS), the predicted sampling effort required to achieve a 15% CV was less than the benchmark effort (451 PSUs) for the three *Orbicella* species. A predicted CV of less than 15% at a typical level of sampling effort would detect a minimum 30% change in density. Although the predicted sampling effort required to achieve a 15% CV was higher than 451 PSUs for *A. cervicornis* for both the AS and HUS scheme, the precision-sample size relationship (Figure 2C) indicated a CV of less than 20% at a sample size of 451 which would detect an approximate 40% change in density or 0.0058 colonies/m$^2$. For *A. palmata* and *M. ferox*, the sampling effort needed to achieve a 15% CV was more than 3 times higher than the benchmark effort. Overall, single-species stratified designs using the NCRMP/DRM stratification-allocation scheme would provide reasonable change detection in density for at least four species.

Surveys are frequently designed using multiple target species to address programmatic priorities and maximize resources (e.g. Smith et al. 2011a, b). Ideally, a survey design targeting the six species in this study would be the most cost effective compared to individual surveys for each species. We used precision-sample size relationships to compare a composite HUS from four species to the AS to determine if it would improve performance of a future multi-species survey for the six ESA-listed species. The composite HUS improved expected precision for all six species. A predicted CV of less than 7.5% at a typical level of sampling effort would detect a minimum 15% change in density for *O. faveolata* and *O. franksi*, or a density change of ±0.0111 colonies/m$^2$ and ±0.0056 colonies/m$^2$ respectively. For *A. cervicornis* and *O. annularis*, the predicted CV of less than 15% would detect a minimum of 30% change in density or ±0.0062 colonies/m$^2$ for *A. cervicornis* and ±0.0041 colonies/m$^2$ for *O. annularis*. The predicted precision for the two rarest species, *M. ferox* and *A. palmata*, was 20% resulting in a 40% change in density or ±0.005 colonies/$m^2$ and ±0.0002 colonies/$m^2$ respectively. The improvement in expected precision for all species including the two rarest species (*A. palmata* and *M. ferox*) using the composite HUS compared to AS showed that a stratification scheme based on spatial distribution of abundance and variance of these threatened species is effective for detecting change in population density at a feasible level of sampling effort in a single survey. The composite HUS also performed better than the species-specific HUS schemes for all four species.

Two abundant species were included in the comparison of the composite HUS and AS schemes to evaluate how a survey designed for ESA-listed species would affect their performance in terms of predicted CV. The predicted precision for these species also improved with the composite HUS scheme. There was a reduction in predicted sample size for *S. siderea* and the CV decreased from approximately 7.5% to less than 5% for *M. cavernosa*. Given the benchmark sampling effort, the composite HUS designed for ESA-listed species could be implemented in the current NCRMP/DRM surveys and maintain high levels of precision for abundant species. The NCRMP reef fish surveys use an analogous strategy and target exploited, less abundant fish species while achieving high levels of precision for abundant species (Smith et al 2011b). This strategy would benefit both the primary goals of the NCRMP and DRM surveys and the ESA recovery evaluation needs.

The composite HUS precision-sample size relationship demonstrates two important aspects of survey design – sample variance with respect to density and practical minimum sample size. Projection of sampling effort at different levels of precision (Table 3B) showed a distinct pattern with the abundance rank of each species. At low levels of population density, the precision was low and thus more samples are required. As the density increases, precision stabilizes, and fewer samples are needed to obtain a precise estimate. Also, the projected sample size ($n^*$) values for *S. siderea* and *M. cavernosa* become exceedingly small as % CV increases (Table 3B). The projected sample size is a theoretical projection and can produce low sample sizes for the most abundant species. The practical minimum sample size for a survey is twice the number of strata to ensure that each stratum has a minimum number of 2 samples. The practical minimum sample size was 60 and 110 for AS and HUS respectively.

The survey data in this study combined three regions in southern Florida. If a region-specific estimate of ESA-listed species is desired, our results showed that sampling to control for precision of density estimates at the regional scale using the composite HUS would require considerably more sampling effort than the sample size needed to control the same level of precision of the entire domain encompassing all three regions (Table 4). For the least abundant species, the sampling effort needed at the regional scale was much higher. Similar results have been found for reef fish species, highlighting the importance of clearly defined objectives for probability-based surveys with respect to target species and management priorities (Smith et al. 2011b, Bryan et al 2016).

Following the listing of all seven ESA-listed species, population status reviews are conducted every five years (NMFS 2020). In Florida, the NCRMP and DRM survey estimates have been incorporated into the most recent population status evaluation of these species along with data from permanent monitoring sites (e.g. Ruzicka et al. 2013) and studies that have investigated genetic structure, reproductive/fertilization success and population dynamic rates of some ESA-listed species (e.g. Kabay 2016, Miller et al. 2016a,b; Williams et al. 2017; Neely et al. 2018; Neely et al. 2020; Williams et al. 2020, Neely et al. 2021). Population and stratum-specific abundance estimates from the NCRMP and DRM surveys serve as a complement to smaller scale studies where localized changes can be placed in context of the larger scale surveys and the population demographic structure estimates could improve predictive modeling efforts. Collectively, these surveys and specific studies address the biological actions needed to assess recovery and improve the evaluation of ESA-listed species. Here we show that moderate adjustments to the current survey design in Florida can increase the precision of change detection in populations of six ESA-listed coral species while retaining the detection power in more abundant species. This further optimization of sampling design would enhance understanding of the ecosystem, better inform management decisions, and decrease the cost of evaluating species of interest.

Probability surveys incorporate a key iterative learning component as standard practice that keeps the design tailored to the changing dynamics of a species. Practically, this means that when planning each survey using the stratification scheme for these rare species, survey performance is evaluated and an optimal (Neyman) allocation of sampling effort is conducted using the three most recent years of survey data. This provides a mechanism for iterative optimization of survey efficiency under changing environmental conditions that potentially impact these species.

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TABLES

Table 1. Regions, subregions, habitat types, and depths that defined analysis strata (AS) in the South Florida coral reef survey. Stratum-specific areas ($A_h$), total possible primary units ($N_h$), and sampled primary units ($n_h$) are listed.

| AS Strata Code | Region/Subregion | Habitat | $n_h$ | $N_h$ | $A_h$ ($km^2$) |
|---|---|---|---|---|---|
| | Dry Tortugas | | | | |
| AS01 | Tortugas Bank (BANK) | Contiguous Reef (CONT), High Relief (HR), all depths | 32 | 1766 | 17.66 |
| AS02 | National Park (DTNP) | CONT, HR, all depths | 5 | 507 | 5.07 |
| AS03 | DTNP | CONT, Medium Relief (MR), all depths | 41 | 1479 | 14.79 |
| AS04 | BANK | CONT, Low Relief (LR), all depths | 10 | 9788 | 97.88 |
| AS05 | DTNP | CONT, LR, all depths | 31 | 7391 | 73.91 |
| AS06 | BANK | Isolated Patch Reef (ISOL), HR, all depths | 5 | 260 | 2.60 |
| AS07 | DTNP | ISOL, HR, all depths | 22 | 510 | 5.10 |
| AS08 | BANK | ISOL, MR, all depths | 10 | 1447 | 14.47 |
| AS09 | DTNP | ISOL, MR, all depths | 12 | 3305 | 33.05 |
| AS10 | BANK | ISOL, LR, all depths | 7 | 268 | 2.68 |
| AS11 | DTNP | ISOL, LR, all depths | 15 | 2767 | 27.67 |
| AS12 | DTNP | Spur and Groove Reef (SPGR), HR, all depths | 11 | 359 | 3.59 |
| AS13 | DTNP | SPGR_LR, all depths | 3 | 1251 | 12.51 |
| | Florida Keys | | | | |
| AS14 | all Subregions | Inshore Patch Reef (IPR), all relief types and depths | 15 | 1684 | 16.84 |
| AS15 | all Subregions | Mid-channel Patch Reef (MPR), all relief types and depths | 76 | 15192 | 151.92 |
| AS16 | all Subregions | Offshore Patch Reef (OPR), all relief types and depths | 53 | 9159 | 91.59 |
| AS17 | all Subregions | Fore reef (FRF), Low relief Rubble (RUBB_LR), all depths | 30 | 1248 | 12.48 |
| AS18 | all Subregions | FRF, SPGR, HR, all depths | 83 | 1170 | 11.70 |
| AS19 | all Subregions | FRF, LR, Shallow (S) (0m - 6m) | 18 | 3238 | 32.38 |
| AS20 | all Subregions | FRF, LR, Mid-Shallow (MS) (≥ 6m - 12m) | 100 | 17807 | 178.07 |
| AS21 | all Subregions | FRF, LR, Mid-Deep (MD) (≥ 12m - 18m) | 33 | 7951 | 79.51 |
| AS22 | all Subregions | FRF, LR, Deep (D) (≥ 18m - 33m) | 7 | 9593 | 95.93 |
| | Southeast Florida | | | | |
| AS23 | Broward-Miami (BM) | Nearshore Ridge (NEAR), LR | 20 | 5568 | 55.68 |
| AS24 | BM | NEAR, HR | 5 | 160 | 1.60 |
| AS25 | BM | Linear Reef Inner (INNER), LR | 10 | 1204 | 12.04 |

| | | | | | |
|---|---|---|---|---|---|
| AS26 | BM | INNER, HR | 11 | 605 | 6.05 |
| AS27 | BM | Linear Reef Middle (MIDR), LR | 48 | 1263 | 12.63 |
| AS28 | BM | MIDR, HR | 25 | 428 | 4.28 |
| AS29 | BM | Linear Reef Outer (OFFR), LR | 5 | 630 | 6.30 |
| AS30 | BM | OFFR, HR | 15 | 1227 | 12.27 |

Table 2. Regions, subregions, habitat types, depths, and spatial management areas that defined condensed field strata (FS-C) in the South Florida coral reef survey.  Stratum-specific total possible primary units ($N_h$) and sampled primary units ($n_h$) are listed. Respective habitat use strata (HUS) for *Orbicella faveolata*, *Orbicella franksi*, *Orbicella annularis*, and *Acropora cervicornis* were delineated by combining FS with similar means and variances of colony density (e.g., Fig. 3).

| | Field Strata, Condensed (FS-C) | | | | | Species -Specific Habitat Use Strata (HUS) | | | |
|---|---|---|---|---|---|---|---|---|---|
| FS-C Strata Code | Region/Subregion | Habitat | Spatial management | n | $N_h$ | *O. faveolata* | *O. franksi* | *O. annularis* | *A. cervicornis* |
| | Dry Tortugas | | | | | | | | |
| AS01/AS02_FSC01 | Tortugas Bank (BANK)/National Park (DTNP) | Contiguous Reef, High Relief (CONT_HR), all depths | Open (OPN) + MPA | 37 | 2273 | 1 | 1 | 1 | 1 |
| AS03_FSC02 | DTNP | CONT, Medium Relief (CONT_MR), all depths | OPN | 21 | 953 | 1 | 1 | 3 | 4 |
| AS03_FSC03 | DTNP | CONT_MR | MPA | 20 | 526 | 1 | 1 | 1 | 4 |
| AS04_FSC04 | BANK | CONT, Low Relief (CONT_LR), all depths | OPN + MPA | 10 | 9788 | 2 | 2 | 2 | 2 |
| AS05_FSC05 | DTNP | CONT_LR, Shallow (S) (< 12m) | Open | 9 | 1590 | 2 | 2 | 2 | 3 |
| AS05_FSC06 | DTNP | CONT_LR_S | MPA | 4 | 883 | 2 | 2 | 2 | 2 |
| AS05_FSC07 | DTNP | CONT_LR, Deep (D) (12m - 33m) | OPN + MPA | 18 | 4918 | 2 | 3 | 1 | 2 |
| AS06_FSC08 | BANK | Isolated Patch Reef, High Relief (ISOL_HR), all depths | OPN + MPA | 5 | 260 | 1 | 1 | 1 | 1 |
| AS07_FSC09 | DTNP | ISOL_HR | OPN + MPA | 22 | 510 | 1 | 1 | 1 | 1 |
| AS08_FSC10 | BANK | ISOL, Medium Relief (MR), Shallow (S) (< 22m) | OPN + MPA | 3 | 336 | 3 | 1 | 1 | 1 |
| AS08_FSC11 | BANK | ISOL_MR, Deep (D) (≥ 22m - 33m) | OPN + MPA | 7 | 1111 | 4 | 1 | 1 | 1 |
| AS09_FSC12 | DTNP | ISOL_MR, Shallow (< 12m) | OPN + MPA | 6 | 1724 | 5 | 1 | 1 | 4 |
| AS09_FSC13 | DTNP | ISOL_MR, Deep (≥ 12m - 33m) | OPN + MPA | 6 | 1581 | 6 | 1 | 1 | 4 |
| AS10_FSC14 | BANK | ISOL, Low Relief (LR), all depths | OPN + MPA | 7 | 268 | 2 | 2 | 2 | 2 |
| AS11_FSC15 | DTNP | ISOL_LR | OPN + MPA | 15 | 2767 | 2 | 2 | 2 | 2 |
| AS12_FSC16 | DTNP | Spur and Groove Reef (SPGR), High Relief (HR), all depths | OPN + MPA | 11 | 359 | 1 | 1 | 4 | 1 |
| AS13_FSC17 | DTNP | SPGR, Low Relief (LR), all depths | OPN + MPA | 3 | 1251 | 2 | 2 | 2 | 2 |

| FS-C Strata Code | Region/Subregion | Habitat | Spatial management | n | $N_h$ | *O. faveolata* | *O. franksi* | *O. annularis* | *A. cervicornis* |
|---|---|---|---|---|---|---|---|---|---|
| | Field Strata, Condensed (FS-C) | | | | | Species -Specific Habitat Use Strata (HUS) | | | |
| | Florida Keys | | | | | | | | |
| AS14_FSC18 | Lower Keys (L) | Inshore Patch Reef (IPR) , all relief types and depths | OPN + MPA | 11 | 701 | 7 | 4 | 5 | 5 |
| AS14_FSC19 | Middle Keys (M) | IPR | OPN + MPA | 1 | 558 | 7 | 4 | 6 | 5 |
| AS14_FSC20 | Biscayne/Upper Keys (B/U) | IPR | Open (OPN) + MPA | 3 | 425 | 8 | 5 | 6 | 5 |
| AS15_FSC21 | L | Mid-channel Patch Reef (MPR), all relief types and depths | Open (OPN) | 25 | 4952 | 9 | 4 | 7 | 6 |
| AS15_FSC22 | L | MPR | MPA | 6 | 277 | 10 | 4 | 8 | 6 |
| AS15_FSC23 | M | MPR | OPN + MPA | 18 | 1909 | 11 | 4 | 9 | 7 |
| AS15_FSC24 | U | MPR | OPN + MPA | 12 | 2793 | 11 | 5 | 9 | 7 |
| AS15_FSC25 | B | MPR | OPN + MPA | 15 | 5261 | 12 | 5 | 9 | 8 |
| AS16_FSC26 | L | Offshore Patch Reef (OPR), all relief types and depths | OPN + MPA | 12 | 2463 | 13 | 4 | 10 | 9 |
| AS16_FSC27 | M | OPR | OPN + MPA | 6 | 979 | 14 | 4 | 11 | 9 |
| AS16_FSC28 | U | OPR | OPN | 16 | 4346 | 15 | 5 | 12 | 10 |
| AS16_FSC29 | U | OPR | MPA | 2 | 56 | 16 | 5 | 12 | 10 |
| AS16_FSC30 | B | OPR | OPN + MPA | 6 | 910 | 17 | 5 | 12 | 10 |
| AS16_FSC31 | U | Inner Line Reef Tract (IRT), all relief types and depths | OPN | 5 | 346 | 15 | 5 | 12 | 11 |
| AS16_FSC32 | U | IRT | MPA | 6 | 59 | 16 | 5 | 12 | 11 |
| AS17_FSC33 | M/L | Fore reef (FRF), Low relief Rubble (RUBB_LR), all depths | OPN + MPA | 23 | 862 | 18 | 6 | 15 | 15 |
| AS17_FSC34 | B/U | FRF_RUBB_LR | OPN + MPA | 7 | 386 | 18 | 6 | 16 | 15 |
| AS18_FSC35 | L | FRF, High Relief Spur and Groove (SPGR_HR), all depths | OPN + MPA | 37 | 461 | 19 | 7 | 13 | 12 |
| AS18_FSC36 | M | FRF_SPGR_HR | OPN + MPA | 26 | 106 | 19 | 7 | 14 | 13 |
| AS18_FSC37 | U | FRF_SPGR_HR | OPN | 6 | 186 | 20 | 8 | 14 | 14 |
| AS18_FSC38 | U | FRF_SPGR_HR | MPA | 6 | 286 | 21 | 8 | 14 | 14 |
| AS18_FSC39 | B | FRF_SPGR_HR | OPN + MPA | 8 | 131 | 22 | 8 | 14 | 14 |

| FS-C Strata Code | Field Strata, Condensed (FS-C): Region/Subregion | Habitat | Spatial management | n | $N_h$ | Species -Specific Habitat Use Strata (HUS): *O. faveolata* | *O. franksi* | *O. annularis* | *A. cervicornis* |
|---|---|---|---|---|---|---|---|---|---|
| | Florida Keys | | | | | | | | |
| AS19_FSC40 | M/L | FRF, Low Relief (LR), Shallow (S) (0m - 6m) | OPN + MPA | 9 | 986 | 23 | 9 | 15 | 16 |
| AS19_FSC41 | B/U | FRF_LR_S | OPN + MPA | 9 | 2252 | 24 | 10 | 16 | 17 |
| AS20_FSC42 | L | FRF_LR, Mid-Shallow (MS) (≥ 6m - 12m) | OPN + MPA | 33 | 4379 | 25 | 9 | 15 | 18 |
| AS20_FSC43 | M | FRF_LR_MS | OPN | 25 | 7199 | 25 | 9 | 15 | 19 |
| AS20_FSC44 | M | FRF_LR_MS | MPA | 19 | 202 | 25 | 9 | 15 | 20 |
| AS20_FSC45 | U | FRF_LR_MS | OPN + MPA | 13 | 3304 | 26 | 10 | 16 | 21 |
| AS20_FSC46 | B | FRF_LR_MS | OPN + MPA | 10 | 2723 | 26 | 10 | 16 | 22 |
| AS21_FSC47 | M/L | FRF_LR, Mid-Deep (MD) (≥ 12m - 18m) | OPN + MPA | 20 | 5483 | 25 | 9 | 15 | 23 |
| AS21_FSC48 | B/U | FRF_LR_MD | OPN + MPA | 13 | 4922 | 26 | 10 | 16 | 24 |
| AS22_FSC49 | M/L | FRF_ LR, Deep (D) (≥ 18m - 33m) | OPN | 6 | 6544 | 27 | 11 | 15 | 23 |
| AS22_FSC50 | B/U | FRF_ LR_D | OPN | 1 | 3049 | 27 | 11 | 16 | 24 |
| | Southeast Florida | | | | | | | | |
| AS23_FSC51 | Broward-Miami (BM) | Nearshore Ridge (NEAR), Low Rugosity (LR) | Open (OPN) | 20 | 5568 | 28 | 12 | 17 | 25 |
| AS24_FSC52 | BM | NEAR, High Rugosity (HR) | OPN | 5 | 160 | 28 | 12 | 17 | 26 |
| AS25_FSC53 | BM | Linear Reef Inner (INNER), Low Rugosity (LR) | OPN | 10 | 1204 | 28 | 12 | 17 | 26 |
| AS26_FSC54 | BM | INNER, High Rugosity (HR) | OPN | 11 | 605 | 28 | 12 | 18 | 26 |
| AS27/AS28/AS29/ AS30_FSC55 | BM | Linear Reef Middle, Low and High Rugosity (MIDR) and Linear Reef Outer, Low and High Rugosity (OFFR) | OPN | 93 | 3548 | 28 | 12 | 17 | 26 |

Table 3. The projected sample size n* to achieve a desired level of precision (%CV) for eight species and two stratification schemes: (A) analysis (30 total strata) and (B) composite species habitat use (55 total strata). Gray shading represents the number of samples at or below the sampling effort of the 2016 NCRMP/DRM survey (n=451). Note that the practical minimum sample size is twice the number of strata: n=60 for the AS scheme (A), and n=110 for the composite species HUS scheme (B).

(A)

| Species | Mean density | Mean proportion occurrence | n* 4% | 5% | 7.50% | 10% | 15% | 20% | 30% | 40% |
|---|---|---|---|---|---|---|---|---|---|---|
| *S. siderea* | 1.2816 | 0.8520 | 393 | 252 | 112 | 63 | 28 | 16 | 7 | 4 |
| *M. cavernosa* | 0.2310 | 0.6155 | 866 | 556 | 248 | 140 | 62 | 35 | 16 | 9 |
| *O. faveolata* | 0.0752 | 0.2602 | 1651 | 1068 | 480 | 271 | 121 | 68 | 30 | 17 |
| *O. franksi* | 0.0379 | 0.1395 | 1287 | 838 | 379 | 214 | 96 | 54 | 24 | 14 |
| *A. cervicornis* | 0.0196 | 0.0423 | 9195 | 6269 | 2978 | 1717 | 777 | 440 | 196 | 111 |
| *O. annularis* | 0.0171 | 0.0462 | 2637 | 1802 | 858 | 495 | 224 | 127 | 57 | 32 |
| *M. ferox* | 0.0011 | 0.0100 | 14624 | 10761 | 5613 | 3361 | 1566 | 896 | 403 | 228 |
| *A. palmata* | 0.0011 | 0.0035 | 8811 | 7381 | 4721 | 3138 | 1602 | 951 | 440 | 251 |

(B)

| Species | Mean density | Mean proportion occurrence | n* 4% | 5% | 7.50% | 10% | 15% | 20% | 30% | 40% |
|---|---|---|---|---|---|---|---|---|---|---|
| *S. siderea* | 1.2319 | 0.8535 | 250 | 160 | 71 | 40 | 18 | 10 | 4 | 3 |
| *M. cavernosa* | 0.2214 | 0.6075 | 674 | 433 | 193 | 109 | 48 | 27 | 12 | 7 |
| *O. faveolata* | 0.0741 | 0.2600 | 1196 | 772 | 346 | 195 | 87 | 49 | 22 | 12 |
| *O. franksi* | 0.0376 | 0.1420 | 993 | 646 | 292 | 165 | 74 | 42 | 18 | 10 |
| *A. cervicornis* | 0.0205 | 0.0425 | 4475 | 3040 | 1438 | 827 | 374 | 212 | 94 | 53 |
| *O. annularis* | 0.0138 | 0.0395 | 2515 | 1724 | 824 | 476 | 216 | 122 | 55 | 31 |
| *M. ferox* | 0.0013 | 0.0110 | 6130 | 4453 | 2284 | 1358 | 629 | 359 | 161 | 91 |
| *A. palmata* | 0.0005 | 0.0011 | 2228 | 2000 | 1475 | 1078 | 610 | 379 | 182 | 106 |

Table 4. Projected number of samples (n*) required to achieve a 15% CV for mean density at the full domain (southern Florida) and region level for two abundant species and six ESA-listed species using the composite habitat use stratification. The species are listed in order of abundance from left to right: *S. siderea* (SSID), *M. cavernosa* (MCAV), *O. faveolata* (OFAV), *O. franksi* (OFRA), *A. cervicornis* (ACER), *O. annularis* (OANN), *M. ferox* (MFER), and *A. palmata* (APAL).

| | | $n^*_{15\%}$ | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sampling frame | NCRMP/DRM n | SSID | MCAV | OFAV | OFRA | ACER | OANN | MFER | APAL | Average |
| Southern Florida | 451 | 18 | 48 | 87 | 74 | 374 | 216 | 629 | 610 | 257 |
| | | | | | | | | | | |
| *Regions* | | | | | | | | | | |
| Broward-Miami | 98 | 80 | 149 | 247 | 575 | 681 | 584 | 3172 | 3172 | 1083 |
| Florida Keys | 185 | 17 | 46 | 78 | 242 | 301 | 204 | 826 | 467 | 273 |
| Dry Tortugas | 168 | 24 | 42 | 149 | 48 | 293 | 1101 | 418 | 3889 | 746 |
| *Region total* | 451 | 121 | 237 | 474 | 865 | 1275 | 1889 | 4416 | 7528 | 2101 |

FIGURE CAPTIONS

Figure 1. Location of 758 Primary Sample Units (PSUs) within the southern Florida study area for NCRMP and DRM surveys in 2013-2016. Sampling encompassed the Broward-Miami subregion in Southeast Florida, four subregions in the Florida Keys (Biscayne, Upper, Middle, Lower Keys), and two subregions in the Dry Tortugas (Dry Tortugas National Park, Tortugas Bank). The Marquesas subregion was not sampled due to limited bathymetry and benthic habitat data.

Figure 2. Relationships between coefficient of variation (CV) of mean density and predicted sample size n* for six ESA-listed coral species and different stratification schemes. Two schemes, analysis strata (AS, gray line) and simple random (SRS, dashed line), were evaluated for all six species. An additional scheme, species-specific habitat use strata (HUS, dashed line), was evaluated for four species (A-D). The projected n* to achieve a 15% CV is denoted.

Figure 3. Construction of habitat use strata (HUS), illustrated for *O. faveolata* in the Florida Keys region. Panels show the spatial pattern of density at progressively smaller spatial scales: (A) cross-shelf patch reef habitats, (B) subregions within Mid-channel patch reefs, and (C) management zones within Mid-channel patch reefs in the Lower Keys subregion. Dashed lines are the area-weighted mean density of individual habitats in each panel. Vertical lines denote delineated HUS based on similarities or differences in the spatial density pattern. Nonparametric tests for the final HUS groupings: Wilcoxon (W) test for differences in means; Conover (C) test for differences in means and variances. Habitat, subregion, and spatial management type codes are defined in Table 2.

FIGURES

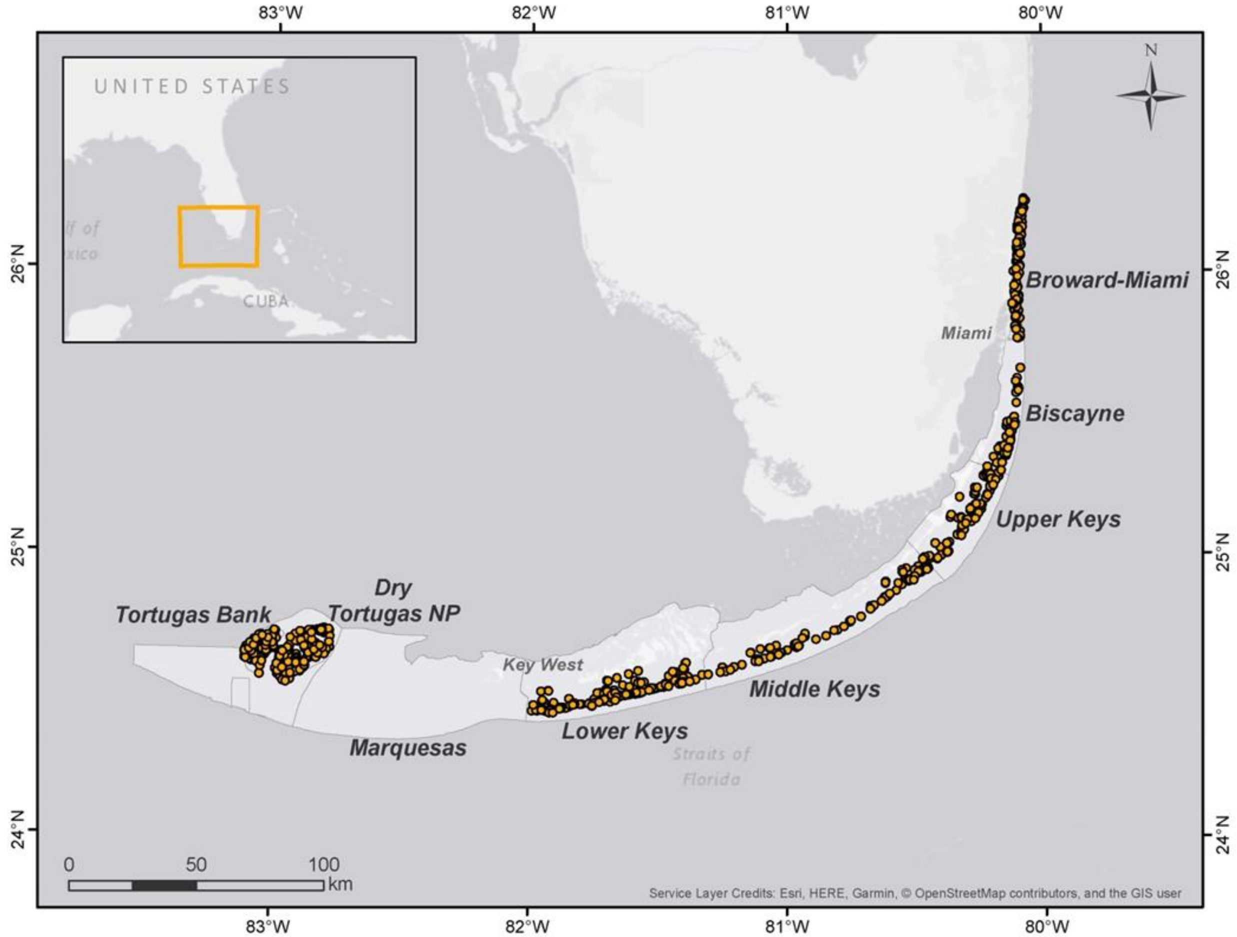



Figure 1.

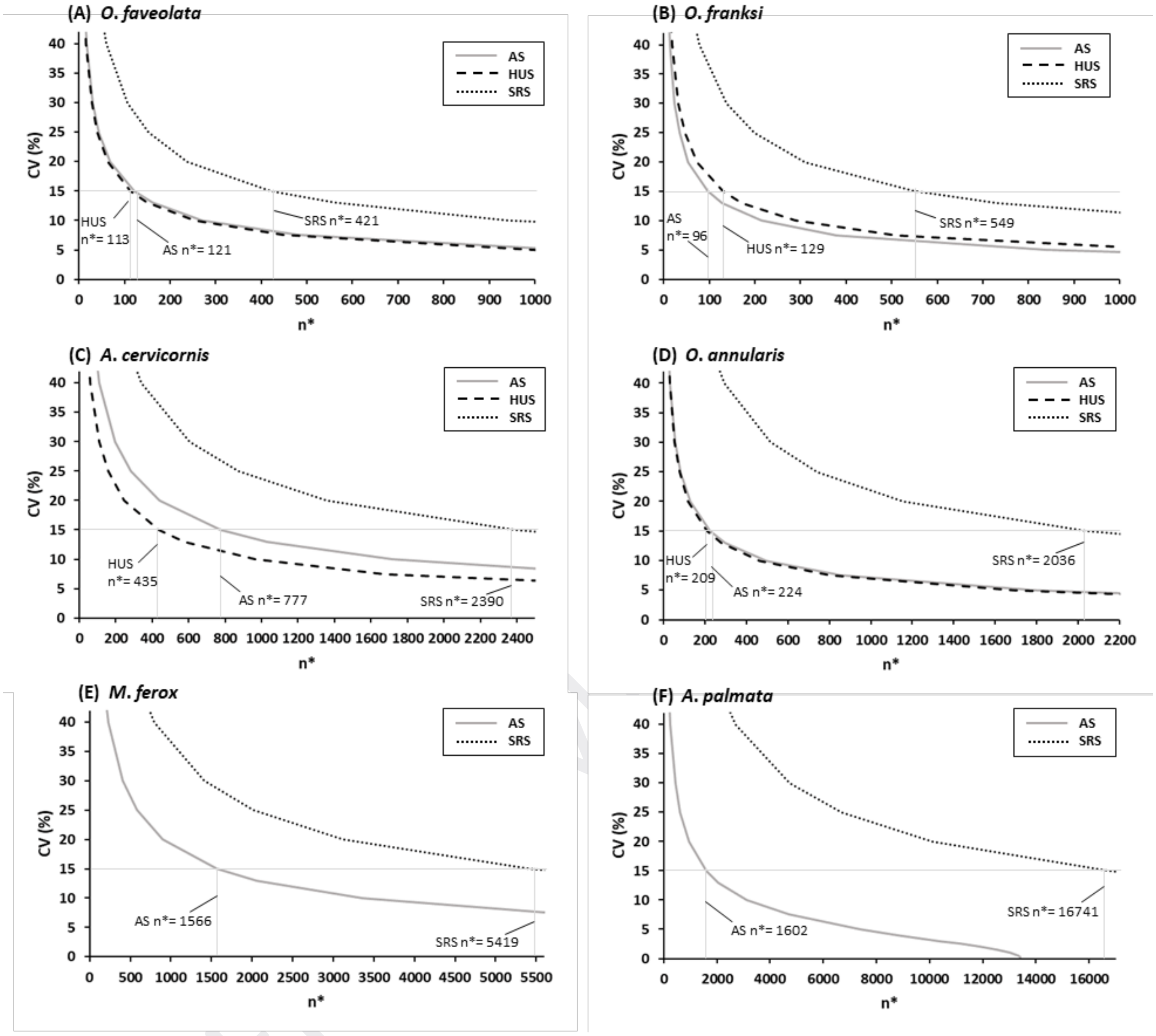
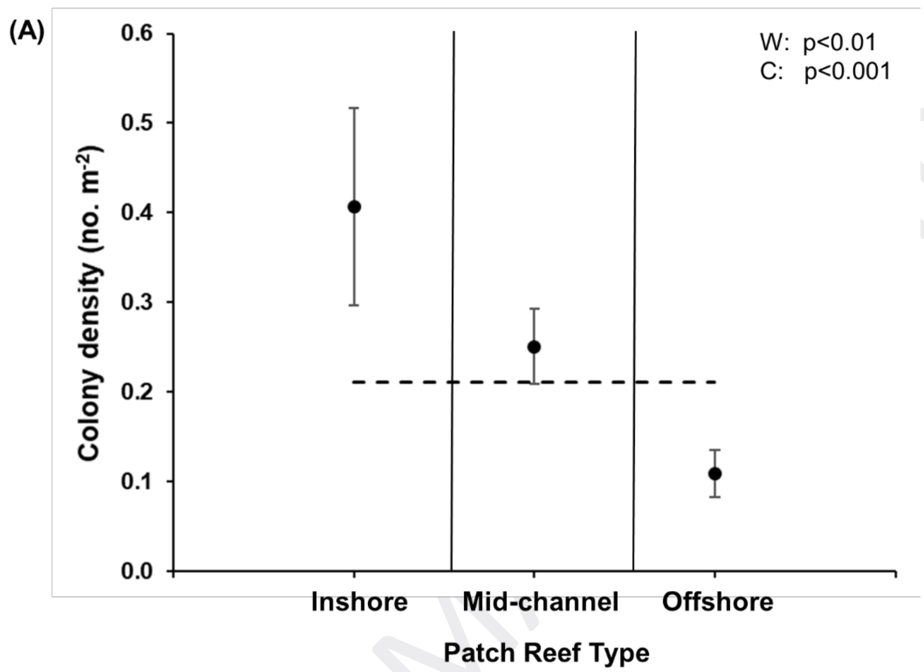

(A) O. faveolata
AS
HUS
SRS
CV (%)
HUS n*= 113
AS n*= 121
SRS n*= 421
n*
(B) O. franksi
AS n*= 96
HUS n*= 129
SRS n*= 549
(C) A. cervicornis
HUS n*= 435
AS n*= 777
SRS n*= 2390
(D) O. annularis
HUS n*= 209
AS n*= 224
SRS n*= 2036
(E) M. ferox
AS n*= 1566
SRS n*= 5419
(F) A. palmata
AS n*= 1602
SRS n*= 16741

Figure 2.


(A)
W: p<0.01
C: p<0.001
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Colony density (no. m-2)
Inshore
Mid-channel
Offshore
Patch Reef Type

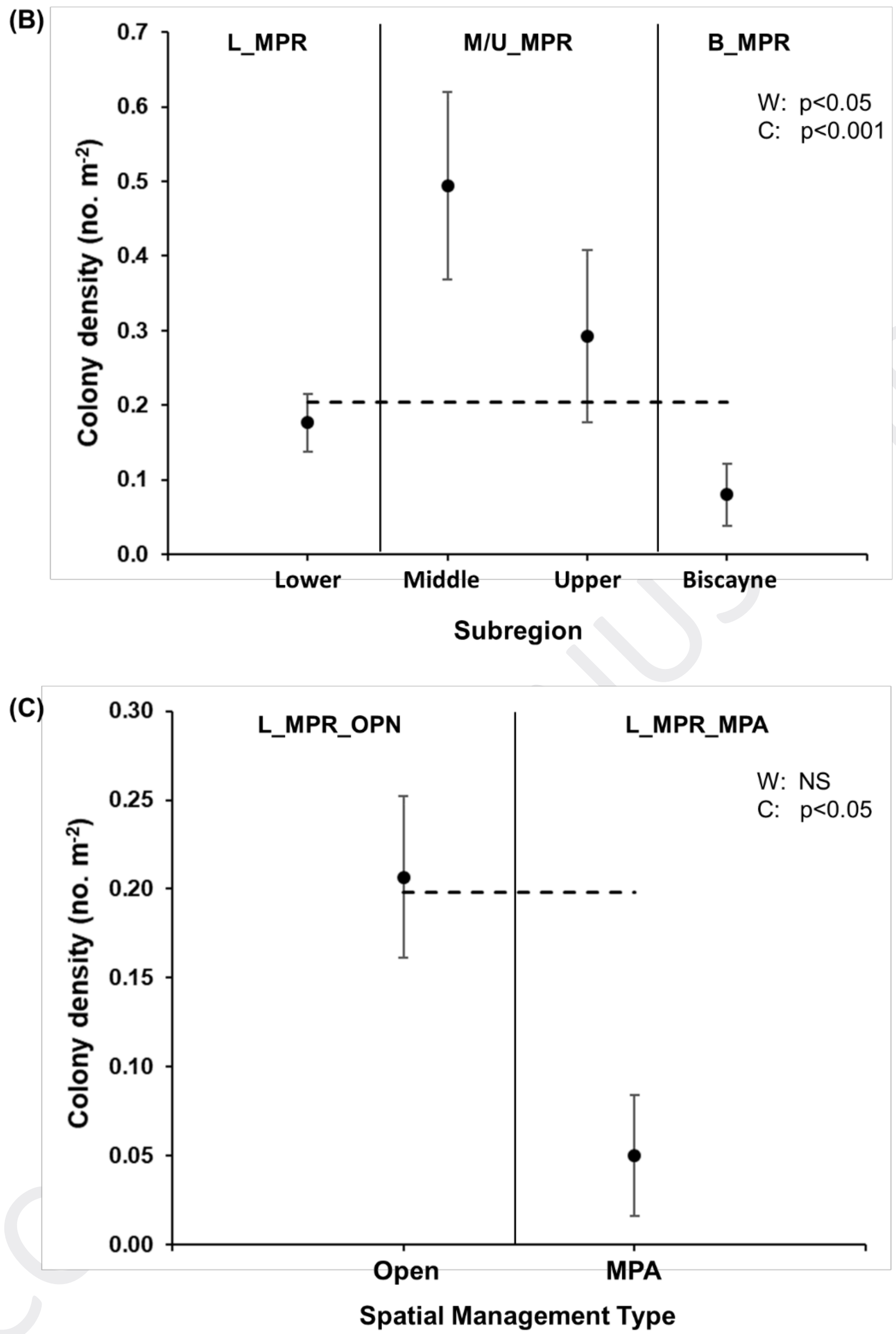

(B)
L_MPR
M/U_MPR
B_MPR
W: p<0.05
C: p<0.001
Colony density (no. m-2)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Lower
Middle
Upper
Biscayne
Subregion
(C)
L_MPR_OPN
L_MPR_MPA
W: NS
C: p<0.05
Colony density (no. m-2)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Open
MPA
Spatial Management Type

Figure 3.