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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 135-146

Published By: American Fisheries Society

URL: <https://doi.org/10.1080/19425120.2015.1082520>

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SPECIAL SECTION: SPATIAL ANALYSIS, MAPPING, AND MANAGEMENT OF MARINE FISHERIES

Feasibility of a Regionwide Probability Survey for Coral Reef Fish in Puerto Rico and the U.S. Virgin Islands

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Abstract

Fishery-independent surveys can provide accurate and precise data for stock assessments and spatial management to sustain fishery resources as a complementary or alternative source of information to fishery-dependent sampling. Four years of underwater visual survey data collected in several local areas in the U.S. Caribbean were used in conjunction with detailed bathymetric and habitat maps to develop a probability sampling design and investigate the feasibility of conducting a regionwide coral reef fish survey. Stratification by depth and habitat produced a more efficient survey design (i.e., one with increased precision at lower sample sizes) for estimating mean fish density than simple random sampling for eight principal exploited and nontarget species. Species with higher sample variance of density required larger sample sizes to improve survey precision. A somewhat counter-intuitive finding was that controlling survey precision over a large spatial scale (i.e., region) required less sampling than controlling precision for multiple smaller areas within the larger survey frame. At regionwide spatial scales relevant for fisheries management, the projected sample sizes for achieving moderately high levels of survey precision were comparable to historical annual sampling efforts. However, controlling survey precision both inside and outside spatial management zones would likely require sample sizes about twice the level of the historical effort. Our findings stress the importance of clearly defining management objectives with respect to spatial scales and target species as a prerequisite for developing precise, cost-effective fishery-independent surveys.

Puerto Rico and the U.S. Virgin Islands (hereafter, the U.S. Caribbean) are located in the northern Caribbean Sea (Figure 1) and are surrounded by a diverse interconnected coral reef ecosystem that supports subsistence, commercial, and sport fisheries as well as an important tourism industry (Matos-Caraballo 2004; Garcia-Sais et al. 2005; Jeffrey et al.

Subject editor: Carl Walters, University of British Columbia, Vancouver

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Received April 4, 2015; accepted August 4, 2015

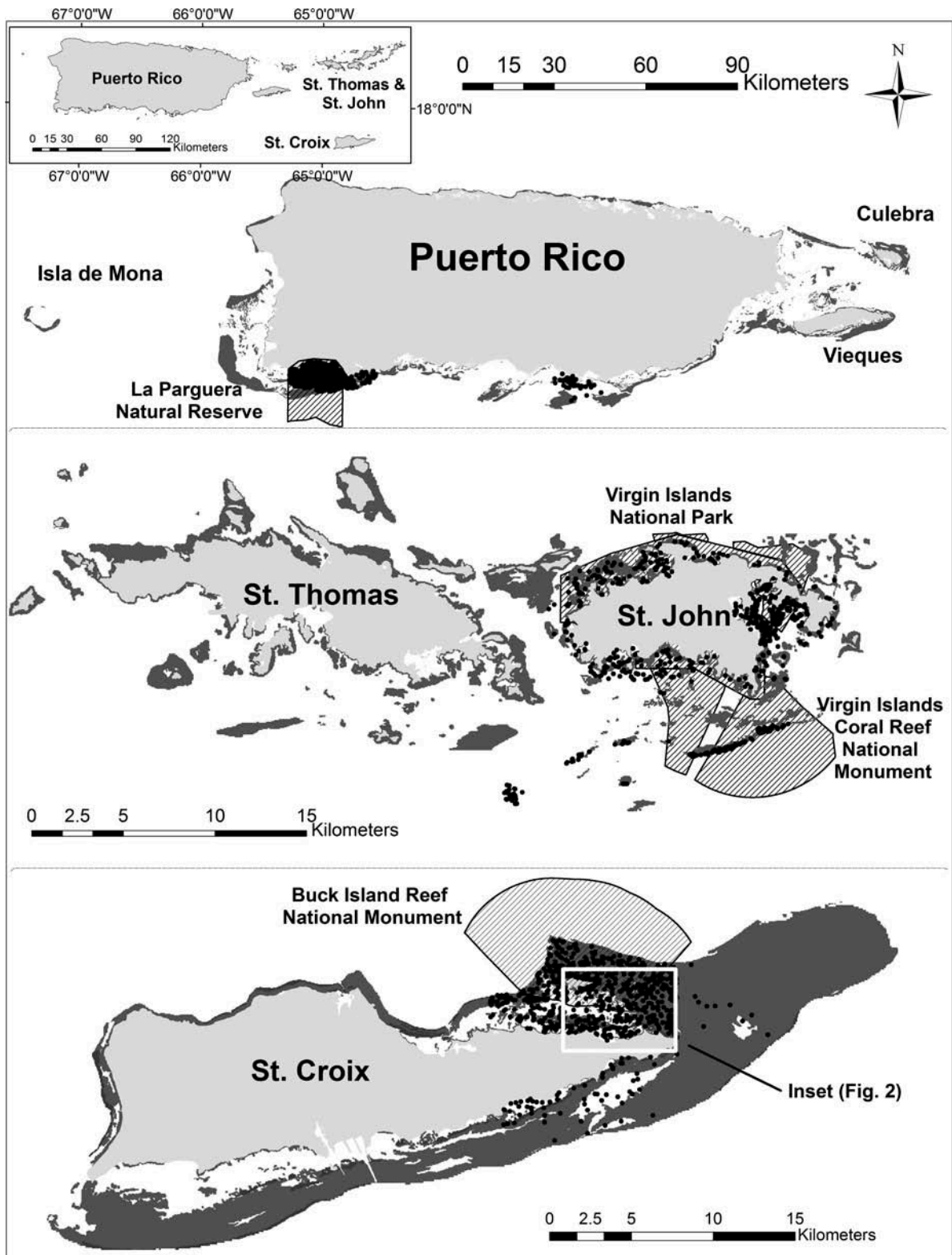


FIGURE 1. Maps of Puerto Rico (top panel) and two subregions of the U.S. Virgin Islands (middle and lower panels) showing management zones (black crosshatching) and the locations of 2007–2010 visual sampling (black circles) on all habitats. Mapped hard-bottom habitats <30 m deep (dark gray) constituted the sample frame. The area shown in detail in Figure 2 is denoted by the white rectangle in the lower panel.

2005). Declines in coral reef fishery resources over the past several decades have raised concerns over their long-term sustainability (Appeldoorn et al. 1992; Rogers and Beets 2001; Ault et al. 2008). The fear is that the U.S. Caribbean may be headed toward the same fate as many coral reef ecosystems around the world, where striking fishery declines and changes in fish community structure have been observed as a result of intensive exploitation and systemic degradation of essential habitats (Bellwood et al. 2004). Compounding the problem in the U.S. Caribbean and many other tropical marine ecosystems is the lack of reliable fishery-dependent data for assessing sustainability status and implementing corrective management actions (Salas et al. 2007).

In accordance with the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006, coral reef fishery resources in the U.S. Caribbean are managed with annual catch limits (ACLs). The ACLs were introduced to prevent or end overfishing by limiting catches to less than the maximum sustainable yield to account for scientific uncertainty in stock assessments. However, the dearth of reliable fishery-dependent and fishery-independent data has effectively constrained stock assessments in the U.S. Caribbean. As a consequence, ACLs have been set by averaging recent historical landings (Caribbean Fishery Management Council 2011; Berkson and Thorson 2015; Newman et al. 2015). Unfortunately, since many fish stocks in the region are already overfished (Ault et al. 2008), the imposed ACLs do not relieve excessive fishing intensities. Thus, ACLs determined in this manner have a high probability of prolonging overfishing (Carruthers et al. 2014). The problem has been further exacerbated by setting ACLs for species groups rather than individual species, which can have detrimental effects on low-productivity stocks when such stocks managed with those of substantially higher productivity (Ricker 1975; Hilborn 1985). Hence, accurate and precise fishery-independent data are greatly needed to perform much-needed rigorous stock assessments of coral reef fishes in the U.S. Caribbean.

Fishery-independent surveys in coral reef ecosystems have been increasing in importance over the past decade as a complementary or alternative source of data to fishery-dependent information (Ault et al. 2005a). These surveys can obtain the same abundance-at-size data as fishery-dependent catch sampling programs and thus can be used to estimate population indicator variables (e.g., average size in the exploitable phase, relative abundance, etc.) for determining resource sustainability in stock assessments (Ault et al. 2014). Especially advantageous are surveys employing nonextractive methods such as diver visual sampling that can be used to collect data for exploited and nontarget species throughout multiple life stages inside and outside of restricted fishing zones (Murphy and Jenkins 2010). This broader range of information allows for evaluation of fishery sustainability as well as animal use of habitats, the design and efficacy of spatial protection strategies (e.g., no-take marine reserves), and community structure and

diversity, all of which support the shift from single-species to ecosystem-based fisheries assessment and management (Ault et al. 2005a; Smith et al. 2011).

The main challenge for survey implementation is to collecting fishery-independent information with reasonable levels of precision at spatial scales that are relevant for fish population assessments, given the limited sampling budgets of most resource agencies (Salas et al. 2007). This study examined the feasibility of conducting a large-scale, fishery-independent diver survey of the shallow-water (<30-m) coral reef fish community in the U.S. Caribbean. A stratified random sampling frame was developed utilizing regionwide maps of bathymetry and benthic habitats and visual sampling data collected in several local areas in Puerto Rico and the U.S. Virgin Islands during 2007–2010. The probability sampling frame was used to evaluate sample size requirements for principal exploited and nontarget fishes in relation to the survey precision and spatial scale of estimates of mean density. Annual effort for visual sampling in 2007–2010 was used as a benchmark to evaluate survey feasibility.

METHODS

Historical sampling data.—Our survey design analysis utilized visual sampling data collected during 2007–2010 as part of a general ecological characterization of the demersal reef fish community and benthic habitats inside and adjacent to several marine parks (Figure 1): La Parguera Natural Reserve (LPNR) in Puerto Rico; Virgin Islands Coral Reef National Monument (VICR) and Virgin Islands National Park (VIIS) in St. John; and Buck Island Reef National Monument (BUIS) in St. Croix. Current fishery regulations in these parks range from no restrictions (LPNR) to some gear, effort, and size restrictions (VICR, VIIS) to full closure to extractive activities (BUIS). In certain years, sampling was expanded to include nearby areas in Puerto Rico (2009) and St. Croix (2010). The study area in each location included all cross-shelf habitats extending from the shoreline to depths of 30 m. Within each study area, sampling locations were randomly selected among three principal ecological strata—hard bottom, soft bottom, and mangroves—using benthic habitat maps (Kendall et al. 2001). At each location, a trained scientific diver recorded abundance and length measurements (total length, TL) to the nearest 5-cm interval for each fish species along a 25-m × 4-m belt transect (Brock 1954; Menza et al. 2006). A second diver characterized the benthic habitat features within the transect, including depth, substrate composition (percent hard bottom and soft bottom), and cover of stony corals, algae, seagrasses, sponges, gorgonians, and other benthic fauna.

Regionwide probability sampling frame.—Development of the probability sampling frame entailed the following steps: (1) identifying the principal reef fishes, including both fished and nontarget species, to evaluate the stratification options; (2) creating a survey spatial frame incorporating depth and habitat

class as potential stratification variables; and (3) evaluating different stratification options to determine the scheme that balanced maximizing the precision and minimizing the cost (i.e., sample size) of estimating mean fish density.

Survey design analysis was tailored for exploited and non-target species of interest to both fisheries and park managers. The historical sampling data collected from hard-bottom (HB) habitats were used to estimate the mean species occurrence (\bar{P}_{HB}), mean density (number per 100 m² [\bar{D}_{HB}]), and variance of density (s^2_{HB}) in each study area. Our final selection of principal species for the design analysis was based on the following criteria: (1) mean occurrence being above 5% in each study area, (2) there being a mix of exploited and non-target species, and (3) there being representatives from major reef fish taxonomic families (i.e., Epinephelinae, Lutjanidae, and Scaridae).

The survey spatial frame encompassed all mapped hard-bottom habitats at depths <30 m and was divided into three broad subregions based on management zones, each of which included one of the historical study areas (Figure 1): (1) Puerto Rico and surrounding islands (Vieques, Culebra, etc.), (2) St. Thomas–St. John, and (3) St. Croix. To delineate this survey frame, a gridded map was developed in a geographical information system. A grid cell of 50 m × 50 m was selected because it corresponded to the minimum mapping unit used to classify benthic habitats and systematized the position of 25-m-long belt transects into nonoverlapping areas. Average depth was computed for each grid cell and cells with depths >30 m were excluded from the frame. The area of soft-bottom (i.e., mud, sand, macroalgae, and seagrass) and hard-bottom (i.e., linear reef, patch reef, pavement, and scattered coral-rock in sand) habitat classes was computed for each grid cell, and only cells with hard-bottom habitats were included in the frame. To facilitate habitat stratification, a single habitat class was designated for each grid cell. In cases in which multiple hard-bottom classes occurred within the same cell (12% of cells), habitat classes (Kendall et al. 2001) were first grouped into high- and low-complexity categories, with high complexity comprised of linear reef and patch reef and low complexity of pavement and scattered coral-rock in sand. Cells with combined high-complexity habitats accounting for 20% or more of the area were assigned to the linear reef or patch reef category, depending on which had the most area. Otherwise, the cell was assigned the habitat class with the largest area. Fish data from historical visual transects were assigned the habitat class of the corresponding map grid cell.

Stratification schemes were created by investigating the mean and variance properties of the density estimates for the principal species. Mean ± SD density was calculated for each species by study area/subregion (Puerto Rico, St. John, and St. Croix) and hard-bottom habitat class at 3-m depth intervals. Statistical differences in species mean density among potential depth and habitat strata were tested using nonparametric

analysis of variance (ANOVA; Kruskal–Wallis test), which guided the construction of a depth-only stratification scheme (Figure 2a), a habitat-only scheme (Figure 2b), and a combined depth–habitat scheme (Figure 2c).

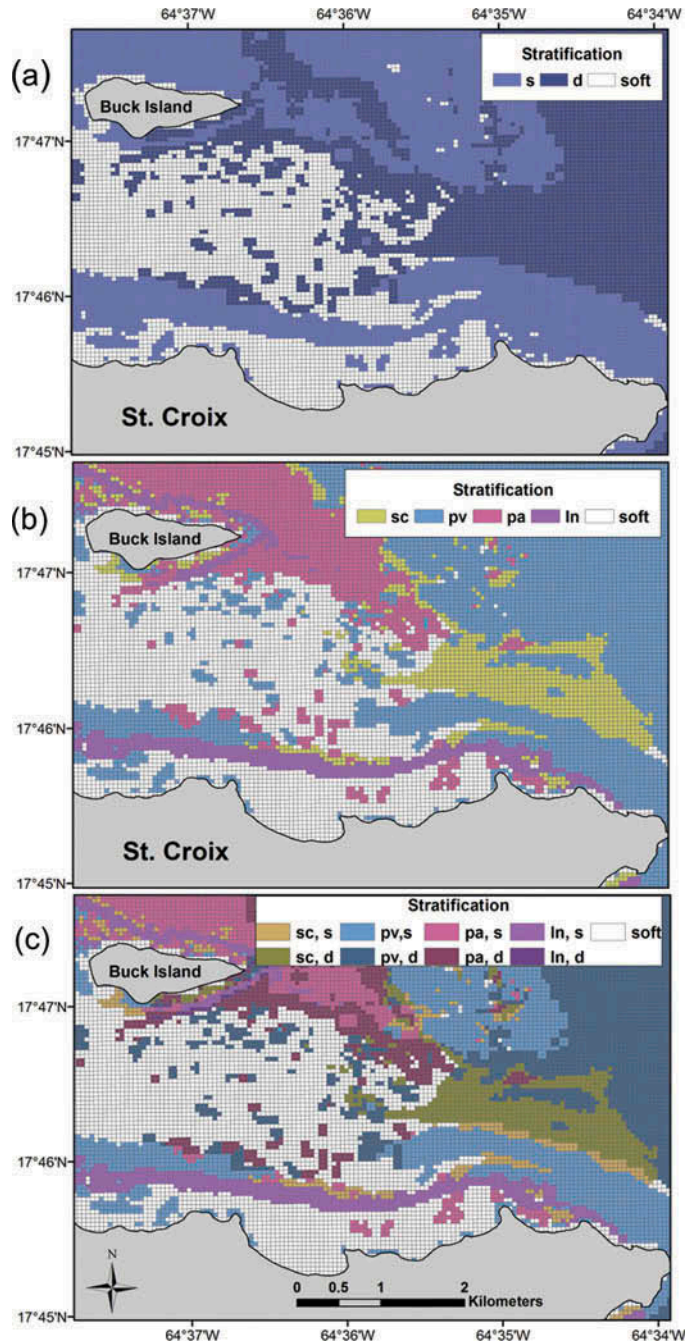


FIGURE 2. Gridded 50-m × 50-m maps of the east end of St. Croix and Buck Island (see Figure 1) illustrating three stratification schemes: (a) depth (shallow [s], <12 m; deep [d], ≥ 12 m), (b) habitat (sc = scattered coral and rock, pv = pavement, pa = patch reef, and ln = linear reef), and (c) combined habitat and depth.

The design performance of the various stratification schemes was evaluated by balancing the trade-off between the precision of the density estimates and survey costs (i.e., sample sizes). The performance measure n^* , the sample size required to achieve a specified variance (Cochran 1977; Ault et al. 1999), was used for the comparison of schemes:

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

where s_h is the standard deviation of density in stratum h , s_h^2 is the sample variance of density in stratum h , w_h is the stratum weighting factor, $V(\bar{D}_{st})$ is the desired variance for the mean density of the survey frame, and N is the total number of possible sample units in the survey frame. Estimation of n^* presumes that sample units are distributed among strata according to a Neyman allocation scheme that accounts for both stratum sizes and variances (Cochran 1977). Desired variance was computed as

$$V(\bar{D}_{st}) = (CV(\bar{D}_{st}) \times \bar{D}_{st})^2, \tag{2}$$

where $CV(\bar{D}_{st})$ is the coefficient of variation of mean density (i.e., the standard error as a proportion of the mean). Following the procedure of Smith and Gavaris (1993), n^* was computed using average strata densities and variances from 2007–2010 visual data. For these data, a sample unit was a single 25-m × 4-m belt transect (100 m²). There were 25 possible sample units per 50-m × 50-m map grid cell (2,500 m²/100 m²). Total sample units N was obtained by summing the number of grid cells in the survey frame and multiplying by 25. The stratum weighting factor was computed as N_h/N ,

where N_h is the number of possible sample units in stratum h . Values of n^* were estimated for the various stratification schemes along with a simple random design for each principal species in each subregion. The optimal design yielding the lowest relative n^* across species and subregions was selected for subsequent feasibility analysis.

Sample size projections.—Using equation (1) and the optimal sampling design, n^* values were projected for U.S. Caribbean-wide surveys that controlled the precision of mean density at three different spatial scales: (1) the entire U.S. Caribbean region with subregions as additional strata, (2) each subregion, and (3) each management zone (inside and outside marine parks) within each subregion. The average annual sample size for the three historical study areas was used as a comparative benchmark to evaluate the feasibility of sampling at a regionwide scale. The dependence of n^* on the size of the sample frame N and the inherent variability of the target population was investigated. Population variability was represented by the scaled metric $CV(D) = s/\bar{D}$, i.e., the sample standard deviation of density expressed as a proportion of the mean.

RESULTS

Regionwide Probability Sampling Frame

Eight ecologically and economically important reef fish species representing seven families were identified to compare stratification schemes and evaluate the feasibility of a regionwide survey (Table 1). Mean percent occurrence ranged from 7% to 83% among species and study areas and generally corresponded with mean density and its associated variance. With the exception of French Grunt, Stoplight Parrotfish, and Queen Triggerfish, species occurrence and density varied among study areas. Together these species comprised a broad range of dietary preferences—e.g., carnivores (Coney,

TABLE 1. Estimates of mean occurrence (\bar{p}_{HB}), mean density (\bar{D}_{HB} [number/100 m²]), and the standard deviation of mean density (s_{HB}) for principal species from historical sampling (2007–2010) on hard-bottom habitat in each subregion. Sample sizes (n) are given for each subregion.

Species	Puerto Rico ($n = 356$)			St. Thomas and St. John ($n = 430$)			St. Croix ($n = 532$)		
	\bar{p}_{HB}	\bar{D}_{HB}	s_{HB}	\bar{p}_{HB}	\bar{D}_{HB}	s_{HB}	\bar{p}_{HB}	\bar{D}_{HB}	s_{HB}
Exploited species									
Coney <i>Cephalopholis fulva</i>	13.5%	0.24	0.75	30.0%	0.98	1.97	54.3%	1.60	2.22
Red Hind <i>Epinephelus guttatus</i>	6.5%	0.07	0.26	34.2%	0.54	1.00	20.5%	0.29	0.66
Yellowtail Snapper <i>Ocyurus chrysurus</i>	46.6%	1.44	3.26	41.4%	1.18	2.44	19.5%	0.50	1.53
French Grunt <i>Haemulon flavolineatum</i> (>10 cm)	35.4%	1.18	4.24	42.1%	0.98	2.34	33.6%	1.08	2.72
Stoplight Parrotfish <i>Sparisoma viride</i>	54.8%	2.03	3.42	57.2%	2.74	3.92	49.8%	2.23	4.25
Queen Triggerfish <i>Balistes vetula</i>	21.3%	0.35	0.90	18.4%	0.29	0.75	22.0%	0.37	0.91
Nontarget and aquarium species									
Foureye Butterflyfish <i>Chaetodon capistratus</i>	71.9%	2.36	2.29	50.9%	1.24	1.82	23.7%	0.50	1.04
Blue Tang <i>Acanthurus coeruleus</i>	50.0%	2.14	6.38	82.6%	4.90	9.41	70.3%	7.21	14.67

TABLE 2. Percent of total area by stratum for each subregion and inside and outside management zones in each subregion. Management zones included La Parguera National Reserve (LPNR), Virgin Islands National Park (VIIS), Virgin Islands Coral Reef National Monument (VICR), and Buck Island Reef National Monument (BUIS). Summed stratum areas and the total number of primary sample units are also provided.

Stratum classification	Puerto Rico			St. Thomas–St. John			St. Croix		
	LPNR (%)	Outside (%)	Subregion Total (%)	VIIS–VICR (%)	Outside (%)	Subregion Total (%)	BUIS (%)	Outside (%)	Subregion Total (%)
Shallow, scattered coral/ rock	5.1	4.0	4.1	5.3	3.8	4.1	4.6	1.3	1.6
Shallow, pavement	5.3	23.9	21.6	24.1	27.0	26.4	40.0	20.0	21.7
Shallow, patch reef	4.1	4.6	4.6	3.6	1.5	2.0	15.2	1.1	2.3
Shallow, linear reef	6.9	7.6	7.5	14.1	8.0	9.2	2.9	4.4	4.3
Deep, scattered coral/rock	4.4	7.0	6.7	6.8	6.9	6.9	2.7	7.1	6.8
Deep, pavement	35.1	41.3	40.5	27.6	33.9	32.6	24.3	63.6	60.2
Deep, patch reef	10.7	8.2	8.5	10.9	4.5	5.8	8.4	0.7	1.4
Deep, linear reef	28.4	3.5	6.5	7.7	14.4	13.0	1.8	1.8	1.8
Total area (km ²)	106.72	779.62	886.34	17.45	68.53	85.98	20.06	216.07	236.13
Total primary sample units	1,067,200	7,796,200	8,863,400	174,475	685,300	859,775	200,600	2,160,700	2,361,300

Red Hind, and Queen Triggerfish), omnivores (Foureye Butterflyfish), and herbivores (Stoplight Parrotfish)—and various schooling and mobility patterns—e.g., large schools with high (Yellowtail Snapper and Blue Tang) and low mobility (French Grunt) as well as solitary species with high (Queen Triggerfish) and low mobility (Coney and Foureye Butterflyfish).

The sum of the 50-m × 50-m hard-bottom grid cells in the U.S. Caribbean survey frame (depth < 30 m) yielded a total area of 1,208 km² and 12,084,475 sample units (100-m² transects) (Table 2). Pavement was the most common habitat class, accounting for 66% of the hard-bottom area. Excluding areas with only 1 year of sampling, the historic study areas in Puerto Rico, St. Thomas–St. John, and St. Croix consisted of 12.8, 38.5, and 15.2% of the mapped hard bottom in each subregion, respectively (Figure 1).

To identify potential stratification variables, the survey frame was partitioned into areas (i.e., strata) with low, moderate, and high variance of mean density based on depth and habitat characteristics (Figure 2). A significant difference in mean density (Kruskal–Wallis test; $P < 0.05$) was detected between depths shallower and deeper than 12 m for 15 of the 24 cases analyzed (8 species × 3 study areas). The differences in mean density (\bar{D}) corresponded to the differences in variance (s^2) since mean and variance were positively correlated. Mean density was significantly different among the four hard-bottom habitat classes in 17 of the 24 cases (Kruskal–Wallis test; $P < 0.05$). A combination depth–habitat scheme was developed using the two depth strata and the four habitat strata. In some cases, mean density and variance

differed mostly by depth (Figure 3a), in others by habitat (Figure 3b) or a combination of depth and habitat (Figure 3c).

Historical (2007–2010) sample sizes by stratum classification (n_h) were generally proportional to stratum areas (w_h) in the different subregions (Table 3). To compare the three stratification schemes, the relationship between survey precision, $CV(\bar{D}_{st})$, and sample size n^* was evaluated (equations 1 and 2) for each scheme and each species–subregion combination. The strata estimates and precision–sample size curves for Blue Tang are presented in Table 3 and Figure 4, respectively. Both the simple random (SRS) and depth–habitat stratified random (StRS) sampling schemes exhibited an initial rapid increase in precision (decline in $CV(\bar{D}_{st})$) with increasing n , followed by a much smaller, asymptotic increase as n increased (Figure 4a). At all values of n , precision was higher for the StRS design than for the SRS design. Likewise, for a fixed level of precision, $CV(\bar{D}_{st})=15\%$, the StRS design required a sample size of $n = 77$, compared with $n = 164$ for the SRS design. Comparisons for the n^* performance measure at $CV(\bar{D}_{st}) = 15\%$ are summarized in Table 4 for each species and subregion. The $n^*_{15\%}$ values estimated for the depth-only and habitat-only StRS designs were in most cases lower than those of the SRS design, indicating that both stratification variables successfully partitioned variance. Subregion was an important stratification variable as well for some species (e.g., Figure 4b). A comparison of n^* estimates among subregions by species suggests that for some species–subregion cases a depth-only or habitat-only scheme

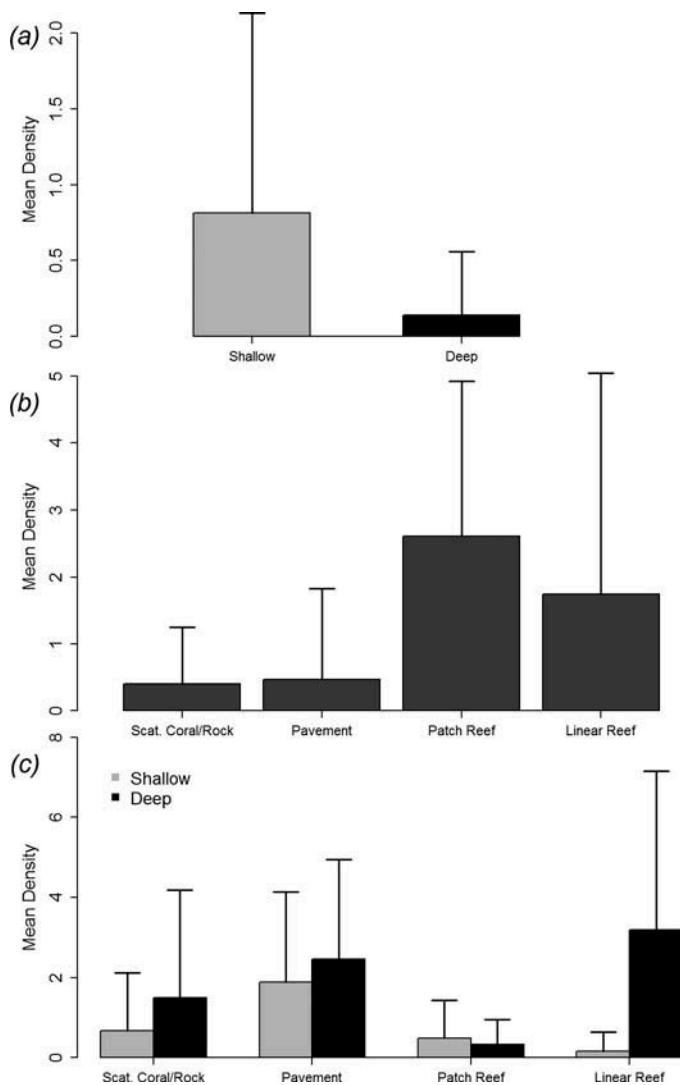


FIGURE 3. Mean densities (number/100 m²) of (a) Queen Triggerfish in St. Croix by depth (shallow, <12 m; deep, 12–30 m), (b) Yellowtail Snapper in St. Thomas–St. John by habitat, and (c) Coney in St. Croix by depth and habitat. Error bars = SDs.

would be the most efficient, but overall the combined depth–habitat stratification scheme provided the lowest estimates of $n^*_{15\%}$ in 59% of the species–subregion cases and the second lowest estimates in an additional 29% of cases.

Sample Size Projections

The projected sample size required for the depth–habitat StRS design to achieve a precision of 15% for $CV(\bar{D}_{st})$ was highly dependent on the spatial frame for controlling precision (Table 5). For each principal species, projected values of $n^*_{15\%}$ for a U.S. Caribbean–wide survey progressively increased as the control of precision changed from the entire region (one overall density estimate), to each subregion (three separate density estimates), to each management zone within

each subregion (six separate density estimates). The projected values of $n^*_{15\%}$ were on average lower than historic sample sizes at the region level, approximately equal to historic sample sizes at the subregion level, and higher at the management zone level.

Estimates of n^* were more dependent on the inherent variance properties of a given target population than on the sheer size of the survey frame (Figure 5). To illustrate this, we computed $CV(D)$, a measure of sample variance, for each species and subregion (Table 3). $CV(D)$ differs from $CV(\bar{D}_{st})$ because it is a measure of the underlying variability in a population, whereas $CV(\bar{D}_{st})$ is a measure of survey precision and can be controlled by the number of samples collected (n). Plots of the estimated values of $n^*_{15\%}$ against $CV(D)$ by species and subregion (Figure 5a) show that sample size requirements increased with increasing variance. Figure 5b portrays the relationship between $n^*_{15\%}$ and N for two species (Blue Tang and Yellowtail Snapper) in two subregions (Puerto Rico and St. Thomas–St. John). Each line was produced using equation (1) by keeping stratum size (w_h) and variance (s_h) constant and varying the size of the associated survey frame N . The graph shows that $n^*_{15\%}$ reached asymptotic values at relatively small survey frame sizes ($N = 1,000$ to 10,000) compared with the actual survey frame sizes of 859,775 for St. Thomas–St. John and 8,863,400 for Puerto Rico. For each species, the asymptotic value of $n^*_{15\%}$ was highest in the more variable subregion, which corresponded to the larger subregion of Puerto Rico for Blue Tang and to the smaller subregion of St. Thomas–St. John for Yellowtail Snapper. Comparison of the relationship of n^* to N between subregions and marine parks within subregions is shown for Blue Tang in Figure 5c. The asymptotic values of $n^*_{15\%}$ were similar for marine parks and their respective subregions, even though the survey frames of the parks comprised a small fraction of the associated subregion survey frames (12% in Puerto Rico and 20% in St. Thomas–St. John). However, estimates of $CV(D)$ for this species were similar between parks and their subregions.

DISCUSSION

By taking advantage of existing mapping and monitoring data (Kendall et al. 2001; Menza et al. 2006; Friedlander et al. 2013), we developed a probability sampling frame for a visual survey of shallow-water reef fishes in the U.S. Caribbean region. Stratification by depth and habitat produced a more efficient survey design (i.e., one with greater precision at lower sample sizes) for estimating mean fish density than simple random sampling. At the spatial scales relevant for fisheries management (i.e., regions or subregions), the projected sample sizes for achieving moderately high levels of survey precision were comparable to historical annual sampling effort. However, controlling survey

TABLE 3. Estimates of the number of samples (n_h), weighting factor (w_h), Blue Tang mean density (\bar{D}_h [number/100 m²]), and standard deviation (s_h) for each stratum h by subregion in 2007–2010 sampling. Totals are given for each subregion, along with the equations used to compute them.

Stratum classification and statistic	Puerto Rico				St. Thomas–St John				St. Croix			
	n_h	w_h	\bar{D}_h	s_h	n_h	w_h	\bar{D}_h	s_h	n_h	w_h	\bar{D}_h	s_h
Shallow, scattered coral/rock	9	0.04	1.33	2.24	35	0.04	2.89	3.61	25	0.02	5.84	7.81
Shallow, pavement	60	0.22	2.83	9.40	89	0.26	5.16	5.60	227	0.22	6.69	15.01
Shallow, patch reef	9	0.05	4.00	3.08	45	0.02	3.64	5.01	56	0.02	13.82	18.29
Shallow, linear reef	48	0.08	5.92	11.36	115	0.09	8.43	16.14	43	0.04	15.91	25.06
Deep, scattered coral/rock	13	0.07	1.31	2.29					20	0.07	1.30	2.25
Deep, pavement	188	0.41	1.04	3.19	102	0.39	2.90	3.33	129	0.60	2.50	4.64
Deep, patch reef	2	0.08	0.50	0.71	10	0.06	3.00	4.94	27	0.01	11.96	12.41
Deep, linear reef	27	0.06	1.67	1.96	34	0.13	2.56	3.20	5	0.02	8.20	8.61
$n = \sum_h n_h$	356				430				532			
$\bar{D}_{st} = \sum_h w_h \bar{D}_h$			1.95				3.98				4.45	
$s_{st} = \sqrt{\sum_h w_h^2 s_h^2}$				2.57				2.54				4.45
$CV(D) = s_{st} / \bar{D}_{st}$				1.32				0.64				1.00

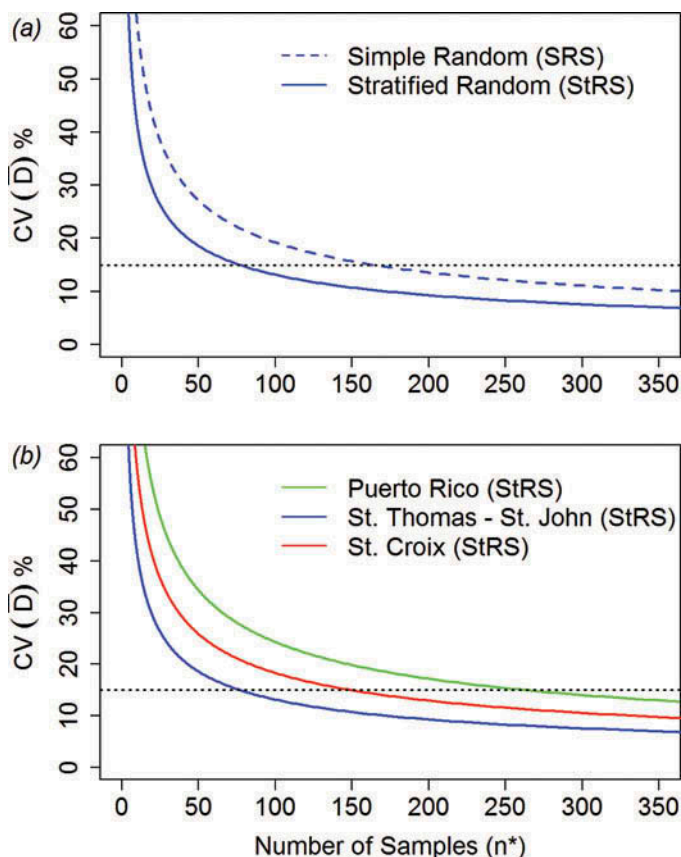


FIGURE 4. Blue Tang (2007–2010) survey precision as a function of sample size for (a) simple random and depth–habitat stratified random sample designs in St. Thomas–St. John and (b) the depth–habitat stratified design in Puerto Rico (green), St. Thomas–St. John (blue), and St. Croix (red). Dotted horizontal lines indicate a $CV(\bar{D}_{st})$ of 15%.

precision at the spatial scales relevant for marine park management (i.e., inside and outside management zones) would likely require sample sizes about twice the level of historical effort.

An underlying assumption in our analysis was that the mean stratum densities (\bar{D}_h) and variances (s_h^2) estimated for the different study areas are representative of the non-sampled areas in the different subregions. Our results show some inconsistencies in the importance of depth and habitat class as stratification variables among subregions, indicating that the study areas may not be fully representative of the larger sampling frame. In the St. Croix study area, a depth-only stratification appeared to be as efficient as the depth–habitat scheme, whereas in Puerto Rico a habitat-only stratification performed as well as the 8-strata combination scheme (Table 4). The strategy of identifying a single stratification scheme (combination of depth and habitat) that performed well for all three subregions and a diverse group of species was an attempt to minimize potential discrepancies in density mean–variance patterns between study areas and their respective subregions. However, we will not know the degree to which this assumption was violated until a regionwide survey has been conducted and analyzed. In the worst case, stratum variances for previously nonsampled areas will likely be higher than those predicted, resulting in less precise estimates than expected. As with any survey, predicted sample sizes are only as good as prior knowledge. As new data are collected, the survey design can be iteratively updated to incorporate the new information and the error of the estimates will decrease.

TABLE 4. Estimated number of samples (n^*) required to achieve a precision of 15% ($CV[\bar{D}_{st}]$) for eight principal species in the Puerto Rico, St. Thomas–St. John, and St. Croix subregions. Four stratification schemes were compared: depth, habitat, habitat and depth, and no stratification, which is equivalent to a simple random design. Gray shading represents the most efficient stratification schemes. Species codes are as follows: CEFU (Coney), EPGU (Red Hind), OCCH (Yellowtail Snapper), HAFL (French Grunt), SPVI (Stoplight Parrotfish), BAVE (Queen Triggerfish), CHCA (Four-eye Butterflyfish), and ACCO (Blue Tang).

Subregion	Stratification	Number of Strata	n^* (15%)							
			CEFU	EPGU	OCCH	HAFL	SPVI	BAVE	CHCA	ACCO
Puerto Rico	Random	1	414	672	228	577	126	294	42	396
	Depth	2	404	682	224	465	107	271	42	279
	Habitat	4	395	611	177	476	92	272	41	283
	Habitat and depth	8	336	646	168	340	101	250	34	263
St. Thomas–St. John	Random	1	179	150	190	252	91	309	95	164
	Depth	2	53	136	267	262	123	111	82	115
	Habitat	4	119	135	177	273	103	182	86	100
	Habitat and depth	8	48	124	214	254	121	96	82	77
St. Croix	Random	1	85	232	414	282	162	272	193	184
	Depth	2	71	207	403	235	160	136	175	156
	Habitat	4	64	224	485	280	151	225	216	205
	Habitat and depth	8	55	209	424	246	120	114	187	149

Our multispecies, multiarea analysis strategy also led to some interesting insights concerning the relationships of survey precision ($CV[\bar{D}_{st}]$) and sample size (n^*) to the size of the sample frame (N) and the inherent variability of the target population ($CV[D]$). Not surprisingly, more-variable target

populations required larger sample sizes to control survey precision (Figure 5). A somewhat counterintuitive finding was that controlling survey precision over a large spatial scale (i.e., region) required less sampling than controlling precision for multiple smaller areas within the larger frame

TABLE 5. Projected number of samples (n^*) required to achieve a precision of 15% ($CV[\bar{D}_{st}]$) for mean density at the region, subregion, and management zone levels for principal species using the habitat–depth stratification. The percentage of hard-bottom habitat inside and outside of the management zones is given in parentheses by subregion. Annual average (2007–2010) historical sampling effort (n) for all habitat types is included as a reference for feasibility. See Table 4 for species codes.

Spatial frame for controlling precision	Historic n	$n^*_{15\%}$								Average
		CEFU	EPGU	OCCH	HAFL	SPVI	BAVE	CHCA	ACCO	
U.S. Caribbean region (1,208 km ²)	545	98	284	196	327	105	184	41	197	179
Subregions										
Puerto Rico (886 km ²)	181	336	646	168	340	101	250	34	263	267
St. Thomas–St. John (86 km ²)	162	48	124	214	254	121	96	82	77	127
St. Croix (236 km ²)	202	55	209	424	246	120	114	187	149	188
Subregion total	545	439	979	807	839	342	460	303	489	582
Management zones within subregions										
LPNR (12.0%)		326	672	100	209	67	200	34	192	225
Outside (88.0%)		394	679	156	350	104	251	35	276	281
Puerto Rico total	181	719	1,351	256	559	171	451	69	467	505
VIIS–VICR (20.3%)		44	93	163	262	73	82	86	84	111
Outside (79.7%)		48	124	233	259	125	95	80	74	130
St. Thomas–St. John total	162	92	218	396	522	198	177	166	158	241
BUIS (8.5%)		44	228	339	163	71	244	116	70	159
Outside (91.5%)		54	209	428	251	128	111	188	153	190
St. Croix total	202	97	437	767	415	199	356	304	223	350
Management zone total	545	909	2,006	1,419	1,495	568	983	539	849	1,096

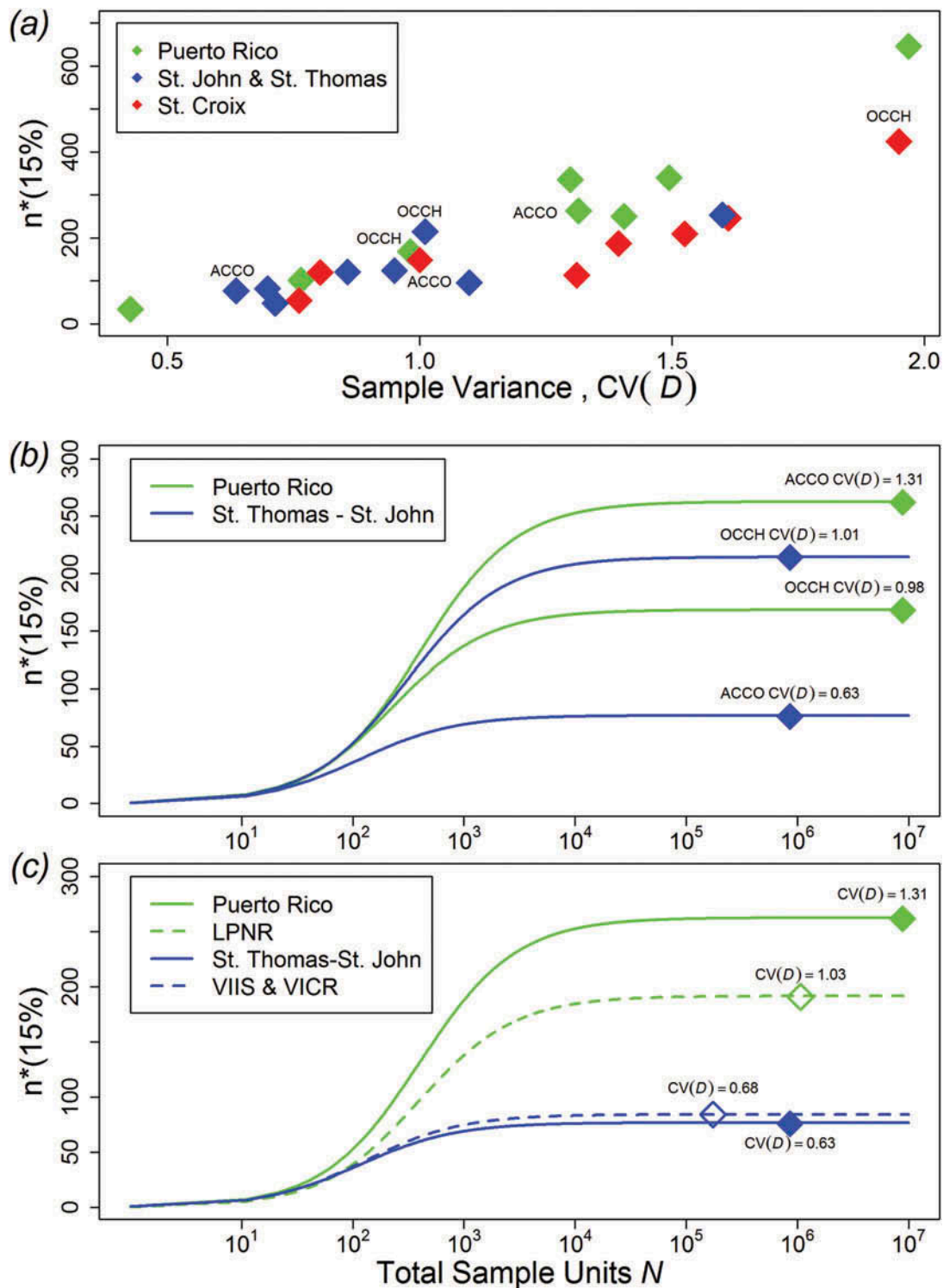


FIGURE 5. Relationships between $n^*(15\%)$ —the number of samples required to achieve a target $CV(\bar{D}_{st})$ of 15%—sample variance ($CV(D)$) and total possible sample units (N). Panel (a) shows a linear relationship between $n^*(15\%)$ and $CV(D)$ for all combinations of species and subregions (24 cases). Panels (b) and (c) illustrate the greater influence of sample variance on $n^*(15\%)$ in comparison to N . Diamonds indicate the true N and estimated n^* for each species and spatial frame. Panel (b) shows values of $n^*(15\%)$ for Blue Tang (ACCO) and Yellowtail Snapper (OCCH) in Puerto Rico (886 km²) and St. Thomas–St. John (86 km²) over a range of hypothetical total survey frame sample units (N). Panel (c) shows values of $n^*(15\%)$ for Blue Tang in Puerto Rico, La Parguera National Reserve (LPNR; 107 km²), St. Thomas–St. John, and Virgin Islands National Park (VIIS) and Virgin Islands Coral Reef National Monument (VICR) (17 km²) over a range of hypothetical values for N .

(Table 5). This property is illustrated in the n^*-N curves of Figure 5b and 5c. For a given level of $CV(D)$, the sample size required to achieve a 15% survey precision was the same over a wide range of survey frame sizes, generally from 10,000–10,000,000, or in terms of area from 1 to 1,000 km². This size range encompasses areas ranging from the smallest management zone of 17 km² (VIIS and VICR in St. Thomas–St. John) to nearly the entire U.S. Caribbean region (1,208 km²). The minimal influence of N on estimates of n^* is exhibited in the species-averaged results (Table 5). These show that controlling precision for surveys in three subregions would require about three times the level of sampling as that for a single regionwide survey and that controlling precision for surveys in six subregion management zones would require about six times the level of sampling.

The properties of survey precision, sample size, and N for probability surveys work in favor of achieving fisheries management objectives. Stock assessments for exploited reef fishes in the U.S. Caribbean region will generally require population data at the region or subregion spatial scales. Our analysis indicates that applying the annual sample sizes achieved in the historical marine park studies would be sufficient for conducting probability surveys at the subregion scale and more than sufficient for surveys at the region scale. Redistributing the sampling effort from the historical study areas to their respective subregion survey frames would increase the complexity of the field operations but would not require a change in the overall n . Population indicator variables (e.g., average size and relative abundance) estimated from a single, well-executed stratified random survey would be of immediate use for an initial determination of reef fish sustainability status via an increasing suite of data-limited assessment methods (Ault et al. 1998, 2005b, 2008, 2014; Hordyk et al. 2014; Nadon et al. 2015). Moreover, conducting these surveys on a regular basis (i.e., every 1–2 years) would eventually provide population-level time series data amenable to potentially more sophisticated stock assessment approaches using biomass-dynamic and age/size cohort-structured models (Quinn and Deriso 1999; Haddon 2011; Methot and Wetzel 2013).

The marine resources of the U.S. Caribbean region are currently managed by multiple local and federal agencies with slightly different objectives and priorities, including both fishery and biodiversity goals. The same properties of probability surveys that are favorable for fisheries management objectives work against the objectives of marine spatial zone management. Our results show that sampling to control precision and thus detect differences in fish density between managed and nonmanaged areas within a subregion (e.g., inside and outside BUIS in St. Croix) would generally require twice the sample size needed to control precision at the same level for the subregion as a whole (St. Croix). In addition, sample size requirements varied substantially

depending on the species and spatial scales for estimation. These findings underscore the importance of establishing clear objectives for probability surveys with respect to target species and management priorities (e.g., stock assessment or spatial management), as discussed in Smith et al. (2011). In situations in which rare species (<5% occurrence) are of management concern, the required number of samples needed to detect significant differences at the 15% level can be far greater than the sample sizes projected here and potentially infeasible given typical survey budgets.

Our analysis of survey feasibility made use of a stratification scheme based on depth and habitat, fundamental factors known to influence the occurrence and abundance of reef fish (Luckhurst and Luckhurst 1978; Friedlander and Parrish 1998; Chapman and Kramer 1999). However, the scheme was fairly simplistic and likely has ample room for improvement. As shown in Figure 4a, improved stratification (and thus more informed partitioning of spatial variance) can improve survey efficiency, resulting in a downward and leftward shift of precision–sample size curves. An initial full-frame survey would provide the fundamental data for refining the stratification scheme using principles of resource selection theory and other analysis techniques for evaluating animal use of habitats (Steffánsson 1996; Manly et al. 2002; Schnute and Haigh 2003). These analyses would focus on identifying improved abiotic and biotic environmental variables (e.g., habitat complexity, patchiness, benthic cover, etc.) that would better partition the variance of fish density (Smith and Gavaris 1993; Ault et al. 1999) and thus lower sample size requirements for tracking populations inside and outside of management zones.

ACKNOWLEDGMENTS

We thank K. Buja for technical mapping assistance. We appreciate the critical review of this manuscript by M. Kendall, R. Clark, and A. Atkinson. We also acknowledge the dozens of divers who collected the significant amount of field data used for these analyses. The research was facilitated through National Park Service (NPS) Cooperative Ecosystems Study Unit Agreement H5000060104 by funding provided by the NPS South Florida and Caribbean Network. Funding for the 2007–2010 surveys was provided by the NPS, the NOAA Coral Reef Conservation Program, and the National Marine Fisheries Service Southeast Fisheries Science Center (NA10OAR4320143). The data are housed at the National Centers for Coastal Ocean Science Web site (<http://www8.nos.noaa.gov/bpdmWeb/>).

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