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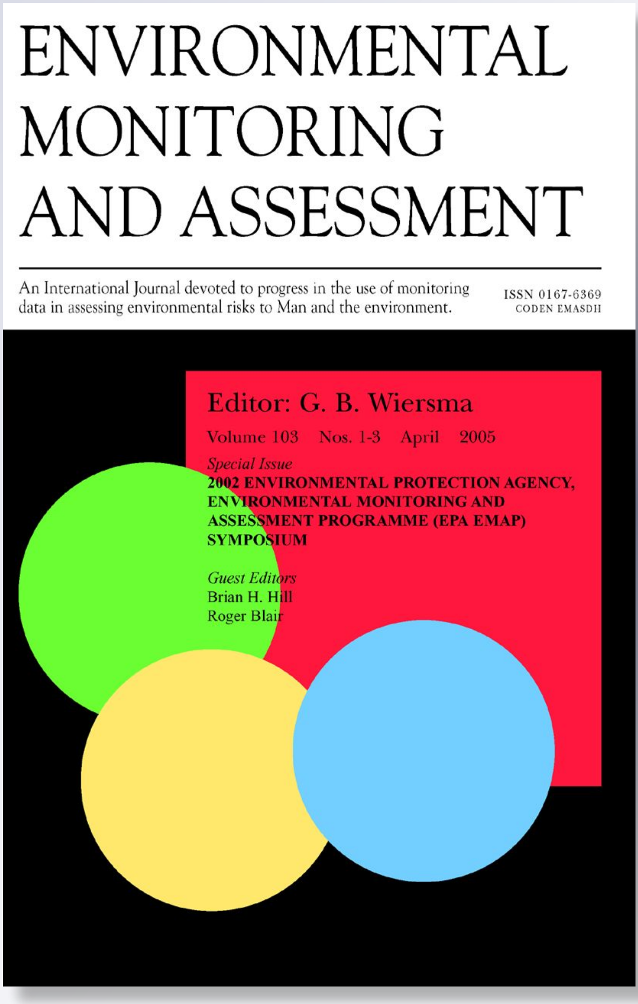

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Abstract Principles of probability survey design were applied to guide large-scale sampling of populations of stony corals and associated benthic taxa in the Florida Keys coral reef ecosystem. The survey employed a two-stage stratified random sampling design that partitioned the 251-km^2 domain by reef habitat types, geographic regions, and management zones. Estimates of the coefficient of variation (ratio of standard error to the mean) for stony coral population density and abundance ranged from 7% to 12% for four of six principal species. These levels of survey precision are among the highest reported for comparable surveys of marine species. Relatively precise estimates were also obtained for octocoral density, sponge frequency of occurrence, and benthic cover of algae and invertebrates. Probabilistic survey design techniques provided a robust framework for estimating population-level metrics and optimizing sampling efficiency.

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Keywords Coral reefs · Stratified random survey design · Population estimation

Introduction

Prior to observations of dramatic coral reef declines in Florida, the Caribbean (Gardner et al. 2003), and the Pacific (Done 1999), monitoring programs focused on questions of ecology, addressing how predation, competition, zonation, and disturbance affected coral community dynamics (e.g., Loya 1972; Lang 1973; Connell 1973). Typically, these studies were conducted at single reefs or were restricted to a limited number of habitat types. Still, much was learned about processes affecting the structure and dynamics of coral reefs (Grigg and Maragos 1974; Burns 1983). By the 1980s, monitoring programs adopted many of the methods and statistics of experimental ecology to assess population status and trends. While these programs documented coral declines at specific sites from various causes such as coastal development, pollution, overfishing, and coral disease and bleaching (Brown and Howard 1985; Glynn 1996; Knowlton 2001), none were conducted in a manner that allowed extrapolation from a single or a few reefs being monitored to the population level.

Interestingly, field methodologies and statistical designs used to monitor and assess coral reefs have changed little since the 1980s. While there is generally little debate about the mechanics of sampling reefs (e.g., transects or quadrats, randomization, etc.), survey designs at the appropriate scale that achieve population-level assessments for coral reefs are rarely implemented (Risk and Risk 1997; Lewis 2004; Santavy et al. 2005). Population-level estimates are fundamental components of ecosystem management (Waddell and Clarke 2008; Levin et al. 2009), and the lack thereof has hindered understanding of coral reef dynamics and how these may be influenced by environmental- and anthropogenic-induced changes.

Survey design is a long-standing, theoretically and methodologically advanced field of statistics developed for the specific purpose of estimating abundance metrics—means, proportions, totals—for a population within a finite spatial domain (Hansen et al. 1953; Cochran 1977; Särndal et al. 1992; Lohr 1999). Probabilistic survey design principles have been successfully applied for decades in a variety of disciplines including agriculture (Sen 1964), human health (Korn and Graubard 1999), and natural resources (Hughes et al. 2000). In marine ecosystems, this approach has been commonly applied in surveys of exploited populations of fishes and macroinvertebrates (Smith and Gavaris 1993; Ault et al. 1999; Folmer and Pennington 2000; Smith and Tremblay 2003; Smith et al. 2011), and has been used in the evaluation of predator–prey interactions between marine mammals and fishes (Wright et al. 2007). These statistical techniques have the advantage of generating population-level metrics, as well as optimizing sampling efficiency to obtain high precision estimates at low sample sizes.

In this paper, we present a novel application of probability survey design principles to guide sampling and estimation of stony coral population density and abundance, benthic cover, and the prevalence of bleaching and disease in the Florida Keys. We show how current design performance can be evaluated through balancing trade-offs between the precision of population density estimates and survey costs, and introduce methods to optimize future surveys.

Methods

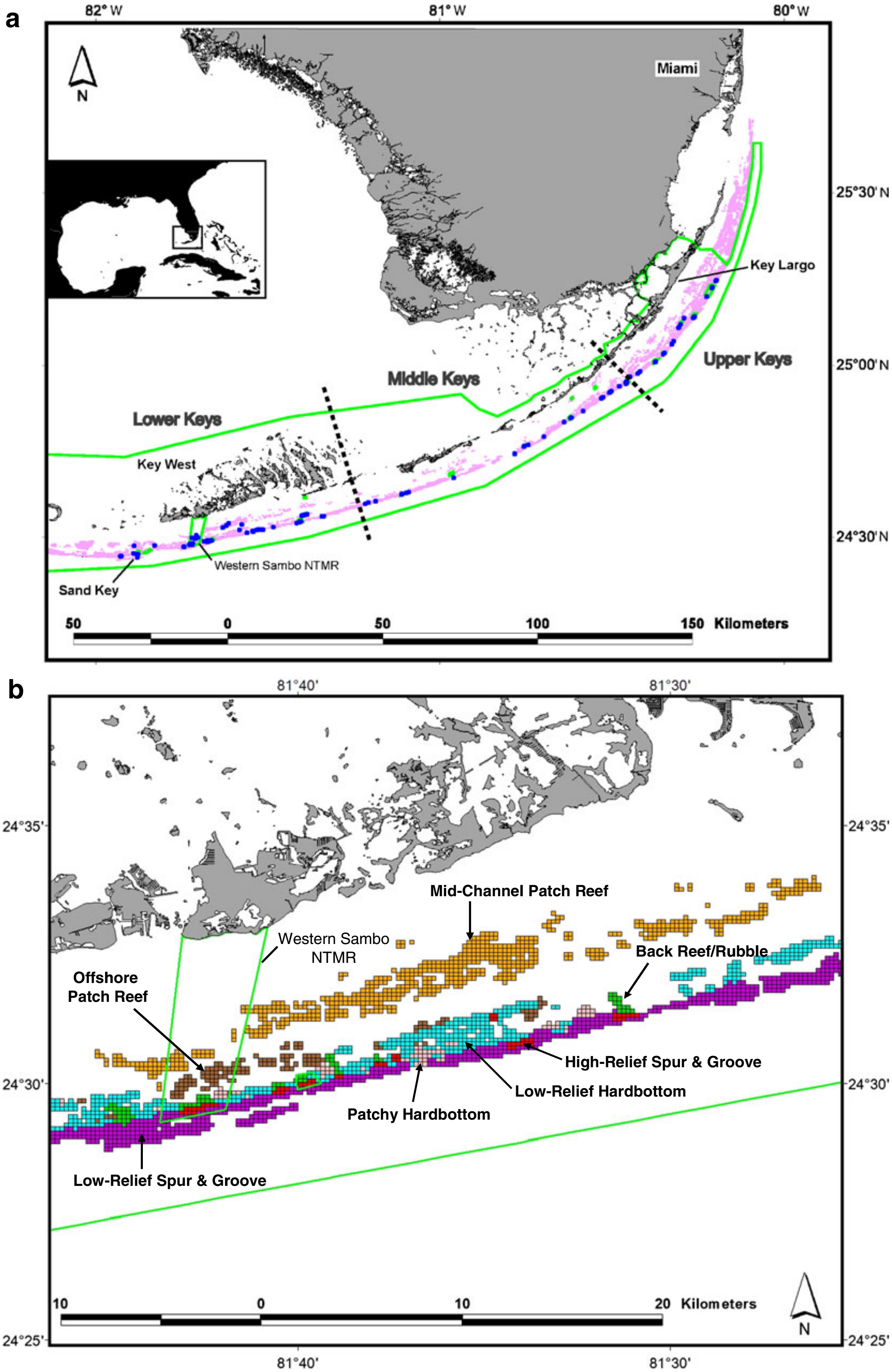
Study area

The study area was the Florida Keys coral reef system (Fig. 1), which is comprised of a semi-continuous series of bank-barrier reefs that extend along the seaward edge of the southeast Florida shelf between Miami and Key West, and includes associated patch reefs located between the fore reef and the barrier islands of the Florida Keys (Jaap 1984; FMRI 1998).

Field protocols

Field sampling protocols were adapted from Aronson et al. (1994) and the Atlantic and Gulf Rapid Reef Assessment program (Kramer and Lang 2003) to capture both community-level metrics such as benthic cover and population-level metrics such as density/abundance and size composition. Stony corals (Order Milleporina and Scleractinia) were the principal focus of the sampling surveys. Stony coral colonies were separated by size into juvenile and adult life stages, with colonies less than 4 cm in maximum diameter considered juveniles following Bak and Engel (1979) and others. Colony density within 10 m^2 belt transects (0.4 m × 25 m) and size measurements (maximum diameter, maximum height, and perpendicular diameter) were obtained for adults of each species present. An individual colony was considered to be a continuous skeletal unit, so that a colony that was part of the same skeleton but divided into two or more separate pieces of live tissue was still considered to be one colony.

Fig. 1 **a** Primary sample unit locations (*blue dots*) for the ▶ Florida Keys sampling survey. Boundaries for the Florida Keys National Marine Sanctuary and associated no-take marine reserves (NTMRs) are shown in *green*, coral reef habitats are shown in *pink*, and geographic regions (upper, middle, lower) are demarcated by *black dashed lines*. **b** Cross-shelf distribution of coral reef and hard-bottom habitat types in the vicinity of Western Sambo NTMR (see **a**) overlain with the 200 m by 200 m primary unit sampling grid


a
82° W
81° W
80° W
N
Miami
25°30' N
Key Largo
Upper Keys
25°00' N
Middle Keys
Lower Keys
Key West
24°30' N
Western Sambo NTMR
Sand Key
50 0 50 100 150 Kilometers
b
81°40'
81°30'
24°35'
Mid-Channel Patch Reef
Western Sambo NTMR
Back Reef/Rubble
Offshore Patch Reef
High-Relief Spur & Groove
24°30'
Low-Relief Hardbottom
Patchy Hardbottom
Low-Relief Spur & Groove
10 0 10 20 Kilometers
N
24°25'

Colony condition factors such as disease, bleaching, and predation were recorded when present.

Octocoral species density and sponge species frequency of occurrence were recorded within 0.4 m by 25 m belt transects. Using the linear point–intercept technique of Liddell and Ohlhorst (1987), benthic cover was determined under points placed at 25 cm intervals along the 25 m transect for a total of 100 points surveyed per transect. Organisms were identified to the lowest taxonomic level possible and placed into several groups: stony corals by species; octocorals by morphology (branching vs. encrusting); sponges; and, algae by functional group (Bradbury et al. 1986).

Spatial sampling framework

The Florida Keys survey area included about 50% of the mapped live coral habitats between Miami and Key West and contained apparent along-shelf and cross-shelf gradients of reef and hard-bottom habitats. Along-shelf components were comprised of fore reef habitats less than 15 m deep extending about 205 km from northern Key Largo to Sand Key southwest of Key West (Fig. 1a). Cross-shelf (nearshore to offshore) components included the patch reefs and fore reef habitats in the lower Florida Keys (Fig. 1b).

To control for spatial variation in population abundance metrics, the survey domain was divided into strata based upon: (1) habitat type; (2) geographic region; and, (3) management zones of the Florida Keys National Marine Sanctuary (FKNMS). Eight cross-shelf habitat types were designated using regional benthic habitat maps (FMRI 1998; Fig. 1b). The reef habitat classification scheme accounted for features that correlate with benthic fauna distributions, including cross-shelf position, topographic complexity, and the proportion of sand interspersed among hard-bottom structures. A geographic regional stratification variable (upper, middle, and lower Keys; Fig. 1a) was used to account for oceanographic and geological features in the Florida Keys that influence the distribution, community dynamics, and biotic composition of reefs (Marszalek et al. 1977; Shinn et al. 1977). FKNMS management zones (i.e., no-take marine reserves) were incorporated as a third stratification variable that delineated areas open and closed to consumptive activities (Fig. 1).

A geographic information system containing digital layers for benthic habitat (FMRI 1998), bathymetry (National Geophysical Data Center, Silver Spring, Maryland), and no-take marine reserve boundaries (Florida Keys National Marine Sanctuary, Marathon, Florida) was used to facilitate delineation of the sampling survey area, strata, and sample units. Map resolution was such that the survey domain was divided into a grid with individual cells of size 200 m by 200 m (40,000 m^2) that defined unique habitat types (Fig. 1b). A two-stage sampling scheme following Cochran (1977) was employed to account for the disparity in size between the grid cell minimum mapping unit (40,000 m^2) and the belt transect (10 m^2). Grid cells containing reef habitats were designated as primary sample units. Belt transects were designated as the second-stage sample units (SSU). The size of an individual primary sampling unit allowed divers to swim to the location of any given second-stage sampling unit from a moored vessel.

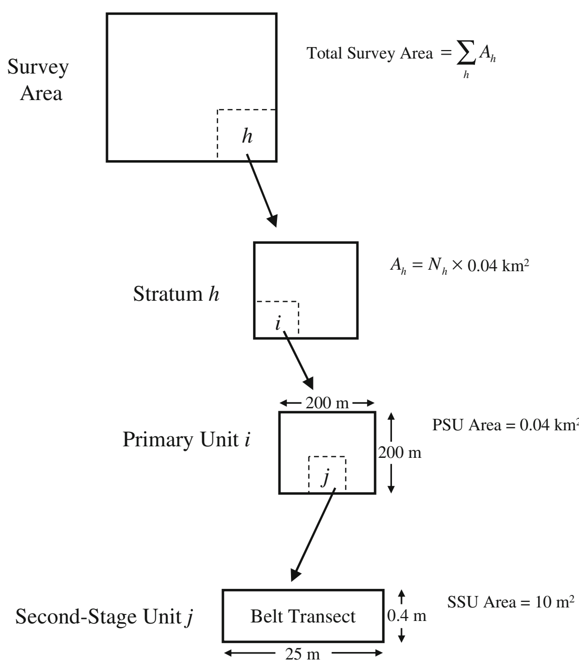


Fig. 2 Conceptual diagram of the survey area, strata, and sample units for a two-stage stratified random survey design. Symbols are defined in Table 1

Table 1 Glossary of statistical symbols and computational formulae used in the Florida Keys coral reef sampling survey

Symbol	Definition	Computational formula	Equation number
h	Stratum subscript		
i	Primary sample unit (PSU) subscript		
j	Second-stage sample unit (SSU) subscript		
M_{hi}	Total possible number of SSUs in PSU i in stratum h		
N_h	Total possible number of PSUs units in stratum h		
A_h	Area of stratum h		
$N_h M_h$	Total possible number of SSUs in stratum h		
w_h	Stratum h weighting factor	$w_h = \frac{N_h M_h}{\sum_h N_h M_h}$	T-1
D_{hij}	Density (individuals) in SSU j in PSU i in stratum h		
m_{hi}	Number of SSUs sampled in PSU i in stratum h		
$\bar{D}_{hi}$	Mean density in PSU i in stratum h	$\bar{D}_{hi} = \frac{1}{m_{hi}} \sum_j D_{hij}$	
n_h	Number of PSUs sampled in stratum h		
$\bar{\bar{D}}_h$	Mean density in stratum h	$\bar{\bar{D}}_h = \frac{1}{n_h} \sum_i \bar{D}_{hi}$	T-2
s_{1h}^2	Sample variance among PSUs in stratum h	$s_{1h}^2 = \frac{\sum_i \left(\bar{D}_{hi} - \bar{\bar{D}}_h\right)^2}{n_h - 1}$	
s_{2h}^2	Sample variance among SSUs in stratum h	$s_{2h}^2 = \frac{1}{n_h} \sum_i \left[\frac{\sum_j \left(D_{hij} - \bar{D}_{hi}\right)^2}{m_{hi} - 1} \right]$	
$\bar{m}_h$	Average number of SSUs sampled per PSU in stratum h	$\bar{m}_h = \frac{1}{n_h} \sum_i m_{hi}$	
$n_h m_h$	Number of SSUs sampled in stratum h		
$\text{var}\left[\bar{\bar{D}}_h\right]$	Variance of mean density in stratum h	$\text{var}\left[\bar{\bar{D}}_h\right] = \frac{\left(1 - \frac{n_h}{N_h}\right)}{n_h} s_{1h}^2 + \frac{\frac{n_h}{N_h}\left(1 - \frac{\bar{m}_h}{M_h}\right)}{n_h m_h} s_{2h}^2$	T-3
$\bar{\bar{D}}_{st}$	Survey-wide mean density	$\bar{\bar{D}}_{st} = \sum_h w_h \bar{\bar{D}}_h$	T-4
$\text{var}\left[\bar{\bar{D}}_{st}\right]$	Variance of survey-wide mean density	$\text{var}\left[\bar{\bar{D}}_{st}\right] = \sum_h w_h^2 \text{var}\left[\bar{\bar{D}}_h\right]$	T-5
$\hat{Y}_h$	Abundance (number of animals) in stratum h	$\hat{Y}_h = \left(\bar{\bar{D}}_h\right)(N_h M_h)$	T-6
$\text{var}\left[\hat{Y}_h\right]$	Variance of abundance in stratum h	$\text{var}\left[\hat{Y}_h\right] = \text{var}\left[\bar{\bar{D}}_h\right](N_h M_h)^2$	T-7
$\hat{Y}_{st}$	Survey-wide abundance	$\hat{Y}_{st} = \sum_h \hat{Y}_h$	T-8
$\text{var}\left[\hat{Y}_{st}\right]$	Variance of survey-wide abundance	$\text{var}\left[\hat{Y}_{st}\right] = \sum_h \text{var}\left[\hat{Y}_h\right]$	T-9
nm	Total SSUs sampled in the survey domain		
n	Total PSUs sampled in the survey domain		
p_{hij}	Proportion cover or occurrence for SSU j in PSU i in stratum h		

Table 1 (continued)

Symbol	Definition	Computational formula	Equation number
$\bar{p}_{hi}$	Mean proportion in PSU *i* in stratum *h*	$\bar{p}_{hi} = \frac{1}{m_{hi}} \sum_j p_{hij}$	
$\bar{\bar{p}}_h$	Mean proportion in stratum *h*	$\bar{\bar{p}}_h = \frac{1}{n_h} \sum_i \bar{p}_{hi}$	
s_{1h}^2	Sample variance among PSUs in stratum *h*	$s_{1h}^2 = \frac{\sum_i \left(\bar{p}_{hi} - \bar{\bar{p}}_h\right)^2}{n_h - 1}$	
s_{2h}^2	Sample variance among SSUs in stratum *h*	$s_{2h}^2 = \frac{1}{n_h}\left[\sum_i \left(\frac{m_{hi}}{m_{hi}-1}\right)(\bar{p}_{hi})(1-\bar{p}_{hi})\right]$	
$\mathrm{var}\left[\bar{\bar{p}}_h\right]$	Variance of mean proportion in stratum *h*	See equation T-3	
$\bar{\bar{p}}_{st}$	Survey-wide mean proportion	$\bar{\bar{p}}_{st} = \sum_h w_h \bar{\bar{p}}_h$	T-10
$\mathrm{var}\left[\bar{\bar{p}}_{st}\right]$	Variance of survey-wide mean proportion	$\mathrm{var}\left[\bar{\bar{p}}_{st}\right] = \sum_h w_h^2 \mathrm{var}\left[\bar{\bar{p}}_h\right]$	T-11
var[ ]	Variance of an estimate (e.g., mean density, abundance)		
SE[ ]	Standard error of an estimate	$SE[] = \sqrt{\mathrm{var}[]}$	T-12
$\mathrm{CV}\left[\bar{\bar{D}}_{st}\right]$	Coefficient of variation of mean density	$CV\left[\bar{\bar{D}}_{st}\right] = \frac{SE\left[\bar{\bar{D}}_{st}\right]}{\bar{\bar{D}}_{st}}$	T-13
s_{uh}	Sample standard deviation in stratum *h*	$s_{uh} = \sqrt{s_{1h}^2 - \frac{s_{2h}^2}{M_h}}$	T-14
m_h^*	Optimum number of SSUs per PSU in stratum *h*	$m_h^* = \frac{\sqrt{s_{2h}^2}}{s_{uh}}$	T-15
$V\left[\bar{\bar{D}}_{st}\right]$	Target variance for survey-wide mean density	$V\left[\bar{\bar{D}}_{st}\right] = \left(CV\left[\bar{\bar{D}}_{st}\right] \cdot \bar{\bar{D}}_{st}\right)^2$	
n^*	Number of PSUs required to achieve a specified variance	$n^* = \frac{\sum_h w_h s_{uh}\left(\sum_h w_h s_{uh} + \sum_h \frac{w_h^2 s_{2h}^2}{m_h^* w_h s_{uh}}\right)}{V\left[\bar{\bar{D}}_{st}\right] + \sum_h \frac{w_h^2 s_{1h}^2}{N_h}}$	T-16
n_h^*	Optimal allocation of PSUs among strata	$n_h^* = n^*\left(\frac{w_h s_{uh}}{\sum_h w_h s_{uh}}\right)$	T-17

The conceptual layout of our two-stage stratified random sampling (StRS) design is shown in Fig. 2, and survey design symbols and definitions are provided in Table 1. The survey area was divided into *h* subregions termed strata. Each stratum was further subdivided into primary sample units *i*, and each primary unit was again subdivided into second-stage sample units *j*. Note that each primary- and second-stage sample unit contains a fixed amount of area; thus, the sum of second-stage sample units within primary units of all strata equals the total survey area. The strata areas A_h and corresponding number of possible primary sample units N_h in the Florida Keys survey area are given in Table 2. Selection of primary and second-stage samples within a given stratum *h* was carried out in two stages. First, the primary units *i* to be sampled were randomly selected without replacement from the complete list of N_h units using a discrete uniform probability distribution (Law and Kelton 2000), which assigned equal selection probability to each primary unit. Second, a

Table 2 Habitat types, regions, and management zones that defined statistical strata in the Florida Keys coral reef sampling survey

Habitat type	Region	Management zone	Stratum (h)	A_h (km^2)	N_h	w_h	n_h
Mid-channel patch reef (MPR)	Lower keys	Open	1	42.52	1,063	0.1694	4
		Protected	2	1.40	35	0.0056	2
Offshore patch reef (OPR)	Lower keys	Open	3	6.04	151	0.0241	6
		Protected	4	2.72	68	0.0108	6
Inner line reef (ILR)	Upper keys	Open	5	2.72	68	0.0108	2
		Protected	6	0.72	18	0.0029	2
Back reef/rubble (BRR)	Lower keys	Open	7	4.32	108	0.0172	5
		Protected	8	1.76	44	0.0070	2
Fore reef, low-relief hardbottom (LHB)	Upper keys	Open	9	40.12	1,003	0.1598	6
		Protected	10	3.96	99	0.0158	6
	Middle keys	Open	11	36.80	920	0.1466	9
		Protected	12	2.48	62	0.0099	6
Fore reef, high-relief spur & groove (HSG)	Lower keys	Open	13	26.64	666	0.1061	6
	Upper keys	Protected	14	2.56	64	0.0102	3
	Middle keys	Protected	15	0.68	17	0.0027	2
	Lower keys	Open	16	1.88	47	0.0075	3
		Protected	17	2.16	54	0.0086	4
Fore reef, low-relief spur & groove (LSG)	Upper keys	Open	18	12.12	303	0.0483	3
	Middle keys	Open	19	24.16	604	0.0963	5
		Protected	20	0.96	24	0.0038	6
Fore reef, patchy hardbottom (PHB)	Lower keys	Open	21	17.32	433	0.0690	13
		Protected	22	0.80	20	0.0032	12
	Middle keys	Open	23	16.16	404	0.0644	8
Total				251.00	6,275	1.000	121

Stratum-specific areas (A_h), total possible primary units (N_h), weighting factors (w_h), and sampled primary units (n_h) are also shown

similar procedure was used to select second-stage units j to be sampled from the total possible M_h units within a primary unit.

Population metrics

Statistical estimation procedures for population abundance metrics—means (e.g., animal density), proportions (e.g., benthic cover), and totals (e.g., animal abundance)—for a two-stage stratified random sampling design were adapted from Cochran (1977; Table 1), and computations were carried out using SAS statistical software. Animal density (colonies per SSU) was the principal metric used to develop and evaluate the statistical sampling design. Survey-wide mean and variance estimates of density (Table 1, equations T-4 and T-5, respectively) were obtained from weighted averages of strata means and variances (equations T-2 and T-3, respectively). A stratum weighting factor (equation T-1) was the proportion of the stratum area relative to the overall survey area. Similar procedures were used to estimate proportions such as benthic cover and frequency of occurrence. Stratum abundance (absolute number of colonies) was estimated by multiplying stratum density by stratum area (equation T-6). The same principle was used to estimate the variance of stratum abundance (equation T-7). Survey-wide abundance (equation T-8) and associated variance (equation T-9) were obtained by summing the respective strata estimates over all strata. Prevalence of coral disease and bleaching was estimated as the proportion of individuals within a population afflicted with the specific condition (Gerstman 2003). Survey-wide estimates of prevalence and associated variance were obtained using the proportion occurrence (equations T-10 and T-11, respectively) of diseased or bleached colonies.

Table 3 Pilot study results for stony corals

Species	n_h	$\bar{m}_h$	$n_h m_h$	10 m^2 (single transect)				20 m^2 (paired transects)			
				$\bar{\bar{D}}_h$	s_{1h}^2	s_{2h}^2	m_h^*	$\bar{\bar{D}}_h$	s_{1h}^2	s_{2h}^2	m_h^*
Millepora alcicornis	9	3.3	30	0.3815	0.1509	0.1243	1	0.3657	0.1070	0.0246	1
Montastraea cavernosa	9	3.3	30	0.2102	0.0123	0.0451	2	0.2148	0.0915	0.0488	1
Montastraea faveolata	9	3.3	30	0.4963	0.6526	0.1322	1	0.4389	0.4456	0.1986	1
Porites astreoides	9	3.3	30	0.2639	0.0518	0.0669	2	0.2329	0.0288	0.0263	2
Stephanocoenia michelini	9	3.3	30	0.0491	0.0034	0.0136	2	0.0519	0.0031	0.0044	2
Siderastrea siderea	9	3.3	30	0.1972	0.0038	0.0508	4	0.2157	0.0053	0.0378	3

Comparison of second-stage unit areas of 10 m^2 versus 20 m^2 with respect to estimates of means $\left(\bar{\bar{D}}_h\right)$, sample variances ($s_{1h}^2$ and s_{2h}^2) and optimal second-stage unit sample sizes (m_h^*) for density (colonies/m^2) of adults of six coral species (>4 cm diameter)

Design performance

Design performance was evaluated by balancing trade-offs between the precision of density estimates and survey costs measured by relative sample sizes. To evaluate design efficacy of past surveys and expected performance of a future survey, three performance measures were used. The first, a measure of relative precision, was the coefficient of variation (CV) of mean density (equation T-13), which is the ratio of the standard error to the mean. The second was m* (equation T-15), the optimum (minimum) number of second-stage sample units required within a primary unit to achieve an asymptotic estimate of the strata variance. Following Cochran (1977), estimates of m* were rounded up to the next integer. The third was n* (equation T-16), the number of primary units required to achieve a specified variance for a future survey. Estimation of n* presumes that primary units will be distributed among strata according to a Neyman or optimal allocation scheme (equation T-17), which accounts for both strata sizes and variances of strata densities. Evaluation of n* treated per unit sampling costs as equal among strata.

Table 4 Pilot study results for stony corals

Species	n_h	$\bar{m}_h$	$n_h m_h$	$\bar{\bar{D}}_h$	m_h^*
M. alcicornis	27	3.4	92	0.6624	1
M. cavernosa	27	3.4	92	0.4743	1
M. faveolata	27	3.4	92	0.4630	1
P. astreoides	27	3.4	92	0.3073	2
S. michelini	27	3.4	92	0.1045	2
S. siderea	27	3.4	92	0.2924	1

Estimates of mean densities (colonies/m^2) and optimal second-stage unit sample sizes for adult corals (>4 cm diameter) for the overall pilot study (transect area 10 m^2)

Results

Pilot study

Prior to conducting the Florida Keys sampling survey, a pilot study evaluated (1) the survey area required for a second-stage unit (i.e., transect), and (2) the minimum number of second-stage sample units within each primary unit for efficient estimation of density of stony corals. Initially, it was assumed that four 20 m^2 second-stage units, each consisting of two 10 m^2 closely-spaced transects, would be required within a primary sample unit.

Table 5 Stratified random survey ($n = 121$, $nm = 242$) estimates of mean density (colonies per SSU, 10 m^2) and associated standard error and coefficient of variation for adult (>4 cm) stony corals

	$\bar{\bar{D}}_{st}$	$SE[\bar{\bar{D}}_{st}]$	$CV[\bar{\bar{D}}_{st}]$ (%)
Milleporina			
M. alcicornis	16.42	1.14	6.9
Scleractinia			
Total (all species)	39.83	2.97	7.5
M. cavernosa	2.70	0.76	28.0
M. faveolata	1.03	0.32	30.8
P. astreoides	6.13	0.68	11.2
S. michelini	7.80	0.93	12.0
S. siderea	11.15	1.21	10.9

Table 6 Stratified random survey ($n = 121$, $nm = 242$) estimates of abundance (number of colonies $\hat{Y}_{st}$) and prevalence ($\bar{\bar{p}}_{st}$) of bleached and diseased colonies of adult stony corals

Taxa	Abundance	Bleached		Diseased	
		Prevalence (%)	SE	Prevalence (%)	SE
Milleporina					
M. alcicornis	412,177,298	1.90	0.472	0.07	0.056
Scleractinia					
Total (all species)	999,628,726	3.64	0.526	1.71	0.766
M. cavernosa	67,795,106	0.38	0.276	1.00	0.604
M. faveolata	25,883,269	1.26	0.824	2.78	1.250
P. astreoides	153,945,165	1.21	0.491	0.23	0.145
S. michelini	195,827,034	1.72	1.366	6.22	3.860
S. siderea	279,877,495	0.25	0.096	0.42	0.232

This configuration was used to sample an initial set of $n_h = 9$ primary units within the same habitat stratum h. Two divers were able to complete, on average, one primary unit each vessel-day.

Transect areas of 10 and 20 m^2 were evaluated by randomly selecting for analysis one transect from the closely-spaced pairs at each second-stage sample unit. Sampling single (10 m^2) or paired (20 m^2) transects yielded similar estimates of mean density $\bar{\bar{D}}_h$, but the sample variances (s^2_{1h} and s^2_{2h}) were generally lower for paired transects (Table 3). For five of the six stony coral species analyzed, however, estimates of optimal sample size m^*_h suggested that two second-stage units provided sufficient sampling effort for either single or paired transects. This indicated that there were no appreciable gains in statistical efficiency by increasing transect area from 10 to 20 m^2. A subsequent set of $n_h = 18$ primary units was sampled in which single 10 m^2 transects were deployed at $m_h = 3$ or 4 second-stage units. Estimates suggested that sampling a target of $m_h = 2$ second-stage units within each primary unit would be sufficient (Table 4).

Sampling two 10 m^2 transects per primary unit allowed two divers sampling stony corals to complete 2 to 2.5 primary units per vessel-day. Second-stage unit sampling effort for other benthic reef fauna was constrained to conform with stony coral sampling. A third team member sampled two transects for octocoral species density and four transects for sponge species presence–absence, while a fourth diver completed four transects for benthic cover.

Florida Keys sampling survey

Sampling was conducted for thirty-seven vessel-days during summer–fall 1999 and 19 vessel-days during summer 2000, yielding $n = 121$ primary units (Fig. 1a, Table 2). This sampling included $nm = 242$ second-stage units for stony corals and octocorals, and $nm = 484$ second-stage units for benthic cover and sponge species presence–absence. Initial target allocation of primary units n_h among strata was proportional to stratum area (i.e., weighting factor w_h) with the following

Table 7 Sampling survey results for octocoral density ($n = 121$, $nm = 242$; units are colonies per SSU)

Taxa	$\bar{\bar{D}}_{st}$	$SE[\bar{\bar{D}}_{st}]$	$CV[\bar{\bar{D}}_{st}]$ (%)
Total octocorals (all species)	129.64	5.92	4.7
Eunicea tourneforti	3.31	0.40	12.0
Gorgonia ventalina	7.34	0.77	10.5
Plexaura flexuosa	8.99	0.79	8.8
Pseudopterogorgia acerosa	9.38	0.88	9.4
Pseudopterogorgia americana	37.08	2.46	6.7

Table 8 Sampling survey results for sponge species percent occurrence ($n = 121$, $nm = 484$)

Taxa	$\bar{\bar{p}}_{st}$ (%)	$SE[\bar{\bar{p}}_{st}]$
Callyspongia vaginalis	89.49	2.09
Ircinia campana	34.24	5.32
Ircinia felix	90.85	2.18
Ircinia strobilina	82.27	2.51
Niphates digitalis	91.20	1.46
Xestospongia muta	62.83	4.10

Table 9 Sampling survey results for benthic cover ($n = 121, nm = 484$)

Taxa	$\bar{\bar{p}}_{st}$ (%)	$SE\left[\bar{\bar{p}}_{st}\right]$
Scleractinia corals	5.28	0.40
Milleporina corals	0.38	0.06
Sponge	5.07	0.40
Octocoral	1.99	0.20
Fine turf algae	40.17	1.60
Crustose coralline algae	2.03	0.33
Macroalgae	29.81	1.71

constraints: (1) each stratum received a minimum of $n_h = 2$ units; (2) each no-take reserve within a management zone stratum received a minimum of two primary units; and, (3) each "open to fishing" management zone stratum for a given habitat-region received at least the same number of primary units as the corresponding "protected" stratum. Actual allocation of primary units among strata achieved during the survey (Table 2) differed somewhat from the target allocation, due principally to inaccuracies in the benthic habitat map.

The Florida Keys-wide survey obtained estimates for: density of 42 stony coral species and 32 octocoral species; frequency of occurrence for 70 sponge species; and, benthic cover for 70 species and functional groups of invertebrates and algae. Mean density for adults of six principal stony coral species ranged from 1 to 16 colonies per SSU (10 m^2; Table 5). Mean and standard error (SE) of density were positively correlated among taxa, that is, SE increased proportionally to density. However, there was an inverse relationship across species between mean density and CV. For adult stony corals, CVs ranged from 7% to 12% for species with mean densities >6 per SSU, while they ranged from 28% to 31% for species with mean densities <3.

Survey-wide prevalence of bleaching and disease is shown for selected stony coral taxa (Table 6). For combined scleractinian corals, prevalence of bleaching and disease was 3.6% and 1.7%, respectively. Among six stony coral species, bleaching prevalence ranged from 0.2% to 1.9%, whereas disease prevalence ranged from 0.1% to 6.2%.

Although the survey was primarily designed for estimating stony coral density, the design also performed well for octocoral density (Table 7), percent occurrence of sponges (Table 8), and benthic cover for a variety of benthic invertebrates and algal taxa (Table 9). Survey-wide CVs of mean octocoral density for five dominant species ranged from about 6% to 12%. For six common sponges, the standard error of mean percent occurrence ranged from 1.5% to 5.5%. For taxa with relatively low mean benthic cover ($\bar{\bar{p}}_{st} < 6\%$), the

Table 10 Evaluation of optimal sample size for second-stage units (m_h^*) for the Florida Keys sampling survey (where $m_h = 2$)

Measurement variable	Number of strata evaluated	Relative frequency (%) of strata		
		$m_h^* \leq 2$	$3 \leq m_h^* \leq 4$	$m_h^* \geq 5$
Coral density				
Milleporina				
M. alcicornis	23	87.0	13.0	0.0
Scleractinia				
Total (all species)	23	82.6	4.3	13.1
M. cavernosa	21	85.7	14.3	0.0
M. faveolata	21	76.2	23.8	0.0
P. astreoides	22	91.0	4.5	4.5
S. michelini	21	100.0	0.0	0.0
S. siderea	22	86.4	13.6	0.0
Octocoral density				
Total (all species)	23	91.4	4.3	4.3
E. tourneforti	21	100.0	0.0	0.0
G. ventalina	23	82.6	8.7	8.7
P. flexuosa	23	87.0	8.7	4.3
P. acerosa	22	86.4	9.1	4.5
P. americana	23	91.3	8.7	0.0

Estimates of m_h^* were made for each stratum where density was non-zero (total possible = 23 strata). Values are the relative frequency of strata corresponding to three levels of m_h^*

Table 11 Post-stratification analysis results for five scleractinian stony coral species based on the Florida Keys sampling survey ($n = 121, nm = 242$)

Design	Stratification variables	Number of strata	$\bar{\bar{D}}_{st}$	n^*(10%)
(a) *Porites astreoides*				
A	Habitat, region, management zone (actual design)	23	6.13	57
B	None (simple random)	1	5.54	197
C	Habitat	8	5.58	79
D	Region	3	5.41	169
E	Management zone	2	5.37	201
F	Habitat-region	14	5.43	74
G	Habitat-management zone	15	6.15	65
H	Region-management zone	6	5.16	153
(b) *Montastraea cavernosa*				
A			2.70	192
B			2.82	272
C			2.52	222
D			2.55	190
E			2.76	313
F			2.39	201
G			2.87	215
H			2.48	212
(c) *Montastraea faveolata*				
A			1.03	189
B			1.46	354
C			1.25	209
D			1.28	255
E			1.06	356
F			1.12	198
G			1.14	225
H			0.92	222
(d) *Stephanocoenia michelini*				
A			7.80	42
B			4.56	485
C			7.46	46
D			3.93	271
E			4.95	493
F			7.41	45
G			7.88	44
H			4.21	267
(e) *Siderastrea siderea*				
A			11.15	28
B			8.63	190
C			10.96	34
D			7.80	109
E			8.44	199
F			10.84	34
G			11.15	28
H			7.65	112

Stratification variables and strata sample sizes are given in Table 2. Density units are colonies per SSU; values of n^* were computed for a target coefficient of variation of 10%

standard error was <0.5%, and <2% when the corresponding mean percent cover $\bar{\bar{p}}_{st}$ for a given taxa was greater than 20%.

Design of future surveys

Three aspects of future design performance were investigated: (1) the level of sampling effort within a primary unit; (2) the effectiveness of the stratification scheme; and (3) the effectiveness of the strategy for allocating primary units to be sampled among strata. Optimal sample size for second-stage units (m^*) within a primary unit was re-examined using the Florida Keys survey data for representative stony corals. Estimates of m^* were made for each stratum h where density was non-zero, and then tallied according to three levels of second-stage sampling effort: $m_h^* \leq 2$, $3 \leq m_h^* \leq 4$, and $m_h^* \geq 5$ (Table 10). Values of m_h^* were two or below in 80% or more of strata for most coral species. These results corroborated pilot study findings (Table 4). Similar to stony corals, the choice of sampling $m_h = 2$ second-stage units within a primary unit also appeared to be satisfactory for octocorals (Table 10).

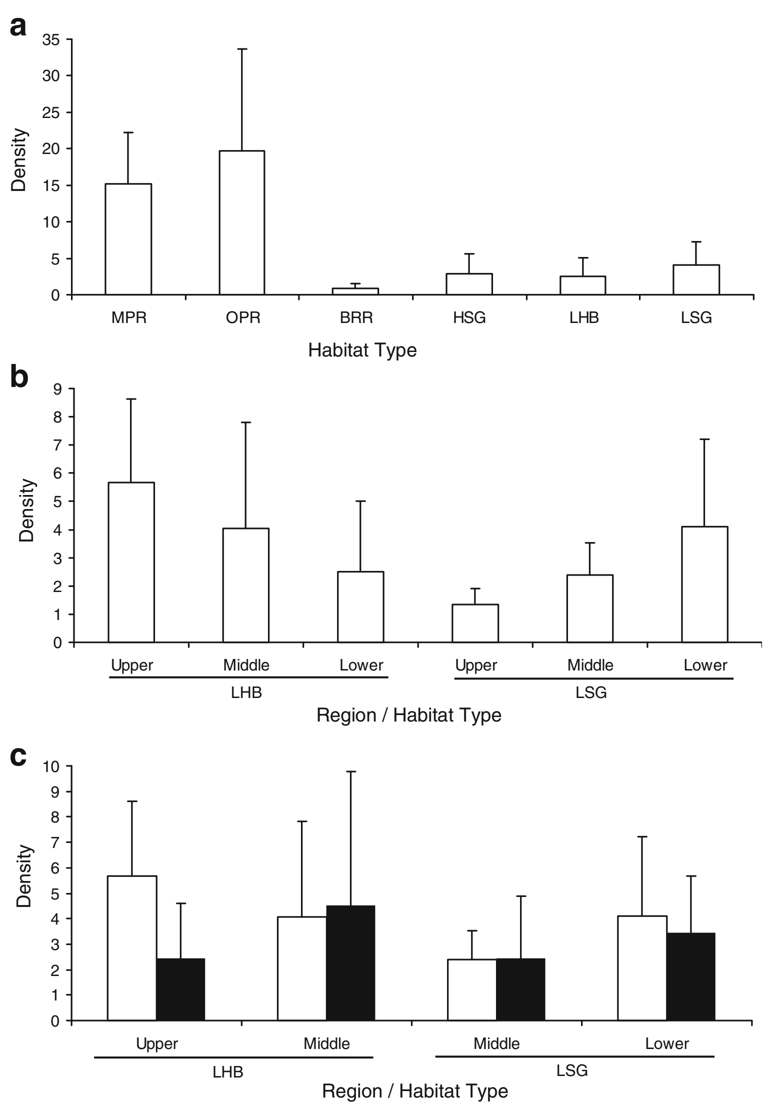


Fig. 3 Spatial density and variance patterns of *Porites astreoides*: **a** by habitat type in the open management zone in the lower Florida Keys region; **b** by region within two habitat types in the open management zone; **c** between open (*open bars*) and protected (*solid bars*) management zones by habitat and region. Habitat codes are given in Table 2; density units are colonies per SSU (10 m^2); error bars denote standard deviation (s_{uh}, equation T-14)

Efficacy of the stratification scheme was evaluated relative to alternative designs using post-stratification analysis that employed various combinations of the three stratification variables: reef habitat type, geographic region, and management zone. Values of $m_h^* = 2$ were used to compute the number of samples required in a future survey (n^*, equation T-16) to achieve a CV of 10%. Results for the scleractinians *Porites astreoides* (Table 11a), *Stephanocoenia michelini* (Table 11d), and *Siderastrea siderea* (Table 11e) showed that designs incorporating habitat type were most efficient. For two of the species (i.e., *Montastraea cavernosa,* Table 11b; *Montastraea faveolata*, Table 11c), additional stratification by region produced the most efficient designs. In all cases, simple random sampling (no stratification) or stratifying solely by management zone yielded the least efficient designs.

As an illustrative case study, post-stratification results for *P. astreoides* are corroborated in Fig. 3. Differences in spatial density and variance of *P. astreoides* were most pronounced among habitat types (Fig. 3a) and less apparent among geographic regions (Fig. 3b) and management zones (Fig. 3c), mirroring the relative importance of the three stratification variables determined from post-stratification analysis (Table 11a). In particular, both mean density and standard deviation in patch reef habitats (Fig. 3a, MPR and OPR; see Table 2 for habitat codes) were four to five times greater compared to fore reef habitats (HSG, LHB, and LSG). Correspondingly, the simple random design for *P. astreoides* was projected to

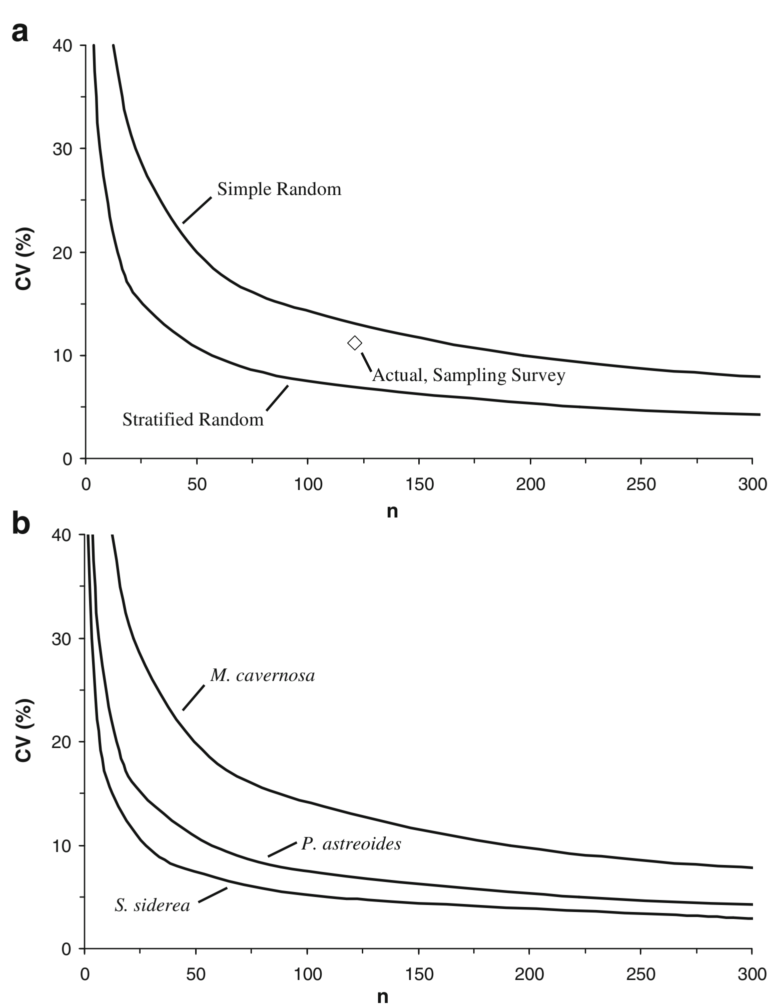


Fig. 4 Relationship between coefficient of variation of mean density, $CV[\bar{\bar{D}}_{st}]$, and predicted sample size n^* estimated using equation (T-16) for: **a** the stony coral *Porites astreoides* based upon the stratified random sampling design employed and for a simple random design; and **b** the stony corals *P. astreoides*, *Montastraea cavernosa*, and *Siderastrea siderea* for the stratified random sampling design employed. Also shown in **a** is the corresponding point value (*diamond*) of the actual coefficient of variation (CV) for *P. astreoides* and sample size for the Florida Keys survey

require 3 to 4 times more sampling effort to achieve a 10% CV compared to the stratified design (Table 11a).

The impact of allocation on design performance is illustrated in Fig. 4a for *P. astreoides*. Equation (T-16) was used to compute the predicted sample size n^* over a range of CV values. Estimates of n^* require estimates of strata variances, and presume that allocation of primary sample units among strata will follow an optimal scheme (equation T-17) in which larger or more variable strata receive more sampling effort compared to smaller or less variable strata. Because reliable estimates of strata variances were not available prior to the Florida Keys survey, allocation of primary units was principally based on stratum size. The substantial difference between the survey CV (diamond in Fig. 4a) and the projected CV at $n = 121$ for the stratified random design (CV–n^* curve, Fig. 4a) reflects the potential gain in precision that could be achieved in a future survey via optimal allocation. The analysis of Fig. 4a suggests that potential improvements in sampling efficiency due to effective stratification (simple random vs. stratified random CV–n^* curves) may be undone by suboptimal allocation. A CV–n^* curve represents a minimum bound of CV that could be achieved in practice for a given stratification scheme combined with optimal allocation; however, the analysis of Fig. 4b indicates that what may be achievable may differ among species for the same design.

Discussion

Design performance

Well-established principles of probability survey design were applied to guide large-scale sampling of populations of stony corals and associated benthic taxa in the Florida Keys coral reef ecosystem. Stony coral population density and abundance were estimated within a 251 km^2 area with high precision (i.e., CVs of 7%–12%) for four of six principal species given a relatively modest survey effort. In these cases, the precision levels would enable detection of relative changes in population mean density ranging from 14% to 24% (approximately 2 SEs) in a future time period. The CVs obtained in our study are among the lowest reported for comparable surveys of marine species, e.g., American lobster *Homarus americanus* (CVs 4%–10%, Smith and Tremblay 2003), pink shrimp *Farfantepenaeus duorarum* (CVs 6%–14%, Ault et al. 1999), and the sea scallop *Placopecten magellanicus* (CVs 6%–10%, Smith and Lundy 2006). Our survey was generally less precise for species with relatively low densities (<3 colonies/10 m^2).

While this design analysis was primarily focused on density and abundance of stony coral populations, relatively precise estimates were also obtained for density of octocorals, frequency of occurrence for sponges, and benthic cover for invertebrate taxa and algal functional groups. The precision of percent cover for scleractinian corals achieved in the survey would enable detection of an absolute change of 0.8% in a future time period. The same principles of statistical sampling design have also been shown to be effective for integrated ecosystem surveys of coral reefs and associated fishes and macroinvertebrates (spiny lobsters, urchins, conchs) and for evaluating the efficacy of marine protected areas (Chiappone et al. 2002; Miller et al. 2002; Ault et al. 2005, 2006; Smith et al. 2011).

The two-stage sampling scheme was an effective way to deal with the disparity in area between a belt transect and the minimum mapping unit for classifying reef habitat strata. Sampling two 10-m^2 belt transects was shown to be adequate for describing coral density within a 200 m by 200 m grid cell irrespective of habitat type. Reduction in estimate variance was thus best achieved by sampling more primary units within a stratum (scale of about 1 to 20 km) rather than sampling more transects within a primary unit (scale of 10 to 100 m), corroborating the findings of Murdoch and Aronson (1999). In other words, it was better to sample more "sites" (aka primary units) than to sample more transects within a site. The emphasis of most previous evaluations of field designs and sample size requirements for coral reefs has been to facilitate comparisons between specific sites; not surprisingly, five to ten transects or more per site have been recommended to detect differences at these fine spatial scales (e.g., Nadon and Stirling 2006).

Optimizing future surveys

The next challenge in the Florida Keys will be to expand the survey area to encompass the full extent of the mapped live coral hard-bottom habitats between Miami and Key West at depths to 33 m (about 500 km^2; FMRI 1998) while keeping costs (e.g., vessel-days) and precision at reasonable levels. The analysis of stratification and allocation strategies with respect to sampling efficiency, exemplified in the CV–n graphs of Fig. 4, suggested at least three promising ways of accomplishing this. First, increasing the efficiency of sampling effort within a primary unit can provide gains in survey performance. In the Florida Keys survey, results of the pilot study enabled a reduction in effort from four 20 m^2 transects to two 10 m^2 transects within a primary unit. These reductions increased the per day rate of n from 1 to 2, effectively doubling the overall survey n under the allotted vessel-days of the sampling budget. Investigating ways to further streamline underwater sampling operations such as experimentation to determine optimal transect area or to improve coordination of tasks among divers could thus provide a substantial payoff in sampling efficiency. A modest increase from the current average of two primary units per vessel-day to three would yield a 50% increase in survey n without increasing the sampling budget.

Second, as illustrated for *P. astreoides* in Fig. 4a, gains in precision at a given n can be achieved by stratifying the survey area with variables that account for spatial heterogeneity in density. Of the stratification variables utilized in the Florida Keys survey design, cross-shelf habitat type was the most effective at partitioning the area into subareas of differing variance of stony coral density. Along-shelf region was less effective in this regard. The similarities in mean density and variance among some habitat types (e.g., Fig. 3) indicate that the stratification scheme may be improved with refinements in the classification of reef habitats. Extension of fore reef depth from 15 to 33 m in the expanded survey area will likely entail adding depth as a stratification variable in future surveys. While management zone did little to control spatial variation of density, it will need to remain as a stratification variable to be able to track temporal changes in the benthic community that may result from no-take protection of fishes and macroinvertebrates.

Third, gains in efficiency from an improved stratification scheme can only be fully realized when accompanied by optimal (i.e., Neyman) allocation of samples among strata according to both stratum size and variance. Results for *P. astreoides* (Fig. 4a) showed that the actual CV for the Florida Keys survey, in which allocation was mostly proportional to stratum area, was over 50% higher compared to the projected CV for the same stratified design employing optimal allocation. The estimates of strata variances obtained from the Florida Keys survey will enable application of an optimal allocation strategy in a future survey. Studies have shown, however, that estimates of strata variances become more reliable over several successive surveys (Smith and Gavaris 1993; Ault et al. 1999). Thus, it will likely take some time to fully realize gains in efficiency via optimal allocation. A final important attribute of this design will be development of an efficient allocation scheme for multiple target species (e.g., Fig. 4b, Miller et al. 2007), because it is quite possible that low variance strata for some species may be high variance for others.

Population metrics for assessment and management

A key aspect of our probabilistic survey was that it enabled population-level estimation of coral reef abundance metrics. Larger-scale investigations in both the Indo-Pacific (e.g., Done 1999; Hughes et al. 1999) and Caribbean (e.g., Newman et al. 2006) have generally employed experimental design techniques (Hairston 1989; Montgomery 2001) to evaluate relative abundance measures at the habitat-level. The main practical difference between these two approaches is that probabilistic surveys explicitly incorporate survey area (e.g., A_h, N_h, M_h) in the estimation of metrics (e.g., equation T-6) and their associated variances (e.g., equations T-3 and T-7). Statistical software packages such as SAS and R have added procedures in recent years for computing means and variances for probabilistic surveys. An additional practical aspect of our survey was that explicit delineation and enumeration of all possible sample units within the survey area facilitated random selection of sample locations, thus avoiding potential investigator-induced bias due to subjective site selection, which has been a problem in coral reef field studies (Lewis 2004).

Many previous studies of coral reef community structure in the Florida Keys and elsewhere have focused on benthic cover as the abundance metric of choice for stony corals (e.g., Dustan and Halas 1987; Porter and Meier 1992; Porter et al. 2002). In contrast, density and size structure were the primary metrics for stony coral populations in our survey. Benthic cover represents the net outcome of population dynamic rate processes of colony recruitment, growth, and survivorship, whereas density and size structure, the two basic components of cover, provide information on the rate processes themselves as well as on the net outcome. For example, a stratum with high densities of mostly small colonies and a stratum with low densities of mostly large colonies may produce similar estimates of stony coral cover, but the two strata reflect very different demographic histories. The spatially-explicit estimates of coral population density and size structure obtained in this study not only allow for tracking changes in abundance metrics over time, but can also serve as fundamental data for further investigations of population dynamics (e.g., Beverton and Holt 1957; Curry and Feldman 1987; Gutierrez 1996) and community ecology (e.g., Glynn and Ault 2000; Connolly et al. 2005) that may help explain the reasons for the changes. Improved understanding of the natural-environmental and anthropogenic factors contributing to declines in coral populations will circumscribe what resource managers can do to mitigate deleterious effects.

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