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Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition

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ABSTRACT

Principles of statistical sampling design were used to guide refinement of a 30-year multispecies fishery-independent diver visual survey of population abundance and size structure of more than 250 exploited and non-target fishes in the Florida coral reef ecosystem. Reef habitat features and no-take marine reserves (NTMRs) were used to partition the 885 km^2 sampling domain into sub-areas (or strata) to control the variation of fish density. For the period 1999–2008, survey precision of population density and abundance (CV, coefficient of variation, ratio of standard error to mean) ranged from 7% to 20% for the majority of 13 primary exploited species in the Florida Keys and Dry Tortugas regions. Population sustainability metrics like species average length in the exploited life stage were comparable between our fishery-independent survey and fishery-dependent catch-sampling. The survey design also performed well for non-target fishes, yielding CVs between 6% and 15% for population density for the majority of 36 species. Sampling efficiency was improved over time via an iterative learning process by which past survey data was used to refine the stratification and allocation schemes of future surveys. We show how survey data are used to support multispecies stock assessments, evaluate the effectiveness of NTMRs, and assess ecosystem condition for the reef fish community.

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1. Introduction

The southern Florida coral reef ecosystem supports lucrative fishing and tourism economies (Ault et al., 2005a). Fishery-dependent (FD) information has been the principal data source supporting stock assessments to address the key management objectives of preventing overfishing and sustaining benefits from tropical ecosystems with high species diversity (Pauly and Morgan, 1987; Gallucci et al., 1996; Sparre and Venema, 1998). However, there are risks in basing assessments entirely upon data from extractive fishing operations (Walters and Martell, 2004; Rotherham et al., 2007). Numerous sources of bias and uncertainty may arise from the process of obtaining catch-effort data from the wide variety of vessels, capture gears, and landing sites typical of tropical reef fisheries. Also problematic is the non-random strategy of catching fishes employed by fishers with respect to the spatial distributions of species and habitats. Many of these potential biases and uncertainties can be eliminated through the controlled sampling approach offered by fishery-independent (FI) surveys. These surveys can be designed to provide the same size-structured abundance estimates as FD surveys for conducting modern stock assessments (Gunderson, 1993; Ault et al., 1998, 2005b, 2008; Smith and Lundy, 2006). However, FI surveys are usually conducted at much lower levels of sampling effort compared to fishing operations; consequently, FI data have mostly been used as corollary indices to estimate fishing mortality rates and population sustainability benchmarks (Fournier and Archibald, 1982; Deriso et al., 1985; Quinn and Deriso, 1999; Kimura and Somerton, 2006).

Management objectives for coral reefs have now expanded beyond sustainable rates of exploitation for single target species to include the impacts of fishing on ecosystem trophic structure and food-web dynamics (Pauly et al., 1998; Walters and Martell, 2004; Levin et al., 2009), and non-fishing human threats to the productivity of reef-fish stocks from habitat and water quality alterations (Ault et al., 1999b, 2003, 2005a). This ecosystem-oriented perspective has given rise to use of new management tools including no-take marine reserves (NTMRs) that have the dual purpose of controlling exploitation as well as conserving biodiversity in the face of environmental variability (Bohnsack and Ault, 1996). In contrast to FD data sources, FI surveys are well-suited to addressing some of the principal information needs for ecosystem-based management. FI surveys can utilize sampling methods and gears to obtain abundance and size-composition data of both target and

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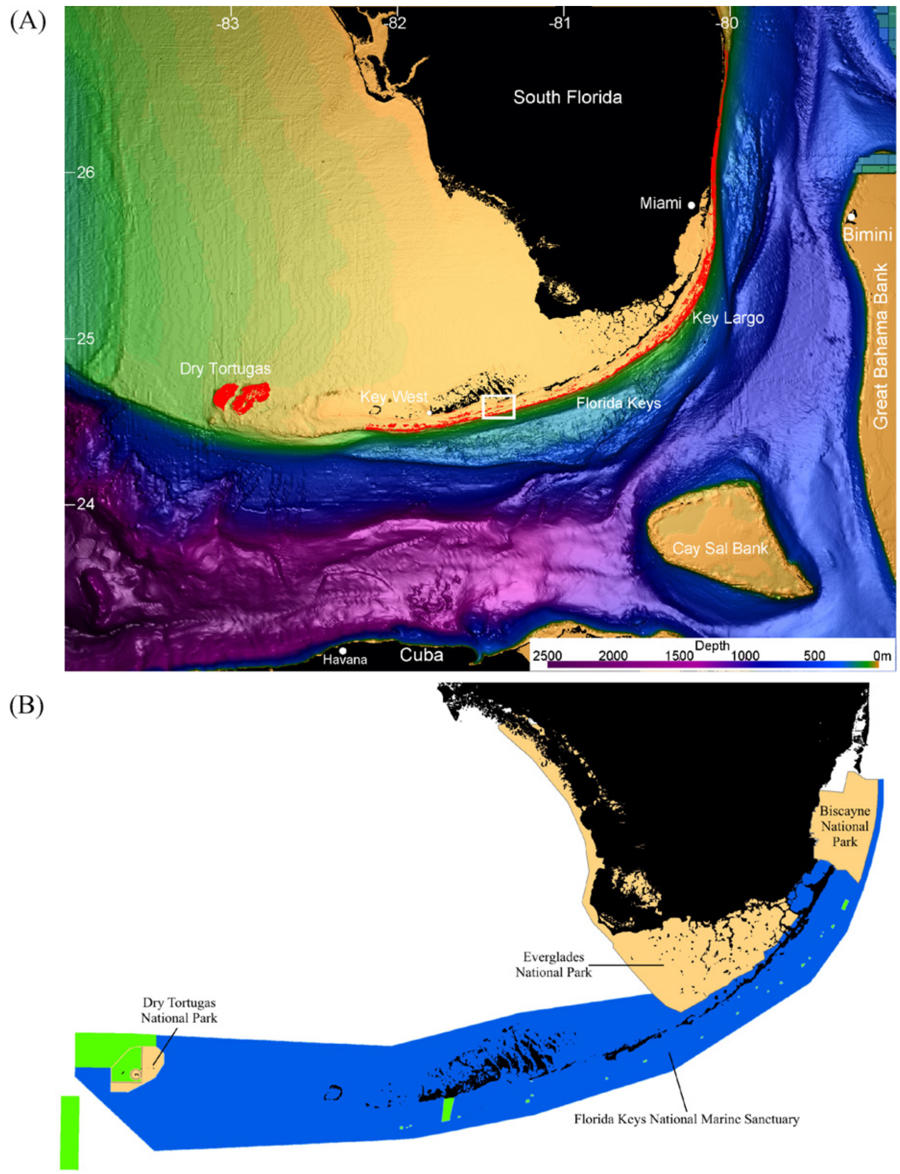

Fig. 1. South Florida reef fish visual survey domain. (A) Seafloor morphology of the coral reef ecosystem and the Straits of Florida with mapped coral reef habitats (red) in the Florida Keys and Dry Tortugas; depths are represented by the color scale; land is black; the rectangle denotes area of detail shown in Fig. 3A. (B) Managed area boundaries for the Florida Keys National Marine Sanctuary (blue), Biscayne, Everglades and Dry Tortugas National Parks (tan), and no-take marine reserves (green).

non-target species, including smaller fishes not subject to capture by a given fishery. FI surveys can also employ sampling designs for evaluating spatially explicit management issues including habitat impacts on stock productivity and the efficacy of NTMRs in reducing exploitation rates (Ault et al., 1999a, 2006).

In this paper we discuss the design and implementation of a fishery-independent, non-destructive, diver visual survey of size-structured population abundance of exploited and non-target fish species in the Florida coral reef ecosystem. We detail how principles of probabilistic sampling design were used to transform a geographically restricted study begun in 1979 to an ecosystem-wide survey in the 1990s that was tailored to provide reliable reef-fish population and community metrics to: (1) support multispecies stock assessments; (2) evaluate the effectiveness of no-take marine reserves (NTMRs) and other spatially explicit management issues; and, (3) estimate metrics of ecosystem condition of the reef fish community. The primary challenge of this research was to design a cost-effective survey that could be conducted annually–biennially over a spatial scale comparable to the commercial and recreational coral reef fisheries in southern Florida, but with enough sampling intensity to provide accurate and precise estimates of population abundance metrics for principal species of the reef-fish community.

2. Material and methods

2.1. Survey sampling approach and spatial domain

A probabilistic sampling approach was used to design a visual survey of reef-fishes that provided population and community metrics for resource management (Cochran, 1977; Thompson, 2002). Visual sampling was conducted along the Florida coral reef tract that extends about 400 km southwest from Miami to the Dry Tortugas (Fig. 1A). The reef tract lies within the management boundaries of the Florida Keys National Marine Sanctuary (FKNMS) and two national parks, Biscayne and Dry Tortugas (Fig. 1B). Our strategy was to use environmental features that correlate with the spatial distribution of reef-fishes to partition the survey area into subareas (i.e., strata) of low, moderate, and high variation in abundance

Table 1A
Habitat stratum (h) characteristics, numbers of primary sample units (N_h), and respective areas (A_h, km^2) for management zones in the Florida Keys region.

Habitat Class	Rugosity	Habitat Stratum	h	Management Zones			
				Open		Protected	
				N_h	A_h	N_h	A_h
Inshore patch reefs	Low-Medium	IPLM	1	169	6.76	32	1.28
Mid-channel patch reefs	Low-Medium	MPLM	2	3483	139.32	56	2.24
Offshore patch reefs	Low-Medium	OPLM	3	1099	43.96	78	3.12
	High	OPRH	4	68	2.72	19	0.76
Fore reef shallow <6 m	High	FRSH	4	102	4.08	156	6.24
	Low	FRSL	5	1374	54.96	113	4.52
Fore reef mid 6–18 m	Low	FRML	6	5489	219.56	355	14.20
Fore reef deep 18–33 m	Low	FRDL	7	1376	55.04	–	–
TOTAL				13160	526.40	809	32.36

(Ault et al., 1999a; Manly et al., 2002). Geo-referenced environmental data including bathymetry (National Geophysical Data Center, Boulder, Colorado; National Ocean Service, Silver Spring, Maryland) and benthic habitat characteristics (FMRI, 1998; Franklin et al., 2003) were compiled for the south Florida coastal ecosystem using a geographic information system (GIS). The spatial domain of the survey encompassed the full extent of mapped Holocene live-coral reef habitats (Fig. 1A, red) to 33 m depths. The domain was subdivided into two regions, the Florida Keys (Miami to Key West; Table 1A) and the Dry Tortugas (Table 1B).

The sampling design was also constructed to evaluate the effects of implementation of a network of NTMRs on reef-fish populations (Fig. 1B, green). This network is comprised of 23 mostly small reserves established in the Florida Keys (FKNMS) in 1997 (Table 1A), and several large reserves established in the Dry Tortugas in 2001 (FKNMS) and 2007 (Dry Tortugas National Park) (Table 1B). Boundaries of these NTMRs were incorporated into the GIS to partition the survey domain into areas open to fishing and closed to fishing.

2.2. Sampling protocols

Abundance and size data for reef-fishes were collected by highly trained and experienced SCUBA divers using a standard, *in situ*, nondestructive monitoring method (Bohnsack and Bannerot, 1986; Brandt et al., 2009). In our protocol, a stationary diver collected reef-fish data while centered in a circular plot of 15 m diameter. This diameter was chosen because extensive field experimentation by Bohnsack and Bannerot (1986) indicated this distance provided unbiased observations of small cryptic species as well as large species that avoided close approach to a diver. The larger economically and ecologically important snapper-grouper species were the focus of our survey design. During a sample, a diver listed all observed fish species for a 5 min period before recording species abundance and fork length measurements to the nearest cm. Data were also collected on depth and benthic habitat features including reef morphology (e.g., isolated patch reefs, spur-groove fore reefs) and topography (e.g., maximum height of reef structures extending above the seafloor). A meter stick with a 30 cm ruler mounted perpendicularly at one end was used as a reference to reduce apparent magnification errors in fish-size estimates, and to facilitate reliable measurements of distinctive habitat features (e.g., rugosity) (Fig. 2A). A large portion of diver training for participation in the visual surveys was devoted to accurate estimation of sizes of fishes at varying distances from the observer (Brandt et al., 2009). In the field, divers periodically calibrated their size estimates in relation to stationary reef components (e.g., sea fans) than can be measured exactly. Divers also carried underwater digital cameras to document benthic habitats and unusual fish species. The average time to complete a circular plot sample ranged from 15 to 20 min, depending on the complexity of the fish community and benthic habitat.

2.3. Statistical design

A probabilistic survey approach required description of the sampling domain (Fig. 1A) as a finite number of sampling units. To accomplish this we used the GIS to grid the digital map layers for bathymetry and benthic habitats into an appropriate cell size (sample unit) for delineating coral reef habitats shallower than 33 m from the complete range of habitat types and depths. Ideally, the minimum grid size for a cell would be the 15 m diameter circular plot used for visual sampling. During initial attempts to use the benthic habitat map of the Florida Keys (FMRI, 1998) to navigate to prominent reef features at well-known dive sites, we found map

Table 1B
Habitat stratum (h) characteristics, numbers of primary sample units (N_h), and respective areas (A_h, km^2) for management zones in the Dry Tortugas region.

Habitat Class	Rugosity	Habitat Stratum	h	Management Zones							
				Open-All		Open-Recreational		Protected-2001		Protected-2007	
				N_h	A_h	N_h	A_h	N_h	A_h	N_h	A_h
Contiguous reef	Low	CRL	1	1100	44.00	1365	54.60	1424	56.96	1023	40.92
	Medium	CRM	2	–	–	189	7.56	–	–	22	0.88
	High	CRH	3	37	1.48	17	0.68	322	12.88	27	1.08
Patch reefs	Low	PRL	4	48	1.92	484	19.36	37	1.48	421	16.84
	Medium	PRM	5	133	5.32	392	15.68	289	11.56	344	13.76
	High	PRH	6	–	–	7	0.28	40	1.60	24	0.96
Spur-groove reef	Low	SGL	7	–	–	273	10.92	–	–	10	0.40
	High	SGH	8	–	–	96	3.84	–	–	23	0.92
TOTAL				1318	52.72	2823	112.92	2112	84.48	1894	75.76

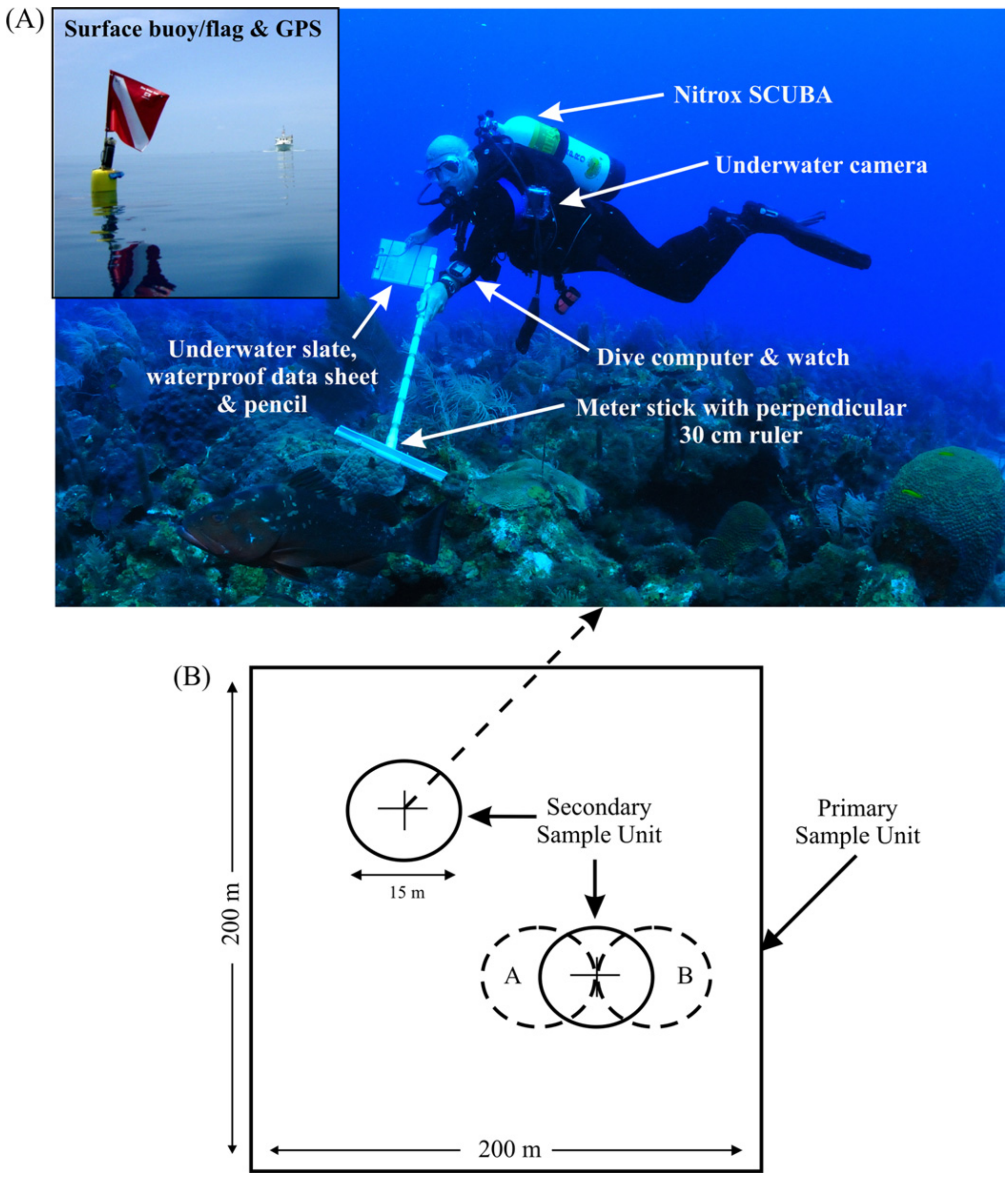

Fig. 2. Visual survey methods. (A) A scientific diver inside the 15 m diameter cylinder measuring a red grouper (*Epinephelus morio*) with the aid of a 30 cm ruler on a meter stick (photo: J. Luo). (B) The spatial layout of primary and second-stage sample units. In practice each second-stage unit is sampled by a buddy team of divers (denoted by dashed circles A and B).

positional errors of as much as 50–100 m without any notable directional bias. In addition, small isolated reef structures may or may not have appeared in the map. Thus, a grid cell of 200 m × 200 m was selected as the minimum mapping unit for defining benthic habitat classes (e.g., spur-groove fore reef, patch reefs). This size was large enough to compensate for positional errors and under-representation of reef habitats in the map, yet small enough to maintain homogeneity of a reef habitat class within a given cell.

A two-stage sampling scheme was employed to account for the disparity in area between a minimum mapping unit (40,000 m^2) for classifying reef habitats and a circular plot sample (177 m^2). The primary sample unit (PSU) was defined as a 200 m × 200 m map grid cell and the second-stage unit (SSU) was defined as a 15 m diameter visual plot (Fig. 2B). Fish density (number per second-stage unit, 177 m^2) was the principal metric used to develop and evaluate the statistical sampling design. Because of diving safety concerns, each SSU was usually sampled by two closely spaced divers (i.e., a "buddy pair" denoted by the dashed circles in Fig. 2B). For analysis, a single plot sample was computed as the arithmetic average of the adjacent stationary counts for a buddy team.

Development of the probabilistic sampling design focused on principal species of the exploited reef-fish complex, and entailed analysis of strategies for stratifying the survey domain and for allocating sampling effort among strata that yielded accurate, precise, and cost-effective estimates of population and community metrics. Estimation procedures for two-stage stratified random sampling were adapted from Cochran (1977; see appendix for computational formulae for density). Estimation of stratum variance (Appendix A, Eq. A-2) was modified to account for situations in which only one second-stage unit was sampled within a primary unit. Specifically, the divisor for s^2_{2h}, the sample variance among second-stage units in stratum h (Eq. A-4), was adjusted to avoid underestimation of this variance term.

Random selection of PSUs to be sampled within a stratum h from the complete list of N_h units was carried out using the discrete uniform distribution to ensure equal probability of selection (Law, 2007). This numerical procedure was not possible in practice for random selection of SSUs to be sampled within a given PSU because of poor map resolution that necessitated the two-stage sampling design. Field procedures were developed to avoid selection bias of SSU locations by divers. Upon reaching a randomly selected PSU, the field team attempted to determine the general location of reef versus non-reef habitats within the grid cell using the vessel's depth finder or by snorkeling, etc., depending on water depth and clarity. Buddy teams of divers were deployed on reef habitat at different locations within the grid cell. Divers descended vertically to the bottom and sampled the first reef habitat encountered. In cases when the same buddy team sampled multiple SSUs during the same dive, the pair were given predetermined randomized directions and distances to swim to subsequent SSU locations (Bohnsack and Bannerot, 1986).

The design performance measure used to evaluate survey precision was the coefficient of variation (CV) of mean density (Eq. A-8), which is the standard error expressed as a proportion of the mean. Performance with respect to survey costs was evaluated in terms of relative sample sizes, of which there are two components in a two-stage design. The first was m^* (Eq. A-9), the optimum number of second-stage units required within a primary unit. The second was n^*, the projected number of primary units needed to achieve a specified precision of mean density (Eq. A-11, derived from Cochran's (1977) equation 10.46 for population variance). Estimation of n^* presumes that primary units will be allocated among strata following an optimal Neyman allocation scheme (Eq. A-12) incorporating both strata areas and variances of density estimates.

2.4. Population and community metrics

The survey produced estimates by species for three standard abundance metrics (Cochran, 1977): frequency of occurrence (proportion of SSUs occupied by a species), mean density (number per SSU), and abundance (total number). Estimates of abundance ($\hat{Y}$) and associated variance were computed using mean density ($\bar{\bar{D}}$),

$$\hat{Y}_h = (\bar{\bar{D}}_h)(N_h M_h)$$

$$var[\hat{Y}_h] = var[\bar{\bar{D}}_h](N_h M_h)^2,$$

where N_h is the total possible PSUs in stratum h and M_h is the total possible SSUs per PSU. Domain-wide abundance and associated variance were obtained by summing the respective strata estimates over all strata.

Additional derived metrics included species richness (average number of species observed), a community measure of biodiversity, and metrics using species length compositions. Species richness was computed on the basis of a primary sample unit rather than per SSU to ensure a sufficient search area for reliable estimates. Population abundance-at-length was estimated by computing stratum abundance for each length class, and then summing across strata by length class. Average length in the exploited phase, a population sustainability metric, was estimated following the procedures of Ault et al. (2005b).

3. Results

3.1. Design evolution: stratification and sample allocation

3.1.1. Historical development

The stratified random sampling design was developed in the Florida Keys region utilizing digital benthic habitat maps and historical visual survey data. Visual sampling using the circular plot method has been conducted annually during May–September in the Florida Keys since 1979 (Bohnsack et al., 1999). During the early years of the survey (1979–1991) the focus was to evaluate reef fish community abundance and population structure in shallow fore-reef habitats at several locations along an exploitation gradient running from the upper to lower Florida Keys. The specific objective was to compare reef fish composition at specific reefs under different management regulations (e.g., with and without spearfishing, Bohnsack, 1982). Over the years, the survey expanded to providing data for stock assessments and for marine spatial planning in terms of locating and evaluating NTMRs for the FKNMS. To accomplish these tasks required a significant expansion of scope with respect to the range of reef habitats sampled and geographical coverage from Key Biscayne to Key West.

In 1994, the survey design was substantially modified to sample matching habitat types both inside and outside an anticipated network of NTMRs. The specific boundaries of 23 individual NTMRs were finalized prior to the 1997 survey and the network was implemented on 1 July 1997 (Bohnsack and Ault, 1996; FKNMS, 1997). The digital map of classified benthic habitats of the Florida Keys became available after the 1998 sampling season, enabling explicit delineation of the reef sampling domain.

Table 2
Primary sample units (PSU, n) and second-stage sample units (SSU, nm) for Florida Keys reef-fish surveys 1997–2001, and the allocation of sampling effort (as % of SSU) among habitat and management zone strata. Habitat strata are defined in Table 1A; O is open area, P is protected area.

Habitat Stratum	Zone	Percent Allocation of SSU				
		1997	1998	1999	2000	2001
IPLM	O	6.1	8.2	2.7	4.9	2.2
	P	6.4	6.3	0.9	3.0	1.1
MPLM	O	7.6	13.0	9.1	10.2	12.8
	P	3.4	2.6	0.9	2.7	1.6
OPLM	O	2.9	2.6	2.3	4.2	4.6
	P	4.7	3.9	3.2	4.2	1.1
OPRH, FRSH	O	7.4	10.8	5.2	4.2	12.7
	P	21.3	21.0	20.0	12.9	18.1
FRSL	O	7.4	10.4	5.9	8.3	12.5
	P	7.4	10.0	1.4	3.8	5.4
FRML	O	17.6	9.3	38.2	33.4	18.6
	P	7.8	1.7	10.2	8.2	6.1
FRDL	O	–	–	–	–	3.4
Total SSU (nm)		408	461	440	527	742
Total PSU (n)		66	76	161	228	305

3.1.2. Pilot design: analysis of 1997–1998 surveys

Data from the 1997 and 1998 surveys were analyzed to identify a potential stratification scheme that partitioned the sampling domain into sub-areas of low to high variance of fish density. Matched habitat types inside and outside the NTMRs became the initial basis for stratification. Five cross-shelf habitat classes were delineated extending from the shoreline to the outer fore reef: inshore, mid-channel, and offshore patch reefs, followed by shallow (0–6 m) and mid-depth (6–18 m) fore reefs (Tables 1A and 2; Fig. 3A). The 18 m depth corresponded with the maximum depths of the NTMRs. Given the very short time that NTMRs had been in effect, fish density data were pooled among management zones by cross-shelf habitat class. The cross-shelf scheme was somewhat effective in circumscribing lower and higher variance habitats of principal exploited species as illustrated by yellowtail snapper (Fig. 3B). In general, mean density differed among some cross-shelf habitats, and the mean and variance of density were positively correlated. Differences were also observed in the spatial distributions of juveniles and adults of the same species, suggesting that life stages based on reproductive maturity (or exploitation phase, which often coincides with the adult life stage) should be treated as separate biological entities for development of the sampling design.

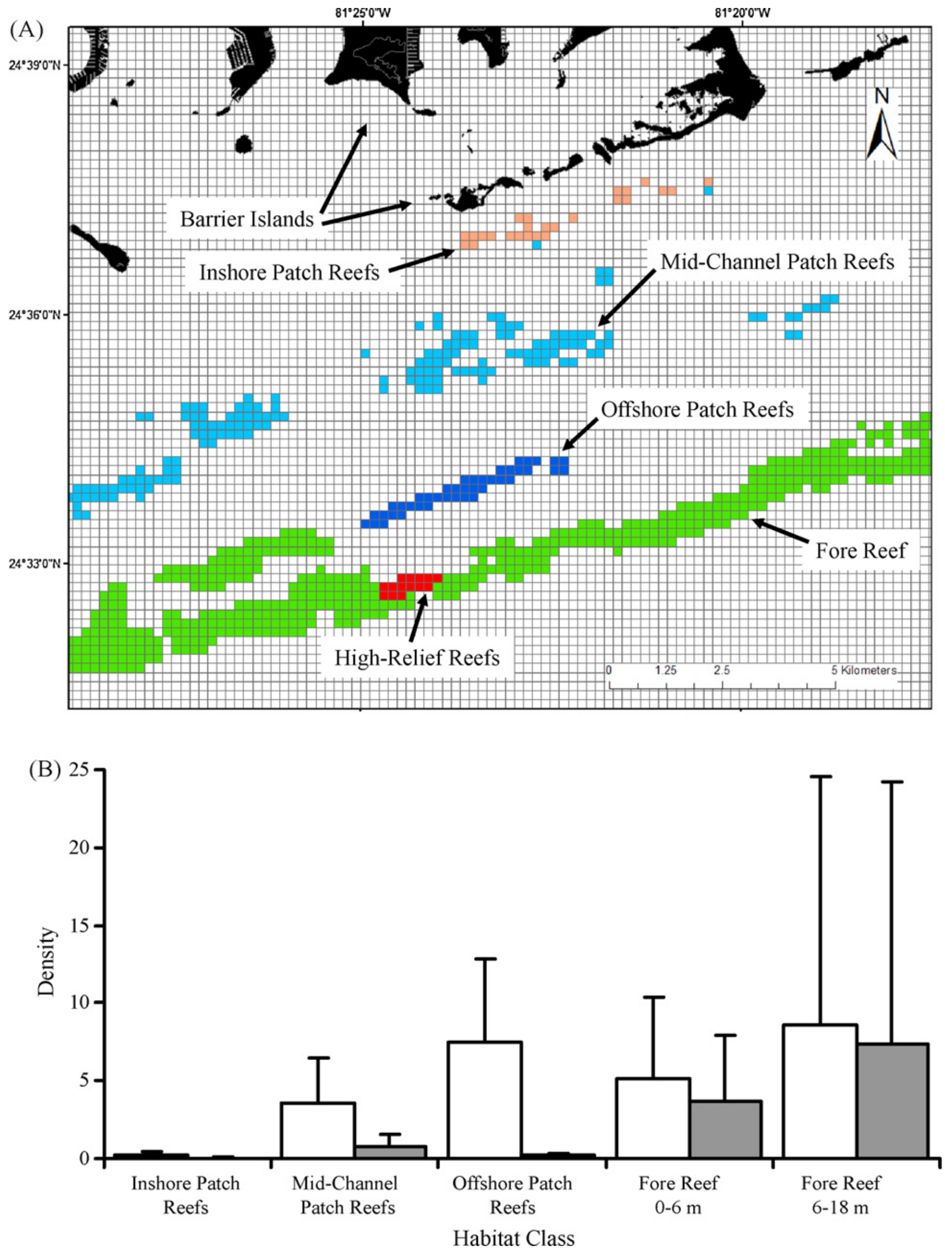

Fig. 3. Spatial relationships between reef fish habitats and density-variance. (A) Detail of Florida Keys sampling grid (rectangle in Fig. 1A) showing reef habitat classes; squares are primary sample units (200 m × 200 m). (B) Mean density (Eq. A-1) and associated standard deviation (Eq. A-10) by cross-shelf habitat class for yellowtail snapper (*Ocyurus chrysurus*) juveniles (open bars) and adults (shaded bars) estimated from the 1997 Florida Keys survey.

Table 3
Estimates of optimal second-stage unit sample sizes, m^* (equation A-9), from 1997 and 1998 surveys by cross-shelf habitat class for life stages of five principal exploited reef-fish species.

Habitat Class	Year	White grunt (*Haemulon plumieri*)		Gray snapper (*Lutjanus griseus*)		Yellowtail snapper (*Ocyurus chrysurus*)		Hogfish (*Lachnolaimus maximus*)		Black grouper (*Mycteroperca bonaci*)
		Juv	Adult	Juv	Adult	Juv	Adult	Juv	Adult	Juv
Inshore patch reefs	1997	1.3	1.9	1.0	1.5	1.6	3.1	2.6	2.2	2.9
	1998	1.2	1.7	0.8	1.6	2.0	3.0	2.1	2.5	1.5
Mid-channel patch reefs	1997	1.2	1.3	1.6	1.7	2.0	2.1	2.2	2.4	1.7
	1998	1.4	1.6	1.0	2.5	1.3	1.8	2.0	2.0	1.7
Offshore patch reefs	1997	1.1	1.7	2.1	1.5	1.9	1.7	2.2	1.1	2.8
	1998	1.8	1.6	1.3	1.0	0.8	1.9	1.5	1.4	2.5
Fore reef, shallow	1997	1.8	1.8	1.4	1.7	1.7	1.5	2.6	2.1	1.9
	1998	2.0	1.7	1.2	1.3	1.9	1.2	2.7	1.7	2.2
Fore reef, mid-depth	1997	1.0	1.6	1.9	1.0	1.2	0.9	2.6	1.6	1.8
	1998	0.7	2.4	1.7	2.3	1.5	2.4	1.9	2.2	1.2

Table 4
Required SSU samples (nm^*, equations A-9 and A-11) to achieve a 15% CV for domain-wide mean density at two levels of within-primary unit sampling effort, $m = 2$ and $m = 6$, estimated from the 1997 and 1998 surveys for life stages (J is juvenile, A is adult) of exploited reef fishes. The target precision was selected to facilitate comparisons of m levels for the various species life stages.

Species	Life stage	SSU samples to achieve 15% CV	
		$m = 6$	$m = 2$
White grunt	J	433	205
	A	1675	897
Gray snapper	J	838	425
	A	3671	1848
Yellowtail snapper	J	1063	514
	A	1781	796
Hogfish	J	1042	645
	A	659	387
Black grouper	J	1284	648

Table 5A
Analysis of 1999–2000 survey data for 5 principal exploited species. Estimated optimal second-stage unit sample sizes; values are the relative frequency of strata corresponding to three levels of m^*.

Species	Life stage	Frequency of Strata		
		$m^* \leq 1.0$	$1.1 \leq m^* \leq 2.0$	$2.1 \leq m^* \leq 2.9$
White grunt	J	30%	70%	0%
	A	20%	75%	5%
Gray snapper	J	0%	100%	0%
	A	15%	85%	0%
Yellowtail snapper	J	30%	70%	0%
	A	15%	80%	5%
Hogfish	J	30%	70%	0%
	A	30%	70%	0%
Black grouper	J	30%	60%	10%

Using the 5-strata cross-shelf scheme, the 1997–1998 data were analyzed to determine the appropriate amount of sampling effort within and among primary units. Estimates of m^*, the optimum number of second-stage units to sample within a primary unit, were generally higher than 1 but less than 3 for most strata for juvenile and adult life stages of 5 principal exploited species in the two survey years (Table 3). These estimates of m^* were in contrast with the actual m of 5–6 second-stage units within each primary unit for 1997 and 1998. Values for nm^* (Eqs. (A-9) and (A-11)), the total second-stage units needed to achieve a specified precision of domain-wide mean density, were estimated for two levels of within-primary unit sampling effort, $m = 2$ and $m = 6$, using strata variances (Eqs. (A-3) and (A-4)) averaged from the 1997 and 1998 surveys. The analysis suggested that a fewer number of second-stage units would be required to achieve the same precision for the strategy of $m = 2$ compared to $m = 6$ (Table 4). The results of Tables 3 and 4 indicated that the two-stage sampling scheme was an effective strategy for controlling variance of density at spatial scales smaller than the minimum mapping unit (200 m × 200 m), but that sampling efficiency could be improved by reducing the number of second-stage units within a given primary unit and using the time savings to sample more primary units.

3.1.3. *Survey implementation and modifications, 1999–2001*

The 5-habitat design was implemented for the 1999 Florida Keys survey. Management zone type (open to fishing, protected from fishing) was incorporated as a second stratification variable, yielding a total of 10 habitat-zone strata. Three key modifications were made to the design of previous years. First, a sample size of $m = 2$ second-stage units was targeted for each primary unit. Second, allocation of primary sample units among strata was based on strata sizes and strata variances for principal species, with a minimum constraint of $n = 2$ primary units for target habitats in each of the 23 NTMRs. This survey sample allocation procedure involved several steps. First, total possible sample size based on the anticipated sampling budget was estimated. Once established, comparisons were made for life stages of six target species (Tables 3 and 4) of the relative proportions of strata sampling effort between 'stratum size' and 'stratum size-variance' allocation schemes. Allocations were adjusted to satisfy the majority of target species' variance-weighted proportions. The net effect of this strategy was to increase primary unit sample sizes in the open management zone, which accounted for 94% of the survey domain (Table 1A). The third modification was that specific primary units to be sampled within a stratum h were randomly selected *a priori* with equal probability from the complete list of N_h units. This formal randomization procedure mostly affected the selection of sampling locations in the open management zone. In earlier years, sampling locations were selected within matched open and protected 'reefs' (e.g., Molasses Reef) of similar habitats that ranged in size from 10 to 20 primary unit grid cells in most cases. For the protected zone, the new procedure essentially drew from the same set of grid cells as for the previous 'protected reefs'. This was not the case for previous 'open reefs', which only constituted a small fraction of the primary unit grid cells in the open zone.

Due to a late-season budget shortfall for sampling in 1999, only about 75% of the planned sites were actually sampled; consequently, some habitat classes were undersampled in each management zone. The same stratification, allocation, and randomization protocols were used for the 2000 survey, which was completed as planned. Further examination of m^* for the 1999–2000 data supported the choice of the two-stage sampling scheme with $m = 2$ second-stage units per primary unit (Table 5A).

During the course of the 1999 and 2000 surveys, a potential problem arose with the cross-shelf stratification scheme. A prominent habitat type inside the NTMRs, namely high complexity reef structures that extended greater than 3–4 m above the sand substrate, was not found among sampling locations in the open management zone. To overcome this discrepancy, additional sampling sites for this habitat type were selected from the matched 'open reefs' of previous years. Features of the benthic habitats were re-analyzed to distinguish three principal categories of general reef complexity: low (average vertical relief of structures <1 m); medium (vertical relief between 1 and 2 m); and high (vertical relief >2 m). High-relief reefs were found to mostly occur in the shallow fore reef, accounting for the majority of reef area for this class within NTMRs, but were quite rare in the open zone (Table 1A). The 1999–2000 data were used to evaluate the effects of stratifying by habitat on design performance. Three scenarios were analyzed: (1) no habitat strata; (2) the actual 5-strata cross-shelf arrangement; and (3) a similar 6-habitat strata design separating high-relief reefs as an additional stratum. All three designs yielded similar estimates of domain-wide mean density for life stages of 5 principal species (Table 5B). Incorporating habitat into the stratification improved survey efficiency for all species life stages analyzed, as measured by a reduction in the projected sample size nm^* required to achieve a CV of 15%. The addition of a high-relief stratum resulted in a modest improvement in efficiency over the 5-strata design in 5 cases, no change in 3 cases, and a decrease in efficiency for 1 species life stage. The 6-strata configuration also corresponded more closely with the matched reef habitat scheme used prior to 1999.

The 6-habitat design was employed in 2001, along with strata for open and protected management zones. The CV of domain-wide mean density for the 2001 survey ranged from 11–25% for the majority of life stages of exploited species (Table 6). CVs were generally higher for life stages with low mean density (e.g., juvenile mutton snapper). In contrast, prior to implementation of the formal

Table 5B
Analysis of 1999–2000 survey data for 5 principal exploited species. The effect of habitat stratification on estimates of mean density ($\bar{D}$, number per SSU) and survey sampling efficiency, as measured by the required SSU samples (nm^*) to achieve a 15% CV. Management zone strata (open, protected) were used in adult life stages computations.

Species	Life stage	No Habitat Strata		5 Habitat Strata		6 Habitat Strata	
		$\bar{D}$	Required SSU to achieve 15% CV	$\bar{D}$	Change in required SSU	$\bar{D}$	Change in required SSU
White grunt	J	3.49	442	4.42	−43.7%	4.62	−45.2%
	A	1.97	732	2.08	−12.6%	2.17	−18.4%
Gray snapper	J	1.66	1457	1.86	−55.8%	1.91	−59.3%
	A	0.95	1095	0.91	−12.8%	0.94	−15.7%
Yellowtail snapper	J	3.84	1170	3.57	−25.1%	3.20	−40.1%
	A	1.45	1207	1.36	−23.2%	1.43	−25.1%
Hogfish	J	0.19	608	0.22	−24.8%	0.23	−25.5%
	A	0.54	316	0.53	−13.3%	0.54	−15.5%
Black grouper	J	0.14	971	0.15	−7.2%	0.14	−1.6%

sampling design, the 1997–1998 surveys yielded CVs above 30% in most cases. The increase in survey precision over the 1997–2001 time frame (Fig. 4A and B) was achieved with no substantial changes in the survey budget in terms of vessel-days and field personnel (divers). The notable increase in sample size nm for 2001 (Table 2) was due to a combination of increased field efficiency (i.e., sampling a greater number of primary units per vessel-day) and additional opportunistic sampling on the vessel of a benthic ecology research group. The survey domain was also expanded in 2001 to include fore reef occurring at depths from 18 to 33 m (Tables 1A and 2), facilitated by the increased availability of enriched air Nitrox. Adding this new stratum resulted in a slight increase in survey precision (Table 6).

3.2. Survey estimates for assessment and management

3.2.1. Design performance: species and community metrics

Survey performance during the period 1980–2008 is illustrated in Fig. 5 for black grouper, a highly prized species. Annual design metrics were computed based on the habitat-zone stratification scheme in effect at the time of sampling. From 1999–2008, the survey domain was fully randomized using the habitat-zone stratification. In 2001 the deep fore reef stratum was added (Table 1A). During 1999–2008, the CVs of mean density for black grouper in the Florida Keys ranged mostly from 12% to 18% (Fig. 5A, solid circles). This level of survey precision enabled statistical detection of relative changes in annual population density of 24 to 36% (i.e., twice the CV approximates the 95% confidence interval in terms of relative standard error). The closeness of the survey CV values for this period to the projected CV dependent on nm^* (Fig. 5A, line) indicates that allocation of circular plot samples within primary units and among strata was close to optimal for the habitat-zone stratified design. The exception during this period was the 2004 survey (CV = 27%) in which an unforeseen shortfall in the field sampling budget mid-way through the survey season resulted in only about 50% completion of the allocated sampling sites. Visual surveys during 1992–1998 were conducted over the entire geographical extent of the Florida Keys region following essentially the same habitat-based spatial framework that was implemented in later years (i.e., 6 habitat strata at 0–18 m depths). The 1998 survey incorporated management zone strata following implementation of NTMRs. Estimates of mean density during this period were less precise, however, with CVs ranging from 25% to 74% (Fig. 5A, open circles). The departure of many of the 1992–1998 survey CV-nm points vertically from the theoretical curve suggests that low precision of estimates was largely due to suboptimal allocation rather than the overall level of sampling effort nm. During the early years of reef-fish surveys (1980–1991, Fig. 5A, open squares), visual sampling was carried out as a component of focused ecological studies in specific habitats and regions of the Florida Keys rather than as a population-wide study; consequently, accuracy and precision of population estimates were low in this time frame. Due to incomplete habitat sampling in 1980–1991, survey estimates were computed for a

Table 6
Estimates of 1997–2001 domain-wide mean density $\bar{D}$ (number per SSU, 177 m^2) and associated CV for seven principal exploited species using a 12-strata (6 habitats × 2 management zones) sampling design. Also shown are estimates for the 2001 survey including the deep fore reef stratum.

Species	Life stage	1997		1998		1999		2000		2001		2001 (with deep stratum)	
		$\bar{D}$	CV	$\bar{D}$	CV	$\bar{D}$	CV	$\bar{D}$	CV	$\bar{D}$	CV	$\bar{D}$	CV
White grunt	J	4.485	15.6	6.770	20.2	4.384	20.9	4.704	12.8	6.747	13.9	6.663	13.5
	A	1.616	35.3	1.259	9.1	1.212	23.5	3.121	15.3	3.932	21.3	4.141	21.0
Mutton snapper (*Lutjanus analis*)	J	0.006	65.8	0.004	100.0	0.012	48.3	0.047	40.2	0.013	41.1	0.012	41.1
	A	0.036	30.4	0.043	49.8	0.045	37.7	0.089	21.1	0.113	17.5	0.125	16.7
Gray snapper	J	0.854	28.5	1.153	14.4	2.552	19.1	1.258	35.0	1.952	30.6	1.788	29.9
	A	0.689	49.2	0.698	32.6	0.720	25.9	1.153	21.4	1.525	20.3	1.517	19.1
Yellowtail snapper	J	5.929	31.6	1.921	35.5	2.282	15.3	2.791	13.2	1.904	13.4	1.968	12.8
	A	3.987	48.9	1.008	54.8	1.359	29.0	1.485	15.6	1.647	18.3	1.888	16.6
Hogfish	J	0.115	46.8	0.145	26.4	0.159	19.0	0.350	12.6	0.232	13.2	0.218	12.8
	A	0.218	24.2	0.233	24.2	0.445	13.2	0.641	11.4	1.292	10.6	1.261	10.0
Red grouper (*Epinephelus morio*)	J	0.037	67.0	0.098	58.6	0.161	19.2	0.199	14.0	0.173	13.6	0.157	13.5
	A	0.005	66.3	0.006	80.8	0.018	42.8	0.016	40.6	0.069	20.4	0.064	19.8
Black grouper	J	0.036	51.2	0.105	51.5	0.080	22.3	0.126	19.0	0.098	16.4	0.159	16.0
	A	0.003	95.5	0.0001	99.4	0.007	63.1	0.006	39.2	0.014	24.7	0.025	22.0

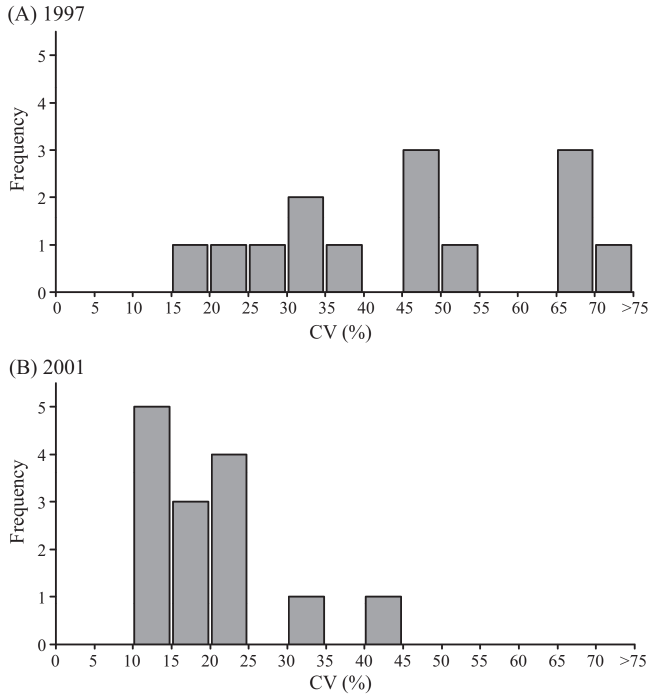

Fig. 4. Frequency histogram of CV of mean density for juvenile and adult life stages of seven principal exploited species (Table 6) showing the improvement in survey precision between (A) 1997 and (B) 2001 in the Florida Keys.

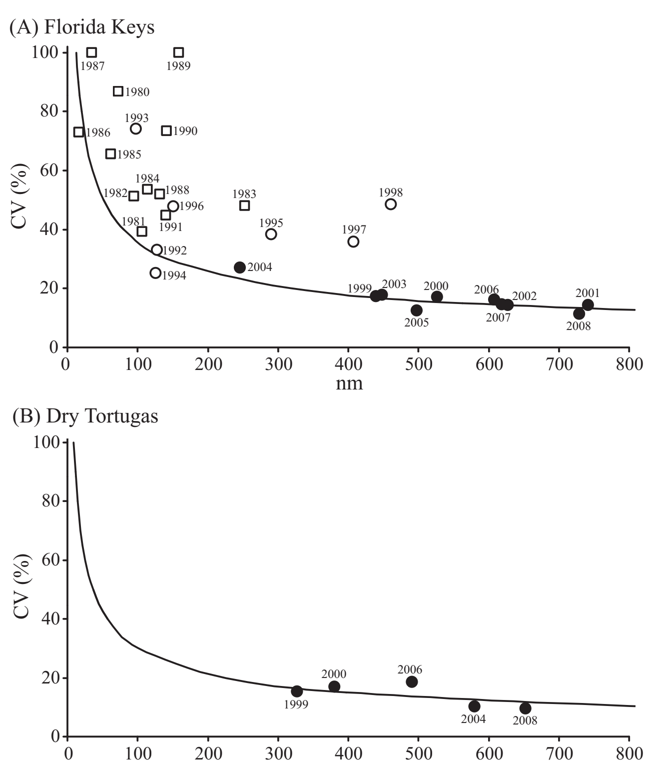

Fig. 5. Coefficient of variation of black grouper mean density (all life stages) dependent upon survey sample size (*nm*) for 1980–2008 in the (A) Florida Keys and (B) Dry Tortugas. Open squares denote 1980–1991 surveys with limited geographical and habitat coverage; open circles denote 1992–1998 surveys with complete coverage of the domain prior to implementation of the formal stratified random sampling design; and, solid black circles denote 1999–2008 surveys post-implementation of the formal design. Solid lines are the predicted CVs at given sample sizes (Eq. A-11) presuming optimal sample allocation.

two-stage simple random design (i.e., no habitat strata) for comparison purposes.

Using the logic of survey design development in the Florida Keys, visual surveys employing a reef habitat-management zone spatial framework were expanded to the Dry Tortugas, a relatively remote region of the coral reef ecosystem located over 110 km west of the nearest human population center of Key West (Fig. 1; Table 1B; Franklin et al., 2003; Ault et al., 2006). Five surveys were conducted in this region between 1999 and 2008. Protected zone strata were incorporated following implementation of NTMRs in 2001 and 2007 (Table 1B). Annual sampling effort was comparable to Florida Keys surveys during this period given the smaller, but spatially compact sampling domain in the Dry Tortugas, 323 km^2 of reef habitat <33 m in depth, compared to 559 km^2 for the Florida Keys (Tables 1A and 1B). Black grouper CVs for the Dry Tortugas surveys ranged from 10 to 18% (Fig. 5B), very similar to the precision in the Florida Keys during 1999–2008.

Survey performance for the period 1999–2008 is compared for 49 species of the broader reef-fish community in Table 7. This comparison includes all reef species with an average frequency of occurrence per SSU above 10% over the ten-year period in both the Florida Keys and Dry Tortugas regions. For 13 exploited species, the 10-year average CV of mean density ranged from 10 to 35% in the Florida Keys and from 7 to 50% in the Dry Tortugas. Average CVs were less than 20% for 9 of 13 species in the Florida Keys and 7 of 13 species in the Dry Tortugas. Only 1 exploited species had an average CV above 25% in the Florida Keys, compared to 5 of 13 species in the Dry Tortugas. Although the sampling design was tailored for exploited species, the surveys of 1999–2008 also performed well for 36 principal non-target species. Average CVs ranged from 6 to 27% in the Florida Keys and from 5 to 27% in the Dry Tortugas. For both regions, average CVs were less than 15% in the majority of cases (27 of 36 non-target species). There was a correspondence between survey precision and mean percent occurrence. For the cases with the highest precision (CVs below 10%), mean percent occurrence generally exceeded 40–50%. In contrast, mean percent occurrence was mostly below 20% for the lowest precision cases (CVs above 25%).

Additional derived community metrics from visual survey data include species richness, a measure of biodiversity. For the 1999–2008 surveys, 257 reef-associated fish species were observed out of a total of 306 species. Strata-weighted estimates of mean richness per PSU were relatively precise for a variety of taxa groupings. For example, in 2008 mean richness was 35.1 ± 0.6 (SE) species in the Florida Keys region and 36.9 ± 0.6 species in the Dry Tortugas. This level of precision would enable statistical detection of changes in mean richness over time of 1.0–1.5 species in both areas. For the 2008 Dry Tortugas survey, mean richness of parrotfishes (14 total species), a principal herbivore family, was 5.0 ± 0.1 species, and mean richness of groupers (17 total species), a principal carnivore family, was 2.3 ± 0.1 species. As illustrated in Fig. 6, PSU observations of richness were associated with reef habitat features for these two families: parrotfish richness was higher in shallower depths and habitats with low rugosity (Fig. 6A), and grouper richness was higher in high rugosity habitats (Fig. 6B). The habitat stratification scheme likely contributed to the high precision of richness estimates in both cases, even though the spatial patterns of richness differed between parrotfishes and groupers.

3.2.2. Size-structured abundance

The survey time-series of abundance-at-length estimates for black grouper are shown in Fig. 7 for the two survey regions. This illustrates a key advantage of fishery-independent over fishery-dependent surveys, viz., the ability to directly estimate abundance for both pre-exploited (<600 mm FL for black grouper) and exploited portions of a stock. The pre-exploited phase esti-

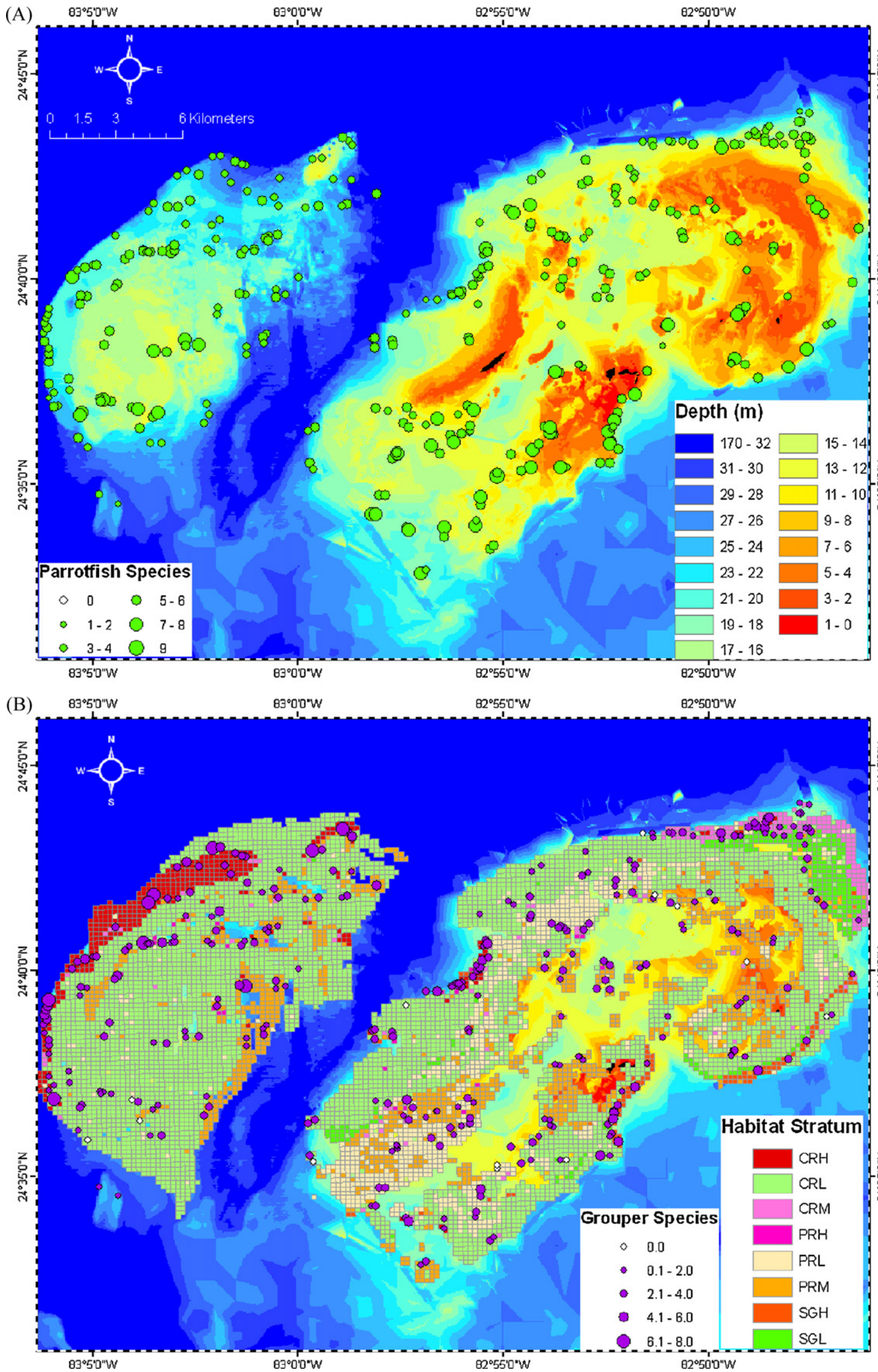

Fig. 6. Spatial distribution of species richness per primary sample unit from the 2008 Dry Tortugas survey for (A) parrotfishes (14 total species) in relation to bathymetry and (B) groupers (17 total species) in relation to reef habitat classes.

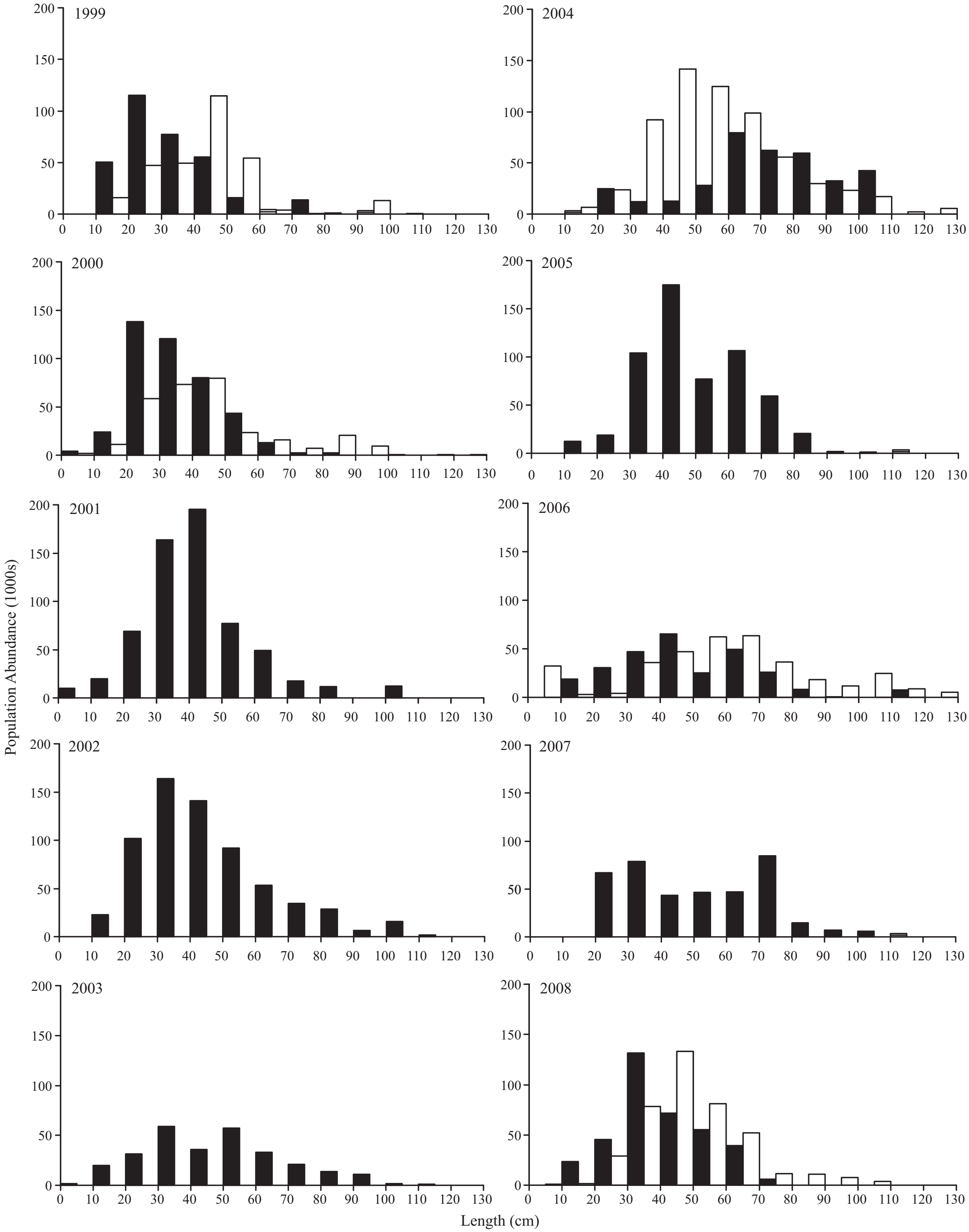

Fig. 7. Black grouper abundance-at-length for the 1999–2008 visual surveys in the Florida Keys (solid bars) and Dry Tortugas (open bars).

Table 7
Average percent occurrence $\bar{P}$ per SSU, average density $\bar{D}$ per SSU, survey precision (CV of $\bar{D}$, percent) and range of CV for the ten year period 1999–2008 for target (exploited) and non-target species in the Florida Keys (10 annual surveys) and Dry Tortugas (5 annual surveys). Species analyzed had average percent occurrence greater than 10% in both regions (49 total species).

Species	Family	Florida Keys			Dry Tortugas		
		$\bar{P}$	$\bar{D}$	CV($\bar{D}$), Range	$\bar{P}$	$\bar{D}$	CV($\bar{D}$), Range
EXPLOITED							
Bar jack (*Caranx ruber*)	Carangidae (jacks)	35.5	2.97	24.2 (18.5, 40.0)	23.4	3.63	26.8 (20.4, 36.8)
Porkfish (*Anisotremus virginicus*)	Haemulidae (grunts)	41.9	1.23	18.3 (11.9, 52.9)	17.8	0.55	34.0 (17.1, 60.4)
Tomtate (*Haemulon aurolineatum*)	Haemulidae	18.5	13.66	34.9 (23.6, 73.9)	31.9	25.96	22.5 (13.8, 29.8)
French grunt (*Haemulon flavolineatum*)	Haemulidae	38.0	3.63	19.7 (15.4, 30.0)	14.9	0.82	30.7 (18.4, 39.7)
White grunt (*Haemulon plumierii*)	Haemulidae	73.5	8.96	14.1 (7.6, 22.8)	79.6	6.58	17.2 (13.8, 21.8)
Hogfish (*Lachnolaimus maximus*)	Labridae (wrasses)	62.5	1.15	10.1 (6.6, 13.6)	48.1	0.55	10.7 (8.6, 13.6)
Mutton snapper (*Lutjanus analis*)	Lutjanidae (snappers)	17.8	0.18	17.5 (10.0, 29.2)	22.8	0.19	14.8 (9.0, 21.8)
Gray snapper (*Lutjanus griseus*)	Lutjanidae	27.5	2.27	22.9 (16.8, 34.0)	15.2	2.73	49.7 (18.3, 70.0)
Yellowtail snapper (*Ocyurus chrysurus*)	Lutjanidae	58.5	4.12	12.3 (7.4, 18.0)	75.7	7.56	15.1 (7.9, 26.9)
Graysby (*Cephalopholis cruentata*)	Serranidae (groupers)	32.1	0.30	10.6 (7.1, 14.7)	31.6	0.27	10.7 (7.0, 13.8)
Red grouper (*Epinephelus morio*)	Serranidae	20.4	0.16	14.2 (10.7, 20.0)	62.2	0.62	6.7 (5.9, 7.8)
Black grouper (*Mycteroperca bonaci*)	Serranidae	16.2	0.14	16.2 (11.2, 27.0)	22.2	0.22	14.1 (9.6, 18.4)
Great barracuda (*Sphyraena barracuda*)	Sphyraenidae (barracudas)	10.7	0.11	23.3 (15.5, 33.7)	17.1	0.21	30.1 (14.9, 52.0)
NON-TARGET & AQUARIUM							
Ocean surgeon (*Acanthurus bahianus*)	Acanthuridae (surgeonfishes)	79.7	3.53	7.3 (5.7, 10.9)	60.5	1.21	10.5 (8.0, 14.4)
Doctorfish (*Acanthurus chirurgus*)	Acanthuridae	56.2	2.18	12.0 (8.5, 17.0)	30.0	0.50	16.8 (14.5, 19.0)
Blue tang (*Acanthurus coeruleus*)	Acanthuridae	77.5	2.92	9.7 (6.4, 15.8)	77.7	2.25	8.1 (7.0, 10.1)
Foureye butterflyfish (*Chaetodon capistratus*)	Chaetodontidae (butterflyfishes)	41.5	0.60	10.5 (7.0, 24.5)	39.8	0.59	9.1 (6.0, 10.9)
Spotfin butterflyfish (*Chaetodon ocellatus*)	Chaetodontidae	42.8	0.53	8.5 (6.2, 12.1)	53.7	0.69	6.9 (5.3, 7.6)
Reef butterflyfish (*Chaetodon sedentarius*)	Chaetodontidae	32.5	0.45	10.4 (7.2, 14.7)	27.0	0.29	13.3 (10.6, 17.1)
Squirrelfish (*Holocentrus adscensionis*)	Holocentridae (squirrelfishes)	10.2	0.14	24.6 (19.6, 36.5)	13.4	0.17	26.7 (16.8, 41.0)
Spanish hogfish (*Bodianus rufus*)	Labridae (wrasses)	23.8	0.25	13.7 (9.6, 19.1)	21.5	0.19	14.6 (8.8, 18.5)
Slippery dick (*Halichoeres bivittatus*)	Labridae	70.0	4.85	8.8 (7.6, 10.7)	77.2	7.18	7.8 (6.0, 9.6)
Yellowhead wrasse (*Halichoeres garnoti*)	Labridae	67.7	3.30	8.3 (5.1, 18.5)	81.6	3.95	7.4 (4.2, 11.8)
Clown wrasse (*Halichoeres maculipinna*)	Labridae	56.4	2.31	8.7 (6.7, 11.4)	42.6	0.89	13.0 (9.6, 20.3)
Puddingwife (*Halichoeres radiatus*)	Labridae	27.2	0.25	12.1 (7.9, 18.7)	11.9	0.09	21.3 (15.3, 36.2)
Bluehead (*Thalassoma bifasciatum*)	Labridae	92.1	17.69	6.6 (4.0, 9.4)	94.8	15.58	8.1 (4.8, 15.8)
Spotted goatfish (*Pseudupeneus maculatus*)	Mullidae (goatfishes)	35.9	0.67	19.1 (8.4, 57.0)	62.0	1.10	9.7 (8.0, 12.0)
Yellowhead jawfish (*Opistognathus aurifrons*)	Opistognathidae (jawfishes)	10.7	0.25	26.7 (16.8, 46.1)	49.8	2.59	14.2 (10.1, 17.5)
Blue angelfish (*Holacanthus bermudensis*)	Pomacanthidae (angelfishes)	16.6	0.14	16.5 (12.2, 23.3)	57.1	0.83	7.2 (5.5, 8.6)
Queen angelfish (*Holacanthus ciliaris*)	Pomacanthidae	27.2	0.23	12.7 (7.9, 19.7)	23.4	0.20	12.9 (9.0, 15.3)
Gray angelfish (*Pomacanthus arcuatus*)	Pomacanthidae	58.1	0.82	10.1 (5.4, 23.1)	46.0	0.58	12.7 (7.6, 27.3)
French angelfish (*Pomacanthus paru*)	Pomacanthidae	21.1	0.19	14.8 (11.9, 20.1)	14.3	0.12	17.3 (13.5, 20.7)
Blue chromis (*Chromis cyanea*)	Pomacentridae (damselfishes)	21.9	1.37	17.2 (12.4, 27.2)	23.3	0.95	24.7 (11.3, 43.9)
Beaugregory (*Stegastes leucostictus*)	Pomacentridae	24.2	0.27	14.8 (8.7, 23.9)	34.6	0.58	12.0 (10.1, 13.5)
Bicolor damselfish (*Stegastes partitus*)	Pomacentridae	81.0	19.55	8.4 (5.7, 12.2)	73.9	7.71	8.6 (6.7, 11.2)
Threespot damselfish (*Stegastes planifrons*)	Pomacentridae	28.6	0.61	14.5 (9.9, 20.2)	36.0	1.08	12.1 (8.7, 20.5)
Cocoa damselfish (*Stegastes variabilis*)	Pomacentridae	55.1	0.89	9.5 (5.8, 14.0)	91.8	5.07	5.2 (4.3, 6.5)
Striped parrotfish (*Scarus iseri*)	Scaridae (parrotfishes)	80.2	7.55	7.1 (5.2, 9.9)	91.6	11.22	13.4 (4.5, 41.5)
Princess parrotfish (*Scarus taeniopterus*)	Scaridae	16.7	0.34	21.5 (12.5, 27.4)	12.0	0.28	21.7 (13.0, 30.8)
Greenblotch parrotfish (*Sparisoma atomarium*)	Scaridae	40.9	1.01	12.3 (7.7, 18.4)	49.7	1.10	12.9 (9.0, 22.5)
Redband parrotfish (*Sparisoma aurofrenatum*)	Scaridae	88.5	3.97	6.0 (3.9, 8.2)	83.9	2.94	13.0 (4.8, 23.2)
Redtail parrotfish (*Sparisoma chrysopterum*)	Scaridae	27.3	0.57	18.4 (12.2, 25.6)	14.5	0.18	25.7 (18.8, 32.5)
Yellowtail parrotfish (*Sparisoma rubripinne*)	Scaridae	19.7	0.34	20.9 (12.2, 30.1)	11.0	0.13	23.0 (15.9, 30.3)
Stoplight parrotfish (*Sparisoma viride*)	Scaridae	64.2	1.41	8.7 (6.4, 11.9)	60.5	1.20	9.9 (5.8, 12.5)
Butter hamlet (*Hypoplectrus unicolor*)	Serranidae (basslets)	32.9	0.33	11.1 (7.2, 19.4)	48.4	0.62	9.4 (5.9, 17.3)
Tobaccofish (*Serranus tabacarius*)	Serranidae	9.9	0.12	23.6 (16.9, 32.5)	14.6	0.18	23.7 (19.2, 36.0)
Harlequin bass (*Serranus tigrinus*)	Serranidae	35.4	0.35	9.6 (7.6, 12.5)	34.0	0.34	12.2 (8.7, 17.9)
Saucereye porgy (*Calamus calamus*)	Sparidae (porgies)	35.3	0.45	13.1 (9.4, 25.1)	75.5	1.43	8.8 (7.1, 11.5)
Sharpnose puffer (*Canthigaster rostrata*)	Tetraodontidae (puffers)	44.4	0.48	8.7 (5.7, 12.4)	30.9	0.28	13.3 (7.1, 19.0)

mates facilitate analysis of stock-recruitment dynamics and natural mortality rate processes, while the exploited component provides the more typical inputs for size (and age)-based assessments of sustainability status. The black grouper abundance-size histograms also highlight potential differences in stock structure between the Florida Keys and Dry Tortugas regions. Exploited phase animals were generally more abundant in the smaller region of the Dry Tortugas (Fig. 7, open bars) compared to the Florida Keys (solid bars). The average length in the exploited phase was also somewhat higher in the Dry Tortugas (Fig. 8A, open circles) relative to the Florida Keys (solid circles). This was also observed in other principal exploited species, including mutton snapper (Fig. 8B) and hogfish (Fig. 8C). Fishery-dependent estimates of average length of the exploited phase for the recreational fleet in south Florida (Fig. 8, open triangles and squares) more or less corresponded with our fishery-independent estimates. The spatial domain of the recreational fleet includes the areas open to fishing in our Florida Keys and Dry Tortugas survey domains, the unmapped area lying between these two regions, and some additional deeper (>33 m) reef habitats (Fig. 1). It is interesting to note that both fishery-dependent and -independent estimates of average length were below the estimated average length for a stock fished at maximum sustainable yield (upper solid horizontal line) for all three species. These examples suggest that expansion of the reef-fish visual survey to the farthest extent of the south Florida coral reef ecosystem appears to have provided more complete data for assessment of stock reproductive capacity and exploitation status.

3.2.3. No-take marine reserves

Another objective of the survey was to facilitate evaluation of the effects of the network of NTMRs on reef fishery resources. As illustrated for black grouper in the Florida Keys region, mean

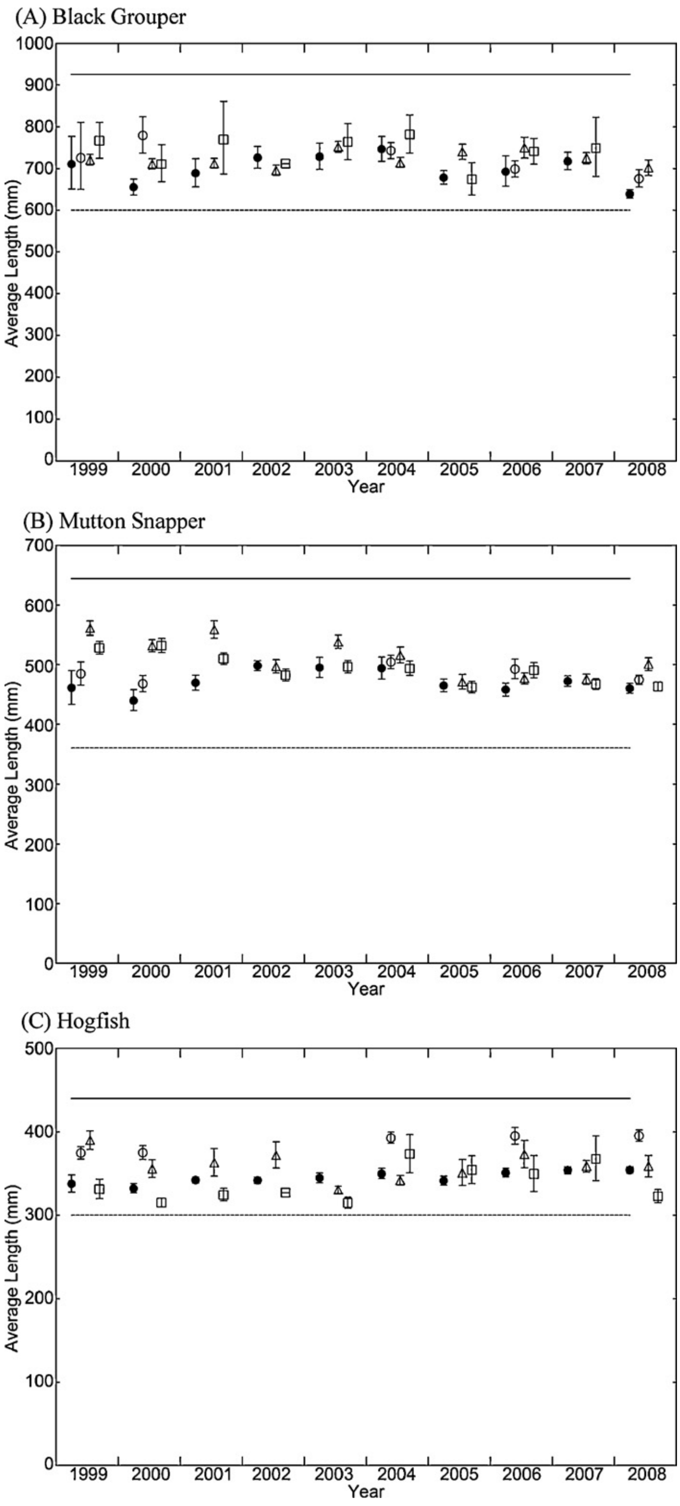

Fig. 8. Visual survey estimates of average length (±SE) of exploited phase fishes during 1999–2008 in the Florida Keys (solid circles) and Dry Tortugas (open circles) for (A) black grouper, (B) mutton snapper, and (C) hogfish. Also shown are average length estimates from fishery-dependent surveys of the recreational fleet (open triangles, Marine Recreational Fisheries Statistical Survey; open squares, Headboat Survey) in south Florida. The lower dashed lines are the respective minimum legal lengths of capture, and the upper solid lines are the respective average lengths at maximum sustainable yield. Average lengths in the exploited phase and at maximum sustainable yield were estimated using the methods of Ault et al. (2005b).

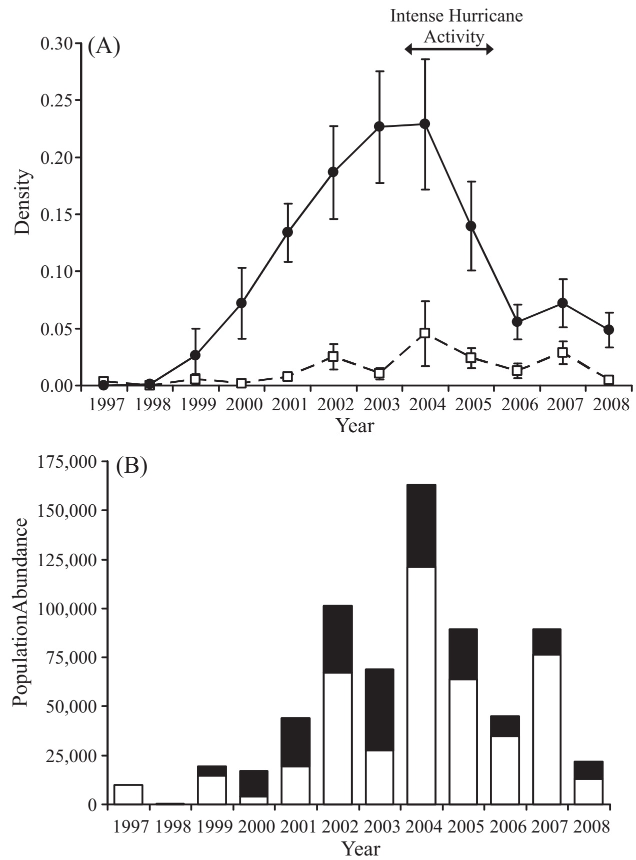

Fig. 9. Survey estimates for evaluating performance of NTMRs in the Florida Keys, 1997–2008; NTMRs were implemented in 1998; intense hurricanes impacted the sampling domain in 2004 and 2005. (A) Habitat-stratified mean densities per SSU and associated standard errors for exploited phase black grouper (total length ≥600 mm) in the open access (open squares) and protected (solid circles) management zones. (B) Population abundance for exploited phase black grouper, denoting the proportions inhabiting protected (dark bars) and open access (open bars) management zones.

density of exploited phase fishes (FL ≥ 600 mm) increased substantially inside the protected management zone in the years following reserve implementation and prior to the period of intense hurricane activity, 1998–2003 (Fig. 9A). In contrast, mean density in the zone open to fishing remained very low from 1998–2001, and then exhibited a modest increase in 2002. Differences in mean density between the protected and open zones were able to be statistically detected by the 2000 survey, three years after NTMR implementation. These analyses excluded the deep fore reef stratum which does not occur in the protected zone (Table 1A) and was not sampled until 2001. Changes in relative abundance of black grouper translated to significant changes in absolute abundance as well (Fig. 9B). By the years 2002–2004, about 40% of exploited phase black grouper inhabited the NTMRs, even though this zone only accounted for 6% of the domain area. Mean density and abundance in both management zones declined following the intense hurricane seasons of 2004–2005. Ault et al. (2006) documented changes in reef-fish abundance following the 2001 implementation of NTMRs in the Dry Tortugas.

4. Discussion

4.1. Survey performance

In this study principles of statistical sampling design were used to develop and conduct an ecosystem-scale, fisheries-independent visual survey of over 250 coral reef-fishes in southern Florida. The annual–biennial survey provides a suite of population metrics for stock assessment, spatial planning, and fisheries ecosystem management. Following implementation of the stratified random design in 1999, survey estimates of density and abundance for about 50 principal exploited and non-target species have been relatively precise, with CVs ranging from 10 to 20% in most cases. This general level of precision ranked somewhat lower than comparable single-species surveys of marine shrimps and lobsters (Ault et al., 1999a; Smith and Tremblay, 2003), but ranked higher compared to surveys targeting multiple species of marine fishes (Smith and Gavaris, 1993).

Several historical developments were instrumental in these achievements. First, the visual stationary plot methodology, the principal sampling method, was designed from its inception in 1979 to obtain density and length composition data for all observable fish species, whether exploited or not (Bohnsack and Bannerot, 1986). These observations are the basis for estimating fundamental metrics for conducting modern stock assessments (Ault et al., 1998; Quinn and Deriso, 1999) and ecological community analyses (Blanchard et al., 2005; Mueter and Megrey, 2005). The non-destructive aspect of the methodology became particularly advantageous for sampling in NTMRs, the first of which were established in 1997. Second, the development of digital benthic habitat maps (FMRI, 1998; Franklin et al., 2003) enabled explicit delineation and enumeration of the geo-referenced sample units comprising the reef sampling domain. Third, visual sampling in the 1980s and 1990s provided historical data on the spatial densities of fishes that facilitated classification of the digital maps into effective sampling strata. Building upon these developments, sampling efficiency was improved over time via an iterative learning process by which past survey data was used to refine the stratification and allocation schemes of future surveys (Smith and Gavaris, 1993; Ault et al., 1999a).

4.2. Stock assessment

The utility of visual surveys for serving the needs of assessment and management of reef-fish resources hinges on the accuracy and precision of survey estimates and their cost. The primary focus was to obtain estimates of density-abundance and size structure for conducting stock assessments of principal exploited reef species, i.e., the snapper-grouper complex (Ault et al., 1998, 2005a,b, 2008). As reported in many studies, application of standard design principles of stratification and allocation led to improvements in sampling efficiency of target species, where efficiency was measured as the relation between precision and sample size or cost (Gavaris and Smith, 1987; Ault et al., 1999a; Folmer and Pennington, 2000; Smith and Tremblay, 2003; Smith and Lundy, 2006; Smith et al., in press). Our analysis showed that stratifying by habitat features including reef structure, rugosity, and depth was effective in partitioning the spatial heterogeneity of reef-fish density, and thus contributed to increased sampling efficiency; however, there may be room for future improvement to this stratification scheme. Analytical investigations of how specific biotic and abiotic factors may be configured to comprise strata that better delineate low, moderate, and high variance regions may yield significant improvements in design performance (Schnute and Haigh, 2003). Treating juveniles and adults of the same species as separate biological entities with respect to stratification also contributed to design efficiency by accounting for potential changes in spatial distribution patterns at the onset of reproductive maturity.

Dramatic reductions in the CVs of population estimates for target species occurred following implementation of the formal survey design in 1999 (Table 6). As illustrated for black grouper (Fig. 5A), the CVs of mean density were about 40–45% in 1997 and 1998 compared to 17% in 1999, even though the stratification scheme and overall sampling effort were nearly the same in all three years. Two changes in the sample allocation strategy in 1999 appear to have contributed to these increases in sampling efficiency. First, sampling effort was reduced at a site (primary unit), enabling the diversion of effort to visiting more sites and thus greater coverage of the survey domain. Second, Neyman allocation of sites among strata enabled re-distribution of samples to larger and more variable habitats.

The two-stage approach was an effective way to deal with the disparity in area between a diver circular plot sample and the minimum mapping unit for classifying reef habitat strata. Future improvements in the spatial resolution of the benthic habitat map may eventually eliminate the need for the two-stage design. At a minimum, increased map resolution would facilitate more formal randomization methods for selecting SSUs within PSUs.

The accuracy of visual survey population estimates was controlled by implementing procedures to guard against bias at each spatial scale of the sampling and estimation process. At the level of a circular plot sample, the ability of divers to accurately identify, count, and size fishes was addressed by extensive training prior to participation in the surveys and by the cross-checking of recorded observations between divers in the same buddy team. At the stratum level, random selection of sample units with equal probability was expected to yield unbiased estimates of mean density, proportion occurrence, etc., following the theoretical properties of probabilistic survey design (Cochran, 1977). Weighting strata estimates by their respective areas controlled for bias of population estimates within the total survey area.

The issue of survey accuracy from a fisheries assessment perspective relates to the larger question of whether a representative sample is being drawn from a given exploited stock. There are potential accuracy and bias problems in this regard for both our fishery-independent visual survey and the more traditional fishery-dependent surveys of reef-fish catches. While our visual survey has expanded over time to include large portions of the Florida Keys coral reef ecosystem, the domain does not include some areas fished by the commercial and recreational fleets, including an unknown amount of deeper (>33 m) reef habitats that occur below safe diving limits and the unmapped section of the reef tract between Key West and the Dry Tortugas (Fig. 1A). On the other hand, our survey obtains information on significant portions of reef-fish stocks that reside within NTMRs and are not available to the fishing fleets. It is also generally unknown whether fishers are sampling reef-fish stocks in an unbiased manner, i.e., in relation to the spatial distribution of fishes among reef habitats, or whether the subsequent catches are representatively sampled at the docks. Despite these potential discrepancies, we found good correspondence in estimates of average length of the exploited life stage, a population sustainability metric, between fishery-dependent and -independent reef-fish surveys for several principal species (Fig. 8). In particular, estimates of average length from both sources were very similar in terms of their relative position between the minimum legal size (L_c) and the expected average length of a stock exploited at maximum sustainable yield. These findings suggest that both the visual and catch-sampling surveys are more or less sampling the area occupied by the same reef-fish stocks, but also highlight the need to cross-validate data from multiple survey sources prior to conducting quantitative stock assessments (Mayfield et al., 2008).

The evolution of the visual survey design over the past 30 years places some time and space constraints on producing population estimates for stock assessment. For retrospective analyses, the longest consistent time-series of sampling occurred in the Florida Keys region. The habitat stratification scheme has been in effect since the survey's inception in 1979; however, prior to 1992 sampling was incomplete in any given year with respect to certain habitat classes and geographical coverage. With the implementation of the formal stratified random design in 1999 the precision of estimates in the Florida Keys greatly improved. The Florida Keys survey area was increased by about 10% in 2001 by adding the deep fore reef stratum; as a result, this requires accounting for historical densities in the new areas when producing population-level estimates before and after the change. To obtain the most representative population estimates of size-structured abundance, our analysis suggests combining the regional surveys of the Florida Keys and Dry Tortugas. This is possible beginning in 1999 for the subset of years in which both regions were surveyed.

4.3. *Spatially explicit management performance*

Another focus of the visual survey design was to facilitate evaluation of potential changes in fish density and other metrics following implementation of NTMRs. Our approach was to incorporate spatial management zones as an additional stratification variable. The resulting spatial framework of habitat-zone strata (Tables 1A and 1B) offered some distinct advantages over the more typical localized inside–outside study designs (Currie and Sorokin, 2009; Lester et al., 2009). The common objective of inside–outside studies is to compare relative measures of abundance (e.g., density) between protected and open zones. Our stratification scheme enabled estimation of habitat-weighted densities and associated variances in each zone (e.g., Fig. 9A), thereby accounting for zonal differences in habitat composition. For example, in the Florida Keys region high-relief reefs comprised 21.6% of the area in the protected zone but only 1.3% in the zone open to fishing (Table 1A). Fully randomizing sample locations by habitat type both inside and outside NTMRs avoided potential investigator-induced bias due to subjective site selection, e.g., the choice of "control" sampling sites within the open zone. An additional advantage of the StRS approach is the ability to evaluate management zones in terms of absolute measures of abundance (e.g., Fig. 9B), which are likely more relevant for understanding stock sustainability impacts of NTMRs compared to relative abundance measures.

Our sample allocation strategy for evaluating NTMR responses was in some respects a tradeoff in survey precision with the strategy for producing population estimates for stock assessment, especially in the Florida Keys region where NTMRs comprised only 6% of the coral reef area. There are 23 separate protected areas in the Florida Keys, each differing in terms of total area and the composition of habitats. The constraint of allocating at least some sampling effort (a minimum of 2 PSUs) to each principal habitat type in each individual reserve was done in an attempt to representatively sample this diverse network of NTMRs. As a result, about one-third of the sampling effort for the Florida Keys (Table 2, 1999–2001) was expended in the small area protected from fishing. A Neyman allocation strategy for optimizing the precision of Florida Keys-wide population estimates would have shifted some of the sampling effort in NTMRs to the open management zone.

4.4. *Ecosystem condition of the reef-fish community*

Although our survey design was tailored for exploited species, it also performed well for other species of the reef-fish community that are not targeted by recreational or commercial fisheries. Many of the non-target species were encountered more frequently (i.e., higher percent occurrence or occupancy rate, Table 7) compared to exploited species, and higher percent occurrence generally corresponded with higher survey precision. By attempting to control survey precision for higher trophic-level exploited species with relatively lower occupancy rates (mostly <40%), this strategy *de facto* resulted in relatively high precision for lower trophic-level non-target species. The sample sizes needed to achieve the same level of precision were thus lower for non-target vs. exploited species. In turn, controlling for the precision of abundance metrics at the species level appears to have contributed to high precision of community metrics such as species richness.

As illustrated for parrotfishes and groupers (Fig. 6), the survey's habitat stratification generally matched the spatial distribution of many species and taxa groups. However, the parrotfish and grouper example also showed that the spatial patterns of abundance may be in direct opposition, e.g., one taxa group may prefer high rugosity habitats while another may prefer low rugosity environments. A sample allocation strategy that is optimal for one species or taxa group may thus be suboptimal for other taxa. Several studies have demonstrated that the benefits to survey performance from a stratification scheme that effectively partitions spatial variance can be outweighed by an ineffective allocation scheme (Smith and Gavaris, 1993; Ault et al., 1999a). In our survey, allocation of samples among habitat strata was somewhat of a compromise for the full suite of high-priority exploited species and was likely suboptimal for any particular species life stage. Further exploration of numerical optimization techniques for allocating samples in multi-objective stratified surveys (Kimura and Somerton, 2006; Miller et al., 2007) may improve overall performance of future surveys. Allocation in our survey was likely suboptimal for many of the non-target species, yet survey precision was still relatively high. The generally higher sample sizes that we allocated to achieve high-precision estimates for target exploited species may have compensated for suboptimal strata allocation for non-target species.

4.5. *Feasibility and transferability of ecosystem monitoring*

As fisheries assessment and management and marine spatial planning move towards an ecosystem perspective, the information requirements will not be met by fishery-dependent sources alone. Our results demonstrate the feasibility of conducting relatively precise and cost-effective fishery-independent monitoring in coral reef environments that can provide species- and community-level metrics for exploited and non-exploited fishes to address resource management issues at spatial scales ranging from habitats to management zones to the ecosystem.

The principles of probabilistic sampling applied in our study should be transferable to other coral reef systems, especially those in the US Caribbean and Pacific under the respective jurisdictions of the Caribbean and Western Pacific fishery management councils. Digital maps of benthic habitats and bathymetry have already been developed for many of these areas (NCCOS, 2005; Zitello et al., 2009). The respective areas of shallow-water (0–33 m) coral reef habitats in principal regions like Puerto Rico, the US Virgin Islands, the Northwestern Hawaiian Islands, and the Northern Marianas Islands are similar in magnitude to our southern Florida survey domain (885 km^2). In addition, habitat-scale visual monitoring of coral reef fishes has been conducted in many of these regions (DeMartini et al., 2005; Monaco et al., 2007). The basic elements are thus in place for development of large-scale fishery-independent surveys. Perhaps the most important consideration up front is to prioritize the survey's objectives in terms of resource management issues and species. Our experience suggests that the total amount and spatial pattern of sampling effort for optimizing survey performance may be very different for addressing fishery sustainability issues at the species level compared to addressing habitat management issues at the community level, for example, and that pursuing one management objective may involve sacrificing survey performance for another objective.

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Appendix A. Computational formulae for the two-stage stratified random sampling design used for reef-fish visual surveys

Symbol	Definition	Computational Formula	Equation Number
$\bar{\bar{D}}_h$	Mean density (individuals/unit area) in stratum h	$\bar{\bar{D}}_h = \frac{1}{n_h}\sum_i \bar{D}_{hi}$	A-1
n_h	Number of primary units sampled in stratum h		
$\bar{D}_{hi}$	Mean density in primary unit i in stratum h	$\bar{D}_{hi} = \frac{1}{m_{hi}}\sum_j D_{hij}$	
m_{hi}	Number of second-stage units sampled in primary unit i in stratum h		
D_{hij}	Density in second-stage unit j in primary unit i in stratum h		
$\mathrm{var}\left[\bar{\bar{D}}_h\right]$	Variance of mean density in stratum h	$var[\bar{\bar{D}}_h] = \frac{(1-n_h/N_h)}{n_h}s_{1h}^2 + \frac{n_h/N_h(1-\bar{m}_h/M_h)}{n_h m_h}s_{2h}^2$	A-2
N_h	Total possible number of primary units in stratum h		
s_{1h}^2	Sample variance among primary units i in stratum h	$s_{1h}^2 = \frac{\sum_i (\bar{D}_{hi}-\bar{\bar{D}}_h)^2}{n_h-1}$	A-3
$\bar{m}_h$	Average number of second-stage units sampled per primary unit in stratum h		
M_h	Total possible number of second-stage units per primary unit in stratum h		
$n_h m_h$	Number of second-stage units sampled in stratum h		
s_{2h}^2	Sample variance among second-stage units j in stratum h	$s_{2h}^2 = \frac{1}{n'_h}\sum_i \left[\frac{\sum_j (D_{hij}-\bar{D}_{hi})^2}{m_{hi}-1}\right]$	A-4
n'_h	Number of primary units i sampled in stratum h in which $m_{hi} > 1$		
$\bar{\bar{D}}_{st}$	Domain-wide mean density for a stratified random survey	$\bar{\bar{D}}_{st} = \sum_h w_h \bar{\bar{D}}_h$	A-5
w_h	Stratum h weighting factor	$w_h = \frac{N_h M_h}{\sum_h N_h M_h}$	A-6
$\mathrm{var}\left[\bar{\bar{D}}_{st}\right]$	Variance of domain-wide mean density	$var[\bar{\bar{D}}_{st}] = \sum_h w_h^2 var[\bar{\bar{D}}_h]$	A-7
$\mathrm{SE}\left[\bar{\bar{D}}_{st}\right]$	Standard error of domain-wide mean density	$SE[\bar{\bar{D}}_{st}] = \sqrt{var[\bar{\bar{D}}_{st}]}$	
$\mathrm{CV}\left[\bar{\bar{D}}_{st}\right]$	Coefficient of variation of mean density	$CV\left[\bar{\bar{D}}_{st}\right] = \frac{SE\left[\bar{\bar{D}}_{st}\right]}{\bar{\bar{D}}_{st}}$	A-8
$m^*{}_h$	Optimum number of second-stage unit samples per primary unit in stratum h	$m_h^* = \frac{\sqrt{s_{2h}^2}}{s_{uh}}$	A-9
s_{uh}	Sample standard deviation in stratum h	$s_{uh} = \sqrt{s_{1h}^2 - \frac{s_{2h}^2}{M_h}}$	A-10
n^*	Number of primary unit samples required to achieve a specified variance	$n* = \frac{\sum_h w_h s_{uh}\left(\sum_h w_h s_{uh} + \sum_h \frac{w_h^2 s_{2h}^2}{m_h^* w_h s_{uh}}\right)}{V[\bar{\bar{D}}_{st}] + \sum_h \frac{w_h^2 s_{1h}^2}{N_h}}$	A-11
$V\left[\bar{\bar{D}}_{st}\right]$	Target variance for domain-wide mean density	$V[\bar{\bar{D}}_{st}] = (CV[\bar{\bar{D}}_{st}] \cdot \bar{\bar{D}}_{st})^2$	
$n^*{}_h$	Optimal allocation of primary units among strata	$n_h^* = n^*\left(\frac{w_h s_{uh}}{\sum_h w_h s_{uh}}\right)$	A-12

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