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BUILDING SUSTAINABLE FISHERIES IN FLORIDA'S CORAL REEF ECOSYSTEM: POSITIVE SIGNS IN THE DRY TORTUGAS

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ABSTRACT

In a series of synoptic research cruises including 4000 research dives, we surveyed reef-fish populations and habitats before and 3 yrs after 2001 implementation of no-take marine reserves covering approximately 566 km^2 in the Dry Tortugas, Florida. Species richness and composition of 267 fishes remained stable between 1999–2000 and 2004 within the overall survey domain. Reef-fish biodiversity was highest in the more rugose habitats. Domain-wide abundances of several exploited and nonexploited species increased; no declines were detected. In the Tortugas Bank reserve, we found significantly greater abundances and shifts in length composition toward a higher proportion of exploited-phase animals in 2004 than in 1999–2000 for some species. Consistent with marine reserve theory, we detected no declines in exploited species in the reserve, whereas we detected both increases and declines in nontarget species, but the increases in exploited populations may also have been influenced by factors other than protected status. Although the recovery process is still in an early stage, our results after 3 yrs are encouraging and suggest that no-take marine reserves, in conjunction with traditional management, can help build sustainable fisheries while protecting the Florida Keys coral-reef ecosystem.

Sustainability of marine ecosystems is a worldwide concern. Intensive fishing has diminished top trophic levels and affected the ecological dynamics and resilience of fisheries by reducing the numbers and lengths of food webs (Pauly et al., 2002; Zeller and Russ, 2004). Resource management focused on single-species production has historically ignored the ecosystem consequences of overfishing (Botsford et al., 1997; National Research Council, 2001; U.S. Commission on Ocean Policy, 2004). Proposed solutions intended to promote sustainability include more stringent applications of the precautionary approach and establishment of marine protected areas under the rubric of ecosystem-based fishery management (National Research Council, 2001; Lubchenco et al., 2003a; Pew Oceans Commission, 2003; Hilborn et al., 2004a,b; Meester et al., 2004; Pikitch et al., 2004; U.S. Commission on Ocean Policy, 2004). An extensive literature has touted the use of "no-take" marine reserves (NTMRs—areas protected from all extractive uses) as the means of reversing declining trends in tropical coral-reef ecosystems (Polunin, 1990, 2002; Roberts and Polunin, 1991; DeMartini, 1993; Bohnsack and Ault, 1996; Roberts, 1997; Allison et al., 1998; Guénette et al., 1998; Meester et al., 2001, 2004; Ault et al., 2002, 2005a; Halpern and Warner, 2002, 2003; Gell and Roberts, 2003; Hastings and Botsford, 2003; Lubchenco et al., 2003b; Willis et al., 2003; Bohnsack et al., 2004; Hooker and Gerber, 2004; Mangel and Levin, 2005).

In the Florida Keys, increased fishing pressure from rapid regional human population growth and environmental changes associated with coastal development have raised concerns about fisheries sustainability and persistence of the coral-reef ecosystem (Porter and Porter, 2001; Ault et al., 2005a; Pandolfi et al., 2005). Historically intense commercial and rising recreational fishing pressures have resulted in

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unsustainable rates of exploitation for 70% of the “snapper-grouper complex” (Ault et al., 1998, 2005b), which consists of over 50 species, mainly of groupers and snappers, but also of grunts, jacks, porgies, and hogfish. Over the last 40 yrs, the number of registered recreational vessels in southern Florida has grown by more than 500%. Sport-fishing effort is expected to continue to grow in proportion to regional human populations, which have doubled about every 20 yrs (Ault et al., 2005a). The recreational fleet now accounts for a substantial proportion of the total regional catches for some key exploited species (NOAA MRFSS Database; Florida Fish and Wildlife Conservation Commission Trip Ticket Database; Coleman et al., 2004), and this increasing trend will probably continue.

Reef fisheries in the Florida Keys ecosystem are complex and regulated by several entities, including the Florida Fish and Wildlife Conservation Commission (http://www.myfwc.com), the National Park Service (http://www.nps.gov/drto), and the National Marine Fisheries Service in conjunction with the South Atlantic Fishery Management Council (http://www.safmc.net) and the Gulf of Mexico Fishery Management Council (http://www.gulfcouncil.org). In response to declining trends in reef-fishery catches, many regional, federal, and state management regulations were imposed, including recreational bag limits, minimum size limits, commercial quotas and trip limits, seasonal closures, gear restrictions, limited commercial entry, closed fisheries, species moratoria, imposition of game-fish status, and restrictions on sale and possession. These regulations were implemented to stabilize catches, protect spawning-stock biomass, and reduce fishing mortality rates. In general, the history of regional regulations for reef fishes has been complex, and they have tended to be more restrictive over time, but nonetheless recent fishery assessments indicated that, for example, black grouper spawning stock biomass was < 10% of its historical size (Ault et al., 2005b).

In recent years, new ecosystem-based management measures have been enacted in the Florida Keys, including the 1997 implementation of a network of 23 NTMRs by the Florida Keys National Marine Sanctuary (http://floridakeys.noaa.gov). These are relatively small (mean 2 km^2, range 0.16–31 km^2), comprising only 46 km^2 in total area (U.S. Department of Commerce, 1996), and have varying levels of protection: four allow catch-and-release surface trolling, and four require a special permit for access. In July 2001, the Florida Keys network was expanded to become the largest in North America with the implementation of two NTMRs in the Dry Tortugas region that cover about 566 km^2. This region is believed to be an extremely important source of recruitment of coral-reef fishes because of its upstream location in the Florida Current, which facilitates advective dispersion and transport of eggs and larvae to the rest of the Keys (Lee and Williams, 1999; Dahlgren and Sobel, 2000; Lindeman et al., 2000; Ault et al., 2002; Yeung and Lee, 2002; Domeier, 2004; Fig. 1A).

Implementation of conventional management measures or of spatial controls like NTMRs is expected to rebuild reef-fish population biomass and age-structure, and in the long run, unrestricted growth of biomass within reserves should result in resource export through reserve boundaries to surrounding areas as either larval dispersal to proximal natal sites or diffusive movements of fishable biomass (Bohnsack, 1998; Roberts et al., 2001; Pauly et al., 2002; Russ, 2002; Zeller and Russ, 2004; Bohnsack et al., 2004). The rate at which these impacts occur and can be detected depends greatly on the species’ life history, demographic characteristics, and survey precision. Because snapper and grouper life spans are often measured in decades, the effects of management actions could take 20 yrs or more to reach their full potential (e.g., Beverton and Holt, 1957).

Here we report results from fisheries-independent surveys in the Tortugas region that assessed reef-fish populations before and after the establishment of Tortugas NTMRs in July 2001. The survey design incorporated habitats and management zones chosen to control the precision of spatial data for reef-fish populations. To evaluate potential impacts of NTMRs and other factors on reef-fish sustainability in the Florida Keys coral reef ecosystem, we analyzed temporal changes of relatively simple population and community metrics (e.g., frequency of occurrence, abundance, size compositions, and species richness) for the Tortugas region both within and outside NTMRs.

Materials and Methods

Study Area.—The Florida Keys coral reef ecosystem extends 380 km from Miami to the Dry Tortugas (Fig. 1A). The Tortugas study area was located about 113 km west of Key West (Fig. 1A) and encompassed approximately 1686 km^2 in two principal areas: Dry Tortugas National Park (managed by Department of the Interior) and Tortugas Bank (managed by Department of Commerce) (Fig. 1B).

Survey Design.—We employed a stratified random diver visual survey to obtain fishery-independent data on the spatial distribution, abundance, size composition, and habitats of coral reef fishes in the Tortugas region (Bohnsack and Bannerot, 1986; Ault et al., 1998, 2002; Bohnsack et al., 1999). The survey domain encompassed coral-reef habitats < 33 m deep in Tortugas Bank and Dry Tortugas National Park (Fig. 1). The sampling domain was partitioned into habitat strata based on the degree of vertical relief (e.g., rugosity, complexity) and the degree of patchiness (e.g., amount of soft-bottom substrate interspersed among reef structures) of the hard-bottom substrate (Fig. 2, Table 1; Ault et al., 2002; Franklin et al., 2003). This habitat-based stratification procedure was developed from the 1999 and 2000 baseline surveys (Fig. 1A) and was shown to be effective in partitioning the domain into areas of high, moderate, and low levels of mean fish density and associated variance for many principal reef species (Ault et al., 2002), thereby improving sampling efficiency and cost-effectiveness (Smith and Ault, 1993; Ault et al., 1999, 2003). Three management zones were incorporated as a second spatial stratification variable. The first, Tortugas Bank Fished (the fished area), was open to all types of commercial and recreational fishing under regional regulations. The second, Dry Tortugas National Park (the park), was open to only recreational hook-and-line fishing. Commercial fishing has been prohibited since 1935, when the area became a national monument, and recreational lobster diving was prohibited in 1980. After it became a national park in 1992, protection increased, and headboats for recreational fishing were excluded in 1995. The third, Tortugas Bank NTMR (the reserve), a no-take and no-anchoring reserve, also known as the Tortugas North Ecological Reserve, has been closed to all types of fishing since 1 July 2001 (Fig. 1B).

We used a geographical information system (GIS) and digital spatial databases of benthic habitats, bathymetry, and management zone boundaries to facilitate spatial delineation of the survey domain, sampling strata, and sample units. The Tortugas sampling domain was overlaid with a GIS grid of 200 × 200-m cells that represented the minimum mapping units for benthic habitat types (Fig. 2).

A two-stage stratified-random sampling design was employed in which the primary sample unit was the 200 × 200-m habitat grid cell and the second-stage unit was a circular visual-census plot 15 m in diameter (described below). Stratum (h) sizes in terms of area (A_h) consisting of N_h possible primary sampling units are given in Table 1. Allocation among strata of the number of primary units to be sampled was based on stratum area and variance of fish density for a representative suite of species (i.e., a Neyman allocation scheme; Cochran, 1977).

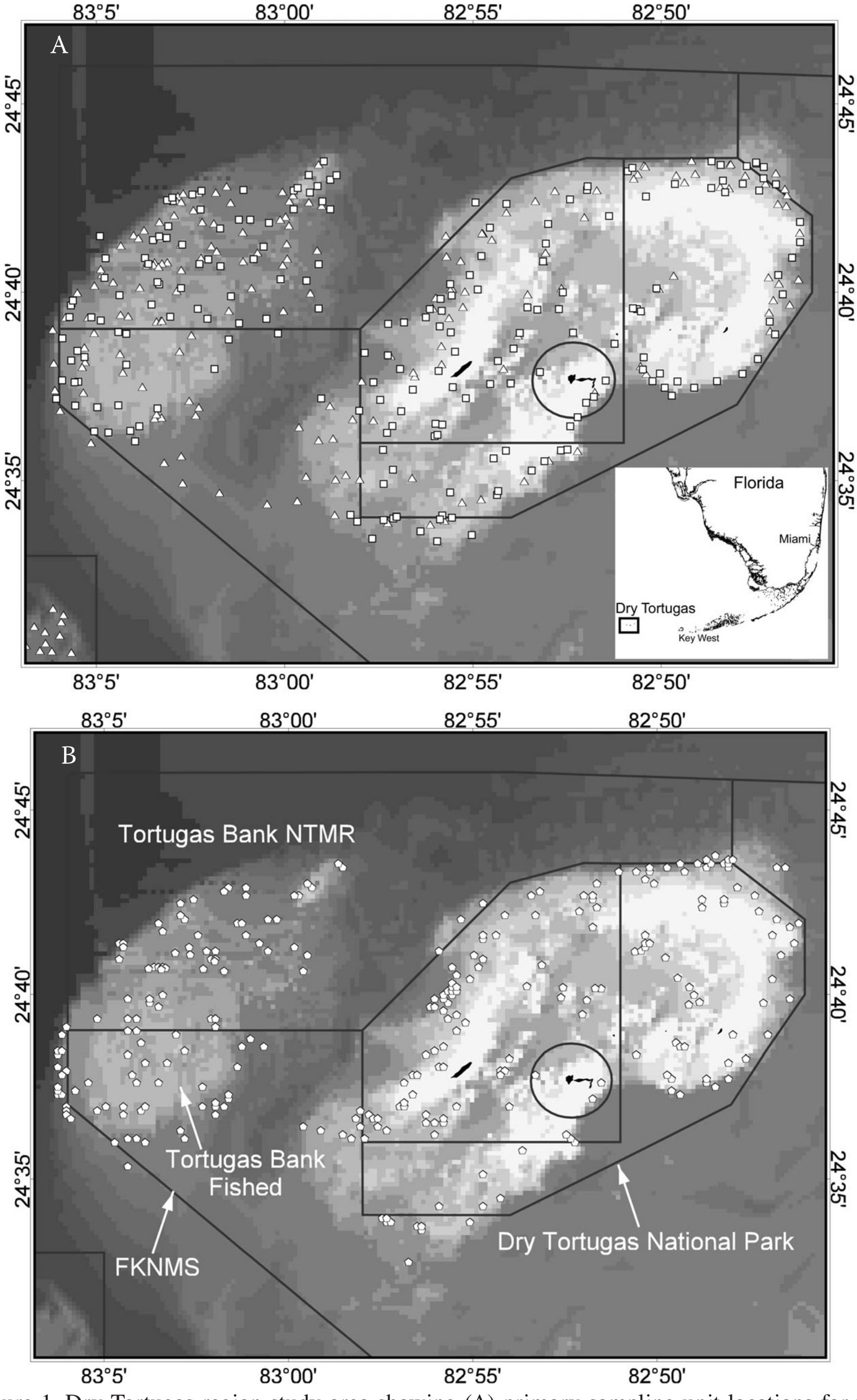

Figure 1. Dry Tortugas region study area showing (A) primary sampling-unit locations for the 1999 (open triangles) and 2000 (open squares) reef-fish surveys and (B) spatial management boundaries and primary units sampled by the reef-fish team (open pentagons) during the 2004 survey. Bathymetry is denoted by light to dark shading (white, 0–3 m; black, >50 m). NTMR, no-take marine reserve; FKNMS, Florida Keys National Marine Sanctuary.

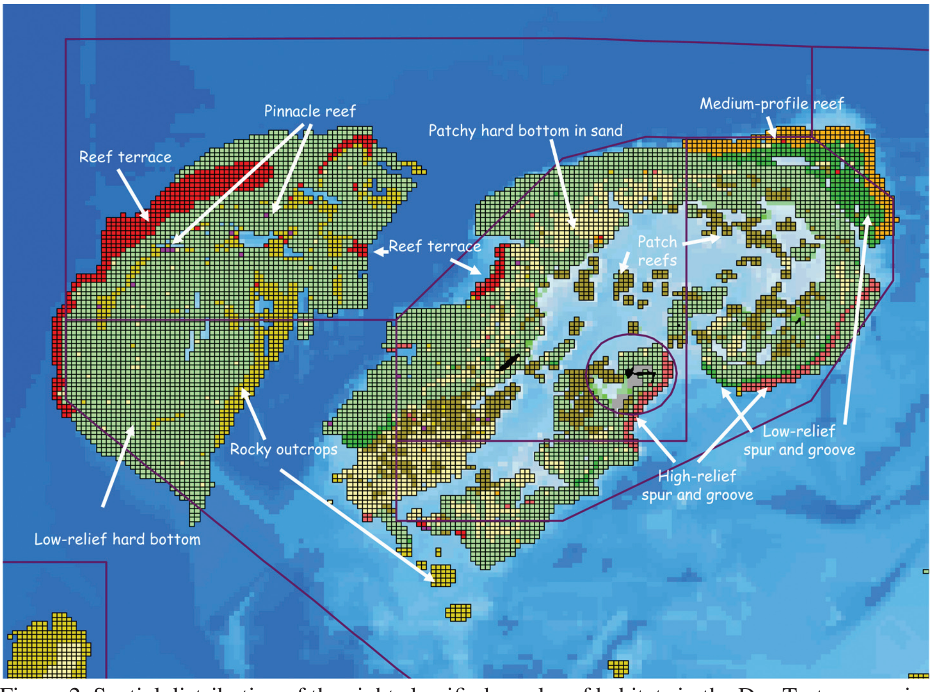

Figure 2. Spatial distribution of the eight classified coral-reef habitats in the Dry Tortugas region overlain by the 200 × 200-m primary unit sampling grid used in monitoring surveys.

Within a stratum, specific primary units to be sampled were randomly selected a priori with equal probability from the complete list of N_h units according to a discrete uniform distribution (Law and Kelton, 2000). To ensure replication, two pairs of second-stage sample units (i.e., diver visual census plots) were randomly positioned within each selected primary unit. Because of diving-safety concerns and statistical concerns about sample autocorrelation, in our computations each second-stage unit estimate consisted of the arithmetic average of stationary plots from two individual divers (i.e., a "buddy pair"). Each primary sample unit location in Figure 1 therefore denotes a place where at least four scientific divers were deployed to conduct visual census samples (i.e., one pair of divers at each of two second-stage locations within a primary sampling unit).

Highly trained and experienced divers collected biological data using Nitrox SCUBA and the reef-fish visual census (RVC) protocol, a standard, nondestructive, in situ visual monitoring method. In the RVC protocol, a stationary diver collects reef-fish data while centered in a randomly selected circular plot 15 m in diameter (Bohnsack and Bannerot, 1986; Bohnsack et al., 1999; Ault et al., 2002). First, for 5 min, all fish species observed within 7.5 m of the diver in an imaginary cylinder extending from the bottom to the limits of vertical visibility (usually the surface) were listed. Data are then collected on the abundance and minimum, mean, and maximum lengths for each species sighted. A ruler connected perpendicularly to the end of a meter stick was used as a reference to reduce apparent magnification errors in fish-size estimates. We also designed and deployed a laser and digital video-camera system to increase the precision of sizing and counting of reef fishes. For each plot, depth, bottom substrate composition, estimated benthic percentage cover, and vertical relief characteristics of the seafloor were recorded from the polar perspective of the centrally located observer. Digital photographs taken at each station assisted with habitat classification and identification of uncommon fish species. The time required to record each sample averaged 15–20 min, depending on the habitat.

Table 1. (A) Habitat stratum (h) characteristics and sizes in terms of primary sampling units (N_h) and area (A_h) for the Dry Tortugas sampling domain. (B) Habitat stratum sizes for three management zones within the Dry Tortugas sampling domain; dashes denote habitats not found in a given management zone. NTMR, no-take marine reserve.

(A)

Reef habitat classification	Habitat code	Degree of patchiness	Degree of vertical relief	Domain-wide area	
				N_h	A_h (km^2)
Low-relief hard bottom	LRHB	Low	Low	4,909	196.36
Low-relief spur and groove	LRSG	Moderate	Low	296	11.84
Patchy hard bottom in sand	PHBS	High	Low	913	36.52
Medium-profile reef	MDPR	Low	Moderate	194	7.76
Rocky outcrops	RKOC	Moderate–High	Moderate	1164	46.56
Reef terrace	RFTC	Low	High	422	16.88
High-relief spur and groove	HRSG	Moderate	High	127	5.08
Pinnacle reef	RFPN	High	High	57	2.28
Total				8,082	323.28

(B)

Habitat code	Tortugas Bank Fished		Tortugas Bank NTMR		Dry Tortugas National Park	
	N_h	A_h (km^2)	N_h	A_h (km^2)	N_h	A_h (km^2)
LRHB	1,108	44.32	1,438	57.52	2,363	94.52
LRSG	—	—	—	—	296	11.84
PHBS	38	1.52	35	1.40	840	33.60
MDPR	—	—	—	—	194	7.76
RKOC	134	5.36	282	11.28	748	29.92
RFTC	47	1.88	327	13.08	48	1.92
HRSG	—	—	—	—	127	5.08
RFPN	—	—	29	1.16	28	1.12
Total	1,327	53.08	2,111	84.44	4,644	185.76

Synoptic survey cruises were conducted in the Dry Tortugas region in 1999 and 2000 (before implementation of the reserve in July 2001) and again in 2004. Each 3-wk cruise was carried out during late May to early July from a 30-m, live-aboard dive vessel equipped with four compressor banks of Nitrox (M/V Spree, Gulf Diving, Houston, TX). During 2002, a Keys-wide survey focused some sampling effort in Dry Tortugas National Park, but we did not include these data because they lacked comparable effort on Tortugas Bank. The onboard scientific crew, consisting of 20–24 persons on any given sampling day, comprised a fish-census team and a benthic-habitat team (and/or a spiny-lobster, *Panulirus argus* (Latreille), team), as well as two full-time divemasters to oversee the complex diving operations. Visual survey data were entered onboard into a digital database with a laptop-based data-entry system that includes extensive error-checking and validation protocols. For the 2004 survey, the laptop computers were linked to a centralized server through a shipboard wireless network.

Our statistical analyses focused on changes between baseline years 1999 and 2000 (before) and 2004 (after). We evaluated change statistically with a community metric, species richness, and two population metrics: frequency of occurrence and abundance. Statistical estimation procedures followed Cochran (1977) for a two-stage stratified random sampling design. In these procedures, stratum means and variances of a given metric are weighted by stratum sizes; i.e.,

$$W_h = N_h \Big/ \sum_h N_h ,$$

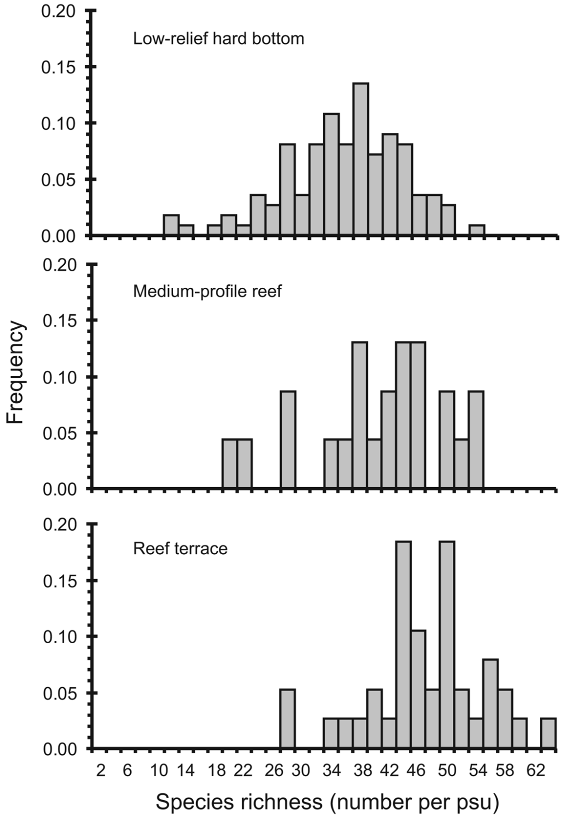

Figure 3. Relative frequency of observations of coral-reef fish species richness (number of species seen per 200 × 200-m primary sample unit) for three benthic habitat classes from the 2004 Tortugas survey. psu, primary sample unit.

to produce overall means and variances either for specific management zones or for the entire Tortugas domain. We estimated species richness on the basis of primary sample unit (i.e., the number of unique species observed within a primary unit by the group of divers) to ensure a sufficient search area for reliable estimates. In this case, the statistical sample size was n, the number of sampled primary units. Both frequency of occurrence and abundance were estimated by species on a second-stage-unit basis, the standard approach for two-stage designs (Cochran, 1977), where the number of second-stage units nm was the statistical sample size. Because benthic habitat classification, digital mapping, and development of the Tortugas survey design occurred concurrently with the baseline surveys of 1999 and 2000 (Ault et al., 2002), we estimated each population and community metric as a composite of the two baseline years to alleviate problems of misclassification of habitats and misallocation of samples among habitat strata. In this procedure, stratum means and variance components were computed as 2-yr averages weighted by respective sample sizes in 1999 and 2000.

Species chosen for detailed analyses reflected the range of population-dynamic processes (growth and survivorship) for relatively abundant exploited and nonexploited components of the reef-fish community. Statistical tests for differences among estimates of mean density, total abundance, and mean proportion of samples for the sampling design configuration were conducted by inspection of confidence intervals (CI) with Bonferroni adjustments (Cochran, 1977). Detection of change was defined as the ability to discriminate between the 95% CI of mean responses for the two time periods. We used the Bonferroni CI t-test because it is more suited to sample design statistics and does not require homogenous variance in two distributions to test differences in the mean responses. Changes in length compositions between time periods were tested with standard two-sample chi-square tests (Agresti, 1996). The absolute ability to detect changes was thus determined by the precision of the survey estimates (e.g., standard error).

Results

In all, 4092 scientific dives totaling more than 668 hrs bottom time, including 3234 fish-survey dives, were made during 1999–2004 cruises in the Tortugas region. Diving depths ranged from 3 to 33 m, but use of enriched-air Nitrox permitted a substantial diving effort at depths > 18 m and ≤ 33 m (> 63% of all dives). Table 2 shows statistical sample sizes in terms of primary (n) and second-stage (nm) sample units by year, habitat, and management zone.

Over the 1999–2004 period, we observed 267 fish species in RVC surveys in the Tortugas region. Fish species richness ranged from 8 to 64 species per primary sample unit (psu) and, in general, was correlated with habitat class. Greatest reef-fish species diversity (63–64 species per psu) was found in high-rugosity habitats (reef terrace and reef pinnacles), the lowest (8–11 per psu) in low-rugosity habitats (low-relief hard bottom and patchy hard bottom in sand), as illustrated in Figure 3 for the 2004 survey. For the Tortugas sampling domain, we detected no change in mean species richness (mean number of species per psu) between the 1999–2000 (37.1 ± 0.7 SE) baseline and 2004 (38.1 ± 0.5 SE), even though we could have detected a change >1.4 species (i.e., approximately 2 SE). We found similar results for selected taxa; for example, mean richness for species of exploited snappers and groupers was 7.8 ± 0.2 SE for both 1999–2000 and 2004. Species richness (diversity) of the snapper-grouper complex was also related to reef rugosity, in that it was highest on reef terrace and pinnacle habitats found on the northwestern Tortugas Bank and western Dry Tortugas National Park, and also in medium-profile reef in the northwestern portion of the park (Fig. 4). It was lowest in low-relief hard bottom and patchy hard bottom in sand habitats.

The relatively stable community structure shown for richness was also reflected in domain-wide estimates of frequency of occurrence or sighting frequency. Although ranks changed slightly between years, only four of the top 50 species for the 2004 survey were not among the top 50 for the 1999–2000 surveys (Table 3). The top 50 included 12 (of 55 total) species from the exploited snapper-grouper complex.

Estimates of frequency of occurrence and abundance for representative species of principal families are given in Tables 4 and 5, respectively. We illustrate analyses of change between 1999–2000 and 2004 using black grouper (*Mycteroperca bonaci*) as an example. Domain-wide percentage occurrence for black grouper increased from 19.5% in 1999–2000 to 28.8% in 2004 (Table 4; $P < 0.01$), as did abundance, by 124% (Table 5A; $P < 0.001$). Detection of temporal change in abundance was facilitated by a decrease in the survey coefficient of variation (CV = SE/mean) from 14.5% to 10.3%. The increase in domain-wide abundance was accompanied by a shift in the length composition between 1999–2000 and 2004 toward a higher proportion of exploited-phase individuals (Fig. 5A; chi-square $P < 0.001$ for lengths >30 cm). Abundance estimates for black grouper increased in all three management zones but statistically so only in the reserve and the park (Table 5B). A spatial perspective on temporal changes in occurrence and density/abundance of black grouper is illustrated in the maps of Figure 6. In 2004, population size structure appeared to expand in the reserve and park areas but was highly truncated above the minimum legal size in the

Table 2. Reef-fish-survey sample sizes in terms of primary (n) and second-stage (nm) units by habitat class and management zone for (A) 1999, (B) 2000, and (C) 2004. Habitat codes are defined in Table 1; dashes denote habitats not found in a given management zone.

Habitat code	Tortugas Bank Fished		Tortugas Bank NTMR		Dry Tortugas National Park		Domain-wide	
	n	nm	n	nm	n	nm	n	nm
(A) 1999								
LRHB	11	22	16	29	24	47	51	98
LRSG	—	—	—	—	15	30	15	30
PHBS	5	10	4	7	7	12	16	29
MDPR	—	—	—	—	4	8	4	8
RKOC	4	8	12	23	8	14	24	45
RFTC	4	8	28	53	5	10	37	71
HRSG	—	—	—	—	12	24	12	24
RFPN	—	—	8	16	3	6	11	22
Total	24	48	68	128	78	151	170	327
(B) 2000								
LRHB	10	20	17	31	34	64	61	115
LRSG	—	—	—	—	5	9	5	9
PHBS	10	20	11	20	25	45	46	85
MDPR	—	—	—	—	9	17	9	17
RKOC	2	4	11	17	28	52	41	73
RFTC	0	0	17	31	7	12	24	43
HRSG	—	—	—	—	12	22	12	22
RFPN	—	—	5	10	4	7	9	17
Total	22	44	61	109	124	228	207	381
(C) 2004								
LRHB	22	41	9	18	81	146	112	205
LRSG	—	—	—	—	14	26	14	26
PHBS	11	19	2	4	24	44	37	67
MDPR	—	—	—	—	23	39	23	39
RKOC	10	19	27	54	24	45	61	118
RFTC	5	9	16	32	17	33	38	74
HRSG	—	—	—	—	4	8	4	8
RFPN	—	—	9	18	7	14	16	32
Total	48	88	63	126	194	355	305	569

fished area. Changes in length compositions within management zones paralleled changes in abundance (Fig. 5B); proportion of exploited-phase individuals was higher in the reserve ($P < 0.05$) and park ($P < 0.001$). No change in length composition was detected in the fished area.

Significant increases in domain-wide occurrence and abundance were also detected for mutton snapper (*Lutjanus analis*), corresponding with significant increases in abundance in the reserve and the park. In general, trends in occurrence mirrored those for abundance for species with relatively small population sizes.

No change in either occurrence or abundance was detected for red grouper (*Epinephelus morio*) domain-wide, but we detected a significant decrease in abundance in the fished area and a significant increase in the reserve. We also noted increases in

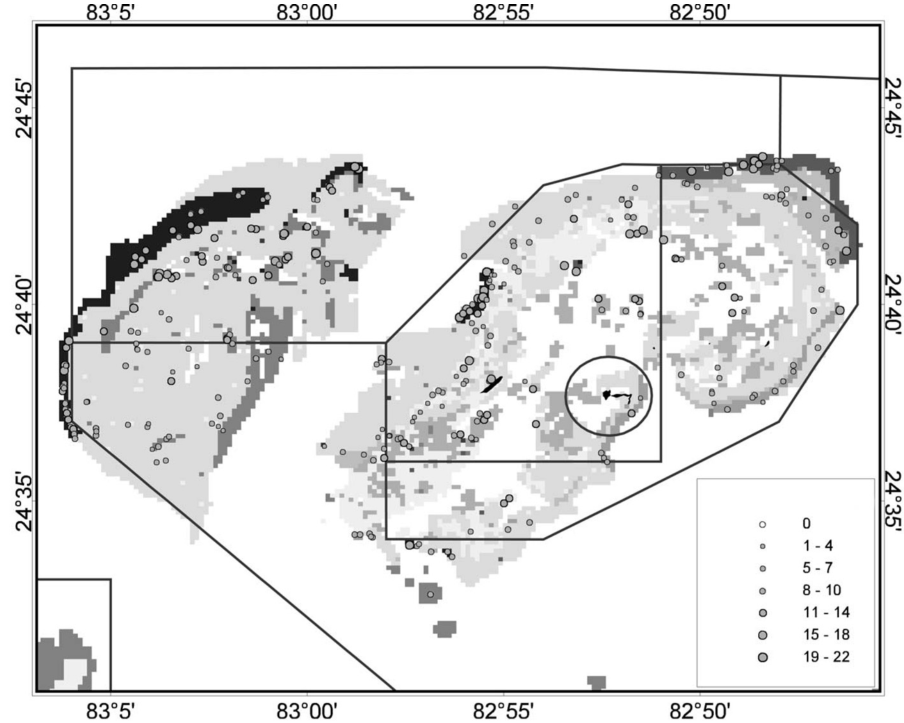

Figure 4. Spatial distribution of snapper-grouper species richness for the 2004 Tortugas survey in relation to benthic habitat types (Fig. 2).

the population proportion of larger (older) individuals for red grouper (Fig. 5A; chi-square P < 0.001 for lengths > 30 cm).

We detected a marginal decrease in domain-wide occurrence for yellowtail snapper (*Ocyurus chrysurus*) but a domain-wide increase in abundance corresponding with a significant increase in the park. Evidently, more fish were seen at fewer sites, but the observed decline in percentage occurrence probably had little biological significance. As a result, abundance may be a better metric of population change. This disparity between occurrence and abundance was also observed for other schooling species: gray snapper (*Lutjanus griseus* (Linnaeus, 1758)), hogfish (*Lachnolaimus maximus)*, and white grunt (*Haemulon plumieri)*.

Domain-wide occurrences of goliath grouper, *Epinephelus itajara* (Lichtenstein, 1822), and Nassau grouper, *Epinephelus striatus* (Bloch, 1792), two species under fishing moratoria, remained low over the survey period. We observed goliath grouper in one primary sampling unit in 1999, two units in 2000, and 10 units in 2004 (seven in the park and three in the reserve), a pattern perhaps encouraging for its recovery but not a statistically significant change in frequency of occurrence.

Among unexploited species, domain-wide increases in both occurrence and abundance were detected for spotted goatfish (*Pseudupeneus maculates*), purple reeffish (*Chromis scotti*), and striped parrotfish (*Scarus iseri*). On the other hand, we detected increases in domain-wide occurrence but no changes in abundance for foureye butterflyfish (*Chaetodon capistratus*) and redband parrotfish (*Sparisoma aurofrenatum*). For blue tang (*Acanthurus coeruleus*), bicolor damselfish (*Stegastes partitus*), and stoplight parrotfish (*Sparisoma viride*), no changes were detected in domain-wide

Table 3. Changes in rank percentage occurrence between 1999–2000 and 2004 for the top 50 reef-fish species. Common names marked with asterisks denote species in the exploited snapper-grouper complex.

Common name	Scientific name	Family	Occurrence rank 2004	Occurrence rank 1999–2000	Change
Bluehead	*Thalassoma bifasciatum* (Bloch, 1791)	Labridae	1	1	=
Striped parrotfish	*Scarus iseri* (Bloch, 1791)	Scaridae	2	2	=
Cocoa damselfish	*Stegastes variabilis* (Castelnau, 1855)	Pomacentridae	3	3	=
Redband parrotfish	*Sparisoma aurofrenatum* (Valenciennes, 1840)	Scaridae	4	5	+
Yellowhead wrasse	*Halichoeres garnoti* (Valenciennes, 1839)	Labridae	5	10	+
Blue tang	*Acanthurus coeruleus* Bloch & Schneider, 1801	Acanthuridae	6	8	+
Bicolor damselfish	*Stegastes partitus* (Poey, 1868)	Pomacentridae	7	11	+
Spotted goatfish	*Pseudupeneus maculatus* (Bloch, 1793)	Mullidae	8	20	+
White grunt*	*Haemulon plumieri* (Lacepède, 1801)	Haemulidae	9	4	-
Slippery dick	*Halichoeres bivittatus* (Bloch, 1791)	Labridae	10	7	-
Yellowtail snapper*	*Ocyurus chrysurus* (Bloch, 1791)	Lutjanidae	11	9	-
Saucereye porgy*	*Calamus calamus* (Valenciennes, 1830)	Sparidae	12	6	-
Stoplight parrotfish	*Sparisoma viride* (Bonnaterre, 1788)	Scaridae	13	15	+
Bridled goby	*Coryphopterus glaucofraenum* Gill, 1863	Gobiidae	14	12	-
Red grouper*	*Epinephelus morio* (Valenciennes, 1828)	Serranidae	15	13	-
Purple reeffish	*Chromis scotti* Emery, 1968	Pomacentridae	16	28	+
Ocean surgeon	*Acanthurus bahianus* Castelnau, 1855	Acanthuridae	17	18	+
Blue angelfish	*Holacanthus bermudensis* Goode, 1876	Pomacanthidae	18	16	-
Spotfin butterflyfish	*Chaetodon ocellatus* Bloch, 1787	Chaetodontidae	19	17	-
Butter hamlet	*Hypoplectrus unicolor* (Walbaum, 1792)	Serranidae	20	29	-
Greenblotch parrotfish	*Sparisoma atomarium* (Poey, 1861)	Scaridae	21	24	+
Masked goby	*Coryphopterus personatus* (Jordan & Thompson, 1905	Gobiidae	22	25	+
Blue hamlet	*Hypoplectrus gemma* Goode & Bean, 1882	Serranidae	23	38	+
Yellowhead jawfish	*Opistognathus aurifrons* (Jordan & Thompson, 1905)	Opistognathidae	24	21	-
Gray angelfish	*Pomacanthus arcuatus* (Linnaeus, 1758)	Pomacanthidae	25	23	-

Table 3. Continued.

Common name	Scientific name	Family	Occurrence rank 2004	Occurrence rank 1999–2000	Change
Hogfish*	*Lachnolaimus maximus* (Walbaum, 1792)	Labridae	26	19	-
Foureye butterflyfish	*Chaetodon capistratus* Linnaeus, 1758	Chaetodontidae	27	32	+
Clown wrasse	*Halichoeres maculipinna* (Müller & Troschel, 1848)	Labridae	28	26	-
Threespot damselfish	*Stegastes planifrons* (Cuvier, 1830)	Pomacentridae	29	30	+
Beaugregory	*Stegastes leucostictus* (Müller & Troschel, 1848)	Pomacentridae	30	34	+
Harlequin bass	*Serranus tigrinus* (Bloch, 1790)	Serranidae	31	27	-
Saddled blenny	*Malacoctenus triangulatus* Springer, 1959	Labrisomidae	32	14	-
Barred hamlet	*Hypoplectrus puella* (Cuvier, 1828)	Serranidae	33	31	-
Neon goby	*Elacatinus oceanops* Jordan, 1904	Gobiidae	34	22	-
Graysby*	*Cephalopholis cruentata* (Lacepède, 1802)	Serranidae	35	37	+
Black grouper*	*Mycteroperca bonaci* (Poey, 1860)	Serranidae	36	44	+
Blue chromis	*Chromis cyanea* (Poey, 1860)	Pomacentridae	37	45	+
Mutton snapper*	*Lutjanus analis* (Cuvier, 1828)	Lutjanidae	38	52	+
Tobaccofish	*Serranus tabacarius* (Cuvier, 1829)	Serranidae	39	46	+
Bar jack*	*Caranx ruber* (Bloch, 1793)	Carangidae	40	40	=
Queen angelfish	*Holacanthus ciliaris* (Linnaeus, 1758)	Pomacanthidae	41	43	+
Great barracuda*	*Sphyraena barracuda* (Edwards, 1771)	Sphyraenidae	42	49	+
Sharpnose puffer	*Canthigaster rostrata* (Bloch, 1786)	Tetraodontidae	43	39	-
Spanish hogfish	*Bodianus rufus* (Linnaeus, 1758)	Labridae	44	47	+
Tomtate*	*Haemulon aurolineatum* Cuvier, 1830	Haemulidae	45	41	-
Princess parrotfish	*Scarus taeniopterus* Desmarest, 1831	Scaridae	46	61	+
Reef butterflyfish	*Chaetodon sedentarius* Poey, 1860	Chaetodontidae	47	36	-
French grunt*	*Haemulon flavolineatum* (Desmarest, 1823)	Haemulidae	48	50	+
Cero	*Scomberomorus regalis* (Bloch, 1793)	Scombridae	49	117	+
Bucktooth parrotfish	*Sparisoma radians* (Valenciennes, 1840)	Scaridae	50	101	+

Table 4. Domain-wide estimates of percentage occurrence for representative exploited and nontarget fish species for baseline years 1999–2000 and the 2004 survey. Levels of statistically significant difference between baseline years and 2004: NS, not significant; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

	% Occurrence (SE)		
Taxon	1999–2000	2004	Change
Snapper-Grouper complex			
Groupers (Serranidae)			
Goliath grouper (*Epinephelus itajara*)	0.5 (0.4)	1.3 (0.5)	NS
Red grouper	67.0 (3.3)	62.8 (3.1)	NS
Nassau grouper (*E. striatus*)	1.0 (0.6)	0.3 (0.2)	NS
Black grouper	19.5 (2.5)	28.8 (2.4)	**
Snappers (Lutjanidae)			
Mutton snapper	14.8 (2.4)	25.8 (3.0)	***
Gray snapper (*Lutjanus griseus*)	17.3 (2.5)	12.2 (1.5)	*
Yellowtail snapper	74.7 (3.2)	68.1 (3.1)	*
Wrasses (Labridae)			
Hogfish	52.8 (3.5)	42.6 (3.0)	**
Grunts (Haemulidae)			
White grunt	82.0 (2.7)	71.5 (2.7)	***
Bluestriped grunt (*Haemulon sciurus* (Shaw, 1803))	6.4 (1.7)	7.7 (1.2)	NS
Nontarget fishes			
Surgeonfishes (Acanthuridae)			
Ocean surgeon	54.9 (3.3)	60.3 (2.7)	NS
Blue tang	76.4 (3.1)	80.9 (2.2)	NS
Butterflyfishes (Chaetodontidae)			
Foureye butterflyfish	34.0 (3.3)	42.3 (2.8)	*
Spotfin butterflyfish	56.4 (3.4)	49.9 (3.0)	NS
Goatfishes (Mullidae)			
Spotted goatfish	50.7 (3.6)	71.7 (2.2)	***
Angelfishes (Pomacanthidae)			
Blue angelfish	57.9 (3.2)	55.9 (2.7)	NS
Gray angelfish	45.5 (3.3)	43.9 (2.8)	NS
Damselfishes (Pomacentridae)			
Purple reeffish	37.2 (3.4)	62.2 (3.1)	***
Bicolor damselfish	72.7 (2.9)	72.6 (2.3)	NS
Cocoa damselfish	87.7 (2.3)	90.0 (2.0)	NS
Parrotfishes (Scaridae)			
Striped parrotfish	88.4 (2.4)	94.3 (1.3)	*
Redband parrotfish	80.8 (2.9)	86.9 (1.9)	*
Stoplight parrotfish	59.3 (3.5)	64.5 (3.3)	NS

occurrence, but we detected increases in domain-wide abundance. Domain-wide increases in spotted goatfish corresponded to significant increases in abundance in all three management zones. Domain-wide increases in abundance of blue tang, purple reeffish, and stoplight parrotfish corresponded to increased abundances in the park. Increases in domain-wide abundance of bicolor damselfish and striped parrotfish were accompanied by significant abundance increases in the reserve. In several cases, management zone changes in abundance were detected that did not correspond to domain-wide changes.

Table 5. (A) Domain-wide estimates of abundance (and associated coefficient of variation CV) and changes between baseline years 1999–2000 and 2004 for representative exploited and nontarget fish species. (B) Population abundance changes between 1999–2000 and 2004 within management zones in the Dry Tortugas region. Levels of statistically significant difference between baseline years and 2004; NS, not significant, * P < 0.05; ** P < 0.01; *** P < 0.001.

Taxon	(A) 1999–2000 Abundance (millions)	1999–2000 CV (%)	2004 Abundance (millions)	2004 CV (%)	Change		(B) Tortugas Bank fished		Tortugas Bank NTMR		Dry Tortugas National Park	
Snapper-grouper complex												
Red grouper	1.260	6.8	1.237	6.5	–2%	NS	–43%	*	+38%	*	–9%	NS
Black grouper	0.277	14.5	0.622	10.3	+124%	***	+84%	NS	+120%	*	+128%	***
Mutton snapper	0.216	21.2	0.452	13.2	+109%	***	–45%	NS	+303%	**	+142%	***
Gray snapper	3.714	54.3	5.155	74.0	+39%	NS	–96%	NS	–51%	NS	+270%	NS
Yellowtail snapper	8.257	13.0	23.169	27.2	+181%	*	–19%	NS	+367%	NS	+132%	***
Hogfish	1.121	10.7	0.910	12.0	–19%	NS	–27%	NS	+6%	NS	–25%	NS
White grunt	9.317	15.5	9.644	21.6	+4%	NS	+7%	NS	+24%	NS	+2%	NS
Bluestriped grunt	0.330	47.0	0.854	42.0	+159%	NS	+50%	NS	+13%	NS	+242%	NS
Nontarget fishes												
Ocean surgeon	2.045	13.3	2.275	8.0	+11%	NS	+2%	NS	+75%	**	–9%	NS
Blue tang	3.474	9.7	5.747	7.8	+65%	***	+13%	NS	+28%	NS	+99%	***
Foureye butterflyfish	0.960	10.8	1.083	7.5	+13%	NS	+86%	*	–18%	NS	+32%	NS
Spotfin butterflyfish	1.315	7.5	1.256	6.8	–5%	NS	+35%	NS	–31%	*	0%	NS
Spotted goatfish	1.076	10.7	3.204	9.8	+198%	***	+133%	**	+326%	***	+175%	***
Blue angelfish	1.555	8.0	1.525	6.8	–2%	NS	–18%	NS	–20%	NS	+31%	*
Gray angelfish	0.868	9.2	1.588	27.2	+83%	NS	–24%	NS	+58%	NS	+120%	NS
Purple reeffish	11.518	17.8	20.219	13.0	+76%	***	+31%	NS	+42%	NS	+263%	***
Bicolor damselfish	12.914	10.4	17.269	7.8	+34%	**	+6%	NS	+73%	**	+17%	NS
Cocoa damselfish	7.654	5.9	7.384	4.9	–4%	NS	–28%	NS	–21%	NS	+6%	NS
Striped parrotfish	16.117	18.3	22.290	10.1	+38%	*	+51%	NS	+127%	*	+9%	NS
Redband parrotfish	4.565	16.2	7.096	23.3	+56%	NS	+121%	***	+26%	NS	+56%	NS
Stoplight parrotfish	1.936	9.7	3.012	10.3	+56%	***	+9%	NS	+26%	NS	+84%	***

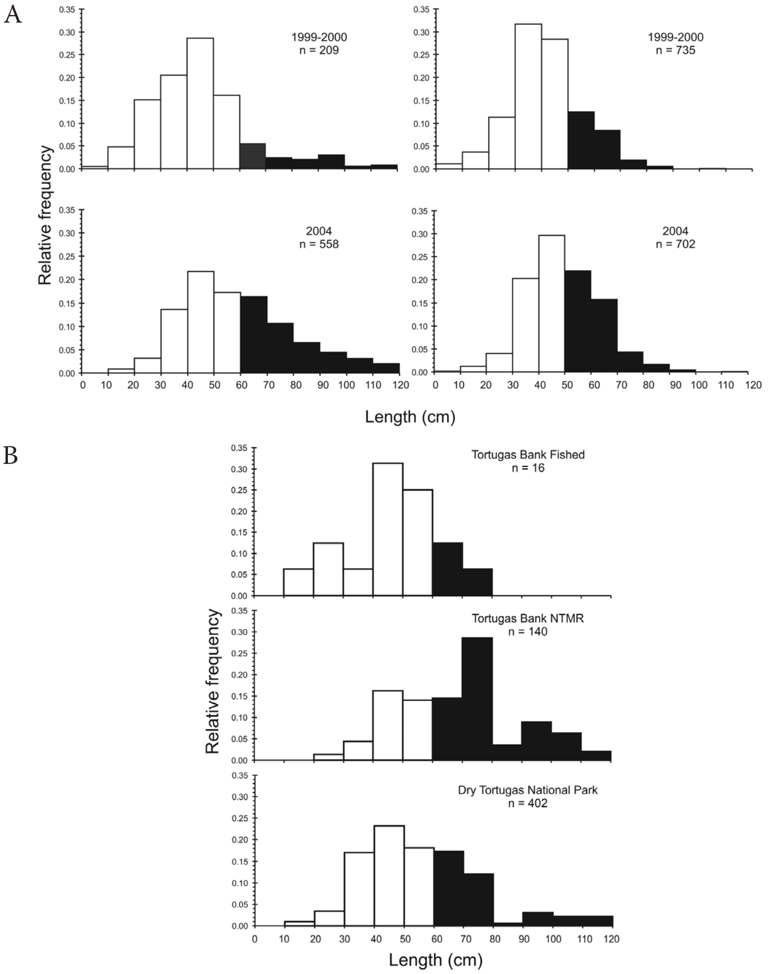

Figure 5. (A) Domain-wide comparisons of length compositions for black grouper (left panels) and red grouper (right panel) between 1999–2000 (top) and 2004 (bottom) surveys. (B) Comparison of the three spatial zones for black grouper for 2004. Open bars are preexploited-phase; shaded bars are exploited-phase animals. Number of length observations is given on each panel.

An occurrence in the 2004 survey, unexpected on the basis of our previous cruises, was the sighting of large (> 2000 fish) schools of large (> 9 kg) permit (*Trachinotus falcatus*) at eight primary-sampling-unit locations. The timing and schooling behavior of these mature permit suggests that these may have been spawning aggregations. Seven of the eight schools were sighted on Tortugas Bank, either inside or just outside the reserve.

Discussion

The Tortugas region represents a de facto adaptive management experiment in which three discrete, contiguous areas are being managed under different levels of resource protection. Determining the efficacy of the suite of management approaches is one of Florida's most critical resource-management problems and a unique challenge for science-based resource management.

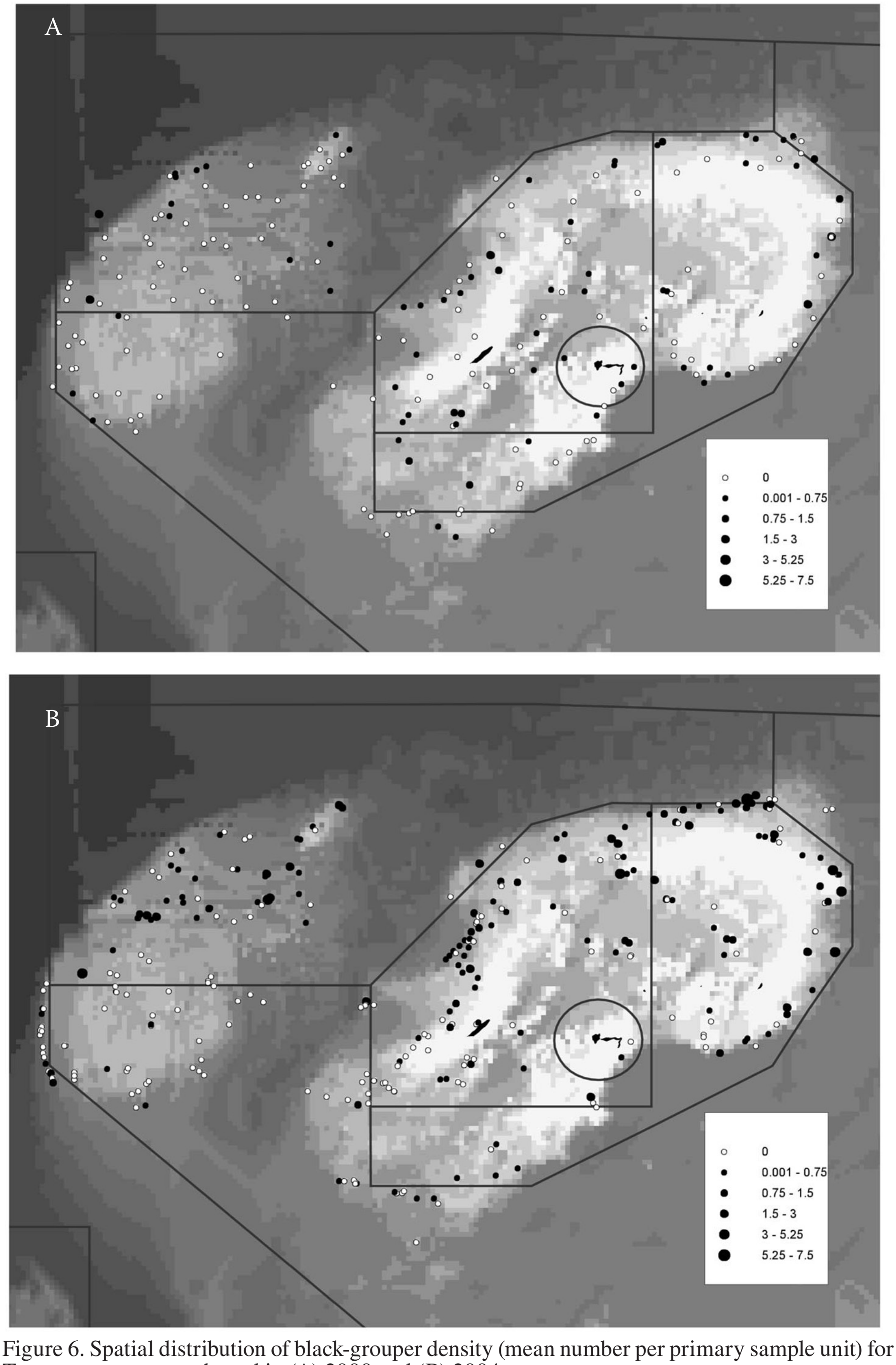

Figure 6. Spatial distribution of black-grouper density (mean number per primary sample unit) for Tortugas surveys conducted in (A) 2000 and (B) 2004.

A number of authors have pointed out that detection of changes in population abundance and biomass in response to any fishery management action has often suffered from lack of rigor in the design of both fishery-dependent and fishery-independent surveys (e.g., Hurlbert, 1984; Stewart-Oaten et al., 1986; Underwood, 1990, 1993; Willis et al., 2003; Hilborn et al., 2004a; Sale et al., 2005). Relative to traditional fishery-dependent approaches, quantitative assessments of NTMRs present their own unique challenges because no catches from closed areas are available for examination and data must be spatially explicit. In addition, data must be collected that reflect community dynamics, not just exploited-species dynamics, for evaluation of the performance of ecosystem-based management. These principles were the impetus for our survey-sampling approach in the Tortugas region.

The fisheries-independent RVC surveys provided fairly precise estimates of species richness and frequency of occurrence. However, while also a precise measure, abundance was more indicative of population change because it tracked population variability at both low and high population sizes. In general, our population detection limits for changes in abundance ranged between 15% and 30%; i.e., twice the measured CV. In some cases precise estimates of abundance were difficult to obtain. For example, low sighting frequency coupled with relatively high abundance at few sites yielded high CVs for gray snapper. Overall, we found our CI *t*-tests to be a conservative application of statistical methods because they required detection of differences in mean abundance with respect to each time period. The method became less robust as the size of the spatial unit (e.g., management zone, habitat type) decreased.

Principles of probability and statistics and of sampling theory (e.g., Cochran, 1977; Levy and Lemeshow, 1999; Johnson and Wichern, 2002) were used to promote survey efficiency and precision of estimates in a cost-effective way for the Tortugas reef-fish sampling operations. Our habitat-based stratification was effective because it capitalized on the statistical covariance between fish abundance and coral-reef habitat types determined from previous surveys (Ault et al., 2002, Franklin et al., 2003). In addition, a number of logistical factors enabled divers to obtain high sample size over substantial areas quickly and at relatively low costs: (1) use of a large, live-aboard dive vessel equipped with Nitrox SCUBA; (2) "live-boating" at dive sites where the vessel never anchored but deployed divers at specified coordinates and picked up the free-swimming groups after samples are taken; (3) use of highly trained professional divemasters to oversee the complex dive operations; and (4) conducting the annual surveys within 2–3 wks during periods (May–June) of minimum winds.

The impacts of management actions on population biomass could take years to occur and be detected (e.g., Beverton and Holt, 1957), but we observed signs of recovery in the Tortugas reef fish community over a relatively short time after implementation of NTMRs. We have shown that metrics of the reef fish community (e.g., richness and species composition) were very stable over the study time period, but of a representative suite of 21 reef fishes, we detected increases in domain-wide abundance for three exploited species (black grouper, mutton snapper, yellowtail snapper) and six nontarget species (blue tang, spotted goatfish, purple reeffish, bicolor damselfish, striped parrotfish, and stoplight parrotfish). No decreases in domain-wide abundance were detected for any of the species analyzed.

Where abundance changes occurred, the observed contrasts between exploited and nontarget species suggest that spatial protection may have been an important contributing factor in region-wide changes. We detected abundance increases for nontarget species in all three management zones, but only one species, the spotfin butterflyfish (*Chaetodon ocellatus*) decreased, and that occurred in the reserve. For exploited species, significant abundance increases were confined to the reserve and the park, whereas the only significant abundance decrease occurred in the fished area. Moreover, we detected significant shifts in length compositions toward larger individuals for black grouper and red grouper. In addition, in the fished area, black grouper size-frequency distributions showed continued truncation of fish above the legal minimum size limit, consistent with continued fishing pressure. Similar responses to spatial protection have been observed in the region for heavily exploited spiny lobster and mutton snapper (Davis and Dodrill, 1980; Burton et al., 2005; Cox and Hunt, 2005).

Our results also suggest, however, that the population increases observed in the reserve and park could have been augmented by co-occurring regional fishery management actions or favorable environmental conditions. Increases in abundance of larger individuals would also be expected in response to traditional management measures such as bag and size limits. For example, minimum size limits for black grouper have been increased from 18 in (45.7 cm) in 1985 to 20 in (50.8 cm) in 1990 and to 22 in (55.9 cm) for recreational fishers and 24 in (61.0 cm) for commercial fishers in 1999. The last regulation brought the minimum size up to the minimum size of sexual maturity (Ault et al., 2005b). Generally, abundance changes in nontarget species would not be expected to occur in direct response to fishery management policy. Increases in nontarget species abundance suggest that the environment plays an important role and may have contributed to good recruitment events in recent years. Random variability in year-class strengths or the passing of several hurricanes in the late-1990s may also have influenced recruitment for both exploited and nontarget reef fishes. In reality, many of the factors probably interact.

Similar observations of recovery of fish populations, but usually over longer time frames, have been made in other coral-reef ecosystems (cf. Halpern and Warner, 2002; Russ et al., 2004; Alcala et al., 2005). According to population-dynamics theory, not enough time has elapsed since implementation of the Tortugas NTMR to explain our findings fully, so not all the observed changes are likely to reflect a direct response to NTMR implementation. Furthermore, potential impacts on reef-fish community dynamics are complex and may be influenced by shifts in composition, trophic cascades promulgated by predator-prey responses, and habitat competition. Our next research challenge will be to develop and refine methods for improved understanding of the relative contributions of NTMRs, various fishery-management actions, community interactions, and environmental factors with the goal of building sustainable fisheries.

As this rebuilding process proceeds and reef ecosystems respond to management actions over the next several decades, a continued concern will be balancing fishing with resource protection. A particular concern is the likely continued growth in demand from the recreational fleet and in its fishing power as a result of technological improvements. Although failure to control fishing mortality adequately can have potentially detrimental consequences for the stocks and the economy (Steele and Hoagland, 2003), removal of units of fishing effort once they have been established will be difficult, because of the "ratchet" effect (Ludwig et al., 1993). In the long run, a precautionary ecosystem-based approach to management using multiple control methods offers promise for providing fishery sustainability and persistence of the

Florida Keys coral-reef ecosystem. As noted by Stefansson and Rosenberg (2005), combining catch controls with large closed areas may be the most effective system of reducing risk of stock collapse while maintaining short- and long-term economic performance and buffering uncertainty.

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