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Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA

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ABSTRACT

The efficacy of no-take marine reserves (NTMRs) to enhance and sustain regional coral reef fisheries was assessed in Dry Tortugas, Florida, through 9 annual fishery-independent research surveys spanning 2 years before and 10 years after NTMR implementation. A probabilistic sampling design produced precise estimates of population metrics of more than 250 exploited and non-target reef fishes. During the survey period more than 8100 research dives utilizing SCUBA Nitrox were optimally allocated using stratified random sampling. The survey domain covered 326 km^2, comprised of eight reef habitats in four management areas that offered different levels of resource protection: the Tortugas North Ecological Reserve (a NTMR), Dry Tortugas National Park (recreational angling only), Dry Tortugas National Park Research Natural Area (a NTMR), and southern Tortugas Bank (open to all types of fishing). Surveys detected significant changes in population occupancy, density, and abundance within management zones for a suite of exploited and non-target species. Increases in size, adult abundance, and occupancy rates were detected for many principal exploited species in protected areas, which harbored a disproportionately greater number of adult spawning fishes. In contrast, density and occupancy rates for aquaria and non-target reef fishes fluctuated above and below baseline levels in each management zone. Observed decreases in density of exploited species below baseline levels only occurred at the Tortugas Bank area open to all fishing. Our findings indicate that these NTMRs, in conjunction with traditional fishery management control strategies, are helping to build sustainable fisheries while protecting the fundamental ecological dynamics of the Florida Keys coral-reef ecosystem.

1. Introduction

Sustainability of marine ecosystems is a worldwide concern because intensive fishing has diminished top trophic levels and altered the ecological dynamics and resilience of fisheries. While the use of spatial no-fishing zones (i.e., “no-take” marine reserves, NTMRs—areas protected from all extractive uses) have been touted as an effective fisheries management tool, in practice they have had their fair share of proponents and skeptics (e.g., Gell and Roberts, 2003; Hooker and Gerber, 2004; Bohnsack et al., 2004; Meester et al., 2004; Hilborn, 2006; Mora and Sale, 2011).

The Florida shallow coral reef ecosystem extends about 400 km southwest from Miami to the Dry Tortugas (Fig. 1A), and supports lucrative tourism and fishing industries (Ault et al., 2005a). The sustainability of reef fisheries is in question because the ecosystem’s multispecies snapper-grouper complex has been intensively fished since at least the late 1960s, and a majority of the region’s snapper-grouper species are currently fished unsustainably (Ault et al., 1998, 2005b, 2009; Hallac and Hunt, 2007). Sustainability refers to the ability of an exploited stock to produce goods and services, including yields at suitable levels in the short term, while maintaining sufficient stock reproductive capacity to continue providing these goods and services into the indefinite future (Ault et al., 2008). The number of recreational vessels in Florida, an index of sportfishing fleet exploitation intensity, has risen in proportion to increases in the human population. From 1960

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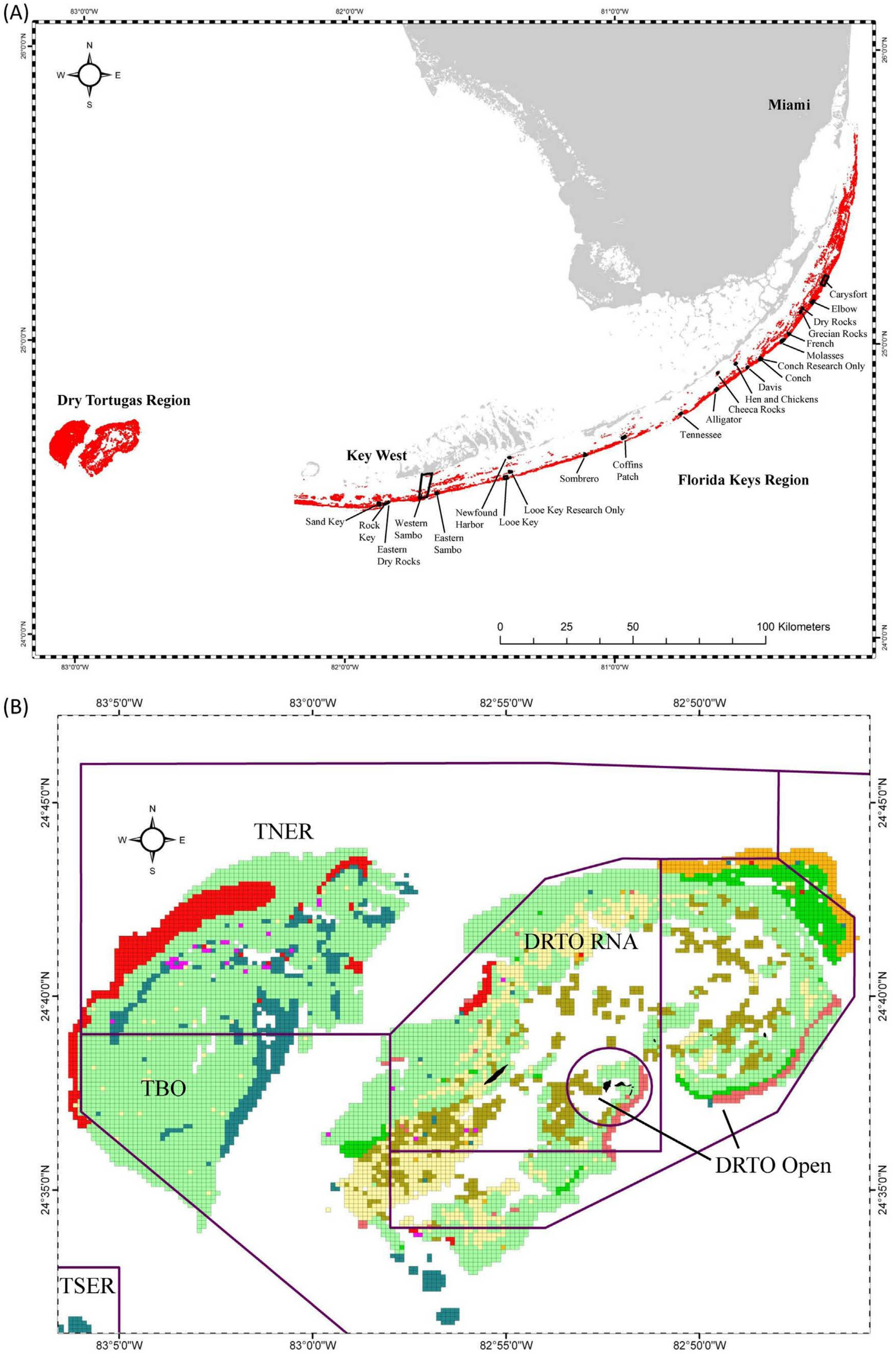

Fig. 1. (A) South Florida reef fish visual survey domain (red, mapped coral reef habitats), with managed no-take marine reserve (NTMR) boundaries (black) for the Florida Keys region. (B) Survey domain for the Dry Tortugas region showing spatial management zones and primary sample unit (PSU, 200 m × 200 m) gridding of coral reef habitat types (colored grid cells comprise 326 km^2). TNER is Tortugas North Ecological Reserve, a NTMR; TSER is Tortugas South Ecological Reserve, a NTMR; TBO is Tortugas Bank Open access to commercial and recreational fishing; DRTO Open is Dry Tortugas National Park open to recreational angling; and DRTO RNA is Dry Tortugas National Park Research Natural Area, a NTMR.

to 2010, Florida's human population increased by 379% from 4,961,560 to 18,801,310 persons (http://www.stateofflorida.com/), while registered recreational vessels increased by 698% from 128,430 to 896,093 vessels. The commercial fleet, in contrast, has decreased by 10% from 27,394 to 24,658 during this same period (http://www.hsmv.state.fl.us/dmv/vslfacts.html). Nonetheless, the nominal efficiency of these fleets has been greatly enhanced by technological innovations in fishing gear, GPS, hydroacoustic fish-finders and communication networks.

Because of growing stresses on regional fisheries and coral reefs, a broad series of traditional management actions were implemented beginning in the 1990s, including regulatory controls of minimum size limits, bag limits, gear restrictions, etc. (Bohnsack and Ault, 1996; Ault et al., 2005a, 2006). Between 1997 and 2007, non-traditional spatial controls of fishing were added to these traditional fishery management approaches. An initial network of 23 mostly small no-take marine reserves (NTMRs, mean area 2 km^2) was formed in the Florida Keys in 1997, mainly to limit conflicts between fishers and divers (Department of Commerce, 1996; Fig. 1A). In 2001, two substantially larger NTMRs were established in the Dry Tortugas region (i.e., Tortugas North and South Ecological Reserves, 566 km^2, TNER and TSER, respectively), followed in 2007 by implementation of a Research Natural Area (a NTMR, DRTO RNA) covering 158 km^2 in the western half of Dry Tortugas National Park (DRTO) (Fig. 1B). All of DRTO has been closed since the 1960s to commercial fishing, recreational spearfishing, and lobstering and open only to recreational hook-line angling, which is still allowed in the eastern portion of DRTO (DRTO Open, Fig. 1B).

The Dry Tortugas was selected as the location for large NTMRs for two principal reasons. First, the region contains known reef fish spawning grounds, and its upstream location in the Florida Current facilitates advective dispersion and transport of eggs and larvae to the rest of the Keys and southern Florida (Lee and Williams, 1999; Schmidt et al., 1999; Dahlgren and Sobel, 2000; Domeier, 2004; Burton et al., 2005). Second, its distance from the nearest human population center (>110 km west of Key West, Florida) minimized the displacement of fishers from the protected areas (V.R. Leeworthy, personal communication). The NTMRs in the Dry Tortugas region were thus implemented with the goal of improving the condition and sustainability of reef fisheries throughout the Florida coral reef ecosystem.

Ault et al. (2006) reported on intensive fishery-independent visual surveys conducted in the Dry Tortugas region in 1999, 2000, and 2004, before and after implementation of the Tortugas North Ecological Reserve (TNER) and the Tortugas South Ecological Reserve (TSER) (Fig. 1B). They found initial beneficial effects of reserve implementation based on the occupancy, abundance and size structure of exploited reef fish species. In this article we present results from continued visual surveys conducted in the Dry Tortugas region during 2006–2011 (Smith et al., 2011), which includes the period before and after implementation of the NTMR in Dry Tortugas National Park (DRTO RNA, Fig. 1B). To evaluate potential impacts of Tortugas spatial management zones on reef fishes, we analyzed temporal changes in several population abundance metrics (e.g., occupancy, density, abundance, and size composition) within and among management zones in the Dry Tortugas region, and evaluated the larger ecological role of the Tortugas zones for providing habitat for juveniles and adults of fishery species in the context of the broader Florida Keys coral reef ecosystem.

2. Materials and methods

Fishery-independent visual surveys in a two-stage stratified random sampling design (Ault et al., 2002; Smith et al., 2011) were conducted from 1999 to 2011 in the Dry Tortugas region to assess the status of the coral reef fish community; specifically, to evaluate potential differences in species abundance and size composition metrics between the fished and nonfished areas before and after implementation. Reef fish sampling design and field methods are thoroughly detailed in Smith et al. (2011).

The Tortugas mapped survey domain of 326 km^2 encompassed coral reef habitats <33 m deep on Tortugas Bank and DRTO. The statistical field design partitioned the domain into sub-regions, or strata, based on reef habitat characteristics (i.e., complexity and patchiness of reef structures, depth) mapped at 200 m × 200 m scales (i.e., primary sample unit, PSU), and spatial management zones (Fig. 1B). This habitat-based stratified survey design, developed in 1999 and 2000, has been shown to provide accurate, precise, and cost-effective abundance metrics for reef fishes in the Tortugas region (Ault et al., 2006; Smith et al., 2011). Tortugas region-wide surveys were conducted during 1999, 2000, 2004, 2006, 2008, and 2010. In addition, DRTO-specific surveys were conducted in 2002, 2009, and 2011.

The field sampling method employed highly trained and experienced divers using SCUBA Nitrox to collect biological data following a standard, non-destructive, in situ monitoring protocol in which a stationary diver records reef-fish data (number and sizes of each species) while centered in a randomly selected circular plot 15 m in diameter (i.e., second-stage unit, SSU; Bohnsack and Bannerot, 1986; Brandt et al., 2009). A principal abundance metric evaluated was reef fish species density (i.e., the number of individuals per unit sample area of 177 m^2, the area of a diver circular plot). A second abundance metric evaluated was frequency of occurrence (i.e., "occupancy" or the percentage of diver visual samples in which at least 1 individual of a given species was observed; MacKenzie et al., 2006). The occupancy statistic provides a measure of the occupancy rate, the percentage of the coral reef habitat area that is occupied

Table 1
Sample sizes within three management zones in Dry Tortugas, Florida (see Fig. 1): Tortugas Bank Open (TBO); Tortugas North Ecological Reserve (TNER); and, Dry Tortugas National Park (DRTO). Shown are primary sample units (PSU), second-stage units (SSU), and individual diver counts for surveys conducted during 1999–2011. Zones not sampled in a given year are denoted by '–'.

Year	TBO			TNER			DRTO			Total
	PSU	SSU	Diver counts	PSU	SSU	Diver counts	PSU	SSU	Diver counts	Diver counts
1999	24	48	90	68	128	230	78	151	316	636
2000	26	52	82	61	109	207	124	228	456	745
2002	–	–	–	–	–	–	99	191	343	343
2004	48	88	200	63	126	241	199	362	681	1122
2006	42	81	135	65	124	241	155	299	577	953
2008	49	98	191	76	150	285	213	405	817	1293
2009	–	–	–	–	–	–	217	421	805	805
2010	51	100	183	85	162	292	228	442	847	1322
2011	–	–	–	–	–	–	229	445	887	887
Total										8106

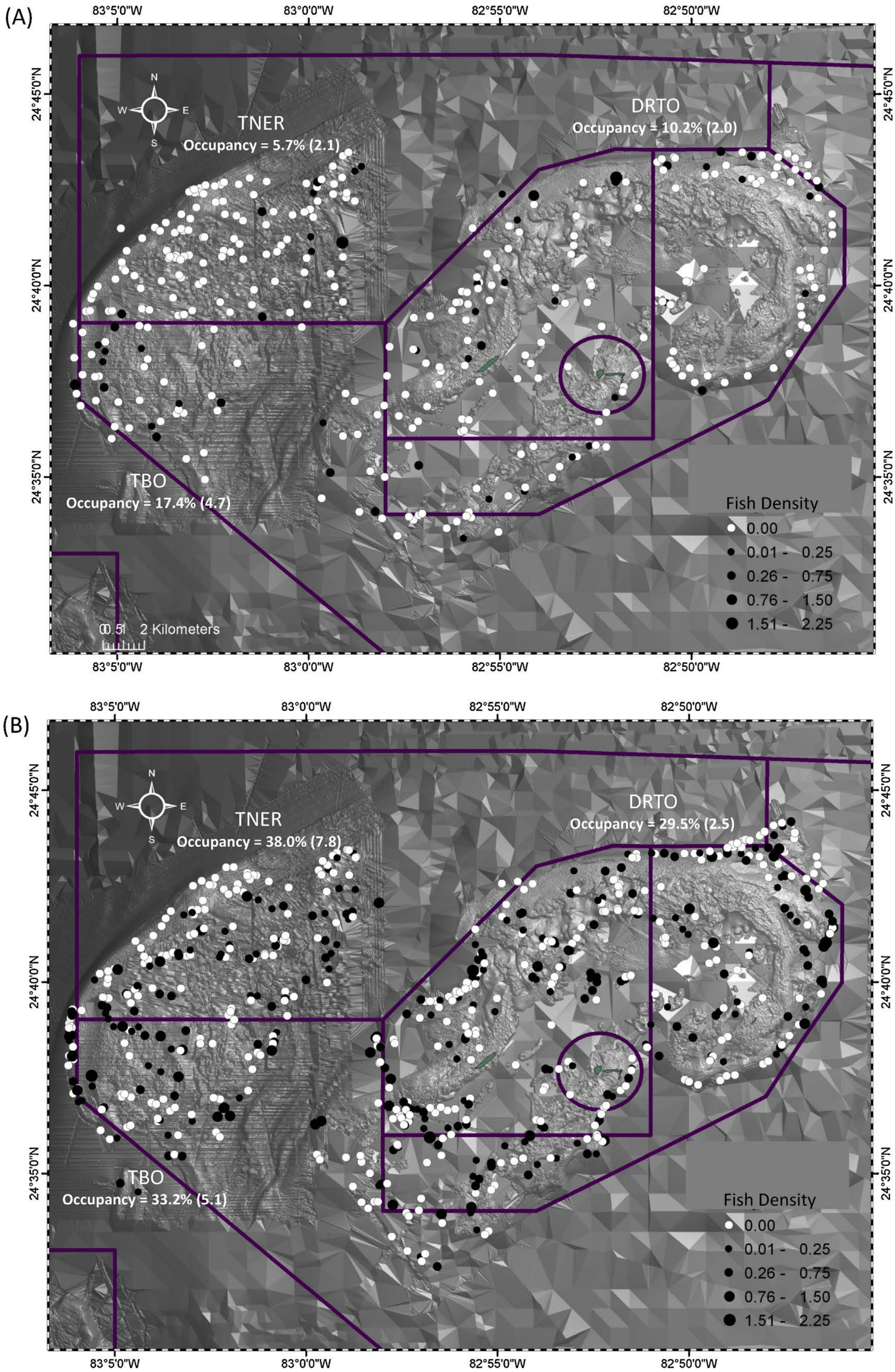

Fig. 2. Spatial distribution of density for exploited life-stage mutton snapper (mean number of fish per SSU, 177 m^2) from Tortugas region visual surveys conducted in (A) 1999–2000; and, (B) 2008 and 2010. Each point is the average of the SSUs within a PSU (200 by 200 m grid cell). Also shown are mean occupancy rates (SE) for three principal management zones (described in Fig. 1B).

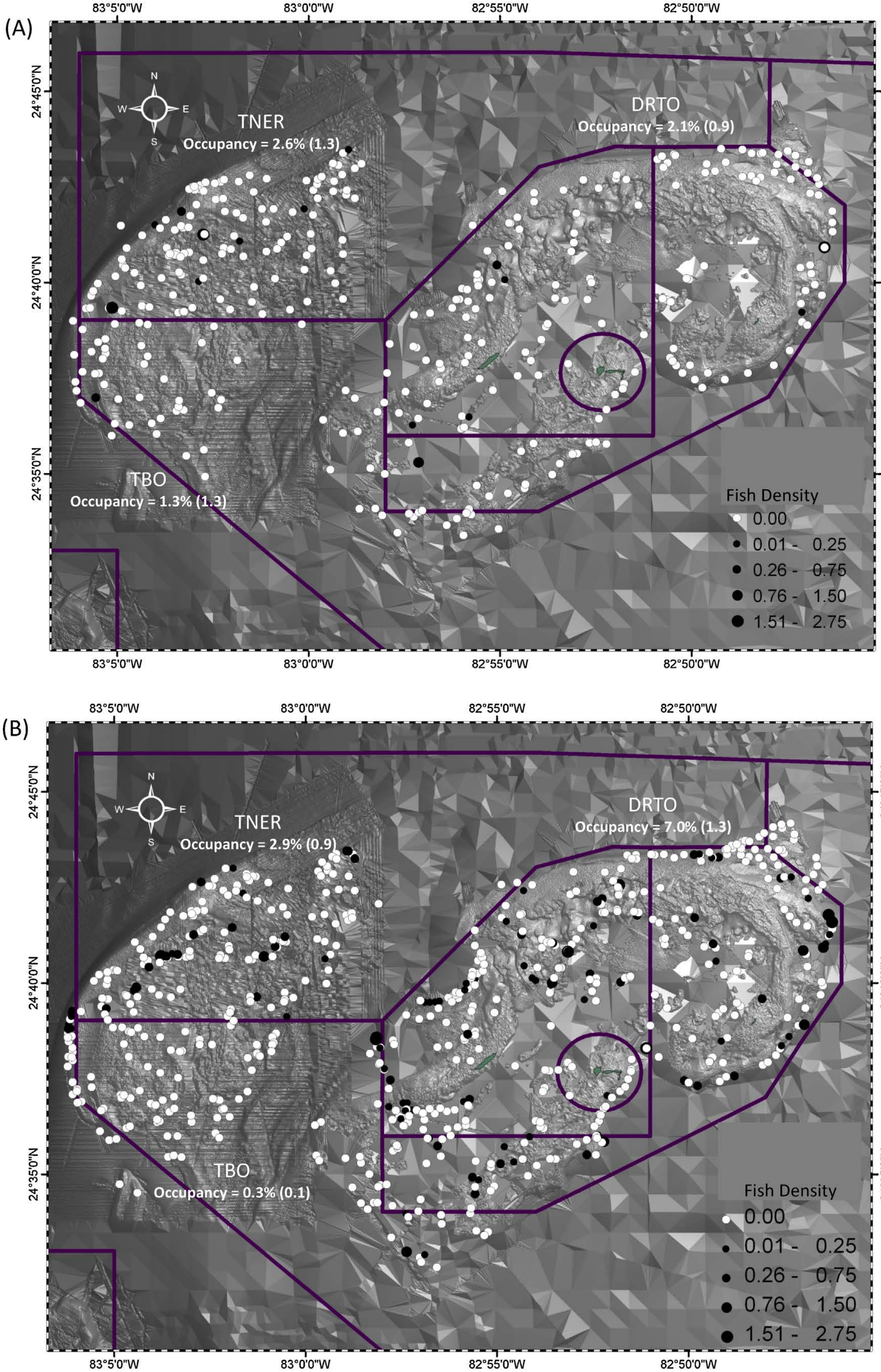

Fig. 3. Spatial distribution of density for exploited life-stage black grouper (mean number of fish per SSU) from Tortugas region visual surveys conducted in (A) 1999–2000 and (B) 2008 and 2010. Each point is the average sample value within a PSU. Also shown are mean occupancy rates (SE) for three principal management zones.

by a particular species. Statistical estimation procedures followed Cochran (1977) and Thompson (2012) for a two-stage stratified random sampling design. Computational methods are detailed in Smith et al. (2011). For the visual surveys, the primary sample unit (PSU) was a 200 by 200 m habitat grid cell, and the second-stage unit (SSU) was a diver circular plot. In most cases, each SSU was sampled by a buddy pair of divers. For analysis, each SSU metric was computed as the arithmetic average of the stationary counts for a buddy team.

Standard statistical procedures were used to test for differences among estimates of mean density, total abundance, and mean occupancy within each zone between the baseline level and each post-baseline survey year by inspection of confidence intervals (CI) following Ault et al. (2006). 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 CI *t*-test because it was more suited to sample design statistics and did not require homogenous variance of two distributions to test differences in mean responses. Detecting a change thus depended on the survey precision in a post-baseline year as well as the precision of the baseline survey. In some cases, data were pooled among consecutive surveys for analysis. Means and variances of abundance metrics were computed as 2-year or 3-year averages weighted by the respective annual sample sizes. Species selected for analysis circumscribed the range of population-dynamic processes (growth, survivorship and recruitment relationships) for relatively abundant and high occupancy rate exploited and non-target components of the reef fish community (Ault et al., 2006).

3. Results

Sample sizes for visual surveys conducted during 1999–2011 are provided in Table 1. In almost all cases, two SSUs were sampled within each PSU, and each SSU was sampled by a buddy pair of divers. Reef-fish population metrics were assessed from three distinct perspectives: (1) changes at the regional scale from 1999 to 2010 before and after implementation of both the TNER and DRTO RNA; (2) changes within DRTO focusing on the 2006–2011 time period before and after implementation of the DRTO RNA; and, (3) analysis of the ecological role of Tortugas management zones for

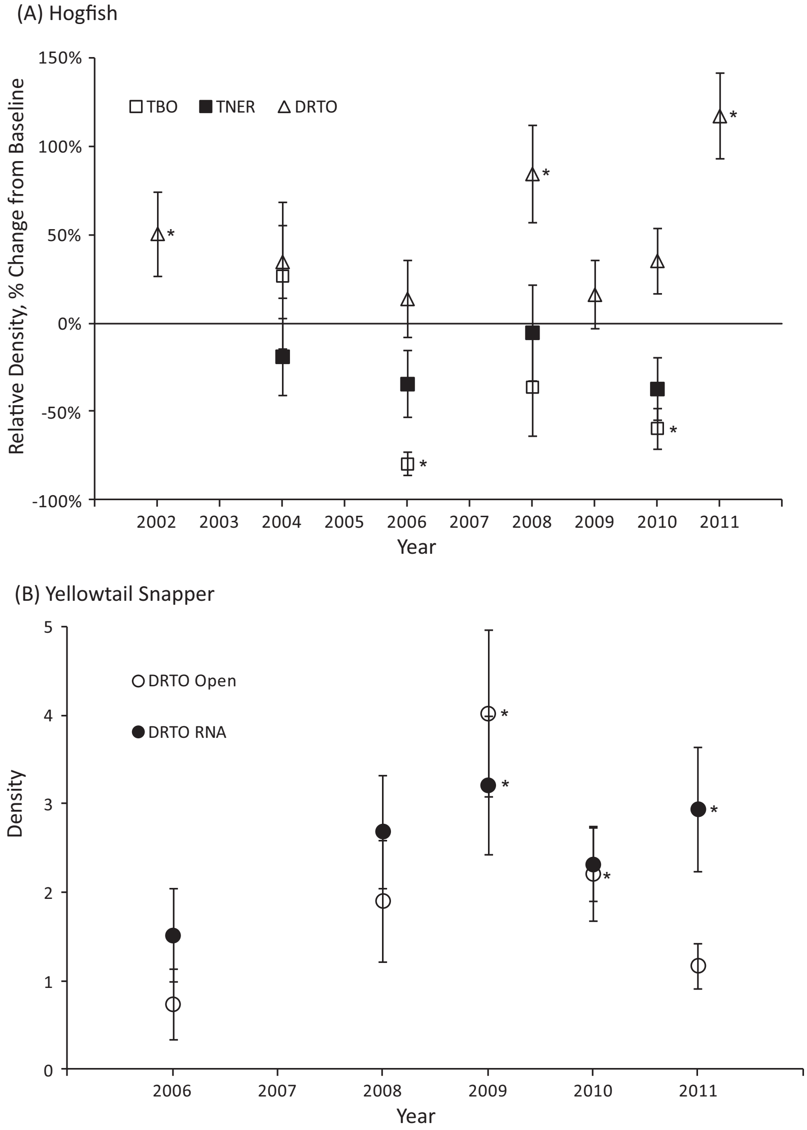

Fig. 4. (A) Visual survey estimates of relative mean density (±SE) for the exploited life-stage of hogfish, 1999–2011, for three management areas. Density (number of fish per SSU) is expressed as percent change from 1999 to 2000 baseline levels (solid line); asterisks denote surveys detecting significant changes from the baseline. (B) Visual survey mean densities (±SE) for the exploited life stage of yellowtail snapper in DRTO, 2006–2011, for two management zones. Asterisks denote surveys detecting significant changes from the 2006 pre-RNA baseline.

providing habitats for juveniles and adults within the Florida coral reef ecosystem.

Visual survey abundance metrics were evaluated for the region through time, beginning with the baseline pre-NTMR implementation surveys in 1999–2000, through implementation of the TNER and TSER (2001) and DRTO RNA (2007) management zones, and concluding in 2011. Maps of spatial density are illustrated in Fig. 2 for mutton snapper (*Lutjanus analis*) and Fig. 3 for black grouper (*Mycteroperca bonaci*) in their respective exploited life stages, i.e., fish above the minimum legal size of capture (Ault et al., 1998, 2005b). These maps also illustrate spatial patterns of occupancy (presence, solid dots; absence, white dots). As shown for mutton snapper in Fig. 2, the occupancy rate increased in all three management zones ($p < 0.05$) between the pre-implementation baseline (1999–2000) and post-implementation of the TNER and DRTO RNA (2008 and 2010), with more dramatic increases occurring in TNER and DRTO. In contrast, the occupancy rate for black grouper increased between 1999–2000 and 2008–2010 in DRTO only ($p < 0.05$), with no changes detected in the other two zones (Fig. 3).

Changes in density over the 1999–2011 survey period are illustrated for exploited phase hogfish (*Lachnolaimus maximus*) in Fig. 4A. To account for potential differences in baseline densities among zones, density was expressed in terms of the percent change from 1999 to 2000 baseline levels for each management zone. For hogfish, statistically significant densities ($p < 0.05$) above the baseline were detected in DRTO in three surveys (2002, 2008, and 2011), whereas densities below baseline levels were only detected in the Tortugas Bank Open (TBO) in two surveys (2006 and 2010). Hogfish densities in TBO were never above baseline at any time. No differences from baseline levels were detected in the TNER.

The analysis of change in density from baseline levels is summarized in Table 2 for a suite of key reef fish species. Increases in density above baseline levels for exploited life stages of principal fishery species were detected in the TNER and DRTO for a number of surveys. Only one increase was detected in TBO. In contrast, decreases in density below baseline levels were only detected in the TBO. The magnitude of minimum changes in density detected by the surveys for exploited species ranged from 50 to 300%. The pattern of density change was different for species fished in the aquaria trade as well as those not targeted by fishers, with densities fluctuating above and below baseline levels irrespective of management zone. The pattern of change was mixed for two species (goliath grouper, *Epinephelus itajara*; Nassau grouper, *E. striatus*) under fishing moratoria since 1994. Densities above baseline were detected for goliath grouper in both the TNER and DRTO, whereas the density of Nassau grouper below the baseline was detected in DRTO during one survey. In nearly all species analyzed, detected increases and decreases in density in relation to the baseline were accompanied by respective increases and decreases in occupancy rates.

Comparisons of length composition among management areas and time periods from the visual survey are illustrated for black grouper in Fig. 5. A general increase between 1999–2000 and 2008–2010 in the proportion of fish at sizes above the legal minimum was observed in the TNER and particularly in DRTO. These changes are characteristic of a relaxation of fishing pressure (fishing mortality rate) over the time frame, during which more fish

Table 2

Summary of 1999–2011 visual survey results for changes in density from baseline of 4 categories of reef fishes: exploited, aquaria, non-target, and moratorium. Baseline surveys were conducted in 1999–2000. The numbers of surveys conducted post-baseline by management zone were: 4 in Tortugas Bank Open (TBO); 4 in Tortugas North Ecological Reserve (TNER); and, 7 in Dry Tortugas National Park (DRTO). Minimum change detection from baseline was based on a 95% CI.

Family	Species	Minimum change (%) detected	Number of surveys where change was detected from baseline					
			TBO		TNER		DRTO	
			Increase	Decrease	Increase	Decrease	Increase	Decrease
Exploited								
Groupers (Serranidae)	Red grouper (*Epinephelus morio*)	66.2	0	3	0	0	0	0
	Black grouper (*Mycteroperca bonaci*)	307.3	0	0	1	0	2	0
Snappers (Lutjanidae)	Mutton snapper (*Lutjanus analis*)	69.1	1	0	2	0	7	0
	Yellowtail Snapper (*Ocyurus chrysurus*)	169.4	0	0	0	0	4	0
Wrasses (Labridae)	Hogfish (*Lachnolaimus maximus*)	50.8	0	2	0	0	3	0
	Total detections, exploited		1	5	3	0	16	0
Aquaria								
Angelfishes (Pomacanthidae)	Blue angelfish (*Holacanthus bermudensis*)	35.7	0	2	0	3	1	2
	Gray angelfish (*Pomacanthus arcuatus*)	26.7	0	0	0	2	1	0
Butterflyfishes (Chaetodontidae)	Foureye butterflyfish (*Chaetodon capistratus*)	54.2	0	1	0	2	0	2
	Spotfin butterflyfish (*C. ocellatus*)	53.4	0	0	0	1	0	3
Groupers	Butter hamlet (*Hypoplectrus unicolor*)	44.1	1	0	0	1	5	0
	Total detections, aquaria		1	3	0	9	7	7
Non-target								
Damselfishes (Pomacentridae)	Bicolor damselfish (*Stegastes partitus*)	48.4	2	1	2	1	3	1
	Threespot damselfish (*S. planifrons*)	46.1	1	0	0	4	1	3
Parrotfishes (Scaridae)	Princess parrotfish (*Scarus taeniopterus*)	62.7	2	0	0	2	2	1
	Striped parrotfish (*S. iseri*)	67.2	0	0	1	0	1	0
	Stoplight parrotfish (*Sparisoma viride*)	49.5	0	0	0	1	2	1
Porgies (Sparidae)	Saucereye porgy (*Calumus calumus*)	38.1	2	0	0	1	2	1
Groupers	Harlequin bass (*Serranus tigrinus*)	53.3	1	1	2	0	0	2
Surgeonfishes (Acanthuridae)	Ocean surgeon (*Acanthurus bahianus*)	38.8	0	0	1	0	0	1
	Blue tang (*A. coeruleus*)	35.7	0	1	0	0	2	0
Wrasses	Yellowhead wrasse (*Halichoeres garnoti*)	42.4	4	0	3	0	6	0
	Puddingwife (*H. radians*)	45.3	0	0	0	0	1	2
	Total detections, non-target		12	3	9	9	20	12
Moratorium								
Groupers	Goliath grouper (*Epinephelus itajara*)	904.6	0	0	1	0	3	0
	Nassau grouper (*E. striatus*)	98.0	0	0	0	0	0	1
	Total detections, moratorium		0	0	1	0	3	1

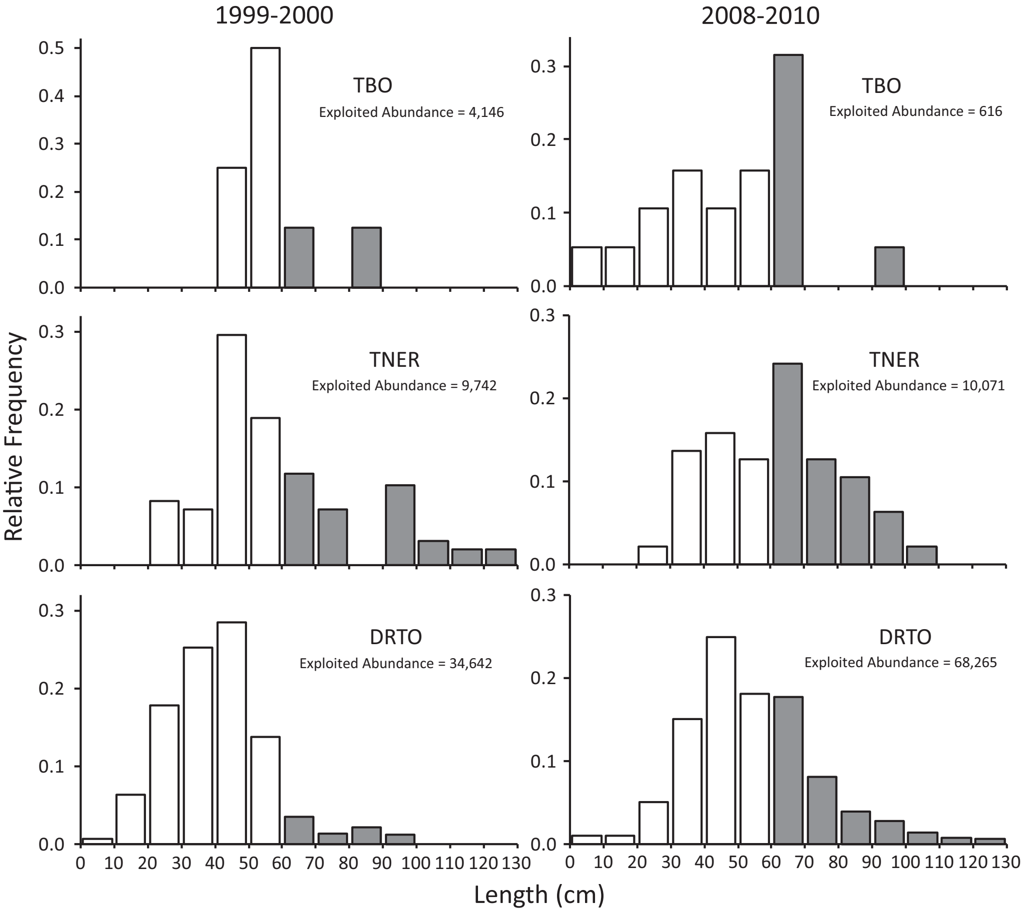

Fig. 5. Comparisons of visual survey length compositions for black grouper among 3 management zones for two time periods: the pre-implementation baseline, 1999–2000; and, post-implementation of the TNER and DRTO RNA, 2008–2010. Open bars are the pre-exploited life stage; shaded bars are exploited (fished) life stage animals. Exploited phase abundance is noted on each panel.

survived and grew to larger mature sizes. In contrast, there were very few exploited phase fish observed in the TBO in both time periods. Similar time-space patterns of change in length composition were observed for red grouper (*E. morio*), mutton snapper, and hogfish.

Visual survey densities within DRTO over the 2006–2011 time period are illustrated for exploited phase yellowtail snapper (*Ocyurus chrysurus*) in Fig. 4B. Increases in density relative to the 2006 pre-RNA baseline were detected during the post-RNA period 2008–2011, but the pattern was inconsistent: significant increases occurred in both the DRTO Open and DRTO RNA zones in 2009, only in the Open zone in 2010, and only in the RNA in 2011. Similar inconsistent patterns of post-RNA density changes were also observed for hogfish, red grouper, and mutton snapper. No changes were detected in either zone for black grouper, and length composition was similar in the two zones for all exploited species analyzed.

The Tortugas region-wide visual surveys were analyzed to evaluate the ecological role of management zones in providing habitat for juvenile and adult life stages (sexually immature and mature, respectively; Ault et al., 2005b) of principal fishery species. While DRTO contains about 60% of the Tortugas survey area (live coral reef habitats, 0–33 m depth), the percentage of juvenile abundance in DRTO in 2008–2010 was similar to or greater than this percentage, ranging from 64 to 93% for the 5 species analyzed (Table 3A). The proportion of adult spawner abundance, which includes the exploited life stage, increased by about 10% or more in DRTO between 1999–2000 and 2008–2010 for 4 of 5 fishery species (Table 3B). By 2008–2010, DRTO contained 60–87% of adult spawners in the Tortugas region for 4 of the 5 species. Concomitantly, the proportion of adults declined between 1999–2000 and 2008–2010 in the TBO for all 5 species. The analysis of adult spawners was expanded to include the combined Dry Tortugas and Florida Keys survey areas (mapped live coral habitats, 0–33 m depth), which were conducted concurrently over the 1999–2010 time period (Smith et al., 2011). Between 1999–2000 and 2008–2010, total spawner abundance doubled or more ($p < 0.05$) for 4 of the 5 species, the exception being red grouper (Table 3C). For the combined Florida Keys-Dry Tortugas regions, DRTO contained 22% of the total survey area yet harbored a disproportionately larger percentage of the adult spawners in 2008–2010 for 4 of the 5 fishery species (range: 30–53%). Similarly, in 2008–2010 the TNER had a disproportionately larger percentage of adult spawners for 3 of the 5 species.

4. Discussion

The visual survey enabled quantitative evaluation of changes in the assemblage of reef fish populations in the Dry Tortugas region over the 1999–2011 period of study. Several key management and environmental events occurred over those years: (1) implementation of the TNER and TSER in 2001; (2) intense hurricane activity in 2004–2005; and, (3) implementation of the DRTO RNA in 2007. Prior to 2007, DRTO allowed recreational hook-line fishing throughout the Park, but notably banned recreational spearfishing, commercial fishing, and "party-boat" fishing from large recreational charter vessels. These regulations are still in effect for the

Table 3

Estimates of total abundance (numbers) and the percentage of abundance among management zones for 5 exploited reef fish species that are the principal focus of management: (A) Dry Tortugas region (domain area = 326 km^2), juveniles (i.e., immature, 2008–2010); (B) Dry Tortugas region, adults (1999–2000 and 2008–2010); and, (C) Florida Keys-Dry Tortugas ecosystem (domain area = 326 + 559 km^2 = 885 km^2), adults, (1999–2000 and 2008–2010). Dry Tortugas management zones (Fig. 1B) are: TBO, Tortugas Bank Open; TNER, Tortugas North Ecological Reserve; and DRTO, Dry Tortugas National Park. Florida Keys management zones (Fig. 1A) are: Keys open-use, open to fishing; and Keys NTMRs, no-take marine reserves. The percentage shown beside the area acronym is the proportion of reef area.

(A) Dry Tortugas region: Juveniles (2008–2010)

Species	Total juvenile abundance (×1000)	Percentage of juvenile abundance		
		TBO (16.5%)	TNER (23.7%)	DRTO (59.8%)
Red Grouper	382.3	12.3	20.8	66.9
Black Grouper	159.7	2.6	5.2	92.2
Mutton Snapper	25.5	33.7	2.0	64.3
Yellowtail Snapper	9254.5	9.3	25.5	65.2
Hogfish	46.9	4.1	14.2	81.7

(B) Dry Tortugas region: Adults (1999–2000 and 2008–2010)

Species	Time period	Total adult abundance (×1000)	Percentage of adult abundance		
			TBO (16.5%)	TNER (23.7%)	DRTO (59.8%)
Red Grouper	1999–2000	468.1	20.5	28.4	51.1
	2008–2010	400.3	6.9	33.0	60.1
Black Grouper	1999–2000	48.5	8.5	20.1	71.4
	2008–2010	78.0	0.8	12.7	86.5
Mutton Snapper	1999–2000	177.5	26.8	12.5	60.7
	2008–2010	589.5	22.5	23.5	54.0
Yellowtail Snapper	1999–2000	3379.5	17.2	33.5	49.2
	2008–2010	10,511.5	4.6	24.4	71.0
Hogfish	1999–2000	1067.7	21.9	21.6	56.5
	2008–2010	924.9	14.0	20.0	66.0

(C) Florida Keys-Dry Tortugas Ecosystem: Adults (1999–2000 and 2008–2010)

Species	Time period	Total adult abundance (×1000)	Percentage of adult abundance				
			TBO (6.2%)	TNER (8.9%)	DRTO (22.4%)	Keys open-use (58.9%)	Keys NTMRs (3.6%)
Red Grouper	1999–2000	521.9	18.4	25.5	45.8	9.7	0.6
	2008–2010	511.1	5.4	25.8	47.1	20.0	1.7
Black Grouper	1999–2000	68.2	6.1	14.3	50.8	15.1	13.7
	2008–2010	128.3	0.5	7.7	52.6	34.7	4.5
Mutton Snapper	1999–2000	416.5	11.4	5.3	25.9	53.7	3.7
	2008–2010	1046.6	12.7	13.2	30.4	40.4	3.3
Yellowtail Snapper	1999–2000	7703.2	7.6	14.7	21.6	38.4	17.7
	2008–2010	15,393.2	3.2	16.6	48.5	27.4	4.3
Hogfish	1999–2000	2796.9	8.4	8.2	21.6	59.5	2.3
	2008–2010	4258.4	3.1	4.3	14.3	74.9	3.4

eastern DRTO Open zone after implementing the western DRTO RNA. Survey sampling precision was sufficient to detect statistically significant increases and decreases in population occupancy, density, and abundance within management zones for a suite of exploited and non-target species of the reef-fish community.

Results from the Tortugas visual surveys show clear evidence that spatial control of fishing activities can improve the condition of exploited stocks. Increases in density and abundance of fish above the minimum legal size of capture (i.e., exploited phase of the population) occurred for four principal fishery species (black grouper, mutton and yellowtail snapper, and hogfish) in the TNER, DRTO, or both of these zones following the implementation of the TNER and DRTO RNA, that is, between the baseline years (1999–2000) and 2010. Density increases were usually accompanied by increases in both the occupancy rate and the size of fishes in the exploited phase of the population (i.e., minimum legal size of capture to the maximum size). In contrast, decreases in density below baseline levels occurred only in the TBO. Density for a fifth fishery species, red grouper, remained stable in the TNER and DRTO, but decreased in the TBO. Density and occupancy rates for a suite of aquaria and non-target reef fishes showed a different spatial pattern of change over the period 1999–2010, with fluctuations above and below baseline levels occurring in each management zone, but depending on the species.

The movement behaviors of fishery species in relation to the size of the spatial protection areas were likely factors contributing to the observed increases in abundance and size metrics in the TNER and DRTO. The acoustic telemetry tagging study conducted in the Tortugas region by Farmer and Ault (2011) found that red and black groupers, and mutton and yellowtail snappers, exhibited home range movement behaviors, with estimated home range areas ranging from 1.4 to 7.6 km^2. These are fairly small in relation to the areas of the TNER (285 km^2) and DRTO (259 km^2), increasing the likelihood that fishes will spend enough time within the spatial protection zones to reduce their chances of being captured by fishers (Barret, 1995; Meester et al., 2001, 2004).

Within DRTO, the visual survey detected some increases in density and occurrence for principal fishery species before (2006) and after (2008–2011) implementation of the RNA; however, these increases occurred in the open-use and RNA zones with nearly equal frequency. Acoustic telemetry tagging studies found that the principal fishery species occasionally moved between the DRTO RNA and Open zones, both of which comprise a similar mix of reef habitat types (Fig. 1B) and depths, as well as between the RNA in the northwest portion of DRTO and adjacent TNER and TSER (Farmer and Ault, 2011; Feeley et al., 2012). These movement fluxes between zones, coupled with the fairly stringent controls on fishing in the DRTO Open zone, perhaps explain the lack of a clear NTMR effect for exploited species thus far post-establishment of the RNA in 2007. From a broader fishing perspective, there were more and larger reef fish available for capture by recreational anglers in the DRTO open-use zone in 2011 as compared to 1999, prior to implementation of the TNER and DRTO RNA.

It should also be noted that six hurricanes impacted the Tortugas region between the surveys of 2004 and 2006, and many fishery and non-target species experienced declines in density and abundance during this period of intense tropical storm activity. While Fig. 5 shows similar abundance for exploited phase black grouper in the TNER in 1999–2000 and 2008–2010, for example, in 2004 prior to the intense hurricane period, abundance of exploited phase black grouper in the TNER had more than doubled over 1999–2000 baseline levels (Ault et al., 2006).

Visual surveys conducted concurrently in the Dry Tortugas and Florida Keys regions (Ault et al., 2006; Smith et al., 2011) provide a unique perspective on the ecological role of the TNER and DRTO in both the Tortugas region and in the larger Florida Keys-Dry Tortugas coral reef ecosystem. DRTO comprises 60% of the coral reef habitat in the Tortugas region, yet it harbors a disproportionately greater number (64–92%) of juveniles (i.e., immature phase) of principal fishery species in the region. This is likely attributed to the wider range of depths and reef habitats found within DRTO as compared to Tortugas Bank (Fig. 1B), as well as the presence of shallow seagrass habitats in DRTO which are known nursery habitats for juvenile reef fishes (Lindeman et al., 2000; Ault et al., 2005a). DRTO also contains a disproportionately greater number of adult spawning fishes (>60% in most cases; Table 3B) of exploited species found in the region, likely owing to the combination of favorable adult reef habitats in DRTO as well as the fishing restrictions, i.e., recreational angling only. Viewed from the larger perspective of the entire Florida coral reef ecosystem, the role of DRTO with respect to reef fish spawning stock is even more striking. Although DRTO accounts for about 22% of the total reef habitat area, it contains one-third to one-half of the adult spawners for 4 of the 5 principal exploited species analyzed (Table 3C). The TNER and DRTO combined account for over 60% of the population's spawning adults of red grouper, black grouper, and yellowtail snapper within the ecosystem. These results, combined with studies of regional oceanography and larval transport (Lee and Williams, 1999; Domeier, 2004), indicate that the TNER and DRTO are major source points of recruits to populations of principal reef fishery species in the Florida Keys. It now appears that DRTO, in particular, was an ideal location to establish a NTMR as a place of refuge and replenishment for juveniles and adults of principal reef fishery species to live, grow, and reproduce with minimal human impacts, thereby enhancing the prospects for sustainability of these important resources in southern Florida. This effect is especially important given the prospects of increasing regional human population and accompanying impacts on this fragile coastal tropical marine ecosystem.

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