# Coral reef fish response to FKNMS management zones: the first ten years (1997-2007) 

Progress Report to the Florida Keys National Marine Sanctuary

> by

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## Introduction

On July 1, 1997, the Florida Keys National Marine Sanctuary (FKNMS) established a network of "no-take" marine reserves (NTMRs) along the Florida Keys Reef Track east of Key West, comprised of 22 Sanctuary Preservation Areas (SPAs) (mean $=0.85 \mathrm{~km}^{2}$, range $0.16-5.15 \mathrm{~km}^{2}$ ), and a larger ( $18.7 \mathrm{~km}^{2}$ ) Western Sambo Ecological Reserve (WSER) (US DOC 1996). This report focuses on research to assess the effectiveness of these NTMRs by comparing trends in population metrics between areas closed and open to fishing for key exploited reef fish species and two non-exploited reef species. We show trends from a four year baseline period before reserve establishment (1994-1997), to 10 years following reserve establishment (1998-2007). This report does not include results for the Tortugas region west of Key West which are reported elsewhere (Ault et al. 2002, 2005c, 2006, 2008).

## Methods

Reef fishes were visually monitored in situ by highly trained and experienced SCUBA divers using the Reef fish Visual Census (RVC) methodology, a standard nondestructive, fishery-independent, spatially-explicit monitoring method (Bohnsack and Bannerot 1986, Bohnsack and Ault 1996, Bohnsack et al., 1999; Brandt et al., in review). RVC data include species composition of visually observed reef fishes and their abundance, size structure, and frequency of occurrence within 7.5 m radius circular plots. Ultimately, these data were used to determine trends in species composition, population abundance, and individual size throughout the Florida Keys, in specific geographically
defined areas, and by habitat. Data can be used to determine species-specific habitat associations and ontogenic habitat shifts, and assess reef fish population and community responses to ecosystem changes resulting from anthropogenic or natural disturbances, such as hurricanes, climate change, or effects of management measures employed to regulate fisheries.

RVC data used in this study were collected annually from 1994 through 2007 in coral reef habitat the along the Florida reef tract from Miami to Key West (Table 1). Baseline data were collected at various reefs in the Florida Keys from 1994 through 1997 before NTMRs were established in 1997. Because the final locations of FKNMS management zones was not determined with certainty until 1996, some previously monitored sites ended up in NTMRs while others remained in areas open fishing. In most years data were collected from May through August before hurricane disturbances. Figure 1 shows an example of the distribution of RVC sampling effort for 2007. During most of the baseline period (1994-1997) we did not know what reef areas would be included in the final FKNMS reserves boundaries for SPAs or ERs. Because of this, not all reef habitats were sampled every year from 1994 to 1996, therefore data for 1994-1997 were combined to form baselines for comparative purposes. When combined, the baseline included all representative reef habitats that are used in the subsequent stratified random sampling design. The final NTMR boundaries that were implemented in 1997 included reef areas with disproportionately more high relief coral habitat than is represented in the FKNMS (Table 2). As a result, we calculated two baseline ranges for various population metrics: One included sampling sites within the final NTMR boundaries and the second included sampling sites in areas that remained opened to fishing. The resulting baseline metric ranges differ among species due to their specific habitat preferences.

Table 1. Total annual RVC sampling effort and significant management and stormrelated events for the period 1994 to 2007.

| Total |  |  |  | Comments and Significant Events |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Year | $\begin{gathered} \hline \text { RVC } \\ \text { surveys } \end{gathered}$ | Primary units | $\begin{gathered} \hline \text { Sea } \\ \text { days } \end{gathered}$ |  | Date |
| 1994 | 282 | 25 | 14 | Pre-reserve baseline period |  |
| 1995 | 672 | 61 | 34 | Pre-reserve baseline period |  |
| 1996 | 326 | 27 | 13 | Pre-reserve baseline period |  |
| 1997 | 787 | 66 | 29 | End of 1994-1997 pre-reserve baseline period |  |
|  |  |  |  | Transition year, no enforcement |  |
| 1998 | 791 | 75 | 31 | Data collected before Hurricane Georges (Cat. 2) | 25-26 Sep |
|  |  |  |  | Data collected before Tropical Storm Mitch | 5-Nov |
| 1999 | 677 | 161 | 51 | Data collected before Hurricane Irene (Cat. 1) | 15-Oct |
| 2000 | 880 | 233 | 53 |  |  |
| 2001 | 1,197 | 306 | 67 |  |  |
| 2002 | 1,224 | 278 | 48 |  |  |
| 2003 | 933 | 232 | 46 |  |  |
| 2004 | 815 | 217 | 44 | Data collected before Hurricane Charlie (Cat. 3) | 12-13 Aug |
| 2004 |  |  |  | Data collected before Tropical Storm Ivan | 22-Sep |
|  |  |  |  | Data collected before Hurricane Dennis (Cat. 2) | 9-Jul |
| 2005 | 1,134 | 284 | 66 | Data collected before Hurricane Katrina (Cat. 1) | 26-Aug |
| 2005 | 1,134 | 284 |  | Data collected before Hurricane Rita (Cat. 2) | 20-Sep |
|  |  |  |  | Data collected before Hurricane Wilma (Cat. 1) | 24-Oct |
| 2006 | 1,081 | 332 | 39 |  |  |
| 2007 | 1,279 | 327 | 44 |  |  |
| Total | 12,078 | 2,624 | 579 |  |  |



Figure 1. Reef fish Visual Census (RVC) sampling sites along the FL Keys in 2007. Each dot represents 4 census dives.

Starting in 1999 with funding from the NOAA Coral Reef Conservation Program (CRCP), monitoring was improved to more efficiently monitor reef fish populations and expand coverage throughout the Florida Keys. The effort to optimize sampling performance was greatly facilitated by the availability of new benthic habitat maps for the Florida Keys coral reef tract (FMRI 1998). These base habitat maps required additional configuration to make them amenable to sampling survey design. By adopting a habitat-based, stratified random sampling approach allowed us to better assess habitat preferences by different species. Sampling effort was stratified according to the relative coverage of distinct habitat types (Table 2).

Table 2. Area of survey sampling domain open to fishing and protected within NTMRs.

| Habitat Class | Fished |  | NTMR |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Area $\left(\mathrm{km}^{2}\right)$ | Percent of Fished Area | $\begin{gathered} \text { Area } \\ \left(\mathbf{k m}^{2}\right) \end{gathered}$ | Percent of SPA Area |
| Patch Reefs, Hawk's Channel | 192.8 | 40.9 | 7.3 | 24.8 |
| Forereef, Depth 0-6 m, High- | 4.1 | 0.9 | 6.2 | 21.3 |
| Relief |  |  |  |  |
| Forereef, Depth 0-6 m, Low-Relief | 55.0 | 11.7 | 4.6 | 15.7 |
| Forereef, Depth 6-18 m | 219.6 | 46.5 | 11.2 | 38.2 |
| Total | 471.4 | 100.0 | 29.3 | 100.0 |

In this report we present population density trends for representative economically and ecologically important species in fished areas and reserves protected from fishing (22 SPAs and the WSER). We selected seven species targeted by fishing for analysis, including three snapper (Lutjanidae), three grouper (Serranidae), and one wrasse (Labridae). Six of these are the most important reef species in the Florida Keys based on total landings, accounting for $\sim 80 \%$ of the total snapper and over $90 \%$ of the total grouper landed
(Bohnsack et al. 1994). Graysby, a minor target species, was included because it was not regulated by state or federal regulations. For this report, we selected two ecologicallyimportant parrotfishes, stoplight and striped parrotfish (Scaridae), not targeted by fishing as reference species for comparison purposes. We then tested predictions that the abundance of exploited species should increase in no-take reserves because of relaxed fishing pressure compared to similar habitat in fished areas subjected to fishing. Reference species not directly targeted by fishing are not predicted to increase directly in response to relaxed fishing pressure. We also analyzed changes in the proportion of adults (i.e. number of spawning individuals) inside reserves compared to the entire Florida Keys sampling domain.

## Results

## Exploited species

Yellowtail snapper (Ocyurus chrysurus, Fig. 2). In reserves, mean density increased starting in 1998 and peaked in 2000, ~340\% above the mean 1994-1997 baseline level for reef sites included in FKNMS reserves. Mean annual density exceeded and remained above the upper 95\% confidence interval (CI) baseline performance range from 2000 through 2005 and then dropped below the upper baseline $95 \%$ CI in 2006, following two consecutive years of hurricanes. In 2007 mean density increased to approach the upper baseline 9\%\% CI. In fished areas, mean yellowtail snapper density increased for most of the decade but never exceeded the upper 95\% CI of the baseline performance range for sites not included in reserves. Except for 2006, mean density was significantly higher in NTMRs than fished areas from 1999 through 2007 ( p < 0.05).

Gray snapper (Lutjanus griesus, Fig. 3). In reserves, mean density approached the baseline upper 95\% CI for five years (2000-2004) and was marginally significantly higher
than the baseline ( $\mathrm{p}<0.10$ ) only in 2002. Mean densities dropped in 2005 and 2006 following hurricane events, but increased again in 2007. In fished areas, gray snapper density exceeded the upper baseline $95 \%$ CI in 2000, 2001, 2003, and 2005, but was within the baseline range in other years. Trend lines showed similar trends in density changes in reserves and fished areas over the study period. For example, densities increased in NTMRs and fished areas from 1999 through 2002 and declined in 2003 and 2006. However, density increases were consistently higher in NTMRs than in fished areas and significantly higher in 2000, 2002, and 2007 ( $\mathrm{p}<0.05$ ).

Mutton snapper (Lutjanus analis, Fig. 4). In reserves, mutton snapper mean density increased significantly above the baseline performance range starting in 2000 and remained significantly above the baseline range through the rest of the study. In fished areas, mean mutton snapper density also increased significantly above the baseline range starting in 2001 and remained there through the rest of the study. Starting in 2000, mean mutton snapper density was about twice as high in NTMRs as in fished areas except for 2004 and 2007.

Black grouper (Mycteroperca bonaci, Fig. 5). In reserves, mean density increased rapidly after 1999 and peaked in 2004, ~32 fold above the baseline level. The overall average increase during the study was 15 fold above the baseline. Starting in 2000, mean densities increased above the upper baseline $95 \% \mathrm{CI}$ and remained there throughout the remainder of the study. Mean densities in NTMRs declined significantly in 2005 and again in 2006 ( $\mathrm{p}>0.05$ ). In fished areas, mean black grouper density increased significantly above the baseline in 2002, 2004, and 2007. Increases in mean black grouper density were about two orders of magnitude higher in NTMRs than in fished areas from 2000 through 2007.

Red grouper (Epinephelus morio, Fig. 6). In reserves, mean density increased between 2000 and 2003 and then dropped starting in 2004 and 2005. In fished areas, density also increased in a similar pattern as in NTMRs except that the magnitude of the increase tended to be significantly higher in NTMRs than in fished areas. In both strata baseline abundance started at very low levels.

Graysby (Cephalopholis cruentata Fig. 7). Mean graysby density increased significantly in reserves above baseline levels from 2000 through 2004 ( < 0.05) and then declined into the baseline range in 2005 through 2007. In fished areas, mean density remained within the baseline range except in 2005 when it exceeded the upper 95\% CI.

Hogfish (Lachnolaimus maximus, Fig. 8) Mean hogfish density increased significantly starting in 2000 and remained well above the baseline performance range in both fished area and NTMRs through 2007. Mean annual hogfish densities, however, were not significantly different between fished and reserve areas except in 2001 when densities were significantly higher in fished areas.

## Non-fishery reference species

Stoplight parrotfish (Sparisoma viride, Fig. 9) is a large, ecologically important herbivore not normally a target of fishing in the FKNMS. In reserves, mean density remained below the baseline range, except in 2004. We conclude that the high baseline densities observed for NTMRs was probably an artifact of the sampling in early years of the study. Most likely the baseline values for stoplight parrotfish were inflated and not representative of overall density in NTMRs because the baseline monitoring included a disproportionate amount of high relief fore reef habitat, a favored habitat of stoplight parrotfish. Mean density variation in NTMRs, however, was small, ranging from about 1.5 to less than 3 individuals per sample. In fished
areas, mean density increased slightly over the study period from about 1 to less that 2 individuals per sample. Mean density in reserves was about twice that in fished areas.

Striped parrotfish (Scarus iseri, Fig. 10) is a small herbivore not targeted by fishing. Mean annual density variation was small on an arithmetic scale and ranged from slightly above to slightly below baseline performance ranges in fished area and NTMRs. Mean annual density was not significantly different between fished and NTMRs, and showed high concordance in variation.

## Proportional abundance of spawning adults in reserves.

Changes in the abundance of spawning adults for exploited species in NTMRs were calculated as a proportion of the total adults in the sampling domain (Fig 11). Since NTMRs represent $5.8 \%$ of the total area in the FKNMS, a dashed red line in each figure at 0.58 represents the proportion of adults expected in reserves if adults were randomly distributed throughout the FKNMS. A horizontal dotted line shows the mean proportion of spawning adults in reserve sites during the pre-reserve baseline period (2004-2007). Two solid black horizontal lines show 95\% CI for the baseline mean. NTMR locations were not randomly selected, however, and tended to selectively include a disproportionate amount of shallow, high relief, reef habitat. Therefore, species that preferentially select habitats included in NTMRs will have mean baseline abundance levels above the red dashed line. Those that avoid reserve habitats fall below the red line.

Species that benefit from reserve protection should show an increased proportion of spawning adults in NTMRs over time. Mean densities that exceed the baseline $95 \%$ CI range indicated significant spawning benefits ( $\mathrm{p}<0.05$ ) from NRMRs. Species that do not benefit from NTMRs should continue to fluctuate within the 95\% CI performance
range. Increased proportional spawning stock abundance in reserves compared to the baseline period was detected for yellowtail snapper (Fig. 11a), black grouper (Fig. 11d), and mutton snapper (Fig. 11c). No significant changes in the proportion of spawning adults were detected for gray snapper (Fig 11b), red grouper (Fig.11e), or hogfish (Fig. 11f). In 2000 no black grouper were observed in fished habitats resulting in $100 \%$ of spawning adults being observed in reserves. Note, however, the high uncertainty of this estimate based on the 95\% confidence intervals.

## Discussion

Marine reserve theory predicts increased density of exploited reef fish species in NTMRs after reserves are established. In fished areas, densities of exploited species could initially remain unchanged, if fishing pressure is unchanged in areas open to fishing, or they could decline if fishing pressure increases in areas open to fishing. Over time, density in fished areas could increase from spillover or increased spawning and dispersal of eggs and larvae from NTMRs, but after an indefinite lag period in which NTMR populations can grow in average size and total abundance.

After FKNMS reserves were established in 1997, mean densities of exploited reef fish species increased significantly in reserves over the following decade as predicted. Compared to the baseline period, significant increased density ( $\mathrm{p}<0.05$ ) was detected in NTMRs for 6 of 10 years for yellowtail snapper, mutton snapper (8 yrs), black grouper (8 yrs), red grouper (7 yrs), graysby (5 yrs), and hogfish (8 yrs). A marginally significant increase ( $\mathrm{p}<0.10$ ) was detected for gray snapper in one year. In fished areas, significant increases were also detected for five exploited species, including gray snapper (4 yrs), mutton snapper (7 yrs), black grouper (5 yrs), and red grouper (6 yrs), and hogfish (8 yrs). No
significant increases were detected for yellowtail snapper or graysby in fished areas. The magnitude of density increases tended to be significantly higher in NTMRs than in fished areas with the exception of hogfish, a large ecologically and economically important wrasse that prefers low profile hard bottom reef habitat.

Compared to large changes in mean density observed for exploited species, mean density for the two reference non-targeted species remained relatively constant in NTMRs and fished areas. Mean annual density for stoplight parrotfish in reserves was 2.0 (range 1.4 - 2.8) and 7.5 (range 4.7 - 12.0) for stripped parrotfish.

## Hurricane disturbance

Other factors besides NTMRs likely influenced density trends in the FKNMS. Hurricane and tropical storm disturbance, for example, was prominent in the decade following FKNMS NTMR establishment (Table 1). A total of nine events impacted the Florida Keys over four years including Hurricane Georges and Tropical Storm Mitch in 1998; Hurricane Irene in 1999; Hurricane Charlie and Tropical Storm Ivan in 2004; and Hurricanes Dennis, Katrina, Rita and Wilma in 2005 (Fig. 12).

The scientific literature and this study indicate that hurricane disturbance can cause individual fish to become disoriented and displaced from home reefs. Normally reef fish tend to be sedentary and display high reef residency and site fidelity. Lindholm et al. (2005), for example, used tagging studies to show long term residency of black grouper and yellowtail snapper at Conch Reef in the Keys. Hurricane disturbance effectively "homogenize" populations by mixing and redistributing existing fish populations. Thus, NTMRs with high initial densities of target fishery species would likely show net declines after disturbance because the pulsed dispersal of fishes will result in net fish
movement away from small marine reserves with high densities to adjacent larger fished areas with lower density. Despite hurricane disturbances, densities of most exploited species in reserves tended to remain significantly above pre-reserve baseline levels.

Physical disturbance is the most likely mechanism to explain observed post hurricane population declines in FKNMS reserves. In this study, mean density for most exploited species declined in 2005 and 2006 following two hurricanes in the fall of 2004 and four in 2005. The density tended to increase 2007 following a year without hurricanes. Because most visual sampling occurred in May through August each year, any population effect from hurricane disturbance is reflected in data from the following year. In each case, mean density declined in reserves for most exploited species a year later, including yellowtail snapper, gray snapper, and in particular black grouper. Despite large declines in some cases, mean density remained significantly above the pre-reserve baseline.

Robins (1957) observed that many coastal fishes were stressed and unable to feed after storms because of prolonged turbidity Long-term resident reef fishes on reefs in the U.S. Virgin Islands disappeared after Hurricane events, apparently because high turbidity and storm surge caused them to become disoriented and lost. Many eventually ended up being redistributed to other locations. We hypothesize that many reef fish in the FKNMS also end up getting displaced and redistributed to other locations. The net result is reef populations become more mixed and homogeneous. Areas with high initial population concentrations likely would show net declines while areas with low initial concentrations may show net increases. SPAs, with high density were especially likely to loose individuals following hurricane disturbance because of their small size.

Tagging studies elsewhere support the hypothesis that hurricane disturbance can result in population redistribution and mixing. Tagging studies at artificial reefs in the

Gulf of Mexico showed that red snapper were highly residential except after hurricane Opal in 1995 (Patterson et al., 2001). Maximum recapture displacement distance from the tagging site was 29 km for fish tagged and recaptured before the hurricane, 12 km for fish tagged and recaptured after the hurricane, and 270 km for fish tagged before and recaptured after the hurricane. The percentage of fish displaced less than 1 km when recaptured for these groups, respectively, was $77 \%$ before, $80 \%$ after, and $23 \%$ for fish exposed to the hurricane.

## Other factors

Several exploited species showed significant increased density in both fished and reserve areas. Because NTMRs covered a small total area of ( $\sim 45 \mathrm{~km}^{2}, 0.058 \%$ of the FKNMS), it is unlikely that any significant fishery benefits outside of reserves could be detected. Other possibilities to explain increased density in fished areas include good recruitment year classes for some species (perhaps by chance); beneficial effects of more restrictive regional fishing regulations on exploited stocks; and the seasonal closure of Riley's hump to all fishing to protect mutton snapper spawning aggregations starting in 1993 and its permanent closure in 2001 as part of the Tortugas South Ecological Reserve. The increased density of red grouper in both NTMRs and fished areas starting in 2001, for example, is consistent with an unusually successful 1999 year class (SEDAR 12, 2006) that influenced NTMRs and fished zones.

Most exploited species also have undergone increased regulation before or during the study period which may have influenced the observed results. Florida established a minimum size limit of 12 " for mutton and yellowtail snapper in 1985 and 10" for gray
snapper in 1994. Minimum size was increased to 16 " for mutton snapper in 1994 which may partially explain the overall increased density observed starting in 2000. Minimum sizes began at 18 " for red and black grouper in 1985 and increased to 20 " in 1990. In 1998 a two fish daily recreational bag limit was established for black grouper and in 2001, minimum size was raised to 22 ". Overall population density increased for red and black grouper following these measures, although the increase was much more substantial in reserves than fished areas for both species. The overall increased population abundance of red grouper starting in 2001 reflected a strong 1999 year class (SEDAR 12, 2006).

Graysby is a small grouper not regulated by fishing regulations. Its density increased significantly in reserves during the study, but remained within the baseline performance range in fished areas. This observed increase in reserves is most easily explained by reserve protection.

Hogfish minimum size limits were set at 12" in 1994 which may explain the increased density observed in both fished and reserve areas starting in 2000. Bohnsack et al. (2006) noted that hogfish prefer low relief hard bottom over high relief habitats prevalent in existing SPAs. This habitat preference is consistent with the fact that the proportion adult spawners in SPAs (Fig. 11f) was consistently below the 0.058 proportion expected in SPAs if hogfish were randomly distributed throughout the Sanctuary based on area alone.

Seasonal and permanent fishery closures outside the study domain may have influenced the observed results. Riley's Hump southwest of the Dry Tortugas was closed seasonally in May and June to protect mutton snapper spawning aggregations starting in
1993. Riley's Hump was closed permanently in 2001 as part of the FKNMS 60 na $\mathrm{mi}^{2}$ Tortugas South Ecological Reserve (TSER). Since then, partial spawning recovery has been documented at Riley's Hump (Burton et al. 2005). Also in 2001, the Tortugas North Ecological Reserve (TNER) covering 90 na $\mathrm{mi}^{2}$ was closed to fishing. These temporary and permanent fishery closures may partially explain increased densities observed in fished and reserve areas (Ault et al. 2005, 2006, 2008). In 2008, Dry Tortugas National Park established a 47 na $\mathrm{mi}^{2}$ Research Natural Area, a no-take reserve, but after the period covered in this study.

Although NTMRs covering a small total area ( $\sim 0.058$ of the domain), they had a disproportionately large influence on the total projected abundance of spawning adults for some exploited species (Fig. 11). Mutton snapper showed a slight preference for reserve habitat and yellowtail snapper, gray snapper, and black grouper showed strong preference for reserve habitats. The proportion of adult spawning sized yellowtail snapper, black grouper, and mutton snapper increased significantly in reserves following reserve establishment probably as the result of reserve protection and their preference for high relief habitat included in reserves. In contrast, adult hogfish were consistently under represented in reserve area based on total area. The fact that the proportion of spawning hogfish never exceeded 0.058 indicates low hogfish preference for NTMR habitat. Spawning sized gray snapper and red grouper were disproportionately more abundant in reserves than fished areas, but their density did not increase significantly above baseline levels.

## Conclusions

Monitoring results in FKNMS no-take marine reserves were consistent with predictions of marine reserve theory. Density increased for the seven exploited species examined (three grouper, three snapper, and a wrasse) during the decade after reserves were established and no biologically significant increases were detected for two reference parrotfish species not targeted by fishing.

The study also showed significant impacts of six hurricanes in 2004 and 2005 on population density. Mean density of all exploited species declined significantly in marine reserves in years following these hurricanes. The simplest explanation for these declines is that hurricanes caused population mixing between marine reserves and fished areas. While most reef species are normally residential and show high site fidelity, hurricane surge and turbidity can disturb and disorient individuals causing them to get lost and redistributed. The net result is a more homogenous density caused by a 'pulsed dispersal' in which individuals at high density in small marine reserves are more likely to move to larger adjacent areas with lower density than vice versa. Because of their high initial densities, density declines of fishery species in marine reserves following disturbance would be more detectable than small density gains in fished areas spread over large areas. Despite fish redistribution following hurricane disturbance, densities of most exploited species in reserves remained significantly above pre-reserve baseline levels.

Other factors besides reserve protection and hurricanes likely contributed to the observed results. Mean density also increased significantly for five exploited species in fished areas although those increases tended to be significantly less than those observed in marine reserves with the exception of hogfish. Because the 23 reserves were small and
covered less than $6 \%$ of the total study domain, they were unlikely to have greatly contributed to any density increases observed in fished areas. Thus, despite the high densities observed in reserves, their total absolute spawning contribution should be low. Also, 10 years of reserve existence is a short time compared to the longevity of exploited reef fish species which is measured in decades. Other possible explanations for increased density in fished areas are good recruitment year class strength by chance and the influence of more restrictive fishery regulations imposed before and during the study, including larger minimum size limits, smaller bag limits, and the seasonal and permanent spawning area closures at Riley's Hump and Tortugas North, both up-current of the study area. Except for graysby, effects of marine reserve protection is somewhat confounded by effects of other regulations.

Finally, because the intensity of fishing in reserves was the only factor directly changed by NTMR zoning, the magnitude and speed of the density increases in no-take reserves suggests that fishing is a stronger influence on exploited reef fish populations in the FKNMS than other environmental concerns such as water quality.

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## Figure Captions

Figure 1. Location of stationary fish sample sites in the Florida Keys National Marine Sanctuary, Biscayne National Park, and Dry Tortugas National Park sampled during the 2002 Keys-wide cruise.

Figure 2. Comparison of yellowtail snapper density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal finely dashed (SPAs) and darker dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 3. Comparison of gray snapper density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted/dashed (SPAs) and dashed/dotted (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 4. Comparison of mutton snapper density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted/dashed (SPAs) and dashed/dotted (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show 95\% confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 5. Comparison of black grouper density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 6. Comparison of red grouper density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 7. Comparison of graysby density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 7. Comparison of hogfish density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 9. Comparison of stoplight parrotfish density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 10. Comparison of striped parrotfish density trends in fully protected "no-take" Sanctuary reserves (SPAs and WSER, solid upper line) and exploited reference areas (dashed lower line). Vertical line shows when no-take protection initiated. Horizontal dotted (SPAs) and dashed (reference areas) bands show null model predictions based on 1994-1997 95\% annual performance measures projected to 2003. Whiskers show $95 \%$ confidence intervals. Asterisks denote significantly different densities from the "no significant change" projection.

Figure 11. Proportional abundance of spawning adults in FKNMS reserves in the study spatial domain (1998-2007) for a. yellowtail snapper, b. gray snapper, c. mutton snapper, d., black grouper, e. red grouper, and f. hogfish. Red dotted horizontal line shows the proportion of area in the FKNMS with no-take reserves established in 1997. Horizontal dotted line shows the mean proportion of spawning adults in reserves during the pre-reserve baseline period (20042007) and two solid black horizontal lines show 95\% CI for the mean.

Figure 12. Hurricane trajectories and intensity projections in southern Florida in 2004 (top) and 2005 (bottom).


Fig 2


Fig 3


Fig 4


Fig 5


Fig 6


Fig 7


Fig 8


Fig 9


Fig 10


Figure 11. Proportional abundance of spawning adults in FKNMS reserves in the study spatial domain (1998-2007) for a. yellowtail snapper, b. gray snapper, c. mutton snapper, d., black grouper, e. red grouper, and f. hogfish. Red dotted horizontal line shows the proportion of area in the FKNMS with no-take reserves established in 1997. Horizontal dotted line shows the mean proportion of spawning adults in reserves during the pre-reserve baseline period (2004-2007) and two solid black horizontal lines show 95\% CI for the mean.


Figure 12. Hurricane trajectories and intensity projections in southern Florida in 2004 (top) and 2005 (bottom).

