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Do no-take reserves benefit Florida's corals? 14 years of change and stasis in the Florida Keys National Marine Sanctuary

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Abstract With coral populations in decline globally, it is critical that we tease apart the relative impacts of ecological and physical perturbations on reef ecosystems to determine the most appropriate management actions. This study compared the trajectories of benthic assemblages from 1998 to 2011 in three no-take reserves and three sites open to fishing, at 7–9 and 15–18 m depth in the Florida Keys. We evaluated temporal changes in the benthic assemblage to infer whether fisheries bans in no-take reserves could have cascading effects on the benthos in this region. Coral cover declined significantly over time at our sites and that trend was driven almost exclusively by decline of the *Orbicella* (formerly *Montastraea*) *annularis* species complex. Other coral taxa showed remarkable

stasis and resistance to a variety of environmental perturbations. Protection status did not influence coral or macroalgal cover. The dynamics of corals and macroalgae in the 15 years since the reserves were established in 1997 suggest that although the reserves protected fish, they were of no perceptible benefit to Florida's corals.

Keywords Coral reefs · Florida Keys · FKNMS · *Montastraea* · *Orbicella* · Marine protected areas

Introduction

Coral reefs have degraded worldwide in recent decades, leaving at least one-third of coral species at long-term risk of extinction (Carpenter et al. 2008). Once-dominant coral taxa have been particularly hard hit, leading to shifts in the absolute and relative abundances of coral species (Aronson and Precht 2001; Knowlton 2001; Green et al. 2008; van Woesik et al. 2011). The coral reefs of the Florida Keys National Marine Sanctuary (FKNMS) are no exception to these trends (Porter and Meier 1992; Precht and Miller 2007; Somerfield et al. 2008).

The primary causes of the recent coral decline and the controls on reef recovery have been long-standing points of contention. At the heart of this debate is the question of how local-scale, ecological interactions, such as herbivory and competition, act in combination with larger-scale physical perturbations such as thermal anomalies. In the Florida Keys, coral disease, coral bleaching, hurricane damage, and declining water quality have all contributed to the decline in coral cover over the last 30 years (Precht and Miller 2007; Causey 2008). Although the ecological implications of these stressors are widely acknowledged, some researchers have suggested that long-term overfishing

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provided the precondition for degradation by reducing the ability of reefs to recover from disturbance (Jackson et al. 2001; Pandolfi et al. 2003; Bellwood et al. 2004).

This line of thinking led to a global focus on establishing networks of no-take reserves with the goal of sustaining populations of important marine organisms and promoting resilience in tropical habitats (Hughes et al. 2003; Bellwood et al. 2004; Mora et al. 2006; Keller et al. 2009). Marine reserves generally increase populations of targeted fish species (Alcala et al. 2005; Bohnsack et al. 2007; Kramer and Heck 2007; McCook et al. 2010), but proponents of reserve-based management further suggest that reduced fishing pressure will, as a rule, have positive effects on the benthos. In theory, reduced exploitation of herbivorous fishes should result in higher rates of herbivory, which should reduce macroalgal biomass and enhance the recruitment and survival of hard corals. Some investigators predict, therefore, that no-take reserves will increase the ability of reefs to recover from disturbance (Bellwood et al. 2004; Mumby et al. 2006, 2007; Mumby and Harbone 2010).

The presumption of enhanced coral recruitment in protected areas is apparently supported in a few locations where populations of herbivorous fish had been exploited (Mumby et al. 2006, 2007; Mumby and Harbone 2010), but increased herbivory has not led to healthier reefs in most places where the relationship has been examined (e.g., Coelho and Manfrino 2007; Kramer and Heck 2007; Huntington et al. 2011; Carassou et al. 2013). A series of meta-analyses evaluating the global impact of no-take reserves on coral assemblages found that although coral declines were generally less severe in no-take reserves (Selig and Bruno 2010), reserves have neither reversed the declines in coral cover nor conferred resilience to further disturbance (Selig et al. 2012). If reserve-based management does not, in general, benefit coral populations, then one or more links in the theoretical cascade must be missing. For reserves to benefit corals, each of the following conditions must be met: (1) herbivore abundance must be higher in reserves, (2) higher abundance of herbivores must result in increased grazing on macroalgae, (3) increased grazing must reduce macroalgal cover, and (4) reduced cover of macroalgae must benefit coral recruitment or coral growth. In some areas, including the FKNMS, herbivorous fishes are not currently important targets of fisheries (Bohnsack et al. 2007; <https://www.flrules.org/gateway/ChapterHome.asp?Chapter=68B-42>); nevertheless, the abundances of some taxa of large, herbivorous fishes were greater in no-take areas relative to reference sites in the FKNMS (Bohnsack et al. 2007; Kramer and Heck 2007). The difference in the abundance of herbivorous fishes was most likely a result of differences in the quality of reef habitat between no-take reserves and reference sites,

rather than reduced fishing pressure (Bohnsack et al. 2007; cf. Jones et al. 2004). Regardless of the underlying drivers of herbivore abundance, there should be differences in the benthic assemblages in the no-take reserves if the abundance of herbivorous fishes drives reef condition. Kramer and Heck's (2007) study of inshore patch reefs in the FKNMS showed, however, that more herbivores in reserves did not result in reduced macroalgal cover or higher densities of juvenile corals within the reserves. Maintaining large populations of herbivorous fishes does not, therefore, guarantee increases in the impact of herbivory or changes in the benthic assemblages of coral reefs.

Furthermore, because the observed increase in macroalgae in the Caribbean has generally followed coral mortality rather than causing mortality, competitive overgrowth of adult corals by macroalgae has not been the proximal cause of the decline in coral cover (Aronson and Precht 2006). Some macroalgae inhibit coral recruitment (Kuffner et al. 2006) and reduce the growth and survival of juvenile corals (Lirman 2001; Box and Mumby 2007). Macroalgae, however, do not, in general, dominate reefs of the wider Caribbean, including reefs in Florida (Bruno et al. 2009; Schutte et al. 2010; Côté et al. 2013). If macroalgae are not, in fact, significant contemporary competitors of Caribbean corals, then the relationship between the density of herbivorous fishes and the cover of hard corals is weak by default.

Understanding the interactive causes of coral decline and determining the measures necessary to promote recovery are crucial steps to managing reef ecosystems in a rapidly changing world. A growing body of research suggests that the theoretical cascade from fisheries protection to enhanced coral populations may be an oversimplification. If the ecological interactions between herbivorous fishes and corals are less important than originally conceived, the solutions to the coral-reef crisis may lie largely outside the scope of local fisheries management. No-take reserves provide the opportunity to test the relative importance of ecological and physical controls on coral-reef dynamics.

We evaluate the impacts of reserve-based management on coral reefs over the period 1998–2011 to test four hypotheses. Hypothesis 1: Because of the high frequency of disturbance in the FKNMS, the cover of hard corals should have declined over time, resulting in declines of dominant taxa, and increases in the abundance of 'weedy' corals (Aronson and Precht 2001; Knowlton 2001) and other non-coral benthic components [sponges (Pawlik 2011), gorgonians (Ruzicka et al. 2013), and zoanthids]. Hypothesis 2: Although the abundance of herbivorous fishes is higher in Florida's no-take reserves than outside the reserves, herbivory is likely to be high throughout the

FKNMS because herbivorous fishes are not currently targeted by fishers (Bohnsack et al. 2007). For this reason, and because of the inconsistent impacts of reserve-based management elsewhere, the trajectories of coral cover, and the relative and absolute abundances of dominant coral taxa, should not have differed between no-take reserves and reefs open to fishing. Hypothesis 3: Reserves also should not have affected the cover of macroalgae or bare space; coral cover should have been decoupled from algal dynamics in the FKNMS, as has been demonstrated elsewhere (Edmunds 2013). Instead, changes in coral cover should have been modulated primarily by changes in the physical environment. Thermal stress (including both elevated temperature and high irradiance) has been an important cause of coral decline in the FKNMS (Causey 2008). Because of relatively lower irradiance and, possibly, lower temperatures in deeper water, deeper habitats should have provided a refuge that increased the resilience of reefs to further disturbance. This leads to Hypothesis 4: Declines in coral cover and shifts in the species composition of corals should have been less pronounced in deeper water than in shallower depths. In conjunction with testing these hypotheses, we compare our results with other assessments from within the FKNMS during the same period.

Materials and methods

Study area

The FKNMS is a 9,850-km² reserve that extends from Key Biscayne to the Dry Tortugas (Fig. 1). The fish populations of the FKNMS have a long history of exploitation (Ault

et al. 1998; McClenachan and Kittinger 2012). Herbivorous fishes were harvested until the early 1990s when they were regulated as part of the ornamental-fish trade (<https://www.frules.org/gateway/ChapterHome.asp?Chapter=68B-42>).

Their harvest is now minimal compared with species targeted by traditional fisheries (Bohnsack et al. 1994, 2007). Recreational and commercial fisheries, however, continued to reduce populations of predatory fish through the 1990s until stricter regulations were implemented (Bohnsack et al. 1994; Ault et al. 1998; <http://myfwc.com/fishing/saltwater/recreational/rules-by-species/>).

One response was to prohibit fishing within no-take zones on 23 coral reefs within the FKNMS beginning in 1997 (Bohnsack et al. 1994; Keller et al. 2009). Our study did not directly assess fish populations in the FKNMS; however, the existing literature suggests the abundances of most commercially important fishes—serranids (grouper) and lutjanids (snappers)—have increased in no-take reserves since 1997 (Bohnsack et al. 2007). Furthermore, the abundances of these taxa are now significantly higher in no-take reserves than in adjacent fished areas (Bohnsack et al. 2007; Kramer and Heck 2007). Adult scarines (parrotfish), acanthurids (surgeonfish), and pomacentrids (damselfish) are also more abundant within marine reserves (Kramer and Heck 2007; Bohnsack et al. 2007); however, these among-site differences preceded the establishment of the reserves (Bohnsack et al. 2007) and are, therefore, most likely a reflection of among-reef habitat variability rather than a cascading impact of protection per se. Although the mechanisms for maintaining large populations of herbivorous fishes at our sites are different from the processes controlling those populations in most reserves, the fact that these herbivores are apparently more abundant in Florida's

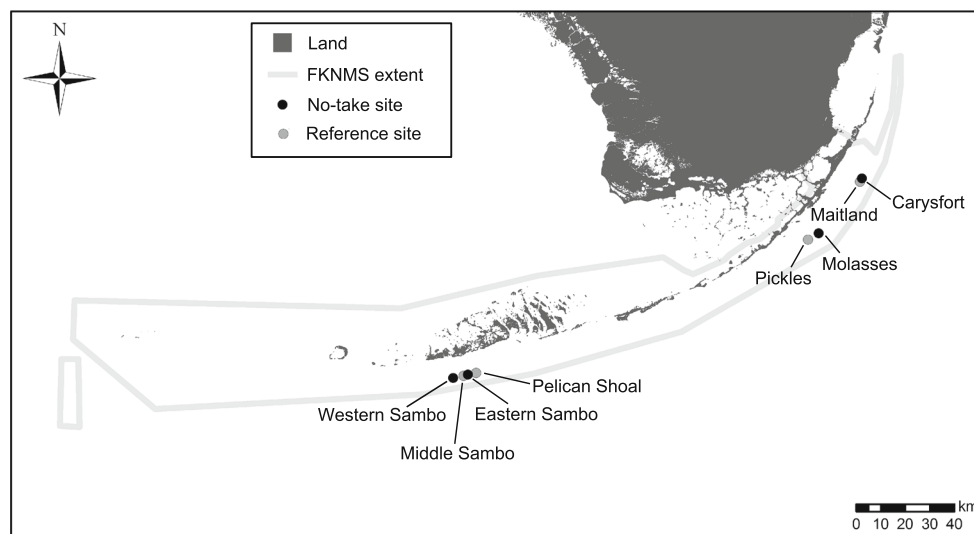


Fig. 1 Map of the Florida Keys showing the extent of the FKNMS and locations of the study sites

reserves than outside the reserves nevertheless allows us to test hypotheses that elevated abundances of herbivorous fishes in reserves will confer positive benefits to the benthos on Florida's reefs (Hypotheses 2 and 3).

By the time the no-take reserves were established, coral cover was already low throughout the FKNMS; however, after the 1997–98 El Niño event and the impact of hurricane Georges that same year, average coral cover dropped below 10 % (Precht and Miller 2007; Causey 2008). Our study assesses changes in the benthic assemblages of reefs in the FKNMS following the disturbances of 1997–98. After 1998, a variety of disturbances continued to compromise Florida's reefs. Hurricanes impacted our study sites in 1999, 2006, 2007, and 2008, but the most significant storm damage occurred in 2005, when four storms passed in close proximity (<http://www.nhc.noaa.gov/>). Two additional mass bleaching events affected Florida's reefs in 2005 and in 2010 (Causey 2008; Brandt and McManus 2009; Wagner et al. 2010), and an extreme cold water event in 2010 also caused high coral mortality, especially on inshore reefs (Lirman et al. 2011). Although the prevalence of disease has been low in the FKNMS in general, coral disease has also been a persistent source of morbidity and mortality over the last 15 years, especially following bleaching events (Santavay et al. 2005; Brandt and McManus 2009).

Our long-term dataset, which spanned the period 1998–2011, assessed changes in the benthic assemblages at 'intermediate' (7–9 m) and 'deeper' (15–18 m) depths in fore-reef habitats within three no-take reserves: Western Sambo, Eastern Sambo, and South Carysfort reefs. Western Sambo and Carysfort reefs were chosen because they are the largest protected areas in the Lower and Upper Keys, respectively. Eastern Sambo was chosen because it is a research only area. We also surveyed three reefs where fishing was allowed: Middle Sambo, Pelican Shoal, and Maitland (Fig. 1). These reference sites were chosen to be adjacent to and comparable in size with the reserve sites. All sites supported the spur-and-groove habitat typical of offshore, fore-reef habitats in the Florida Keys.

A rectangular plot was established on each reef in each depth range, for a total of 12 plots. The plots extended 25 m downslope along the spurs and 80 m along the depth contours, perpendicular to the spurs. The center of each plot, henceforth termed a study site, was marked with a submerged buoy, and site maps were created to allow annual surveys.

Data collection

We conducted videographic surveys using an underwater transecting method (Aronson et al. 1994; Murdoch and Aronson 1999) at each of the twelve 25 m × 80 m study

sites. Within each study site, 10 to 12, 25-m transect lines were laid along the tops of haphazardly chosen reef spurs. No more than one transect line was laid per spur per sampling time. A diver swam slowly along each transect, holding a video camera in a waterproof housing and recording the reef surface in a 25 m × 40 cm swath: an area of 10 m². A vertical bar projecting forward from the housing maintained the camera's lens a standard 40 cm above the reef surface. Underwater video lights were used under low-light conditions. No transects were laid in expansive areas of sand.

We surveyed the study sites each summer from 1998 to 2011, with the exceptions of 2006 and 2009. In addition, Maitland Reef and the intermediate-depth sites at Pelican Shoal were not surveyed in 2005. Our overall sampling design is summarized in Electronic Supplementary Material (ESM) Fig. 1.

Image analysis

Non-overlapping still images were extracted from each video transect using Capture It[®] or Sony Vegas Pro Studio[®] software. Random points were overlain on each image using Coral Point Count with Excel extensions (Kohler and Gill 2006) or using a software program developed by T.J.T.M. Between 1998 and 2005, 50 images were collected from each video transect and ten random points were projected onto each image (Aronson et al. 1994), for a total of 500 points per transect. In 2007, a high-definition camera was used for the surveys, which necessitated a change to a wide-screen video format. The shorter vertical span reduced the total area captured in each image. We, therefore, increased the number of captured images to 55 in 2007 and in all subsequent analyses and reduced the number of points per frame to nine, for a total of 495 points per transect.

Macroalgae, sponges, gorgonians, zoanthids, and sand beneath the random points were identified categorically. Because branching gorgonians bend with water motion, we only counted points falling on the holdfasts. For cases in which points fell on gorgonian branches in the still images, we examined the video to identify the benthic constituents beneath. An aggregate category, including crustose coral-line algae, fine-turf algae, and bare substrate (CTB; Aronson and Precht 2000), was also identified categorically. Hard corals (Scleractinia and Milleporina) were identified to the lowest possible taxonomic level. Hard corals were generally identified to species, but occasionally only generic identifications were possible. Some corals were grouped into broader categories for statistical analysis of the data. These corals included the three species of the *Orbicella annularis* species complex [*O. annularis*, *O. franksi*, and *O. faveolata*: formerly in the genus

Montastraea (Budd et al. 2012) and hereafter termed the *O. annularis* complex], *Agaricia* spp. (primarily *A. agaricites*, but also *A. fragilis*, *A. grahamae*, *A. humilis*, *A. lamarki*, and *A. undata*), *Siderastrea* spp. (*S. siderea* and *S. radians*), branching *Porites* spp. (*P. divaricata* and *P. furcata*; *P. porites* was considered separately), and *Millepora* spp. (*M. alcicornis*, *M. complanata*, and *M. squarrosa*). Colonies in the *O. annularis* complex were almost exclusively *O. faveolata* and *O. franksi*, but uncertainty in identifications of small colonies from the video frames necessitated pooling the *Orbicella*. During the last four years of the study—2007, 2008, 2010, and 2011—the use of a high-definition video camera allowed us to identify macroalgae to the genus level. These data were not analyzed statistically, but we describe overall trends in the composition of the macroalgal assemblages.

Point-count data were used to estimate covers of the broad categories of sessile benthos, and the absolute and relative covers of hard-coral taxa. We estimated the absolute cover of all sessile benthos after removing the points falling on loose sand from the total number of points for each transect. Estimates of benthic cover were, therefore, limited to hard substrate. To calculate the relative cover of a coral taxon, we divided the cover of that taxon by the total coral cover at the same site in the same year.

Statistical analysis

Using a repeated measures analysis of variance (RM-ANOVA), we tested the hypotheses that (1) coral cover declined over time, (2) declines in coral cover led to increases in other taxa, (3) the covers of coral, macroalgae, and CTB did not differ between no-take reserves and sites open to fishing, and (4) declines in coral cover were less extreme in deeper reef zones. We considered site, rather than transect, as the sampling unit to avoid the problem of spatial autocorrelation among transects within a given site. Proportional-cover data were used in preference to percentages so we could employ the most appropriate transformation for this type of data: the logit transformation (Warton and Hui 2011). The RM-ANOVA carries three assumptions: homoscedasticity, normality, and sphericity (Zar 1999). It is not possible to test for sphericity of the data when the number of repeated measures (years) exceeds the number of replicates (sites), as was the case in our analysis. As a precaution, we used the Huynh–Feldt correction for violations of sphericity to avoid type I errors. The raw data on the cover of hard corals conformed to the assumptions of homoscedasticity (Levene’s test: $P > 0.05$) and normality (Shapiro–Wilk test: $P > 0.05$) for all years. Gorgonian cover conformed to the parametric assumptions after logit transformation. Cover data for macroalgae, CTB, sponges, and zoanthids were still heterogeneous or non-

normal after transformation, so rank transformations were applied to those data. When a parametric test such as ANOVA is applied to ranked data, as we did here, the analysis is equivalent to a nonparametric test, rendering moot the problems associated with violations of the parametric assumptions (Conover and Iman 1981). Patterns over time and between no-take and reference sites in the cover of hard corals, macroalgae, sponges, gorgonians, zoanthids, and CTB, were evaluated in a two-way RM-ANOVA design, with depth (intermediate vs. deeper) and protection (no-take vs. reference) as fixed factors. Because Maitland Reef and the intermediate-depth site at Pelican Shoal were not visited in 2005, that year was excluded from the statistical analyses; however, the remaining data for 2005 were included in the figures. Pairwise differences among years were assessed with Tukey’s HSD a posteriori analysis.

Changes in the absolute and relative cover of the six commonest hard-coral taxa—the *O. annularis* complex, *Montastraea cavernosa*, *Siderastrea* spp., *Agaricia* spp., *Porites astreoides*, and *Millepora* spp.—were evaluated using a two-way RM-ANOVA, with protection and depth as fixed factors. Total coral cover was low throughout our study, and the temporal variability in taxon-specific coral cover was high. We, therefore, examined the total change in the absolute and relative covers of the dominant coral taxa from 1998 to 2011, rather than trying to isolate year-to-year changes. These analyses tested the hypothesis that overall declines in coral cover were associated with declines in the dominant taxa (the *O. annularis* complex) and increases in weedy taxa. The sphericity assumption was not a problem because it is always met when there are only two levels of the repeated measure, which in our case were the years 1998 and 2011; therefore, no correction was applied to the result of the RM-ANOVA for the taxon-specific analyses of coral cover. The raw data for the absolute and relative covers of *M. cavernosa*, *Millepora* spp., the absolute covers of *P. astreoides*, *Agaricia* spp., and *Siderastrea* spp. and the relative cover of the *O. annularis* complex conformed to the assumptions of homoscedasticity (Levene’s test: $P > 0.05$) and normality (Shapiro–Wilk test: $P > 0.05$). The absolute cover of the *O. annularis* complex and the relative cover of *Millepora* spp. were transformed using a logit transformation. The relative cover data of *Siderastrea* spp. and *Agaricia* spp. were transformed using a rank transformation.

We used regression analysis to test the hypothesis that differences in macroalgal cover were related to changes in coral cover on Florida’s reefs. One assumption of regression analysis is that the data are independent and not temporally autocorrelated. To overcome the problem of autocorrelation, we used the difference in cover between sequential time steps for the regression. We tested the

statistical hypotheses that (1) changes in coral and macroalgal cover were negatively related within the same time step, which tests the hypothesis that macroalgae were actively overgrowing corals (cf. Lirman 2001) and (2) a change in macroalgal cover during 1 year negatively influenced change in coral cover the following year (i.e., there was a 1-year time lag). We were generally able to detect newly recruited corals 1 year after recruitment (~5 mm in diameter) with our video survey methods (Toth, personal observation). The latter analysis, therefore, tested the hypothesis that macroalgal cover impacted coral recruitment. The residuals of the regressions were both non-normal (Shapiro–Wilk test: $W_{107} = 0.889$, $P < 0.001$ and $W_{120} = 0.077$, $P < 0.001$), so we used Kendall's rank regression. All univariate statistical analyses were conducted using IBM SPSS® version 20.

Results

Temporal changes in hard-coral cover

The initial cover of hard corals at our sites ranged from 1 to 13 %, with a mean cover of 5.1 % (± 1.1 SE). Coral cover declined significantly through time ($F_{2,19} = 7.972$, $P = 0.002$; Fig. 2; Hypothesis 1) and reached its lowest value in 2008. Overall, coral cover declined in relative terms by more than half after 1998. Although coral cover showed some recovery during the last two surveys (2010 and 2011), most notably at the no-take sites (Fig. 2), by 2011 average cover of hard corals at our sites was only 2.4 % (± 1.1 SE; ESM Table 1).

The decline in overall hard-coral cover was driven by a significant reduction in the absolute and relative covers of the *O. annularis* complex between 1998 and 2011 (Fig. 3; $F_{1,8} = 9.770$, $P = 0.014$ and $F_{1,8} = 12.647$, $P = 0.007$; ESM Tables 4–7; Hypothesis 1). The *O. annularis* complex was the dominant space occupant in 1998, averaging 2.2 % (± 0.9 SE) of benthic cover and 30.6 % (± 7.4 SE) of hard-coral cover at our sites. By 2011, the average absolute cover of the *O. annularis* complex was reduced to 0.2 % (± 0.1 SE) and the average relative percent cover of this taxon was only 6.0 % (± 1.6 SE). Most of the decline in cover of the *O. annularis* complex can be attributed to the partial mortality of large colonies, which in some cases were initially several meters in longest horizontal dimension.

Although we did not detect significant temporal changes in absolute cover of the other five dominant coral species, the ~92 % reduction in cover of the *O. annularis* complex led to increases in the relative abundance of some other taxa. There were significant increases in the relative covers of both *Siderastrea* spp. and *Millepora* spp. between

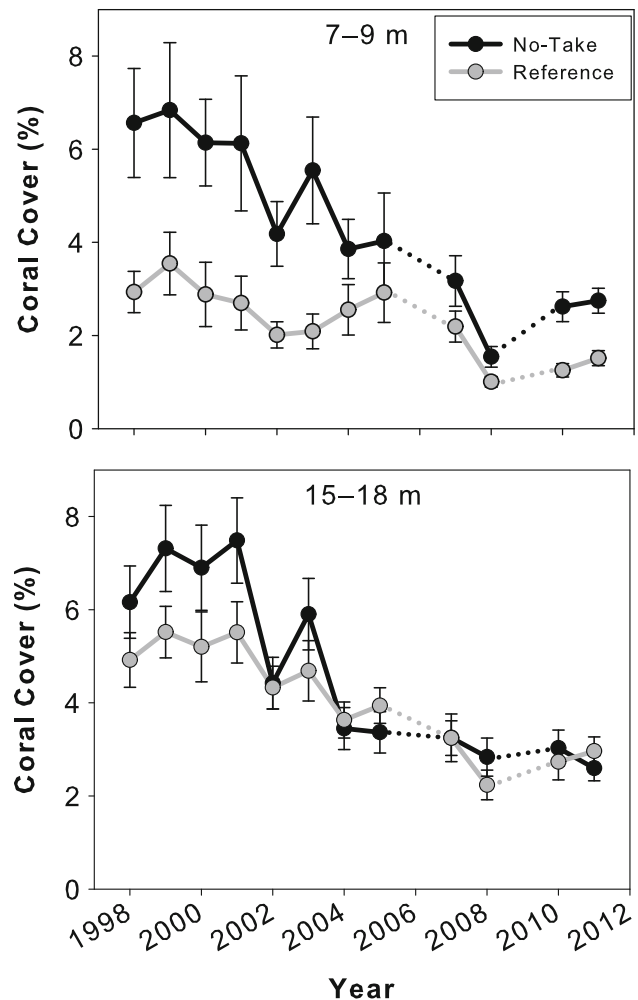


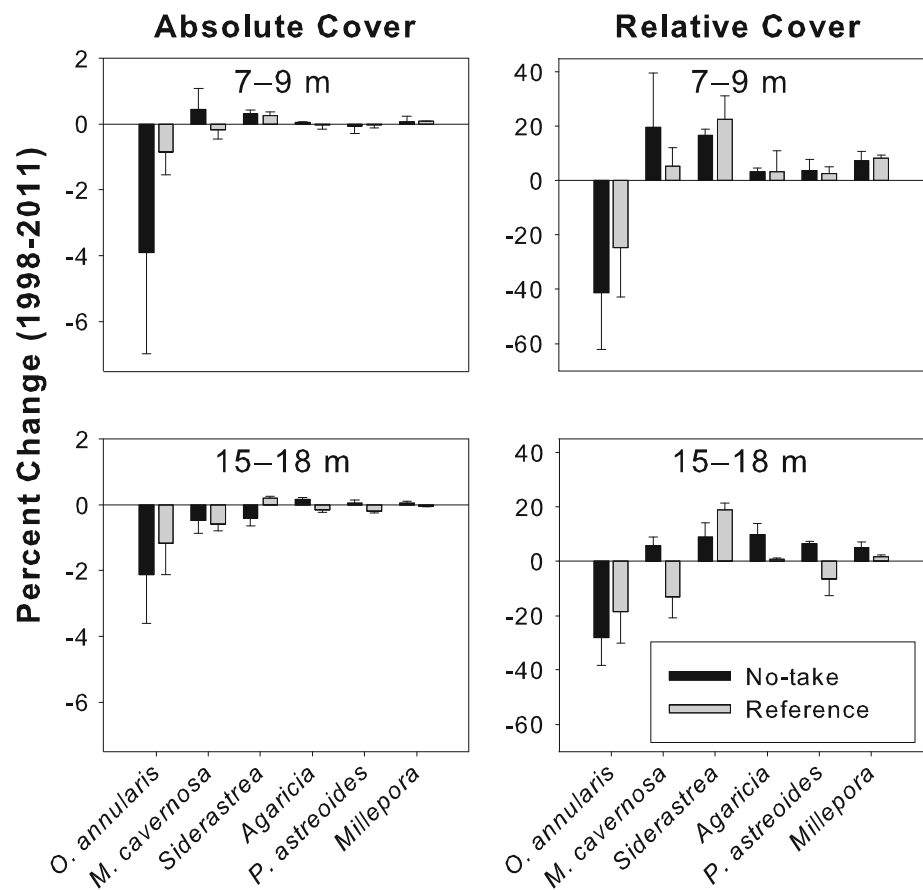
Fig. 2 Trajectories of hard-coral cover mean (\pm SE) at no-take and reference sites in intermediate and deeper depths. Dotted lines span years of missing data in this and subsequent figures

1998 and 2011 (Fig. 3; $F_{1,8} = 46.582$, $P < 0.001$ and $F_{1,8} = 26.207$, $P = 0.001$; ESM Tables 8–15; Hypothesis 1). Temporal differences in the absolute and relative covers of *Agaricia* spp., *P. astreoides*, and *M. cavernosa* were all nonsignificant (ESM Tables 16–27).

Impacts of no-take reserves on hard-coral cover

The largest absolute reduction in both total coral cover and cover of the *O. annularis* complex over the study period was at the no-take sites, which had higher initial coral cover than the reference sites (Fig. 2); however, there was no difference in total coral cover or cover of the *O. annularis* complex between the no-take and reference sites (ESM Tables 2–7; Hypothesis 2). There were significant interactions between year and protection for the absolute and relative covers of *Agaricia* spp. ($F_{1,8} = 5.650$, $P = 0.045$ and $F_{1,8} = 10.947$, $P = 0.011$). This effect was likely a result

Fig. 3 Changes in the mean (\pm SE) absolute and relative cover of the six dominant coral taxa between 1998 and 2011 at no-take and reference sites in intermediate and deeper depths



of larger temporal change in the relative cover of *Agaricia* spp. in the no-take reserves compared with the reference sites (Hypothesis 2). The absolute and relative cover of *Siderastrea* spp., *Millepora* spp., *P. astreoides*, and *M. cavernosa* did not differ significantly between reserves and reference sites (ESM Tables 8–15 and 20–27).

Differences in hard-coral cover between depths

There was no difference in total coral cover between the intermediate (7–9 m) and deeper (15–18 m) sites (Fig. 2; ESM Table 3; Hypothesis 4); however, the relative cover of *Siderastrea* spp. was significantly higher at the deeper depths than at the intermediate depths ($F_{1,8} = 8.332$, $P = 0.020$), and there was a significant interaction between year and depth for the absolute cover of *Siderastrea* spp. ($F_{1,8} = 7.345$, $P = 0.027$; Hypothesis 4). There were no significant differences in either absolute or relative cover of the other dominant taxa between depths (ESM Tables 4–7 and 12–27).

Algal dynamics

Taken together, macroalgae and CTB accounted for the largest percentage—89.4 % (± 0.4 SE)—of the benthic assemblages across years, depths, and sites, with CTB

generally dominating. *Dictyota* spp. dominated the macroalgal assemblage, accounting for 31.2 % (± 1.8 SE) of benthic cover across years, depths, and sites. *Halimeda* spp. were also common, constituting 2.2 % (± 1.3 SE) of total benthic cover. Other taxa, especially *Styopodium zonale* and *Lobophora variegata*, were abundant at some sites during some years, but were not generally a significant proportion of the benthic assemblage (ESM Fig. 5).

It is clear from Fig. 4 that macroalgae and CTB fluctuated in a reciprocal manner between 1998 and 2011 (ESM Table 1), and temporal variations in macroalgae and CTB were highly significant ($F_{10,80} = 15.393$, $P < 0.001$ and $F_{10,80} = 13.172$, $P < 0.001$, respectively). Trends in macroalgal and CTB cover were similar between depths and between no-take and reference sites (ESM Tables 28–31). Furthermore, the relationships between changes in macroalgal and coral cover were nonsignificant (Kendall's rank regression: $\tau = -0.096$, $P = 0.061$; with a 1-year lag in coral cover: $\tau = 0.031$, $P = 0.321$). Taken together, these results reflect the negligible impact of protection on the algal dynamics of reefs at our study sites.

Other benthos

The cover of gorgonians varied significantly over time ($F_{7,59} = 6.570$, $P < 0.001$), averaging 2.3 % (± 0.2 SE) of

Fig. 4 Temporal changes in mean (\pm SE) cover of macroalgae and CTB (crustose coralline algae, fine-turf algae, and bare substrate) at no-take and reference sites in intermediate and deeper depths

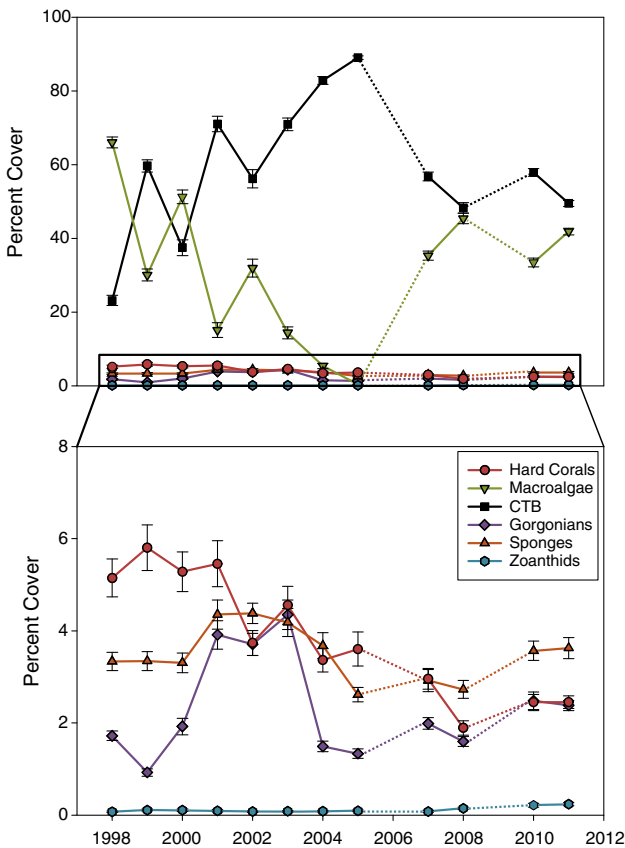
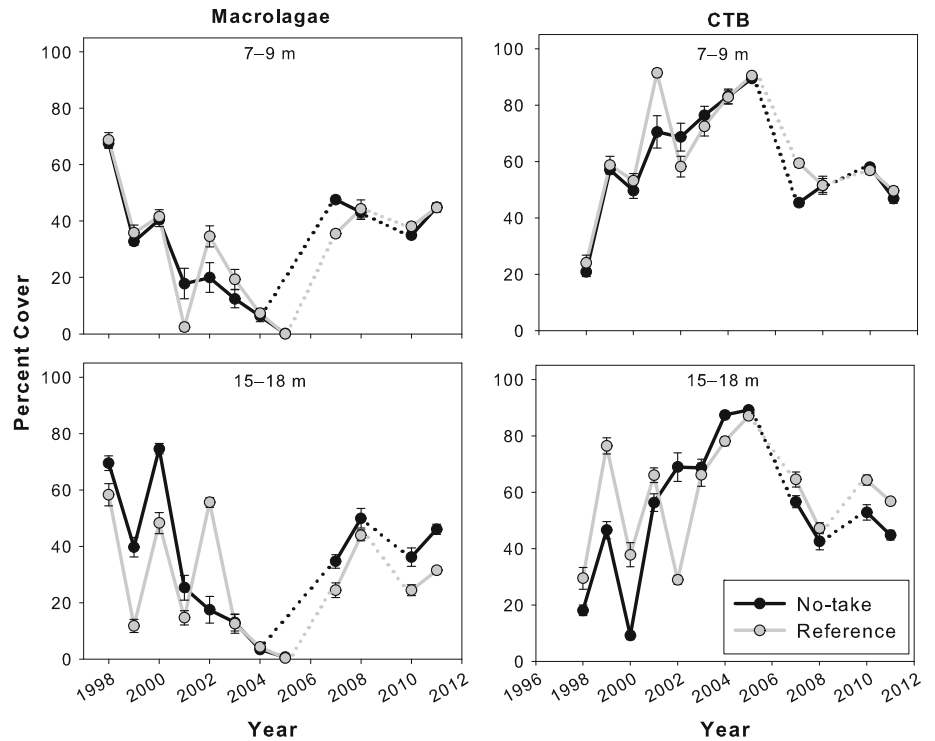


Fig. 5 Temporal trends in the cover (mean \pm SE) of hard corals, macroalgae, CTB, gorgonians, sponges, and zoanthids, pooled across sites and depths

the benthic cover across depths, years, and sites (Fig. 5). Gorgonian cover was highest in 2001–2003, but was low for the remainder of the study (ESM Table 1; ESM Fig. 2). There was no difference in the cover of gorgonians between depths or between no-take reserves and reference sites (ESM Tables 32, 33); however, there was a significant interaction between year and depth ($F_{10,79} = 5.902$, $P < 0.001$).

The cover of sponges, which on average accounted for 3.5 % (± 0.2 SE) of benthic cover, varied significantly through time ($F_{10,79} = 7.216$, $P < 0.001$; Fig. 5; ESM Table 1) and was higher at deeper depths ($F_{1,8} = 51.804$, $P < 0.001$; ESM Fig. 3). There was, however, no significant difference in sponge cover between no-take and reference sites (ESM Tables 34, 35). Other than a significant interaction between year and depth ($F_{10,79} = 4.269$, $P < 0.001$), all other interactions between year, depth, and protection were nonsignificant (ESM Tables 34, 35).

The cover of zoanthids was low throughout our study, typically accounting for $<0.2\%$ of the total benthic assemblage (mean $0.1 \pm <0.1$ SE; Fig. 5; ESM Table 1). Zoanthid cover varied significantly through time ($F_{10,80} = 2.299$, $P = 0.020$; ESM Fig. 4) and was significantly higher in 2010 and 2011 compared with all other years (Tukey’s HSD: $P < 0.05$). Zoanthid cover was also significantly higher at intermediate depths ($F_{1,8} = 28.899$, $P = 0.001$). Differences among depths were especially pronounced in later study years, which may explain the

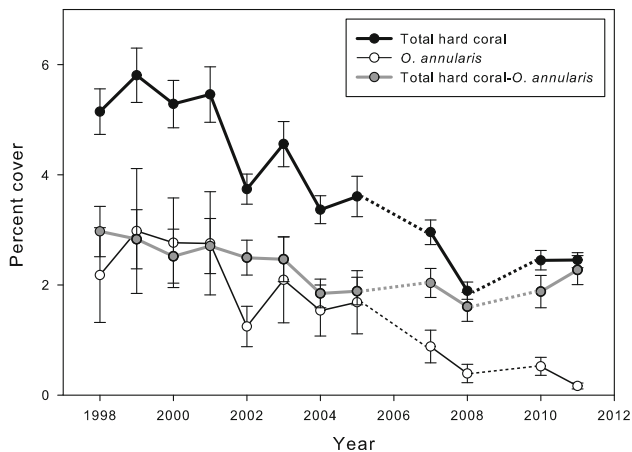


Fig. 6 Temporal changes in the cover (\pm SE) of all hard corals, the *O. annularis* complex, and hard corals minus the *O. annularis* complex. Data are pooled across sites and depths

significant interactions between year and depth ($F_{10,80} = 2.861$, $P = 0.004$) and year and protection ($F_{10,80} = 2.580$, $P = 0.009$; ESM Fig. 4). Zoanthid cover did not differ between no-take and reference sites, and all other interaction effects were nonsignificant (ESM Tables 36, 37).

Discussion

Changes in the benthic assemblages of Florida's reefs

Coral cover at our study sites declined over the 14-year period from 1998 to 2011. Disease outbreaks, hurricane damage, and thermal stress were likely the most significant causes of coral loss (Brandt and McManus 2009; Lirman et al. 2011; Ruzicka et al. 2013); however, local-scale factors, including hydrography, nutrient levels, and predation, have doubtless interacted with regional- to global-scale events (Precht and Miller 2007; Wagner et al. 2010). The loss of cover was similar at both depths, falsifying our hypothesis that depth provided a refuge from disturbance (Hypothesis 4).

The decline was driven almost entirely by reduction in the cover of the once-dominant *O. annularis* complex (Fig. 6; see Ruzicka et al. 2013). Other investigators observed similar patterns of coral decline driven by the loss of the *O. annularis* complex in Curaçao (Bruckner and Bruckner 2006), the U.S. Virgin Islands (Edmunds and Elahi 2007), and Puerto Rico (Bruckner and Hill 2009). In contrast, abundance of the *O. annularis* complex has remained relatively stable on Florida's patch reefs (Ruzicka et al. 2013; but see Lirman et al. 2011). Subtracting the

O. annularis complex from total coral cover in our data, we found essentially no change in the absolute cover of the remaining corals (Fig. 6). The persistence of five sub-dominant taxa—*M. cavernosa*, *Siderastrea* spp., *Agaricia* spp., *P. astreoides*, and *Millepora* spp.—through multiple perturbations was likely due in part to their relatively high recruitment rates and eurytopic proclivities (Chiappone and Sullivan 1996; Moulding 2005). At our sites, the complete or, more often, partial mortality of colonies of the *O. annularis* complex increased the relative abundance of the 'weedy' coral taxa *Siderastrea* spp. and *Millepora* spp. (Knowlton 2001), which supports Hypothesis 1.

Concurrent with the decline in coral cover after 1998, Ruzicka et al. (2013) detected a trend of increasing cover of gorgonians in the FKNMS. That was not a consistent pattern in our data. There are two likely reasons for the difference: (1) we measured the cover of gorgonian hold-fasts only, whereas Ruzicka et al. measured canopy cover; and (2) Ruzicka et al. primarily observed increases in shallow habitats (1–6 m depth), whereas our surveys were conducted in deeper habitats. Our data, like those of Ruzicka et al. (2013), do not support the suggestion that sponges are becoming more abundant on Floridian reefs (McMurray et al. 2010; Pawlik 2011).

Impact of no-take reserves

As predicted by Hypothesis 2, there were no significant differences in coral cover between our sites in no-take reserves and reference areas. Declines in coral cover were actually greater (although not significantly so) in the no-take reserves, the opposite of expectation if the reserves had conferred resistance or resilience to coral assemblages. It is unlikely, however, that protective status per se was responsible for the difference. Instead, because coral cover was initially higher at the no-take sites (Miller et al. 2000), the absolute decline at these sites was more substantial.

The declines in coral cover at all our sites, irrespective of protective status, add to a growing body of work showing that, across multiple reef-habitat types, increasing the abundance of herbivorous fishes does not guarantee cascading impacts on corals. We did not directly assess fish abundance in this study, and the lack of a reserve effect could be a result of high levels of herbivory throughout the FKNMS; however, if the greater abundance of herbivorous fishes in Florida's no-take reserves had resulted in significantly higher herbivory, as is commonly assumed, then macroalgal cover should have been lower and the cover of CTB should have been higher within the reserves. In reality, as predicted by Hypothesis 3, we found no significant difference in the cover of CTB and macroalgae between no-take reserves and reference sites at both depths.

Apparently, one or more steps of the predicted cascade are not occurring within Florida's no-take reserves.

The macroalgal assemblages were dominated by *Dictyota* spp., a taxon that has been shown to limit coral recruitment (Kuffner et al. 2006), reduce the growth of juvenile corals (Lirman 2001; Box and Mumby 2007), and cause partial colony mortality due to shading (Lirman 2001). Macroalgal cover on Florida's reefs varies among habitats, seasons, and years (Lirman and Biber 2000; Ruzicka et al. 2013). In general, however, macroalgal cover is highest in the summer months (Lirman and Biber 2000) when we conducted our surveys, which coincides with the spawning season of most corals in this region (van Woesik 2010). Coral recruitment and post-settlement survival are the processes most sensitive to competition with macroalgae (Kuffner et al. 2006; Box and Mumby 2007). If, therefore, macroalgae were a central driver of changes coral cover in the Florida Keys, the effects would have been most significant during this critical period. The reciprocal patterns of cover of macroalgae and CTB and the lack of correlation between coral and macroalgal cover suggest that coral and macroalgal cover are presently decoupled on Florida's reefs (Fig. 5), as Ruzicka et al. (2013) also observed. The trajectories of corals and algae are also decoupled on reefs elsewhere (Aronson et al. 2012; Edmunds 2013), suggesting that the primary drivers of change in benthic assemblages now operate at regional to global scales (Toth et al. 2012).

The no-take reserves in our study did not benefit corals or confer resilience to disturbance at the spatial and temporal scales of our study. On Florida's reefs, the elevated abundance of herbivorous fishes at no-take sites do not necessarily translate to significant changes in macroalgal cover (Kramer and Heck 2007). Furthermore, macroalgae do not dominate most coral reefs in Florida or elsewhere, and there is no evidence that macroalgae control the abundance of corals at our sites. Our results contribute to a growing body of work that suggesting that cascading benefits of no-take reserves to corals may be the exception, rather than the rule (Coelho and Manfrino 2007; Kramer and Heck 2007; Selig and Bruno 2010; Huntington et al. 2011; Selig et al. 2012; Carassou et al. 2013).

Prospects for recovery

When the no-take reserves were established within the FKNMS in 1997, Florida's reefs had already lost almost all their acroporid corals to white-band disease in the 1980s (Aronson and Precht 2001; Precht et al. 2004). The remaining corals were about to experience a series of disturbances that included the most extreme thermal-stress event on record: the 1997–98 El Niño. As a result, our sites were highly degraded at the outset of our study, and

additional perturbations over the 14-year period degraded the reefs even further by reducing the cover of the *O. annularis* complex. The *O. annularis* complex and *Acropora* spp. were the primary framework builders of Florida's reefs, and their loss will likely compromise future reef accretion (Aronson and Precht 2001; Precht and Miller 2007).

By the end of our study, coral cover averaged only 2.4 % at our sites. The relative cover of hard corals, across all study sites and depths, dropped by more than 50 % during the study period. Although that figure sounds dramatic, it is misleading because coral cover was initially very low. During our 14-year study, the absolute cover of hard corals dropped by an average of only about 3 %. In functional terms, coral cover was low in 1998 and somewhat lower in 2011.

Recruitment levels of the *O. annularis* complex were very low during the study period. In 512 permanent, 95 × 65 cm quadrats at the study sites, one of us (S.R.S., unpublished data) recorded only 15 recruits of the *O. annularis* complex from 1998 to 2008. Recruitment of the *O. annularis* complex has been rare throughout the Caribbean even when adult colonies have been abundant (Edmunds and Elahi 2007). It is, therefore, unlikely that the *Orbicella* populations of the Florida Keys will recover within the next few decades in the face of continued perturbation (Edmunds and Elahi 2007; Bruckner 2012).

Our study tested four hypotheses about the controls on benthic assemblages in the FKNMS. As we predicted with Hypothesis 1, coral cover declined significantly over a period of 14 years, primarily as a result of significant reductions in the cover of the *O. annularis* complex. These declines resulted in increases in the relative abundances of *Siderastrea* spp. and *Millepora* spp., but no change in the absolute cover of any of the sub-dominant corals, which suggests these taxa may be particularly resistant or resilient to environmental perturbations. Coral cover declined at all sites irrespective of protective status, as predicted by Hypothesis 2. In fact, although coral cover was significantly higher in no-take reserves at the outset of our study, the coral assemblages were similar at all of our sites by the end. Despite the putatively higher abundance of herbivorous fishes in no-take reserves, the algal dynamics of Florida's reefs were also independent of protective status, as predicted by Hypothesis 3. Finally, we did not observe a difference in coral cover between depths, as predicted by Hypothesis 4, which suggests that the environmental perturbations driving coral declines may not be modulated by depth refugia in the bathymetric range examined.

Coral assemblages in the spur-and-groove habitats that characterize our study sites have converged on the composition of hardground communities, which constitute 98 % of the hard-bottom habitat in the Florida Keys

(Precht and Miller 2007). This convergence is a manifestation of a general trend to biotic homogenization of coral assemblages across habitat and latitude on Florida's reefs (Burman et al. 2012). Protective status did nothing to hamper that transition. Although no-take reserves clearly benefit target species of fishes, the cascading benefits of reserves on the benthic assemblages are not always realized. For many locations, including the Florida Keys, the remedies for the benthic assemblages must be sought elsewhere.

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