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SEAGRASS HABITATS AS NURSERIES FOR REEF—ASSOCIATED FISH: EVIDENCE FROM FISH ASSEMBLAGES IN AND ADJACENT TO A RECENTLY ESTABLISHED NO—TAKE MARINE RESERVE IN DRY TORTUGAS NATIONAL PARK, FLORIDA, USA

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Abstract: Scientists and managers worldwide have increasingly advocated the use of marine protected areas (MPAs) to protect at—risk fish stocks. Most MPAs, however, have been established to protect reefs, while nonreef habitats, such as seagrasses, have received less consideration. In January 2007, an MPA called the Research Natural Area (RNA), was established as a no—take marine reserve in the Dry Tortugas National Park, Florida (DTNP), becoming the first MPA within the park boundaries to offer direct protection to seagrasses and reef habitat. We conducted a study using small—mesh Antillean Z—traps to (1) characterize fish assemblages in seagrass and reef habitats and (2) assess if differences in community structure existed between the RNA and adjacent open—use areas. Over 3 sampling events (Fall 2009, Spring 2010, Fall 2010), 3,163 individuals of 38 species were collected from 129 stations. Fish assemblages differed significantly among sampling events and between habitat types, but no differences were evident between the RNA and open—use areas. Unlike previous sampling efforts that focused on larger—bodied fish in the DTNP, Z—traps targeted small—bodied reef— and seagrass—associated fishes. Juvenile *Haemulon plumierii* and *Epinephelus morio* strongly contributed to community structure and were more abundant in seagrass habitats, which may serve as an important nursery area. Because the RNA was only established 2 years before this study was conducted, it could still be several years before benefits to the juvenile population become evident, but this study establishes the importance of considering seagrass habitats when developing a reef—associated no—take marine reserve.

Key words: Community structure, fish traps, marine protected areas

Introduction

Marine protected areas (MPAs) have been receiving increased attention worldwide as a tool for effectively managing a variety of fishery resources. Numerous studies have demonstrated that exploited stocks generally exhibit increased abundance and an expanded size structure following the establishment of MPAs (Dugan and Davis 1993, Johnson et al. 1999, Nemeth 2005, Kramer and Heck 2007, Claudet et al. 2011), even though these benefits are not universal (Lipej et al. 2003). Recent MPA planning has targeted areas in which reef fish spawning aggregations occur, but limited field and modeling studies have indicated that this approach may not increase exploitable biomass (Gruss et al. 2014). Overexploited stocks typically receive the greatest benefit from MPAs, but other stocks can also benefit (Côté et al. 2001, Apostolaki et al. 2002). The density of commercially important fishes has also been found to increase with the size of no—take MPAs, so small MPAs may not be as effective for some species (Claudet et al. 2008). Although MPA effectiveness is likely influenced by several interrelated factors (Lester et al. 2009, Claudet et al. 2010), recent planning has involved creating networks of MPA nodes over large areas (Sundblad et al. 2011, Saarman et al. 2012) so recruitment in one node can sustain local populations while supplying larvae to other nodes and nonreserve areas that experience poor recruitment (Berumen et al. 2012, Sponaugle et al. 2012).

Many MPAs also protect habitats and fisheries from destructive activities like bottom trawling, dynamite fishing, and dredging (Tittensor et al. 2007, Lester and Halpern 2008), so their establishment fosters an ecosystem approach to fisheries management that serves to stabilize at—risk stocks and helps preserve biodiversity and habitat. Furthermore, MPAs may serve as insurance against the uncertainty and unpredictability inherent in traditional fishery management (Ballantine 1997, Lauck et al. 1998). For developing nations that cannot afford to collect the data required for traditional stock assessments, MPAs are especially attractive if enforcement is possible. Challenges in the governance of MPAs can arise if management does not take into account the expectation of stakeholders and encourage their involvement and if consistent site—specific monitoring and enforcement does not take place (Christie and White 2007, Álvarez—Fernández et al. 2017).

Many MPAs established in recent decades have focused on protecting coral reef habitats, and include a disproportionately small area of seagrass habitats (Geoghegan et al. 2001, Prado et al. 2008, Nagelkerken et al. 2012) even though seagrass loss worldwide is comparable to that in mangrove and reef habitats (Waycott et al. 2009). Seagrass habitats provide important ecosystem services, such as nutrient cycling, serve as refuge and feeding habitat for various species of fish, birds, invertebrates, and marine mammals, and often function as nursery habitat for juvenile reef fishes (Nagelkerken and van

der Velde 2004, Bartels and Ferguson 2006, Verweij et al. 2006, Faunce and Serafy 2007, Waycott et al. 2009). Interactions among seagrass, mangrove, and coral reef habitats in providing ontogenetic connectivity for many reef fish species is well established (Heck and Weinstein 1989, Nagelkerken et al. 2000a, Cocheret de la Morinière et al. 2002, Jones et al. 2010). Proximity to associated nursery habitat (i.e., seagrasses or mangroves) is often more important than protection from fishing in determining areas with enhanced reef fish populations (Nagelkerken et al. 2012), and the size of seagrass meadow influences the effectiveness of protected areas for various herbivores (Prado et al. 2008). Because MPAs are often created based on opportunity rather than ecology, ecological representation and connectivity between habitats should be periodically assessed through systematic sampling (Sundblad et al. 2011, Saarman et al. 2012). The importance of seagrasses and other nursery habitats as a component of MPAs, therefore, should be considered and investigated as a benchmark for success.

The ecosystems of Dry Tortugas National Park (DTNP) are unique in the variety and complexity of available habitat, including extensive seagrass beds and a diverse range of coral reef habitats (Franklin et al. 2003, Ault et al. 2006). Commercial fishing, recreational spearfishing, and lobstering have been restricted since the 1960s, but recreational hook—line angling is still allowed in the eastern portion (Ault et al. 2013). The remoteness of the DTNP (>110 km west of Key West, FL) may alleviate some of the reduction in the quality and quantity of benthic habitat under anthropogenic stressors (e.g., water quality, boating, anchoring, diving) seen in the greater Florida Keys region (Palandro et al. 2008). However, many reef fishes in DTNP and the greater Florida Keys region are overfished (Ault et al. 1998, 2002, 2005). To mitigate the effects of fishing and habitat loss, a MPA (119.14 km^2) called the Research Natural Area (RNA) was established in January 2007 as a no—take marine reserve where fishing and other possibly destructive activities are restricted or were eliminated (Ziegler and Hunt 2012). Together with 2 other no—take marine reserves established in 2001, the RNA brings the total protected area in the DTNP to 672.35 km^2 (Rogers et al. 2007). While all 3 areas protect a large quantity of coral reef habitat, the RNA was the first protected area in the DTNP to directly protect seagrass habitat. Exploited fishes generally respond to the establishment of an MPA through increasing abundance and expanding size structure (Russ and Alcala 1996, Roberts et al. 2001, Bohnsack 2002), but for unexploited species the effects of MPAs are less predictable (Claudet et al. 2010, Ault et al. 2013). Numerous resident and transient fishes use seagrasses as habitat at some point in their life history and are expected to respond positively when the quality and quantity of seagrass habitat improves in an MPA (Lindholm et al. 2001, Rodwell et al. 2003). These ecosystem—level changes highlight the importance of considering exploited and unexploited species and habitat types when assessing the effectiveness of no—take marine reserves, especially in terms of ecosystem function. In association with the establishment of the RNA in 2007, the National Park Service (NPS) and the Florida Fish and Wildlife Conservation Commission (FWC) developed a research and monitoring program using several methods (i.e., visual surveys, creel surveys, acoustic telemetry, fish traps, and hook and line) to evaluate the effectiveness of the RNA in protecting reef fishes and associated habitats (SFNRC and FWC 2007, Ziegler and Hunt 2012). In this study, small Antillean Z—traps (Sheaves 1992, 1995) were deployed over seagrass and reef habitats to target and assess small—bodied fish assemblages within DTNP. Accordingly, fish community structure in seagrass and reef habitats was compared between the DTNP RNA and adjacent open—use areas and provides baseline data for future analyses.

Materials and Methods

Study Area

A stratified—random sampling survey was conducted in fall (September) 2009, spring (May) 2010, and fall (September) 2010 and was restricted to the southern half of DTNP (south of 24°40.5′ N; Figure 1) to maximize comparability between our results and other studies within DTNP (Ziegler and Hunt 2012). Sampling stations over seagrass and reef habitat were randomly selected and equally partitioned between 2 spatial strata, the DTNP RNA and adjacent open—use areas (Figure 1).

Field Methods

Antillean Z—traps (Sheaves 1992, 1995) were used to collect fishes from seagrass and reef habitats and were constructed of 12.8 mm coated—wire mesh and measured 0.6 × 0.7 × 1.1 m (H × W × L) with a throat opening of 200 × 55 mm (H × W). Paired traps spaced 25 m apart and baited with cut Atlantic mackerel (*Scomber scombrus*) were deployed at each station and fished for at least 90 min. Sampling occurred during daytime hours only, beginning about 1h after sunrise and ending 1h before sunset. At each sampling station, habitat type (reef or seagrass) was verified by a surface snorkel dive or a tethered digital drop camera. Water depth (m) was recorded, and water quality parameters including temperature (°C), salinity, and dissolved oxygen (mg/l) were profiled (measurements taken 0.2 m from the surface, at mid—depth, and at 0.2 m from the bottom) with a YSI water—quality datasonde.

Once the gear had been deployed and fished for at least 90 min, each Z—trap was brought to the surface, where its contents were emptied into an aerated live well. Specimens were identified to the lowest practical taxonomic level and up to 40 individuals per species were measured to the nearest mm standard length (SL). Most specimens were then released, but when satisfactory field identification was not possible, they were retained for identification in the laboratory.

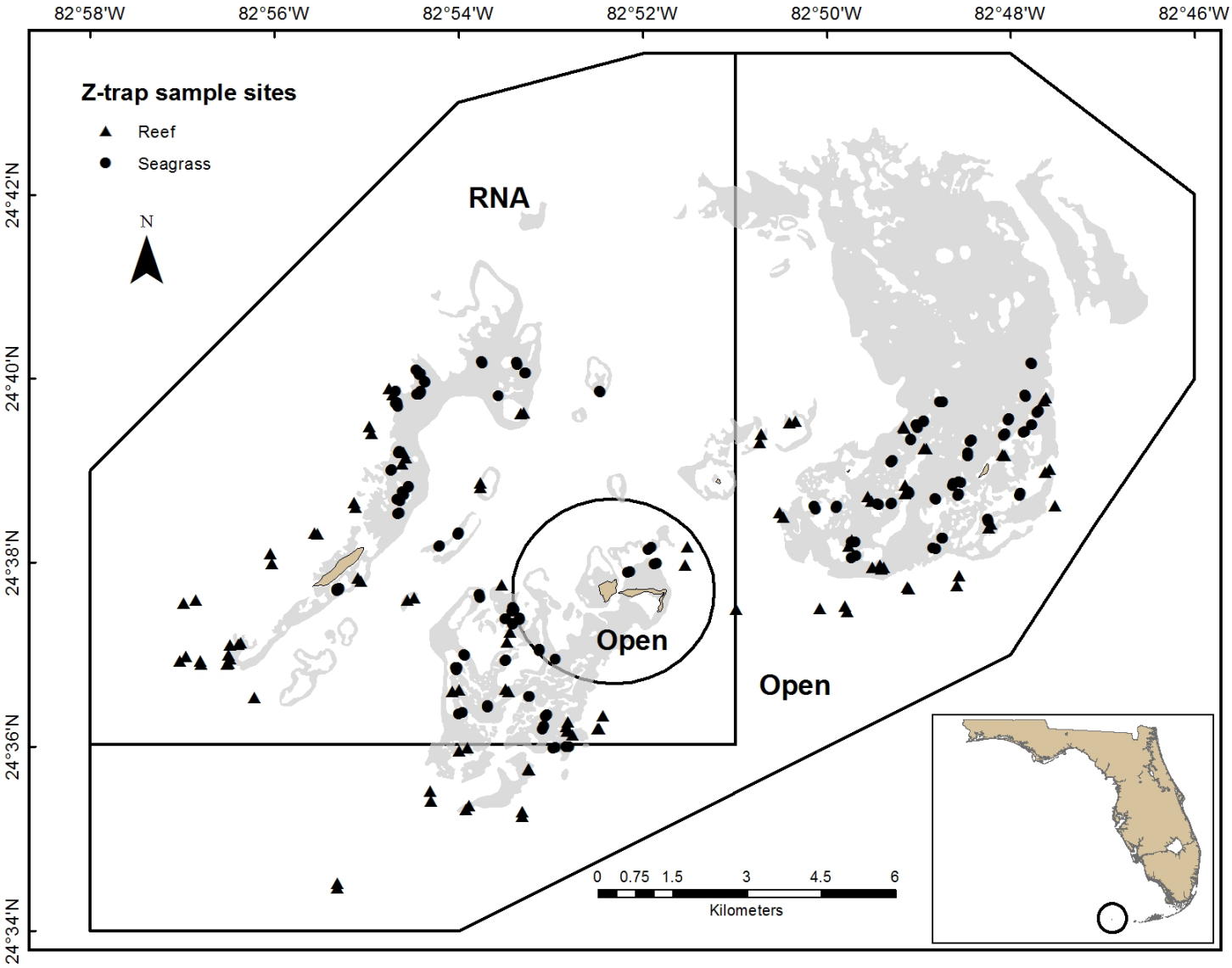

FIGURE 1. *Map of Z-trap sampling stations in the Dry Tortugas National Park (DTNP), fall 2009–fall 2010. Boundaries designate DTNP open-use areas surrounding Garden Key (i.e., central island) and to the east and south, while the Research Natural Area (RNA) is situated to the north and west. Shading indicates extent of seagrass per a 2004 aerial survey (Yarbro 2013). Symbols indicate habitat type (triangles represent reef, circles represent seagrass).*

Analytical Methods

Seagrass habitats were sampled at water depths of 1.7–10.1 m, whereas reef habitats were sampled at water depths from 2.0–24.0 m. To facilitate comparisons between habitat types and to account for the depths where seagrass beds are common, all reef sites sampled at depths of >11 m were excluded from analyses. Thus, the number of samples analyzed differed among the 3 sampling seasons.

Statistical analyses were conducted to compare fish assemblages among sampling events by habitat (seagrass vs. reef) within the RNA and open—use areas. For abundant species with a wide size range in the dataset (i.e., *Epinephelus morio* (Red Grouper), *Haemulon plumierii* (White Grunt), and *Ocyurus chrysurus* (Yellowtail Snapper)), we defined pseudospecies based on appropriate size classes by either length frequencies or changes in diet from the literature (Nagelkerken et al. 2000b, Verweij et al. 2008) to separate life history stages and examine potential ontogenetic differences in assemblage structure. We summarized overall catch—per—unit—effort (CPUE; individuals per soak—hour) and the total number of species and individuals collected during each sampling event within each habitat and area.

Differences in fish assemblage structure among sampling events and between habitats in the RNA and adjacent open—use areas were explored using PRIMER software with the PERMANOVA add on (Clarke and Warwick 2001, Clarke and Gorley 2006, Anderson et al. 2008). Abundance data were calculated as the sum of individuals collected at a station across the paired trap deployments to more accurately represent the community and were square—root transformed to reduce the influence of numerically—dominant species (Clarke and Warwick 2001, Clarke and Gorley 2006). A Bray—Curtis

dissimilarity resemblance matrix (Bray and Curtis 1957) was calculated on the transformed abundance data and a distance—based linear model (DISTLM, Anderson et al. 2008) was used to determine the multivariate relationship between the species resemblance matrix and a combination of associated continuous variables (water depth, temperature, salinity, dissolved oxygen, and soak time); significant variables were added into the subsequent PERMANOVA analyses. To visualize the patterns in assemblage structure, an ordination was constructed using non—metric multidimensional scaling (nMDS) calculated on the area by habitat by sampling event centroids. Contributions to similarity patterns of the fish assemblages were represented by correlation vectors (> 0.2) on the nMDS plot. Groupings between samples were also determined based on a 60% similarity level calculated using hierarchical clustering (CLUSTER, Clarke and Warwick 2001). The statistical significance and relative importance of area (a fixed factor with 2 levels: RNA and Open), habitat (a fixed factor with 2 levels: seagrass and reef), and sampling event (a fixed factor with 3 levels: Fall 2009, Spring 2010, and Fall 2010) were investigated using permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) on the full set of data at the replicate level. Analyses included all interaction terms, significant covariates from the DISTLM analyses, and were conducted using type III sums of squares; p—values were obtained using 9,999 permutations under a reduced model. Abundances (based on square root transformed abundance data) were then averaged to identify taxa contributing to observed area, habitat, and sampling event—associated differences in assemblage structure. Similarity percentages (SIMPER) analyses were conducted on significant factors to determine the species that contributed up to 90% of community structure differences.

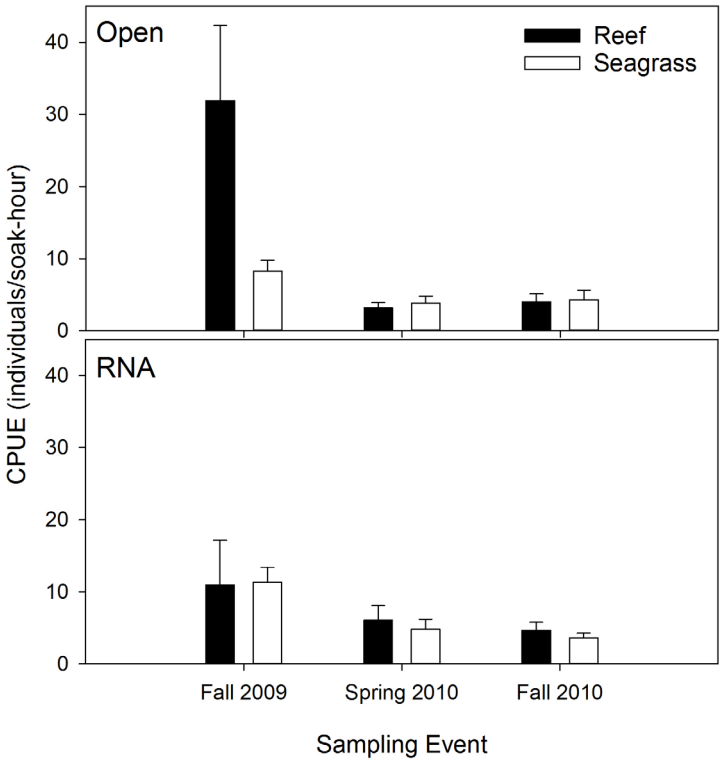

FIGURE 2. *Overall mean catch-per-unit-effort (CPUE; individuals/soak-hour) for fish collected with Z-traps in the Dry Tortugas National Park, fall 2009–fall 2010 averaged over sampling event, area (open vs. Research Natural Area (RNA)), and habitat (reef vs. seagrass). Error bars indicate standard error.*

Size composition was summarized with length—frequency histograms for 4 commonly collected or economically important species (*E. morio*, *H. plumierii*, *Halichoeres bivittatus* (Slippery Dick), and *O. chrysurus*). Length distributions were compared between habitats by area using Kolmogorov—Smirnov (KSa) tests (SAS Institute, Inc. 2006).

Results

Sampling was conducted during fall 2009 (37 stations sampled), spring 2010 (41 stations sampled), and fall 2010 (51 stations sampled), and spatial distribution of sampling effort was consistent across all 3 sampling seasons (Figure 1, Table 1). The mean soak time per trap set was above the target soak time, and the standard error was minimal (120.7 ± 2.9 minutes). A total of 3,163 individuals of 38 species were collected from 129 paired Z—trap stations, over half of which were collected in fall 2009 (n = 1,710; Figure 2, Table 1). Eleven species were found only in reef habitats, and 13 species were found only in seagrass habitats, whereas 14 species were found exclusively in the RNA, and 6 species were found only in the open—use area (Table 1). *Ocyurus chrysurus* (combined size classes) was the most numerically abundant species collected (n = 1,298), followed by *H. bivittatus* (n = 751), and *Haemulon aurolineatum* (Tomtate; n = 439); the latter species was only collected in reef habitats (Table 1). The mean size of fish collected with Z—traps was relatively small, and varied slightly between areas and habitats (Open, reef: 91.6 mm SL; Open, seagrass: 106.8 mm SL; RNA, reef: 127.1 mm SL; RNA, seagrass: 117.5 mm SL), however, these values are highly influenced by the numerically abundant species mentioned above. Sizes of fishes collected ranged from 18 mm SL (*Chaetodon ocellatus*, Spotfin Butterflyfish) to 652 mm SL (*Sphyraena barracuda*, Great Barracuda).

The DISTLM analyses determined the multivariate relationship between fish assemblages and water depth was the most significant (Pseudo—F = 5.3542, p = 0.0001, AIC 1014.8) and explained 4.07% of the variability in the resemblance matrix. Water depth was therefore incorporated into the PERMANOVA analysis described below.

Nekton community structure differed between habitats and sampling events but did not differ between the RNA and open—use areas (Table 2, Figure 3). Results from PERMANOVA analyses identified a significant 2—way interaction between area and habitat, but the 3—way interaction with sampling event was not significant and was pooled

TABLE 1. *Summary of fish collected with Z-traps by sampling event, area, and habitat in the Dry Tortugas National Park, fall 2009–fall 2010. Fish are ordered phylogenetically by family (using Nelson et al. 2016) and then alphabetically by species. n = number of stations.*

	Fall 2009				Spring 2010				Fall 2010				Totals
	Reef		Seagrass		Reef		Seagrass		Reef		Seagrass		
Family Species	**RNA n=4**	**Open n=7**	**RNA n=13**	**Open n=13**	**RNA n=9**	**Open n=10**	**RNA n=12**	**Open n=10**	**RNA n=14**	**Open n=11**	**RNA n=12**	**Open n=14**	**n=129**
Muraenidae													
Gymnothorax moringa	0	0	0	0	0	2	0	0	0	0	0	0	2
Pomacentridae													
Stegastes adustus	0	5	0	0	0	0	0	0	0	0	0	0	5
Stegastes leucostictus	0	1	3	3	0	4	0	1	8	4	6	0	30
Stegastes partitus	0	0	0	0	0	0	0	0	0	1	1	0	2
Stegastes planifrons	1	0	0	0	0	0	0	0	0	0	0	0	1
Stegastes sp.	0	0	0	0	0	0	0	0	0	0	1	0	1
Stegastes variabilis	10	15	1	0	7	16	3	0	12	10	5	12	91
Sphyraenidae													
Sphyraena barracuda	0	0	0	0	0	0	0	1	0	0	0	0	1
Aulostomidae													
Aulostomus maculatus	0	0	0	0	0	1	0	0	0	0	0	0	1
Labridae													
Halichoeres bivittatus	2	169	106	159	14	15	67	66	47	14	64	28	751
Halichoeres poeyi	0	0	1	2	0	0	0	0	0	0	2	0	5
Thalassoma bifasciatum	0	2	0	1	0	2	0	0	2	0	0	0	7
Scaridae													
Cryptotomus roseus	0	0	2	0	0	0	0	0	0	0	0	0	2
Scarus iseri	0	6	0	0	0	0	0	0	0	0	0	2	8
Sparisoma atomarium	0	0	0	0	0	0	0	0	0	0	0	1	1
Sparisoma aurofrenatum	0	1	0	0	0	0	0	0	0	0	0	0	1
Sparisoma radians	0	0	31	6	0	0	1	0	0	0	3	2	43
Mullidae													
Pseudupeneus maculatus	0	3	0	0	1	0	0	0	0	0	0	5	9
Serranidae													
Cephalopholis cruentata	0	0	4	0	0	0	0	0	0	0	0	0	4
Diplectrum formosum	1	0	0	0	0	0	0	2	0	0	0	0	3
Epinephelus morio (<200 mm SL)	0	0	1	0	0	3	1	0	0	0	3	0	8
Epinephelus morio (≥200 mm SL)	1	1	2	0	4	5	0	2	7	5	1	1	29
Hypoplectrus puella	1	3	0	0	0	1	0	0	1	0	0	0	6
Hypoplectrus unicolor	0	1	0	0	2	2	0	0	0	0	0	1	6
Mycteroperca bonaci	0	0	0	0	0	0	2	0	0	0	2	0	4
Serranus tigrinus	0	0	0	0	0	1	0	0	0	0	0	0	1
Chaetodontidae													
Chaetodon ocellatus	0	0	0	0	0	0	0	0	2	2	4	1	9
Haemulidae													
Haemulon aurolineatum	11	312	0	0	72	0	0	0	8	36	0	0	439
Haemulon chrysargyreum	0	1	0	0	0	0	0	0	0	0	0	0	1
Haemulon flavolineatum	0	2	0	0	0	0	0	0	0	0	0	0	2
Haemulon melanurum	0	4	0	0	0	0	0	0	0	4	0	0	8
Haemulon plumierii (<75 mm SL)	4	71	54	13	2	2	12	13	4	44	16	11	246
Haemulon plumierii (≥75 mm SL)	3	40	12	1	11	18	2	3	9	3	19	0	121
Lutjanidae													
Lutjanus synagris	0	0	0	1	0	0	0	0	0	0	2	0	3
Ocyurus chrysurus (<150 mm SL)	71	174	134	83	44	44	11	5	55	8	14	42	685
Ocyurus chrysurus (≥150 mm SL)	7	10	86	65	92	9	115	17	92	44	37	39	613
Scorpaenidae													
Scorpaena plumieri	0	0	0	0	0	0	0	1	0	0	0	0	1
Acanthuridae													
Acanthurus chirurgus	0	0	0	0	0	0	0	0	0	0	1	0	1
Sparidae													
Calamus nodosus	0	0	3	1	0	0	3	1	1	0	1	0	10
Monacanthidae													
Monacanthus ciliatus	0	0	0	1	0	0	0	0	0	0	0	0	1
Stephanolepis hispidus	0	0	0	1	0	0	0	0	0	0	0	0	1
Totals	**112**	**821**	**440**	**337**	**249**	**125**	**217**	**112**	**248**	**175**	**182**	**145**	**3,163**

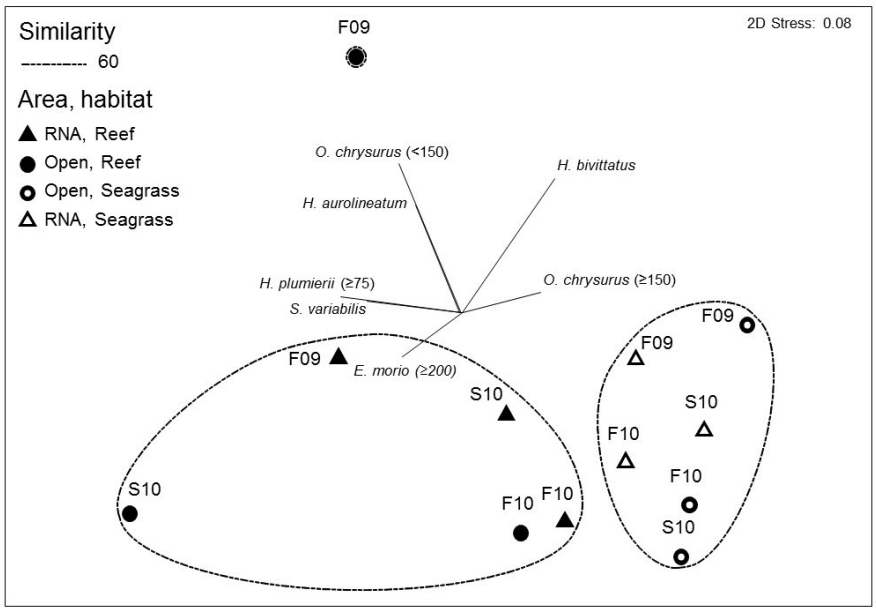

FIGURE 3. *MDS ordination for fish collected with Z-traps in the Dry Tortuga National Park, fall 2009–fall 2010 averaged over sampling season, area, and habitat. Labels indicate sampling season (F09 = fall 2009, S10 = spring 2010, F10 = fall 2010); symbols indicate area (triangles = Research Natural Area (RNA), circles = open-use areas); colors indicate habitat (black = reef habitat; white = seagrass habitat). Ellipses represent groups that had community structures at a 60% (dashed line) similarity level as determined from CLUSTER analysis. Vectors for taxa that contributed 0.2 or more to assemblage structure are also included.*

(Table 2). Accordingly, we conducted pairwise comparisons of area and habitat separately for each combination of the other factor. Fish assemblages differed significantly between reef and seagrass habitats in open—use areas (p = 0.0005) and marginally within the RNA (p = 0.0508). Fish assemblages did not differ within habitat regardless of area (Reef p = 0.1263, Seagrass p = 0.5776). The 2—way interaction between sampling event and area was not significant (p = 0.592), and the interaction between sampling event and habitat was only marginally significant (p = 0.0501), so pairwise comparisons were conducted directly among sampling events. Community structure in fall 2009 was significantly different from fall 2010 (p = 0.0027) and marginally different from spring 2010 (p = 0.0955). Habitat (5.71% of variation explained) was a more important driver of fish assemblage structure than sampling event (2.78% of variation explained), water depth (1.31%), or area (0.27%).

Sampling in fall 2009 differed from the other sampling events as a result of greater numbers of *H. bivittatus*, *H. aurolineatum*, and the smaller size classes of *O. chrysurus* (<150 mm SL) and *H. plumierii* (<75 mm SL), and *Sparisoma radians* (Bucktooth Parrotfish; Figures 3 and 4, SIMPER analyses). In addition, 5 species were only collected during this sampling event (*Cephalopholis cruentata* (Graysby), *Stegastes planifrons* (Threespot Damselfish), *Stegastes adustus* (Dusky Damselfish), *Haemulon flavolineatum* (French Grunt), and *Haemulon chrysargyreum* (Smallmouth Grunt)).

Differences in assemblage structure between habitat types were driven primarily by greater abundances in seagrass habitats of *S. radians* (2.6% contribution as calculated through SIMPER analyses), *H. bivittatus* (11.4%), large *O. chrysurus* (11.8%), and small *E. morio* (1.9%), and by greater abundances over reef habitats of *Stegastes variabilis* (Cocoa Damselfish, 10.4%), small *O. chrysurus* (11.0%), and large *H. plumierii* (9.0%; Figures 3 and 5). *Haemulon aurolineatum* (9.6%) was one of the most abundant species and was collected only over reef habitat, while comparable numbers of juvenile *H. plumierii* (4.5%) were found across reef (n = 127) and seagrass (n = 119) habitats (Figures 3 and 5, Table 1). Although not major contributors to differences in community structure, economically important *C. cruentata* (n = 4, ranging from 189 to 224 mm SL), *Lutjanus synagris* (Lane Snapper, n = 3, ranging from 63 to 193 mm SL), and juvenile *Mycteroperca bonaci* (Black Grouper; n = 4, ranging from 87 to 153 mm SL) were collected in only seagrass habitats (Figure 5, Table 1).

Nekton community structure did not differ between the RNA and open—use areas due to similar abundances of dominant species. Species that were found exclusively in one area or another were those in very low abundance; in only 2 instances were more than 5 individuals of a certain species more abundant in either area (*Scarus iseri*, Striped Parrotfish and

TABLE 2. *PERMANOVA results for the analysis of fish assemblages in the Dry Tortugas National Park, fall 2009–fall 2010 on the basis of the Bray-Curtis dissimilarity measure in response to depth, area, sampling event, and habitat. df = degrees of freedom, MS = mean square error, Sqrt variation = square root component of variation.*

Source	df	MS	Pseudo-F	p	Sqrt variation	% of variation
Depth	1	6,170	2.43	0.0208	6.3945	1.31%
Area	1	2,054	0.81	0.5855	–2.9048	0.27%
Sampling event	2	5,776	2.28	0.0078	9.2985	2.78%
Habitat	1	11,474	4.52	0.0004	13.327	5.71%
Area * Sampling event	2	4,200	1.66	0.0592	9.0182	2.61%
Area * habitat	1	5,189	2.05	0.0460	9.4859	2.89%
Sampling event * habitat	2	4,310	1.70	0.0501	9.549	2.93%
Pooled (includes residuals and three way interaction)	117	2,537			50.371	81.50%
Total	**127**					

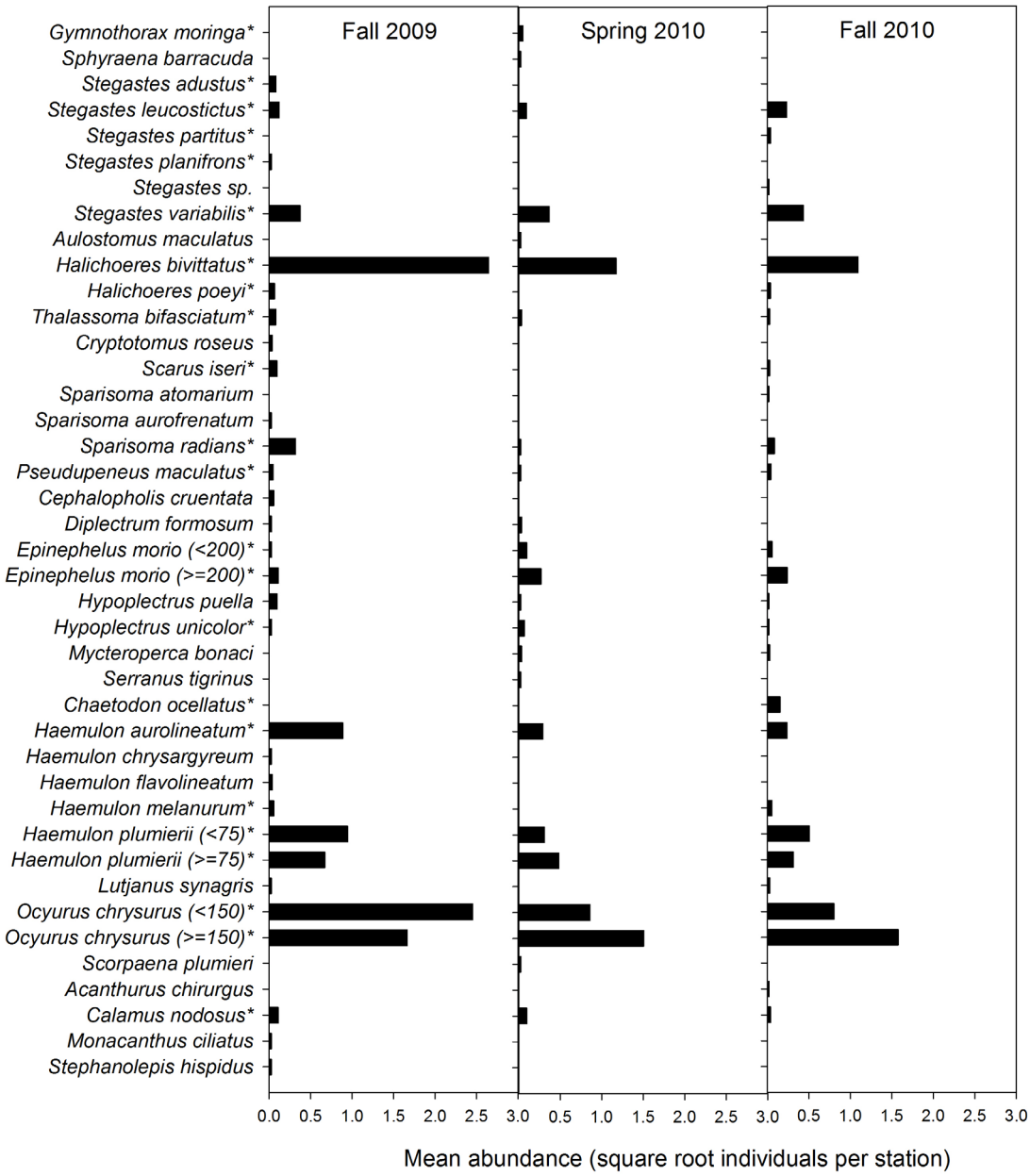

FIGURE 4. *Average abundance, by sampling event, for fish collected with Z-traps in the Dry Tortugas National Park, fall 2009–fall 2010. Fish are ordered phylogenetically by family and then alphabetically by species as in Table 1. Species that contributed to up to 90% to the differences among seasons through SIMPER analysis are noted with an asterisk.*

Haemulon melanurum, Cottonwick) and were only encountered in the open—use area (Figure 6, Table 1).

Size structure for the 4 species selected for length frequency analysis (*E. morio*, *H. bivittatus*, *H. plumierii*, and *O. chrysurus*) differed by area and habitat combinations (Figure 7). Size structure of *E. morio* did not differ by habitat in open—use areas (KSa_{16} (Open) = 0.79, p = 0.5672), but were significantly smaller within seagrass than reef habitats of the RNA (KSa_{19} (RNA) = 1.46, p = 0.0281). Within each area, *H. plumierii* were also significantly smaller in seagrass than reef habitats (KSa_{207} (Open) = 2.47, p < 0.0001, KSa_{146} (RNA) = 2.93, p < 0.0001), while *O. chrysurus* were significantly larger in seagrass habitats (KSa_{516} (Open) = 2.83, p < 0.0001, KSa_{732} (RNA) = 3.36, p < 0.0001). Size structure of *H. bivittatus* did not differ by habitat in the RNA (KSa_{295} (RNA) = 1.17, p = 0.1303), but they were significantly smaller within seagrass habitats of the open—use areas (KSa_{438} (Open) = 1.65, p = 0.0088).

Discussion

This study represents an important contribution to understanding the use of seagrasses by reef—associated species in DTNP, and demonstrates that these potential nursery habitats should be considered within no—take marine reserves to enhance connectivity between juvenile and adult reef fish habitats (Nagelkerken et al. 2012). *Epinephelus morio* and *H. plumierii* exhibited clear evidence of seagrass habitat use at smaller sizes, suggesting its potential use as a nursery, while *H. bivittatum* was more abundant over seagrass habitat, suggesting its utility as a refuge for small resident species. Although the greater Dry Tortugas benthic environment has been studied extensively (Franklin et al. 2003) and a long—running, reef fish visual census has provided valuable data for reef—associated species (Ault et al. 2002, 2006), monitoring data on seagrass—associated species and highly cryptic smaller—bodied fishes are generally lacking. Large—mesh Antillean fish traps have limitations such as increased catchability of mobile species and a positive correlation with low habitat complexity (Robichaud et al. 2000), however, the use of small—mesh Z—traps with short soak times have been associated with higher catch rates (Sheaves 1995). In this study, small—mesh Z—traps allowed for nondestructive and highly targeted sampling of reef and seagrass habitats in open—use and protected areas in the DTNP and provided data on a

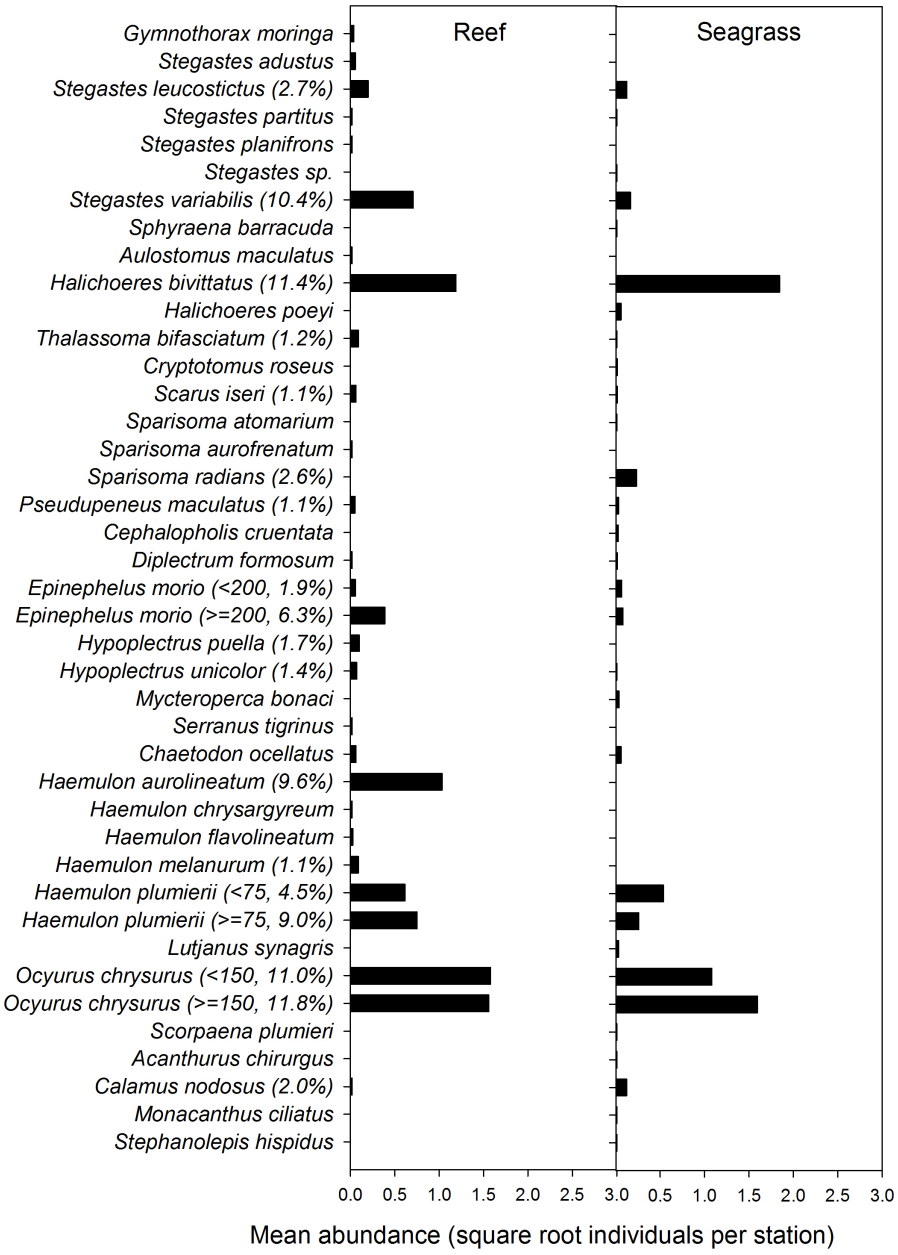

FIGURE 5. *Average abundance, by habitat, for fish collected with Z-traps in the Dry Tortugas National Park, fall 2009–fall 2010. Fish are ordered phylogenetically by family and then alphabetically by species as in Table 1. The percent contribution of species that contributed up to 90% to the differences between habitats through SIMPER analysis is in parentheses.*

broad size range of economically and ecologically important fishes, some of which, such as the different species of *Stegastes* and juvenile *Haemulon*, would be difficult to discern in a visual survey. Therefore, this study complements other ongoing research (Ziegler and Hunt 2012) into the nursery function and conservation efficacy of habitats in DTNP.

Overall, fish community composition did not differ strongly between the RNA and adjacent open—use areas. Upon initial examination, it might seem surprising that no short—term (~3 years; RNA established in 2007) differences in fish community structure were evident in either reef or seagrass habitats. After all, the RNA offers direct protection to seagrasses, which are known to directly support numerous small resident fishes and indirectly sustains the productivity and ontogeny of transient fishes (such as exploited reef fishes) through habitat connectivity (i.e., foraging and nursery areas; Unsworth and Cullen 2010). One might expect the fish community to respond positively through increased abundance and diversity as the quality and quantity of seagrass habitat improves (Lindholm et al. 2001, Rodwell et al. 2003), although these benefits may be partly offset through increased predation from reef—associated species that generally receive the greatest protection from no—take marine reserves and are known to forage in adjacent seagrass meadows at night (Robblee and Zieman 1984, Babcock et al. 1999, Shears and Babcock 2003). Visual surveys conducted on reef habitat during the same time period documented increases in density and abundance for exploited sizes of several reef fish species (*M. bonaci*, *Lutjanus analis* (Mutton Snapper), *O. chrysurus*, and *Lachnolaimus maximus* (Hogfish)), but not in nontarget fish species (Ault et al. 2013). For exploited reef fishes, protection is generally thought to lead to increasing reproductive capacity that, presumably, would first be detected through enhanced juvenile recruitment; no such enhanced recruitment was evident from targeted sampling of smaller size classes with Z—traps. It is possible that too little time has passed since the RNA was established or that our study was too short in duration for increases in the abundance of exploited or unexploited species to be evident. In addition, the overall recovery of fish communities in no—take marine reserves can be slow (Russ et al. 2004), especially in species such as those in the grouper—snapper complex that mature later and have a high probability of discard mortality for undersized individuals (Coleman et al. 1996, 1999). Studies have also shown that small reef fish were relatively greater in biomass when nursery habitats were nearby than when only a fishing closure was in effect (Nagelkerken et al. 2012), so fish community composition may be inherently more affected by habitat use than by protection status especially in remote areas like the DTNP. In addition, area closures related to fishing and other recreational activities may not have discernible direct benefits to nontarget species, even exhibiting decreases in abundance in

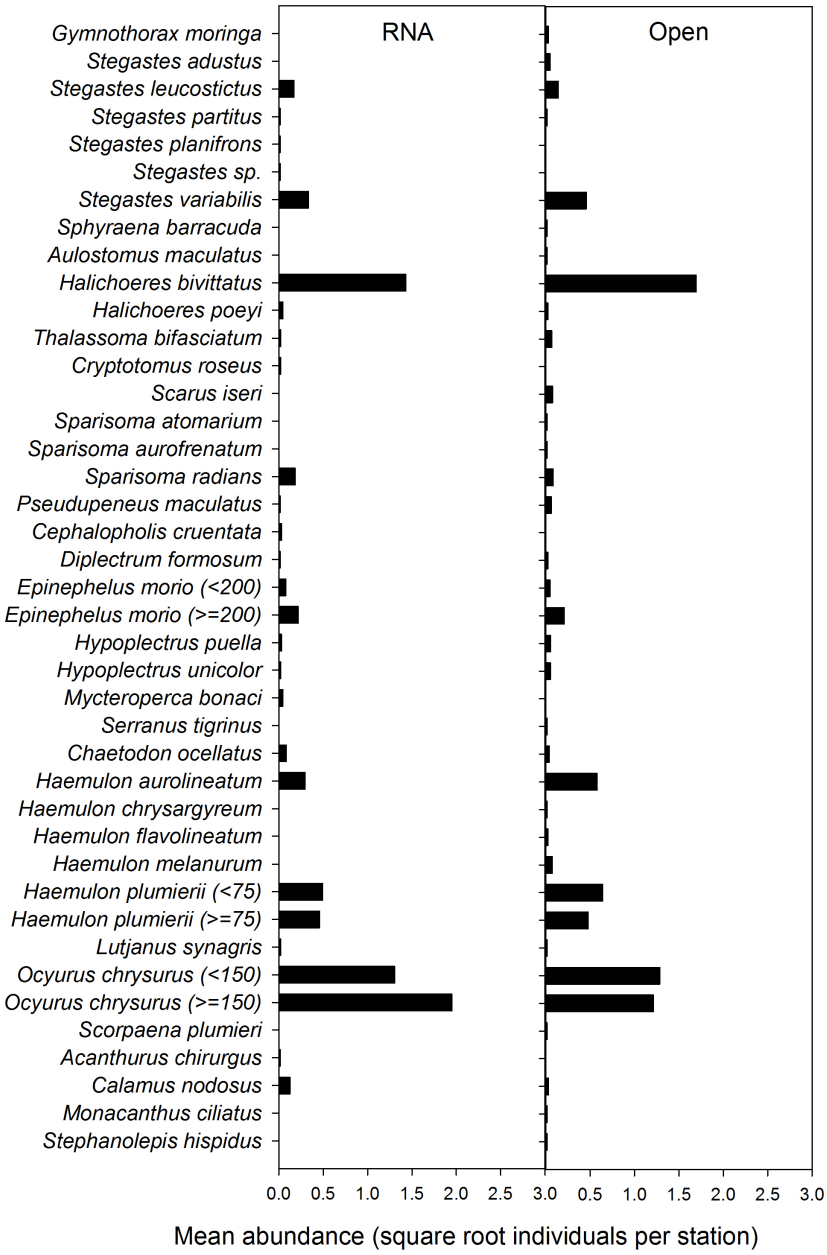

FIGURE 6. *Average abundance, by habitat, for fish collected with Z-traps in the Dry Tortugas National Park, fall 2009–fall 2010. Fish are ordered phylogenetically by family and then alphabetically by species as in Table 1.*

some cases (Claudet et al. 2010). Regardless, these data represent an important baseline to compare changes within the RNA to less protected areas within the DTNP.

As expected, fish community structure differed significantly between seagrass and reef habitats. Although reef habitats in the DTNP are important centers for spawning of many exploited species (Ault et al. 2002, 2006, Rogers et al. 2007), little research has been done on the function of DTNP seagrass habitats, even though they serve as valuable nursery habitat in other coral reef systems (Nagelkerken et al. 2001, 2002, Nagelkerken and van der Velde 2004, Unsworth et al. 2008). It is well known that many reef fish juveniles settle into seagrass beds before moving into nearby reef habitats as adults (Chittaro et al. 2005, Casey et al. 2007, Nagelkerken et al. 2012, Flaherty–Walia et al. 2015, Switzer et al. 2015), and this study documented smaller sizes of *E. morio* and *H. plumierii* in seagrass habitats than in reef habitats. Additional research is needed to confirm this result for *E. morio* due to small sample size (n = 8, ≤ 200 mm SL), however. The opposite trend is true for *O. chrysurus*, and although not significantly contributing to community structure differences, juveniles of the economically–important *M. bonaci* were exclusively collected in seagrass habitats, suggesting further research and additional sampling would be beneficial to delineate trends for some species. Habitat segregation among species or life stages of coral reef fishes along a seagrass–coral reef gradient can be affected by competition, feeding ecology, ontogenetic shifts, or the spatial arrangement of the habitats (Dorenbosch et al. 2005, 2007), so any of these factors could help explain the differences in community structure. The spatial characteristics of MPAs, environmental perturbations, and the level of enforcement of no–take areas can also influence how effective MPAs are at protecting the multiple habitats used during ontogeny (McNeill 1994, Rogers and Beets 2001, Christie and White 2007, Ortiz and Tissot 2012). This study represents an initial examination of the community structure of juvenile and small–bodied fishes within seagrass and reef habitats receiving different levels of protection in the DTNP.

Although differences in fish community structure were most pronounced between habitat types, differences were also evident among sampling events. Observed patterns were not seasonally consistent; rather, fall 2009 differed from both spring 2010 and fall 2010, and most differences occurred in open–use areas with reef habitat. Without a long–term data set using Z–traps, it is difficult to say if the greater abundances of *H. bivittatum*, *H. aurolineatum*, and the smaller size classes of *O. chrysurus* and *H. plumierii* during fall 2009 were unusual. Differences in fish community structure between fall 2009 and spring 2010 could have been related to an extreme cold event during the winter of 2010 that caused massive mortality of patch reefs in the Florida Keys and subtropical fish species in various regions of Florida (Colella et al. 2012, Stevens et al. 2016). An additional possibility is that 2009 was an exceptionally good recruitment year, especially for the summer–spawning *O.*

chrysurus (Garcia et al. 2003). Similar findings were reported from ongoing visual surveys that documented greater densities of *O. chrysurus* in the RNA and open—use areas in the spring of 2009 than in previous years (Ault et al. 2013). Furthermore, by chance, reef sites in the open—use area during fall 2009 had shallower water than in other years which may have added to community structure differences. Conducting periodic monitoring over time would help in defining baseline seasonal variability and its effects on regional and habitat—related community structure.

Z—traps allowed us to obtain valuable data on reef— and seagrass—associated fishes in DTNP. Catches were dominated by juvenile and small resident fishes, some of which would be difficult to discern in a visual survey. Juvenile *H. plumierii* and *E. morio* were found in greater abundance in seagrass habitats in DTNP, suggesting that seagrasses may function as nurseries and should be considered an important component of no—take marine reserves associated with coral reef habitat. Further research is needed to quantify if a greater than average number of individuals are contributed to the adult population from seagrass areas than other habitats used by juveniles within the DTNP (Beck et al. 2001, Heck et al. 2003), preferably with a sampling design constrained by depths at which seagrass beds occur (< 11m), so that all sites are comparable. These results also highlight the importance of considering all life—history stages when establishing no—take marine reserves, not simply reproductively active adults. Although our study did not detect differences in fish communities between the RNA and adjacent open—use areas, establishment of the RNA may still be too recent for its effects on exploited or unexploited species to be evident. Only by integrating results from this and other ongoing studies and with continued, regular sampling over time can the effects of the RNA's establishment be fully assessed.

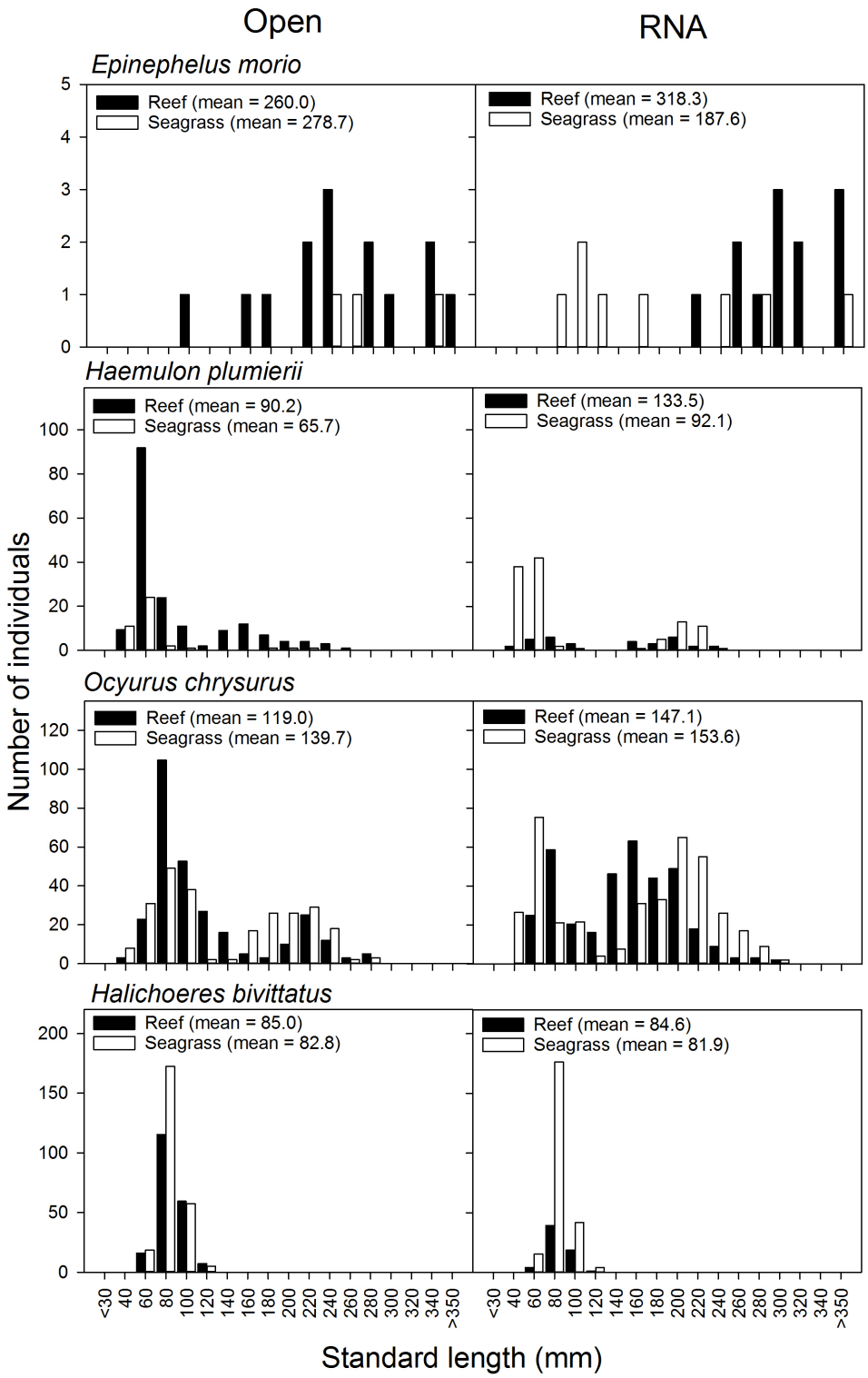

FIGURE 7. *Length frequency by 20 mm size bins and sampling area for selected fish collected in Z-traps in Dry Tortugas National Park open-use (Open) and Research Natural Area (RNA) areas, fall 2009–fall 2010. Colors indicate habitat (black = reef; white = seagrass).*

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Literature Cited

Álvarez—Fernández, I., N. Fernández, N. Sánchez—Carneroc, and J. Freired. 2017. The management performance of marine protected areas in the Northeast Atlantic Ocean. Marine Policy 76:159—168. https://doi.org/10.1016/j.marpol.2016.11.031

Anderson, M.J., R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER—E: Plymouth, UK, 214 pp.

Apostolaki, P., E.J. Milner—Gulland, M.K. McAllister, and G.P. Kirkwood. 2002. Modelling the effects of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences 59:405–415. https://doi.org/10.1139/f02—018

Ault, J.S., J.A. Bohnsack, and G.A. Meester. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fishery Bulletin 96:395–414.

Ault, J.S., S.G. Smith, G.A. Meester, J. Luo, J.A. Bohnsack, and S.L. Miller. 2002. Baseline multispecies coral reef fish stock assessment for the Dry Tortugas. Technical Report NMFS—SEFSC—487. National Marine Fisheries Service, Miami, FL, USA. 127 p.

Ault, J.S., J.A. Bohnsack, S.G. Smith, and J. Luo. 2005. Towards sustainable multispecies fisheries in the Florida, USA, coral reef ecosystem. Bulletin of Marine Science 76:595–622.

Ault, J.S., S.G. Smith, J.A. Bohnsack, J. Luo, D.E. Harper, and D.B. McClellan. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. Bulletin of Marine Science 78:633–654.

Ault, J.S., S.G. Smith, J.A. Bohnsack, J. Luo, N. Zurcher, D.B. McClellan, T.A. Ziegler, D.E. Hallac, M. Patterson, and M.W. Feeley. 2013. Assessing coral reef fish population and community changes in response to marine reserves in the Dry Tortugas, Florida, USA. Fisheries Research 144:28–37. https://doi.org/10.1016/j.fishres.2012.10.007

Babcock, R.C., S. Kelly, N.T. Shears, J.W. Walker, and T.J. Willis. 1999. Changes in community structure in temperate marine reserves. Marine Ecology Progress Series 189:125–134.

Ballantine, B. 1997. "No—take" marine reserve networks support fisheries. In: D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer, eds. 2nd World Fisheries Conference. CSIRO Publishing, Collingwood, Australia, p. 702–706.

Bartels, C.T., and K.L. Ferguson. 2006. Preliminary observations of abundance and distribution of settlement—stage snappers in shallow, nearshore seagrass beds in the middle Florida Keys. Proceedings of the Gulf and Caribbean Fisheries Institute 57:235–248.

Beck, M.W., K.L. Heck Jr., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, and R.J. Orth. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site—specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51:633–641. https://doi.org/10.1641/0006—3568(2001)051[0633:TICAMO]2.0.CO;2.

Berumen, M.L., G.R. Almany, S. Planes, G.P. Jones, P. Saenz—Agudelo, and S.R. Thorrold. 2012. Persistence of self—recruitment and patterns of larval connectivity in a marine protected area network. Ecology and Evolution 2:444–452. https://doi.org/10.1002/ece3.208

Bohnsack, J.A. 2002. Preliminary analysis of no—take reserves on world records at Cape Canaveral, Florida. American Fisheries Society Symposium 30:234–236.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Casey, J.P., G.R. Poulakis, and P.W. Stevens. 2007. Habitat use by juvenile gag *Mycteroperca microlepis* in subtropical Charlotte Harbor, Florida (USA). Gulf and Caribbean Research 19:1–9. https://doi.org/10.18785/gcr.1901.01

Chittaro, P.M, P. Usseglio, and P.F. Sale. 2005. Variation in fish density, assemblage composition and relative rates of predation among mangrove, seagrass and coral reef habitats. Environmental Biology of Fishes 72:175–187.

Christie, P. and A.T. White. 2007. Best practices for improved governance of coral reef marine protected areas. Coral Reefs 26:1047–1056.

Clarke, K.R. and R.N. Gorley. 2006. PRIMER v6: User Manual/Tutorial. PRIMER—E, Plymouth, U.K. 190p.

Clarke, K.R. and R.M. Warwick. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition. Natural Environment Research Council, Plymouth Marine Laboratory, Plymouth, U.K.

Claudet, J., C.W. Osenberg, L. Benedetti—Cecchi, P. Domenici, J.—A. García—Charton, Á. Pérez—Ruzafa, F. Badalamenti, J. Bayle—Sempere, A. Brito, F. Bulleri, J.—M. Culioli, M. Dimech, J.M. Falcón, I. Guala, M. Milazzo, J. Sánchez—Meca, P.J. Somerfield, B. Stobart, F. Vandeperre, C. Valle, and S. Planes. 2008. Marine reserves: size and age do matter. Ecology Letters 11:481–489. https://doi.org/10.1111/j.1461—0248.2008.01166.xS

Claudet, J., C.W. Osenberg, P. Domenici, F. Badalamenti, M. Milazzo, J.M. Falcón, I. Bertocci, L. Benedetti—Cecchi, J.—A. García—Charton, R. Goñi, J.A. Borg, A. Forcada, G.A. De Lucia, Á. Pérez—Ruzafa, P. Afonso, A. Brito, I. Guala, L. Le Diréach, P. Sanchez—Jerez and P. J. Somerfield. 2010. Marine reserves: Fish life history and ecological traits matter. Ecological Applications 20: 830—839. https://doi.org/10.1890/08—2131.1

Claudet, J., J.A. Garcia—Charton, and P. Lenfant. 2011. Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. Conservation Biology 25:105–114. https://doi.org/10.1111/j.1523—1739.2010.01586.x

Cocheret de la Morinière, E., B.J. Pollux, I. Nagelkerken, and G. Van der Velde. 2002. Post—settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. Estuarine, Coastal, and Shelf Science 55:309–321. https://doi.org/10.1006/ecss.2001.0907

Colella, M.A., R.R. Ruzicka, J.A. Kidney, J.M. Morrison, and V.B. Brinkhuis. 2012. Cold—water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. Coral Reefs 31:621–632. https://doi.org/10.1007/s00338—012—0880—5

Coleman, F.C., C.C. Koenig, and L.A. Collins. 1996. Reproductive styles of shallow—water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environmental Biology of Fishes 47:129–141. https://doi.org/10.1007/bf00005035

Coleman, F.C., C.C. Koenig, A.M. Eklund, and C.B. Grimes. 1999. Management and conservation of temperate reef fishes in the grouper—snapper complex of the southeastern United States. American Fisheries Society Symposium 23:233–242.

Côté, I.M., I. Mosqueira, and J.D. Reynolds. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta—analysis. Journal of Fish Biology 59:178–189. https://doi.org/10.1111/j.1095—8649.2001.tb01385.x

Dorenbosch, M., M.G.G. Grol, I. Nagelkerken, and G. Van der Velde. 2005. Distribution of coral reef fishes along a coral reef–seagrass gradient: edge effects and habitat segregation. Marine Ecology Progress Series 299:277–288.

Dorenbosch, M., W.C.E.P. Verberk, I.A. Nagelkerken, and G. van der Velde. 2007. Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Marine Ecology Progress Series 334:103–116.

Dugan, J.E. and G.E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 50:2029–2042. https://doi.org/10.1139/f93—227

Faunce, C.H. and J. Serafy. 2007. Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. Bulletin of Marine Science 80:473–495.

Flaherty—Walia, K.E., T.S. Switzer, B.L. Winner, A.J. Tyler—Jedlund, and S.F. Keenan. 2015. Improved ability to characterize recruitment of gray snapper in three Florida estuaries along the Gulf of Mexico through targeted sampling of polyhaline seagrass beds. Transactions of the American Fisheries Society 144:911–926. https://doi.org/10.1080/00028487.2015.1054516

Franklin, E.C., J.S. Ault, S.G. Smith, J. Luo, G.A. Meester, G.A. Diaz, M. Chiappone, D.W. Swanson, S.L. Miller, and J.A. Bohnsack. 2003. Benthic habitat mapping in the Tortugas region, Florida. Marine Geodesy 26:19–34. http://dx.doi.org/10.1080/01490410306706

Garcia, E.R., J.C. Potts, R.A. Rulifson, and C.S. Manooch. 2003. Age and growth of yellowtail snapper, *Ocyurus chrysurus*, from the southeastern United States. Bulletin of Marine Science 72:909–921.

Geoghegan, T., A.H. Smith, and K. Thacker. 2001. Characterization of Caribbean marine protected areas: an analysis of ecological, organizational, and socio—economic factors. Caribbean Natural Resources Institute (CANARI), CANARI Technical Report No. 287, Laventille, Trinidad, 140 p.

Gruss, A., J. Robinson, S.S. Heppell, S.A. Heppell, and B.X. Semmens. 2014. Conservation and fisheries effects of spawning aggregation marine protected areas: What we know, where we should go, and what we need to get there. ICES Journal of Marine Science 71:1515–1534. https://doi.org/10.1093/icesjms/fsu038

Heck, K.L. Jr. and M.P. Weinstein. 1989. Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. Bulletin of Marine Science 45:629–636.

Heck, K.L. Jr., G. Hays, and R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253:123–136.

Johnson, D.R., N.A. Funicelli, and J.A. Bohnsack. 1999. Ef-

fectiveness of an existing estuarine no—take fish sanctuary within the Kennedy Space Center, Florida. North American Journal of Fisheries Management 19:436–453. http://dx.doi.org/10.1577/1548—8675(1999)019<0436:EOAEEN>2.0.CO;2

Jones, D.L., J.F. Walter, E.N. Brooks, and J.E. Serafy. 2010. Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. Marine Ecology Progress Series 401:245–258. https://doi.org/10.3354/meps08404

Kramer, K.L. and K.L. Heck, Jr. 2007. Top—down trophic shifts in Florida Keys patch reef marine protected areas. Marine Ecology Progress Series 349:111–123. https://doi.org/10.3354/meps07083

Lauck, T., C.W. Clark, M. Mangel, and G.R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8:S72–S78. https://doi.org/10.1890/1051—0761(1998)8[S72:ITPPIF]2.0.CO;2

Lester, S.E. and B.S. Halpern. 2008. Biological responses in marine no—take reserves versus partially protected areas. Marine Ecology Progress Series 367:49–56. https://doi.org/10.3354/meps07599

Lester, S.E., B.S. Halpern, K. Grorud—Colvert, J. Lubchenco, B.I. Ruttenberg, S.D. Gaines, S. Airamé, and R.R. Warner. 2009. Biological effects within no—take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33–46. https://doi.org/10.3354/meps08029

Lindholm, J.B., P.J. Auster, M. Ruth, and L. Kaufman. 2001. Modeling the effects of fishing and implications for the design of marine protected areas: juvenile fish responses to variations in seafloor habitat. Conservation Biology 15:424–437. https://doi.org/10.1046/j.1523—1739.2001.015002424.x

Lipej, L., M.O. Bonaca and M. Sisko. 2003. Coastal fish diversity in three marine protected areas and one unprotected area in the Gulf of Trieste (northern Adriatic). Marine Ecology 24:259–273. https://doi.org/10.1046/j.1439—0485.2003.00843.x

McNeill, S.E. 1994. The selection and design of marine protected areas: Australia as a case study. Biodiversity and Conservation 3:586–605.

Nagelkerken, I. and G. van der Velde. 2004. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. Marine Ecology Progress Series 274:153–159.

Nagelkerken, I., G. van der Velde, M.W. Gorissen, G.J. Meijer, T. van't Hof, and C. den Hartog. 2000a. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes: using a visual census technique. Estuarine, Coastal, and Shelf Science 51:31–44. https://doi.org/10.1006/ecss.2000.0617

Nagelkerken, I., M. Dorenbosch, W.C.E.P. Verberk, E. Cocheret de la Morinière, and G. van der Velde. 2000b. Importance of shallow—water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Marine Ecology Progress Series 202:175–192.

Nagelkerken, I., S. Kleijnen, T. Klop, R.A.C.J. van den Brand, E. Cocheret de la Morinière, and G. van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology Progress Series 214:225–235.

Nagelkerken, I., C.M. Roberts, G. van der Velde, M. Dorenbosch, M.C. van Riel, E. Cocheret de la Morinière, and P.H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral—reef fish? The nursery hypothesis tested on an island scale. Marine Ecology Progress Series 244:299–305.

Nagelkerken, I., M.G.G. Grol, and P.J. Mumby. 2012. Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. PloS One 7(6):e36906. https://doi.org/10.1371/journal.pone.0036906

Nelson, J.S., T.C. Grande, and M.V. Wilson. 2016. Fishes of the world. Fifth Edition. John Wiley and Sons. Hoboken, New Jersey, USA, 752 p.

Nemeth, R.S. 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. Marine Ecology Progress Series 286:81–97.

Ortiz, D.M. and B.N. Tissot. 2012. Evaluating ontogenetic patterns of habitat use by reef fish in relation to the effectiveness of marine protected areas in west Hawaii. Journal of Experimental Marine Biology and Ecology 432–433:83–93. https://doi.org/10.1016/j.jembe.2012.06.005

Palandro, D.A., S. Andréfouët, C. Hu, P. Hallock, F.E. Müller—Karger, P. Dustan, M.K. Callahan, C. Kranenburg, and C.R. Beaver. 2008. Quantification of two decades of shallow—water coral reef habitat decline in the Florida Keys National Marine Sanctuary using Landsat data (1984–2002). Remote Sensing of Environment 112:3388–3399. https://doi.org/10.1016/j.rse.2008.02.015

Prado P., S. Farina, F. Tomas, J. Romero, and T. Alcoverro. 2008. Marine protection and meadow size alter fish herbivory in seagrass ecosystems. Marine Ecology Progress Series 371:11–21. https://doi.org/10.3354/meps07662

Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920–1923. https://doi.org/10.1126/science.294.5548.1920

Robichaud, D., W. Hunte, and M.R. Chapman. 2000. Factors affecting the catchability of reef fishes in Antillean fish traps. Bulletin of Marine Science 67:831—844

Robblee, M.B. and J.C. Zieman. 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. Bulletin of Marine Science 34:335–345.

Rodwell, L.D., E.B. Barbier, C.M. Roberts, and T.R. McClanahan. 2003. The importance of habitat quality for marine reserve–fishery linkages. Canadian Journal of Fisheries and Aquatic Sciences 60:171–181. https://doi.org/10.1139/f03—009

Rogers, C.S. and J. Beets. 2001. Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the U.S. Virgin Islands. Environmental Conservation 28:312–322. https://doi.org/10.1017/s0376892901000340

Rogers, C.S., G.E. Davis, and C. McCreedy. 2007. National Parks and Caribbean Marine Reserves Research and Monitoring Workshop: St. John, U.S. Virgin Islands, July 11–13, 2006. Natural Resource Technical Report NPS/NRPC/WRD/NRTR—2007/015. National Park Service, Fort Collins, CO, USA. 50 p.

Russ, G.R. and A.C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132:1–9. https://doi.org/10.3354/meps132001

Russ, G. R., A.C. Alcala, A.P. Maypa, H.P. Calumpong, and A.T. White. 2004. Marine reserve benefits local fisheries. Ecological Applications 14:597–606. https://doi.org/10.1890/03—5076

Saarman, E., M. Gleason, J. Ugoretz, S. Airame, M. Carr, E. Fox, A. Frimodig, T. Mason, and J. Vasques. 2012. The role of science in supporting marine protected area network planning and design in California. Ocean and Coastal Management 74:45–56. https://doi.org/10.1016/j.ocecoaman.2012.08.021

SAS Institute Inc. 2006. Base SAS® 9.1.3 Procedures Guide, 2nd ed., Volumes 1–4. SAS Institute Inc., Cary, NC, USA.

SFNRC and FWC (South Florida Natural Resources Center and the Florida Fish and Wildlife Conservation Commission). 2007. Assessing the conservation efficacy of the Dry Tortugas National Park Research Natural Area. South Florida Natural Resources Center, Everglades and Dry Tortugas National Parks, Homestead, FL, and the Florida Fish and Wildlife Conservation Commission, Tallahassee, FL, USA. 47 p.

Shears, N.T. and R.C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no—take marine reserve protection. Marine Ecology Progress Series 246:1–16. https://doi.org/10.3354/meps246001

Sheaves, M.J. 1992. Patterns of distribution and abundance of fishes in different habitats of a mangrove—lined tropical estuary, as determined by fish trapping. Australian Journal of Marine and Freshwater Research 43:1461–1479. https://doi.org/10.1071/MF9921461

Sheaves, M.J. 1995. Effect of design modifications and soak time variations on Antillean—Z fish trap performance in a tropical estuary. Bulletin of Marine Science 52:474–489.

Sponaugle, S., K.D. Walter, K. Grorud—Colvert, and M.J. Paddack. 2012. Influence of marine reserves on reef fish recruitment in the upper Florida Keys. Coral Reefs 31:641–652. https://doi.org/10.1007/s00338—012—0915—y

Stevens, P.W., D.A. Blewett, R.E. Boucek, J.S. Rehage, B.L. Winner, J.M. Young, J.A. Whittington, *and* R. Paperno. 2016. Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. Ecosphere 7(8):e01400. https://doi.org/10.1002/ecs2.1400

Sundblad, G., U. Bergström, and A. Sandström. 2011. Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. Journal of Applied Ecology 48:112–120. https://doi.org/10.1111/j.1365—2664.2010.01892.x

Switzer, T.S., S.F. Keenan, P.W. Stevens, R.H. McMichael Jr., and T.C. MacDonald. 2015. Incorporating Ecology into Survey Design: Monitoring the Recruitment of Age—0 Gags in the Eastern Gulf of Mexico, North American Journal of Fisheries Management, 35:1132–1143. https://doi.org/10.1080/02755947.2015.1082517

Tittensor, D.P., F. Micheli, M. Nyström, and B. Worm. 2007. Human impacts on the species–area relationship in reef fish assemblages. Ecology Letters 10:760–772. https://doi.org/10.1111/j.1461—0248.2007.01076.x

Unsworth, R.K.F. and L.C. Cullen. 2010. Recognising the necessity for Indo—Pacific seagrass conservation. Conservation Letters 3:63–73. https://doi.org/10.1111/j.1755—263X.2010.00101.x

Unsworth, R.K.F., P. Salinas de León, S.L. Garrard, J. Jompa, D.J. Smith, and J.J. Bell. 2008. High connectivity of Indo—Pacific seagrass fish assemblages with mangrove and coral reef habitats. Marine Ecology Progress Series 353:213–224. https://doi.org/10.3354/meps07199

Verweij, M.C., I. Nagelkerken, D. de Graaff, M. Peeters, E.J. Bakker, and G. van der Velde. 2006. Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Marine Ecology Progress Series 306:257–268.

Verweij, M.C., I. Nagelkerken, I. Hans, S.M. Ruseler, and P.R.D. Mason. 2008. Seagrass nurseries contribute to coral reef fish populations. Limnology and Oceanography 53:1540–1547. https://doi.org/10.4319/lo.2008.53.4.1540

Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, W. J. Kenworthy, F.T. Short, and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12377–12381. https://doi.org/10.1073/pnas.0905620106

Yarbro, L. A. 2013. Seagrass Integrated Mapping and Monitoring Program mapping and monitoring report No. 1. FWRI Technical Report TR—17. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA. 135 pp.

Ziegler, T.A. and J. Hunt (eds.). 2012. Implementing the Dry Tortugas National Park Research Natural Area Science Plan: The 5—year Report 2012. South Florida Natural Resources Center, Everglades and Dry Tortugas National Parks, Homestead, FL, USA and the Florida Fish and Wildlife Conservation Commission, Tallahassee, FL, USA. 63 p.