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research paper

A quantitative assessment of the status of reef fish communities from a large-scale probability survey in southern Florida

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Advances in Ecosystem-Scale Coral Reef Visual Surveys

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ABSTRACT.—Numerous reef fish monitoring programs worldwide produce the data necessary to describe the status and trends of coral reefs; however, quantitative description of status at ecosystem scales has been challenging. Our goal was to use southern Florida's coral reefs as the template to complete a holistic, ecosystem-scale evaluation of reef fish community status using large-scale diver surveys that sampled across a spatial gradient of human urbanization, exploitation, and fishery protection. Key aspects of the analysis were: (1) identification of a low human impact reference area as the basis for quantifying resource condition; (2) selection of indicator variables that helped discriminate two classes of impacts: habitat quality and fishing; (3) application of estimation methods that facilitated distinguishing anthropogenic impacts from inherent productivity of different habitats; and (4) use of a sustainability benchmark to gauge the resource condition of the reference area. The reference-centering analysis approach reduced reliance on qualitative judgements by an expert panel and produced results on a scale that was informative and could be easily interpreted by a variety of audiences. Our findings identified habitat quality issues in the most urbanized region, southeast Florida, and pervasive fishing issues throughout the ecosystem, including the remote Dry Tortugas region.

Worldwide declines in coral reefs and their associated fisheries have been documented for at least the past four decades (Hughes and Tanner 2000, Bellwood et al. 2004, Chin et al. 2011, Jackson et al. 2014, Nadon et al. 2015). Direct and indirect human pressures have contributed to these declines, including coastal development, overfishing, invasive species, terrestrial and marine pollution, and climate changes (Connell et al. 1997, Nyström et al. 2000, Hughes et al. 2003, Pandolfi et al. 2003, 2005). In the United States (US), coral reef assessment and management has been conducted on regional scales (e.g., southern Florida, Puerto Rico, Hawaii, etc.) by a combination of federal, state, and local entities that can be separated into two groups that focus on: (1) water quality and habitat issues [e.g., US Environmental Protection Agency (EPA), Florida Department of Environmental Protection]; and (2) fishing and habitat issues [e.g., National Oceanic and Atmospheric Administration (NOAA) Fisheries, South Atlantic Fishery Management Council, Florida Fish and Wildlife Conservation Commission]. From a legal standpoint, this is understandable because fishery management agencies do not have authority to regulate water quality, and water quality management entities do not have authority to regulate fishing. From a practical scientific standpoint, these two types of processes act in concert, making it difficult to determine which are primarily responsible for observed declines in resource condition(s).

Recognizing the scientific limitations of a narrower focus, in recent years, both the EPA and NOAA have initiated research efforts to evaluate coral reef ecosystems in a more holistic manner. Both agencies support large-scale coral reef monitoring programs. The EPA's approach was adapted from freshwater ecosystems and has expanded their historical emphasis on strictly water quality and benthos to include the reef fish community (USEPA 2016, Cicchetti et al. 2017, Bradley et al. 2020). NOAA's Coral Reef Conservation Program (CRCP) focuses on sampling reef fish and stony coral populations, but also includes some water quality parameters (NOAA Coral Program 2021). Both agencies attempt to distill coral reef habitat and animal data into analysis products to inform policymakers tasked with regulatory responsibilities and to guide future scientific monitoring and assessment activities. Examples are the EPA's Biological Condition Gradient (BCG) analyses of benthic invertebrates and reef fishes (USEPA 2016, 2021, Santavy et al. 2022a,b), and NOAA CRCP's National Coral Reef Monitoring Program's (NCRMP) ecosystem status report cards that include analyses of four categories: benthic community, reef fish community, climate, and socioeconomics (Towle et al. 2022, Viehman et al. 2024).

A recent application of the BCG to evaluate resource status of the Puerto Rico reef fish community highlighted its potential utility and practical difficulties (USEPA 2021). The conceptual model for BCG is a graph of resource condition dependent on the level of several combined stressors. Resource response runs from pristine (i.e., not impacted by humans—high condition, low stressor level) to impaired (i.e., greatly impacted by humans—low condition, high stressor level). The Puerto Rico study defined various attributes of the reef fish community (e.g., herbivore densities, higher trophic level predator presence, etc.) using diver survey data to generate composite scores that placed sampling sites along the condition-stressor gradient. Analyses yielded an unclear spatial gradient of human impacts (i.e., coastal development, land-based sources of pollution, fishing). Since there was no reference area for human impacts, an expert panel was convened to infer what might constitute pristine conditions as the basis for interpreting site scores. Another practical difficulty was clear quantification of multi-attribute fish community metrics into a single composite score that did not obscure the underlying human and/or environmental reasons for low-scoring sites.

The southern Florida coral reef ecosystem afforded a unique opportunity to develop assessment methods with the goal of improving ecosystem status evaluations. Intensive diver surveys of the reef fish community have been conducted over several decades across three regions with distinct gradients of human impacts: urbanization, coastal development, fishing intensity, and spatial protections (Table 1, Fig. 1). These regions include: (1) highly urbanized southeast Florida with no spatial fishing restrictions; (2) less-urbanized Florida Keys with minor spatial fishing restrictions; and (3) remote Dry Tortugas with minimal human presence (i.e., National Park Service personnel) and major spatial fishing restrictions (e.g., NPS 2005, Ault et al. 2022). As a consequence, the present study's objectives were to: (1) delineate a low-impact reference area as the basis for conducting fish community status evaluations in the three southern Florida regions; (2) use regional diver survey data to define a set of community metrics that indicated habitat quality and another set that indicated fishing impacts; and (3) develop and apply an estimation approach that accounted for inherent habitat productivity characteristics across the ecosystem to facilitate discernment of anthropogenic impacts.

Methods

Diver Probability Surveys.—This study used reef fish community data from annual-biennial diver probability surveys conducted in the Dry Tortugas, Florida Keys, and southeast Florida regions (Fig. 1). Region-scale surveys began in the late 1990s in the Dry Tortugas and Florida Keys, and in 2012 in southeast Florida. Recent surveys collected as part of NOAA CRCP's NCRMP from 2016 and 2018 were the focus of status evaluations in the three regions (the 2020 surveys were not fully completed due to the COVID-19 pandemic). The survey frame (i.e., sampling domain) encompassed the full extent of mapped reef habitats shallower than 33 m. Field sampling collected biological data following a standard, nondestructive, in situ monitoring protocol in which a stationary diver records reef fish data (numbers-at-length of each species) while in a randomly selected circular diver-centered plot 15 m in diameter (Bohnsack and Bannerot 1986, Brandt et al. 2009). Each site was sampled by a pair of divers, and biological metrics (e.g., fish density, number per 176.71 m^2) were computed as the arithmetic average of the stationary counts from each diver's circular plot. Divers also collected benthic habitat data at each location, including depth, reef morphology (e.g., patch reefs, contiguous hardbottom), substrate composition (e.g., % hardbottom, % softbottom), and reef rugosity-complexity measures.

Sampling was carried out according to a two-stage, stratified-random design (Smith et al. 2011). For randomized site selection, the sample frame was gridded into 100-m^2 cells, i.e., primary sample units (PSUs), and stratified by reef habitat characteristics (depth, substrate rugosity, reef zonation) and spatial management zones (fishing zones, no-take marine reserves). Allocation of PSUs among habitat and management zone strata was based on strata sizes (i.e., amount of habitat area) and strata variances of density for principal species, i.e., a Neyman allocation strategy (Cochran 1977). The second-stage unit (SSU) was a circular diver-centered plot, sampled by a pair of divers. At least two SSUs were randomly sampled within each PSU.

Low-Impact Reference Area.—The Dry Tortugas was designated as the reference area to evaluate reef fish community status because it was least affected

Table 1. Regional habitat and exploitation (fishing) characteristics along Florida's coral reef tract. Habitat characteristics are discussed further in the Online Supplementary Material ("Florida's Coral Reef Tract") and fishing characteristics were derived from NCRMP's sample frame.

Characteristic	Region		
	Dry Tortugas	Florida Keys	Southeast Florida
Habitat			
Proximity to human population center	113 km	Adjacent	Adjacent
Proximity to coastal bay nursery grounds	150 km	Adjacent	Proximal
Coastal bay & offshore mangrove shorelines	Limited, natural	Extensive, natural	Mostly replaced by seawalls
Dredging for navigation	Limited, one small navigational channel	Moderate, one small naval and cruise ship port, many small navigational channels & canals	Extensive, two major naval and cruise ship ports, numerous navigational channels & canals
Dredging for aesthetics	None	None	Extensive beach nourishment
Fishing	310 km^2	676 km^2	230 km^2
% Reef habitat: no-take marine reserves	47.10%	4.10%	0
% Reef habitat: closed to spearfishing and commercial fishing	25.00%	4.40%	0
% Reef habitat: size/bag limits & seasonal closure regulations	- - -	14.40%	0
% Reef habitat: additional state fishery regulations	27.90%	77.10%	100%

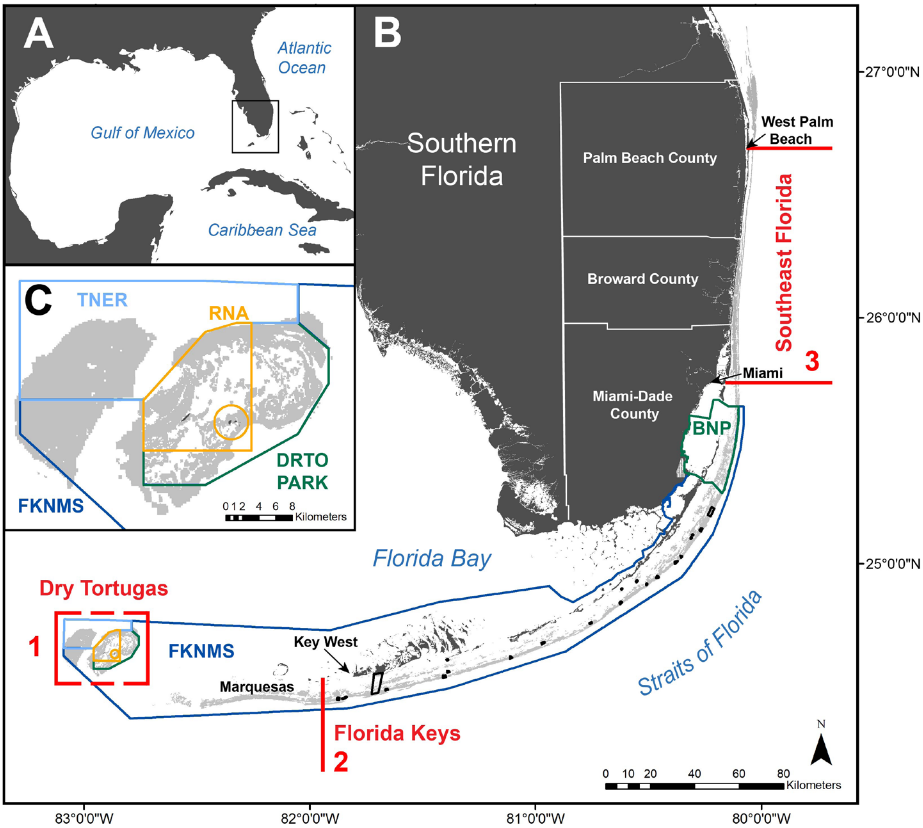

Figure 1. (A) Study area in southern Florida, United States. (B) Three regional survey sampling areas (outlined in red): (1) Dry Tortugas, (2) Florida Keys (west of Sand Key near Key West to Government Cut, Miami), and (3) southeast Florida (north of Government Cut, Miami, to West Palm Beach inlet). Surveys occurred within the sampling frame shown in light grey (i.e., reef habitat from 0 to 33 m of water depth). Management areas in the Florida Keys are outlined in colored polygons: Biscayne National Park (BNP; green), Florida Keys National Marine Sanctuary (FKNMS; dark blue), and Sanctuary Preservation Areas (SPAs; black). (C) NOAA and NPS management areas in the Dry Tortugas are outlined in colored polygons: Dry Tortugas National Park (DRTO PARK; green), FKNMS (dark blue), Tortugas North Ecological Reserve (TNER; light blue), and the selected reference area for this study, the Research Natural Area (RNA; yellow).

by anthropogenic stressors including fishing pressure and land-based sources of pollution (Table 1; Online Supplementary Material, "Florida's Coral Reef Tract"). Several options within the Dry Tortugas region were discussed with an expert panel (n = 30; Online Supplementary Material, "Expert Panel"). A no-take marine reserve within Dry Tortugas National Park, the Research Natural Area (RNA; Fig. 1C) was selected as the reference area based on the following characteristics: (1) remote location approximately 113 km from the mainland Keys, affording less overall human interaction (lower historical fishing pressure, less land-based pollution, etc.); (2) closure to landings by recreational and commercial fisheries; (3) large size (69.5 km^2 of mapped reef habitat) accounting for 22.3% of the Dry Tortugas sampling domain;

Table 2. Commercial and recreational fishery species used to compute community density metrics for "Target Adults" and "Target Juveniles". Juvenile and adult life stages were defined by length at 50% maturity L_m following Stevens et al. (2019).

Family		Species		L_m (cm)
Common	Scientific	Common	Scientific	
Triggerfishes	Balistidae	Gray triggerfish	*Balistes capriscus*	21
Groupers	Epinephelidae	Red grouper	*Epinephelus morio*	29
		Black grouper	*Mycteroperca bonaci*	83
		Yellowmouth grouper	*Mycteroperca interstitialis*	42
		Gag	*Mycteroperca microlepis*	54
		Scamp	*Mycteroperca phenax*	33
		Yellowfin grouper	*Mycteroperca venenosa*	54
Wrasses	Labridae	Hogfish	*Lachnolaimus maximus*	18
Snappers	Lutjanidae	Mutton snapper	*Lutjanus analis*	32
		Schoolmaster	*Lutjanus apodus*	25
		Blackfin snapper	*Lutjanus buccanella*	24
		Cubera snapper	*Lutjanus cyanopterus*	54
		Gray snapper	*Lutjanus griseus*	25
		Dog snapper	*Lutjanus jocu*	48
		Lane snapper	*Lutjanus synagris*	24
		Yellowtail snapper	*Ocyurus chrysurus*	23
Barracuda	Sphyraenidae	Great barracuda	*Sphyraena barracuda*	80

and (4) presence of the full range of depths and habitat classes in the respective regional domains. In conjunction with the expert panel, a reference time frame of 2011–2014 was selected for comparative analysis with the 2016–2018 surveys in the three regions. Fish densities in the Dry Tortugas region, including the RNA, substantially improved from the late 1990s following the establishment of marine reserves in the 2000s (adjacent to the RNA in 2001, RNA in 2007), and had generally plateaued by 2011 (Ault et al. 2013). In addition, three surveys were conducted in the RNA (2011, 2012, 2014) during the four-year reference time frame.

Indicator Variables.—Several community-level metrics, developed in conjunction with the expert panel, were used to define indicator variables for habitat quality and fishing impacts. Analysis focused on reef-associated, noncryptic species, which are important components of the reef fish community that are consistently sampled by the stationary-point-count method (Online Table S1). Nonreef (e.g., flatfishes), small cryptic (e.g., blennies, gobies), and rare species only observed at a single PSU in the surveys analyzed were excluded. Species richness, or alpha diversity, was selected as a simplistic community metric to characterize all fishes observed during surveys. Species richness was defined as the number of unique fish species observed in a given SSU. Reef fish density, the number of individuals per SSU (per 15-m diameter visual plot; 176.71 m^2), was estimated for three categories of species: (1) fishery-target adults, (2) fishery-target juveniles, and (3) species restricted or protected from fishing. Fishery-target species were selected based on multiple criteria, including commercial and recreational importance as well as published data on species-specific life history parameters, specifically length at maturity (L_m; Stevens et al. 2019) to determine the adult and juvenile groups (Table 2). Fishery-restricted species are those that have received a "Marine Life" (i.e., aquaria) designation by the Florida Fish and Wildlife Conservation Commission, and must be landed alive (Online Table S1). Many of these aquaria species also have maximum legal sizes to focus extraction on smaller individuals. Protected species were historically fished but under complete moratoria during the study time frame (Online Table S1). Although these community metrics are affected by a wide array of human activities, species richness and fishery target juvenile density were considered to be primarily indicators of "habitat" quality, and fishery-target adult density and restricted-protected species density were considered to be primarily indicators of fishing impacts (Rakocinski et al. 1996, Lindeman et al. 2000, Knowlton and Jackson 2008, Walker et al. 2009, Cote et al. 2013, Cook et al. 2014, Worm and Lotze 2021, Ault et al. 2022).

A species-level metric, average length ($\bar{L}$) in the exploited life stage ($L \geq L_c$, the minimum legal capture size), was also analyzed as an indicator of fishing mortality rate (Ault et al. 2005). This metric provided further insight into fishing impacts on the exploited component of the reef fish community, and also enabled comparisons with established sustainability benchmarks for $\bar{L}$ (Ault et al. 2019) as a gauge on the condition of the RNA reference area.

Estimation of Status Level, Richness, and Density Indicators.—Depth and rugosity were core ecological variables used in delineating "habitats" in reference and regional sampling domains. We capitalized on definition of six key "habitat" strata h that combined two depth intervals (shallow, <12 m; deep, ≥12 m) and three rugosity levels (low, average vertical relief <0.3 m; moderate, ≥ 0.3 – 0.5 m; high, ≥0.5 m; Table 3A).

For indicator variables y (e.g., species richness and density), reference means $\bar{y}_{ref_h}$ were used to standardize i regional SSU observations $\tilde{y}_{reg_{hi}}$ by strata h,

$$\tilde{y}_{reg_{hi}} = y_{reg_{hi}} - \bar{y}_{ref_h} \qquad \text{(Eq. 1)}$$

These reference-centered SSU observations $\tilde{y}_{reg_{hi}}$ were then used to calculate standardized stratum-level means $\bar{\tilde{y}}_h$ and variances following procedures for a two-stage stratified random sampling design (Cochran 1977, Lohr 2010). Computational formulae are provided in Smith et al. (2011). Survey strata h were a combination of depth-rugosity classes and management zones (marine reserves, fishing zones) in each sampling domain (reference and three regions); additionally, the Florida Keys region incorporated reef zonation (back reef, fore reef) in the stratification scheme (Online Supplementary Material, Online Table S2). Analyses for the 2016–2018 status in the Dry Tortugas region excluded the RNA reference area.

Estimation of region-level indicator means and variances were carried out respectively using

$$\bar{\tilde{y}}_{reg} = \sum_h w_h \bar{\tilde{y}}_h \qquad \text{(Eq. 2)}$$

and

$$\text{var}(\bar{\tilde{y}}_{reg}) = \sum_h w_h^2 \text{var}(\bar{\tilde{y}}_h) \qquad \text{(Eq. 3)}$$

Table 3A. Habitat rugosity (vertical relief) and depth ranges for the six survey strata.

Strata name (depth, rugosity)	Strata abbreviation	Depth	Vertical relief
Shallow, low	SH_L	≤12 m	≤0.3 m
Shallow, medium	SH_M	≤12 m	>0.3 m to ≤0.5m
Shallow, high	SH_H	≤12 m	>0.5 m
Deep, low	DP_L	>12–33 m	≤0.3 m
Deep, medium	DP_M	>12–33 m	>0.3 m to ≤0.5m
Deep, high	DP_H	>12–33 m	>0.5 m

Table 3B. Status scoring based on the level of significant difference between region $\bar{\bar{y}}_{reg}$ and reference $\bar{\bar{y}}_{ref}$ for a given indicator variable, where $\bar{\bar{y}}_{ref} = 0$. The status score color ramp provides a quick way to interpret results: (1) light green indicates the result is the same, (2) dark green and blue indicate that results are significantly higher, and (3) yellow, orange, and red indicate that results are significantly lower than the remote reference area.

$\bar{\bar{y}}_{reg}$	SE	Significance	Status score
> 0	+3	$P < 0.001$	U001
> 0	+2	$P < 0.010$	U01
> 0	+1	$P < 0.050$	U05
= 0	0	NS	NS
< 0	−1	$P < 0.050$	L05
< 0	−2	$P < 0.010$	L01
< 0	−3	$P < 0.001$	L001

where w_h was the proportion of stratum area within the sampling domain. Standard errors $\mathrm{SE}(\bar{\bar{y}}_{reg})$ were computed as the square root of Equation 3. Note that Equation 1 shifts the mean of the distribution of y_{hi} observations relative to the reference mean, but does not affect the sample variance of the distribution; thus, $\mathrm{SE}(\bar{\bar{y}}_h) = \mathrm{SE}(\bar{y}_h)$ and $\mathrm{SE}(\bar{\bar{y}}_{reg}) = \mathrm{SE}(\bar{y}_{reg})$.

For statistical comparisons of region and reference indicator variables, the null hypothesis is $\bar{y}_{reg} = \bar{y}_{ref}$, i.e., $\bar{\bar{y}} = 0$. A t-test was used to determine whether the standardized mean $\bar{\bar{y}}_{reg}$ was different from zero. Following standard methods for probability surveys (Lohr 2010), t-tests were carried out by constructing confidence intervals from region-level indicator means, standard errors, and sample sizes,

$$(1-\alpha)\%\mathrm{CI} = \bar{\bar{y}}_{reg} \pm t_{\alpha,df}\mathrm{SE}(\bar{\bar{y}}_{reg}) \qquad \text{(Eq. 4)}$$

where the degrees of freedom (df) for a two-stage stratified design is the number of SSUs minus the number of PSUs minus the number of strata. Equations 1–4 were also applied to reference area indicators, resulting in confidence intervals for $\bar{\bar{y}}_{ref}$ with a mean of zero. Region and reference indicator means were determined to be significantly different if both of the following conditions were met:

(1) $\bar{\bar{y}}_{reg}$ was outside the CI for $\bar{\bar{y}}_{ref}$,

and

(2) $\bar{\bar{y}}_{ref}$ was outside the CI for $\bar{\bar{y}}_{reg}$.

Testing was conducted for three levels of α: 0.05, 0.01, and 0.001. A status scoring rubric was developed based on the direction and level of significance (P-values) of differences between region and reference indicators (Table 3B).

Evaluation of Average Length.—The fishing mortality rate indicator $\bar{L}$ was estimated for a given exploited species and region using the ratio estimator:

$$\bar{L}_{reg} = \frac{\sum_h w_h \bar{Y}_h}{\sum_h w_h \bar{X}_h}, \qquad \text{(Eq. 5)}$$

where $\bar{X}_h$ is the stratum mean number of fish per SSU (i.e., density) in the exploited life stage, and $\bar{Y}_h$ is the stratum mean of the summed lengths of fish per SSU in the exploited life stage (Ault et al. 2019). Computations of means and variances for Equation 5 were carried out for a two-stage stratified design ratio estimator following Lohr (2010). As shown in Equation 5, $\bar{L}$ is a region-scale metric, and the ratio is not estimated at the stratum level; consequently, the reference-centering procedure of Equation 1 was not applicable in this case. Statistical tests comparing $\bar{L}_{reg}$ and $\bar{L}_{ref}$ were carried out using the confidence interval (Eq. 4) procedure described above. Species-specific results were then summarized for the exploited community in a given region.

Data.—Analyses combined data from three surveys in the reference area (2011, 2012, 2014) and two surveys in each region (2016, 2018). To represent the average time conditions within a spatial sampling domain, stratum means, variances, and sample sizes were averaged across survey years for the various indicator variables. Southeast Florida analyses used data from the southern portion of the region (Miami-Dade, Broward, and south Palm Beach counties), where the reef assemblage was similar to those in the Florida Keys and Dry Tortugas (Ames 2017). Sample sizes for the analysis datasets are provided in Online Table S2. All data are publicly available and can be accessed from NOAA's National Centers for Environmental Information (NCEI), through an associated R package (Ganz and Blondeau 2015), or upon request from NOAA data source contacts.

Results

The status evaluation procedure was completed for the four indicators (i.e., species richness, target juvenile, target adult, and marine life density) and aspects of the status analysis procedures are illustrated for species richness (Table 4, Figs. 2–4). Mean species richness per SSU differed among depth-rugosity classes within the reference area, with the highest average richness of about 35 species in deep-high rugosity strata and the lowest average richness of 23 species in shallow-low rugosity strata (Fig. 2). The reference-centering analysis approach (Eqs. 1–4), shown for southeast Florida in Table 4, scaled regional SSU observations with respect to mean richness in the reference area by each depth-rugosity class, accounting for the inherent differences in richness among habitats. The stratum-weighted mean of scaled richness in southeast Florida ($\bar{\tilde{y}}_{reg}$) was significantly lower than zero ($P < 0.05$), i.e., different from the reference area (Fig. 3). Analyzing scaled richness ($\tilde{y}$) rather than richness (y) also removed the impact of differing habitat compositions between the region and reference area on the region-scale estimates ($\bar{\tilde{y}}_{reg}$). For example, a region was not penalized for having a higher proportion of lower richness habitat compared to the reference area. This was an important feature of the status scoring method, because habitat compositions were substantially different in the sampling domains analyzed (Fig. 4).

Table 4. Illustration of status evaluation procedure for species richness in southeast Florida, using equations 1–4. The stratum weighted reference-centered mean richness for southeast Florida, $\bar{\bar{y}}_{reg} = -1.295$, was significantly less than zero at the $P < 0.05$ significance level. Strata categories included two depths, shallow (SH) and deep (DP); and, three rugosities, low (L), medium (M), and high (H).

	Reference (df = 91)			Southeast Florida (df = 141)		
Stratum	w_h	$\bar{\bar{y}}_h$	$\mathrm{SE}(\bar{\bar{y}}_h)$	w_h	$\bar{\bar{y}}_h$	$\mathrm{SE}(\bar{\bar{y}}_h)$
SH_L	0.2208	0.0	1.201	0.4530	−2.123	0.859
SH_M	0.1071	0.0	1.492	0.0357	0.229	1.573
SH_H	0.0204	0.0	1.178	0.0264	0.291	1.539
DP_L	0.4153	0.0	1.195	0.2430	0.425	0.756
DP_M	0.1410	0.0	0.940	0.1260	−2.173	0.887
DP_H	0.0954	0.0	0.822	0.1159	−1.542	1.110
	$\bar{\bar{y}}_{ref} \sum_h w_h \bar{\bar{y}}_h = 0.00$			$\bar{\bar{y}}_{reg} = -1.295$		
	$\mathrm{SE}(\bar{\bar{y}}_{ref}) = \sqrt{\sum_h w_h^2 [\mathrm{SE}(\bar{\bar{y}}_h)^2]} = 0.605$			$\mathrm{SE}(\bar{\bar{y}}_{reg}) = 0.468$		
	95% CI = [−1.202, 1.202]			95% CI = [−2.220, −0.370]		
Outcome:	$\bar{\bar{y}}_{reg} < \bar{\bar{y}}_{ref}$, $0.01 < P < 0.05 \rightarrow$ L0.05					

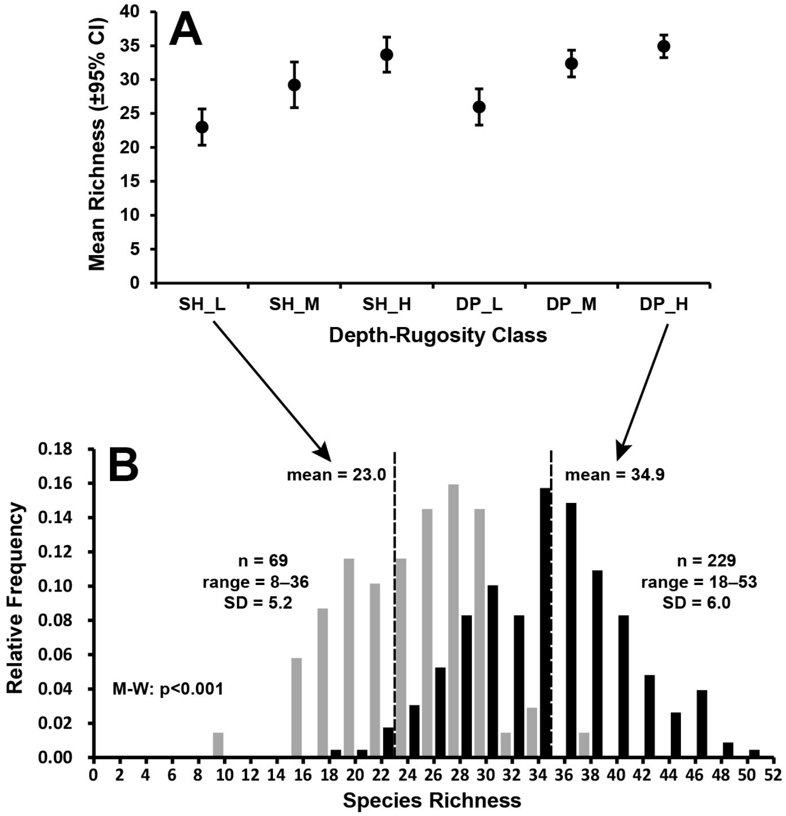

Figure 2. Comparisons of species richness metrics. (A) Means and 95% confidence intervals (CI) of species richness of the reference area by depth-rugosity class (*see* Table 3A and Fig. 1C). (B) Frequency distributions of species richness for two depth-rugosity classes SH_L (gray bars, lowest mean richness) and DP_H (black bars, highest mean richness). Although the means of the two distributions are different at the $P < 0.001$ level (Mann–Whitney U test), their distributions show considerable overlap (*see* Fig. 3).

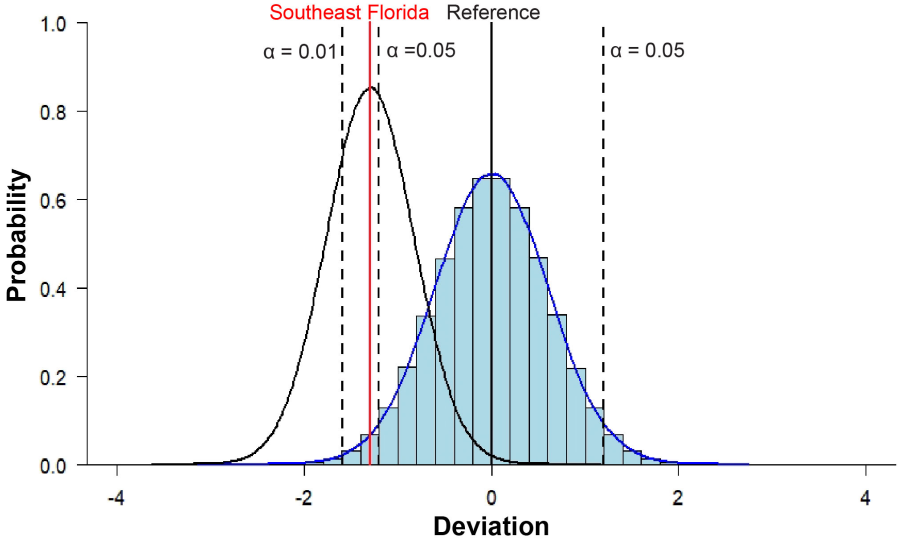

Figure 3. Comparison of the significance of the test distributions from Table 4 showing means for reference (black solid vertical line) and southeast Florida (red solid vertical line). The dashed vertical lines show the $\alpha = 0.05$ and $\alpha = 0.01$ from the $1 - \alpha$ confidence intervals. For this example, southeast Florida was significantly less than the reference area, where $0.01 < P < 0.05$.

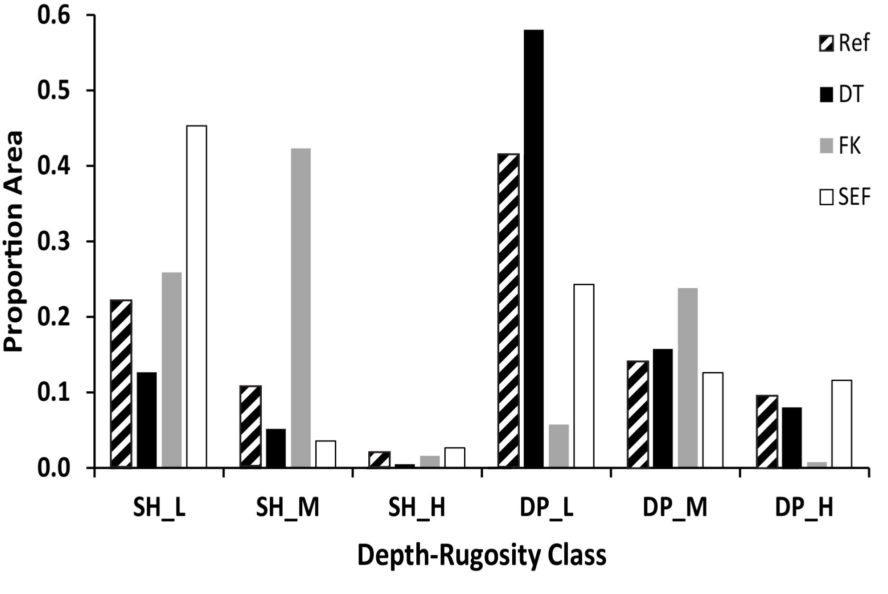

Figure 4. Proportion of area for depth-rugosity classes within the three sampling domains of the reference area (ref), Dry Tortugas (DT), Florida Keys (FK), and southeast Florida (SEF; *see* Table 3A).

Table 5. Reference-centered means ($\bar{\bar{y}}$) and associated standard errors (SE) for community metrics by region. Status scores are defined in Table 3B.

Community metric	Reference (df = 91)		Dry Tortugas (df = 208)			Florida Keys (df = 377)			Southeast Florida (df = 141)		
	Mean	SE	Mean	SE	Status score	Mean	SE	Status score	Mean	SE	Status score
Habitat Quality Indicators											
Richness	0.000	0.605	0.444	0.442	NS	−0.565	0.399	NS	−1.295	0.468	L05
Density, Target Juveniles	0.000	1.361	1.179	0.810	NS	−1.620	0.796	NS	−6.307	0.302	L001
Fishing Impact Indicators											
Density, Target Adults	0.000	0.921	−0.355	0.461	NS	−5.665	0.243	L001	−5.179	0.243	L001
Density, Marine Life-Prohibited	0.000	5.722	−6.308	3.083	NS	1.718	2.920	NS	13.406	4.625	U05

Both community indicators of "habitat" quality, species richness and juvenile density of fishery target species, were significantly lower in southeast Florida compared to the reference area (Table 5). No differences from reference values were found for habitat quality indicators in the Florida Keys and Dry Tortugas. Community indicators of fishing impacts showed densities of species restricted or protected from fishing were not different (Florida Keys) or significantly higher (southeast Florida) than reference levels, while densities of fishery target adults were lower than reference values at the $P < 0.001$ level in both regions. No differences in either indicator from reference levels were observed in the Dry Tortugas. Species-level analysis of fishing impacts confirmed these findings. The average length indicator variable was not different or higher than the reference area in the Dry Tortugas region for all 10 principal fishery species analyzed, but average lengths for 4 of 10 species in the Florida Keys and 4 of 9 species in southeast Florida were significantly below reference levels (Table 6A,B). Average length at sustainability was significantly higher than average length in the reference area for four of the five species (Table 6C).

Discussion

This study furthered the development of holistic evaluations of resource condition for coral reef ecosystems, building from previous efforts using fishes as indicators. The availability of reef fish community data from large-scale probabilistic diver surveys conducted in southern Florida across a spatial gradient of human urbanization and fishery protections was instrumental in overcoming some known difficulties (e.g., Bradley et al. 2020). Key developments in the analysis approach were: (1) identification of a low human impact reference area as the comparative basis for measuring resource conditions; (2) application of statistical estimation methods that were able to distinguish anthropogenic impacts from the inherent productivity characteristics of different habitats; (3) identification and selection of indicator variables that facilitated discrimination of two classes of impacts, habitat quality and fishing, that align with resource agency responsibilities; and (4) use of a robust sustainability benchmark to gauge the resource condition of the selected reference area. The quantitative, statistically based status scoring system made results simple to interpret and identified potential habitat quality issues in southeast Florida, as well as more pervasive fishing issues throughout the southern Florida ecosystem.

From a habitat perspective, the scores of species richness and target juvenile density metrics in the Dry Tortugas and the Florida Keys were both similar to the reference area. These regions support numerous sprawling reefs that offer an abundance of high-quality habitat with plentiful living shorelines that provide key nursery habitats (i.e., mangroves and sea grasses) to many coral reef fishes (e.g., Halley et al. 1997, Lindeman et al. 2000, NPS 2005). In comparison, lower richness and target juvenile density metric scores in southeast Florida coincided with a more uniform, lower quality, and compressed reef tract (Walker et al. 2009, Walker and Gilliam 2013). In southeast Florida, lower quality reef habitat and limited nursery habitats are a response to increased sedimentation and nutrient influx due to dredging, beach nourishment, and intense coastal development (i.e., intercoastal canals and associated retaining walls; Stauble 1993, Reich et al. 2009, Gregg and Karazsia 2013, Miller et al. 2016, Shideler et al. 2017, Ault et al. 2022). Moreover, for the data used in these analyses (2018 status year), the southeast Florida sampling domain was

Table 6A. Comparison of reference with region estimates of average length $\bar{L}$ in the exploited phase ($\bar{L} \geq \bar{L}_c$, the regulated minimum capture length) for principal fishery target species in southern Florida; "- - -" denotes insufficient length observations for analysis.

Species	$\bar{L}_{ref}$	Reference (df = 91)		Dry Tortugas (df = 208)			Florida Keys (df = 377)			Southeast Florida (df = 141)		
		$\bar{L}_{ref}$	SE($\bar{L}_{ref}$)	$\bar{L}_{reg}$	SE($\bar{L}_{reg}$)	Status score	$\bar{L}_{reg}$	SE($\bar{L}_{reg}$)	Status score	$\bar{L}_{reg}$	SE($\bar{L}_{reg}$)	Status score
Red grouper	50	58.6	1.29	59.4	1.79	NS	58.2	1.41	NS	55.8	1.74	NS
Black grouper	60	72.4	4.11	72.7	1.13	NS	67.5	2.59	NS	- - -	- - -	- - -
Mutton snapper	40	54.6	2.06	52.3	1.01	NS	47.8	1.18	L01	43.9	0.73	L001
Schoolmaster	25	30.5	0.92	32.4	1.37	NS	27.5	2.33	NS	27.7	0.48	L01
Gray snapper	30	33.4	1.02	32.9	0.79	NS	34.1	0.52	NS	33.0	3.08	NS
Dog snapper	30	54.1	0.72	58.0	1.10	U001	38.1	3.76	L001	42.4	0.23	L001
Lane snapper	20	23.3	0.07	22.7	1.93	NS	22.0	0.64	L05	23.8	1.41	NS
Yellowtail snapper	26	29.1	0.38	29.0	0.49	NS	29.0	0.50	NS	29.8	0.87	NS
Hogfish	30	38.8	1.20	39.9	1.14	NS	33.6	0.34	L001	35.7	1.16	L01
Great barracuda	38	83.3	14.76	91.7	12.07	NS	82.1	6.13	NS	111.2	11.35	NS

Table 6B. Summary of results from Table 6A, showing the number of species in each status category and the percentage of species with $\bar{L}$ lower than the reference value.

Status score	Dry Tortugas	Florida Keys	Southeast Florida
U001	1	- - -	- - -
U01	- - -	- - -	- - -
U05	- - -	- - -	- - -
NS	9	6	5
L05	- - -	1	- - -
L01	- - -	1	2
L001	- - -	2	2
% Species, Region $\bar{L}_{st}$ < Reference $\bar{L}_{st}$	0%	40%	44%

Table 6C. Comparison of the average lengths for five species from the reference area to sustainability benchmark values of average length ($\bar{L}$ at 40% spawning potential ratio) estimated by Ault et al. (2019, 2022). Status scores are defined in Table 3B.

Species	Reference				Sustainability benchmark	
	$\bar{L}_{ref}$	95% CI	99% CI	99.9% CI	$\bar{L}_{SPR40\%}$	Status score
Red grouper	58.63	(56.07, 61.19)	(55.24, 62.02)	(54.25, 63.01)	59.9	NS
Black grouper	72.36	(64.19, 80.53)	(61.54, 8318)	(58.37, 86.35)	91.5	U001
Mutton snapper	54.61	(50.52, 58.70)	(49.19, 60.02)	(47.61, 61.61)	60.4	U01
Yellowtail snapper	29.06	(28.31, 29.81)	(28.07, 30.06)	(27.78, 30.35)	33.2	U001
Hogfish	38.84	(36.46, 41.22)	(35.69, 41.99)	(34.77, 42.91)	45.8	U001

heavily impacted by stony coral tissue loss disease (SCTLD) that has resulted in substantial declines in many coral species, thus greatly degrading this component of the reef tract's habitat quality (Walton et al. 2018). Although we accounted for regional habitat differences (e.g., latitudinal dissimilarities in reef development) to the extent possible, we acknowledge that southeast Florida is at the northern end of the tropical marine environment (Walker et al. 2009, Walker and Gilliam 2013). It is possible that in pristine conditions indicator metrics may have differed between this region of the reef tract and the reference area. However, our results show very high residual variation for the target juvenile density metric (P < 0.001; Table 5) in southeast Florida that correlates with documented declines in reefs, nursery habitats, and targeted fisheries.

From a fisheries perspective, the lower metric scores for target adult density in the Florida Keys and southeast Florida domains reflect excessively high fishing effort in a region that brings in about US$6 billion dollars of fishing-related revenue annually. This high level of fishing intensity is unsustainable and puts reef fishery resources at great risk (Ault et al. 2005, 2022). This conclusion is further supported in the Florida Keys where target juvenile density is the same as the reference area, but density drops significantly when reef fishes reach sizes available for capture by the fishery. The lower target juvenile density observed in southeast Florida likely reflects reduced regional spawning capacity and lower target adult density in both southeast Florida and the Florida Keys (proximal and upstream). Consequently, low target adult density in southeast Florida is related to both reduced recruitment and high fishing effort. The nonsignificant target adult density metric score in the Dry Tortugas is a function of substantially less fishing pressure due to its remote location, and to the presence of several large marine reserves (Ault et al. 2013). In contrast, the marine life density metric scores show the success of fisheries management regulations that prohibit traditional fishery landing of these colorful aquaria species. Southeast Florida's higher score for this metric likely reflects the limited presence of predators (i.e., low fishery-target densities) due to both lower quality habitat and high fishing pressure (e.g., Johns et al. 2001, Ault et al. 2022), which may have created an opportunity for more generalist, nontargeted marine life species (e.g., Valentine and Heck 2005).

There is utility in holistic evaluations of resource status as first-order screening tools to alert resource agencies to potential problems and to help focus their research and regulatory efforts towards finding solutions. The reference-centering analysis presented here is feasible to implement in other coral reef ecosystems, can be updated periodically as data becomes available, and can be incorporated in regional and national assessments that produce wide-ranging products for a variety of audiences to promote coral reef conservation (e.g., Towle et al. 2022, Viehman et al. 2024). A critical component of this approach was the identification of a suitable reference area. Ideally, reference areas are those minimally impacted by urbanization, human population size, coastal development, land-based sources of pollution, and fisheries. However, some impacts like climate change are ubiquitous. Reference-centering can still be successfully used even with relatively imperfect reference area designations. In our study, fishing impacts were certainly lower in the Dry Tortugas region compared with other regions, but the marine reserve within Dry Tortugas National Park (reference area) was not completely isolated from anthropogenic influences. Unfortunately, a pristine reference area may no longer exist and, as such, scientists must be vigilant to account for shifting baseline syndrome when interpreting results (Pauly 1995, Towle et al. 2022, Viehman et al. 2024).

This reference-centering approach seems particularly promising for identifying impacts of habitat quality (Tables 4 and 5, Figs. 2–4). Assessing indicator variables from potentially impacted regions to the reference area by strata accounted for the inherent productivity characteristics of different habitats (e.g., Fig. 2) and differing compositions of habitat types between the reference area and evaluation region (Table 4, Fig. 4). The fine-scale stratification of these physical system characteristics helps to elucidate patterns that can vary at larger spatial scales due to large differences in individual sites. For example, there were significant differences in species richness between habitat classes, but also considerable overlap in the respective distributions of site-level observations (Fig. 2). As such, our analyses highlighted the need to be cautious when using site-level data to describe regional status. Further, they support the use of stratified reference-region analyses that are amenable to standard methods of statistical hypothesis testing (i.e., inference from comparison of means of two distributions).

The reference-centering approach also changed the role of the expert panel. Historically, expert panels have contributed to generate conceptual models, select metrics, synthesize data, assign scores, and/or interpret results (e.g., Van de Putte et al. 2021). Qualitative expert panel inputs (e.g., scoring and interpreting results) are highly dependent on the individual panel members, their personal frame of reference, and their broader knowledge of reef fishes (e.g., life history, habitat preferences, diet), the fishery (e.g., commercial fleet preferences, regulations, spatial coverage), the habitat (e.g., quantity and quality), and stressors (e.g., climate, pollution; e.g., Hare et al. 2016, Bradley et al. 2020). Expert panels will always be an integral part of ecosystem-scale fish status assessments to provide data inputs (i.e., knowledge of existing data and their limitations), determine the best metrics to evaluate, and provide insight into the relative condition of a reference area to provide a balanced and clear narrative of the assessment results. However, the goal of ecosystem-wide assessments should be to rely on experts as needed and to the extent possible perform quantitative analyses that can be easily reproduced in new regions (Game et al. 2013, Borja et al. 2016).

While the reference-centering approach was beneficial, research challenges remain, including developing more refined ecological metrics that are indicators of habitat and water quality and improved classification of benthic habitats. In addition, for evaluating fishing impacts, comparing region estimates of average length ($\bar{L}$) to sustainability benchmark values may be more appropriate and feasible compared to the reference-centering method. Fishing effort is generally applied at the region or ecosystem scale, and it may not be possible to locate a suitable reference area free from adverse fishing impacts. In our case, fishes in the remote no-take marine reserve inside Dry Tortugas National Park appeared to bear the signature of decades of intensive fishing throughout the southern Florida coral reef ecosystem (Ault et al. 1998, 2022). Substituting a sustainability benchmark for the reference area values in the analysis shown in Tables 6A and 6B and relating these to the unexploited state of the fishery is perhaps a more prudent strategy, and would eliminate the need for identifying a potential reference area and then sampling it sufficiently. However, development of sustainability benchmarks requires demographic life history parameters for age, growth, natural mortality and reproductive maturity (Quinn and Deriso 1999, Ault et al. 2019). The life history synthesis of Stevens et al. (2019) found that only 16 of 84 commercially exploited reef fishes in Florida and the US Caribbean (Puerto Rico and the US Virgin Islands) had reliable demographic parameters for conducting stock assessments. The pressing research need for this approach is thus to conduct life history research on the remaining species in the exploited reef fish complex.

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