Egyptian Journal of Aquatic Biology & Fisheries
Zoology Department, Faculty of Science,
Ain Shams University, Cairo, Egypt.
ISSN 1110 – 6131
Vol. 26(5): 681 – 705 (2022)
www.ejabf.journals.ekb.eg

Herbivorous Reef Fishes of South Sinai Marine Protected Areas (Gulf of Aqaba, Egypt): Influence of Fisheries Management and Protection Status

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ARTICLE INFO

Article History:
Received: Sept. 12, 2022
Accepted: Sept. 24, 2022
Online: Oct. 5, 2022

Keywords:
Fisheries management;
Herbivorous reef fishes,
Marine protected areas,
Gulf of Aqaba,
Red Sea

ABSTRACT

Herbivorous fish play a key role in the resilience of coral reefs to climatic stressors. In the Egyptian Gulf of Aqaba (GoA), many of these herbivores are important targets for artisanal fishing. Moreover, little is known about the status of their biomass and size-structure patterns. Therefore, this study was conducted to investigate the status of herbivorous fish communities at 30 reef sites in eight regions at the western side of the GoA. Notably, these regions are subject to three levels of fishing and protection, ranging from almost unfished (no-take, NT) to moderately fished (gear-restriction, GR) or heavily fished (open-access, OA). The results of this study showed that no-take fishery reserves are the most effective in maintaining the richness, body size, and biomass of all functional groups of herbivorous fishes. Total herbivorous fish biomass was 4.3 and 2.8 times higher on NT reefs and GR reefs, respectively, than on OA reefs. Among GoA regions, only Ras Mohammed and Sharm El-Sheikh (unfished) and Nabq (moderately fished) met the global mean herbivorous fish biomass target of 30 kg/500 m^2. The current work highlighted three important results: (i) size structure of herbivorous fishes was heavily skewed toward smaller individuals, with fishes less than 20 cm accounting for 81.1% of the population at OA (heavily fished) reefs vs. 52.8% at NT (unfished) reefs; (ii) biomass of larger herbivore individuals (> 35 cm) accounted for less than 1% of the total biomass in OA reefs vs. 37% at NT reefs; (iii) large-bodied target species, such as *Cetoscarus bicolor*, *Naso unicorn*, and *Kyphosus* spp., accounted for 15.9% of the total biomass at NT reefs, while they were virtually absent from OA reefs. Collectively, these findings suggest that many principal fishery species in the northern regions of the GoA have been overfished, which in turn can lead to coral reef degradation.

INTRODUCTION

Coral reef ecosystems are among the world's most structurally complex, biodiverse, and valuable ecosystems, supporting nearly a third of all marine fish species **(Wilkinson, 2008; Graham & Nash, 2013; Fisher *et al.*, 2015)**. However, this unique ecosystem is among the most vulnerable to local stressors, mostly from overfishing **(Burke *et al.*, 2011)**. Worldwide, many people depend on coral reefs as a source of food and income, both from reef fisheries and reef-based tourism activities **(Wilkinson, 2008)**. Furthermore, approximately 75% of the world's reefs are in developing countries, and the rapid growth of the reef-based tourism sector has contributed to increasing demand for reef fishes, which in turn has significantly depleted many fish populations **(Ashworth & Ormond, 2005; Burke *et al.*, 2011)**. Indeed, managing the ever-increasing demand for coral reef fisheries while maintaining the functionality and ecological resilience of reefs is one of the most important and challenging issues regarding corals' present and future **(Pratchett *et al.*, 2014; Chung *et al.*, 2019)**.

The Gulf of Aqaba **(GoA)** in the northern Red Sea is home to one of the world's most diverse high-latitude reefs and a coral refuge from global stressors, yet it is also under increasing pressure from local stressors, in particular overfishing and destructive fishing methods **(Burke *et al.*, 2011; Fine *et al.*, 2013; Osman *et al.*, 2018)**. Egypt's coral reefs have a national economic value due to their importance for local artisanal fisheries and tourism, ranking as one of the top ten countries with the highest total coral reef tourism value, accounting for $5.5 billion annually **(Spalding *et al.*, 2017)**. Coral reefs along the Egyptian GoA coast have been fished by the local Bedouin community for generations as part of their traditional activities **(Poonian, 2020)**. To protect and conserve these unique reefs and coral reef fisheries, Egypt established a network of three connected marine protected areas **(MPAs)** in Sinai Peninsula, covering the entirety of Egypt’s GoA **(Pearson & Shehata, 1998)**. However, their management effectiveness has diminished over time due to inadequate staffing and financial resources, especially in the past decade **(Mabrouk, 2015; Samy-kamal, 2015)**. Moreover, non-compliance and weak enforcement of fishing regulations in some of Sinai MPAs may constitute a threat to conservation goals and subsequently the efficacy of the MPAs **(Advani *et al.*, 2015; Gill *et al.*, 2017)**.

Fisheries management systems **(FMSs)** vary widely across GoA regions. In Ras Mohammed and Sharm El-Sheikh (southern GoA), all forms of nearshore fishing are prohibited **(Mabrouk, 2015)**. Whereas in Nabq (north of Sharm El-Sheikh), fishing is permitted only for local Bedouin using their traditional gear (e.g., gillnets and trammel nets) to target mainly herbivorous fish entering the reef flat with the rising tides to feed on algae **(Galal *et al.*, 2002)**. In Abu Galum and Dahab (central GoA), fishing is permitted in the designated areas and prohibited at all dive sites **(Hasler and Ott, 2008)**. On the other hand, fisheries management appears to be more permissive in Nuweiba and Taba (northern GoA), where a variety of fishing gear (e.g., hook and line, nets, traps, and spear guns) are used almost throughout these regions **(Tilot *et al.*, 2008; Poonian, 2020)**.

Local management of herbivorous fish populations (via size limits, gear restrictions, or spatial closures) has been widely acknowledged as an effective tool that reef managers can use to protect or restore herbivorous fish populations and indirectly maintain reef health and resilience **(Bozec *et al.*, 2016; Williams *et al.*, 2016, 2019; Weijerman *et al.*, 2018; Chung *et al.*, 2019)**. Herbivorous fish species are largely classified into four main functional groups; namely, grazers, browsers, scrapers and excavators. Their ecological roles are critical in controlling coral-algal spatial competition **(Burkepile & Hay, 2008; Green & Bellwood, 2009; Cheal *et al.*, 2010)**. Therefore, a growing number of recent studies have concluded that (i) effective management of herbivorous fishes is a critical tool for preserving coral reef resilience, and (ii) monitoring programmes should include fish biomass as the most useful indicator or response metric for evaluating the status of coral reef fisheries in order to set practical management targets **(Green & Bellwood, 2009; Chung *et al.*, 2019; Williams *et al.*, 2019; Campbell *et al.*, 2020; McClanahan *et al.*, 2019, 2021)**.

Herbivorous reef fishes have been studied in many coral reefs throughout the world **(Helyer & Samhouri, 2017; Robinson *et al.*, 2020; Shantz *et al.*, 2020; Cure *et al.*, 2021)**. Moreover, they were addressed in the Red Sea **(Alwany *et al.*, 2009; Afeworki *et al.*, 2013; Khalil *et al.*, 2013, 2017; Kattan *et al.*, 2017)**. In the GoA, a series of studies have described the status of herbivorous fishes **(Ashworth & Ormond, 2005; Tilot *et al.*, 2008; Advani *et al.*, 2015; Naumann *et al.*, 2015; Reverter *et al.*, 2020; El-Haddad *et al.*, 2022)**. However, these studies were generally limited by the fact that they focused on a specific region or a specific fish group. Furthermore, quantitative information on the biomass and size structure of the functional groups of herbivorous fishes in the Egyptian reefs is largely missing, hampering attempts to measure the effectiveness of South Sinai MPAs in maintaining herbivorous fish communities after several decades of their establishment.

The present study, therefore, was intended to provide a better understanding of whether South Sinai MPAs are effective in protecting and sustaining healthy levels of all functional groups of herbivorous fish by investigating four important ecological metrics (species richness, density, biomass, and body size), which are critical to maintain the health and survival of coral reefs.

MATERIALS AND METHODS

1. Study sites and survey design

Underwater visual censuses of herbivorous reef fishes were carried out between April and September 2017. A total of 30 reef sites from eight regions were surveyed. These sites were distributed along 250 km of coastline in the northern Red Sea and the GoA (Table 1 & Fig. 1). In the Egyptian GoA, three FMSs were classified based on the level of conservation and protection, fishing intensity, and compliance with fishery regulations (Table 2). The southern GoA regions (Ras Mohammad and Sharm El-Sheikh) are classified as NT, where near-shore fishing is prohibited; the central GoA regions (Nabq, Dahab, and Abu Galum) as GR, where artisanal reef fisheries are regulated (via limitations on the use of fishing gear), and the northern GoA regions (South Nuweiba, North Nuweiba, and Taba) as OA, where fisheries management appears to be more permissive than other regions where a variety of fishing gear (e.g., hook and line, nets, traps, and spear guns) are used throughout these regions (Table 2 & Fig. 1).

2. Herbivorous fish surveys

Species-level visual censuses targeting four key herbivorous coral reef fish families (Acanthuridae, Kyphosidae, Scaridae, and Siganidae) were conducted using the standard underwater visual belt-transect survey method **(Hill & Wilkinson, 2004)**. At each site, four 50×10 m belt transects were laid along reef crest habitat, oriented parallel to the coastline, and each was separated by a minimum of at least 5 meters to ensure independence between transects. At each transect, herbivorous fishes were counted, and the body length of each fish individual was visually estimated to the nearest 5cm. The surveys focused on counting fish larger than 10cm (total length, TL), and 5cm for the two small acanthurid species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. Each fish was classified into one of the following nine

(5cm) size classes; 6-10, 11-15,..., 41-45, and 46- 50cm. Fish biomass and density were summarized per transect area (500 m^2), whereas fish size and richness were determined per site area (2000 m^2). All surveys were limited to reef crest habitat (1–3 m depth) and conducted during daylight hours between 10:00 and 17:00hr at high tide to ensure that counts were undertaken when the reef crest zone was available for grazing fishes.

Table 1. Details of 30 sites surveyed along the Gulf of Aqaba, Egypt. [Eight regions with different type of fisheries management and protection were surveyed, each comprised of 3-5 sites. Sites were assigned a numerical code (1-30) in order of latitude. The coordinates (in decimal degrees format) indicate survey location on reef site].

Fisheries management	Region	Site ID	Site name	Lat. (N)	Long. (E)
	Ras Mohammad	1	Mangrove Channel	27.724347	34.251272
		2	Yollanda Beach	27.728206	34.256730
		3	Old Quay	27.732875	34.242647
No-take (NT)		4	Eel Garden	27.737806	34.256753
		5	South Bareika	27.766686	34.220025
	Sharm El-Sheikh	6	Umm el-Sidd	27.852033	34.316664
		7	Sheikh Coast	27.932728	34.369997
		8	North Nasrani	27.994628	34.434483
	Nabq	9	Al-Gharqana	28.121594	34.441964
		10	Maria Schroder	28.189000	34.442275
		11	Ras Tantour	28.243642	34.415519
		12	Al-Sheheira	28.409100	34.451550
	Dahab	13	Three Pools	28.435117	34.456586
Gear-restricted (GR)		14	Al-Island	28.477378	34.511703
		15	Al-Canyon	28.556867	34.523172
	Abu Galum	16	Al-Dahayla	28.614869	34.559917
		17	Al-Omayed	28.626903	34.575272
		18	Ras Mamlah	28.731942	34.625756
		19	Al-Sokhn	28.758806	34.623367
	South Nuweiba	20	Al-Sokhn north	28.773244	34.625372
		21	Wadi Miran	28.805558	34.624556
		22	Hobiq	28.879167	34.645350
		23	Hobiq north	28.895678	34.649092
		24	Al-Mazariq	28.920800	34.644264
Open-access (OA)	North Nuweiba	25	AL-Tirabin north	29.063219	34.672967
		26	Ras Shattan	29.126361	34.685983
		27	Basata	29.204842	34.735264
	Taba	28	Al-Mahash	29.325411	34.753739
		29	Morgana Beach	29.359872	34.783369
		30	Taba Heights	29.390611	34.810786

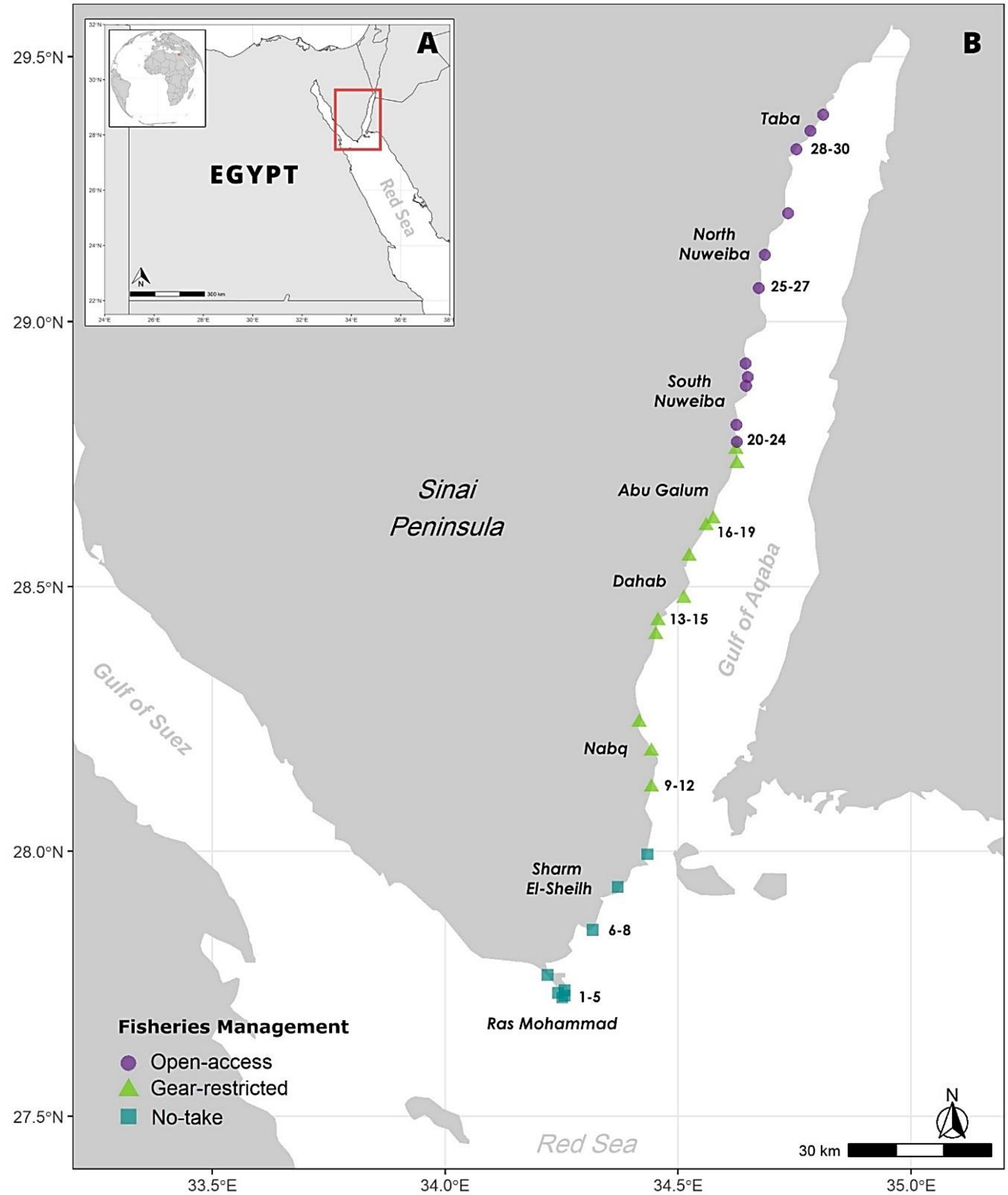

Fig. 1. **(A)** Map of Egypt showing the location of the GoA. **(B)** Map of the GoA showing locations of the eight study regions representing 30 reef sites. Different shapes represent fisheries management type; (square symbols) represent NT, (triangles) represent GR, and (circles) represent OA reefs. Surveyed sites per region were assigned a numerical code (shown next to regions).

Table 2. The potential effects of local stressors on coral reefs in the surveyed regions. The uses allowed (√), permitted in the designated zones (P), or prohibited (x) within each region are shown. Severity of each impact is shown as: (-) non-significant; (+) noticeable; (++) marked; (+++) severe. Adopted from **(Galal, 1999; Ashworth, 2004; Mabrouk, 2015)** to include the northern regions of the GoA.

Local anthropogenic threats	**No-take**		**Gear-restricted**			**Open-access**		
	RM	**SH**	**NQ**	**DB**	**AG**	**SN**	**NN**	**TB**
Fishing	x	x	P	P	P	√	√	√
(Gill & Trammel nets, Hand-lining)	-	-	++	++	++	+++	+++	+++
Harvesting of reef organisms	x	x	P	P	P	√	√	√
(Collection of Shells and Octopus)	-	-	+++	+++	+++	+++	+++	+++
Coastal construction	x	√	P	√	P	x	√	√
(Camps, Villages, Hotels)	-	+++	+	+++	++	-	+++	+++
Recreational activities	√	√	√	√	√	x	√	√
(Snorkeling, SCUBA diving)	+++	+++	+	+++	++	-	+	+

RM= Ras Mohammad, **SH**= Sharm el-Sheikh, **NQ**= Nabq, **DB**= Dahab, **AG**= Abu Galum, **SN**= South Nuweiba, **NN**= North Nuweiba, **TB**= Taba

3. Estimations of fish biomass

Fish densities and length estimates were converted to kilograms (kg) of biomass per unit area (kg/500 m^2) using the allometric length-weight equation: $W= aTL^b$; where, W is weight in kilograms; TL is the total length in cm (taking the midpoint of each size class), and parameters a and b are species-specific constants derived for each species from FishBase **(Froese & Pauly, 2019)** and other published resources in the region **(Abdulghani, 2018; Gabr *et al.*, 2018; Amin *et al.*, 2019)**. Herbivorous fish species were placed into one of four functional feeding groups: excavators, scrapers, grazers and browsers **(Green & Bellwood, 2009)**. However, non- categorized species in the aforementioned references, such as *Chlorurus sordidus* was identified as excavator, and *Siganus stellatus* and *Ctenochaetus striatus* were identified as grazers **(Marshell & Mumby, 2012; Afeworki *et al.*, 2013)**, while *Siganus luridus* and *Siganus rivulatus* were determined as macroalgal browsers **(Ebrahim *et al.*, 2020**

4. Data analyses

For each fish species, the density, biomass, and frequency of occurrence metrics were calculated as a percentage of the grand total for each metric. Subsequently, an index of relative dominance **(IRD)** for each species was created by multiplying the percent frequency of occurrence of the species combination by the relative percent biomass of that species **(Friedlander *et al.*, 2003)**.

4.1. Univariate data analysis

Herbivorous fish characteristics (density, biomass, species richness, body length) among different FMSs were analyzed using generalized linear mixed models (GLMMs). All models included the predictors 'fisheries management' as (fixed effect with three levels: NT, GR, OA), while the two spatial variables (region, site) were as random effects to account for their potential influence upon herbivorous fish characteristics, as response variables. Mean herbivorous fish biomass and body length were modelled using a Gamma distribution (R package lme4) **(Bates *et al.*, 2015)**, which is appropriate for continuous data **(Zuur *et al.*, 2009)**, while species richness and numerical density (abundance) were modelled using a Poisson distribution (R package lme4), which is appropriate for count data **(Zuur *et al.*, 2009)**. All models were fitted with a "log" link function. A Tukey post-hoc test was used to investigate pairwise differences between significant factor levels using the glht function of the multcomp package (Hothorn *et al*., 2008) in R project 4.0.3 **(R Core Team, 2020)**.

4.2. Multivariate data analysis

(a). To examine variability in herbivorous fish biomass and density between FMSs, multivariate statistical and ordination methods were implemented through the R package vegan **(Oksanen *et al.*, 2019)**. At site level, fish species density and biomass for the entire herbivorous fishes and for each individual feeding group were averaged and distance matrices based on Bray–Curtis dissimilarities were created using the vegdist function. First, we conducted permutational multivariate analysis of variance (PERMANOVA) tests using the adonis function to test whether the biomass and density varied significantly among the different types of FMSs. Similarly, a permutational analysis of multivariate dispersion (PERMDISP; betadisper function) within the FMSs was conducted. Adonis Pairwise comparisons were tested using the Pairwise Adonis function **(Martinez, 2020)**. Next, we performed a multivariate ordination (principal coordinates analysis; PCoA) using the betadisper function to display the variation observed in PERMANOVA tests. Statistical significance of the PCoA ordinations was determined by an ANOVA-like permutation test (permutest function). Finally, to determine the species responsible for driving any observed differences in the herbivorous fish density and biomass, we used the simper (similarity percentages) function to identify influential species among FMSs. A cut-off criterion was applied to allow identification of a subset of species, whose cumulative percentage contribution reached 70% of the dissimilarity value. The above-mentioned analyses were conducted in the software R v.4.0.3 **(R Core Team, 2020)**.

(b). To evaluate whether the mean density and biomass of total herbivorous fish were affected by fisheries management, region or site factors, we used a PERMANOVA **(Anderson, 2014)**, based on a Bray–Curtis resemblance matrix with square-root transformed data. The design was based on three factors: (i) FMSs (fixed factor), (ii) region (nested in FMSs, random factor), and (iii) site (nested in region and FMSs, random factor). The relative importance of each factor was quantified through the estimates of component of variation. Next, the potential effect of multivariate dispersion was assessed using PERMDISP **(Anderson, 2006)**. Multivariate patterns were visualized through (canonical analysis of principal coordinates; CAP) **(Anderson & Willis, 2003)**, with herbivorous fish density and biomass data of all replicates. In each CAP biplot, correlation vectors based on Spearman ranking (>0.5) were overlaid on the CAP plots to determine which fish species (vectors) were responsible for the clusters. Analyses and CAP ordination were performed in using PRIMER 6.1.13 and in the PERMANOVA + 1.0.3 add-on **(Clarke & Gorley, 2001; Anderson *et al.*, 2008)**.

RESULTS

1. Herbivorous fish assemblages

A total of 12,542 fish belong to 24 herbivorous species (8 browsing, 3 excavating, 6 grazing, and 7 scarping) were recorded. One-third of the observed herbivore species (10 spp.) were widely distributed, occurring on 80-100% of survey sites **(Table 3)**. Among the encountered species, only two were endemic to the Red Sea region: *C. gibbus* and *C. viridescens*, together comprised only 2.2 and 3.5% of the total density and total biomass, respectively **(Table 3)**. The most dominant species based on **IRD** was *A. sohal*, which was present in 55% of transects and accounting for 25.6% of the total biomass. The next most dominant species were *C. sordidus* and *S. niger*, which together accounted for 18.1% of the total biomass and 14.6% of the total density **(Table 3)**. The overall abundant species in terms of numerical density were the small-bodied grazers *A. nigrofuscus* and *C. striatus*, together accounting for 45.4% of the total density. The most dominant functional group was grazers (61.2 and 37.8% of total density and biomass, respectively), followed by browsers (16.3% and 22.6%), scrapers (12.6% and 26.5%), and excavators (9.9% and 13.0%).

Table 3. Abundance (%) and biomass (%) of the grand total, and frequency of occurrence (total number of transects=120) of observed herbivorous fish species in the study area.
Species are ordered by IRD= (frequency of occurrence × percent biomass) × 100

Functional group	Family	Species	Abundance	Biomass	*Freq.*	IRD
Grazers	Acanthuridae	*Acanthurus sohal*	6.9	25.6	55	**1408.4**
Excavators	Scaridae	*Chlorurus sordidus*	9.1	10.2	97.5	**997.6**
Scrapers	Scaridae	*Scarus niger*	5.5	7.8	96.67	**757.8**
Browsers	Siganidae	*Siganus luridus*	8.6	6.6	84.17	**553.4**
Scrapers	Scaridae	*Hipposcarus harid*	3.1	7.6	61.67	**467.2**
Grazers	Acanthuridae	*Ctenochaetus striatus*	13.4	4.5	98.33	**438.5**
Scrapers	Scaridae	*Scarus ferrugineus*	2.5	5.4	79.17	**424.9**
Grazers	Acanthuridae	*Acanthurus nigrofuscus*	32	3.9	98.33	**385.2**
Grazers	Acanthuridae	*Zebrasoma xanthurum*	5.6	2.1	80	**169.4**
Browsers	Acanthuridae	*Naso unicornis*	1.1	7.5	21.67	**161.7**
Scrapers	Scaridae	*Scarus frenatus*	0.6	3.9	35.83	**138.4**
Browsers	Acanthuridae	*Naso elegans*	1.0	3.3	33.33	**110.3**
Grazers	Acanthuridae	*Zebrasoma desjardinii*	3.1	1.7	66.67	**109.9**
Browsers	Scaridae	*Calotomus viridescens*	1.6	1.6	65.83	**103.3**
Excavators	Scaridae	*Chlorurus gibbus*	0.6	1.9	40	**76.8**
Scrapers	Scaridae	*Scarus fuscopurpureus*	0.6	0.9	25	**24.8**
Browsers	Siganidae	*Siganus rivulatus*	2.6	1.1	20.83	**22.8**
Excavators	Scaridae	*Cetoscarus bicolor*	0.2	0.9	14.17	**12.3**
Browsers	Kyphosidae	*Kyphosus vaigiensis*	0.3	1.2	8.33	**9.7**
Browsers	Siganidae	*Siganus argenteus*	1.0	0.8	6.67	**5.1**
Scrapers	Scaridae	*Scarus ghobban*	0.2	0.7	7.5	**4.9**
Browsers	Kyphosidae	*Kyphosus cinerascens*	0.2	0.7	6.67	**4.7**
Scrapers	Scaridae	*Scarus psittacus*	0.2	0.2	10	**2.2**
Grazers	Siganidae	*Siganus stellatus*	0.2	0.1	5	**0.4**

2. Total herbivorous fish

The grand mean biomass of herbivorous fish was 36.2 ± 2.1 kg per 500 m^2 in unfished locations (NT) and 23.7 ± 4.0 in moderately fished locations (GR), respectively; both were significantly greater by ~4.3 and 2.8 times that of heavily fished locations (OA) (GLMMs, t = -6.65, P<0.001; pairwise test, P<0.001; **(Tables 4a & 5a** and **Fig. 2a**). Herbivore biomass values varied considerably among regions and across sites, ranging from 2.9 ± 0.5 kg at heavily fished (OA) sites of Taba, to 38.4±1.8 kg at unfished (NT) sites of Ras Mohammed **(Table 4a)**. Among GoA regions, the unfished regions (Ras Mohammed and Sharm El-Sheikh) and only one of fished regions (Nabq) met the global mean herbivorous fish biomass target of ~30 kg/500 m^2 **(Edwards *et al.*, 2014)**. Comparing study reef sites-level biomass to the global herbivore biomass target, we found that 87.5% of NT sites exceeded this target, compared to 27.3% of GR sites. Noticeably, none of the OA sites have reached this target **(Table 4a)**.

The grand mean density of herbivorous fish was 136.5 ± 27.6 individuals (ind) per 500 m^2 at GR reefs, which was 1.3 and 1.9 times higher than at NT and OA reefs, though this variation was not significant (GLMMs; P>0.05; (**Tables 4b & 5b** and **Fig. 2b**). Herbivore density varied considerably among regions and across sites, ranging from 48.2 ± 10.0 ind at heavily fished (OA) sites of Taba, to 188.1 ± 59.4 ind at moderately fished (GR) sites of Nabq **(Table 4b)**.

Species richness of herbivores declined significantly with increasing fishing pressure, from 16.9 ± 1.1 species per 2000 m^2 at NT reefs to 11.3 ± 0.5 species at OA reefs (GLMMs; P=0.002; **(Table 4c** and **Fig. 2c**). Notably, six species (four browsers, one grazer and one excavator) were not observed at OA reef sites. A pairwise comparison between NT and GR reefs revealed a non-significant variation (pairwise test, P=0.831; **Table 5b**). At region level, the highest species richness was recorded at Ras Mohammed with 19 ± 0.7 species and the lowest was at Taba with 9.7 ± 0.3 species **(Table 4c)**.

In accordance with biomass variation, herbivorous fish size declined significantly from 25.4 ± 3.9 cm per 2000 m^2 at NT reefs to 19.7 ± 2.5 cm at GR reefs, and to 16.6 ± 2.2 cm at OA reefs (P<0.001 for all comparisons; **(Tables 4d & 5d** and **Fig. 2d**). Size-class distribution of herbivorous fishes in fished (GR and OA) locations were dominated by small-sized individuals (6–20 cm in length) with 77.4% and 81.1% of the total density, representing 30.8% and 37.3% of the total biomass, respectively. However, a moderate frequency of small-sized individuals was recorded in unfished NT locations with 50.8% of the total density representing 12.2% of the total biomass. In contrast, only 8.8% and 3.5% of the total density in fished (GR and OA) locations were larger than 30 cm, compared to 26.1% in NT locations. The variation is even greater in terms of biomass, with NT reefs having more than 45 times the biomass of large (> 35 cm) herbivores when compared with heavily fished OA reefs **(Table 4)**.

3. Functional groups

Biomass, species richness, and size-frequency distributions of the four functional groups of herbivorous reef fishes declined considerably with increasing fishing pressure along the GoA. Generally, these three ecological metrics were lower at heavily fished and moderately fished reefs than at unfished reefs **(Table 4)**.

Three functional groups (scrapers, grazers, and browsers) revealed significant declines in biomass with increasing fishing pressure. This pattern was mostly notable when comparing

NT with OA reefs (GLMMs; $P<0.001$ for the three functional groups **(Table 5**). In respect to scrapers, biomass and density varied significantly between NT and OA reefs (GLMMs: $P<0.001$ for all comparisons (**Table 5**). The size-class distribution of scrapers declined considerably from 31.9 ± 1.0 cm at NT reefs to 27.8 ± 0.4 cm at OA reefs. Biomass and density values of scrapers varied greatly among GoA regions, with Ras Mohammed having the highest value 12.2 ± 2.6 kg and 23.6 ± 6.3 ind., whereas Taba had the lowest biomass value 0.6 ± 0.2 kg, and North Nuweiba had the lowest density with 2.9 ± 1.4 ind. **(Table 4)**.

Biomass results of grazers and browsers revealed high significant differences between NT reefs and OA reefs, though density was not (GLMMs: $P<0.001$ for all comparisons (**Table 5**). At NT reefs, most of the grazers and browsers biomass came from the large-sized classes (more than 30 cm), contrary to GR and OA reefs were in the size classes less than 30 cm **(Fig. 3)**. Among South Sinai regions, the biomass and density of grazers and browsers were considerably greater in Nabq, with (18.1 ± 4.7 and 9.5 ± 2.5 kg) and (107.2 ± 33.5 and 52.2 ± 24.2 ind.), respectively, whereas they were lowest in the heavily fished OA regions **(Tables 4)**. Densities of both functional groups were dominated by medium- and small-sized fishes in all fisheries management systems of South Sinai MPAs.

Biomass of excavators showed a little variation among the investigated FMSs except for the NT reefs, where they showed considerably higher abundance for large size-classes (i.e., >35 cm **(Fig. 3**). At region level, mean biomass and density of excavators were highest at Abu Galum with 3.7 ± 0.4 kg (per 500 m^2) and 13.3 ± 2.0 individuals (per 500 m^2), respectively, followed by Ras Mohammed and Sharm El-Sheikh **(Table 4a)**. Size-class distribution of excavators declined from 27.5 ± 1.2 cm (per 2000 m^2) at NT reefs to 24.5 ± 0.5 cm in GR reefs, and to 23.4 ± 0.6 cm at OA reefs **(Table 4d)**. Furthermore, excavators at fished (GR and OA) reefs were generally dominated by small-sized individuals (6–20 cm in length) with 77.4% and 81.1% of the total density compared to 50.8% at unfished NT reefs. Notably, large-sized excavators (>40 cm) were totally absent from OA reefs, distinguishing this assemblage from that on NT reefs **(Fig. 3)**.

Table 4. Comparisons of fish biomass (kg/500 m^2), density (individual/500 m^2), richness (species number/2000 m^2), and size (body-length in cm/2000 m^2) of the studied functional groups of herbivorous reef fishes (excavators, scrapers, grazers, and browsers) and for all groups combined (total herbivores) in the surveyed regions and fisheries management systems. Values are grand mean values (±SE). Fish biomass and density data were averaged per transect area (500 m^2), whereas fish richness and size data were averaged per site area (2000 m^2).

	RM (n= 5)	**SH (n= 3)**	**Total NT**	**NQ (n= 4)**	**DB (n= 3)**	**AG (n= 4)**	**Total GR**	**SN (n= 5)**	**NN (n= 3)**	**TB (n= 3)**	**Total OA**
(a) Biomass											
Excavators	3.5±0.2	3.1±1.0	**3.4±0.4**	2.6±0.7	2.9±0.9	3.7±0.4	**3.1±0.4**	2.7±0.8	2.3±0.7	0.8±0.2	**2.1±0.4**
Scrapers	12.2±2.6	6.5±1.6	**10.0±1.9**	6.5±1.7	5.7±1.2	4.6±0.6	**5.6±0.7**	4.1±0.6	2.2±0.8	0.6±0.2	**2.6±0.6**
Grazers	13.9±2.7	14.9±5.6	**14.3±2.4**	18.1±4.7	4.1±2.1	4.4±2.3	**9.3±2.8**	3.8±1.0	1.7±0.5	0.9±0.2	**2.5±0.6**
Browsers	8.9±1.5	7.9±6.7	**8.5±2.4**	9.5±2.5	3.9±1.2	3.1±0.6	**5.7±1.3**	1.9±0.5	1.4±0.1	0.5±0.1	**1.4±0.3**
Total	**38.4±1.8**	**32.4±4.3**	**36.2±2.1**	**36.8±5.9**	**16.5±4.9**	**15.9±2.7**	**23.7±4.0**	**12.5±2.7**	**7.5±1.6**	**2.9±0.5**	**8.5±1.8**
(b) Density											
Excavators	10.7±1.0	10.4±5.5	**10.6±1.9**	11.1±2.2	10.6±1.5	13.3±2.0	**11.7±1.1**	13.5±4.0	7.0±0.3	6.6±3.5	**9.9±2.2**
Scrapers	23.6±6.3	14.5±3.3	**20.2±4.3**	14.3±2.2	17.3±1.9	11.7±1.6	**14.2±1.2**	11.6±1.3	2.9±1.4	5.8±4.0	**7.6±1.6**
Grazers	57.9±8.6	68.4±24.6	**61.9±9.7**	107.2±33.5	43.2±10.7	90.4±38.3	**83.6±18.8**	52.9±11.3	40.9±5.9	38.5±9.3	**47.0±6.0**
Browsers	17.0±3.7	9.4±4.7	**14.2±3.0**	52.2±24.2	14.9±1.0	19.8±1.4	**30.2±9.6**	13.3±1.0	5.9±1.3	7.7±4.4	**9.7±1.6**
Total	**109.1±10.8**	**102.7±30.2**	**106.7±11.9**	**188.1±59.4**	**79.2±17.5**	**127.9±39.5**	**136.5±27.6**	**88.2±15.5**	**62.4±8.7**	**48.2±10.0**	**70.2±9.1**
(c) Species richness											
Excavators	3.0±0.0	2.3±0.3	**2.8±0.2**	2.3±0.5	2.0±0.6	2.5±0.3	**2.3±0.2**	1.6±0.2	1.7±0.3	1.0±0.0	**1.5±0.2**
Scrapers	5.6±0.4	3.7±0.3	**4.9±0.4**	6.0±0.3	4.3±0.3	4.5±0.6	**5.0±0.4**	3.8±0.2	3.3±1.3	2.3±0.7	**3.3±0.4**
Grazers	5.2±0.2	4.7±0.3	**5.0±0.2**	5.0±0.4	4.7±0.3	4.3±0.5	**4.6±0.2**	4.2±0.4	4.0±0.0	4.3±0.3	**4.2±0.2**
Browsers	5.2±0.5	2.7±0.7	**4.3±0.6**	4.3±0.3	3.3±0.7	3.8±0.8	**3.8±0.3**	2.4±0.2	2.7±0.3	2.0±0.0	**2.4±0.2**
Total	**19.0±0.7**	**13.3±0.3**	**16.9±1.1**	**17.5±0.9**	**14.3±1.8**	**15.0±1.1**	**15.7±0.8**	**12.0±0.3**	**11.7±1.8**	**9.7±0.3**	**11.3±0.5**
(d) Fish-size (cm)											
Excavators	26.6±0.9	29.1±2.8	**27.5±1.2**	24.0±0.9	24.9±0.9	24.7±0.8	**24.5±0.5**	22.9±0.7	22.5±1.0	25.0±1.5	**23.4±0.6**
Scrapers	31.8±1.1	32.0±2.3	**31.9±1.0**	29.7±0.9	29.0±1.0	26.8±0.9	**28.4±0.6**	27.4±0.8	28.5±0.5	27.6±0.6	**27.8±0.4**
Grazers	23.0±3.9	23.1±4.0	**23.0±2.7**	17.8±1.2	15.4±1.7	14.2±0.4	**15.8±0.8**	14.1±0.6	14.2±1.1	14.4±0.3	**14.2±0.4**
Browsers	30.2±2.2	32.4±5.2	**31.0±2.2**	23.6±2.0	23.3±1.5	21.4±0.2	**22.7±0.8**	20.2±0.9	21.1±1.2	19.6±0.5	**20.3±0.5**
Total	**24.5±0.5**	**26.9±3.9**	**25.4±1.4**	**20.5±1.2**	**20.5±1.4**	**18.3±1.3**	**19.7±0.7**	**18.0±0.6**	**17.0±0.6**	**13.9±0.7**	**16.6±0.6**

Fisheries management systems abbreviations (abbrev.): NT= No-take, GR= Gear-restricted, OA= Open-access.
Region abbrev.: RM= Ras Mohammad, SH= Sharm El-Sheikh, NQ= Nabq, DB= Dahab, AG= Abu Galum, SN= South Nuweiba, NN= North Nuweiba, TB= Taba

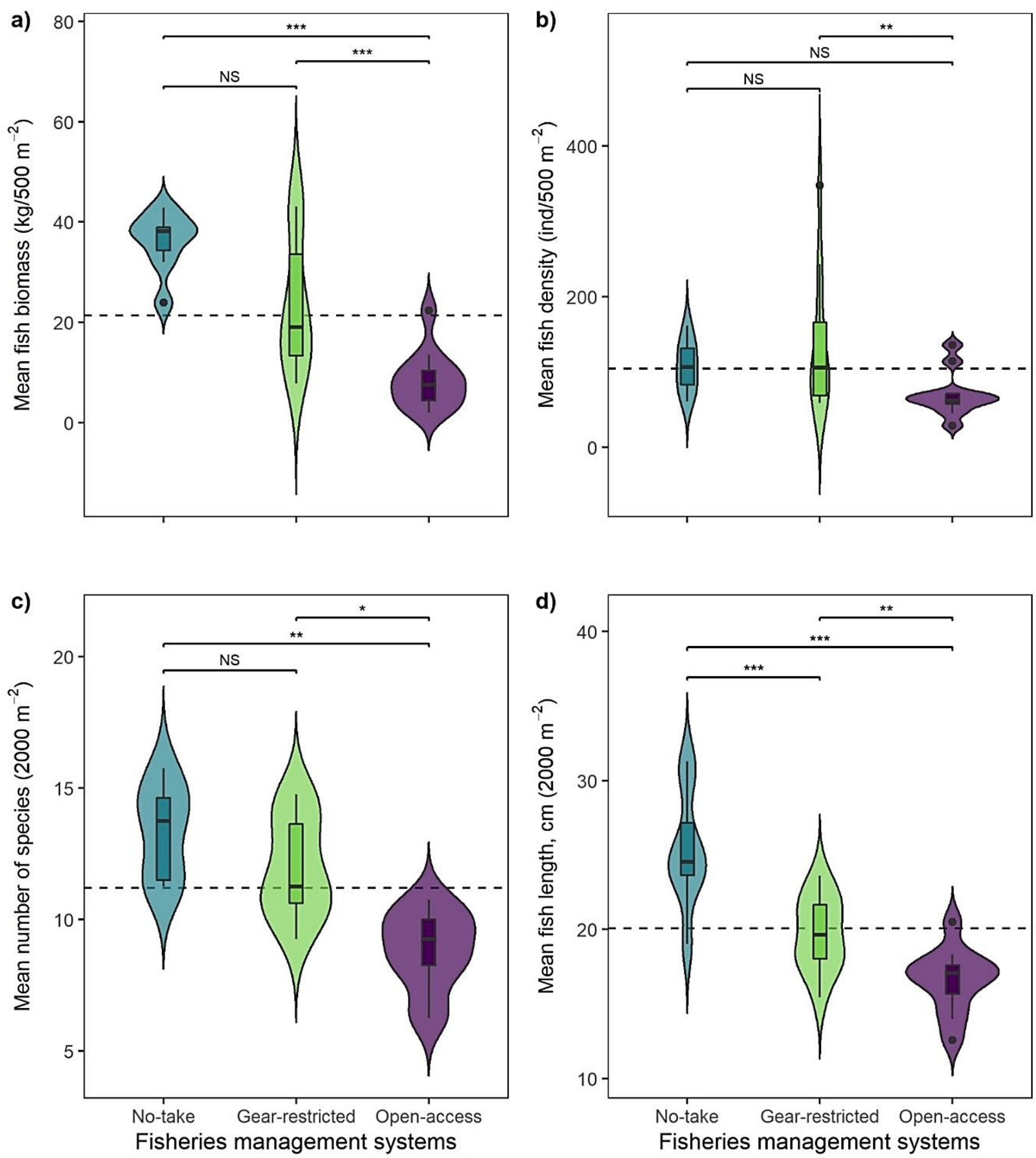

Figure 2. Violin plots with boxplots overlaid, showing the comparison of total herbivorous fish indices between the sampling three fisheries management systems in 2017. Fish biomass **(a)**, Fish density **(b)**, Species richness **(c)** and Fish size **(d)**.

The boxplot shows the median (black line) and interquartile range (top and bottom borders of the box). Tukey post-hoc test used to examine differences in management levels: levels of significance is denoted with asterisks *P<0.05, **P<0.01, ***P<0.001, NS non-significant.

Dashed horizontal line represent the overall mean value for each fish index combined across all management systems.

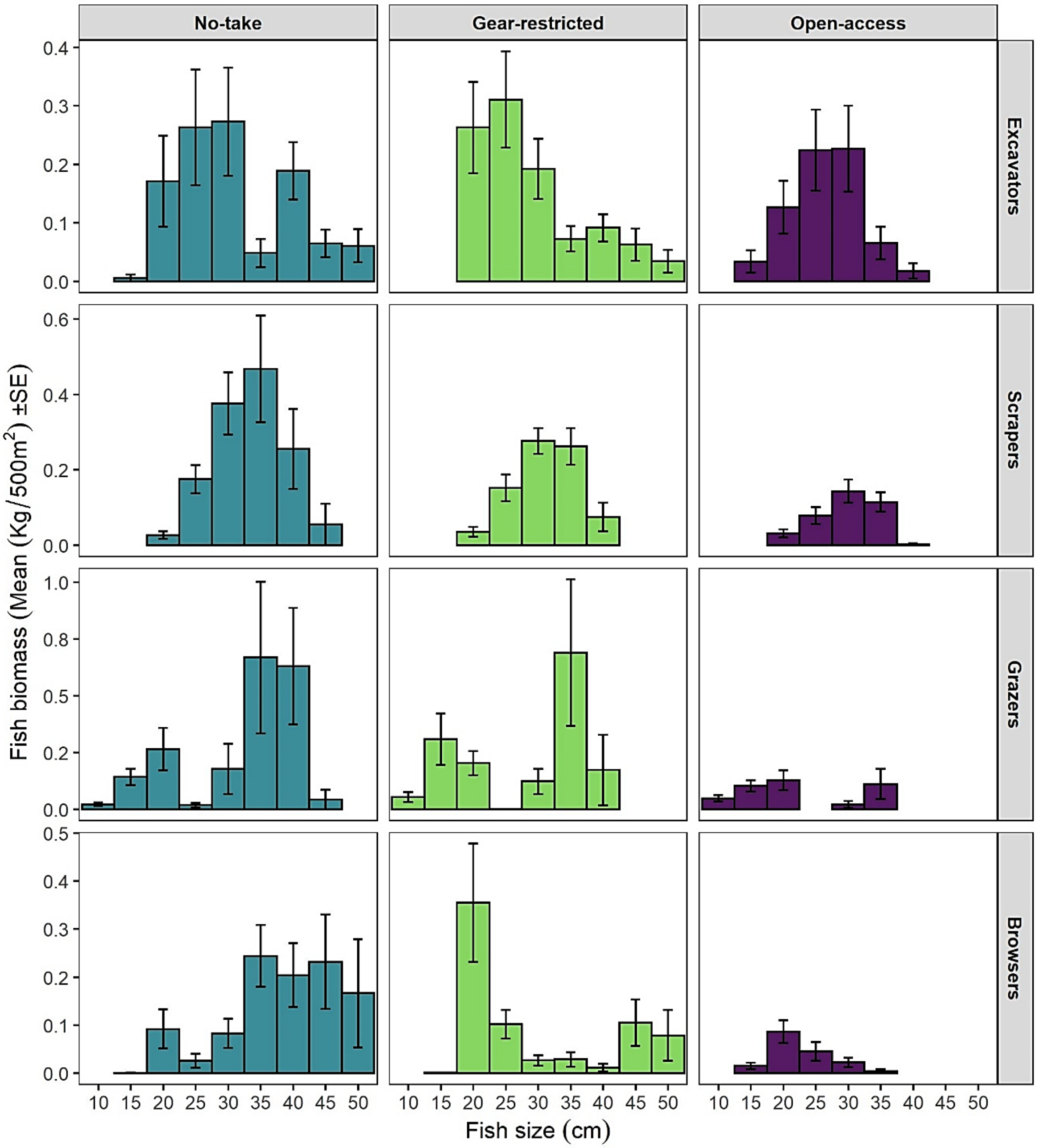

Figure 3. Mean biomass (kg $500^2 \pm$ SE) for each size-class (total length; cm) of herbivorous fishes divided by (functional feeding group) in each fisheries management systems.

Table 5. Results of multiple comparisons of means (Tukey Contrasts) between levels of fisheries management systems for each response variables.

Response variable	Fisheries Management Systems		
	NT vs OA	**GR vs OA**	**NT vs GR**
(a) Biomass			
Total herbivores	< 0.001 ***	< 0.001 ***	0.065
Excavators	0.506	0.545	0.984
Scrapers	< 0.001 ***	0.001 **	0.243
Grazers	< 0.001 ***	0.006 **	0.076
Browsers	< 0.001 ***	< 0.001 ***	0.808
(b) Density			
Total herbivores	0.084	0.009 **	0.831
Excavators	0.531	0.213	0.875
Scrapers	0.005 **	0.015 *	0.807
Grazers	0.465	0.172	0.887
Browsers	0.522	0.013 *	0.294
(c) Species richness			
Total herbivores	0.007 **	0.022 *	0.831
(d) Fish size			
Total herbivores	<0.001 ***	0.005 **	< 0.001 ***

NT refers to no-take reefs, **GR** to gear-restricted reefs and **OA** to open-access reefs.

Values in boldface type are statistically significant at $\alpha = 0.05$, and asterisks indicate levels of significance *P<0.05, **P<0.01, ***P<0.001

4. Herbivorous fish community structure

The total biomass of herbivorous fish communities varied significantly between FMSs (ADONIS; R^2=0.32, P=0.001). SIMPER results showed that over 70% of the dissimilarity in herbivore community structure at NT reefs compared to OA reefs was attributable to the highest biomass of 7 species. In particular, the biomass of the three large-bodied herbivores (the grazer *A. Sohal*, the macroalgal browser *N. unicornis*, and the scraper *H. harid*) contributed most to dissimilarities (53.5%) **(Table 6)**. The biomass structure of total herbivores, and each individual functional group was also significantly influenced by FMSs **(Fig. 4a-d)**. At OA reefs, the decline in herbivorous biomass (either total or functional groups) was mostly driven by the declines in body length **(Table 4** and **Fig. 3)**, particularly the grazer (*A. sohal*), scraper (*H. harid*) and macroalgal browsers (*N. unicornis*, *N. elegans*) **(Table 6)**.

The total density of herbivorous fish communities also varied significantly across FMSs (R^2=0.25, P=0.001). In terms of functional groups, all groups except for the excavators exhibited significant differences in structure across FMSs **(Fig. 4e–h)**. SIMPER results showed that over 70% of the dissimilarity in herbivore community structure at NT reefs compared to OA reefs was attributable to the highest numerical density of 6 species (53.1%) in NT reefs and 2 species (20.7%) in OA reefs. The density of the four large-bodied herbivores (the grazer *A. Sohal*, the scrapers *H. harid* and *S. ferrugineus*, and the excavator *C. sordidus*) contributed most to the dissimilarities (32.6%) between NT and OA reefs. Conversely, the influential small-bodied grazer species *A. nigrofuscus* and macroalgal browser *S. luridus* experienced increases in density in GR and OA reefs.

CAP analysis showed that FMSs effects are the strongest, especially contrasting NT versus either GR or OA along CAP axis-1, in addition to the significant differences between FMSs in terms of fish biomass and density (*P*=0.0001, **Fig. 5**). Unfished NT reef sites were characterized by greater biomass of highly targeted fish browsers (*K. cinerascens, N. elegans, N. unicorn*), grazers (*A. sohal*), and scrapers (*H. harid, S. ferrugineus*), recording 5.8 - 32.9 and 1.9 - 5.7 times greater than the OA and GR reefs, respectively. However, the heavily fished OA reef sites have a greater biomass and density of the only scarid browsers (*C. viridescens*). Lastly, moderately fished GR reef sites were distinct from other management types by having a greater biomass and density of siganid browsers (*S. luridus* and *S. rivulatus*). The observed patterns in CAP ordination were confirmed by results from PERMANOVA test, which showed that, herbivorous fish biomass and density significantly differed among FMSs, regions, and sites (*P<0.05* for all comparisons). For biomass and density, the estimates of component variation (ECV) test in PERMANOVA indicated that site variation was greater followed by fisheries management effects.

Table 6. Results from similarity of percentages analysis (SIMPER) of discriminating species contributing to 70% of the variation in herbivorous fish community structure between fisheries management groups. Mean fish biomass (kg 500m^2) as well as the cumulative contributions (%) of each species to overall community dissimilarity between management groups are given.

Species	Mean biomass		Contribution %	Cumulative %
	No-take	Open-access		
Acanthurus sohal	45.48	3.16	32.6	32.6
Naso unicornis	15.65	0.00	11.3	43.9
Hipposcarus harid	14.61	1.67	9.6	53.5
Naso elegans	8.33	0.25	5.9	59.4
Scarus ferrugineus	7.98	1.38	5.0	64.4
Scarus niger	8.06	5.20	4.8	69.2
Ctenochaetus striatus	6.34	3.52	4.4	73.6
	No-take	Gear-restricted		
Acanthurus sohal	45.48	23.69	29.0	29.0
Naso unicornis	15.65	6.08	11.3	40.3
Hipposcarus harid	14.61	5.43	9.2	49.5
Siganus luridus	3.20	9.89	5.4	54.9
Naso elegans	8.33	1.43	5.4	60.3
Scarus niger	8.06	7.28	4.2	64.5
Scarus frenatus	6.01	2.70	4.1	68.6
Ctenochaetus striatus	6.34	2.30	4.1	72.7
	Gear-restricted	Open-access		
Acanthurus sohal	23.69	3.16	22.5	22.5
Siganus luridus	9.89	3.17	8.9	31.4
Naso unicornis	6.08	0.00	8.9	40.3
Chlorurus sordidus	9.30	7.74	7.5	47.8
Scarus niger	7.28	5.20	6.8	54.6
Hipposcarus harid	5.43	1.67	6.1	60.7
Scarus ferrugineus	5.38	1.38	6.1	66.8
Acanthurus nigrofuscus	6.57	1.14	6.1	72.9

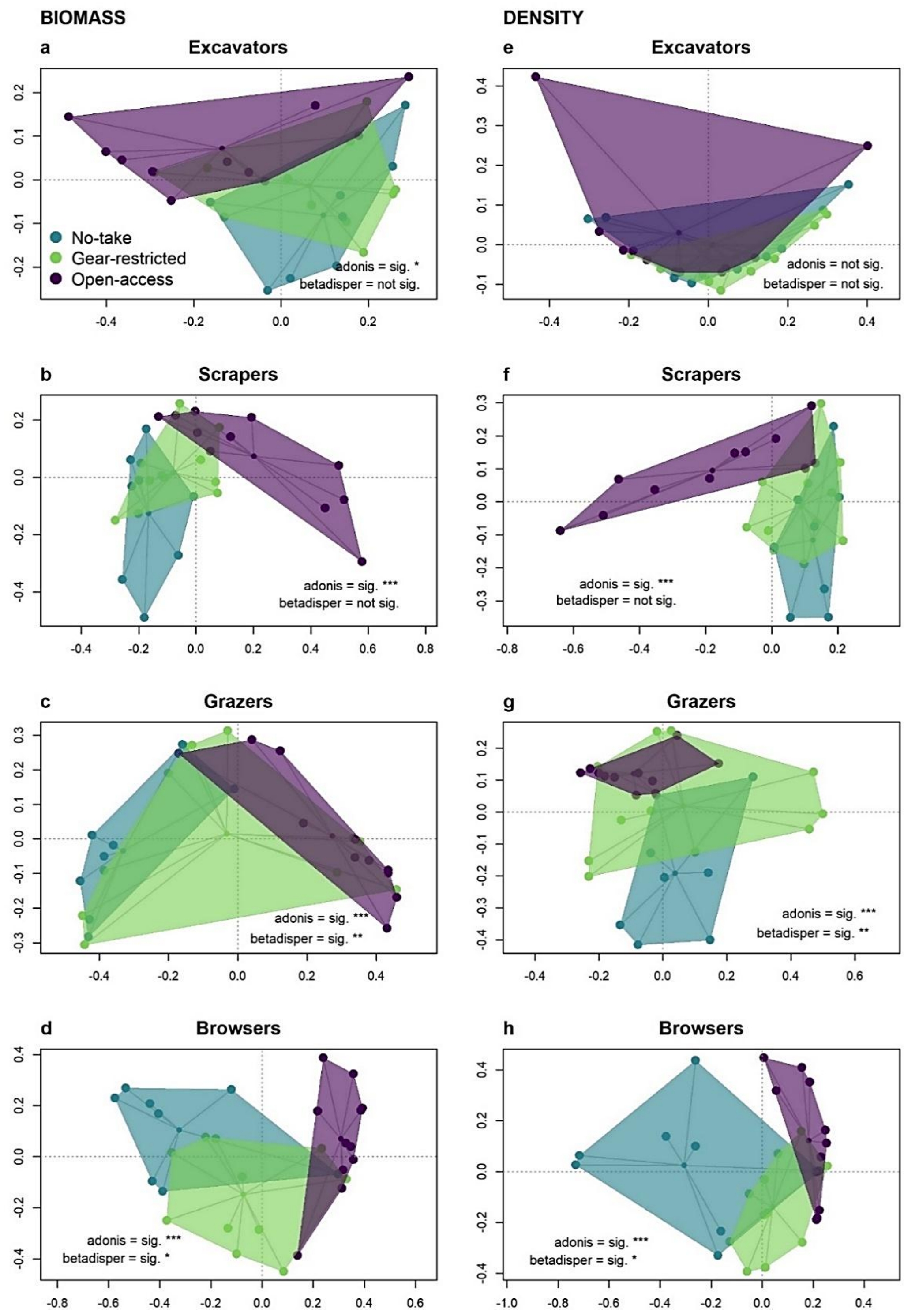

Figure 4. Principal coordinates analysis (PCoA) ordination of distances among the centroids of main effects (fisheries management) based on Bray–Curtis dissimilarities of biomass (left column) and density (right column) for individual herbivores groups; excavators (a, e), scrapers (b, f), grazers (c, g), and browsers (d, h). Points represent individual sites (connected to the centroid point in the center), sites are color-coded by fisheries management systems, and shaded polygons indicate boundaries of observed community structure. Significance level of ADONIS and PERMDISP tests are denoted by ****P*<0.001, ***P*<0.01, **P*<0.05.

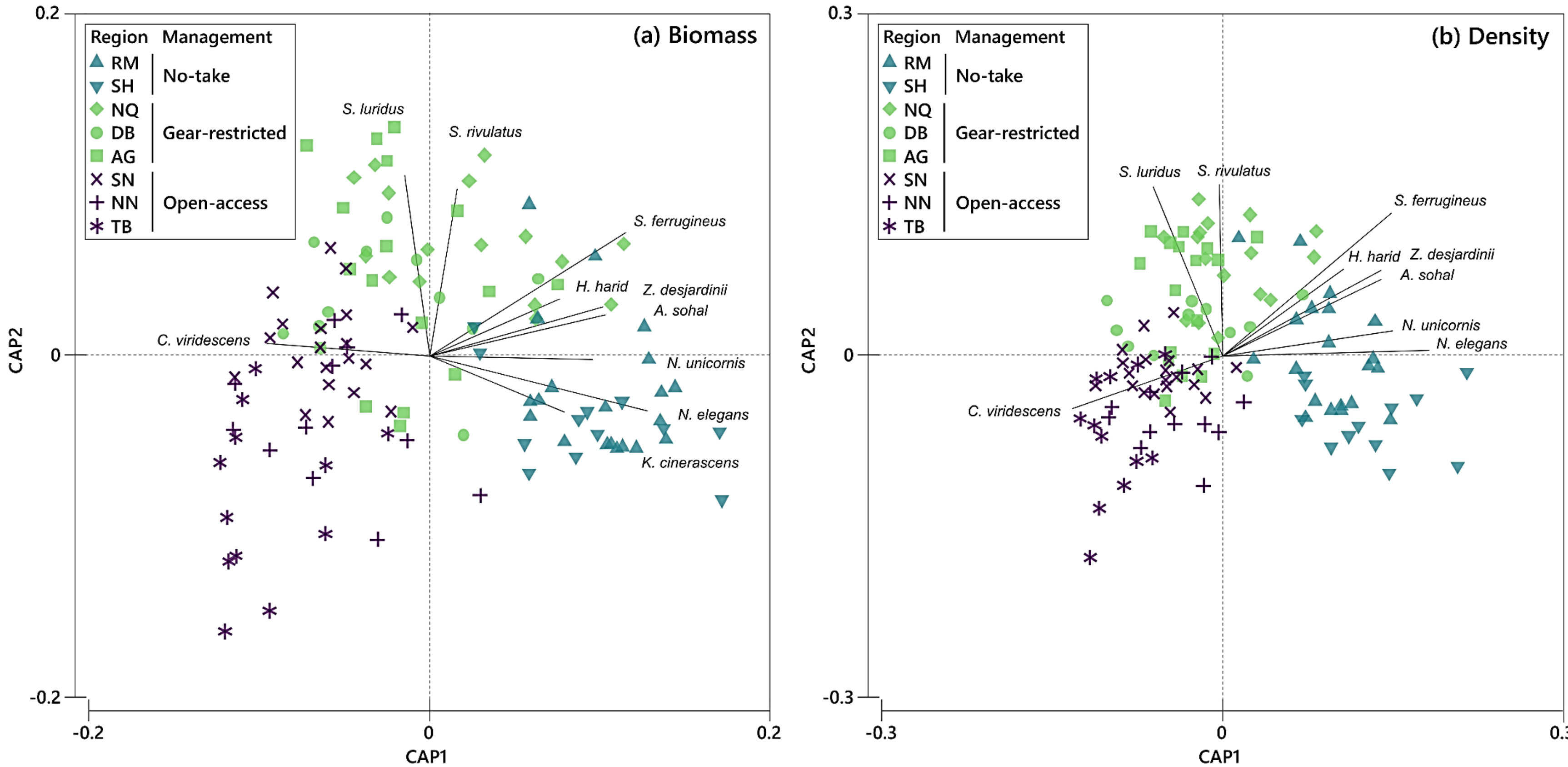

Figure 5. Canonical analysis of principal coordinates (CAP) ordination based on Bray-Curtis similarity for herbivorous fish biomass **(a)** and density **(b)** across three fisheries management systems (NT, GR, OA) and eight regions (RM: Ras Muhammad, SH: Sharm El-Sheikh, NQ: Nabq, DB: Dahab, AG: Abu Galum, SN: South Nuweiba, NN: North Nuweiba, TB: Taba). Each color represents a management type and each shape a study region. Species correlations with the canonical axis are represented as vectors for species with Pearson R value greater than 0.5; e.g. biomass and density of large-bodied algal browsers (*N. unicornis* and *N. elegans*) are positively correlated with NT management. Choice of m = 8 for fish biomass data (Eigenvalues of correlation: 1 = 0.85, 2 = 0.65; Permutation test: P = 0.0001) and m = 10 for fish density data (Eigenvalues of correlation: 1 = 0.86, 2 = 0.69; Permutation test: P = 0.0001).

DISCUSSION

Coral reef managers face the challenge of balancing the ever-increasing demand for reef fisheries with maintaining reef health and resilience. The effective management of herbivorous fish populations is one tool that reef managers can use to complement existing management strategies to improve coral reef resilience. In South Sinai (northern Red Sea), the existing MPAs are subject to different levels of fishing pressure, therefore, understanding the effects and consequences of this stressor on herbivorous fish populations is highly needed to properly manage current and future levels of fishing.

In this study, we found that herbivorous fish assemblages at locations closed to fishing (NT) supported more than 1.5 and 4 times the total biomass, compared to those with restrictions on fishing gears (GR) or open to all fishing gears (OA). This finding is consistent with the growing number of regional and global studies that have noted similar patterns between unfished and fished areas **(Edwards *et al.*, 2014; Advani *et al.*, 2015; Kattan *et al.*, 2017; Steneck *et al.*, 2018; Campbell *et al.*, 2018, 2020; Bejarano *et al.*, 2019; Cinner *et al.*, 2020; Humphries *et al.*, 2020)**. For example, **Edwards *et al.* (2014)** examined the impacts of fishing on herbivorous fishes from 145 locations around the world. They found that biomass is more than twice as high in locations closed to fishing relative to fished locations. **Campbell *et al.* (2018)** observed the same patterns within 22 global marine ecoregions. They showed that herbivorous fish (Scaridae and Siganidae) biomass in unfished reefs were (46% and 330% higher, respectively) than heavily fished reefs. Furthermore, recent findings by **Campbell *et al.* (2020)** corroborate our results that NT and GR reefs were associated with significantly higher biomass of herbivores relative to OA reefs. **Cinner *et al.* (2020)** found that gear-restricted MPAs provided similar conservation benefits as fully protected MPAs for parrotfish family, and thus, for this particular group of fish, gear restrictions can be very effective. To best of our knowledge this is the first study to investigate the variation patterns of biomass and population size structure of herbivorous reef fishes between fished and unfished locations in the GoA (northern Red Sea).

Similar to the observed patterns in total herbivorous fish biomass and body length, species richness also declined with increasing fishing pressure and was considerably higher in unfished reefs (NT). This finding is consistent with previous studies that reported a positive effect of protection on herbivorous fish species richness **(Bejarano *et al.*, 2019; Topor *et al.*, 2019; Altman-Kurosaki *et al.*, 2021)**. Despite consistent patterns in herbivorous fish sizes, biomass and richness, there was no significant difference in numerical density between fished (GR and OA) and unfished (NT) locations. Previous studies which investigated fishing impacts on the abundance of herbivorous fish populations offer conflicted opinions.

Several authors have concluded that fishing reduced herbivorous fish abundances e.g. **(Edwards *et al.*, 2014; Russ *et al.*, 2015; Steneck *et al.*, 2018)**. Whereas observations made by other studies suggested that herbivorous fish abundances, in particular the parrotfish family, appeared to be more influenced by protection status **(Price *et al.*, 2021)**, environmental conditions **(McClanahan and Muthiga, 2020)**, and habitat characteristics **(Vallès and Oxenford, 2014)** rather than fishing effect. On the other hand, density of surgeonfish species were influenced more by the changes of benthic composition rather than protection status **(Russ *et al.*, 2018)**. However, small sized individuals and small-bodied fish species (surgeonfish, rabbitfish and parrotfish) increased with increasing fishing pressure **(Hawkins and Roberts, 2004; Bellwood *et al.*, 2012; Advani *et al.*, 2015; Bejarano *et al.*, 2019)**. Many of the latter observations would appear to corroborate the predator-removal hypotheses developed by **Boaden and Kingsford (2015)**. In our study, the numerical density of herbivorous fish assemblages appeared to be driven by the highly abundant surgeonfish family (Acanthuridae), particularly by the small-bodied grazer *A. nigrofuscus*, which is considerably more abundant in fished locations (GR and OA). Similarly, abundances of the highly targeted rabbitfish family (Siganidae), particularly *S. luridus* and *S. rivulatus*, were also more abundant in fished locations. Our findings support those of **Floeter *et al.* (2006)**, who also found highly targeted herbivore species were significantly more abundant and larger in a highly protected sites.

Predatory species have been recognized as important in maintaining diversity on coral reefs **(Hixon, 2015)**. In the GoA, groupers family (Serranidae) recognized to heavily prey on some herbivores, particularly small acanthurids **(Shpigel and Fishelson, 1989)**, and so, it is likely that interactions may explain the higher density of small-bodied grazers (surgeonfish) in fished areas compared to unfished areas **(Ashworth and Ormond, 2005)**. Neither species of rabbitfish family (Siganidae) are considered to be prey species of groupers **(Shpigel and Fishelson, 1991)**, Accordingly, the predator-removal hypothesis couldn't be a factor determining the higher abundances observed in fished areas (e.g. Nabq). However, this study suggests that the increasing of abundance of rabbitfish family might be affected more by environmental factors as mentioned by **(Olds *et al.*, 2013; Roff *et al.*, 2019)** rather than predation or fishing effect. **Price *et al.* (2021)** found that abundances of grazers and browsers increased in the fished areas with high algal cover. Personal observations suggest the presence of seagrass beds and/or mangroves close to fished reefs (particularly at Nabq), could be an important factor in determining the significance of Siganids associated with them.

Most of fisheries tend to target commercially important reef fishes with larger sizes **(Wilson *et al.*, 2010; Robinson *et al.*, 2017)**. Handline, gillnets and trammel nets are the more widely used traditional fishing methods by Bedouin fishermen along the Egyptian GoA. However, in the last decade, spearfishing has become more frequently practiced by Bedouin **(Poonian, 2020)**. This highly selective method contributes to removing larger size classes and key herbivorous fish species **(Frisch *et al.*, 2012; Bender *et al.*, 2014; Barbosa *et al.*, 2021)**. In many regions around the world, the selectivity of larger herbivore species has been observed **(Edwards *et al.*, 2014; Ford *et al.*, 2016)**, but this is the first study to demonstrate this pattern in the GoA for this fish group. The striking depletion of large-bodied herbivorous fish density and biomass (*A. sohal, H. harid, N. elegans, S. ferrugineus*; > 35 cm TL), was noticeable by the drop from 12.9 and 36.4% of the total density and biomass, respectively on NT reefs to 0.1 and 0.8%, respectively on OA reefs. Moreover, large-bodied target species (*C. bicolor, N. unicorn, Kyphosus* spp.) were virtually absent from OA reefs.

As large-bodied herbivore species have important and unique ecological function in maintaining the health and resilience of coral reefs, hence, protecting and restoring these key herbivores has become a priority **(Heenan and Williams, 2013; Mumby *et al.*, 2016)**. Furthermore, conserving the functional redundancy and complementary roles of diverse herbivorous fish community are critical for maintaining healthy coral reef ecosystems **(Burkepile and Hay, 2008; Cheal *et al.*, 2010; Bellwood *et al.*, 2012)**. Our findings revealed that many of these key herbivore species in the have been overexploited central-northern regions of the GoA (e.g. Dahab, Nuweiba and Taba) and thus may explain the significant increases in turf algae and macroalgae cover that have been reported recently in Dahab **(Naumann *et al.*, 2015; Reverter *et al.*, 2020)**. We believe that more attention should be paid for managing and maintaining the biomass and composition of these key herbivorous fish groups to improve the existing fisheries management strategies in

SSMPAs. All of our findings suggest that if the current fishing levels in the central-northern reefs of the GoA are not managed well, it could reduce the ability of herbivore communities to control algal communities, which in turn could lead to the degradation of coral reefs.

CONCLUSION

To the best of our knowledge, the status of herbivorous reef fishes in the Gulf of Aqaba (Northern Red Sea, Egypt) has not been assessed on such a large scale before, so our results provide important baseline information about herbivorous fish assemblages in this area. The biomass of herbivorous fishes was 4.3 times higher on unfished reefs than locations open for fishing in the northern Gulf of Aqaba (Nuweiba and Taba). Even though fishing had a clear effect on the biomass, species richness, and body length of herbivorous fish in fished reefs, there were no significant differences in the numerical density of herbivores between fished and unfished reefs. This opposite pattern proves that larger-bodied herbivore individuals and species were excessively affected by unregulated fishing activities. As a result, our findings highlight that current levels of fishing (i.e., selectivity of large-bodied herbivores), particularly in the northern sector of the Gulf of Aqaba, may reduce the ability of herbivorous fishes to control turf and macroalgae that grow on reef substratum, which indirectly could reduce the substrate suitable for coral settlement.

In the end, our findings support previous studies showing that fishing-gear restriction provides comparable protection benefits to herbivore groups as in no-take MPAs. Therefore, we suggest that such an approach would help coral reef managers to give the overexploited herbivorous fisheries in Nuweiba and Taba a chance to recover.

ACKNOWLEDGMENT

We would like to thank all the staff of South Sinai MPAs and colleagues who assisted the study, especially *Ahmed El-Sadeq* and *Ismael Abdel Azim*, for their kind assistance throughout field activities. We thank *Eslam Osman*, *Alaaeldin Soultan*, *Yasser Awadalla*, and *Karim Farouk* for their valuable help in data analysis and revision of this manuscript. This work is part of the PhD thesis of the first author.

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