Management effectiveness suggests a role in structuring herbivorous fish communities in Sinai marine protected areas, Gulf of Aqaba

Khaled M. El-Haddad [a,*], Abdel-Hamid A. Ali [a], Mohammed S. Abdel-Rahman [b], Saad Z. Mohammed [c], Tarek A. Temraz [c]

[a] Marine Environment Division, National Institute of Oceanography and Fisheries, Suez, Egypt.
[b] Nature Conservation Sector, Egyptian Environmental Affairs Agency, Cairo, Egypt.
[c] Marine Science Department, Suez Canal University, Ismailia, Egypt.

Corresponding author: elhaddad1379@gmail.com, km.elhaddad@niof.sci.eg
ORCID: 0000-0003-2826-3227

Highlights

- Large-scale assessment of the status of herbivorous fishes in the northern Red Sea.
- Comparison of herbivorous fish assemblages along a fishing pressure gradient.
- Large-bodied herbivore species were either rare or absent at heavily fished reefs.
- Loss of these key herbivores may boost algal dominance, thus diminish reef functionality.
- Promoting local community participation in the fishery management process.

Abstract

Herbivorous reef fishes are critically important for maintaining the health and resilience of coral reefs. In the Egyptian Gulf of Aqaba (GoA), many of these herbivores are important fishery targets and little is known about their population size structure and biomass patterns. Here, we conduct a large-scale (~250 km of coastline) assessment of the status of herbivorous fish populations along a fishing pressure gradient at 30 sites and eight regions in the GoA. These regions are subjected to three levels of fishing and protection, ranging from almost no fishing (No-take, NT), and moderately fished (via Gear-restriction, GR) to heavily fished (Open-access, OA). We found that the NT fishery reserve was the most effective in maintaining herbivorous fish size, biomass, and richness across all functional groups, though numerical density was not. Total herbivore 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 (fished) met the global mean herbivore biomass target of ~30 kg/500 m^2. Our work also highlights three important results regarding the impacts of fishing and fisheries management on herbivorous fish populations: (i) size structure was heavily skewed toward smaller individuals, with fishes less than (20 cm) accounting for 81.1% of the population in heavily fished OA reefs vs. 52.8% at unfished NT 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, and (iii) large-bodied target species, *Cetoscarus bicolor*, *Naso unicorn*, and *Kyphosus* spp., accounting for 15.9% of the total biomass at NT reefs on average, while they were virtually absent from OA reefs. Collectively, these findings suggest that many principal fishery species in the central-northern regions of the GoA have been overexploited, which in turn can lead to reef degradation. Therefore, there is an urgent need to develop a participatory management approach and enforce restrictions on destructive fishing gear in order to promote recovery of herbivore biomass.

Keywords:

Fisheries management, Functional groups, Herbivorous fishes, Marine protected areas, Gulf of Aqaba, Red Sea

1. Introduction

Coral reef ecosystem are among the world's most structurally complex, biodiverse and valuable ecosystems, supporting nearly a third of all marine fish species (Fisher et al., 2015; Graham and Nash, 2013; Wilkinson, 2008). However, this unique ecosystem is among the most vulnerable to local stressors chiefly from overfishing and unsustainable fishing activities (Burke et al., 2011). While more than 25% of the world's coral reefs are located within marine protected areas (MPAs) boundaries, only 6% of reef areas are within adequately managed MPAs (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). Approximately 75% of these reefs are in developing countries and the rapid growth of the reef-based tourism sector has contributed to increasing demand for reef fishes that has significantly depleted many fish populations (Ashworth and 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 challenging issues regarding corals' present and future (Chung et al., 2019; Pratchett et al., 2014).

The 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 they are 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 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 MPAs in South Sinai, covering the entirety of Egypt's GoA (Pearson and Shehata, 1998). However, this role has diminished over time due to inadequate staffing and financial resources, especially in the past decade (Mabrouk, 2015; Samy-kamal, 2015). Additionally, non-compliance and weak enforcement of fisheries regulations in the MPAs may constitute a threat to conservation goals and hence the efficacy of the MPAs (Advani et al., 2015; Gill et al., 2017).

Fisheries management varies widely across GoA regions. In Ras Mohammed and Sharm el-Sheikh (southern of GoA), all forms of nearshore fishing activities are prohibited (Mabrouk, 2015). However, at Nabq (south GoA), fishing is permitted for local Bedouin using their traditional gears (e.g., gillnets and trammel nets) that principally target herbivorous fish species entering the reef flat with the rising tides to feed on algae (Galal et al., 2002). Also, in Abu Galum and Dahab (central GoA), fishing is allowed in certain locations and prohibited at dive sites (Hasler and Ott, 2008). In

contrast, fisheries management appear to be more permissive in Nuweiba and Taba (north GoA), where a variety of fishing gears are used (e.g., hook and line, nets, traps, spear guns) throughout these regions (Poonian, 2020; Tilot et al., 2008). 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 healthy herbivore populations and indirectly maintain reef health and resilience (Bozec et al., 2016; Chung et al., 2019; Weijerman et al., 2018; Williams et al., 2019, 2016).

Healthy herbivorous fish communities are critical in facilitating coral settlement and post-settlement survivorship; and thus maintaining coral reef resilience (Adam et al., 2015; Bellwood et al., 2004; Lirman, 2001). 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 and Hay, 2010, 2008; Cheal et al., 2010; Green and Bellwood, 2009). As a result, a growing number of recent studies have recognized that monitoring and effective management of herbivorous fishes are important tools that reef managers can use to maintain coral reef resilience. Specifically, it has been recommended that fish biomass be included in monitoring programs as the most useful indicator or response metric that allows reef managers to evaluate the status of coral reef fisheries and set practical management targets (Campbell et al., 2020; Chung et al., 2019; Green and Bellwood, 2009; Maynard et al., 2015; Mcclanahan et al., 2015; McClanahan et al., 2021, 2019; Williams et al., 2019).

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

The present study, therefore, is intended to provide a better understanding of the effects of fisheries management strategies on herbivorous fish communities in South Sinai regions that are subjected to different levels of fishing pressure and conservation measures. We aim to understand whether SSMPAs and their fisheries management systems (FMSs) were effective in protecting the herbivorous fish richness, density, biomass, and size; that are essential to sustain the condition of coral reef ecosystems.

2. Materials and Methods

2.1. Study sites and survey design

Underwater visual censuses (UVC) of herbivorous reef fishes were carried out between April-September 2017. A total of 30 reef sites representing eight regions were surveyed. These sites are distributed along 250 km of coastline in the northern Red Sea and the GoA (Figure 1, Table S1). In GoA regions, three FMSs were categorized based on the prevalent human activity, level of conservation measures and protection, fishing intensity, and compliance with fishery regulations (see Table 1). 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 appear to be more permissive than other regions and a variety of fishing gears are used (e.g., hook and line, nets, traps, spear guns) throughout these regions (Figure 1; Table 1).

Table 1.

The surveyed regions were stratified according to fisheries management systems as (no-take, gear-restricted, and open-access). The uses allowed (√), permitted in the designated zones (P), or prohibited (x) within each region are shown. The potential effects of the anthropogenic stressors on coral reefs are also shown. Severity of each impact is shown as: (-) non-significant; (+) noticeable; (++) marked; (+++) severe. Adopted from (Ashworth, 2004; Galal, 1999; Mabrouk, 2015).

	No-take		**Gear-restricted**			**Open-access**		
Local anthropogenic threats	**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

2.2. Survey methods

Species-level visual censuses targeted four key herbivorous fish families (Acanthuridae, Kyphosidae, Scaridae, and Siganidae) were conducted using belt transect method. At each site, four 50m (total 200m) transects were laid end-to-end and parallel to the shoreline, with a minimum of 5m between

adjacent transects. At each transect, herbivorous fishes were counted and the body length of each individual was visually estimated to the nearest 5cm, within 5m to either side of the observer's path, yielding a censused area of 500m^2. Surveys focused on counting fishes (≥10 cm total length, TL), except for the two small surgeonfish, *A. nigrofuscus* and *C. striatus* (≥5 cm, TL). All surveys were limited to reef crest habitat (1–3 m, depth) and took place during daylight hours at high tide to ensure that counts were undertaken when the reef crest area was available for grazing fishes.

From the UVC surveys, fish abundance and length estimates (TL) were converted to kg of biomass per unit area (kg/500m^2) using the allometric length-weight equation: $W= aTL^b$, where W is weight in kilograms, TL is the total length in centimetres (taking the midpoint of each size category), and parameters a and b are species-specific constants derived from FishBase (Froese and Pauly 2019) and other published sources in the region (Table S2). The average biomass of herbivorous fish was summarized into four functional feeding groups (excavators, scrapers, grazers, and browsers) following established classifications (Green and Bellwood, 2009). Species that were not categorized in the aforementioned references, such as *C. sordidus,* was identified as excavator, *S. luridus* and *S. rivulatus* as macroalgal browsers (Ebrahim et al., 2020), *S. stellatus* and *C. striatus* as grazers (Afeworki et al., 2013; Marshell and Mumby, 2012) (Table S3).

2.3. Data analysis

The density, biomass, and frequency of occurrence of each fish species were calculated as a percentage of the total. As a result, an index of relative dominance (IRD) was calculated for each fish species (Friedlander et al., 2003).

2.3.1 Univariate data analysis.

Herbivorous fish characteristics (biomass, density, species richness, body length) among different FMSs were analysed 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 communities. 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 density 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, and 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).

2.3.2 Multivariate data analysis.

Multivariate statistical and ordination methods implemented through: (a) determine variability in herbivorous fish biomass and density by the functional group between FMSs using the 'vegan' package (Oksanen et al., 2019) in R project 4.0.3 (R Core Team 2020); (b) assess variability in herbivorous fish community structure between FMSs and among sampling regions and sites. The relative importance of each factor was quantified through the estimates of component of variation using PRIMER 6.1.13 and in the PERMANOVA + 1.0.3 add-on (Clarke & Gorley 2001, Anderson et al. 2008).

(a). At site level, fish species density and biomass for the total herbivorous fishes and for each individual group were averaged and distance matrices based on Bray–Curtis dissimilarities were created using the *vegdist* function. A permutational multivariate analysis of variance (PERMANOVA, *adonis* function in the R package vegan; (Oksanen et al., 2019) was used to evaluate whether the biomass and density for each functional group varied significantly among the different types of FMSs. Similarly, a permutational analysis of multivariate dispersion (PERMDISP; *betadisper* function) within the groups 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 of mean herbivorous fish biomass and density at each FMSs. Statistical significance of the PCoA ordinations were 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. A cut-off criterion was applied to allow identification of a subset of species whose cumulative percentage contribution reached 70% of the dissimilarity value.

(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: (1) FMSs (fixed factor), (2) region (nested in FMSs, random factor), and (3) site (nested in region and FMSs, random factor). The potential effect of multivariate dispersion was assessed using PERMDISP (Anderson, 2006). Multivariate patterns were visualized through (canonical analysis of principal coordinates; CAP) (Anderson and 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.

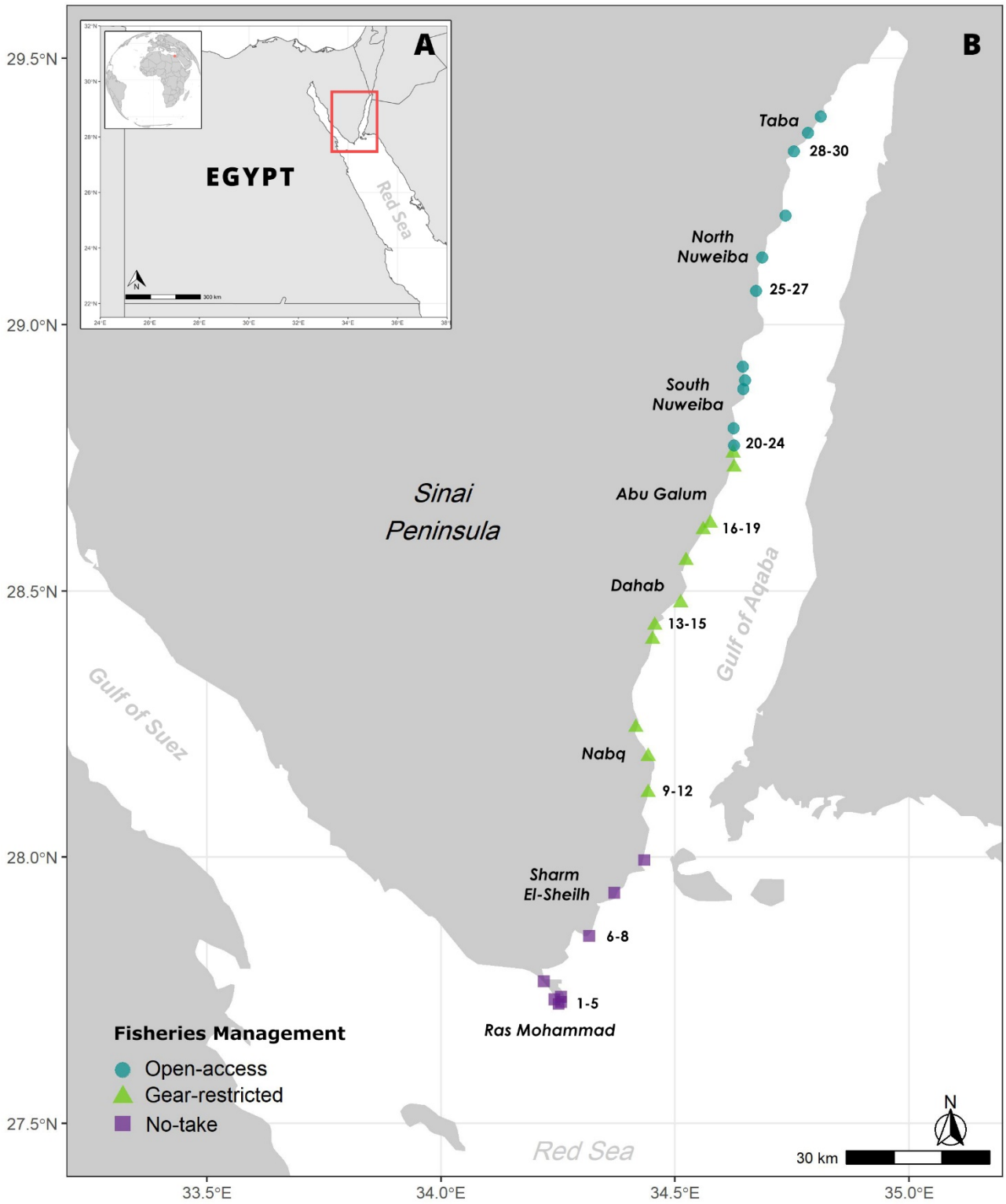

Figure 1.

Map of Egypt, showing the location of the GoA (A). Map of the GoA, showing locations of the eight study regions representing 30 reef sites (B). 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).

3. Results

3.1. Herbivore assemblages

A total of 120 belt-transects covering an area of 60 km^2 were performed on reef crest zone across 30 study sites. Overall, 12,509 individuals belonging to 24 species of herbivorous fishes from the reef crest were recorded, with 8 browsing, 7 scraping, 6 grazing and 3 excavating species (Table S3). One-third of the observed herbivore species (10 spp.) were widespread, occurring on 80-100% of survey sites. Among the encountered species, only two are endemic to the Red Sea region (Golani and Fricke, 2018): *C. gibbus* and *C. viridescens*, together comprised only 2.2 and 3.5% of the total density and total biomass, respectively (Table S4). The most dominant species based on IRD was *A. sohal*, which was present in 55 % of transects and accounting for one-quarter 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 S4). The overall abundant species in terms of numerical density were the small-bodied *A. nigrofuscus* and *C. striatus* grazers, 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%).

3.2. Total herbivorous fish

The grand mean biomass of herbivores at unfished NT reefs with 36.2±2.1 kg (per 500 m^2) and moderately fished GR reefs with 23.7±4.0 kg was significantly greater by ~4.3 and 2.8 times than in heavily fished OA reefs (GLMMs, t = -6.65, P<0.001; pairwise test, P<0.001; Figure 2a; Tables 2, 3). 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 in unfished NT sites of Ras Mohammed (Table S5a). Among GoA regions, the unfished regions (Ras Mohammed and Sharm El-Sheikh) and one of fished regions (Nabq) met the global mean herbivore biomass from unfished reefs of ~30 kg/500 m^2 (Edwards et al., 2014). (Figure S1; Table S5a). Comparing reef site-level biomass to a global mean 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 S5a).

The grand mean density of herbivores in GR reefs with 136.5±27.6 individuals (per 500 m^2) was higher by 1.3 and 1.9 times than at NT reefs and OA reefs, respectively, though not significant (GLMMs; P>0.05; Figure 2b; Tables 2, 3). 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. in moderately GR sites of Nabq (Figure S1; Table S5b). 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 in

OA areas (GLMMs; P=0.002; Figure 2c, Table 2). Notably, six species (four browsers, one grazer and one excavator) were not observed at any of the sites classified as OA fishery. A pairwise comparison between NT reefs and GR reefs revealed non-significant variation (pairwise test, P=0.83, Table 3). At region level, the highest species richness was recorded at Ras Mohammed 19±0.7 species and the lowest at Taba 9.7±0.3 species (Figure S1; Table S6a).

In accordance with the 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 in GR reefs, and to 16.6±2.2 cm in OA reefs (P<0.001 for all comparisons; Figure 2d, Table S6b). Size-class distribution of herbivorous fishes in fished (GR and OA) reefs 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 reefs with 50.8% of the total density representing 12.2% of the total biomass (Figure S2). In marked contrast, only 8.8% and 3.5% of the total density on fished (GR and OA) reefs were larger than 30 cm, compared to 26.1% at NT reefs. 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 (Figure S2).

3.3. Functional groups

Biomass, species richness and size-frequency distributions of the four herbivore functional groups declined considerably with increasing fishing pressure on the GoA (Figure 3; Tables S5 and S6). These three herbivore metrics were all generally lower within heavily fished OA reefs or moderately fished GR reefs compared to unfished NT reefs (Figures 3, S4; Tables S5, S6). Three out of the four functional groups (scrapers, grazers, browsers) revealed significant declines in biomass with increasing fishing pressure. This pattern was most notable when comparing NT with OA reefs (GLMMs; P<0.001 for the three functional groups; Figure 3; Tables 2 and 3). However, the biomass of excavators showed little variation among the investigated FMSs and the only difference was found in NT reefs where they showed considerably higher abundance for size-classes >35 cm (Figure 3). 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 in OA reefs (Table S6b). Furthermore, excavators in 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 (Figure S3). Notably, large-sized excavators (>40 cm) were totally absent from OA reefs, distinguishing this assemblage from that on NT reefs (Figures 3, S3).

With respect to scrapers, biomass and density (GLMMs: $P<0.001$ for all comparisons; Figure 3, S4; Table 2), varied significantly between NT and OA reefs. Size-class distribution of scrapers declined considerably from 31.9±1.0 cm at NT reefs to 27.8±0.4 cm in OA reefs (Table S6b). Among grazers and browsers, the biomass results revealed highly significant differences between NT reefs and OA reefs, density on the other hand revealed no significant differences (GLMMs: $P<0.001$ for all comparisons; Figure 3, S4; Tables 2, 3). However, differences in mean body-length of grazers and browsers between individual FMSs revealed that grazers and browsers were found to be considerably larger on NT reefs than on OA reefs (Figure 3, S4; Table S6b). Both functional groups were dominated by intermediate and small sized fishes on all reefs. 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 (Figure 3).

At region level, Mean biomass and density of excavators were greatest 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 (Figure S4a, Table S5a). Biomass and density values of scrapers varied greatly among 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. Notably, grazers and browsers biomass and density were considerably higher 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, and the lowest values were at heavily fished OA regions (Figure S4b, Table S5b).

3.4. Herbivorous fish community structure

3.4.1. Effects of fisheries management on fish biomass and density

The total biomass of herbivorous fish communities varied significantly between FMSs (R^2=0.32, P=0.001; Table S7). SIMPER results showed that over 70% of the dissimilarity in herbivore community structure in NT compared to the OA fishery was attributable to the highest biomass of 7 species. In particular, the biomass of the three large-bodied herbivores (the grazer *A. Sohal*, the algal browser *N. unicornis*, and the scraper *H. harid*) contributed most to dissimilarities (53.5%) (Table S9). The biomass structure of total herbivores and each individual functional group was also significantly influenced by FMSs (Figures 4a-d, S5; Table S5). In OA reefs, the decline in herbivorous biomass (either total or functional groups) is mostly driven by the declines in body length (Figures 3, S3; Table S5), specifically for the important grazer (*A. sohal*), scraper (*H. harid*) and algal browsers (*N. unicornis*, *N. elegans*) (Table S9).

The total density of herbivorous fish communities also varied significantly across FMS (R^2=0.25, P=0.001; Table S7). In terms of functional groups, all groups except for the excavators

exhibited significant differences in structure across FMSs (Figures 4e–h, S5; Table S5). SIMPER results showed that over 70% of the dissimilarity in herbivore community structure in the NT compared to the OA fishery was attributable to the highest numerical density of 6 species (53.1%) in NT reefs and 2 species (20.7%) in OA reefs (Table S10). 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 the algal browser *S. luridus* experienced increases in density in GR and OA reefs (Table S10).

3.4.2. Effects of site, region and fisheries management on fish biomass and density

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, Figure 5a, b). Unfished NT reefs are 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 reefs have a greater biomass and density of the only scarid browsers (*C. viridescens*). Lastly, moderately fished GR reefs 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, fish biomass and density significantly differed among FMSs, regions, and sites ($P<0.05$ for all comparisons; Table S8). 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 S8).

4. Discussion

Reef managers face the challenge of balancing the ever-increasing demand for coral 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 and fisheries management, and therefore, understanding the effects and consequences of these interventions on herbivorous fish populations is needed to properly manage current and future levels of fishing. Here, we find that herbivorous fish assemblages at locations closed to fishing (NT) support on average more than 1.5 and 4 folds the total biomass, compared to those with restrictions on fishing gears (GR), and open to all fishing gears (OA), respectively. These results are consistent with the growing number of regional and global studies that noted similar patterns between unfished and

fished areas (Advani et al., 2015; Bejarano et al., 2019; Campbell et al., 2020, 2018; Cinner et al., 2020; Edwards et al., 2014; Foo et al., 2021; Humphries et al., 2020; Kattan et al., 2017; Rolim et al., 2018; Steneck et al., 2018). However, this is the first study to investigate this patterns for the biomass and population size structure of herbivorous fishes in the GoA (northern Red Sea). 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. Also, Campbell et al (2018) observed the same patterns within 22 global marine ecoregions. As, unfished reefs most benefited herbivorous fish (Scaridae and Siganidae) biomass (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, and 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.

Despite consistent patterns in herbivorous fish sizes and biomass, there was no significant difference in numerical density between fished (GR and OA) and unfished (NT) locations. Previous studies investigating fishing impacts on the abundance of herbivorous fish populations offer conflicting opinions. Several authors have concluded that fishing reduced herbivorous fish abundances e.g. (Edwards et al., 2014; McClanahan et al., 1999; Russ et al., 2015; Steneck et al., 2018). Alternatively, observations made by other studies suggest that herbivorous fish abundances, in particular parrotfish family appeared to be more influenced by management status (Price et al., 2021), environmental conditions (McClanahan and Muthiga, 2020), and habitat characteristics (Vallès and Oxenford, 2014) rather than fishing effect. Similarly, density of surgeonfish species was influenced more by the changes to benthic composition than protection status (Russ et al., 2018). However, small individuals and smaller surgeonfish, rabbitfish and parrotfish species may actually increase with increasing fishing pressure (Advani et al., 2015; Bejarano et al., 2019; Bellwood et al., 2012; Clua and Legendre, 2008; Hawkins and Roberts, 2004). 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) is known to prey heavily on some herbivores, particularly small acanthurids (Shpigel and Fishelson, 1989), and so it is likely that interactions have been suggested to 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), though it is possible that this couldn't be a factor determining higher abundances observed in fished areas (e.g. Nabq). However, the evidence from this study suggests that populations of Siganidae are more likely to be determined by environmental factors (Olds et al., 2013; Roff et al., 2019) rather than by 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 fisheries tend to typically target commercially important reef fishes with larger sizes (Robinson et al., 2017; Wilson et al., 2010). 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 (Barbosa et al., 2021; Bender et al., 2014; Frisch et al., 2012). 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 these fish groups. The striking depletion of large-bodied herbivorous fish density and biomass (*A. sohal, H. harid, N. elegans, S. ferrugineus*; > 35 cm TL), is so evident by the drop from (12.9 and 36.4% of the total density and biomass, respectively) on NT reefs to (only 0.1 and 0.8%, respectively) on OA reefs. Also, large-bodied target species (*C. bicolor, N. unicorn, Kyphosus* spp.) were virtually absent from OA reefs. Given the unique functional roles of these large-bodied herbivore species in maintaining reef resilience, they highlight the urgent need for their protection and restoration (Heenan and Williams, 2013; Mumby et al., 2016). Our findings from moderately fished (Dahab, GR) and heavily fished (Nuweiba and Taba, OA) regions may explain the significant increases in the cover of turf algae and macroalgae that have been documented recently in Dahab (Naumann et al., 2015; Reverter et al., 2020). Similarly 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 (Altman-Kurosaki et al., 2021; Bejarano et al., 2019; Topor et al., 2019). Functional

redundancy and complementary roles among a highly diverse herbivorous fish community are critical for maintaining healthy coral reef ecosystems (Bellwood et al., 2012, 2006; Burkepile and Hay, 2008; Cheal et al., 2010). We believe that more attention should be paid to managing and maintaining the biomass and composition of these key herbivorous fish groups to complement the existing fisheries management strategies in SSMPAs. Collectively, our findings suggest that if current fishing levels in the central-northern GoA reefs are not effectively managed, it could reduce herbivore communities' ability to maintain top-down control on algal communities and could lead to degradation of coral communities.

4.1. Conclusion

The status of herbivorous reef fishes in the northern Red Sea and Gulf of Aqaba has not been evaluated on such a large scale, so our results provide important baselines for herbivorous fish assemblages in this region. The biomass of herbivorous fishes was 4.3 times higher on unfished reefs than in locations completely open for fishing at the northern Gulf of Aqaba (Nuweiba and Taba). While fishing has a clear effect on biomass, species richness and body length, there is no difference in the numerical density of herbivores between fished and unfished reefs. This contrary pattern proves that larger-bodied individuals and species were excessively impacted by fishing. As a result, our findings highlighting that current levels of fishing (i.e., selectivity of large-bodied herbivores) in the northern Gulf of Aqaba may reduce the ability of grazing fishes to control turf and macroalgae that are growing on the reef substratum and, indirectly, reduce the suitable substrate for coral settlement. Finally, our findings support previous studies showing that fishing-gear restriction provides comparable protection benefits to herbivore groups as 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.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the staff of the South Sinai MPAs for their support, especially Ismael Abdel-Azim and Ahmed El-Sadek for logistic support and assistance in the field. We are grateful to Dr. Eslam O. Osman for his help with the R code for the figures and data analysis. We are also in debt to Yasser Awadalla for his valuable help in revising the English language of the manuscript. This work is part of the PhD thesis of the first author.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

Additional supporting information may be found online in the Supporting Information section.

References

Adam, T.C., Burkepile, D.E., Ruttenberg, B.I., Paddack, M.J., 2015. Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. Mar. Ecol. Prog. Ser. 520, 1–20. https://doi.org/10.3354/meps11170

Advani, S., Rix, L.N., Aherne, D.M., Alwany, M.A., Bailey, D.M., 2015. Distance from a fishing community explains fish abundance in a no-take zone with weak compliance. PLoS One 10, 1–17. https://doi.org/10.1371/journal.pone.0126098

Afeworki, Y., Videler, J.J., Bruggemann, J.H., 2013. Seasonally changing habitat use patterns among roving herbivorous fishes in the southern Red Sea: The role of temperature and algal community structure. Coral Reefs 32, 475–485. https://doi.org/10.1007/s00338-012-1000-2

Altman-Kurosaki, N.T., Smith, C.M., Franklin, E.C., 2021. O‘ahu’s marine protected areas have limited success in protecting coral reef herbivores. Coral Reefs 40, 305–322. https://doi.org/10.1007/s00338-021-02054-5

Alwany, M.A., Thaler, E., Stachowitsch, M., 2009. Parrotfish bioerosion on Egyptian Red Sea reefs. J. Exp. Mar. Bio. Ecol. 371, 170–176. https://doi.org/10.1016/j.jembe.2009.01.019

Anderson, M.J., 2014. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef Stat. Ref. Online 1–15. https://doi.org/10.1002/9781118445112.STAT07841

Anderson, M.J., 2006. Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62, 245–253. https://doi.org/10.1111/J.1541-0420.2005.00440.X

Anderson, M.J., Willis, T.J., 2003. CANONICAL ANALYSIS OF PRINCIPAL COORDINATES: A USEFUL METHOD OF CONSTRAINED ORDINATION FOR ECOLOGY. Ecology 84, 511–525. https://doi.org/10.1890/0012-9658

Ashworth, J.S., 2004. The effects of protected area status on fish and mollusc stocks in South Sinai , Egypt. Philosophy 348.

Ashworth, J.S., Ormond, R.F.G., 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. Biol. Conserv. 121, 333–344. https://doi.org/10.1016/j.biocon.2004.05.006

Barbosa, M.C., Luiz, O.J., Cordeiro, C.A.M.M., Giglio, V.J., Ferreira, C.E.L., 2021. Fish and spearfisher traits contributing to catch composition. Fish. Res. 241. https://doi.org/10.1016/j.fishres.2021.105988

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bejarano, S., Pardede, S., Campbell, S.J., Hoey, A.S., Ferse, S.C.A., 2019. Herbivorous fish rise as a destructive fishing practice falls in an Indonesian marine national park. Ecol. Appl. 29. https://doi.org/10.1002/eap.1981

Bellwood, D.R., Hoey, A.S., Hughes, T.P., 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc. R. Soc. B Biol. Sci. 279, 1621–1629. https://doi.org/10.1098/rspb.2011.1906

Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833. https://doi.org/10.1038/nature02691

Bellwood, D.R., Hughes, T.P., Hoey, A.S., 2006. Sleeping Functional Group Drives Coral-Reef Recovery. Curr. Biol. 16, 2434–2439. https://doi.org/10.1016/j.cub.2006.10.030

Bender, M.G., Machado, G.R., De Azevedo Silva, P.J., Floeter, S.R., Monteiro-Netto, C., Luiz, O.J., Ferreira, C.E.L., 2014. Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. PLoS One 9. https://doi.org/10.1371/journal.pone.0110332

Boaden, A.E., Kingsford, M.J., 2015. Predators drive community structure in coral reef fish assemblages. Ecosphere 6, 1–33. https://doi.org/10.1890/ES14-00292.1

Bozec, Y.M., O'Farrell, S., Bruggemann, J.H., Luckhurst, B.E., Mumby, P.J., 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc. Natl. Acad. Sci. U. S. A. 113, 4536–4541. https://doi.org/10.1073/pnas.1601529113

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs At Risk Revisited, World Resources Institute.

Burkepile, D.E., Hay, M.E., 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS One 5. https://doi.org/10.1371/journal.pone.0008963

Burkepile, D.E., Hay, M.E., 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci. 105, 16201–16206. https://doi.org/10.1073/PNAS.0801946105

Campbell, S.J., Darling, E.S., Pardede, S., Ahmadia, G., Mangubhai, S., Amkieltiela, Estradivari, Maire, E., 2020. Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. Conserv. Lett. 13, 1–9. https://doi.org/10.1111/conl.12698

Campbell, S.J., Edgar, G.J., Stuart-Smith, R.D., Soler, G., Bates, A.E., 2018. Fishing-gear restrictions and biomass gains for coral reef fishes in marine protected areas. Conserv. Biol. 32, 401–410. https://doi.org/10.1111/COBI.12996

Cheal, A.J., MacNeil, M.A., Cripps, E., Emslie, M.J., Jonker, M., Schaffelke, B., Sweatman, H., 2010. Coral – macroalgal phase shifts or reef resilience : links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs (2010) 29, 1005–1015. https://doi.org/10.1007/s00338-010-0661-y

Chung, A.E., Wedding, L.M., Green, A.L., Friedlander, A.M., Goldberg, G., Meadows, A., Hixon, M.A., 2019. Building Coral reef resilience through spatial herbivore management. Front. Mar. Sci. 6, 1–12. https://doi.org/10.3389/fmars.2019.00098

Cinner, J.E., Zamborain-Mason, J., Gurney, G.G., Graham, N.A.J., MacNeil, M.A., Hoey, A.S., Mora, C., Villéger, S., Maire, E., McClanahan, T.R., Maina, J.M., Kittinger, J.N., Hicks, C.C., D'Agata, S., Huchery, C., Barnes, M.L., Feary, D.A., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G.J., Stuart-Smith, R.D., Sandin, S.A., Green, A.L., Beger, M., Friedlander, A.M., Wilson, S.K., Brokovich, E., Brooks, A.J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Tupper, M., Ferse, S.C.A., Sumaila, U.R., Hardt, M.J., Mouillot, D., 2020. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. Science (80-.). 368, 307–311. https://doi.org/10.1126/science.aax9412

Clarke, K. R., & Gorley, R. N. (2001). PRIMER v6 PRIMER-E Ltd. Plymouth, UK.

Clua, E., Legendre, P., 2008. Shifting dominance among Scarid species on reefs representing a gradient of fishing pressure. Aquat. Living Resour. 21, 339–348. https://doi.org/10.1051/ALR:2008036

Cure, K., Currey-Randall, L., Galaiduk, R., Radford, B., Wakeford, M., Heyward, A., 2021. Depth gradients in abundance and functional roles suggest limited depth refuges for herbivorous fishes. Coral Reefs 40, 365–379. https://doi.org/10.1007/s00338-021-02060-7

Ebrahim, A., Martin, T.S.H., Mumby, P.J., Olds, A.D., Tibbetts, I.R., 2020. Differences in diet and foraging behaviour of commercially important rabbitfish species on coral reefs in the Indian Ocean. Coral Reefs 39, 977–988. https://doi.org/10.1007/s00338-020-01918-6

Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P., Williams, I.D., Zgliczynski, B., Sandin, S.A., Smith, J.E., 2014. Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. Proc. R. Soc. B Biol. Sci. 281, 7–11. https://doi.org/10.1098/rspb.2013.1835

Fine, M., Gildor, H., Genin, A., 2013. A coral reef refuge in the Red Sea. Glob. Chang. Biol. 19, 3640–3647. https://doi.org/10.1111/GCB.12356

Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E., Caley, M.J., 2015. Species Richness on Coral Reefs and the Pursuit of Convergent Global Estimates. Curr. Biol. 25, 500–505. https://doi.org/10.1016/J.CUB.2014.12.022

Floeter, S.R., Halpern, B.S., Ferreira, C.E.L., 2006. Effects of fishing and protection on Brazilian reef fishes. Biol. Conserv. 128, 391–402. https://doi.org/10.1016/j.biocon.2005.10.005

Foo, S.A., Walsh, W.J., Lecky, J., Marcoux, S., Asner, G.P., 2021. Impacts of pollution, fishing pressure, and reef rugosity on resource fish biomass in West Hawaii. Ecol. Appl. 31, 1–15. https://doi.org/10.1002/eap.2213

Ford, A.K., Bejarano, S., Marshell, A., Mumby, P.J., 2016. Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 790–805. https://doi.org/10.1002/aqc.2623

Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R., Rodgers, K.S., 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22, 291–305. https://doi.org/10.1007/s00338-003-0317-2

Frisch, A.J., Cole, A.J., Hobbs, J.P.A., Rizzari, J.R., Munkres, K.P., 2012. Effects of Spearfishing on Reef Fish Populations in a Multi-Use Conservation Area. PLoS One 7. https://doi.org/10.1371/journal.pone.0051938

Galal, N., 1999. Studies on the coastal ecology and management of the Nabq Protected Area, South Sinai, Egypt (BL) . PQDT - UK Irel. . University of York.

Galal, N., Ormond, R.F.G., Hassan, O., 2002. Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. Mar. Freshw. Res. 53, 199–205. https://doi.org/https://doi.org/10.1071/MF01158

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holst, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543, 665–669. https://doi.org/10.1038/nature21708

Golani, D., Fricke, R., 2018. Checklist of the Red Sea Fishes with delineation of the Gulf of Suez, Gulf of Aqaba, endemism and Lessepsian migrants, Zootaxa. https://doi.org/10.11646/zootaxa.4509.1.1

Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 2012 322 32, 315–326. https://doi.org/10.1007/S00338-012-0984-Y

Green, A.L., Bellwood, D.R., 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience : a practical guide for coral reef managers in the Asia Pacific region (No. 7), IUCN resilience science group working paper series.

Hasler, H., Ott, J.A., 2008. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea. Mar. Pollut. Bull. 56, 1788–1794. https://doi.org/10.1016/j.marpolbul.2008.06.002

Hawkins, J.P., Roberts, C.M., 2004. Effects of fishing on sex-changing Caribbean parrotfishes. Biol. Conserv. 115, 213–226. https://doi.org/10.1016/S0006-3207(03)00119-8

Heenan, A., Williams, I.D., 2013. Monitoring herbivorous fishes as indicators of coral reef resilience in American Samoa. PLoS One 8. https://doi.org/10.1371/journal.pone.0079604

Helyer, J., Samhouri, J.F., 2017. Fishing and environmental influences on estimates of unfished herbivorous fish biomass across the Hawaiian Archipelago. Mar. Ecol. Prog. Ser. 575, 1–15. https://doi.org/10.3354/meps12235

Hixon, M.A., 2015. Predation: Piscivory and the ecology of coral reef fishes. Ecol. Fishes Coral Reefs 41–52. https://doi.org/10.1017/CBO9781316105412.007

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. Biometrical J. 50, 346–363. https://doi.org/10.1002/bimj.200810425

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Curr. Biol. 17, 360–365. https://doi.org/10.1016/j.cub.2006.12.049

Humphries, A.T., McClanahan, T.R., McQuaid, C.D., 2020. Algal turf consumption by sea urchins and fishes is mediated by fisheries management on coral reefs in Kenya. Coral Reefs 39, 1137–1146. https://doi.org/10.1007/s00338-020-01943-5

Kattan, A., Coker, D.J., Berumen, M.L., 2017. Reef fish communities in the central Red Sea show evidence of asymmetrical fishing pressure. Mar. Biodivers. 47, 1227–1238. https://doi.org/10.1007/s12526-017-0665-8

Khalil, M.T., Bouwmeester, J., Berumen, M.L., 2017. Spatial variation in coral reef fish and benthic communities in the central Saudi Arabian Red Sea. PeerJ 2017, 1–23. https://doi.org/10.7717/peerj.3410

Khalil, M.T., Cochran, J.E.M., Berumen, M.L., 2013. The abundance of herbivorous fish on an inshore Red Sea reef following a mass coral bleaching event. Environ. Biol. Fishes 96, 1065–1072. https://doi.org/10.1007/s10641-012-0103-5

Lirman, D., 2001. Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19, 392–399. https://doi.org/10.1007/s003380000125

Mabrouk, A. M. H. (2015). The role of marine protected areas in maintaining sustainable fisheries in the Egyptian Gulf of Aqaba, Red Sea. Michigan State University.

Marshell, A., Mumby, P.J., 2012. Revisiting the functional roles of the surgeonfish Acanthurus nigrofuscus and Ctenochaetus striatus. Coral Reefs 2012 314 31, 1093–1101. https://doi.org/10.1007/S00338-012-0931-Y

Martinez Arbizu, P. (2020). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4

Maynard, J.A., McKagan, S., Raymundo, L., Johnson, S., Ahmadia, G.N., Johnston, L., Houk, P., Williams, G.J., Kendall, M., Heron, S.F., van Hooidonk, R., Mcleod, E., Tracey, D., Planes, S., 2015. Assessing relative resilience potential of coral reefs to inform management. Biol. Conserv. 192, 109–119. https://doi.org/10.1016/j.biocon.2015.09.001

McClanahan, T.R., Friedlander, A.M., Graham, N.A.J., Chabanet, P., Bruggemann, J.H., 2021. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. Aquat. Conserv. Mar. Freshw. Ecosyst. 31, 28–42. https://doi.org/10.1002/aqc.3448

Mcclanahan, T.R., Graham, N.A.J., Macneil, M.A., Cinner, J.E., 2015. Biomass-based targets and the management of multispecies coral reef fisheries. Conserv. Biol. 29, 409–417. https://doi.org/10.1111/cobi.12430

McClanahan, T.R., Muthiga, N.A., 2020. Change in fish and benthic communities in Belizean patch reefs in and outside of a marine reserve, across a parrotfish capture ban. Mar. Ecol. Prog. Ser. 645, 25–40. https://doi.org/10.3354/meps13357

McClanahan, T.R., Muthiga, N.A., Kamukuru, A.T., Machano, H., Kiambo, R.W., 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. Biol. Conserv. 89, 161–182. https://doi.org/10.1016/S0006-3207(98)00123-2

McClanahan, T.R., Schroeder, R.E., Friedlander, A.M., Vigliola, L., Wantiez, L., Caselle, J.E., Graham, N.A.J., Wilson, S., Edgar, G.J., Stuart-Smith, R.D., Oddenyo, R.M., Cinner, J.E., 2019. Global baselines and benchmarks for fish biomass: Comparing remote reefs and fisheries closures. Mar. Ecol. Prog. Ser. 612, 167–192. https://doi.org/10.3354/meps12874

Mumby, P.J., Steneck, R.S., Adjeroud, M., Arnold, S.N., 2016. High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. Oikos 125, 644–655. https://doi.org/10.1111/oik.02673

Naumann, M.S., Bednarz, V.N., Ferse, S.C.A., Niggl, W., Wild, C., 2015. Monitoring of coastal coral reefs near Dahab (Gulf of Aqaba, Red Sea) indicates local eutrophication as potential cause for change in benthic communities. Environ. Monit. Assess. 187, 1–14. https://doi.org/10.1007/s10661-014-4257-9

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., 2019. Vegan. Encycl. Food Agric. Ethics 2395–2396. https://doi.org/10.1007/978-94-024-1179-9_301576

Olds, A.D., Albert, S., Maxwell, P.S., Pitt, K.A., Connolly, R.M., 2013. Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific. Glob. Ecol. Biogeogr. 22, 1040–1049. https://doi.org/10.1111/geb.12072

Osman, E.O., Smith, D.J., Ziegler, M., Kürten, B., Conrad, C., El-Haddad, K.M., Voolstra, C.R., Suggett, D.J., 2018. Thermal refugia against coral bleaching throughout the northern Red Sea. Glob. Chang. Biol. 24, e474–e484. https://doi.org/10.1111/gcb.13895

Pearson, M.P., Shehata, A.I., 1998. Protectorates management for conservation and development in the Arab Republic of Egypt. Parks 8, 29–35.

Poonian, C., 2020. Coral reef fisheries of the Mzeina Bedu in South Sinai. https://doi.org/10.13140/RG.2.2.11937.02409

Pratchett, M.S., Hoey, A.S., Wilson, S.K., 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr. Opin. Environ. Sustain. 7, 37–43. https://doi.org/10.1016/j.cosust.2013.11.022

Price, N.W., Chen, K., Chen, C.A., Wen, C.K., 2021. Scraping and grazing herbivorous/detritivorous sh display opposite feeding behaviours under different protection regulations 1–22.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Reverter, M., Jackson, M., Daraghmeh, N., von Mach, C., Milton, N., 2020. 11-yr of coral community dynamics in reefs around Dahab (Gulf of Aqaba, Red Sea): the collapse of urchins and rise of macroalgae and cyanobacterial mats. Coral Reefs 39, 1605–1618. https://doi.org/10.1007/s00338-020-01988-6

Robinson, J.P.W., McDevitt-Irwin, J.M., Dajka, J.C., Hadj-Hammou, J., Howlett, S., Graba-Landry, A., Hoey, A.S., Nash, K.L., Wilson, S.K., Graham, N.A.J., 2020. Habitat and fishing control grazing potential on coral reefs. Funct. Ecol. 34, 240–251. https://doi.org/10.1111/1365-2435.13457

Robinson, J.P.W., Williams, I.D., Edwards, A.M., McPherson, J., Yeager, L., Vigliola, L., Brainard, R.E., Baum, J.K., 2017. Fishing degrades size structure of coral reef fish communities. Glob. Chang. Biol. 23, 1009–1022. https://doi.org/10.1111/gcb.13482

Roff, G., Bejarano, S., Priest, M., Marshell, A., Chollett, I., Steneck, R.S., Doropoulos, C., Golbuu, Y., Mumby, P.J., 2019. Seascapes as drivers of herbivore assemblages in coral reef ecosystems. Ecol. Monogr. 89. https://doi.org/10.1002/ecm.1336

Rolim, F.A., Langlois, T., Rodrigues, P.F.C., Bond, T., Motta, F.S., Neves, L.M., Gadig, O.B.F., 2018. Network of small no-take marine reserves reveal greater abundance and body size of fisheries target species. bioRxiv 1–22. https://doi.org/10.1101/422147

Russ, G.R., Payne, C.S., Bergseth, B.J., Rizzari, J.R., Abesamis, R.A., Alcala, A.C., 2018. Decadal-scale response of detritivorous surgeonfishes (family Acanthuridae) to no-take marine reserve protection and changes in benthic habitat. J. Fish Biol. 93, 887–900. https://doi.org/10.1111/jfb.13809

Russ, G.R., Questel, S.-L.A., Rizzari, J.R., Alcala, A.C., 2015. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar. Biol. 2015 16210 162, 2029–2045. https://doi.org/10.1007/S00227-015-2728-3

Samy-kamal, M., 2015. Status of fisheries in Egypt : reflections on past trends and management challenges. Rev. Fish Biol. Fish. 25, 631–649. https://doi.org/10.1007/s11160-015-9404-z

Shantz, A.A., Ladd, M.C., Burkepile, D.E., 2020. Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. Ecol. Monogr. 90, 1–17. https://doi.org/10.1002/ecm.1403

Shpigel, M., Fishelson, L., 1991. Experimental removal of piscivorous groupers of the genus Cephalopholis (Serranidae) from coral habitats in the Gulf of Aqaba (Red-Sea). Environ. Biol. Fishes 31, 131–138. https://doi.org/https://doi.org/10.1007/BF00001014

Shpigel, M., Fishelson, L., 1989. Food habits and prey selection of three species of groupers from the genus Cephalopholis (Serranidae: Teleostei). Environ. Biol. Fishes 24, 67–73. https://doi.org/https://doi.org/10.1007/BF00001611

Spalding, M., Burke, L., Wood, S.A., Ashpole, J., Hutchison, J., zu Ermgassen, P., 2017. Mapping the global value and distribution of coral reef tourism. Mar. Policy 82, 104–113. https://doi.org/10.1016/J.MARPOL.2017.05.014

Steneck, R.S., Mumby, P.J., MacDonald, C., Rasher, D.B., Stoyle, G., 2018. Attenuating effects of ecosystem management on coral reefs. Sci. Adv. 4, 1–12. https://doi.org/10.1126/sciadv.aao5493

Tilot, V., Leujak, W., Ormond, R.F.G., Ashworth, J.A., Mabrouk, A., 2008. Monitoring of South Sinai coral reefs: Influence of natural and anthropogenic factors. Aquat. Conserv. Mar. Freshw. Ecosyst. 18, 1109–1126. https://doi.org/10.1002/AQC.942

Topor, Z.M., Rasher, D.B., Duffy, J.E., Brandl, S.J., 2019. Marine protected areas enhance coral reef functioning by promoting fish biodiversity. Conserv. Lett. 12, 1–9. https://doi.org/10.1111/conl.12638

Vallès, H., Oxenford, H.A., 2014. Parrotfish size: A simple yet useful alternative indicator of fishing effects on Caribbean reefs? PLoS One 9. https://doi.org/10.1371/journal.pone.0086291

Weijerman, M., Gove, J.M., Williams, I.D., Walsh, W.J., Minton, D., Polovina, J.J., 2018. Evaluating management strategies to optimise coral reef ecosystem services. J. Appl. Ecol. 55, 1823–1833. https://doi.org/10.1111/1365-2664.13105

Wilkinson, C., 2008. Status of coral reefs of the world: 2008.

Williams, I.D., Kindinger, T.L., Couch, C.S., Walsh, W.J., Minton, D., Oliver, T.A., 2019. Can Herbivore Management Increase the Persistence of Indo-Pacific Coral Reefs? Front. Mar. Sci. 6, 1–15. https://doi.org/10.3389/fmars.2019.00557

Williams, I.D., White, D.J., Sparks, R.T., Lino, K.C., Zamzow, J.P., Kelly, E.L.A., Ramey, H.L., 2016. Responses of Herbivorous Fishes and Benthos to 6 Years of Protection at the Kahekili Herbivore Fisheries Management Area, Maui. PLoS One 11, e0159100. https://doi.org/10.1371/JOURNAL.PONE.0159100

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecol. Appl. 20, 442–451. https://doi.org/https://doi.org/10.1890/08-2205.1

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, 1st ed, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/https://doi.org/10.1007/978-0-387-87458-6

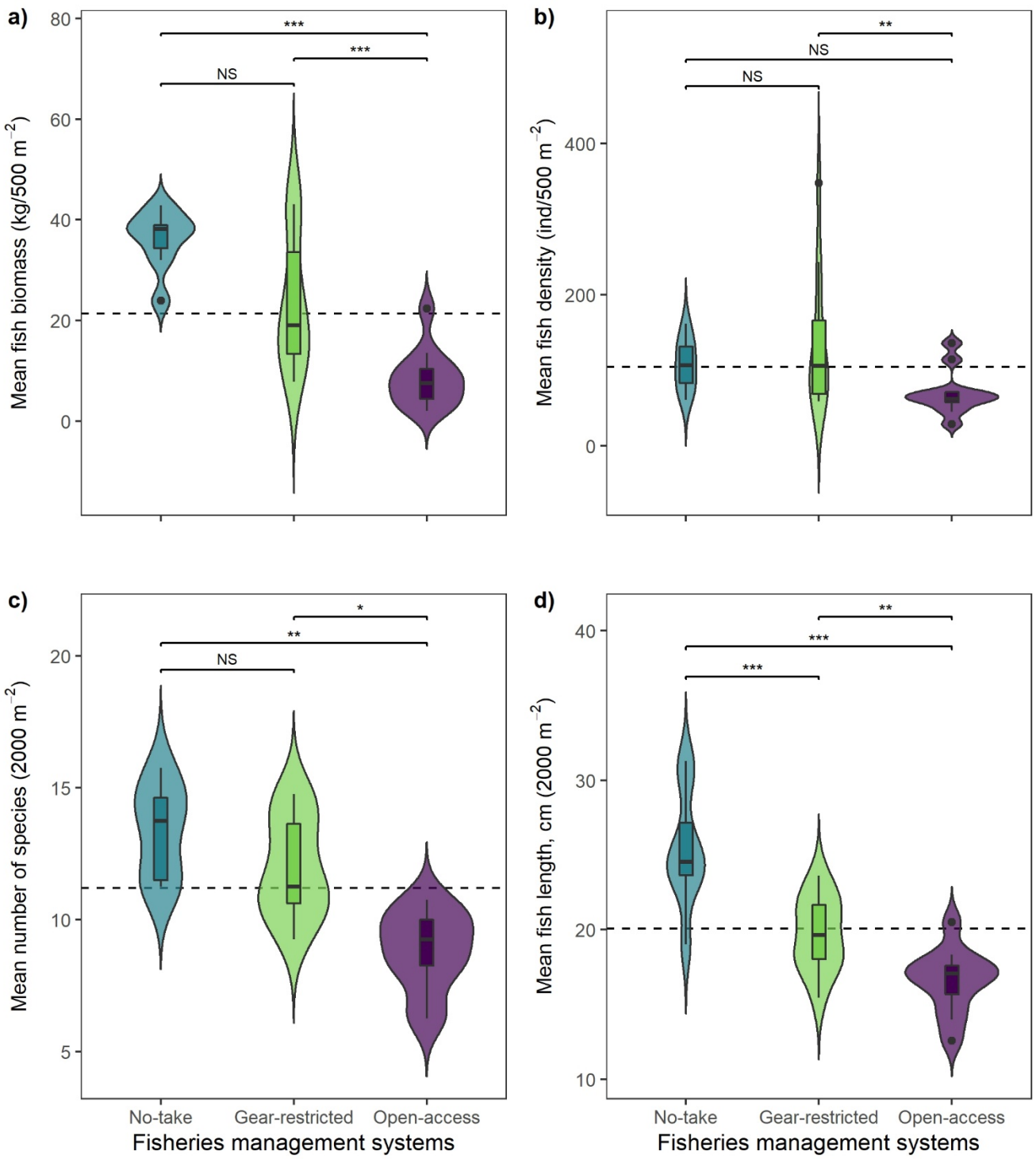

Figure 2. Violin plots with boxplots overlaid, showing the comparison of total herbivorous fish indices between the sampling three fisheries management systems in 2017. Fish biomass (a), Fish density (b), Species richness (c) and Fish size (d). The boxplot shows the median (black line) and interquartile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

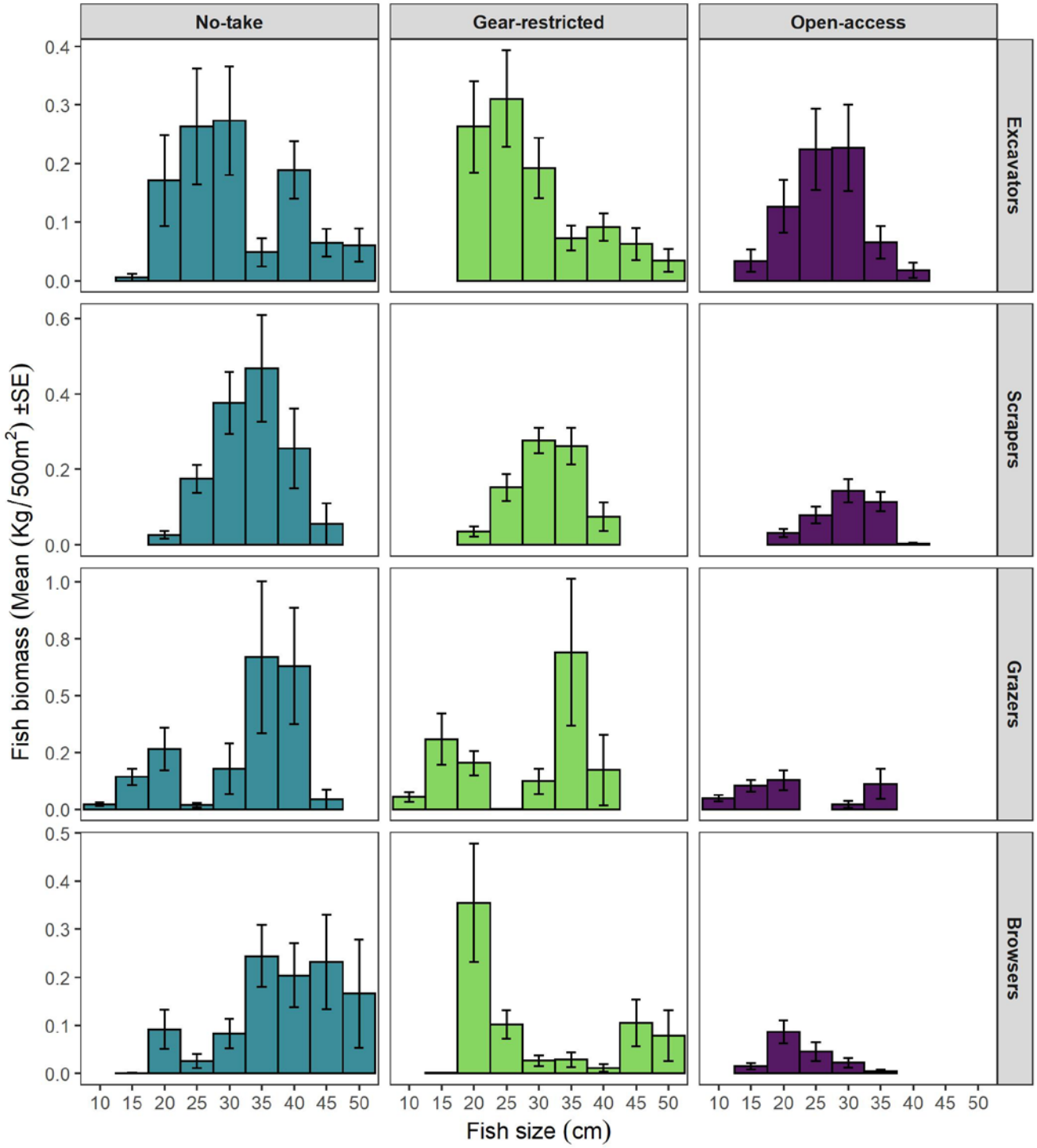

Figure 3. Mean biomass (kg 500^2 ± SE) for each size-class (total length; cm) of herbivorous fishes divided by (functional feeding group) in each fisheries management systems

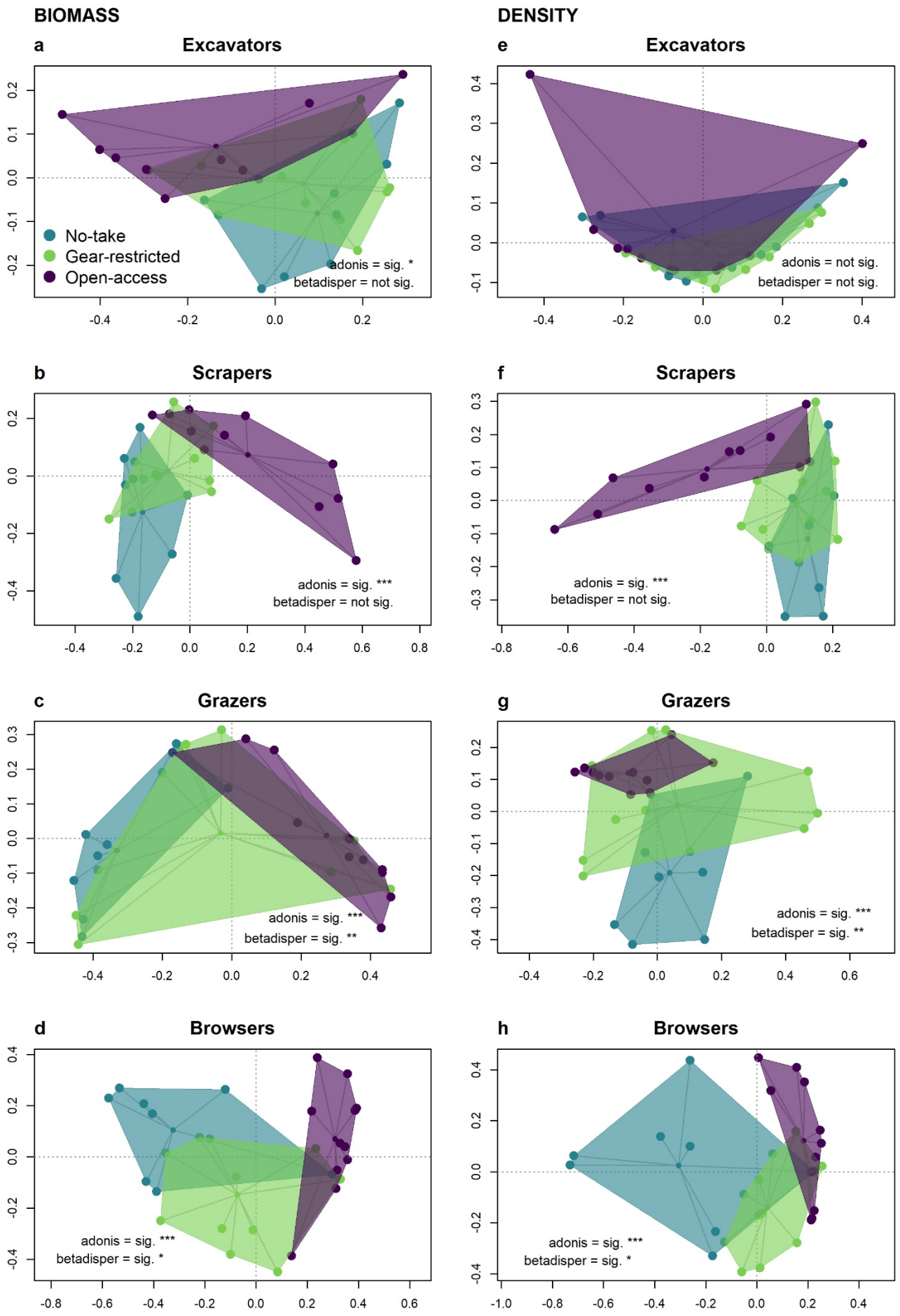
BIOMASS
a
Excavators
No-take
Gear-restricted
Open-access
adonis = sig. *
betadisper = not sig.
b
Scrapers
adonis = sig. ***
betadisper = not sig.
c
Grazers
adonis = sig. ***
betadisper = sig. **
d
Browsers
adonis = sig. ***
betadisper = sig. *
DENSITY
e
Excavators
adonis = not sig.
betadisper = not sig.
f
Scrapers
adonis = sig. ***
betadisper = not sig.
g
Grazers
adonis = sig. ***
betadisper = sig. **
h
Browsers
adonis = sig. ***
betadisper = sig. *

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 ***$p<0.001$, **$p<0.01$, *$p<0.05$.

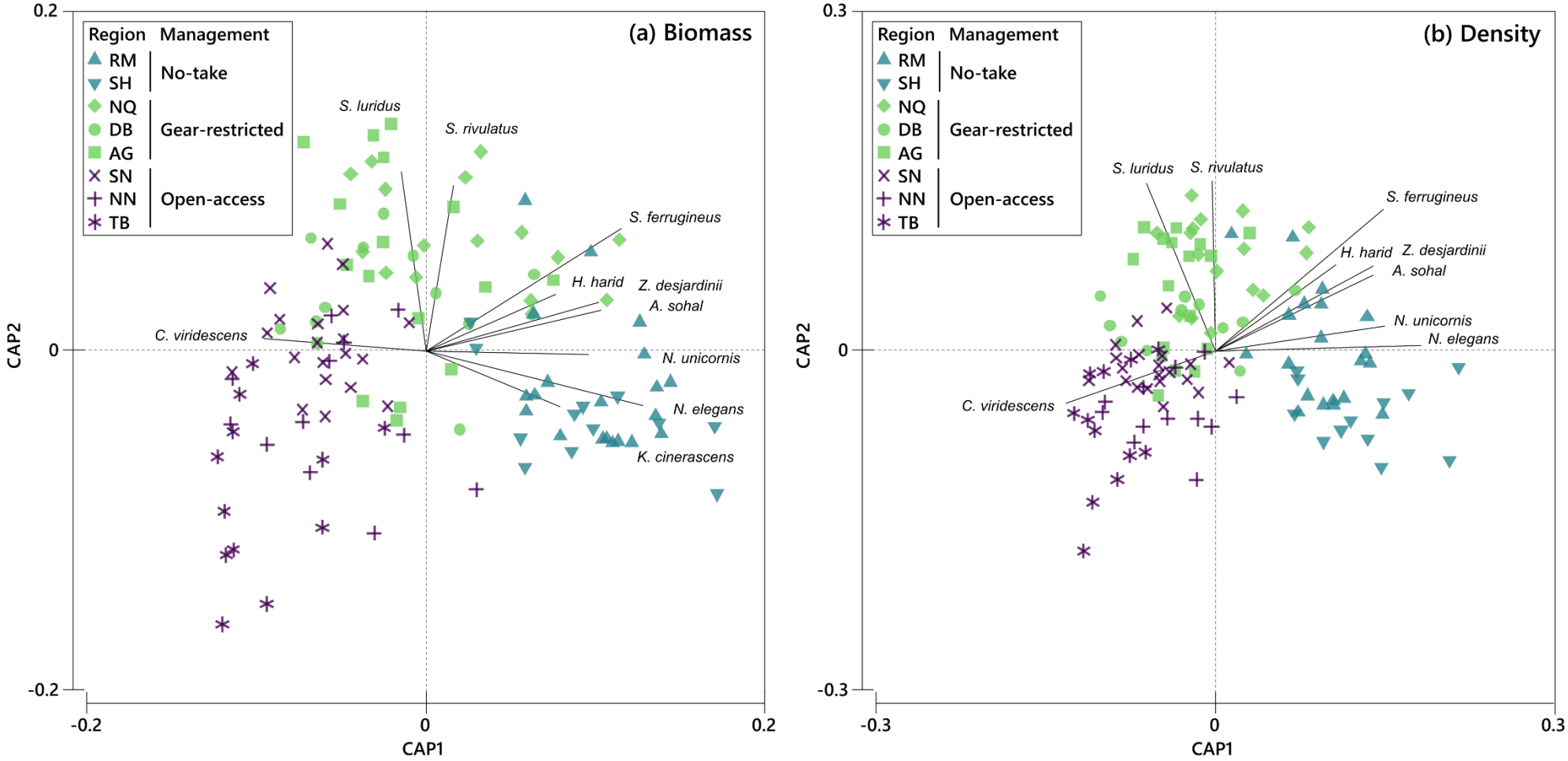

Figure 5. Canonical analysis of principal coordinates (CAP) ordination based on Bray-Curtis similarity for herbivorous fish biomass (a) and density (b) across three fisheries management systems (NT, GR, OA) and eight regions (RM: Ras Muhammad, SH: Sharm El-Sheikh, NQ: Nabq, DB: Dahab, AG: Abu Galum, 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).

Table 2.

Summary of generalized linear mixed-effects models (GLMMs) results used to examine the differences in fish biomass, density, species richness and body length. Models contain the fixed effect: fisheries management systems (no-take, gear-restricted, and open-access). SE = standard error, Gamma distribution models use a *t* value while Poisson models use a *z* value.

Response variable	Predictor variable	Estimate	SE	*t/z value*	*p value*
Biomass					
All herbivores	Intercept	4.9610	0.1884	26.333	< 0.001 ***
	Open-access	-1.6455	0.2476	-6.646	< 0.001 ***
	Gear-restricted	-0.5543	0.2476	-2.239	0.025 *
Excavators	Intercept	2.5311	0.4740	5.339	< 0.001 ***
	Open-access	-0.6818	0.6129	-1.112	0.266
	Gear-restricted	-0.1055	0.6125	-0.172	0.863
Scrapers	Intercept	3.5700	0.2540	14.053	< 0.001 ***
	Open-access	-1.6126	0.3339	-4.830	< 0.001 ***
	Gear-restricted	-0.5357	0.3339	-1.605	0.109
Grazers	Intercept	3.9424	0.2972	13.267	< 0.001 ***
	Open-access	-1.9482	0.3905	-4.988	< 0.001 ***
	Gear-restricted	-0.8473	0.3905	-2.170	0.030 *
Browsers	Intercept	3.1213	0.2792	11.178	< 0.001 ***
	Open-access	-1.6041	0.3668	-4.374	< 0.001 ***
	Gear-restricted	-0.2279	0.3666	-0.622	0.534
Density					
All herbivores	Intercept	6.0105	0.1605	37.452	< 0.001 ***
	Open-access	-0.4519	0.2125	-2.127	0.033 *
	Gear-restricted	0.1220	0.2106	0.579	0.562
Excavators	Intercept	3.6468	0.1770	20.606	< 0.001 ***
	Open-access	-0.2538	0.2366	-1.072	0.284
	Gear-restricted	0.1138	0.2311	0.492	0.622
Scrapers	Intercept	4.2388	0.3047	13.910	< 0.001 ***
	Open-access	-1.2588	0.4021	-3.131	0.002 **
	Gear-restricted	-0.2462	0.3948	-0.624	0.533
Grazers	Intercept	5.4232	0.1944	27.900	< 0.001 ***
	Open-access	-0.3017	0.2557	-1.180	0.238
	Gear-restricted	0.1192	0.2555	0.467	0.641
Browsers	Intercept	3.8109	0.2819	13.517	< 0.001 ***
	Open-access	-0.3978	0.3664	-1.086	0.278
	Gear-restricted	0.5423	0.3635	1.492	0.136
Species richness					
All herbivores	Intercept	2.93784	0.08138	36.101	< 0.001 ***
	Open-access	-0.35213	0.11607	-3.034	0.002 **
	Gear-restricted	-0.06273	0.10840	-0.579	0.563
Fish size					
All herbivores	Intercept	3.22531	0.04587	70.319	< 0.001 ***
	Open-access	-0.42615	0.06028	-7.070	< 0.001 ***
	Gear-restricted	-0.25130	0.06028	-4.169	< 0.001 ***

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

Table 3.

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

	Fisheries Management Systems		
Response variable	**NT vs OA**	**GR vs OA**	**NT vs GR**
Biomass			
All 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
Density			
All 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
Species richness			
All herbivores	0.007 **	0.022 *	0.831
Fish size			
All herbivores	<0.001 ***	0.005 **	< 0.001 ***

NT refers to No-take, GR refers to Gear-restricted and OA refers to Open-access. 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