

Fisheries restrictions and their cascading effects on herbivore abundance and macroalgae removal at Kenyan coral reefs

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ABSTRACT

The increase of macroalgae at degraded reefs impedes several ecosystem services and calls for effective methods to facilitate a return to coral dominance. Removal of macroalgae (browsing) is typically realized by fish, but the role and identity of browsers at the heavily-fished East African coast is still largely unknown. This study investigated how browsing pressure at Kenyan reefs (−4.700, 39.396) related to fisheries management and herbivore community. From October 2018 to January 2019, consumption during 24-h buffet assays using the brown macroalgae *Sargassum* and *Padina* was determined and video recorded at six sites: two in fished zones, two in marine reserves (traditional fishing allowed) and two in no-take zones. Herbivorous fish composition, biomass and sea urchin density were also determined. Consumption of *Sargassum* and *Padina* was nearly three-fold lower in the fished zones (26% and 28% of macroalgal biomass consumed, respectively) compared to the no-take zones (62% and 82%), with intermediate consumption in the marine reserves (48% and 71%). Herbivore biomass was seven-fold higher in no-take zones and included substantially more browsers (mainly unicornfishes, *Naso* spp.) and scrapers (scarids), which were associated with the higher browsing pressure. Browsers and scrapers were predominantly responsible for the consumption of macroalgae as determined by video recordings, though key species differed across sites. In contrast, damselfish-dominated fished sites were associated with high sea urchin densities and low browsing pressure. These results indicate that fishing restrictions are likely to support reef resilience by increasing herbivorous fish biomass of key species and thereby promote macroalgae removal.

1. Introduction

Important ecosystem services such as coastal protection and sustainable fisheries provision become reduced when coral reefs degrade into seascapes dominated by macroalgae (Pratchett et al., 2014; Rogers et al., 2018). Herbivores, especially fish, play a crucial role in promoting coral over macroalgal dominance (Holbrook et al., 2016; Hughes et al., 2007) either by preventing the establishment of macroalgal recruits through continuous removal of algal turf (i.e. grazing) or by reversing macroalgal dominance through selective removal of mature macroalgae (i.e. browsing). Grazing of algal turf creates favourable conditions for coral growth and settlement and thereby supports coral dominance (Lefcheck et al., 2019) and consequently reef biodiversity and resilience (Nyström et al., 2008). However, with climate change induced temperature stress weakening the competitive potential of numerous corals (Sully et al., 2019) in combination with overfishing (Edwards et al.,

2014) and eutrophication (Norström et al., 2009), impaired grazer communities become increasingly unable to prevent macroalgae establishment. First and predominantly observed in the Caribbean (Bruno et al., 2009; Done, 1992), coral to macroalgae phase shifts are now occasionally reported from Indo-Pacific reefs as well (Chong-Seng et al., 2014; Ledlie et al., 2007; McClanahan et al., 2001). Once established, macroalgae can prevent a return to a coral-dominated state by suppressing the survival, fecundity and recruitment of corals (Hughes et al., 2007; Schmitt et al., 2019). It is thought that reversal of such phase shifts can be achieved mainly through the active removal of macroalgae by browsers (Puk et al., 2016). Therefore, a good understanding on the distribution of key browsing species and the factors influencing their potential to control macroalgae is important.

The use of functional groups has proven helpful to understand the principles of ecological processes and coral reef resilience (Heenan and Williams, 2013). Even though herbivory is a well-studied process on

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coral reefs, research focussed on browsers specifically has been challenging and results often defy generalization. Identification of key species responsible for macroalgae removal based on their abundance alone has proven difficult for several reasons. Biomass estimates from visual surveys tend to underestimate browser diversity and biomass due to the cautious nature of browsers (Hoey and Bellwood, 2010; Michael et al., 2013), though the use of video-recorded macroalgae buffet assays have provided a wealth of additional information on browsers (Bennett and Bellwood, 2011). Browsing on macroalgae seems to be commonly done by only a small subset of the diverse browser community due to spatial, temporal and behavioural variation (Bennett and Bellwood, 2011; Lefèvre and Bellwood, 2011; Puk et al., 2016), and is sometimes even dominated by species traditionally not considered as browsers (Bellwood et al., 2006; Chong-Seng et al., 2014; Tebbett et al., 2020). In addition to these various groups of fishes, sea urchins can also contribute to the control of macroalgae (McClanahan et al., 1994) and this has been especially important on Caribbean reefs (Francis et al., 2019). Increasing numbers of sea urchins have become more dominant in macroalgal control at certain overfished Indo-Pacific reefs as well (Humphries et al., 2014), but also contribute heavily to reef erosion through their scraping feeding method (Carreiro-Silva and McClanahan, 2001). The apparent plasticity in functional roles of the browser community complicates the use of browser biomass alone to predict browsing pressure, an indicator deemed relevant for reef resilience (Brandl and Bellwood, 2014; Nyström et al., 2008).

Mismatches between abundance and ecological relevance of browsing species have important management implications, where protection of certain species might not result in the desired coral reef resilience (McClanahan, 2008). A good understanding on which species contribute most to macroalgae removal can enable managers to increase reef resilience and the likelihood of phase shift reversal when restoration towards coral dominance is desired. Although several studies on the well-protected Great Barrier Reef have proven invaluable to identify dominant browsers and potential drivers for the regional variability in browsing pressure (Bennett and Bellwood, 2011; Hoey and Bellwood, 2009; Michael et al., 2013; Streit et al., 2015), the application of this knowledge to other geographical areas and sites with higher fishing pressure may be limited. Indeed, superimposed on geographic differences (Heenan et al., 2016) is the divergent fishing pressure among coastal populations, in which large-bodied fishes such as browsers are often preferred targets (Edwards et al., 2014). The susceptibility of browsers to fishing pressure (see also Froese and Pauly, 2015) and their important yet complex role in the coral-algae balance call for a better understanding of these dynamics in general and variability among geographical areas in particular.

This study aimed to further improve our understanding on browsing by expanding the geographic scope and including the impact of fisheries management within the study domain. We provide an identification of key browsers and quantification of their browsing capacity at six Kenyan reefs, which form part of a mostly intensely-utilized fringing reef in the Western Indian Ocean. Here, the enforcement of three distinct fisheries management zones (open access fished zones, marine reserves for traditional fishing only and well-enforced no-take zones) are well suited to investigate the impact of management on the browser community and their influence on reef resilience. Through video-recorded macroalgae buffet assays we identified key browsing species and their browsing pressure and related this to biomass estimates from stationary fish surveys and sea urchin counts. We hypothesised that the increasing levels of fisheries restrictions would result in higher herbivorous fish biomass and more effective control of macroalgae.

2. Materials and methods

2.1. Study sites

The study was performed around Wasini Island in southern Kenya

from October 2018 till January 2019 during the dry northeast monsoon. Tidal differences reach over four meters during spring tide and result in moderately strong tidal currents throughout the area. Six study sites were chosen (Fig. 1), equally distributed over three different types of fisheries management. Two study sites are located in a fished zone, where intense and unselective fishing is performed daily by artisanal fishermen using mainly traps, nets, spearguns and hook and line (sites 1 and 2). Two study sites are in the Mpunguti Marine Reserve (11 km² established in 1973), where only traditional fishing methods are allowed (i.e. traps and hook and line) and this is enforced by the Kenyan Wildlife Service (sites 3 and 4). Two well-enforced no-take zones were chosen to complete the comparison, each with one study site: Kisite Marine National Park (28 km² established in 1973) enforced by the Kenya Wildlife Service (site 5), and the Wasini Community Managed Area (0.31 km² established in 2008) enforced locally by the Wasini Beach Management Unit (site 6). Reef zone was standardized by selecting reef slope habitat across study sites and given differences in visibility, this resulted in different depths per site. Sites 1, 2 and 6 are situated in a sea strait between Wasini Island and the mainland and experience relatively turbid water conditions (average visibility ~7 m) and therefore exhibit a shallow (up to 8 m depth) and patchy reef development. These sites had not yet been included in any long-term monitoring program and therefore lack documented data on their habitat such as historical coral cover. Sites 3, 4 and 5, south of Wasini Island, are further offshore and have an average visibility of ~15 m and fringing reef development up to around 16 m depth. Sites 4 and 5 have been monitored extensively and have maintained a moderate to high coral cover and diversity (McClanahan et al., 1999), with a decline and subsequent recovery after the 1998 thermal anomaly (McClanahan et al., 2001; Obura et al., 2002). Site 3 has not been included in past monitoring, but given the hard substrate, clear water and moderate depth and exposure one would expect this site to have been historically suitable for hard corals.

2.2. Benthic and fish surveys

A 20-m point intercept transect with 0.5 m interval was used to map benthic cover in broad categories (hard coral, soft coral, turf algae (< 1 cm), fleshy macroalgae (> 1 cm) and a pooled category 'other' including mainly sand, rubble and uncommon sessile invertebrates such as sponges and tunicates (Hill and Wilkinson, 2004). Within a 2 × 20 m² belt transect sea urchins were identified to species level and counted to determine their density (Hill and Wilkinson, 2004). A stationary fish census (radius of 7.5 m; surveys were only performed on days when visibility exceeded 8 m) was used to quantify the composition and abundance of all diurnal, non-cryptic fishes (Bohnsack and Bannerot, 1986). Fish sizes (fork length) were estimated in classes of 5 cm for fishes smaller than 20 cm, and in 10-cm size classes for larger individuals. Per study site, 10 replicate benthic surveys and 11–15 replicate fish surveys were performed, covering a stretch of around 200 m at each site. Benthic and fish surveys were performed midway the reef slope at study sites with a fringing reef (depth range: 5–9 m) and patch reefs (depth range: 2–6 m).

2.3. Macroalgae buffet assay

At each study site, browsing pressure was determined by recording consumption from macroalgae buffet assays over 24 h (Fig. 2). Two brown macroalgae were used: *Sargassum ilicifolium* and *Padina boergeri* (henceforth referred to by genus name only). These brown algae were chosen as they are the dominant macroalgae in the area and typical representatives of algal climax communities (Humphries et al., 2014). One day before use, the macroalgae were collected from the shallow reef flat at study site 1 and stored in seawater basins. Before and after deployment, the drip-dry wet weight (shaken 10 times to remove excess water) of each macroalgae was determined. The macroalgae were kept in their natural growth form, resulting in the following average starting

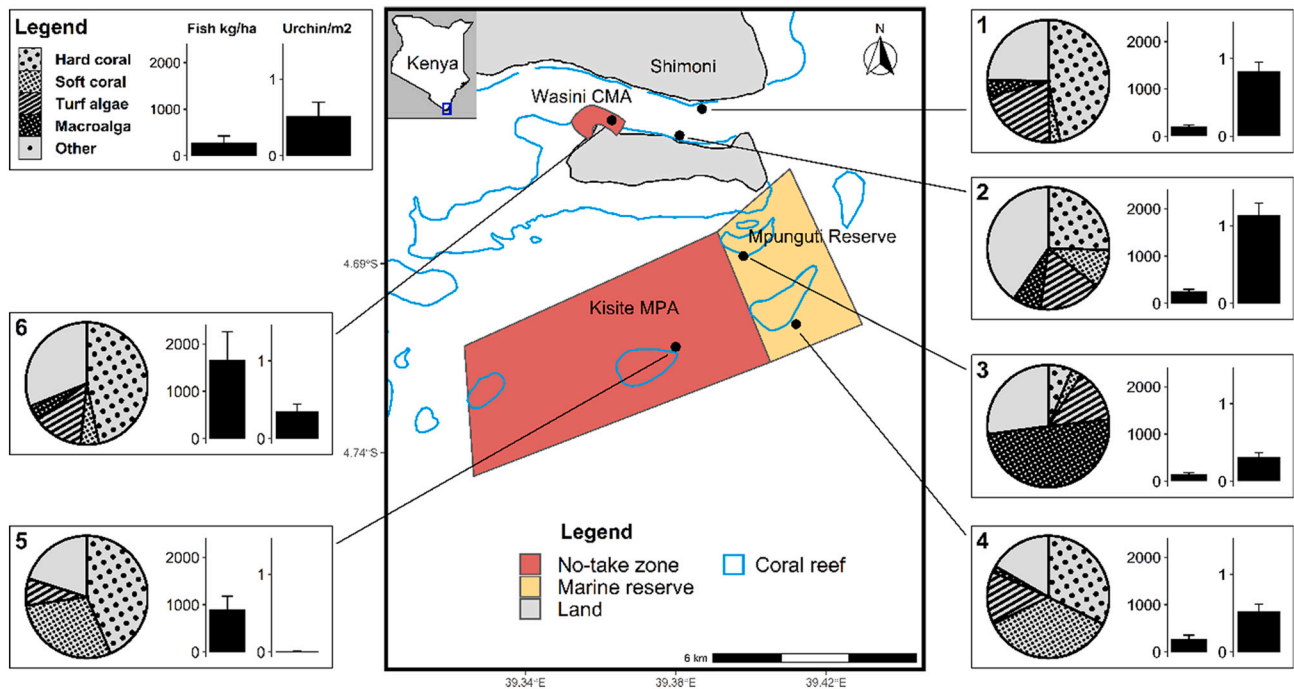


Fig. 1. Map of Kenya showing study area (insert) and detailed map showing the six study sites. Three different fisheries management zones can be identified: unrestricted fished zone (unshaded) including sites 1 (Firefly House Reef) & 2 (Pilli Pipa Restaurant), the Mpunguti Marine Reserve where traditional fishing is allowed (shaded orange) encompassing sites 3 (Lower Mpunguti) & 4 (Dolphin Point) and no-take zones (shaded red) covering sites 5 (Kisite Marine National Park) & 6 (Wasini Community Managed Area). Boxes show additional information for each study site on benthic cover, total fish biomass and sea urchin density. Bars represent means \pm standard error ($n = 10$ for benthic surveys and $n = 11$ – 15 for fish surveys). Credit to H. Mwamlavya for compiling the figure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

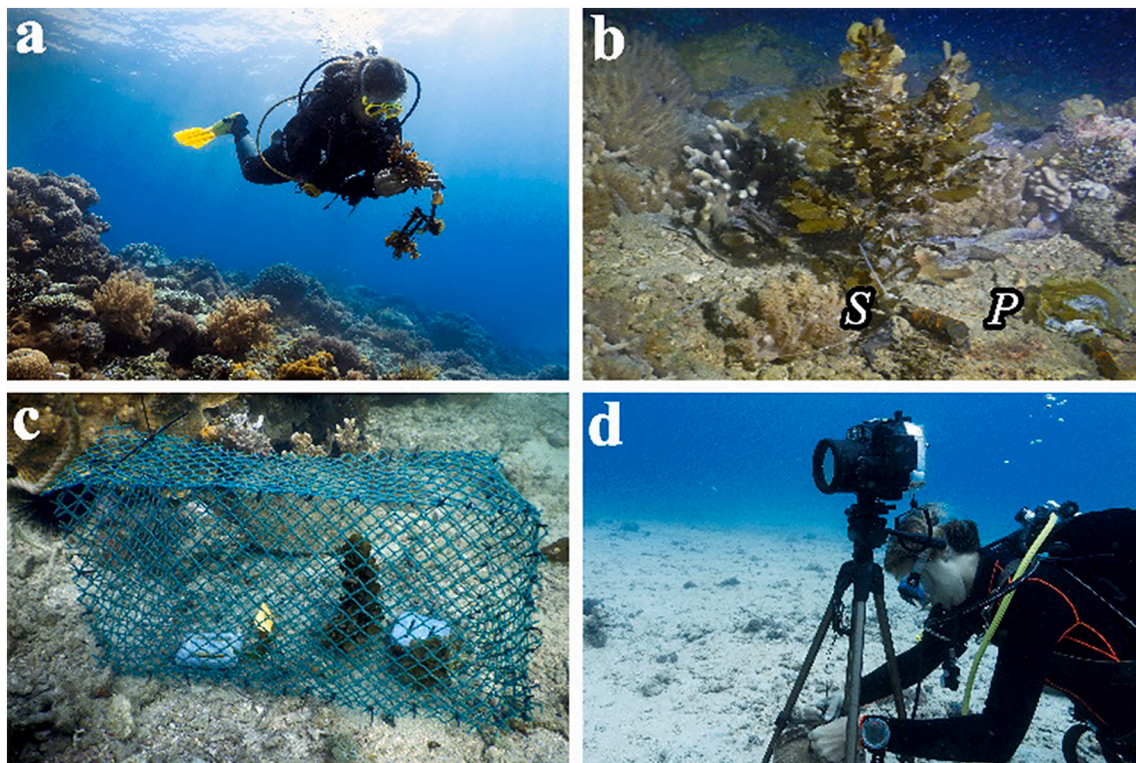


Fig. 2. Experimental setup of the buffet assay. a Diver placing macroalgae on the reef. b Close-up of one assay line positioned on the reef, showing *Sargassum ilicifolium* & *Padina boergeresii*. c Close-up of one assay in the control cage. d Diver preparing the remote underwater video recording. Source a-d: EGK.

weights (mean \pm SD): *Sargassum* (38.3 ± 4.6 g) and *Padina* (18.4 ± 2.9 g). The buffet assay also included the seagrass *Thalassia hemprichii* to allow for comparisons with an older buffet assay study from the Kenyan coast (McClanahan, 2008), but these results are discussed separately in the supplementary data (Appendix A, Fig. S1) as the focus of this report is on macroalgae. For deployment, the three different macrophyte species were strung equidistant and in random order on a 1-m fishing line. The line was weighted with three 10-cm metal pins to enable secure placement on the reef substratum and to provide access to both vertebrate and invertebrate, bottom-dwelling browsers. The macrophytes were transported in basins with seawater and deployed at a similar habitat and depth as where the benthic and fish surveys were performed. One replicate buffet assay consisted of 10 lines, with each line separated approximately 2 m from the next. Per replicate assay, one additional control line was placed inside a weighted plastic cage of $30 \times 30 \times 50$ cm³ with 1.3×1.3 cm² mesh size to exclude all macro-browsers to check for weight loss due to handling, following Seah et al. (2021) among others. For each study site, the assays were repeated on five non-consecutive days throughout the 4-month study period.

2.4. Remote underwater video

To identify the species responsible for the reduction in macroalgae biomass and to quantify their browsing activity with minimum disturbance, the first 75 mins of deployment of each buffet assay were recorded on remote underwater video (RUV). A Canon 600D DSLR camera in a Neewer 40 M case was placed on a weighted tripod, approximately 2 m from one randomly chosen line. The camera was programmed to take 10-min clips, with both a starting delay and subsequent interval of 5 min, resulting in a total recording time of 45 min per assay. Recording took place between 1000 h and 1400 h, which coincides with the peak in foraging activity of most roving (i.e. mobile) herbivorous fishes (Hoey and Bellwood, 2009). In total, 30 recordings were made.

2.5. Data processing and analysis

Data on benthic cover, total fish biomass and grazing sea urchin density is presented descriptively. Grazing sea urchins include all sea urchin species except the burrowing species *Echinostrephus molaris* which feeds on drifting algae only. Data from stationary visual surveys was used to estimate fish biomass using the midpoint of each size class and published length-weight relationships (Froese and Pauly, 2015). Herbivorous fish biomass was subdivided into the following functional groups: browsers, grazers, scrapers and excavators, based on reported species' functional traits following Green and Bellwood (2009). Two additions were made: *Platax* spp. were also considered browsers (Bellwood et al., 2006) and territorial damselfishes were considered as a separate functional group, including the genera *Amblyglyphidodon*, *Plectroglyphidodon* and *Stegastes*. Average herbivorous fish biomass was compared between the three types of *Fisheries management* using a generalized linear model with Gamma distribution and log-link using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2020). Reef type ('Patch' for study sites 1, 2 and 6 and 'Fringing' for sites 3–5) was included as factor during model selection to explore potential confounding environmental parameters related to these different habitats, such as depth, water clarity and exposure. The most parsimonious model was selected based on Akaike's Information Criterion (AIC) using a selection threshold of $\Delta AIC > 6$ (Fox et al., 2015). Study site was included as random factor to account for non-independence of repeated surveys at each site. Model assumptions were validated by visual inspection of DHARMA diagnostic plots for mixed regression models (Hartig, 2021). The Wald Chi-Squared Test from the *car* package (Fox and Weisberg, 2018) was used to determine the significance of fixed factors. Within-level differences between *Fisheries management* were examined using pairwise means comparisons with Tukey adjustment using the *emmeans*

package (Lenth, 2020). A similar approach was repeated to test for differences in herbivorous fish biomass between the specific Study sites, without the need for inclusion of a random factor here.

The fraction consumption of buffet assays was calculated following Bennett and Bellwood (2011): Consumption (F) = $1 - \frac{M_1}{M_0(1-C)}$ where M_0 is the initial macroalgal mass, M_1 the remaining mass after 24 h and C the mean fraction of biomass loss at the control treatment (calculated separately for each site and macroalgae). The mean of 10 lines was taken for both macroalgae species to represent a replicate buffet assay. A beta regression model with logit link was used to account for the proportional nature of the consumption data (Douma and Weedon, 2019) using the *glmmTMB* package (Brooks et al., 2017). A mixed-effects model was built to determine the fixed effects of *Fisheries management* and *Macroalgae species* ('Sargassum' and 'Padina') on consumption. Study site and Assay were included as nested random factors to account for both the non-independence of repeated measurements at each study site and the non-independence of algal species on the same line. Accounting for potential confounding factors, checking model assumptions and performing significance tests were implemented as outlined above. Again, the approach was repeated to specifically test for the effect of individual Study sites.

All RUV recordings were viewed and for each bite the targeted macroalgae and involved fish species were noted. In addition, fish's fork length was estimated (using the buffet line as reference), transformed to weight using published length-weight relationships (Froese and Pauly, 2015) and multiplied by the number of bites taken to calculate mass-scaled bites (ms-bites) following Hoey and Bellwood (2009). Sums of ms-bites were standardized to hour to correct for slight variations in RUV recording length. Bite impact estimated from RUV is thus expressed as ms-bites in kg h⁻¹. This data is presented descriptively.

A distance-based redundancy analysis (db-RDA; Legendre and Anderson, 1999) was performed using fisheries management, as well as average macroalgae consumption and sea urchin density per study site as (z-score transformed) environmental parameters fitted to a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) on the herbivorous fish species community using the *vegan* package (Oksanen et al., 2022). A main advantage of db-RDA compared to other ordination methods is that it accepts non-Euclidian dissimilarity matrices, such as the ecologically-relevant Bray-Curtis (Ramette, 2007). Significance of the overall db-RDA model and the environmental parameters were assessed using Monte Carlo permutation tests using 999 permutations (Legendre et al., 2011).

3. Results

3.1. Benthos and fish

Average hard coral cover was relatively high across study sites with values ranging between 25 and 47%, except at site 3 where only 6% hard coral cover was found (Fig. 1). In contrast, macroalgal cover was low for all sites (< 8%) except at site 3 where half of the substrate was covered by macroalgae (mainly *Sargassum* spp.). The density of grazing sea urchins (Fig. 1) was highest in the fished zones (0.8 and 1.1 sea urchins m⁻² at sites 1 and 2, respectively) and lower in the marine reserves and no-take zones (< 0.5 sea urchins m⁻² at sites 3–6). Total fish biomass was low in the fished zones and marine reserves, with values ranging between 150 and 285 kg ha⁻¹ for sites 1–4 (Fig. 1). In the no-take zones, total fish biomass was much higher: 898 kg ha⁻¹ for site 5 and 1667 kg ha⁻¹ for site 6.

The biomass of herbivorous fish differed significantly between types of fisheries management ($\chi^2 = 20.903$, df = 2, $p < 0.0001$; Fig. 3) and was higher in the no-take zones compared to both the fished zones (nearly seven-fold higher, $p < 0.0001$) and reserves (over two-fold higher, $p = 0.0040$). The herbivorous fish biomass did not differ significantly between fished zones and reserves. The factor reef type was

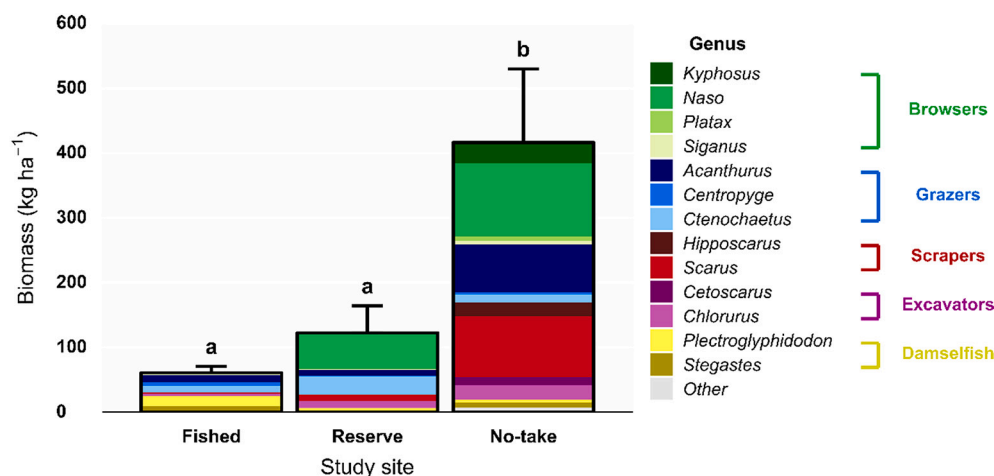


Fig. 3. Herbivorous fish biomass (kg ha^{-1}) per type of fisheries management. Average biomass ($n = 21\text{--}30$ fish surveys nested within 2 study sites each) is stacked by genus. Colours indicate functional groups: browsers (green), grazers (blue), scrapers (red), excavators (purple) and territorial damselfishes (yellow), and shades further identify each genus. Error bars denote the standard error of the mean total herbivore biomass and lower-case letters denote significant differences between fisheries management ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

not included in the final model as it increased the AIC (see Table S1 and Table S2 for model details). There was considerable variation between study sites, with significantly higher biomass at site 4 compared to site 3, both situated in the reserve (Fig. S2). These higher herbivore biomasses at sites 4–6 were not only attributable to more herbivores being present, but also due to the presence of larger (> 30 cm) individuals, which were completely absent from sites 1–3 (Fig. S3). The composition of functional groups within the herbivorous fish community also clearly differed between types of fisheries management (Fig. 3). Browsers were practically absent from fished sites, while they were well represented in the reserves and no-take zones, mainly due to the presence of *Naso* spp. Grazers were present across all study sites and were relatively more abundant in fished areas. *Acanthurus* spp. dominated the grazer community in the no-take zones, whereas smaller-bodied grazers such as *Ctenochaetus* spp. and *Centropyge* spp. were more commonly found in the fished areas and reserves. Scrapers and excavators (predominantly *Scarus* spp.) were only regularly encountered in no-take zones and even made up more than a third of the herbivorous fish community there. Territorial damselfishes were most abundant in fished zones.

3.2. Macroalgae buffet assay

A significant interaction for macroalgae consumption was found between fisheries management and macroalgae species ($X^2 = 10.917$, $df = 4$, $p = 0.0275$; Fig. 4). Reef type was not included as factor, because the resulting improvement in AIC was marginal (see Tables S1–S3 for all model output). For *Sargassum*, the consumption was more than two-fold

higher in no-take zones ($62 \pm 11\%$) compared to the fished zones ($26 \pm 4\%$; $p = 0.0064$), with intermediate results for the marine reserves ($48 \pm 10\%$) that were not significantly different from the other two management types (Fig. 4). For *Padina*, consumption was comparably low in the fished zones ($28 \pm 7\%$) and consumption was over two-fold higher in the marine reserves ($71 \pm 6\%$; $p = 0.0002$) and nearly three-fold higher in the no-take zones ($82 \pm 4\%$; $p < 0.0001$); the marine reserves and no-take zones were again not significantly different from each other. Across all three protection zones, consumption of *Padina* was higher than for *Sargassum* (Fig. 4). Consumption of *Sargassum* was significantly lower at study sites 3 and 6 compared to sites 4 and 5, respectively (Fig. S4).

3.3. Recorded bites

Mass-scaled bites as recorded on RUV were dominated by a few fish species (Fig. 5). Only three species were recorded taking substantial ms-bites of *Sargassum* (*Naso elegans*, *Hipposcarus harid* and *Zebrasoma desjardini*). Bites on *Padina* were predominantly taken by a small group of scarids (*Hipposcarus harid*, *Scarus tricolor* and *Calotomus carolinus*) and the unicornfish *Naso elegans*. All ms-bites were recorded at sites 4–6, with no recorded bites at sites 1–3 (Table S4). At sites 4–6, a different species dominated at each site, with *Naso elegans* taking most ms-bites at site 4, *Scarus tricolor* dominating ms-bites at site 5 and *Hipposcarus harid* taking most ms-bites at site 6 (Table S4).

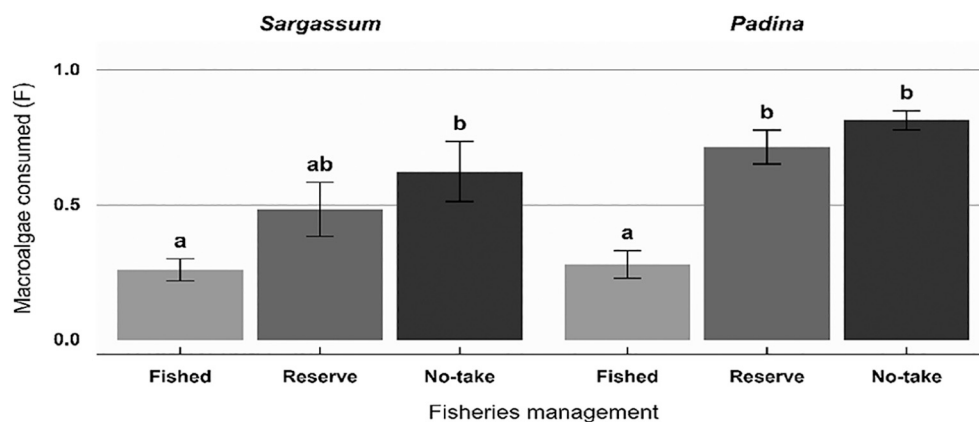


Fig. 4. Fraction of macroalgal biomass consumed in 24 h (F) for both *Sargassum ilicifolium* and *Padina boergesenii*, split between three levels of fisheries management. Bars present mean \pm standard error ($n = 10$ buffet assays nested within two study sites each). Letters above indicate significant differences ($p < 0.05$) between fisheries management for each macroalgae.

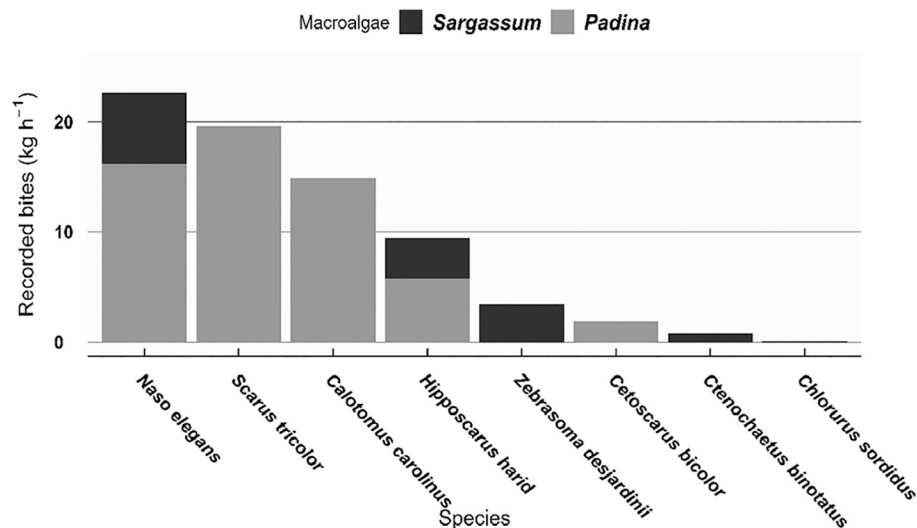


Fig. 5. Recorded mass-scaled bites (kg h^{-1}) on presented macroalgae by fish species recorded on remote underwater video, averaged across all six study sites.

3.4. Ordination

The db-RDA model captured 90% of variation in fish species composition (pseudo- $F = 2.233$, $df = 4$, $p = 0.0278$), with the first two axes capturing 65% of the total explained variation (Fig. 6). The overlay vector for reef type was not significant and not included in the final model. The overlay vector for fisheries management (pseudo- $F = 2.427$, $df = 2$, $p = 0.0389$) contributed to the separation of fished sites versus reserves and no-take zones on the first axis, and the separation of reserves and no-take zones on the second axis. The overlay vector for browsing pressure (pseudo- $F = 2.524$, $df = 1$, $p = 0.0389$) was positively associated with the no-take zones and reserves. The overlay vector for sea urchin density, though not significant, was negatively associated

with no-take zones, reserves and browsing pressure and instead associated positively with the fished zones. Fish species associating most strongly with reserves, no-take zones and higher browsing pressure included two *Naso* species, various parrotfishes and a kyphosid. In contrast, the fish community associating with the fished zones and high sea urchin densities were predominantly damselfishes.

4. Discussion

A risk to coral reefs and the people dependent on their current services is the phase shift from corals towards macroalgae, promoted by eutrophication and warmer waters and exacerbated by the removal of herbivorous fish by overfishing (Hughes et al., 2007; Ledlie et al., 2007; Pratchett et al., 2014). Key browsing species, their impact on reefs and the relationships to fisheries management are geographically variable and still largely unknown from the East African coast. We characterized the herbivore community and quantified their browsing pressure at six Kenyan reefs within three distinct fisheries management zones. Browsing pressure on the presented macroalgae was over two-fold greater in areas with partial fishing restrictions and nearly three times higher at fully protected reefs. Biomass of herbivores were respectively two-fold and seven-fold higher in areas with partial and full fishing restrictions compared to fished areas, with substantially higher biomasses of browsing unicornfishes (*Naso* spp.) and scraping parrotfishes. In contrast, sea urchins, damselfishes and small-bodied grazers were dominant in fished areas. In line with previous studies, only a select few dominant browsers were identified to consume the presented macroalgae (Puk et al., 2016), with key species varying strongly across reefs (Cvitanovic and Bellwood, 2009) and also including herbivores not specifically classified as browsers (Chong-Seng et al., 2014). Overall, our results affirm that fishing restrictions can have a strong positive influence on herbivorous fish biomass and highlight how this can be expected to increase reef resilience by supporting higher rates of macroalgae browsing by key species.

Consumption of *Sargassum* in the no-take zones and marine reserves was higher than found in a previously studied community managed area in northern Kenya where only 20% was consumed in 24 h (Humphries et al., 2015), but somewhat lower and more variable than consumption rates (81–92% in 24 h) found on the Great Barrier Reef (Hoey and Bellwood, 2010). *Padina* consumption fell broadly within the ranges previously found (Humphries et al., 2015; Plass-Johnson et al., 2015). It seems that despite widely varying herbivore species compositions across broad geographic scales browsing pressure at unfished reefs can be quite comparable (Tebbett et al., 2020), highlighting the role local drivers

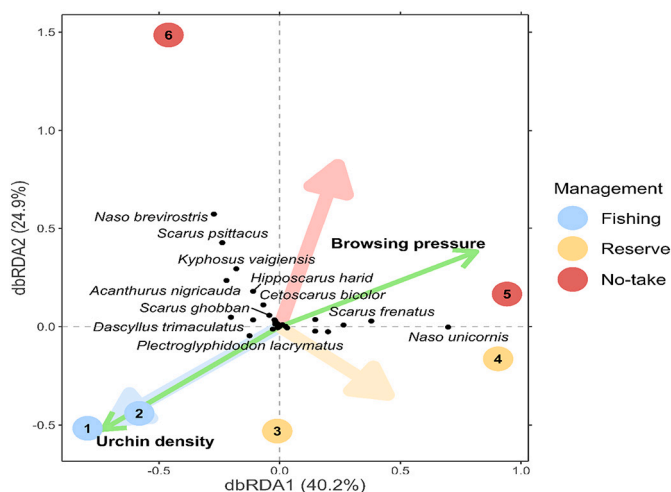


Fig. 6. Distance-based redundancy analysis (db-RDA) plot based on environmental parameters (vectors) per study site (numbered points) fitted to the herbivorous fish community (labelled points). Each point indicates an herbivorous fish species, though only species explaining >40% of the variation are shown. Each number represents a study site, their distances based on the Bray-Curtis dissimilarity matrix. Vectors and their length indicate the direction and strength of the parameter effect in the ordination plot. The vectors for fisheries management have been coloured according to their level of protection and their widths have been increased to aid visual distinction between overlapping vectors. Monte Carlo permutation tests (999 permutations) showed that browsing pressure and fisheries Management were significant ($p < 0.05$) predictors in the model.

such as fisheries management can play in determining browsing pressure. An effect of reef type, such as the combined greater depth and clearer water at offshore sites, was not found to affect fish biomass or browsing pressure in this study. Though the low replications relative to the inherent variation of the data might have obscured some patterns, it is worth highlighting that the effect of fisheries management clearly stood out. Interestingly, consumption at the fish-depauperate and macroalgae-dominated study site 3 was also relatively high. This result contrasts with previous studies where higher densities of macroalgae were associated with lower browsing rates, supposedly through feeding dilution (Chong-Seng et al., 2014) or predator avoidance (Hoey and Bellwood, 2011). The combination of both low fish and sea urchin biomass, the absence of browsing recorded on RUV, but relatively high macroalgae consumption at this structurally-eroded and macroalgae-dominated site is indeed surprising. It should be noted that the high consumption was mainly driven by removal of *Padina*, the macroalgae which appeared overall more palatable in this and other experiments (Humphries et al., 2015), compared to *Sargassum*, the macroalgae which dominated this reef and is most often associated with phase shifts (Hughes et al., 2007). As the stationary survey method likely reduces fish behavioural disturbance (Colvocoresses and Acosta, 2007) and also no browsers were identified through RUV, it appears unlikely that macroalgae removal was driven by (wary) herbivorous fish. Thus, the organism responsible for the high removal of *Padina* at this site remains unidentified and could possibly include overlooked species such as nocturnal crabs (Francis et al., 2019). At the two fished study sites, consumption was higher compared to reports of other overfished or macroalgae-dominated reefs. For example, *Sargassum* sp. removal rates of only 2% in 4.5 h were found on macroalgae-dominated reefs in the Seychelles (Chong-Seng et al., 2014). In the fished areas studied here, macroalgae removal might still be realized by small-bodied grazers and sea urchins.

The differences in the herbivore community and functional absence of browsing, scraping and excavating herbivores found at the fished study sites confirm results found at the central Kenyan coast (Humphries et al., 2015), and potentially undermine the resilience of these reefs (Holbrook et al., 2016; Nyström et al., 2008). Herbivorous fish biomass in the no-take zones and marine reserve (except site 3) was comparable with worldwide averages from protected reefs (Edwards et al., 2014) and this biomass was considerably higher compared to the sites without fishing restrictions. An exception was the macroalgae-dominated study site 3 in the marine reserve, which had an equally low fish biomass as the fished reefs. At this site and at the fished reefs, no large herbivores (> 30 cm) were recorded, indicative of severe overfishing (McClanahan et al., 2008), habitat degradation (Rogers et al., 2018) or both. The observed low biomasses were most striking for large-bodied and functionally important fishes such as browsers, scrapers and excavators. This impact of high fishing pressure on key functional groups has been observed worldwide (Edwards et al., 2014; Humphries et al., 2014) and is remarkably severe along the East African Coast (Humphries et al., 2014; McClanahan et al., 2008). It is therefore promising that the small and recently-established community managed no-take zone of Wasini (study site 6) has been able to sidestep this trend and now boasts the highest fish biomass of all the sites studied here, despite its nearshore location (Johansson et al., 2013). Unlike other young community managed reserves in Kenya where only grazers recovered (Humphries et al., 2015), also browsers and scrapers are abundant at Wasini. Our data suggest that of all herbivorous functional groups, grazers are least impacted by high fishing pressure, with 'only' a three-fold lower biomass at fished sites compared to no-take zones and this is conform global trends (Edwards et al., 2014). Sea urchins and territorial damselfishes showed highest densities in fished zones and it is likely that they benefit from reduced competition as well as reduced predation by larger fishes (Ceccarelli et al., 2005; McClanahan, 2008).

The possibility that small-bodied grazers can endure high fishing pressure and control macroalgal establishment could be seen as hopeful

(Cernohorsky et al., 2015; Müller et al., 2021), yet there are several reasons to be cautious. First, small herbivorous fishes are likely to be targeting leaves or epiphytes only, without removing the holdfasts of macroalgae (Streit et al., 2015). Second, small herbivorous fishes appear more vulnerable to bleaching events and the ensuing habitat loss of branching coral (Nash et al., 2016). In addition, when bleaching events open up large areas of space, macroalgal settlement and growth is likely to overwhelm the grazing capacity of small herbivores, increasing chances of a phase shift (Williams et al., 2001). We suppose this could have happened at study site 3 during the strong 1998 El Niño (McClanahan et al., 2001), despite the implemented partial fishing restrictions (Williams et al., 2019). Lastly, while increasing numbers of sea urchins might partially compensate for the loss of herbivorous fish (McClanahan, 2014), the intensity of their scraping feeding method can undermine long-term reef development through bioerosion (Carreiro-Silva and McClanahan, 2001) and hinder coral settlement (Humphries et al., 2020). In addition, browsing pressure by sea urchins (at overfished reefs) appears to be relatively small compared to the browsing pressure by herbivorous fish (at protected reefs). Hence, at overfished reefs, small-bodied fishes and sea urchins may partially take over the role of larger herbivorous fishes in controlling macroalgal growth, but such a change in control is likely to undermine reef resilience.

The apparent limited functional redundancy of browsers at the studied protected reefs may also have implications for reef resilience, as the loss of key species can have large detrimental impacts on ecosystem functioning (Cheal et al., 2013; Nash et al., 2016). In accordance with reports from numerous preceding studies using macroalgae buffet assays, browsing in this study was dominated by a few species only (Puk et al., 2016) and with marked variation in dominant species across sites (Cvitanovic and Bellwood, 2009). *Naso elegans* was among the dominant browsers in this study and closely-related species have been identified as dominant browsers across the Indo-Pacific (Hoey and Bellwood, 2009; Humphries et al., 2015; Knoester et al., 2019; Plass-Johnson et al., 2015), highlighting the importance of this genus in macroalgal control across broad geographic scales. Browsing was not only performed by those classified as browsers and this supports several studies that suggest plasticity in functional roles exists (Bellwood et al., 2006; Chong-Seng et al., 2014; Tebbett et al., 2020). Indeed, scraping parrotfishes were recorded taking substantial amounts of bites as has been found in previous studies (McClanahan et al., 1994), but, in contrast to the browsing *Calotomus* spp. (Humphries et al., 2015), these are more likely to have been targeting epiphytes (Clements et al., 2017; Lefèvre and Bellwood, 2011). Interestingly, *Siganus* spp. and *Kyphosus* spp., species frequently identified as dominant browsers in the Central Indo-Pacific and Great Barrier Reef (Michael et al., 2013; Puk et al., 2016), were not recorded biting in this study. *Siganus* spp. were almost exclusively found in dense seagrass beds during this study, likely targeting epiphytes and turf algae which might be a preferred food source for some species (Ebrahim et al., 2020). *Kyphosus* spp. were situated higher in the water column and might have been feeding on drifting algae instead (Ferguson et al., 2017). Though longer RUV recordings would undoubtedly expand the list of identified browsers, these results align with other browsing studies in the Indo-Pacific in that they identify only a select and sometimes surprising group of species responsible for macroalgal removal from the diverse assemblage of potential browsers present. This variability may in part explain the finding that the reef with the highest herbivore biomass in this study did not bolster the highest browsing pressure, and especially consumption of *Sargassum* was relatively low here. Thus, in addition to the biomass of herbivores present, realized browsing pressure is likely also depending on many more factors such as spatial restrictions (Puk et al., 2016), behavioural variation (Bennett and Bellwood, 2011) as well as temporal variation (Lefèvre and Bellwood, 2011; Seah et al., 2021).

The variation in browsing pressure found can be indicative of divergent resilience between the studied reefs (Nyström et al., 2008). Three of the six studied reefs harboured an herbivore biomass that was

just above the identified threshold of 50 kg ha⁻¹ below which coral reefs might shift to macroalgal dominance (Holbrook et al., 2016; Plass-Johnson et al., 2015). On two of these reefs, coral is still dominant over macroalgae. Nevertheless, reefs like these might be pushed to macroalgal dominance through an external disturbance such as coral bleaching (Williams et al., 2001). The minimum herbivore biomass needed to absorb such increasingly common disturbances remains unknown for the Indo-Pacific (Roff and Mumby, 2012) and likely varies depending on the local community composition given the large influence of key species. In the marine reserve, a coral-dominated and a macroalgae-dominated reef co-exist under roughly equal browsing pressure. This co-existence could possibly be indicative of alternative steady states (Holbrook et al., 2016) and would then illustrate that shifts to alternative stable states can be difficult to reverse even when ambient browsing pressure is relatively high (Schmitt et al., 2019). If such reefs were historically indeed dominated by hard corals, one might consider to combine the protection of herbivorous fish with manual removal of macroalgae and attempt to push the ecosystem back to coral dominance (Ceccarelli et al., 2018; Williams et al., 2019). More effective, however, would be to keep herbivore levels well above potential phase-shift thresholds and prevent macroalgal dominance in the first place (Anthony et al., 2015; Mumby and Steneck, 2008). Our results indicate that fisheries management through marine reserves and no-take zones in particular, even small-scale and community-managed (Bonaldo et al., 2017; Kawaka et al., 2017), have the potential to safeguard the diversity and biomass of functionally important herbivorous fishes. Following effective management, a high level of macroalgal control is realized as especially large-bodied browsing and scraping fishes seem to benefit from fisheries protection. Although reasonable levels of browsing were still realized at fished study sites, the long-term resilience of these fished reefs is uncertain given the eroding nature of sea urchin browsing (Carreiro-Silva and McClanahan, 2001), the high susceptibility of small-bodied herbivorous fishes to coral loss (Nash et al., 2016) and their limited capacity to control sudden increases in macroalgae (Streit et al., 2015; Williams et al., 2001). Therefore, we recommend to continue the establishment of a network of community managed no-take zones to allow for the recovery of herbivorous fish biomass and key species, increase ecosystem resilience, promote local stewardship and move towards sustainable use of coral reefs (Topor et al., 2019). Such local management could help restore and maintain coral dominance and provide heightened resilience against large-scale disturbances during the Anthropocene.

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Ethical approval

No approval of research ethics committees was required for this observational study. Applicable international guidelines for monitoring on coral reefs were followed. This study was performed under the research license NACOSTI/21/8896.

Author statement

EG Knoester: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. V Plug: Methodology, Investigation, Writing – original draft. AJ Murk: Conceptualization, Resources, Writing – review & editing, Supervision. SO Sande Conceptualization, Resources, Writing – review & editing, Supervision. R Osinga: Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

Data availability

The datasets analysed and code used are available as a GitHub repository on: <https://github.com/ewoutknoester/HerbivoryBrowsing>

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2022.151850>.

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