Coral Reefs
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RESEARCH

Differential changes in the taxonomic and functional composition of herbivorous fishes from shallow to mesophotic coral ecosystems at the Coral Sea Marine Park, Australia

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Abstract Mesophotic coral ecosystems (MCEs: 30–150 m) are characterized by environmental conditions and biological assemblages that are distinct from those of shallow reefs (< 30 m). Several studies have described changes in species richness, abundance and composition of reef fish assemblages, from shallow reefs to MCEs; however, few have considered how different functional groups change over the same gradient. Here, remotely operated vehicle (ROV) surveys were used to examine how depth (2–98 m) and slope orientation influence the abundance, biomass, richness and composition of all herbivorous fishes, and the abundance and biomass of five functional groups of herbivorous fishes (scrapers, excavators, algal croppers, browsers and detritivores) on oceanic reefs of the Coral Sea Marine Park, Australia. While the abundance, biomass and species richness of herbivorous fishes generally declined with depth, the rate of decline varied among groups. The rate of decline in abundance of excavating (7.0% m^{-1}) and detritivorous (7.4% m^{-1}) fishes was nearly double that of croppers (4.2% m^{-1}) and scrapers (3.9% m^{-1}), while rates of decline in biomass of detritivores (3.5% m^{-1}) was ~ 50% higher than croppers (2.4% m^{-1}). Further, gentle to moderate slope orientations (6–45°) generally supported higher richness, abundance and biomass of herbivorous fishes than both flatter (< 5°) and steeper (> 81°) orientations. These results show that the response of herbivorous fishes to depth is not homogenous and varies among functional groups, and may be related to changes in resource availability, slope orientation and predation from shallow reefs to MCEs.

Keywords Remotely operated vehicles · Deep coral reefs · Depth gradient · Ecological roles · Algae · Geomorphology

Introduction

Mesophotic coral ecosystems (MCEs) are extensions of shallow (< 30 m) coral reef habitats that are typically situated at depths of 30 to 150 m (Lesser et al. 2018). Although characterized by light-dependent benthic communities, a key feature of MCEs is light levels that are 1–10% of surface irradiance (Lesser et al. 2018; Kahng et al. 2019). Several other environmental variables (e.g., temperature, nutrients) also vary with depth, and together with changes in light, influence the composition of reef-associated species from shallow reefs to MCEs (Lesser et al. 2018; Spalding et al. 2019). For example, changes in the abundance and physiological and/or morphological adaptations of corals and macroalgae with depth have been related to changes in light and/or temperature (Littler et al. 1986; Norris and Olsen 1991; Kahng et al. 2019). Notably, corals in MCEs typically have flattened morphologies presumably to maximize the exposure of tissues to incident light; however, they also reduce

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the physical structure they provide (Kahng et al. 2010; Swanborn et al. 2022). Similarly, macroalgae adopt simple morphologies with small sizes to maximize photosynthetic efficiency (Littler et al. 1986; Runcie et al. 2008; Voerman et al. 2023). Given the well-established relationship between benthic habitats and reef fish community structure (Roberts and Ormond 1987; Syms and Jones 2000; Richardson et al. 2017), these changes in benthic communities may influence the distribution of reef-associated organisms such as reef fishes at MCEs. Indeed, reef fishes typically exhibit a general decline in species richness, abundance and biomass, and changes in taxonomic composition from shallow reefs to MCEs (e.g., Pyle et al. 2016; Semmler et al. 2017; Rocha et al. 2018; Pinheiro et al. 2023). Such declines in species richness are hypothesized to be related to niche reduction because most MCEs have low habitat heterogeneity and resource availability or quality (Pinheiro et al. 2023), while declines in abundance and biomass have been suggested to be related to declines in the availability and productivity of dietary resources (Thresher and Colin 1986; Brokovich et al. 2010). These reductions are pronounced for primary consumers such as herbivorous fishes, which typically have limited distribution in MCEs.

Herbivorous fishes are often described as a key group in shallow reef ecosystems because of their perceived importance in preventing, or potentially reversing, the proliferation of macroalgae (Lewis and Wainwright 1985; Bellwood et al. 2006; Burkepile and Hay 2008 but see Russ et al. 2015; Clements et al. 2016). The distribution of herbivorous fishes, and hence any impact of their feeding, is influenced by differences in environmental variables across a range of spatial scales (e.g., Floeter et al. 2005; Heenan et al. 2016; Bejarano et al. 2017), including water depth (e.g., Bouchon-Navaro and Harmelin-Vivien 1981; Lewis and Wainwright 1985). However, most initial studies that examined the depth distribution of herbivorous fishes and/or herbivory were limited to depths of < 40 m (Hay 1984; Nemeth and Appeldoorn 2009; Hoey and Bellwood 2010) and only recently have advances in underwater technologies [e.g., remotely operated vehicles (ROVs), rebreathers] facilitated studies of MCEs (Armstrong et al. 2019; Pyle 2019). While these recent studies have shown that species richness and abundance of herbivorous fishes generally declines with depth (e.g., Gulf of Eilat: Brokovich et al. 2010; Hawaii: Fukunaga et al. 2016, Asher et al. 2017; Western Atlantic and Pacific: Pinheiro et al. 2023), few have considered how individual species or functional groups of herbivorous fish change with depth (see Cure et al. 2021 for exception). Herbivorous fishes have considerable variation in diet, feeding substrata and feeding behavior among taxa (e.g., Burkepile and Hay 2008; Hoey et al. 2013; Streit et al. 2019) that may influence their depth distribution patterns. To date, the only study that has investigated the distribution of herbivorous fish functional groups from shallow reefs to MCEs reported differential responses among groups, with grazers and detritivores exhibiting a mid-depth maximum, scrapers exponentially decreasing with depth and browsers showing slight increases with depth (Cure et al. 2021). However, this study was restricted to a small island (~ 0.1 km^2) off the Western Australian coast, and it is not clear whether these patterns are representative of reefs elsewhere.

Herbivorous fishes can be broadly differentiated into grazers and browsers based on the substrata from which they bite (Gerking 1994). Browsers typically bite larger (> 5 cm) fleshy macroalgae (Hoey and Bellwood 2011; Puk et al. 2016), whereas grazers typically bite turf-covered substrata (i.e., substrata colonized by filamentous algae, cyanobacteria, propagules of larger fleshy macroalgae and microbes; Wilson et al. 2001). Grazers can be further subdivided into turf croppers, scrapers, excavators and detritivores based on the morphology of the feeding apparatus, dietary targets and impacts on the underlying substrata (Bellwood and Choat 1990; Green and Bellwood 2009; Hoey et al. 2013; Streit et al. 2015). Croppers generally remove the upper portions of algae and/or cyanobacteria, leaving the basal components intact (Hoey et al. 2013), and in areas where they are abundant maintain turf assemblages in a low standing biomass but productive state (Russ 2003). Scrapers and excavators gouge the underlying substrata when feeding, targeting protein-rich epilithic and endolithic microorganisms (e.g., cyanobacteria; Clements et al. 2016; Nicholson and Clements 2020) and are important agents of external erosion of reef carbonates (Bellwood and Choat 1990; Hoey and Bellwood 2008). Detritivores target detrital aggregates within turf assemblages, and while they contribute little to the removal of benthic algae, they are conduits of energy in detrital pathways (Tebbett et al. 2017). The distribution of these herbivore functional groups and their contribution to ecological processes in MCE's is largely unknown.

While MCEs are primarily structured by light and temperature, physical habitat characteristics may also influence the distribution of reef fishes with depth (Locker et al. 2010; Bennett et al. 2018; Galbraith et al. 2021). In shallow reefs, reef zonation (e.g., flat, crest, slope) and their associated environmental conditions (e.g., intensity of wave exposure, accessibility of food) are known to influence the abundance or biomass of herbivorous fishes (Russ 2003; Hoey and Bellwood 2010; Heenan et al. 2016; Bejarano et al. 2017). Benthic characteristics within reef zones in shallow reefs may also influence herbivorous fishes such as when highly complex habitats may have lower abundance of herbivores (Adam et al. 2011; Russ et al. 2015). While little is known on how habitat characteristics influence herbivorous fishes across depth gradients, differences in light attenuation and substrate availability between shallow reefs and MCEs (Lesser et al. 2021a, b) may influence the settlement and growth of benthic taxa that serve as habitat and/or food for herbivorous fishes (Purcell and Bellwood 2001; Verges et al. 2011; Goatley and Bellwood 2012; Rasher et al. 2012). Although one study conducted in MCEs (Swanborn et al. 2022) demonstrate the importance of habitat characteristics for total abundance of reef fishes, knowledge on the effects of habitat characteristics for specific functional groups across the gradient of shallow reefs to MCEs is lacking.

It is widely accepted that the different functional groups of herbivores contribute to different ecological processes on shallow reefs; however, the distribution of these groups and their potential importance to functioning of deeper reefs has not been examined. While initial studies suggested that MCEs may provide refuge for benthic and fish taxa to many of the stressors to which shallow reefs are exposed (i.e., the depth refuge hypothesis: Lesser et al. 2009; Bongaerts et al. 2010), recent works revealed that MCEs may be just as vulnerable as shallow reefs (Rocha et al. 2018). For example, storms (Abesamis et al. 2018), marine heat waves (Smith et al. 2016), invasive species (Lesser and Slattery 2011) and plastic pollution (Pinheiro et al. 2023) have been reported to impact MCEs. This potential vulnerability emphasizes the need to understand how ecological processes, such as herbivory, may contribute to the functioning of MCEs. The aim of this study was to examine the effects of depth, reef zones, slope orientation and benthic complexity on herbivorous fish assemblages in the Coral Sea Marine Park, Australia. Specifically, differences in (i) species richness and assemblage composition of herbivorous fish assemblages and (ii) the abundance and biomass of all herbivorous fishes collectively, and five herbivore functional groups (browser, cropper, scraper, excavator and detritivore) independently among depths (2–98m), reef zones, slope orientations and benthic complexity were examined. Given that each functional group derives nutrition from different components of benthic algae, it was hypothesized that the rates of decline with depth varied among functional groups and that the differential rates of decline affected their potential ecological roles in MCEs. Moreover, it was hypothesized that herbivore assemblages varied with reef zone, slope orientations and benthic complexity due to changes in physical characteristics that may affect light availability and substrate condition.

Methods

Study site

The study was conducted in Australia's Coral Sea Marine Park (CSMP). The CSMP extends from the eastern boundary of the Great Barrier Reef Marine Park to approximately 1,200 km from the Queensland coast and covers an area of approximately 984,000 km^2 (Fig. 1). Within the CSMP are a variety of coral reef geomorphologies, including steep-sided seamounts rising from deep waters (up to 3000m deep), atolls atop major geological plateaus and submerged banks (Ceccarelli et al. 2013; Bridge et al. 2019). The reefs of the CSMP possess a variety of habitats including extensive deep-water lagoons (up to 70m deep), shallow coral reefs and MCEs (Bongaerts et al. 2011; Englebert et al. 2017; Galbraith et al. 2024). Due to its offshore location, the CSMP experiences reduced local anthropogenic stressors, such as nutrient runoff and fishing (Hoey et al. 2021). Fifty sites across 17 reefs spanning the northern, central and southern CSMP were surveyed during 5 voyages between 2021 and 2023. Within each reef, 1–4 sites spanning depths of 2–98m and a range of reef zones (lagoons, inner reefs, outer reefs and channels between the lagoon and outer reef) were surveyed using an ROV. MCE habitats in the present study were defined according to Pyle and Copus (2019), which are reef ecosystems situated at depths of typically 30-150m, characterized by low light, and benthic communities that contain scleractinian corals and other heterotrophic benthic organisms such as sponges and gorgonians.

Lagoon zones were located at the center of each atoll reef, typically had a maximum depth of 60m with relatively flat or gentle slope profiles and were characterized by sparsely distributed coral bommies primarily composed of hard consolidated substrata with little sand cover. Inner reefs were classified as contiguous coral reefs within lagoons, essentially the back reef of outer seaward reef crests that extend into the central lagoon with similar depth and slope profiles. Both inner reef and lagoon zones were typically sheltered from oceanic swells by the outer reef zones to their south and/or east. Channel zones were passages between areas of contiguous reef that connected the lagoon/inner zones with exposed outer reef zones and had depth and bathymetric profiles similar to lagoons and inner reefs, with maximum depth of ~ 60m and flat or gentle slope profiles. Outer reef zones were located on the seaward side of the reefs surveyed, with the highest exposure to waves and surrounded by deep oceanic waters. Of the zones sampled, outer reefs had the deepest depth surveyed (≥ 90m) and were characterized by steep slopes and walls. Details on the number of reefs, sites and transects surveyed together with their depth range and habitat profiles are provided in Table S1.

ROV surveys

A BlueRobotics (BlueROV2 heavy configuration) was fitted with a forward-facing stereo-video system (SVS) and was used to survey coral reef fish assemblages at each site. Paired video cameras (Paralenz Dive Camera +) were mounted to the front of the ROV with the cameras converging at an orientation of 5° and calibrated using the software CAL (www.seagis.com.au/bundle.html) and associated calibration cube

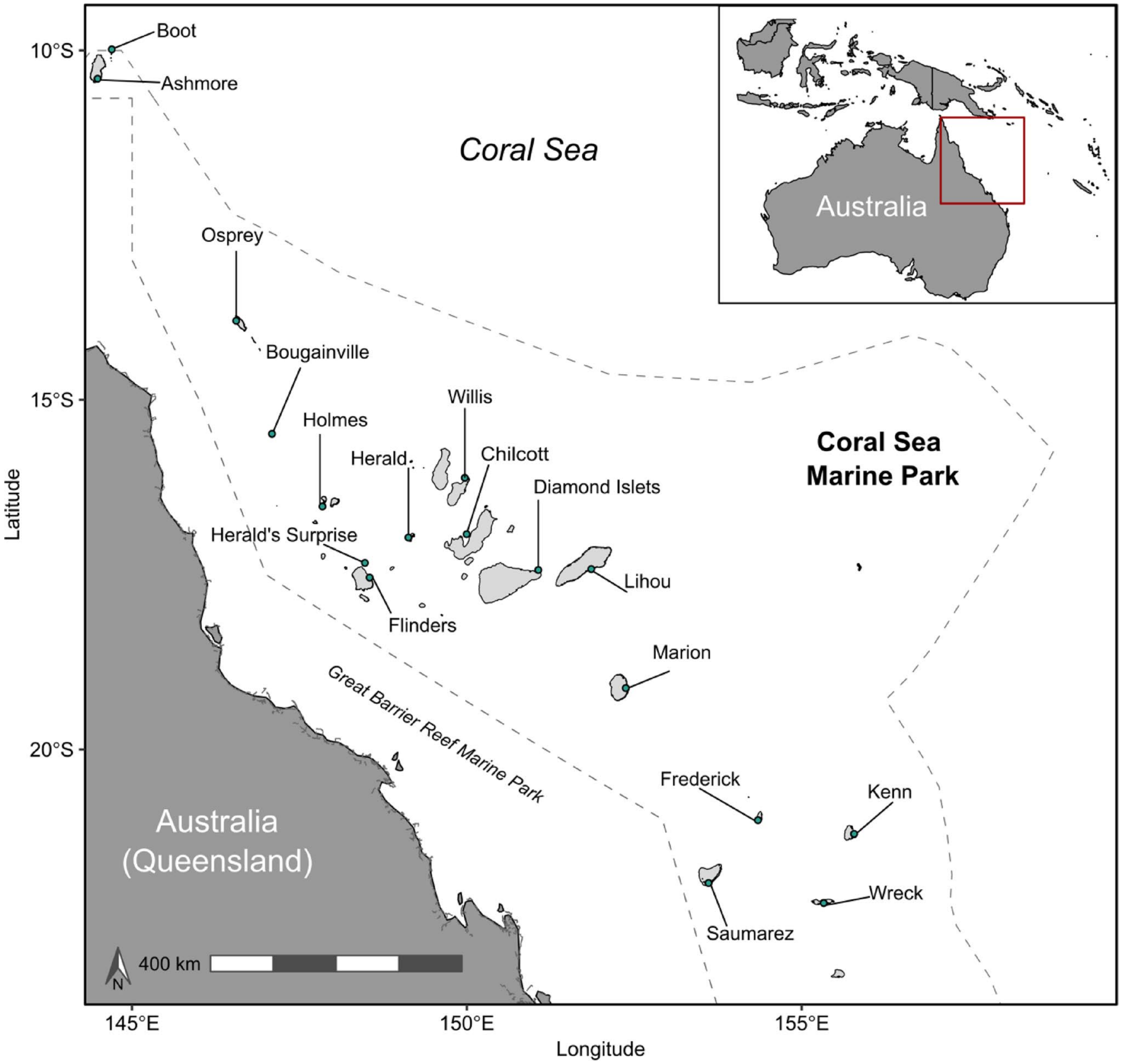


Fig. 1 Map of the 17 surveyed reefs in the Coral Sea Marine Park (CSMP), Australia. Dashed line shows the border of the CSMP relative to the neighboring Great Barrier Reef Marine Park to the west and the wider Coral Sea to the east. Inset in the top right shows the location of the CSMP relative to mainland east coast Australia

and methods (Harvey and Shortis 1998; Shortis and Harvey 1998). ROVs have been increasing used to survey MCE ecosystems (Armstrong et al. 2019) and have been shown to yield comparable estimates of richness and abundance of reef fish to those of diver operated stereo-video (stereo-DOV) surveys, but comparisons with underwater visual census remain scarce and have yielded variable results (UVC) (Jessop et al. 2022). Nevertheless, despite the natal state of the application of ROVs in coral reef video surveys, ROVs are an important tool for investigating MCEs that are difficult to access safely using other survey methods. To conduct transect-based sampling, an ROV specific dive methodology was developed to attain suitable replication along the depth gradient at each site while balancing the logistical requirements of deploying the ROV. The ROV was launched from a small vessel (< 6m) and piloted to the deepest targeted sampling depth (~ 100m in outer reef habitats and the maximum depth of lagoons and channels). Two 2.5-min timed swims were conducted at the maximum depth, with the ROV piloted at a constant speed of 0.2 m/s, thereby covering approximately 30 m during each transect. Transects within each depth were separated horizontally by a minimum of 5 m using time and speed to estimate this distance. After completing two transects at a depth, the ROV was ascended ~ 10 m and two 2.5-min transects were conducted as described above. This process was repeated until the ROV was at a depth of < 10 m. Once transects at the shallowest depth were complete, the ROV was recovered to the vessel and moved ~ 100 m along the reef using the initial marked deployment location (Navionics boating app). A second dive was then conducted following the procedure described above, yielding two ROV dives per site and four transects per depth per site. At some sites, the number of dives was constrained by sea state, weather and/or water currents, restricting safe vessel maneuvers along the reef. In the lagoon, inner reef and channel zones, ROV surveys were typically conducted at a single depth (the maximum depth for a given site: ~ 40–60 m) due to the absence of reef habitat at shallower depth in these zones.

Video analyses

ROV stereo-video surveys were analyzed using the software EventMeasure Stereo (https://www.seagis.com.au/event.html). Stereo-video analysis methods followed established standard operating procedures outlined in Goetze et al. (2019). Briefly, all herbivorous fish within 2.5m either side and directly in front of the camera field of view (< 8–10m) were counted and identified. Transect width and distance from the ROV were determined within the EventMeasure software. Each fish identified was measured (fork length) to obtain size estimates from video footage. Biomass was estimated using the length–weight relationship of fishes ($\text{Weight} = a * \text{Length}^b$) and species-specific allometric growth coefficients (Froese and Pauly 2024). Herbivorous fish species were then classified into one of five functional groups: browsers, croppers, detritivores, excavators and scrapers with reference to Green and Bellwood (2009) and Hoey et al. (2013). The slope of the substratum of each transect was visually estimated at the end of each video transect and classified using a five-point scale: flat (0–5º), gentle slope (6–30º), moderate slope (31–45º), steep slope (46–80º) and wall (> 81º) following Englebert et al. (2017). Benthic complexity was also visually estimated at the end of each video transect using the six-point scale of Wilson et al. (2007), with 0 being the lowest and 5 the highest complexity.

Statistical analyses

All statistical analyses were conducted in R statistical software version 4.3.2 (R Core Team 2024) with basic data handling and visualization conducted using the tidyverse suite of packages (Wickham et al. 2019). Fully reproducible code is available at https://github.com/tjrq/CSMP_Herb_Functional_Group/tree/main.

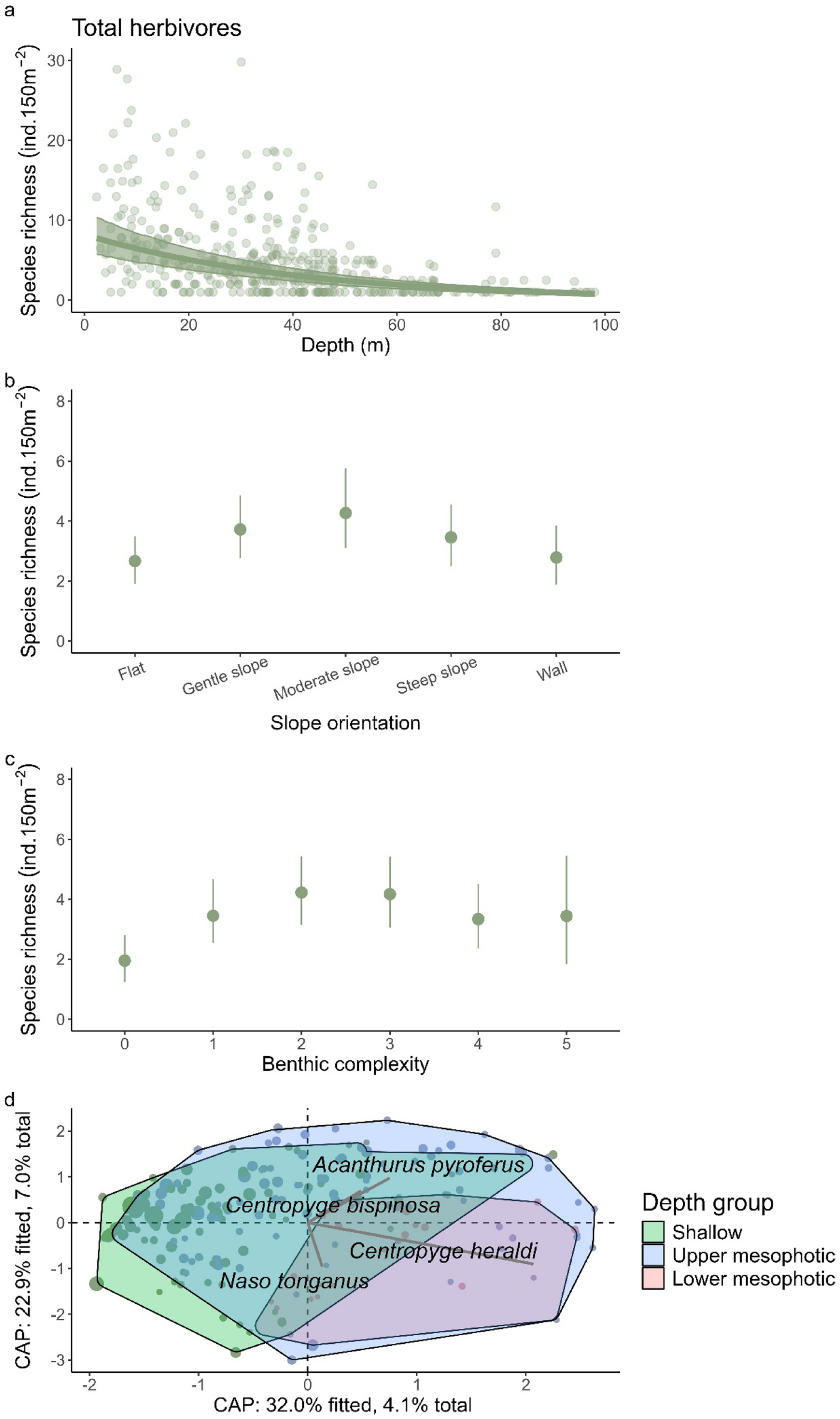
Species richness, abundance, biomass

A series of Bayesian generalized linear mixed-effects models (GLMMs) were fitted using the package brms (Burkner 2017) to examine differences in transect-level species richness, abundance and biomass of total herbivores and/or for each functional group (browsers, croppers, detritivores, excavators, scrapers) across depth (continuous), reef zone (categorical: lagoon, inner reef, channels, outer reef), slope orientation (categorical: flat, gentle slope, moderate slope, steep slope and wall) and benthic complexity (categorical: 0–5). The group-level effects were sites nested in reefs (categorical: Table S1). Prior to model fitting, rarefaction curves were performed to estimate asymptotic species richness using the R package iNEXT, with these estimates based on ChaoRichness (Chao et al. 2014). The estimated asymptotic species richness for all herbivores was then used as the response variable for the model.

The species richness model used a lognormal distribution with an identity link; the abundance model used a negative binomial distribution with log-link; and the biomass model used a hurdle lognormal distribution. All models used weakly informative priors, with sampling chain diagnostics conducted in bayesplot (Gabry and Mahr 2024), and model validation was conducted using the DHARMa package (Hartig 2002). Species richness was not modeled for each functional group because of the low species numbers at deeper depths for some groups. Post hoc model investigation was conducted using the package emmeans (Lenth 2024) and tidybayes (Kay 2023). Median trends ± 95% highest posterior density (HPD) interval were extracted directly from the model posterior and associated exceedance probabilities calculated.

Herbivore assemblages

To examine differences in herbivore species assemblages among depths and slope orientation, a multivariate analysis was conducted using the R package vegan (Oksanen et al. 2017). A canonical analysis of principal coordinates (CAP) was conducted using the function capscale, based on fourth-root-transformed and Wisconsin double-standardized abundance data. The dissimilarity coefficient in the ordination was based on a Bray–Curtis dissimilarity matrix. The predictor depth in the CAP was treated as a categorical variable [shallow (< 30 m), upper (31–60 m), lower mesophotic (> 60 m)] to aid visualization in the ordination plot. Similarly, gentle, moderate and steep slope orientations were combined into a single category "slope" for better visualization. To examine whether herbivore assemblages


a
Total herbivores
Species richness (ind.150m^{-2})
30
20
10
0
0
20
40
60
80
100
Depth (m)
b
Species richness (ind.150m^{-2})
8
6
4
2
0
Flat
Gentle slope
Moderate slope
Steep slope
Wall
Slope orientation
c
Species richness (ind.150m^{-2})
8
6
4
2
0
0
1
2
3
4
5
Benthic complexity
d
CAP: 22.9% fitted, 7.0% total
2
1
0
-1
-2
-3
-2
-1
0
1
2
CAP: 32.0% fitted, 4.1% total
Acanthurus pyroferus
Centropyge bispinosa
Centropyge heraldi
Naso tonganus
Depth group
Shallow
Upper mesophotic
Lower mesophotic

◂**Fig. 2** Differences in the species richness and composition of herbivorous fish assemblages in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of herbivorous fish species richness (n. individuals per 150 m^{-2}) across depth (**a**), slope orientations (**b**) and benthic complexity (**c**). **a** the line is the modeled relationship, ribbons are the 95% upper and lower credible intervals and circles the species richness for each transect from the raw data. **b**, **c** the solid points are the modeled median, with lines representing the 95% upper and lower credible intervals. **d** Canonical analysis of principal coordinates (CAP) ordination of the composition of herbivorous fish assemblages (abundance-weighted) among depths. Points are scaled to size based on the total abundance of herbivores in a site and depth. Species displayed were highly ($p < 0.001$) correlated to the two principal axes of the ordination plot

differed among depths [categorical: shallow (< 30 m), upper (31–60 m), lower mesophotic (> 60 m)], reef zone (categorical: as described above), slope orientation (categorical: flat, slope, wall) and benthic complexity (categorical: as described above), a PERMANOVA with 10,000 permutations was used with the function adonis2. To identify herbivore species associated with variation in the multidimensional space, the two ordination axes were correlated with the species composition matrix using the function envfit, with statistical significance examined using 10,000 permutation tests. Only highly correlated ($p < 0.001$) species were visually displayed in the ordination plot. Moreover, patterns of abundance for these highly correlated species among depth bands were also visualized with mean and standard error presented.

Results

Species richness and composition

Seventy-two species of herbivorous fish from six families (Acanthuridae, Labridae: Scarini, Pomacanthidae, Kyphosidae, Pomacentridae and Siganidae) were recorded across the 385 transects from depths of 2 to 98 m (Table S2). There was strong evidence ($P = 1$) that herbivore species richness decreased with depth from 2 to 98 m, with species richness declining by 2.5% m^{-1} (95% HPD: 2.1–2.9) (Fig. 2a). There was strong evidence ($P = 0.95$) that species richness of herbivorous fish assemblages was influenced by slope orientation, with richness generally greater on gentle, moderate and steep slope orientations (i.e., 5–80º), and decreased on both flat (< 5º) and wall (> 80º) orientations (Fig. 2b; Fig. S1a). There was strong evidence ($P = 0.97$) that benthic complexity influenced the richness of herbivorous fishes, with intermediate complexity (scores of 2 and 3) having the greatest richness and the lowest complexity (score of 0) having the lowest richness of herbivorous fishes (Fig. 2c; Fig. S2). There was no evidence ($P = 0.62$) to suggest that reef zones influenced the richness of herbivorous fishes in the CSMP (Fig. S3).

The first two axes of the constrained component of canonical analysis of principal coordinates (CAP) explained 54.9% of the variance in herbivore assemblage composition (Fig. 2c). The PERMANOVA indicated that depth ($F_{(2, 226)} = 7.3$, $p < 0.001$; Fig. 2c), reef zone ($F_{(5, 226)} = 1.8$, $p < 0.001$; Fig. S4a) and slope orientation ($F_{(2, 226)} = 2.8$, $p < 0.001$; Fig. S4b) influenced the composition of herbivorous fish assemblages. There was no statistically detectable influence of benthic complexity on herbivorous fish assemblages ($F_{(5, 226)} = 1.1$, $p = 0.18$). The greatest difference in species composition was the higher abundance of pygmy angelfish *Centropyge heraldi* that characterized the lower mesophotic (61–98 m) and higher abundance of *Acanthurus pyroferus* and *Naso tonganus* in the upper mesophotic (31-60 m) (Fig. S5).

Abundance

There was strong evidence ($P = 1$) that the abundance of herbivorous fishes, both collectively and for functional groups independently, declined with depth (Fig. 3). There were, however, differences in the rate of decline among groups. The median abundance of all herbivorous fishes declined at a rate of 5.1% m^{-1} (95% HPD 4.6–5.6) (Fig. 3a), with scrapers (3.9% m^{-1}: 95% HPD 3.0–4.8) and croppers (4.1% m^{-1}: 95% HPD 3.6–4.7) (Fig. 3c, f) decreasing at a lower rate than browsers 6.8% m^{-1} (95% HPD 5.2–8.5; Fig. 3b), excavators 6.8% m^{-1} (95% HPD 5.2–8.1; Fig. 3e) and detritivores 7.4% m^{-1} (95% HPD 6.4–8.4; Fig. 3d).

There was evidence or weak evidence that the abundance of total herbivores ($P = 0.87$), browsers ($P = 0.85$), croppers ($P = 0.87$) and detritivores ($P = 0.93$) varied with reef zones (Fig. 4a–d; Fig. S6a-d). For total herbivores and browsers, abundance was greater in the lagoon than the inner and outer reefs (Fig. 4a, b). In contrast, croppers were more abundant in lagoon and inner reefs compared to outer reefs (Fig. 4c), while detritivores were more abundant on outer reefs than in lagoon and inner reefs (Fig. 4d). There was no evidence to suggest that excavator ($P = 0.71$) and scraper ($P = 0.72$) abundance varied with reef zone (Fig. 4e, f, Fig. S6 e–f).

There was strong evidence ($P = 0.98$) that overall herbivore abundance was greatest on moderate slopes and declined on both flatter and steeper orientations (Fig. 5a; Fig. S1b). This pattern of higher abundance on moderate slopes were also recorded for detritivores ($P = 0.88$; Fig. 5d; Fig. S7c), scrapers ($P = 0.92$; Fig. 5f; Fig. S7e) and excavators ($P = 1$; Fig. 5e; Fig S7d). For croppers, the greatest abundance was recorded on both moderate and gentle slopes ($P = 0.90$; Fig. 5c; Fig. S7b), while there was no evidence ($P = 0.55$) to suggest an effect of slope orientation for browsers (Fig. 5b; Fig. S7a).

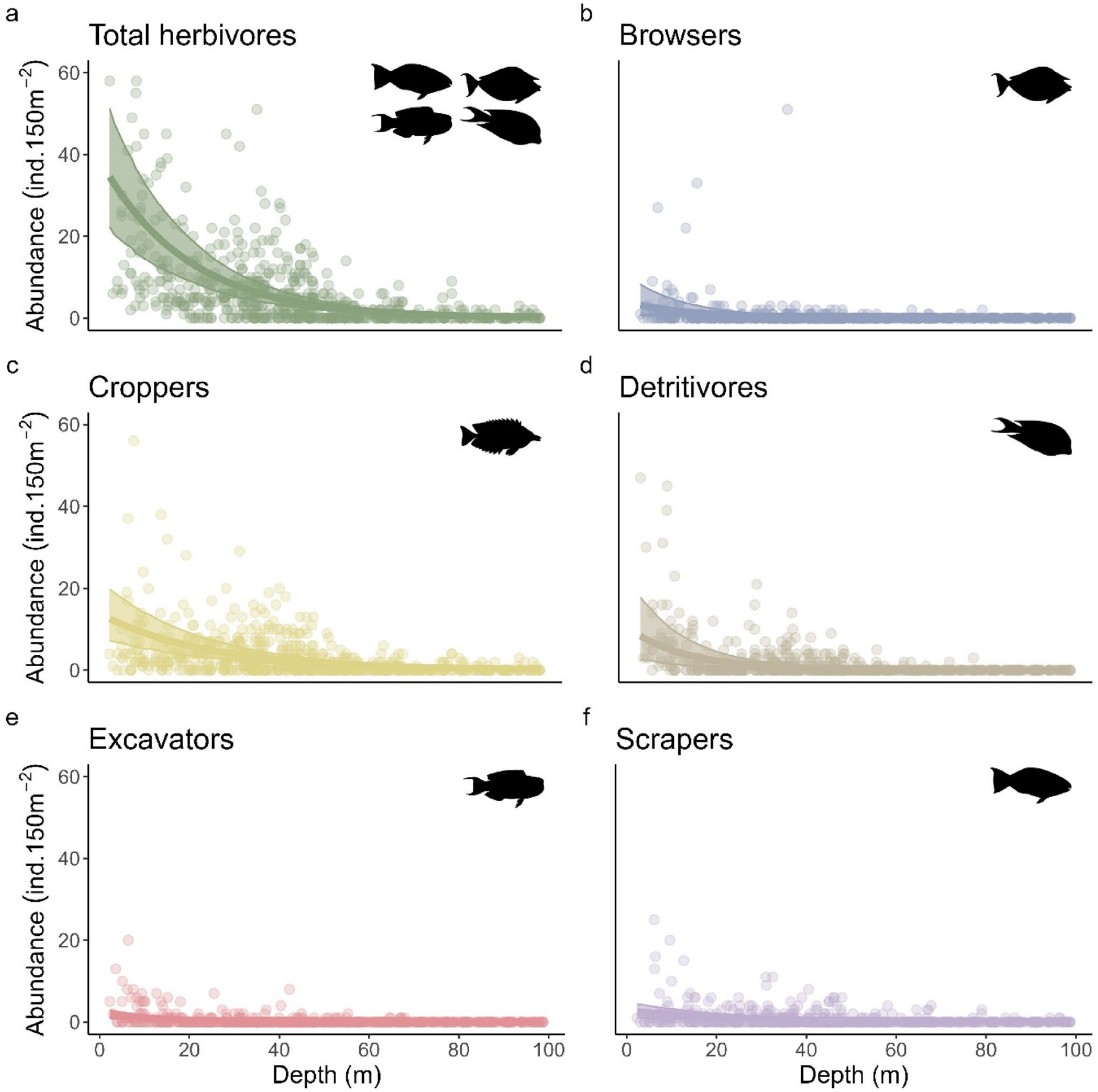


Fig. 3 Changes in the abundance of herbivorous fishes with depth in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of changes in abundance (n. individuals per 150 m^{-2}) with depth for **a** herbivorous fishes collectively and **b**–**f** each functional group independently. Lines are the modeled relationship with ribbons representing the 95% upper and lower credible intervals. Circles are the abundance for each transect from the raw data

There was strong evidence ($P = 0.99$) that benthic complexity influenced the abundance of total herbivorous fishes and four of the five functional groups (browsers: $P = 0.91$; croppers: $P = 0.98$; detritivores: $P = 0.90$; scrapers: $P = 0.93$), the exception being excavators ($P = 0.72$). The abundance of all herbivores collectively and the four functional groups (except excavators) was lower in areas with low benthic complexity (i.e., scores at 0 and 1) than those with intermediate to high complexity (i.e., scores of 2 to 5) (Fig. 6; Fig. S8).

Biomass

There was strong evidence ($P = 1$) to suggest that biomass of all herbivorous fishes collectively decreased with depth, but again the rate of decline varied among

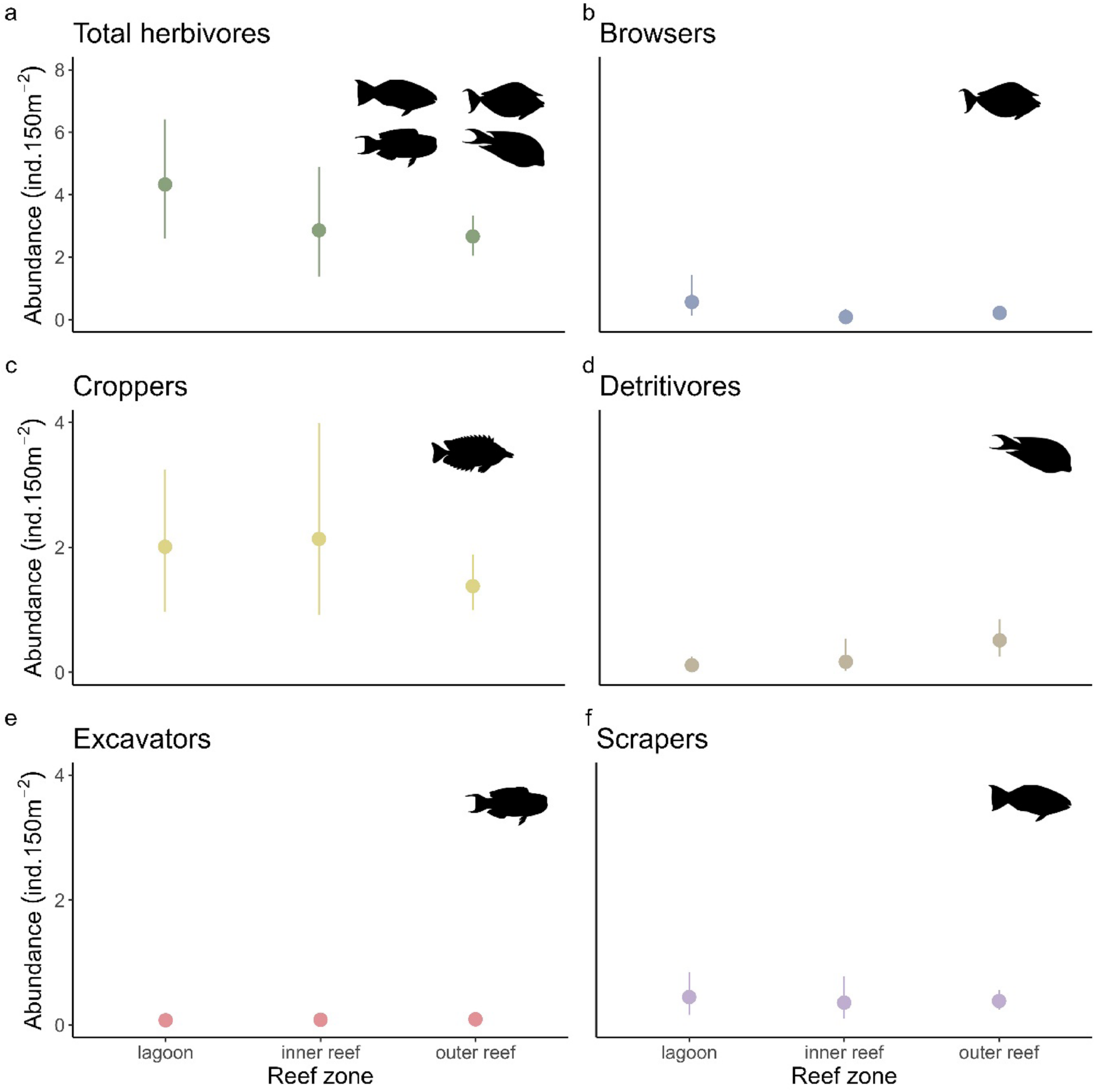


Fig. 4 Differences in the abundance of herbivorous fishes among reef zones in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of abundance (n. individuals per 150 m^{-2}) for **a** all herbivorous fishes collectively and **b–f** each functional group independently are shown. Points represent the median, and the lines represent the 95% upper and lower credible intervals

functional groups (Fig. 7). The median biomass of all herbivorous fishes decreased by 3.2% m^{-1} (95% HPD 1.7–4.7) with increasing depth (Fig. 7a). Detritivores ($P = 0.99$) decreased at a rate of 3.1% m^{-1} (95% HPD 1.2–4.9; Fig. 7d) while croppers ($P = 0.99$) decreased by 2.3% m^{-1} (95% HPD 0.8–3.8; Fig. 7c). There was no evidence to suggest depth affected the biomass of browsers ($P = 0.63$), scrapers ($P = 0.84$) and excavators ($P = 0.52$; Fig. 7b, e, f).

There was no evidence to suggest that total herbivore biomass ($P = 0.63$) and biomass for each functional group (browsers: $P = 0.62$; croppers: $P = 0.69$; detritivores: $P = 0.76$; excavators: $P = 0.74$; scrapers: $P = 0.66$) varied with reef zone (Fig. S9).

There was weak evidence ($P = 0.88$) that the biomass of herbivorous fishes was greatest in gentle and moderate slope orientations compared to flat, steep slopes and/

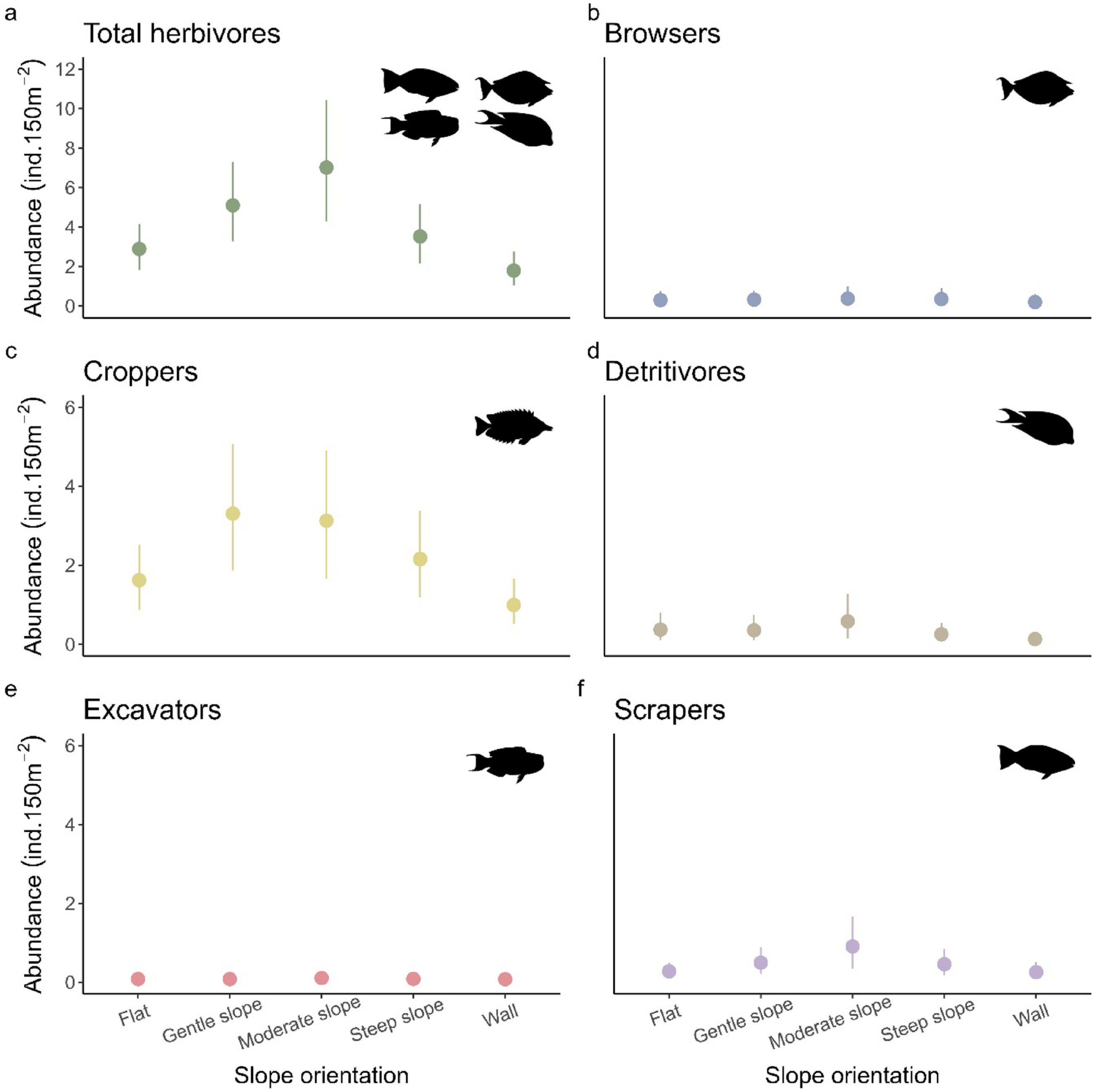


Fig. 5 Differences in the abundance of herbivorous fishes among slope orientations in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of abundance (n. individuals per 150 m^{-2}) for **a** all herbivorous fishes collectively and **b**–**f** each functional group independently are shown. Points represent the median, and the lines represent the 95% upper and lower credible intervals

or walls (Fig. 8a; Fig. S1c). The effect of slope orientation on biomass varied among functional groups, with croppers ($P=0.90$; Fig. 8c; Fig. S10b) having the highest biomass on gentle slopes; excavators ($P=0.87$; Fig. 8e; Fig. S10d) and scrapers ($P=0.85$; Fig. 8f; Fig. S10e) on moderate slopes; detritivores on flats and/or gentle and moderate slopes ($P=0.86$; Fig. 8d; Fig. S10c). There was no evidence to suggest that browser biomass varied with slope orientation ($P=0.71$; Fig. 8b; Fig. S10a).

There was evidence to suggest that the biomass of total herbivores ($P=0.94$), croppers ($P=0.90$), detritivores ($P=0.89$) and scrapers ($P=0.92$) varied with benthic complexity (Fig. S11-S12). Biomass of total herbivores, detritivores and scrapers was greatest in areas of low benthic complexity (i.e., score of 1), whereas the biomass of croppers was greatest in areas of high complexity (i.e., score of 5). There was no evidence to suggest that benthic

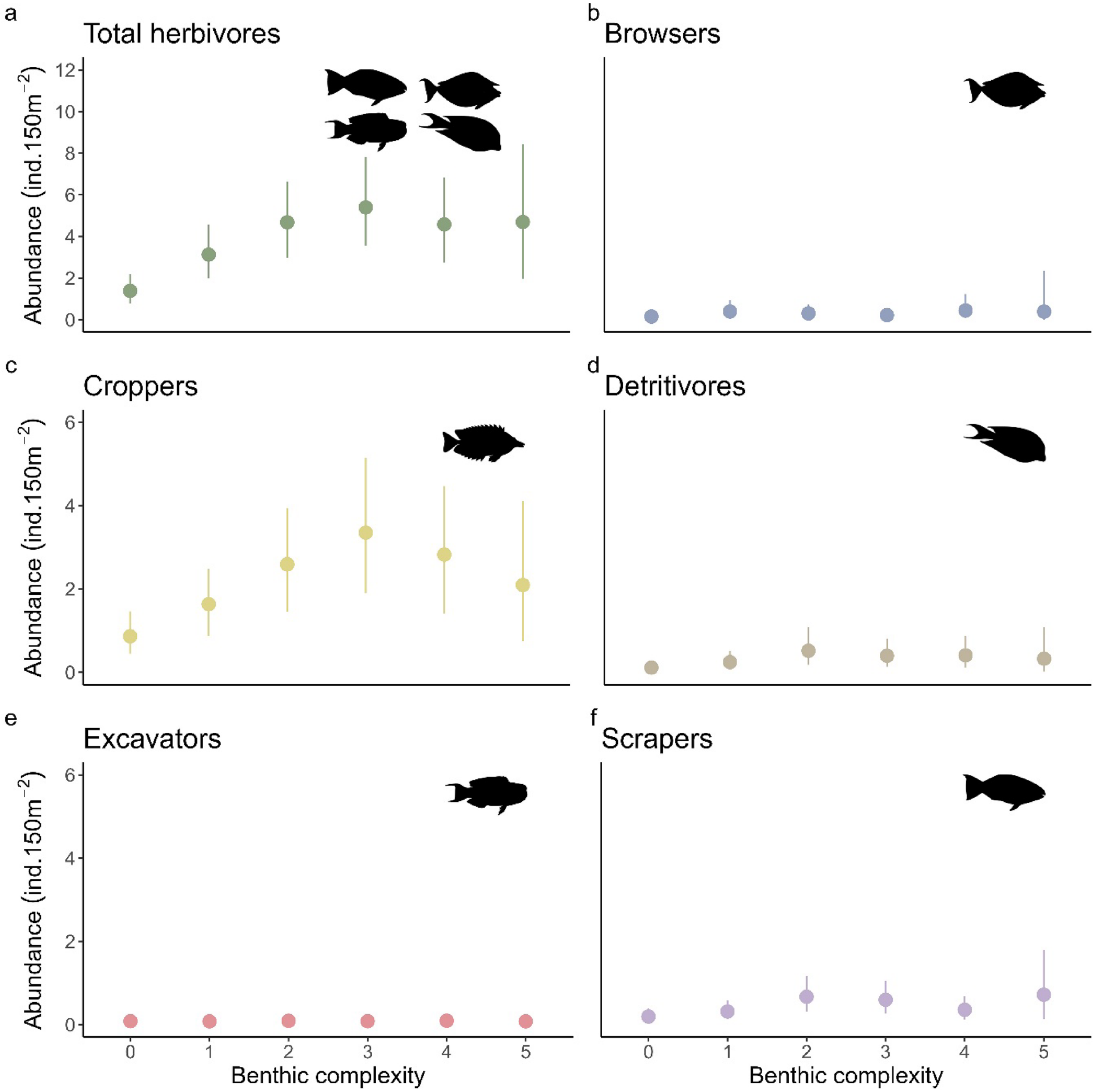


Fig. 6 Differences in the abundance of herbivorous fishes among benthic complexity in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of abundance (n. individuals per 150 m^{-2}) for **a** all herbivorous fishes collectively and **b**–**f** each functional group independently are shown. Points represent the median, and the lines represent the 95% upper and lower credible intervals

complexity influenced the biomass of excavators ($P = 0.54$) or browsers ($P = 0.66$).

Discussion

Changes in the taxonomic and trophic composition of reef fishes from shallow reefs to MCEs are well documented (e.g., Rocha et al. 2018; Pinheiro et al. 2023), but few studies have examined how depth and slope orientation influences the functional composition of herbivorous fishes. The present study showed that while the taxonomic richness, abundance and biomass of herbivorous fishes were greatest in shallow (< 10 m) habitats and declined with depth, the rates of decline for both abundance and biomass varied among functional groups. The rate of decline in abundance of excavating and detritivorous fishes was nearly double that of cropping and scraping fishes.

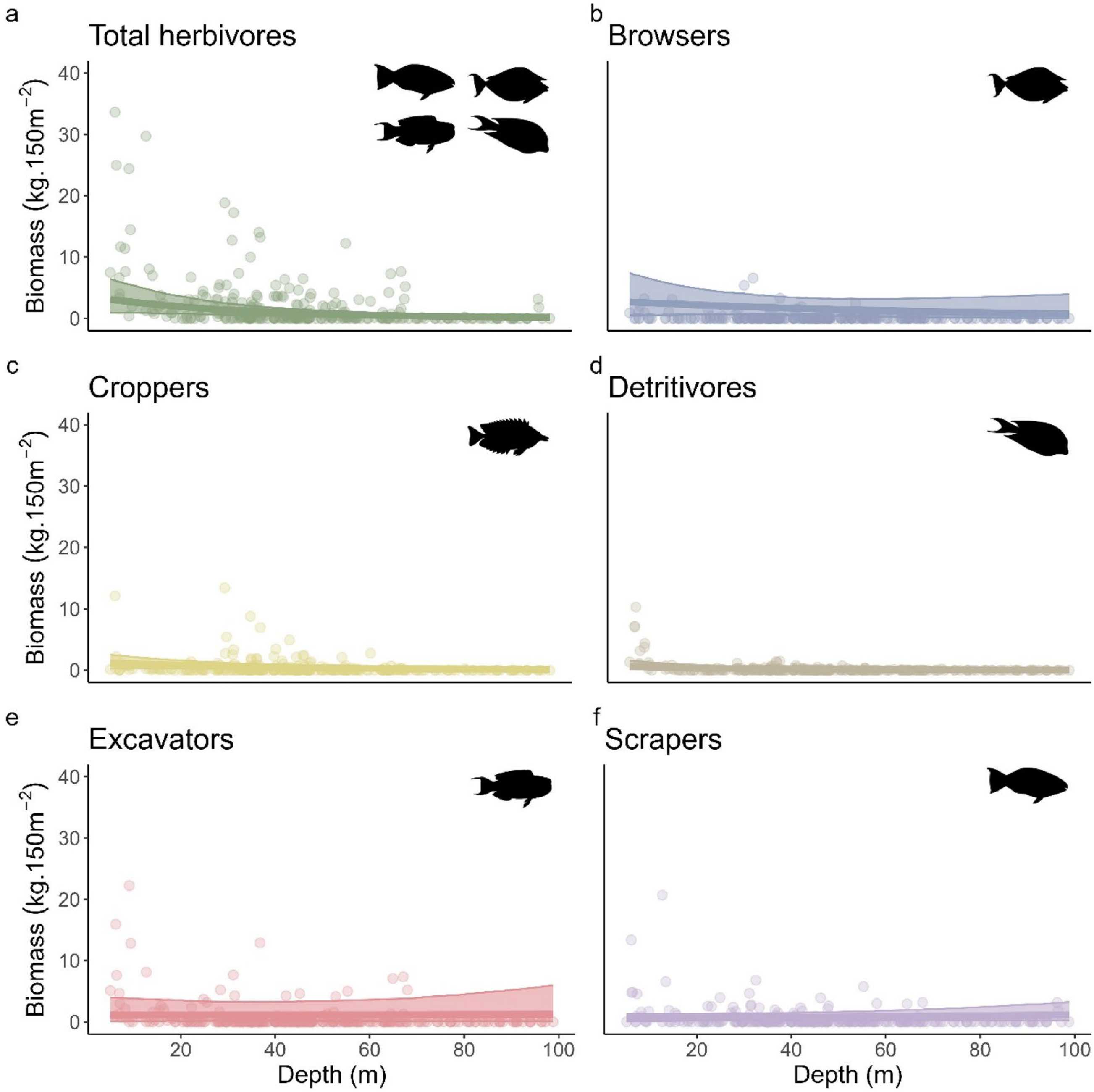


Fig. 7 Changes in the biomass of herbivorous fishes with depth in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of the relationship between biomass (kg per 150 m^{-2}) and depth for **a** all herbivorous fishes collectively and **b**–**f** each functional group independently from shallow to MCEs. Lines are the modeled relationships with ribbons representing the 95% upper and lower credible intervals. Circles are the biomass for each transect from the raw data

Similarly, the rates of decline in biomass of detritivorous fishes was ~ 50% higher compared to cropping fishes. Given that these functional groups derive their nutrition from different components of the photoautotroph assemblage, the different rates of decline with depth may reflect variation in the availability or nutritional quality of their dietary resources from shallow reefs to MCEs (Brokovich et al. 2010; Strait et al. 2022), or alternatively differences in predation risk with depth (Lindfield et al. 2016; Pimentel et al. 2022).

The decline in the abundance, richness and biomass of herbivorous fishes with increasing depth within the CSMP is consistent with studies from other Indo-Pacific (e.g., Fukunaga et al. 2016; Pinheiro et al. 2023) and tropical Atlantic reefs (Pinheiro et al. 2016; Stefanoudis et al. 2019). These declines in herbivorous fishes (collectively) have generally

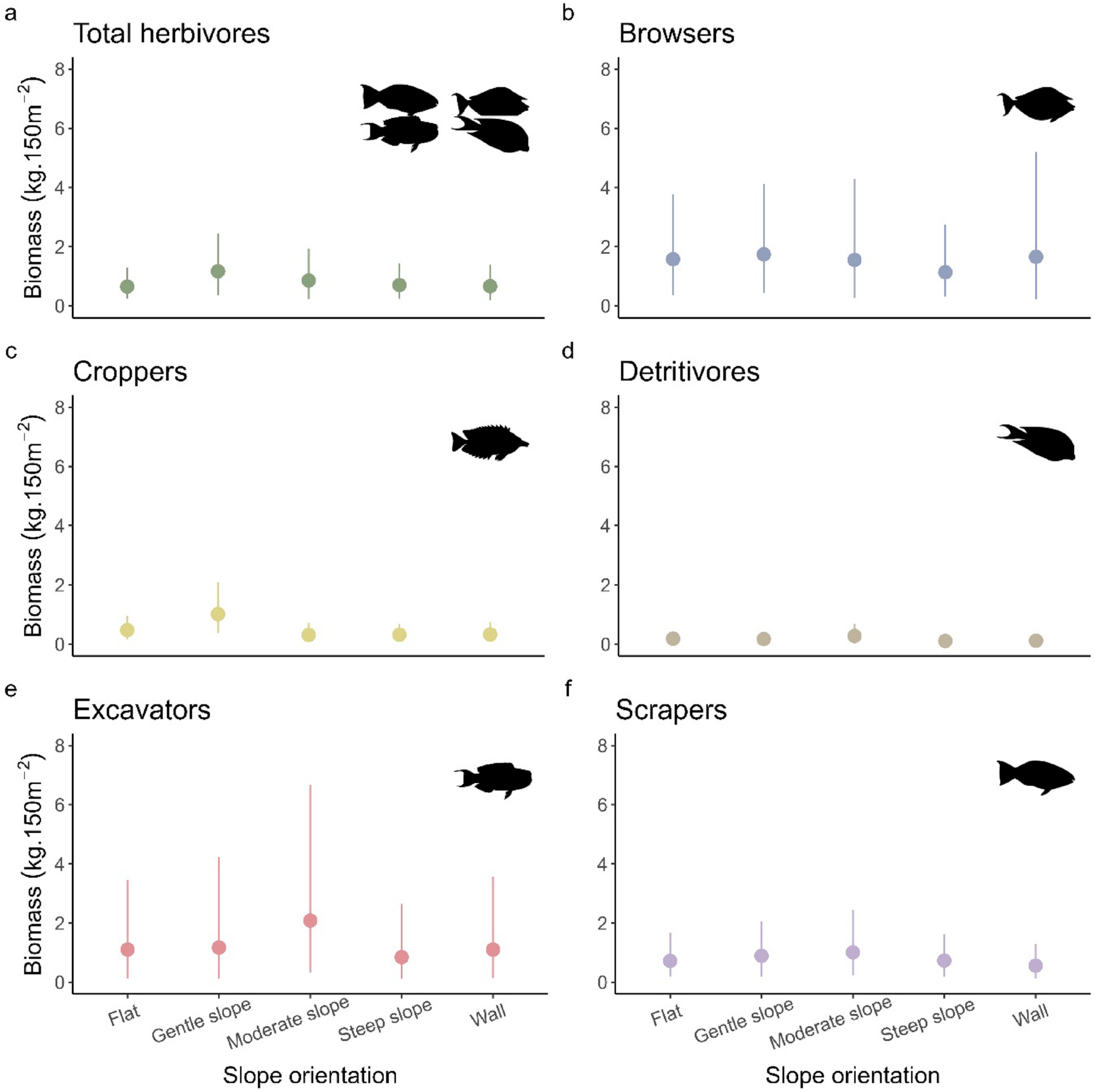


Fig. 8 Differences in the biomass of herbivorous fishes among slope orientations in the Coral Sea Marine Park (CSMP). Marginal posterior predictions of the biomass (kg per 150 m^{-2}) of **a** all herbivorous fishes collectively and **b**–**f** each functional group independently among slope orientations. Points represent the median biomass, while the lines represent the 95% upper and lower credible intervals

been related to changes in the availability, composition and/or nutritional quality of dietary resources with increasing depth (Brokovich et al. 2010; Pinheiro et al. 2023). MCEs are primarily defined by lower light levels relative to shallow reefs (Lesser et al. 2018; Kahng et al. 2019), with numerous studies on shallow reef ecosystems demonstrating that reductions in incident light can influence the composition, and reduce the cover and/or productivity of benthic photoautotrophs (e.g., turfs, macroalgae, microbes) (Littler et al. 1986; Klump and McKinnon 1989; Vogel et al. 2000; Aponte and Ballantine 2001; Perry and Macdonald 2002; Tebbett and Bellwood 2021; Fabricius et al. 2023).

The differences in the rates of decline in abundance (and/or biomass) among herbivore functional groups with depth may reflect changes in the availability and/or quality of their preferred dietary resources. For example, the abundance of excavating parrotfishes decreased with depth at a rate nearly twice that of scraping parrotfishes. While both excavating and scraping parrotfishes have been shown to target micro-photoautotrophs (Nicholson and Clements 2020), there are interspecific differences in both the composition of micro-photoautotroph assemblages and the calcareous substrata targeted by parrotfishes when feeding (Nicholson and Clements 2023). Notably, the excavating parrotfish *Chlorurus microrhinus* has been reported to target the endolithic chlorophytes *Ostreobium* and *Phaeophila* (Nicholson and Clements 2020, 2023) and highly bioeroded reef substrata (Nicholson and Clements 2021). Although *Ostreobium* is adapted to low light (Tandon et al. 2023) and has been recorded in MCEs (Littler et al. 1985), its abundance (Vogel et al. 2000) and ability to micro-bioerode the substrata may decrease with increasing depth (Weinstein et al. 2019). The lower availability of *Ostreobium* and weakly eroded substrata with depth may contribute to the greater rates of decline for excavating parrotfishes in MCEs. In contrast, scraping parrotfishes of the genus *Scarus* generally target filamentous cyanobacteria with the taphonomy of their feeding substrata varying from recently dead coral to highly bioeroded, depending on the species (Nicholson and Clements 2021, 2023). Although filamentous cyanobacteria are present in MCEs (Olson and Kellogg 2010), information on their changes in availability and composition with depth is unknown and is an area for future research. The broader range of substrate taphonomy targeted by scraping parrotfishes may contribute to their lower rate of decline with depth compared to excavators.

The rate of decline of the abundance and biomass of detritivores with depth was nearly double that of croppers and/or browsers. While turf assemblages and macroalgae, the feeding substrata of croppers and browsers, respectively, both occur in MCEs (e.g., Littler et al. 1986; Aponte and Ballantine 2001; Kane and Tissot 2017; Slattery and Lesser 2014), the lower productivity of turfs (Brokovich et al. 2010; Tebbett and Bellwood 2021) and the greater physical and/or chemical defenses (Lesser and Slattery 2011; Slattery and Lesser 2014; Spalding et al. 2019) and lower nutritional quality of macroalgae with increasing depth (Strait et al. 2022) may contribute to the reductions in croppers and browsers in MCEs. In contrast, detritivorous fishes target detrital aggregates within turf assemblages (Wilson et al. 2003). Studies of shallow reefs (down to 17 m deep) have shown that the standing biomass of detritus declines with depth and is greatest on shallow reef flats because of low wave energy that allows the accumulation of detrital material (Purcell and Bellwood 2001; Max et al. 2013). Although surface wave energy attenuates with increasing depth (Bradbury and Young 1981), turbulence through subsurface currents and/or internal waves (Wolanski et al. 2004; Kahng et al. 2010) may minimize detrital build up with depth. Further, seamounts and other similar steep-sided coral reef geomopholoies are known to experience strong hydrodynamic conditions due to site-specific interactions between surrounding currents, upwellings and the abrupt physical structure (Lavelle and Mohn 2010; Leitner et al. 2021; Galbraith et al. 2022). Strong currents at mesophotic depths on seamounts in the Coral Sea may be further enhanced due to the offshore locations of these reefs and their exposure to large regional ocean circulation systems (Choukroun et al. 2021). Moreover, the lower densities and perhaps feeding/defecating activities of reef fishes in MCEs may limit detritus enrichment and nutritional quality (Wilson et al. 2001).

Predation is a key process in coral reef ecosystems that can contribute to prey mortality, or through non-consumptive (fear) effects (NCEs; Mitchell and Harborne 2020) that alters prey morphology and/or behavior (e.g., swimming capabilities; feeding behavior). These NCEs may also interact with habitat availability with variation in predation risk among shelter and nursery types (Coker et al. 2014; Harborne et al. 2015; Catano et al. 2016). Some MCEs have been reported to have greater richness and/or abundance of predators, including highly mobile jacks and sharks, compared to shallow reefs (e.g., Fukunaga et al. 2016; Pinheiro et al. 2016; Lindfield et al. 2016) suggesting greater predation risk with increasing depth at these locations. However, reefs within the CSMP appears to be counter to this pattern, with the richness and abundance of predators declining from shallow reefs to MCEs (Cresswell et al. 2025). Moreover, if predation was a major driver of the declines in abundance/biomass, then fishes of similar body size may be expected to decline at similar rates as predation risk is generally thought to be greater for smaller compared to larger individuals (Mihalitsis and Bellwood 2021). However, the differences in rates of decline among herbivore functional groups within the CSMP are not consistent with size-related predation. For example, detritivores and croppers are generally small-bodied and have similar maximum body sizes, yet detritivores declined at a rate 50% greater than that of croppers. While predation effects on herbivorous fishes in the CSMP were modest, NCEs may have affected behavior (e.g., bite rates), but this remains to be examined. Moreover, the abundance of four of the five groups of herbivorous fishes was positively associated with benthic complexity, suggesting the availability of shelter may be an important driver of herbivorous fish abundance in MCEs in the CSMP. However, further studies are required to isolate the potential effects of predation and shelter on herbivorous fish assemblages cumulatively and among functional groups.

Slope orientation influences the light intensity and sediment accumulation in MCEs, with vertical orientations (e.g., reef walls) receiving ~ 25% less incident light compared to sloping orientations (Lesser et al. 2021a). Generally, abundance or biomass of functional groups were higher on gentle (5–30°) and moderate (31–45°) slopes compared to walls (> 81°) suggesting the importance of light and its influence on the photoautotrophic assemblages. Indeed, experimental work using limestone tiles in shallow reefs suggest that algae assemblages differed on tiles oriented vertically versus horizontally, with crustose coralline algae the dominant group in vertical orientations (Duran et al. 2018). Despite the higher incident light on horizontal surfaces, the abundance or biomass of detritivores, scrapers and excavators was generally lower on flat ($<5°$) compared to gentle, moderate and steep slope orientations. Horizontal surfaces retain more sediments than inclined surfaces (Sherman et al. 2016), which has been shown to reduce the feeding activities of herbivores (Goatley and Bellwood 2012; Gordon et al. 2015). The abundance and biomass of most functional groups was greatest on moderate slopes and may reflect a balance between light availability, sediment accumulation and the availability of different microhabitat (or surface orientation) types that can support the preferred grazing substrata of herbivores (Brandl and Bellwood 2014). In contrast, cropper biomass was highest on gentle slopes suggesting croppers may be less sensitive to sedimentation (Tebbett et al. 2017; Pessarrodona et al. 2022) and perhaps more influenced by light availability and consequent turf productivity.

In conclusion, while herbivorous fishes cumulatively decreased in taxonomic richness, abundance and biomass with depth, supporting previous observations from studies in other locations (e.g., Fukunaga et al. 2016; Pinheiro et al. 2016, 2023; Stefanoudis et al. 2019), the rates of such declines varied among functional groups. Differential changes in the availability and/or quality of dietary resources with depth appear to be the most likely cause for these differences in declines among functional groups; however, the potential role of variation in predation should not be discounted. These functional group-specific responses to depth suggest that MCEs may provide limited depth refuge for all herbivorous fish groups (but see Pinheiro et al. 2016; Lindfield et al. 2016). Importantly, these variable reductions among functional groups with depth may translate to disproportionate deliveries of their ecological functions in MCEs. For example, the greater rates of decline in the abundance or biomass of excavators, detritivores and browsers with depth compared to croppers and scrapers, may limit piscine bioerosion, browsing and detritivory and thereby disrupt carbonate budgets (Mallaela and Fox 2018), macroalgae removal (Hoey and Bellwood 2009) and energy transfer (Max et al. 2013; Munsterman et al. 2021), respectively, in MCEs. The net effects of functional groups will, however, also depend on the relative production of turfs, cyanobacteria, macroalgae, detritus and microbes among depths. Moreover, lagoon habitat, slope orientations between 6 and 45° and benthic complexity scores between 2 and 5 generally supported higher richness and abundance suggesting the influence of geomorphological characteristics in the distribution of herbivorous fishes in MCEs. This study highlights that the influence of depth on herbivorous fishes are not homogenous but varies with functional groups, with such differences perhaps related to changes in resource availability and predation from shallow reefs to MCEs.

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Author contributions TJRQ, ASH and GFG conceptualized the study. GFG, BJC, AB and ASH collected data. GFG, BJC and TJRQ conducted video analyses. Statistical analyses were performed by TJRQ with consultation from GFG and BJC. The first draft of this manuscript was written by TRJQ with all authors contributing to the revisions. All authors read and approved of the final manuscript.

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Data availability Data and reproducible R codes are available at https://github.com/tjrq/CSMP_Herb_Functional_Group/tree/main.

Declarations

Conflict of interest The authors declare no competing interests.

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