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Deep-Reef Fish Communities of the Great Barrier Reef Shelf-Break: Trophic Structure and Habitat Associations

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Abstract: The ecology of habitats along the Great Barrier Reef (GBR) shelf-break has rarely been investigated. Thus, there is little understanding of how associated fishes interact with deeper environments. We examined relationships between deep-reef fish communities and benthic habitat structure. We sampled 48 sites over a large depth gradient (54–260 m) in the central GBR using Baited Remote Underwater Video Stations and multibeam sonar. Fish community composition differed both among multiple shelf-break reefs and habitats within reefs. Epibenthic cover decreased with depth. Deep epibenthic cover included sponges, corals, and macro-algae, with macro-algae present to 194 m. Structural complexity decreased with depth, with more calcified reef, boulders, and bedrock in shallower depths. Deeper sites were flatter and more homogeneous with softer substratum. Habitats were variable within depth strata and were reflected in different fish assemblages among sites and among locations. Overall, fish trophic groups changed with depth and included generalist and benthic carnivores, piscivores, and planktivores while herbivores were rare below 50 m. While depth influenced where trophic groups occurred, site orientation and habitat morphology determined the composition of trophic groups within depths. Future conservation strategies will need to consider the vulnerability of taxa with narrow distributions and habitat requirements in unique shelf-break environments.

Keywords: deep reefs; shelf-break habitats; BRUVS; multibeam bathymetry; fish-habitat associations; trophic structure

1. Introduction

In coastal oceans, the shelf-break is defined as the point where the continental shelf ends and the continental slope begins. It is characterized by steep increases in depth and associated changes in biotic and abiotic conditions. While tropical shelf-break ecosystems, such as deep reefs (i.e., >50 m depth), support a variety of ecologically and economically important fishes, there is a lack of information on the links between these fish communities, depth, and benthic composition, which limits our ability to effectively assess ecological impacts and manage stocks. While deep-reef fish communities include many species endemic to these habitats, they may also provide habitat extensions or 'refuges' for numerous shallow water fishes [1–3], and can support key ontogenetic stages [4,5] or large, highly fecund individuals [6]. Consequently, deeper habitats can represent critical reservoirs of biodiversity [7], while maintaining fisheries resilience and safeguarding local and global biodiversity [8].

Despite their potential importance, the majority of deep reefs globally are afforded little or no protection [9] with current management measures either insufficient or non-representative of geographic scope or ecological importance. One partial exception is Australia's Great Barrier Reef (GBR) where deep habitats are afforded some protection due to the comprehensive marine reserve network that includes continental shelf and slope habitats in addition to the better-known shallow-water coral reefs. The GBR marine reserve network was designed using conservation objectives that explicitly accounted for latitudinal and cross-shelf gradients in geophysical and environmental conditions likely to influence spatial patterns of biodiversity, which is an approach that resulted in reasonable representation of deepwater habitats despite a lack of biological data [10]. Fish stocks within the GBR also receive some additional protection from overlapping Queensland State and Commonwealth fishery regulations. Despite reasonable representation of deepwater habitats within the GBR marine reserve network, no information is currently available on finer-scale biological or ecological factors that are critical for managing particular species or ecosystems. For example, there is limited information on the ecology of deep reef ecosystems, the life history traits of associated fishes, and the role of deep habitat as a mediator of the fish community structure.

In shallow marine environments (<30 m depths), biotic and abiotic habitat characteristics that influence individual or population fitness impact the distribution and abundance of fish species. For instance, many fish associate with structurally or biologically complex benthic habitats [11–16] since these can provide a greater abundance of food resources, shelter, and reproductive opportunities. Increasing complexity can also mediate important processes such as predator-prey interactions, recruitment, and competition [17–20], which, in turn, can promote greater fish community diversity [21]. The widespread disturbance of shallow benthic habitats, as a result of climate change and other anthropogenic impacts, has led to decreased habitat complexity and loss of ecosystem function, and has corresponded with local and global declines in fish abundance and diversity [22,23]. While the significance of habitat complexity as a mediator of the fish population structure and biodiversity is well documented for shallow reef systems, its role within deep reef ecosystems is poorly documented. However, given the potential economic and ecological value of these systems, increasing varied anthropogenic pressure should be applied to them [24,25] to understand the importance of deep-reef habitat composition for fish communities is critical for effective future management.

Our current understanding of shelf-edge reef fish communities and fish-habitat interactions is generally poor [26–31]. Some studies have examined entire fish assemblages associated with deeper reefs (>50 m). However, a number of potential interactions between habitat characteristics and the associated fish community have been identified. For example, studies of fish assemblages from tropical Indo-Pacific and Atlantic shelf-breaks have reported the partitioning of trophic groups with depth [2,8,26,30,32–36]. With increasing depth, the abundance of herbivores decreases and the abundance of planktivores increases [37]. However, the majority of these studies sampled depths <80 m, and the distribution of other groups, such as piscivores, showed no consistent depth-related patterns.

The abundance and composition of benthic fauna, especially habitat-forming species, such as corals, sponges, and algae, are the primary drivers of fish community composition [38]. The distribution of these benthic organisms is often highly depth-dependent. For instance, scleractinian corals are generally the most important component of shallower communities [2,34,36], while the representation of heterotrophic taxa such as sponges and gorgonians increase with depth as light decreases [26,39]. Similarly, other studies have suggested that physical attributes of the underlying benthos that increase habitat complexity, such as overall rugosity or the presence of key elements such as boulders or bedrock, often affects fish abundance [30], even in the absence of habitat-forming sessile invertebrates and algae.

Our limited understanding of mesophotic fish-habitat relationships is largely due to the difficulty of studying them. Direct observations traditionally require the use of expensive and logistically restrictive equipment such as technical diving [40], Remotely Operated Vehicles (ROVs, e.g., [41,42]), Autonomous Underwater Vehicles (AUVs, e.g., [43]) or submarines (e.g., [44,45]). However, Baited Remote Underwater Video Stations (BRUVS) and other single or stereo video systems (e.g., BotCam, stereo-BRUVS, stereo video-lander) are practical, cost-effective alternatives that can be deployed on complex topographies in a variety of habitats [46–52]. The underwater video can effectively identify both community patterns (species richness and abundance) and whole assemblage composition without depth restrictions, and can increase potential sampling time, replication rate, and sampling area relative to cost. Importantly, BRUVS are less selective or destructive than fishery-dependent methods [53] and, since all deployments are filmed, images can be easily archived for future use. While BRUVS sample representative trophic groups and relative abundance at similar rates to diver-based surveys [54], they can document higher species richness [55,56] as well as small fishes missed by divers [56]. Shallower GBR BRUVS studies have identified strong cross-shelf gradients and weak latitudinal patterns, likely due to varying topographical complexity and the distribution of key habitats, as well as depth-related but variable changes to fish communities [57]. In deeper deployments, baited units have greater sampling efficiency than un-baited units, which records a greater abundance of demersal species and allows more accurate species identification [48]. While BRUVS have been used extensively in the GBR [53,58], they have rarely been deployed below 100 m depths. Deeper deployments have added challenges, including increased pressure at depth, low ambient light for cameras, strong currents, longer deployment, and retrieval times, and substantial gear requirements. BRUVS methods have inherent biases and, for deeper deployments, both bait and light could be attractants for some species or trophic groups preferentially over others. The biases of BRUVS have been reviewed [59,60] and should be carefully considered. However, for studies sampling fishes below 150 m (below this depth, the ambient light may not be sufficient to accurately identify species), there are few cost-effective and statistically robust options. Since the field-of-view of the BRUVS is limited, the parallel use of additional sampling techniques, such as multibeam echo-sounding technology, can rapidly gather complimentary high-resolution information on seafloor characteristics. Differences in substratum type (e.g., sand or bedrock), relief (i.e., elevational change), rugosity (i.e., relative topographical position), and complexity (i.e., three-dimensional structure) [61] can help explain fish community patterns over varying spatial scales.

Depth had a great influence on fish assemblages [62] and we predicted that the complex mosaic of habitats would affect the distribution of fishes. Specifically, we examined how variation in the fish community composition related to benthic habitat among and within multiple locations along the GBR shelf-break. We described some deep reefal and inter-reefal habitats and investigated how multivariate metrics of biotic and abiotic components may be responsible for community patterns that may be masked by depth. We also assessed community patterns of trophic groups and species co-occurrence, which could have important implications for future conservation management strategies of shelf-break habitats.

2. Materials and Methods

2.1. Study Locations

Submerged shoals along the margin of the GBR support a wide range of ecosystems, largely due to the diverse range of shelf-edge reef morphologies that occur [63]. The central GBR is particularly morphologically distinctive (Figure 1, [64]). In this region, very few major reefs reach sea-level within eight kilometers landward of the shelf-edge, and only one emergent reef is found on the edge itself (Myrmidon Reef, [64]). The shelf-edge here is characterized by one to three lines of submerged reefs, which indicates periods of active development during lower historical sea levels [65]. The central GBR shelf-break is located >100 km from shore, which is a greater distance than in the northern GBR (north of Cairns), but much less than the southern GBR (up to 250 km). Gradients on the upper continental slope in the central GBR are also comparatively low compared to the northern GBR, with a combination of subsidence [66] and sediment input [67] as the likely drivers for this morphology. The region commonly experiences nutrient enrichment as the seasonal thermocline of the adjacent Coral Sea shallows [68], which, in turn, transports nutrient-rich waters to the continental shelf [69].

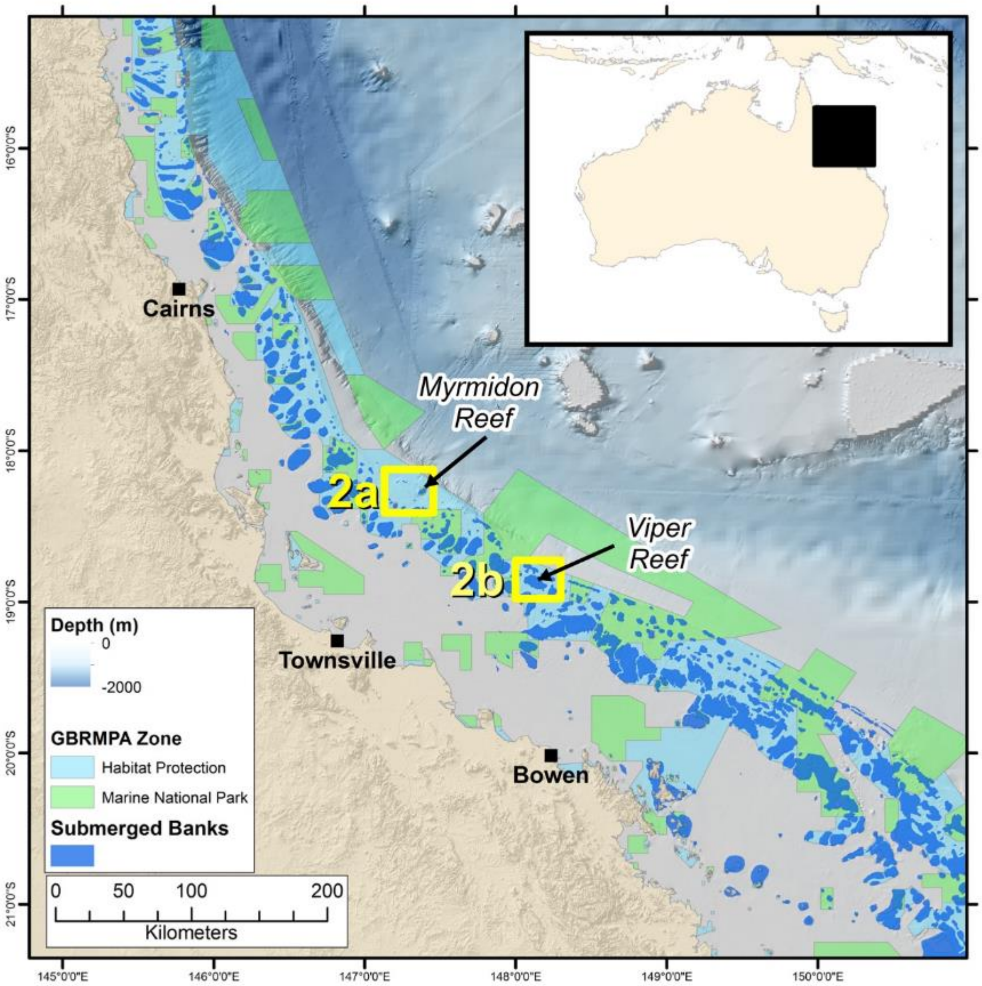


Figure 1. Map showing shelf-break areas of the central Great Barrier Reef sampled: (**a**) Myrmidon Reef, Northern Submerged Shoals, an inter-reefal transect, and (**b**) Viper Reef. The shelf-break is over 100 km offshore and the adjacent continental slope drops off to depths of hundreds of meters. Within the Great Barrier Reef Mark Park, activities are managed by the Great Barrier Reef Marine Park Authority (GBRMPA) in Zones. Marine National Park Zones (green) are 'no-take' areas where extractive activities such as fishing and collecting are not allowed without a permit. Habitat Protection Zones (blue) are set aside to protect habitats from potentially damaging activities. See Fernandes et al., 2005 for a description of the zonation. Submerged banks from Harris et al., 2013 are depicted in darker blue.

In order to assess variation in habitats along the upper continental slope environment, four distinct shelf-edge locations were targeted using the multibeam sonar and BRUVS: Myrmidon Reef, a suite of unnamed shoals 15 km northwest of Myrmidon ('Northern Submerged Shoals'), an inter-reef transect (Figure 2a), and two submerged shoals 30 km east of the Viper Reef ('Viper Reef', Figure 2b). The mesophotic benthic communities of the central GBR are composed of a diverse range of habitat-forming taxa such as hard and soft corals (including Scleractinia, zooxanthellate, and azooxanthellate Octocorallia), sponges, seagrasses, and algae [70,71]. Hard substratum above ~60 m is typically dominated by shallow-water zooxanthellate corals such as *Montipora*, *Porites*, *Seriatopora*, and Xeniidae. However, below 60 m, the communities are increasingly dominated by azooxanthellate octocorals [39,72]. Inter-reefal habitats between 50–80 m are generally composed of either bare sand or dense fields of calcareous *Halimeda* macroalgae, with this species becoming sparse below 80 m in the central GBR [71] but present down to 100 m in the northern GBR [63], and where shelf-edge bathymetry allows nutrient upwelling to occur [73]. The shelf-edge between 90–140 m includes extensive hard reef substratum formed during lower Pleistocene sea levels that now supports dense forests of gorgonians [39,74]. Beyond 140 m, this hard reef substratum is less abundant, with a correlated decline in the abundance of octocorals and other habitat-forming species. The one exception may be the eastern side of the Myrmidon Reef, where a steep rocky slope extends to depths well below 150 m and continues to support azooxanthellate octocorals (T. Bridge pers. obs. from this study).

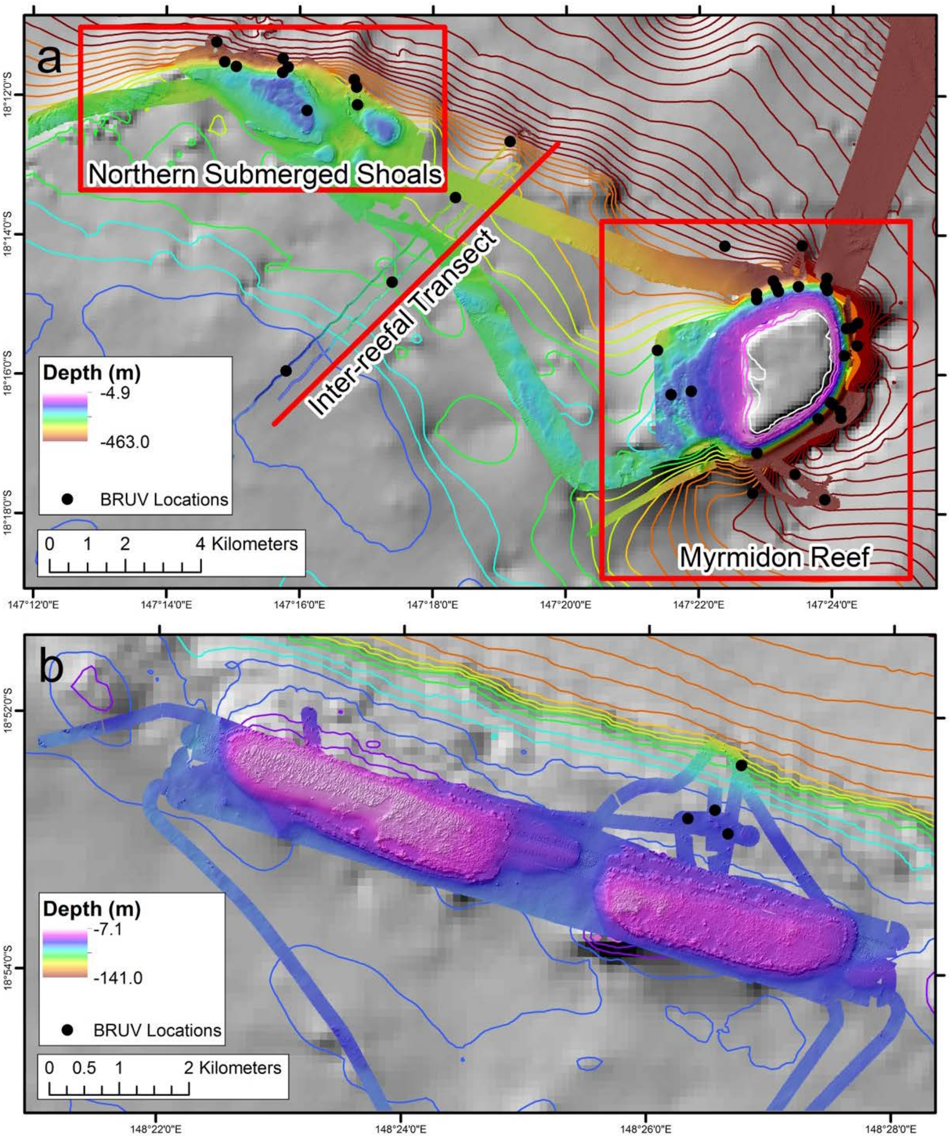


Figure 2. Regional and detailed multibeam bathymetry for (**a**) Myrmidon Reef, an inter-reefal transect, and the adjacent Northern Submerged Shoals, and (**b**) the submerged shoals adjacent to the Viper Reef. Sites of BRUVS deployments are shown as black circles and depth (- meters below the surface from shallower to deeper depths) as a color gradient (from high to low).

Within the Great Barrier Reef Marine Park (GBRMP), locations have varying levels of protection based on the activities that are permitted. Approximately 33% of the area is designated Marine National Park Zone as 'no-take', where fishing is not allowed [75]. Other zone types occur within the GBRMP. However, the locations included in this study are all under habitat protection, with Myrmidon Reef the only location in a 'no-take' zone.

2.2. Baited Remote Underwater Video Stations (BRUVS)

To sample fish assemblages and habitats in situ, 48 single BRUVS deployments were conducted over three research cruises (May, June, and September 2014), all during daylight hours (0700–1800). BRUVS were depth-stratified targeting depths of ~100 m, ~150 m, and over 200 m to investigate depth gradients. Since Viper Reef has the shallowest slope environment, some deployments were placed at depths <100 m to ensure similar width of spacing between BRUVS at the other locations. All BRUVS were set at a minimum distance of 200 m between units to minimize the effects of bait plumes and reduce the likelihood of fish being re-sampled [76]. BRUVS were deployed at sites between 54 to 260 m depth and sampling a total of three reefs and one inter-reefal transect (Figure 2).

A high-definition camera (Sony HDR-CX110E) was housed in an aluminum rollbar-frame for protection during deep deployments while also minimizing damage to benthic habitats (Figure 3). The field-of-view (FOV) of each BRUVS was illuminated by a white spotlight (550 lumen) to overcome diminished light with depth and aid in species identification. The camera focus was set to manual infinity to maximize the FOV. BRUVS were attached to a bridled rope configuration with sufficient rope (8-mm diameter polypropylene, approximately twice the water depth of the deployment because of the strong currents), ballast weights, and a float-flag assembly for retrieval. A plastic mesh bag filled with one kilogram of crushed pilchards (*Sardinops sagax*) was attached to the BRUVS via a flexible plastic conduit as an attractant. BRUVS were left to soak for 45 min, but, due to the time to reach the bottom, tapes were an average of 54 min (27 to 84 min). BRUVS units were retrieved from the surface using a hydraulic pot-hauler.

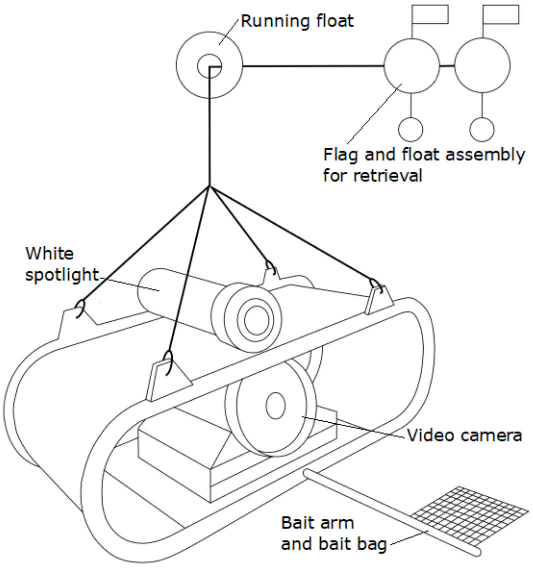


Figure 3. Illustration of Baited Remote Underwater Video Station unit for deepwater (<300 m) deployments. A high-definition video camera was in a water-tight housing and an additional white spotlight above the camera aided species identification. Bait arm of plastic mesh filled with ~1 kg of crushed pilchards extended into the camera's field-of-view. At surface-level, there was a flag-float assembly for retrieval and a running float was used to keep track of the slack line. This figure is a schematic not drawn to scale.

Videos were read to the full length, then standardized for number of fishes per hour, using purpose-built software developed by the Australian Institute of Marine Science (AIMS). Fishes were identified to the lowest possible taxonomic level with the help of multiple ichthyologists via correspondence. Time on the seabed, visibility, time of first appearance of each species, abundance *N* of each species until the time when *MaxN* was reached (i.e., the greatest number of individuals of a species per frame [51]), and time of the end of sampling (i.e., when the video left the bottom or when the video camera stopped recording) were recorded. Video stills of all fish identified were indexed for inclusion in the AIMS reference image library. *MaxN* is a conservative estimate of abundance and is used to avoid recounting individuals that exit and re-enter the FOV [77] and provides a minimum estimate of true abundance [78]. Species richness and total abundance were added for each deployment and standardized by effective sampling time to be estimates per hour filmed at the seabed. Individual BRUVS deployments were treated as independent sites and the sites sampled were divided into four locations (Myrmidon Reef, Viper Reef, Northern Submerged Shoals, and the inter-reefal transect).

We hypothesized that some components of the epibenthos and substratum would affect the fish community composition. Benthic habitat information at each site was estimated from the FOV. This included identifying major abiotic and biotic habitat characteristics based on a standardized, tripartite, benthos classification scheme developed for a project that used similar methods to describe patterns in fish and fauna of deeper shoals on the GBR continental shelf with a range of habitat, spatial, and temporal variables [79]. Substratum categories used were bedrock, boulder, calcareous reef, mud/silt, gravel (2–64 mm), rubble, sand, and 'indeterminate' (i.e., where substratum could not be determined reliably due to the angle or visibility of the FOV). Bedform categories included qualitative descriptors such as bioturbated sand, boulder field, sand dunes, sand ripples, rubble field, flat gravel/sand/silt, *Halimeda* beds, high-relief reef, and low-outcrop reef. Benthic community categories included coral, gorgonian, and sea-whip garden, low-relief rubble field, macroalgae bed, open sandy seabed, and seagrass bed. In addition, the following benthic community components were also qualitatively summarized in the same way: anemones, bryozoans/encrusting animals, coralline algae, gorgonian fans, forams, *Halimeda*, hard coral, hydroids, macroalgae, seagrass, soft coral, sponges, sea whips, zoanthids, and 'none.' Each component was given a percentage score 0–100 in increments of 10. Rarer categories of substratum or epibenthos were pooled with related categories for fewer covariates (Table 1).

2.3. Multibeam Sonar Acquisition

Reef architecture can affect the distribution of fishes. For this reason, we obtained a broader suite of information on the underlying habitat structure of shelf-break environments, with multibeam bathymetry and backscatter information describing a number of neighborhood characteristics. High-frequency multibeam sonar produces accurate, high-resolution digital bathymetric models [80]. While this technology is in wide use, it has only recently been applied to study shelf-break reefs and fish communities on the GBR [81,82]. Multibeam information has the potential to characterize fine-scale spatial relationships between deeper habitats and fish [83]. Multibeam echo sounders collect bathymetry and backscatter information over a wide swath of the seafloor [80,84], with the relative acoustic backscatter, i.e., the 'acoustic reflectivity of the seabed,' which provides a useful proxy for seabed substratum [84]. Multibeam sonar surveys using a Reson 8101 were conducted in 2014 onboard James Cook University's *RV James Kirby* (24, 25 May) and Australian Institute of Marine Science's *RV Cape Ferguson* (03–09 Sept). Multibeam mapping in water depths of 10–250 m was conducted at a speed of 5–6 knots. The Reson 8101 emits 101 acoustic beams of $1.5^\circ \times 1.5^\circ$, covering an angular sector of up to 150° for a total swath approximately seven times the water depth. A Kongsberg Seatex motion reference unit corrected for pitch, roll, and heave. A Fugro OmniSTAR 9200-XP differential GPS recorded positioning, with a quoted accuracy of 1.0 m RMS in the X and Y plane. Data from all peripheral sensors were recorded using QPS QINSy acquisition software. A Sontek CastAway CTD system corrected the acoustic profile. Predicted tides generated from XTide software [85] corrected the bathymetric data by tidal datum over the survey period. Raw multibeam data files were converted to Extended Triton Format (XTF) and imported to Caris HIPS/SIPS post-processing software. All multibeam data post-processing included noise editing, tide, and sound velocity corrections. Bathymetry data were visually inspected and spurious soundings removed to create a level and clean dataset relative to the mean sea level. The error of estimation for vertical soundings reported is estimated to be a maximum of ±0.2 m. The final digital models were produced using Caris HIPS/SIPS software with a 5-m cell size.

2.4. Secondary Datasets from Multibeam

Multibeam sonar datasets measures both the seabed structure through bathymetry and seabed composition with acoustic backscatter [80]. To improve the predictive power of the multibeam sonar datasets, a variety of secondary datasets, potentially correlating with seafloor properties, were produced from the raw bathymetry and backscatter data using neighborhood-based statistics and terrain analysis techniques [84,86]. Neighborhood operations produce an output raster dataset in which each cell location is a function of the input value at a cell location and the values of the cells in a specified kernel (i.e., neighborhood) around that location. The configuration (size and shape) of the kernel determines which cells surrounding the input cell are included in the output value. The most typical kernel size is 3 × 3 cells (i.e., a radius of 1 grid cell), which incorporates the processing cell and its closest eight neighbors.

Multi-scale terrain analysis is predicted to be the most efficient method for characterizing features at multiple spatial scales [86–88] and, for this study, we wanted to compare differences between sites on local and broad scales. Derivative datasets that accounted for both high-frequency and low-frequency variations in the multibeam data, and variations in the kernel (neighborhood size), were included in the analyses. All derivatives of the bathymetry and backscatter were chosen because they have a potential influence on the fish community ecology (Table 1) and are commonly used within the marine habitat and seabed characterization (see Reference [89] for a review and Figure S1 for demonstrative examples of backscatter and bathymetry derivatives used in this study). Progressively lower frequency neighborhood analyses were applied to the multibeam bathymetry and backscatter to investigate multiple spatial scales in two ways. Some neighborhood functions (Easting, Northing, Slope, Topographic Position Index, Topographic Ruggedness Index, Surface Ratio, Total Curvature, Planar Curvature, and Profile Curvature) are used to quantify the 'shape' of the kernel. As a result, they are calculated from the surrounding eight pixels (a 3 × 3 kernel) and were applied to the bathymetry raster only. Therefore, to achieve progressively 'lower frequency' derivatives of these metrics, the bathymetry rasters were low-pass filtered (5 times) using an 11 × 11 kernel-averaging filter. Each time the averaging low-pass filter was applied, the nine neighborhood functions were then calculated to create derivative raster datasets at that resolution (designated '**' in Table 1). Neighborhood functions that could be applied to larger kernel sizes were applied to both the bathymetry and backscatter grids using kernels with radius values of 5 and 50 pixels (Range, Standard Deviation of Bathymetry, Average Backscatter and Standard Deviation of Backscatter, and these multiple spatial scales were designated with '***' in Table 1). Backscatter information can be interpreted as qualities of the substratum (i.e., 'hard' or 'soft'). Raster calculations were undertaken using the R software [90] and the Raster package [91]. Additional subroutines were written for Curvature measurement based on Zevenbergen and Thorne [92]. For site comparisons within depth strata, multibeam information from the 5 × 5 kernel was used, and, for comparisons among depth strata, multibeam derivatives from the 50 × 50 kernel were used.

Table 1. Explanatory covariates from multibeam echo sounding technology and estimates from the Baited Remote Underwater Video Station field-of-view (FOV). Some epibenthic and substratum categories were pooled for combined groups of benthos. Primary and secondary (derived) features from bathymetry and backscatter raster datasets: * Raw raster data. ** Applied as a 3 × 3 kernel on bathymetry after it was averaged using kernels with a radius of 5 and 50 pixels. *** Applied kernels with a radius of 5 and 50 pixels. References where these multibeam derivatives are described are in bold. Example references where these factors have been highly influential on fish or benthic assemblages are noted in italics.

Covariate Name (Abbreviation)	Covariate Type	Definition	Reference
Bedrock	% composition of seafloor by substratum categories	FOV estimated % Bedrock	
Boulder	% composition of seafloor by substratum categories	FOV estimated % Boulder	*Moore et al., 2009* [93]
Calcified reef	% composition of seafloor by substratum categories	FOV estimated % Calcareous reef	*Moore et al., 2009*
Gravel	% composition of seafloor by substratum categories	FOV estimated % Gravel (2–64mm)	*Haywood et al., 2008* [94] *Holmes et al., 2008* [95] *Malcolm et al., 2016* [96]
Indeterminate	% composition of seafloor by substratum categories	FOV estimated % Indeterminate	
Mud	% composition of seafloor by substratum categories	FOV estimated % Mud/silt	*Haywood et al., 2008*
Rubble	% composition of seafloor by substratum categories	FOV estimated % Rubble	
Sand	% composition of seafloor by substratum categories	FOV estimated % Sand	*Malcolm et al., 2016* *Kane & Tissot 2017* [36]
Filtering organisms	% composition of seafloor by epibenthic categories	% combined Fans, Hydroids, Sponges, Whips	*Holmes et al., 2008*
Encrusting organisms	% composition of seafloor by epibenthic categories	FOV estimated % combined Bryozoans/encrusting animals, coralline algae	
Coral	% composition of seafloor by epibenthic categories	FOV estimated % combined Hard coral and Soft coral	*Garcia-Sais 2010* [2] *Kane & Tissot 2017*
Bare	% composition of seafloor by epibenthic categories	FOV estimated % no epibenthic cover	
Plants	% composition of seafloor by epibenthic categories	FOV estimated % combined Macro-algae and Seagrass	*Holmes et al., 2008*
Halimeda	% composition of seafloor by epibenthic categories	FOV estimated % *Halimeda*	

Name	Source	Description	Possible Ecological Context	Reference
Depth * (m)	Vessel depth sounder	Depth below sea-level	Location relative to Photic Zone Potential impact by waves and storms Location relative to thermoclines/haloclines	*Costa et al., 2014* [97] *Oyafuso et al., 2017* [98] *Kane & Tissot 2017* *Moore et al., 2009* *Moore et al., 2011* [99]
Latitude	Handheld GPS unit	Position of the deployment	Location relative to latitudinal gradients	*Cappo et al., 2007*
Longitude	Handheld GPS unit	Position of the deployment	Location relative to longitudinal gradients	*Cappo et al., 2007*
Easting **	Bathymetry derivative	Easterly component of the kernel azimuth	Level of exposure or protection from oceanographic processes	**Hirzel et al., 2002** [100]

Table 1. *Cont.*

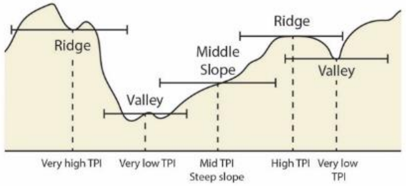
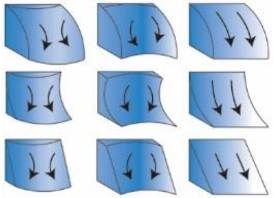
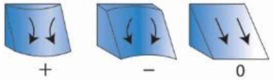
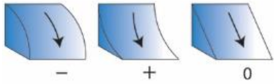
Name	Source	Description	Possible Ecological Context	Reference
Northing **	Bathymetry derivative	Northerly component of the kernel azimuth	Level of exposure or protection from oceanographic processes	**Hirzel et al., 2002**
Slope ** (Degree)	Bathymetry derivative	Change in elevation as a function of distance within the kernel	Indicate activity of gravity driven processes Indication of hard substratum	**Dartnell and Gardner 2004** [101] *Misa et al., 2013* [102] *Moore et al., 2009*
Topographic Position Index ** (TPI)	Bathymetry derivative	Difference between center kernel value and the average of all kernel values. Example of TPI interpretation as defined in Weiss 2001 (SD is standard deviation of bathymetry): Ridge: $z_0 > SD$ Upper slope: $SD \geq z_0 > 0.5\ SD$ Middle slope: $0.5\ SD \geq z_0 \geq -0.5\ SD$, slope > 5° Flat area: $0.5\ SD \geq z_0 \geq -0.5\ SD$, slope $\leq 5°$ Lower slope: $-0.5\ SD > z_0 > -SD$ Valley: $z_0 < -SD$	Relative topographic position in the neighborhood: Positive TPI values are higher than their surroundings (i.e., ridges) and negative TPI values are lower than their surroundings (i.e., valleys). TPI values near zero are flat areas.  (re-drawn from [103])	**Weiss 2001** [104] *Iampietro et al., 2005* [105] *Moore et al., 2009*
Terrain Ruggedness Index **	Bathymetry derivative	Average of the absolute difference between the center kernel values and each of the other kernel values	Index of surface roughness indicating degree of structural complexity	**Riley et al., 1999** [106]
Range***	Bathymetry derivative	Difference between the maximum and minimum values within the kernel	Index of surface roughness indicating degree of structural complexity	**Dartnell 2000** [107] *Yates et al., 2016* [108] *Moore et al., 2009* *Holmes et al., 2008*
Surface Ratio **	Bathymetry derivative	Ratio of the kernel surface area and planimetric area	Relative vertical relief indicating degree of structural complexity	**Jenness 2004** [109] *Moore et al., 2011*
Standard Deviation *** (m)	Bathymetry derivative	Standard deviation of values within the kernel	Index of surface roughness	**Costa et al., 2014**
Curvature ** (Degrees/m)	Bathymetry derivative	Index of concavity/convexity measured within the kernel	Measure of overall curvature within kernel (planform left to right + −, 0; profile top to bottom, −, +, 0)  (re-drawn from “Curvature type” ArcGIS help files)	**Zevenbergen and Thorne 1987** [92]

Table 1. *Cont.*

Name	Source	Description	Possible Ecological Context	Reference
Planar Curvature ** (Degrees/m)	Bathymetry derivative	Index of concavity/convexity measured perpendicular to slope within the kernel	Identifies ridges, valleys, and flat slopes  (re-drawn from "Curvature type" ArcGIS help files)	**Zevenbergen and Thorne 1987**
Profile Curvature ** (Degrees/m)	Bathymetry derivative	Index of concavity/convexity measured parallel to the slope within the kernel	Concave or convex slopes  (re-drawn from "Curvature type" ArcGIS help files)	**Zevenbergen and Thorne 1987** *Moore et al., 2009*
Acoustic Backscatter * (Decibels)	Backscatter derivative	Acoustic backscatter	Proxy for seabed substratum	**Hughes-Clarke et al., 1996** [80]
Ave Backscatter *** (Decibels)	Backscatter derivative	Average backscatter within the kernel	Proxy for seabed substratum	**Brown et al., 2011** [84]
StdDev Backscatter *** (Decibels)	Backscatter derivative	Standard deviation of values within the kernel	Variation in substratum within the kernel	**Brown et al., 2011**

2.5. Data Analysis

2.5.1. Habitats and Fish Communities Separated by Depth

Depth had a great influence on fish community patterns. However, since numerous ecological factors vary with depth, this can obscure the underlying drivers of fish distributions, including the influence of fish-habitat interactions [62]. Therefore, we investigated habitat differences within and among depth strata. For epibenthic and substratum percent cover comparisons, we divided the sites based on depth categories with n = 16 sites for balance ('Shallow' 54–107 m, 'Middle' 110–156 m, and 'Deep' 160–260 m). We then analyzed patterns of fish and environmental covariates using non-metric multi-dimensional scaling (nMDS) and fitting environmental correlates on the ordination package 'vegan' [110] in R. Fish abundance data was divided into 'Shallow' (54–115m, n = 18 sites), 'Middle' (128–160m, n = 14 sites), and 'Deep' (179–260m, n = 12 sites with no missing values) sites and fish species only occurring at one site were removed from the dataset, which left 72 species. Sites (i.e., BRUVS deployments) were eliminated from the analyses if there were missing habitat values (some multibeam values were 'missing' if the kernels extended beyond the region where multibeam information was collected, which was more frequent at the deepest sites). One site was removed because it did not contain any of the remaining 72 species. Separating sites into three nMDS investigated the differences in habitats with the maximum separation between depth categories.

Ordination by nMDS separated the sites based on community dissimilarities in relative abundances and composition. Separate nMDS identified what species and habitat variables contributed to similarities among locations (function metaMDS, $k = 2$). Non-metric MDS is a flexible and robust ordination method for visualizing patterns that preserve the ranks of dissimilarities in species abundance data. Relative abundances were transformed with a fourth-root to reduce the influence of highly abundant fishes and then scaled using a Wisconsin double-standardization with the Hellinger method where species are standardized by the maxima and sites by the site total. Hellinger accounts for relative rarity and the 'horseshoe effect' where sites are considered more alike by what species are absent from those sites. Species abundance data were then incorporated into a Bray-Curtis resemblance matrix.

To see what environmental covariates were meaningful for distinguishing sites, correlating covariates were fitted as vectors overlaying the plotted sites if they were above the $p < 0.05$ significance level (function envfit, Pearson correlations with 999 permutations). This function estimated the strength of the correlation as well as the direction of the correlation among sites. Multibeam information and FOV information were first evaluated for variables that were highly correlated (>0.8) and those variables were removed. The absolute values of multibeam data from the 5×5 kernel were log(x+1)-transformed. FOV epibenthic/substratum measurements were arcsine-transformed. Environmental variables were scaled and converted into a Euclidean distance-based matrix.

We also investigated community differences among deep reefs using similarity percentages (SIMPER, PRIMER v7, PRIMER-e, Auckland, New Zealand), which estimated the contributions of fish species to the differences in community composition variability between locations within depth strata. SIMPER analysis used presence/absence-transformed community fish data, using a Bray-Curtis resemblance matrix with 70% as the cut-off level for low contributions.

2.5.2. Species-Species Associations

The occurrence and abundance of fishes may be explained by co-existence or competition with other species in the community. Therefore, we investigated between-species correlations. We plotted significant Pearson correlations ($p < 0.05$) for all the possible pairs of the 28 most frequently-occurring species using the packages 'corrplot' [111] and 'Hmisc' (function rcorr, [112]). This subset of 28 species included the relative abundance of fish observed at five or more of the total 48 sites. Significant negative correlations could indicate potentially competing species and significant positive correlations could indicate species co-existing in a similar ecological system.

2.5.3. Trophic Communities

We hypothesized that fishes would have different levels of habitat association and that these levels were likely due to differences in the ecological niche (i.e., what they eat). The degree of habitat specialization between fishes can even be different between closely related species [113,114]. An analysis was conducted to determine differences in the trophic community composition (diversity of feeding groups) between deep-reef habitats. Each species was designated a trophic group based on diet or trophic ecology information, according to Fishbase (herbivore, piscivore, planktivore, general carnivore, benthic carnivore, or unknown [115]). The number of total species per trophic group (presence/absence) per site was summed as a measure of relative trophic richness. Some species' diets could be inferred to the most likely category based on closely-related species (e.g., *Gymnothorax* species tend to be carnivores), but, where there were different trophic niches within a family, these species were left as unknown.

Sites were plotted along the two primary axes (PC1 and PC2) accounting for most of the variation in trophic richness using a Principal Component Analysis (PCA) on Wisconsin-standardized trophic group richness. Wisconsin double-standardization first transformed data by 'species' maxima and then by 'site' totals for a more uniform comparison and common scale among sites with very different numbers of members, reducing the contribution of abundant taxa [116] and improving the gradient detection capability when comparing dissimilarities [117]. Sites were grouped according to the depth category (n = 16, 'Shallow' 54–107 m, 'Middle' 110–156 m, and 'Deep' 160–260 m) and individual habitat measures were correlated to the variance explained in PC1 and PC2. We presumed broad trophic differences would be operating on larger spatial scales, so the multibeam measurements used were from the 50 × 50 kernel (i.e., largest sampling window). This approach compared each single predictor to the combined community response of the principal component. This comparison reduced dimensionality, which increased the ability to identify how much communities respond directly to gradients in the environmental factors [118]. This method determined which habitat variables are most important in explaining the variation among sites.

Animal ethics approval was granted by James Cook University (A1808 and A2207).

3. Results

3.1. Description of Deep-Reef Benthic Shelf-Break Habitats

Epibenthic cover and substratum type varied with depth (54–260 m deep, Figures 4 and 5). The mean abundance cover of macro-algae decreased from 27% at the shallowest sites (54–107 m), to 13% at middle sites (110–156 m), to 5% at the deepest sites (160–260 m, Figure 5). *Halimeda* (kept as a separate category for analyses) was also most prominent in shallower sites (10% mean abundance cover) and was found to a maximum depth of 150 m. Soft corals were seen down to 155 m. Sponges had the greatest representation in the Middle sites (4%–16% average cover). The encrusting community (coralline algae and bryozoans) was most abundant at Shallow sites (~22% mean abundance cover) and decreased with increasing depth. Overall, the average percent cover of the total epibenthic community decreased from Shallow (72%), Middle (43%) to Deep sites (11%), with deeper sites having noticeably more 'bare' coverage (89%). Structural complexity also decreased with greater depth, largely due to the declining abundance of calcified reef (mean 45%, 54–107 m, 8%, 160–260 m). However, other hard substratum categories, such as bedrock and boulder, had limited but relatively consistent average abundance cover (1%–4%). Rubble and sand became more common with increasing depth, while mud only appeared in the middle and deeper sites.

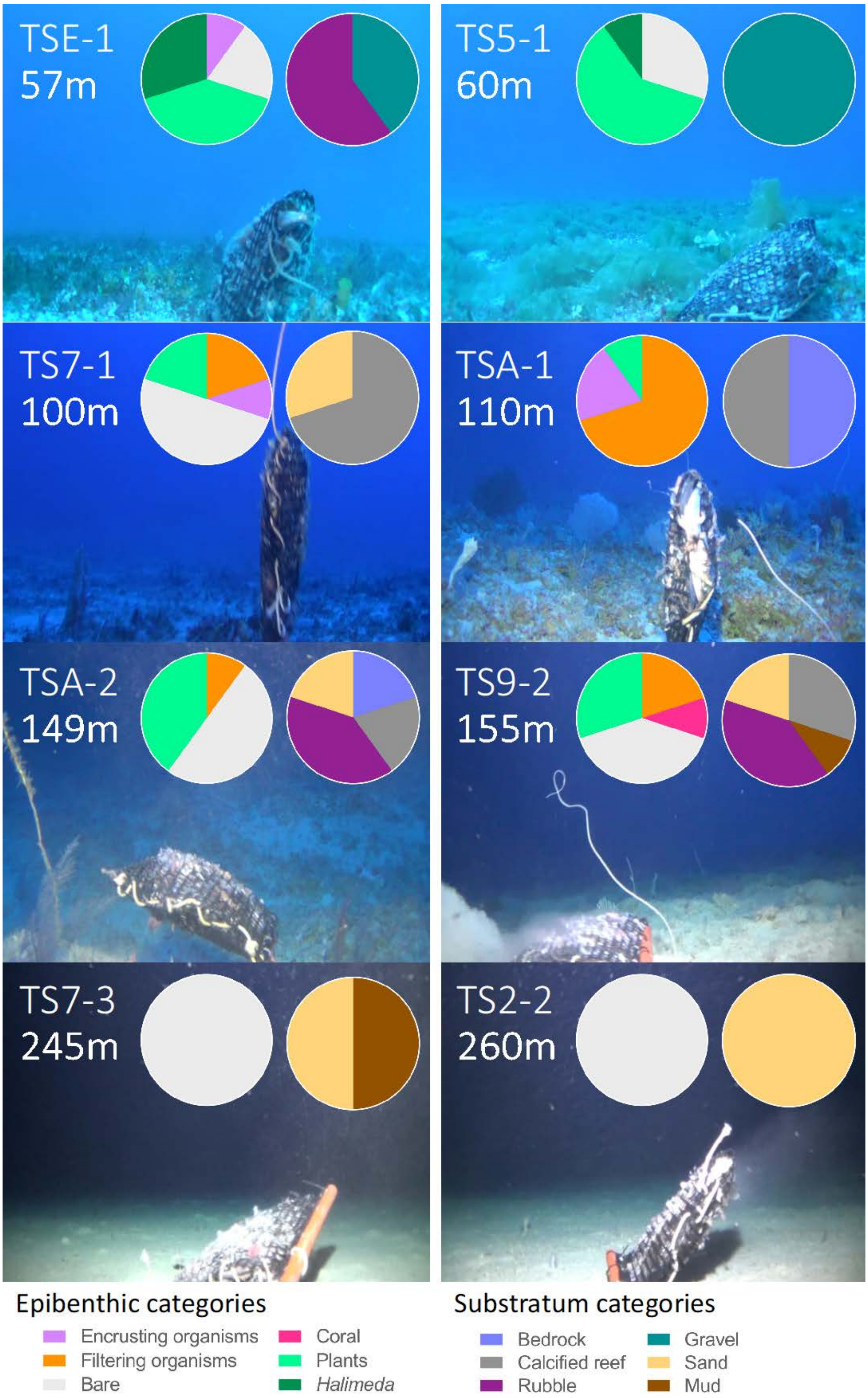


Figure 4. Examples of deep-reef habitats from the field-of-view of Baited Remote Underwater Video Stations (BRUVS). The bait arm extension is visible in the video frame. A unique BRUVS operation code (TS_ removed observer bias) and depth are noted for each site with the relative proportion of epibenthic (left pie chart) and substratum categories (right pie chart).

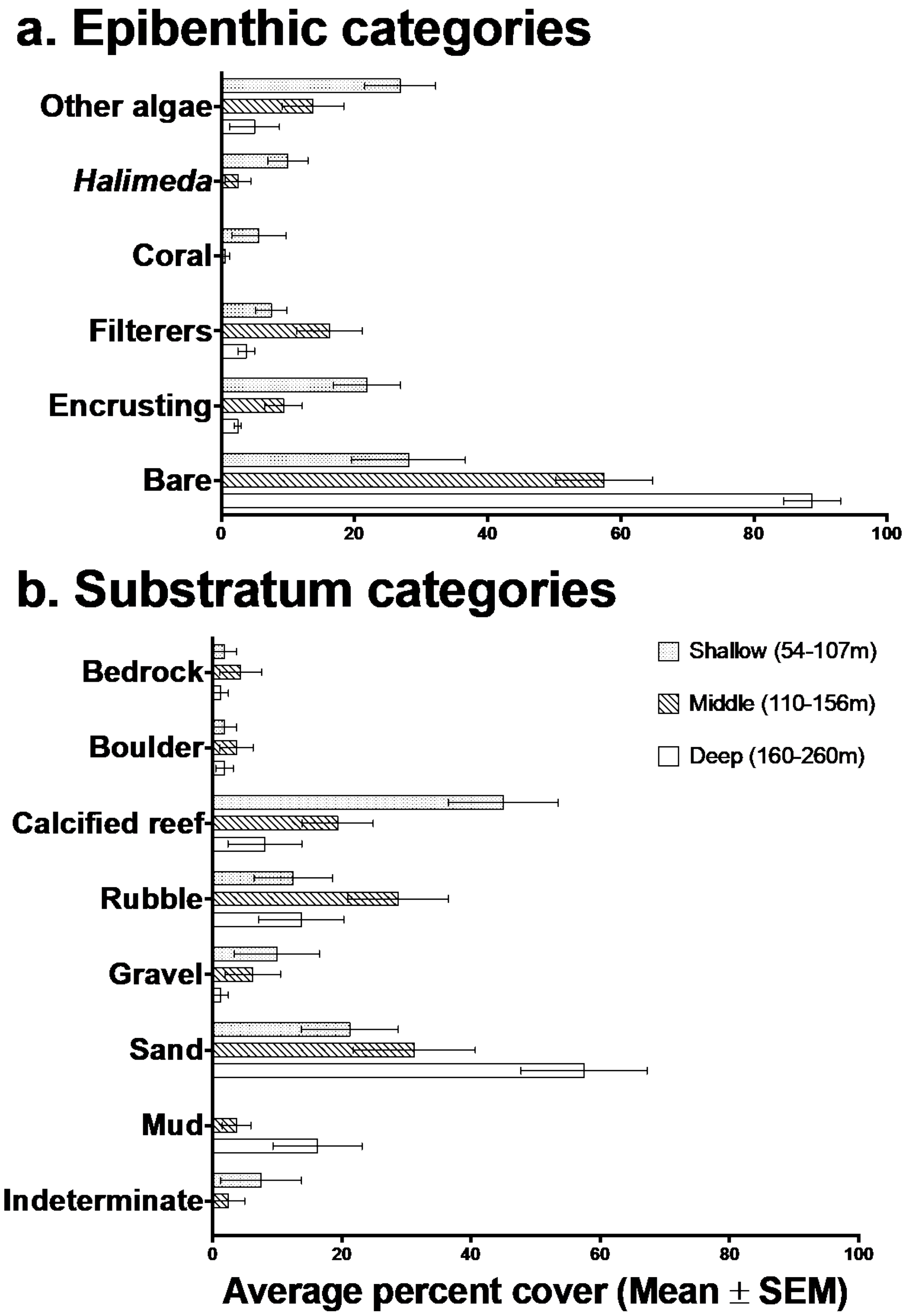


Figure 5. Deep-reef habitats varied by depth, measured by epibenthic and substratum cover in the field-of-view of the camera. Sites were divided into three depth strata: Shallow (54–107 m), Middle (110–156 m), and Deep (160–260 m) represented by three sequentially stacked bars (each n = 16 sites) with error bars for the standard error of the mean percent cover.

There was some notable habitat variation among locations surveyed and also at the level of sites within locations (Figure 4). Overall, epibenthic composition was more similar between Myrmidon Reef and Northern Submerged Shoals than the Viper Reef (Figure S2). While coral was observed at shallow Viper Reef sites, it was absent from other locations (Viper included some shallower sampling depths). In addition, while the abundance of sponges was consistent between the Myrmidon Reef and Northern Submerged Shoals, they were absent from Viper Reef. Macro-algae was abundant at deeper sites of the Northern Submerged Shoals, occurring at three of the four sampling sites and down to 194 m. There were no major differences in substratum by location (Figure S3), but what was visible in the FOV were coarse qualifications of substratum. The number of replicate sites per reef and depth varied (e.g., for inter-reefal sites, there was only one site per depth category), and, therefore, due to low replication at some locations, these results were not analyzed by parametric tests by location.

3.2. Investigating Habitats and Fish Communities within Depth Strata

There was great variation in species composition both among locations and sites nested within locations. The differences among locations were greatest at shallow depths, but there was still an overlap between sites among locations (Figure 6). Of the environmental variables responsible for differences among sites, only a few were significant by depth strata. Slope and the presence of filter-feeding organisms among shallow sites were significant ($p < 0.05$), while Middle sites had the significant separation based on longitude, latitude, and the proportion of sand. The presence of boulder substratum differentiated among sites at Deep sites.

Variation within depth strata show some overall patterns between fish communities by location (Figures S4–S6). Many species are shared among multiple locations, such as *Lethrinus rubrioperculatus*, *Aprion virescens*, *Gymnocranius euanus*, and *Carcharhinus albimarginatus*, indicated by the close clustering of species towards the middle of the ordination (Figure S4). Among Middle sites, the species composition at Northern Submerged Shoals overlapped with Myrmidon sites, and Viper varied the most in species composition (Figure S5). For the within-location similarity between sites, SIMPER analysis showed the species that contributed to each location's community were varied and there were also high levels of unexplained variation within depth strata among locations (Table 2). The species showing greater similarities within a location were often representatives of the Lutjanidae, Lethrinidae, Carcharhinidae, and Carangidae families. At Shallow sites, locations sampled were dissimilar in species assemblages because of high species diversity, with the greatest dissimilarities between the inter-reefal transect and the other reefs sampled. Among sites at Middle depths, Myrmidon and Northern Submerged Shoals were the most similar.

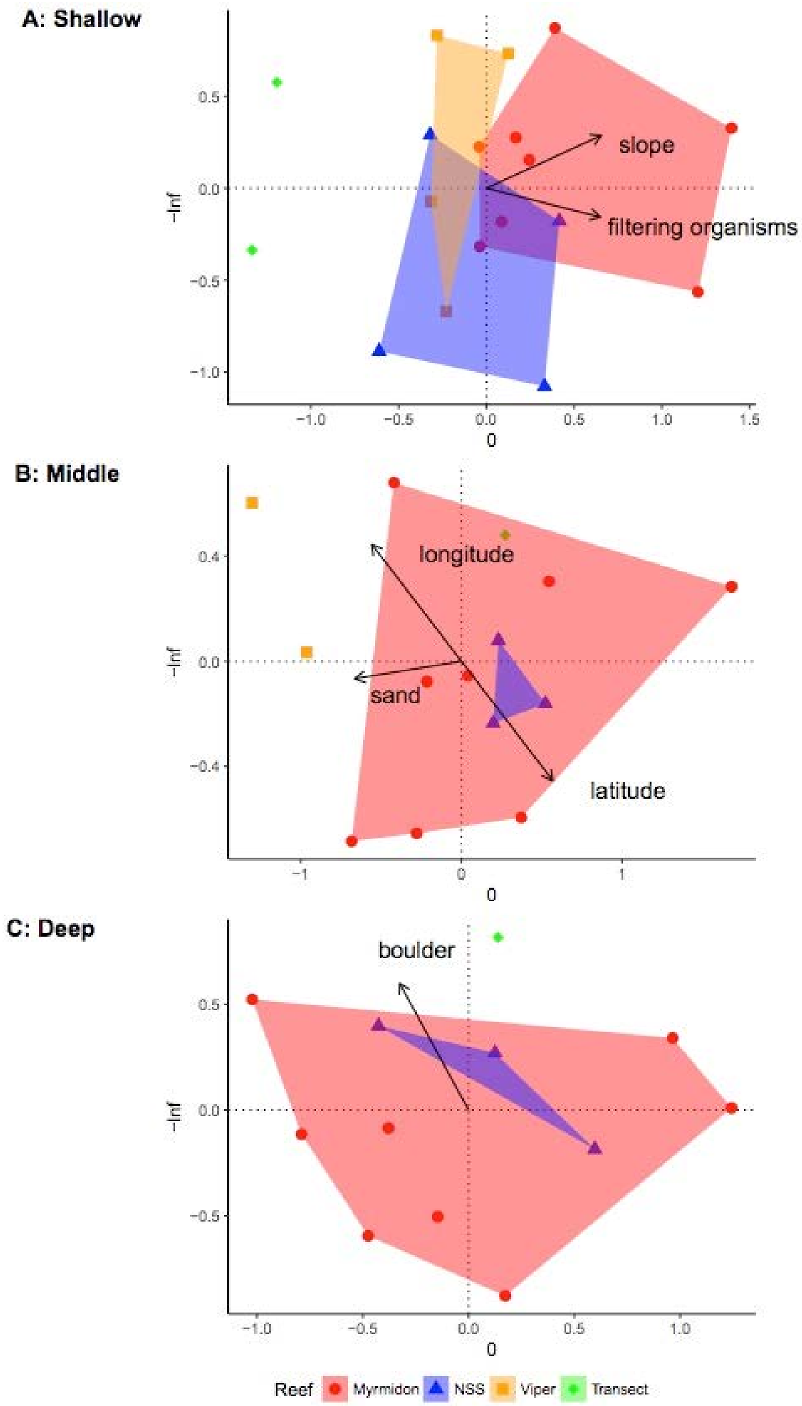


Figure 6. Nonmetric Multidimensional Scaling (nMDS) showed patterns between fish community composition and environmental variables, including epibenthic and substratum measured in the underwater camera field-of-view and multibeam echo sounder measured variables. Sites were separated into Shallow (54–115 m, nMDS non-metric fit, $R^2 = 0.967$, linear fit, $R^2 = 0.827$, stress = 0.21, top), Middle (128–160 m, nMDS non-metric fit, $R^2 = 0981$, linear fit, $R^2 = 0.913$, stress = 0.15, middle), and Deep (179–260 m, nMDS non-metric fit, $R^2 = 0.989$, linear fit, $R^2 = 0.924$, stress = 0.15, bottom) based on depth. Ordination from Bray-Curtis dissimilarities in species abundance data, transformed using fourth-root transformation, and standardized using Wisconsin-double standardization. Colored hulls show the affiliation of each site to a location. Environmental variables that were significant within these depth strata are depicted as vectors on the nMDS ordination ($p < 0.05$, 999 permutations).

Table 2. Similarity percentages (SIMPER) analysis on deep-reef fish community data described the relative contributions of specific species to the dissimilarities between sites (among locations) with percent contribution of individual species to those differences. Species abundances were presence/absence-transformed, and Bray-Curtis similarity measures were used. Species contributing to ~70% combined are listed.

Location		**Myrmidon Reef**	**Northern Submerged Shoals**	**Viper Reef**	**Inter-Reefal Transect**
Depth strata	Shallow (54–115 m)	*n* sites = 8 Average similarity: 28.0% Individual species contributions: *Carangoides caeruleopinnatus*, (15.3%) *Lutjanus bohar* (13.6%) *Carcharhinus amblyrhynchos* (9.9%) *Aphareus rutilans* (8.9%) *Gymnocranius euanus* (8.9%) *Cirrhilabrus roseafascia* (6.0%) *Pristipomoides filamentosus* (5.3%) *Lethrinus miniatus* (5.0%).	*n* sites = 4 Average similarity: 15.9% Individual species contributions: *Carangoides caeruleopinnatus* (21.7%) *Gymnocranius grandoculis* (13.1%) *Carcharhinus albimarginatus* (10.0%) *Lethrinus rubrioperculatus* (9.1%) *Carcharhinus amblyrhynchos* (7.2%) *Pomacanthus imperator* (7.2%) *Plectropomus leopardus* (7.2%)	*n* sites = 4 Average similarity: 25.6% Individual species contributions: *Carangoides dinema* (23.6%) *Echeneis naucrates* (11.4%) *Lethrinus olivaceus* (9.5%) *Aphareus rutilans* (4.7%) *Carcharhinus albimarginatus* (4.7%) *Carangoides fulvoguttatus* (4.7%) *Lutjanus bohar* (4.7%) *Parapercis* sp. (4.7%) *Epinephelus cyanopodus* (4.7%)	*n* sites = 2 Individual species contributions: All similarities are zero
	Middle (128–160 m)	*n* sites = 8 Average similarity: 29.5% Individual species contributions: *Aphareus rutilans* (31.2%) *Pristipomoides typus* (14.3%) *Pristipomoides filamentosus* (13.1%) *Parapercis nebulosa* (10.3%) *Pristipomoides multidens* (9.4%)	*n* sites = 3 Average similarity: 58.3% Individual species contributions: *Bodianus* sp. (10.4%) *Wattsia mossambica* (10.4%) *Aphareus rutilans* (10.4%) *Pristipomoides filamentosus* (10.4%) *Pristipomoides multidens* (10.4%) *Pristipomoides typus* (10.4%) *Gymnosarda unicolor* (10.4%)	*n* sites = 2 Average similarity: 28.57 Individual species contributions: *Carcharhinus albimarginatus* (100%)	*n* sites = 1
	Deep (179–260 m)	*n* sites = 8 Average similarity: 17.0% Individual species contributions: *Pristipomoides argyrogrammicus* (39.0%) *Pristipomoides multidens* (31.2%)	*n* sites = 3 Average similarity: 31.7% Individual species contributions: *Gymnosarda unicolor* (48.9%) *Seriola dumerili* (13.2%) *Pristipomoides argyrogrammicus* (13.2%)	*n* sites = 0	*n* sites = 1

3.3. Relationships among Fish Species

The distribution of fishes among habitats may be both positively and negatively influenced by inter-species interactions. Of the 28 species present at five or more sites, many correlated species were identified (Figures 7 and 8, correlation values with a significance of $p < 0.05$). *L. bohar* abundance was highly correlated with the abundance of *L. ravus* (0.71) and *L. olivaceus* (0.67), and moderately correlated to *Parapercis* sp. (0.50, Family Pinguipedidae). Deeper reefs often had mixed groups of lethrinid species: *L. olivaceus* was often found with *L. ravus* (0.59) and *L. miniatus* (0.57); *L. miniatus* was associated with *L. rubrioperculatus* (0.68), *G. euanus* was often frequented seen with species *L. rubrioperculatus* (0.55) and *L. miniatus* (0.60). Lethrinid and other family co-occurrences were common: *L. rubrioperculatus* and *C. caeruleopinnatus* (0.77), *G. euanus* with *C. caeruleopinnatus* (0.58) or the grey reef shark, *C. amblyrhynchos* (0.62), which also was frequently seen with *L. rubrioperculatus* (0.54) and *L. miniatus* (0.57). The silvertip shark, *C. albimarginatus*, was often seen with an attached sharksucker, *E. naucrates* (0.57). The deep-reef serranid *Epinephelus morrhua* and *P. typus* were frequently observed at the same sites (0.67). *W. mossambica* was weakly correlated in abundance to deepwater lutjanids *P. typus* (0.51), and *P. filamentosus* (0.57), as well as *E. morrhua* (0.67), and *G. unicolor* (0.54, Scombridae). Deep reefs commonly featured *Parapercis* species. *P. nebulosa* and the labrid, *Terelabrus rubrovittatus*, were often seen on the same videos and *Parapercis* sp. abundance was weakly correlated with *L. ravus* abundance (0.51). *T. rubrovittatus* was also frequently seen with an unknown *Selenanthias* sp. (a potential new species for the GBR, 0.59).

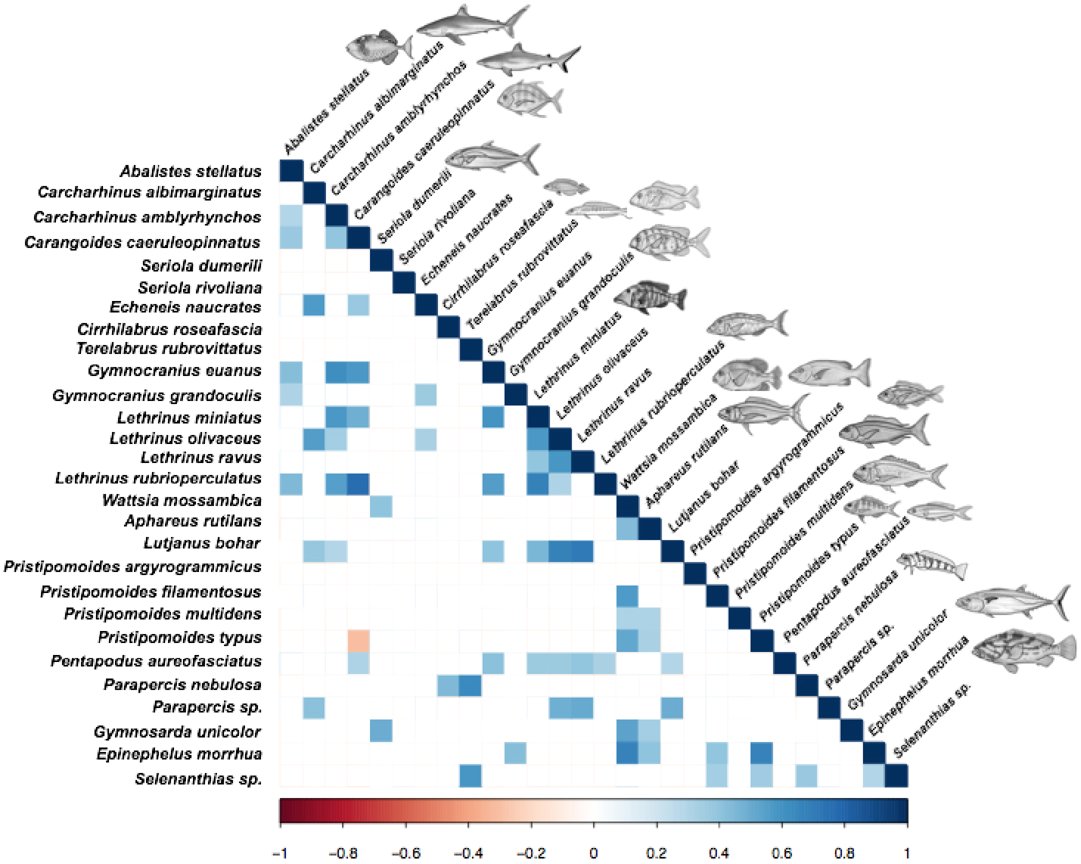


Figure 7. Species correlations of most frequently occurring 28 fish species from Baited Remote Underwater Video Station deployments on shelf-break reefs. Positive Pearson correlation values are depicted in blue and negative correlations in red (only significant correlations where $p < 0.05$ are depicted).

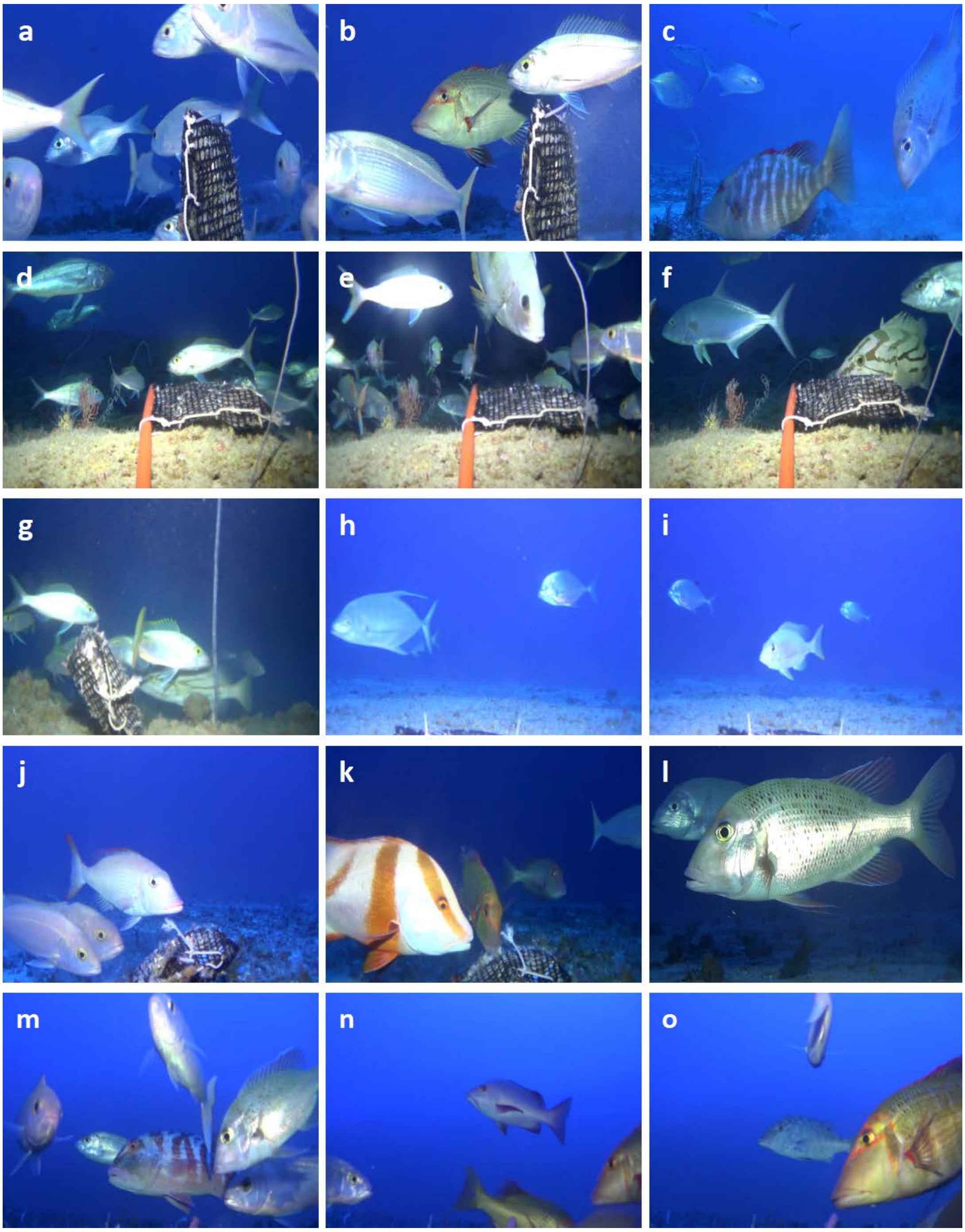


Figure 8. Examples of fish co-occurrences on deep reefs of the Great Barrier Reef shelf-break: (**a**,**b**) West Myrmidon 128 m, (**c**) North Myrmidon 100 m, (**d**–**f**) Northern Submerged Shoals (NSS) 155 m, (**g**) NSS 160 m, (**h**,**i**) West Myrmidon 129 m, (**j**,**k**) North Myrmidon 103 m, (**l**) North Myrmidon 107 m, and (**m**–**o**) North Myrmidon 105 m.

3.4. Deep-Reef Fish Trophic Communities

The reef fishes detected in this study were ecologically diverse. Of the 98 fishes identified to species-level, piscivores (10 species), planktivores (7 species), benthic-associated carnivores (26 species), generalist carnivores (41 species), and four species of combined diets (e.g., planktivorous and piscivorous fishes) were represented, based on the membership of known trophic guilds (Table S1 includes species-specific CAAB code [119]). Twenty species recorded had no published trophic information (according to the Fishbase). However, half of these were assigned to a trophic group based on other family members occupying that same trophic group. Only one species was herbivorous (*Acanthurus xanthopterus*), which is likely due to the decreased availability of edible algae with depth, or the amount of feeding activity around the BRUVS. PC1 and PC2 accounted for a combined 52.5% of the variation among sites, with the presence of general carnivores against the other trophic guilds accounting for the greatest separation and approximately 30% of the total variation (Figure 9). Shallower sites tended to have a greater variety of feeding modes and less overlap with the other depth categories. However, overall, there was a great degree of trophic overlap, especially between the middle and deeper sites (110–260 m).

Several environmental variables were found to have an influence on trophic diversity across PC1 and PC2 (Table S2). Depth, aspect (orientation), planar curvature, and surface ratio dimensions contribute toward the differences in communities along PC1. Fish communities were affected by the local topography and habitat position, presumably because some habitats will be cliff-like features facing the prevailing currents. Proportional measures of bare, plants, bedrock, calcified reef, and presence of sand also correlated with differences along PC1. Slope and standard deviation of the bathymetry were found to explain the variation in PC2.

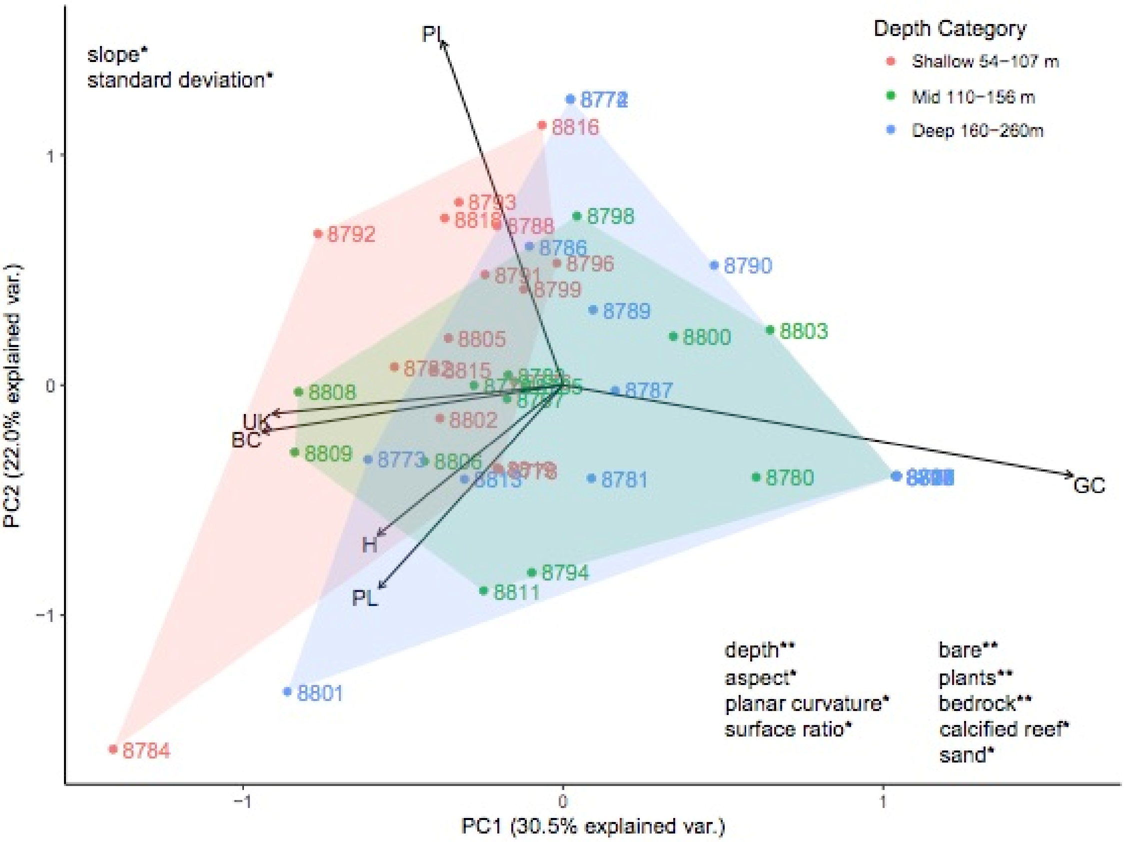


Figure 9. Principal Component Analysis show trophic community differences of fishes between sites sampled on shelf-break reefs. The first two principal components explain 52.5% of the variation in trophic diversity between sites. Sites are grouped by depth category and each has a unique number. Vectors depicting the principal feeding strategies (H = herbivores, PI = piscivores, PL = planktivores, BC = benthic carnivores, GC = general carnivores, UK = unknown) show some of the key differences between sites. Environmental variables found to significantly contribute to the community differences along PC1 and PC2 are summarized next to the corresponding axis (** $p < 0.01$ and * $p < 0.05$).

4. Discussion

Habitat type varied with depth and within depth strata. These differences in reef architecture and benthic cover affected both community and trophic composition of fish communities. While the shelf-break sites sampled all exhibited a steep vertical gradient, individual habitats were highly heterogenous, which varied in both biotic and abiotic characteristics. These factors influenced the distribution and abundance of many fish taxa, as well as broad trophic groups. Many habitat differences corresponded with increasing depth, which is likely driven by vertical variation in temperature, light, and pressure. However, habitats also varied within depth strata with regard to the benthic community composition and underlying substrate type. Most multibeam variables did not correlate with changes in overall fish community composition even though a few (slope, aspect, planar curvature, and surface ratio) could distinguish sites with different trophic communities. This may be because the measures of habitat from different spatial scales, from relatively small scales with BRUVS (<10 m^2) and multibeam derivatives describe broader spatial information (~10–100s m^2). Topographical features of the habitat, such as slope angle, aspect (i.e., sites facing prevailing currents), rugosity, and planar curvature (e.g., local ridges or valleys) may contribute to the local availability of food and shelter. Among the shallow-depth and middle-depth sites sampled, the fish community composition at the Viper Reef was clearly distinct from other locations. The Viper was located on a shallower portion of the shelf-break, where the reef bottoms out to a maximum depth of 150 m and the slope is less steep. The maximum extent (i.e., deepest depth) of the reef may account for some of the variability in fish communities [33].

Trophic group composition and structure varied with depth, with a greater trophic diversity at upper mesophotic depths and increasing reliance on general carnivores at the deepest depths. This suggested that the ecology of deeper reef fish communities is fundamentally different from those found at shallower depths. Some previous studies have noted a greater abundance of certain trophic groups, such as piscivores, on outer-shelf reefs along the GBR [120]. However, this is the first assessment of depth-related changes in trophic structure below 50 m. Worldwide, many mesophotic habitats are characterized by low herbivore abundances and high planktivore abundances (e.g., the Red Sea, Puerto Rico, Northwest Hawaiian Islands, Brazil, Main Hawaiian Islands, [8,35,121–125]). While this study identified low numbers of planktivorous and piscivorous species compared to other feeding strategies (7%–10%), this is largely due to the lack of trophic specificity available (some of the species observed had 'unknown' feeding modes). Depth-related trophic variation indicates a dramatic shift from shallow reef food-web dynamics to strategies that rely more on plankton and other mobile resources. It has been postulated that mobile invertivores [35,122] and anthiine fishes [126,127] are key links within other mesophotic food webs, and the high proportion of carnivores and piscivores found at mesophotic depths within the GBR suggests similar strategies are operating there. Even within the same species of *Stegastes partitus*, deeper habitat-associated subpopulations had broader diet niches in those in shallower depths [128]. Future trophic comparisons should include relative measures of trophic-level hierarchy, mobility, and prey size [122], as well as quantifying how reliant these predators are on food sources that originate at shallower depths and use vertical diel movements to target benthic prey [129] if there are 'trophic subsidies' in operation where oceanic planktonic and nektonic resources make up the deficit for dwindling primary productivity at deeper depths [130].

Identifying where species co-occur is an important consideration in ecosystem-based fisheries management used to predict the degree that species interact. Species distributions that are highly correlated will also affect fishing mortality estimates in multispecies fisheries [131]. More connected species are thought to have a higher vulnerability to combined anthropogenic threats as well as detrimental changes to the community structure [132]. The species co-occurrences identified in this study suggest the presence of both inter-family and intra-family interactions, similar habitat needs, or greater food availability. However, since the majority of overlapping fish species are upper-level predators, these are likely examples of competition or niche partitioning rather than predator-prey interactions. In addition to differences in trophic groups with depth, there was substantial variation in overall fish community composition both between and within-depths, with this information on variability critical for future management plans. Previous surveys of mesophotic and sub-mesophotic shelf-break reefs suggested species composition is often highly heterogeneous [133] with potentially high proportions of both rare species [134] and endemism [7,135]. New and highly unique fish communities are being frequently described, as mesophotic research effort increases [24,124,136]. Our surveys identified a number of new potential species as well as new location records for the GBR.

Variation in fish community structure among and within depths likely reflects differences in the biotic and abiotic components of shelf-break reefs, with these habitats distinctive from shallower reefs along the continental shelf. A greater proportion of sponges and macro-algae within the benthic community, and the presence of boulders, distinguish shelf-break environments from shallower habitats, as well as differences among shelf-break reef habitats. Not only were significant differences in the community composition found between the sampled reefs, but also between reefs and inter-reefal areas. This is especially true at the shallower depths where a steep slope angle and a high abundance of filter-feeding invertebrates were characterizing features. Sponges and filters are an important habitat-forming component of the upper mesophotic zone along the central GBR [26,137], compared to shallow reefs where coral is the primary ecosystem engineer. Dominant benthic taxa shift from photosynthetic to obligate heterotrophic in deeper, mesophotic Indo-Pacific environments [39,72,138]. The central GBR shelf-break has similar benthic habitats to other clear, tropical mesophotic regions, where *Halimeda* and corals are observed down to >150 m [37,139,140]. While the lower mesophotic zone is dominated by depth-specialist benthic communities that are distinct from shallower areas [141], coral communities have been documented in transitional depths of 60 to 75 m at multiple sites [39,82]. The lower depth-limits of corals vary, with isolated coral colonies documented to at least 125 m in some locations in the GBR and neighboring Coral Sea [64,142], this study). *Halimeda* bioherms, while not explicitly studied here, are common macro-algal components of deep reef ecosystems and provide important deposits of calcium carbonate that promotes reef growth. In this study, we observed photosynthetic algae at deeper depths than reported in other MCEs worldwide, which is likely due to well-documented nutrient upwelling. Macro-algal communities in other mesophotic locations have also found new mesophotic-specific species [143,144]. At the deepest depths surveyed, boulders replaced reef-building organisms in creating structural complexity. It is clear that, in the GBR, the shelf-edge should be considered an ecologically unique ecosystem and fundamentally different from shallow reefs, which is similar to other MCEs [24,134,145].

Shelf-break reefs are likely critical habitats for key ecological processes, and it is not yet known to what extent these habitats are necessary for certain species to thrive. Anecdotally, several of the BRUVS deployments observed juvenile fish at mesophotic depths. While it was not always possible to identify juvenile fish to the species-level (and single BRUVS only allow an estimated size), some fish appear to complete most of the life cycle in solely deep habitats, such as the grouper *Epinephelus morrhua* (Figure 10). In general, the juvenile habitats of the deep-reef species we observed are not well-documented. For instance, juvenile habitats of *Pristipomoides* sp. were only accidentally discovered over deep (65–100 m), flat, soft habitats in Hawaii [146]. Dogtooth tuna, *Gymnosarda unicolor*, were observed in groups of 1–3 in all BRUVS deployments except one (Figure 10c). This behavior could be a spawning aggregation, to increase safety from predators, or to increase hunting success. Certain Lutjanidae and Serranidae spawning aggregations are reliable and infamous worldwide [147–149]. The use of different habitats by many species to complete their life cycle is not known for the GBR, and future research should attempt to describe and quantify how deep reefs are important for spawning, ontogenetic shifts and life history cycles.

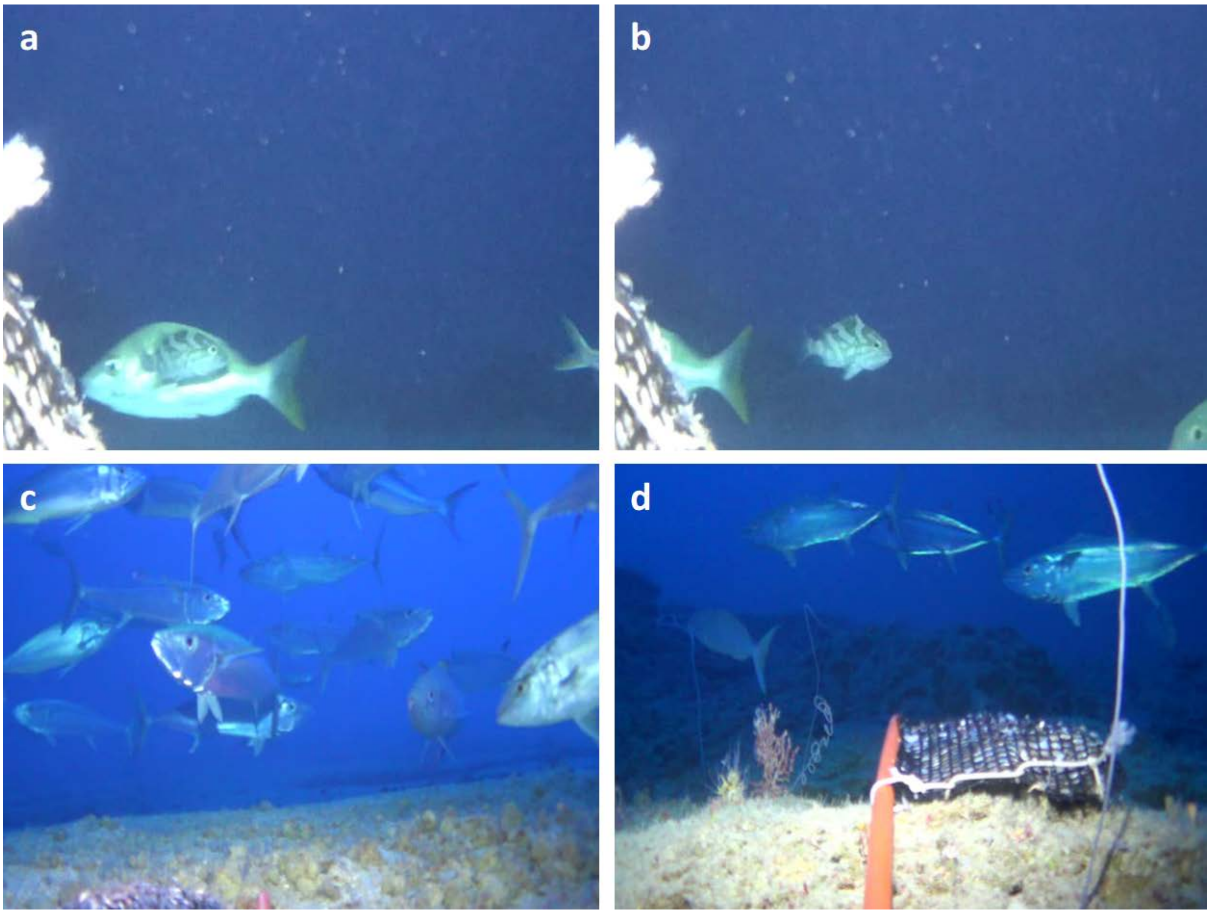


Figure 10. Some deep Baited Remote Underwater Video Stations captured juvenile fishes, including this *Epinephelus morrhua* at 194 m (**a**,**b**). Another deployment captured a large aggregation of *Gymnosarda unicolor* and other species (**c**). Most often *G. unicolor* were found in small groups of one to three individuals (**d**).

5. Conclusions

This study has shown that benthic composition can influence the distribution and abundance of mesophotic fish communities. Therefore, further research on the distribution and composition of deep-reef habitats is critical to understanding mesophotic biodiversity. A greater sampling effort of the GBR shelf-break along its latitudinal extent would fill in existing knowledge gaps on these deeper marine biomes and would be useful for future conservation strategies. When the GBR Marine Park (GBRMP) protection and mixed-use zonation was determined a decade ago, only coarse environmental data was available for the deeper habitats within the GBRMP [10]. The strategy of the conservation zones allowed for some uncertainty and was designed to protect unknown habitats [75], and incidentally ~30% of submerged banks are within no-take areas and 88% of banks are protected from bottom-trawling [10,150]. Of the locations sampled, only Myrmidon is afforded greater protection as a 'no-take' area with the other locations under habitat protection. However, this research showed community differences between reefs and also between reefal and inter-reefal sites. In the future, it will be important to compare species richness and abundance over different protection levels and to include inter-reefal areas for habitat protection, since currently there is no information if existing habitat protection measures are sufficient to safeguard deep-reef fish communities. More detailed benthic habitat mapping and biotic surveys have improved the representative distributions of habitats and fishes in other marine conservation parks in Australia [96,151]. Therefore, increasing the understanding of GBR shelf-break habitats should be a priority. While BRUVS have some biases and limitations, such as the effects of light, bait, and the field-of-view, BRUVS proved to be useful for gaining a better understanding of deep-reef fish communities and habitats. The species composition of fishes varied greatly among habitats. Although depth was important, habitat preferences clearly had a role in determining the distribution of species and trophic groups. Potential predictors of fish distributions on the shelf-break are depth, reef architecture, and benthic cover. The narrow spatial extent of the mesophotic areas on the GBR and other locations makes them vulnerable to fisheries.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/11/2/26/s1, Figure S1: Examples of multibeam bathymetry, backscatter and derivatives for the Northern Submerged Shoals Figure S2: Epibenthic habitat measures by reef, Figure S3: Substratum habitat measures by reef, Figure S4: Non-metric multidimensional scaling showing fish community composition for Shallow sites (54–115 m), Figure S5: Non-metric multidimensional scaling showing fish community composition for Middle sites (128–160 m), Figure S6: Non-metric multidimensional scaling showing fish community composition for Deep sites (179–260 m); Table S1: Ecology of deep-reef fishes seen in deep Baited Remote Underwater Video Stations, Table S2: Habitat variables to understand variation in fish trophic communities.

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