



Fish community dynamics in remote northern Australia: the role of habitat and seascape

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A B S T R A C T

Associations between fish and benthic habitats are shaped by structural complexity, resource availability, and positioning within the larger seascape. In the remote Gulf of Carpentaria in northern Australia, there is very little scientific information on how fish communities interact with their habitats within a heterogeneous seascape, despite their ecological and cultural value. This is the first study of how habitat characteristics and seascape configuration influence demersal fish communities in Marra Sea Country in the southwestern Gulf of Carpentaria. Baited remote underwater video stations were used to observe species richness, relative fish abundance, and community structure at 95 sites. We determined that site (seagrass, algae, benthic macroinvertebrate (BMI) cover, and depth) and seascape characteristics (distance to reef (km), distance to major river mouth (km), distance to habitat-forming seagrass meadows (km), and distance to Kurrulinya (km) (Maria Island)) influence fish species richness and relative abundance. We also found that the three major habitats in Marra Sea Country (bare substrate, benthic macroinvertebrates, and seagrass meadows) support statistically distinct fish communities, with community differences in seagrass and BMI being driven by specific associated species, while community differences in bare substrate are driven by the presence of both BMI- and seagrass-associated species. Our results indicate that both habitat type and seascape configuration are important for determining fish assemblage distributions. Variation in fish assemblages across benthic habitats and their spatial arrangement underscores the need for seascape-scale management to support marine conservation in Marra Sea Country and other tropical ecosystems.

1. Introduction

Benthic habitats are key components of coastal marine ecosystems, providing vital resources such as food, shelter, and fish nursery grounds (Rossi et al., 2020). In tropical ecosystems, benthic habitats are foundational to support biodiversity and supply ecosystem services to coastal populations (Cullen-Unsworth et al., 2014; Kathiresan and Bingham, 2001; Ullmann and Grimm, 2021; Wilson et al., 2000). Fish use of habitats is determined by resource availability, substrate diversity, and structural complexity (Graham and Nash, 2013; Messmer et al., 2011; Pickens et al., 2021; Sell and Kröncke, 2013). Additionally, many fish species utilize different habitat types at different life stages (Compton et al., 2012; Robertson and Duke, 1990; Stuart-Smith et al., 2021), making access to multiple habitat types within an ecosystem vital for supporting stable fish populations. Within tropical oceans, the relationship between fish communities and coral reefs has been most

extensively studied (Abdul Wahab et al., 2018; Almany, 2004; Eduardo et al., 2018; Srinivasan, 2003). Examining fish-benthic habitat associations from a multi-dimensional, seascape-wide perspective offers a more complete understanding of their dynamics (Davis et al., 2014; Tokeshi and Arakaki, 2012).

In tropical seascapes, coral reefs, seagrass meadows, mangrove forests, macroalgal beds, and bare substrate are often linked through the exchange of energy and materials as well as spatial proximity, forming a heterogeneous mosaic of interconnected habitats (Davis et al., 2014; Olds et al., 2016). Seagrass meadows and mangroves are particularly important to reef-associated fish through providing foraging grounds and nursery habitats for juveniles (Dorenbosch et al., 2005; Harborne et al., 2016; Verweij et al., 2006). Reefs adjacent to these vegetated habitats experience higher fish abundance and diversity (Berkström et al., 2020; Hill et al., 2025; Mumby et al., 2004; Olds et al., 2012). Structurally complex and diverse tropical vegetated habitats, including

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seagrass meadows and macroalgal beds, can also increase fish abundance and diversity (Gullström et al., 2008; Jones et al., 2021). For seagrass, canopy height (Gullström et al., 2008) and cover (Jones et al., 2021; Malesa et al., 2022) are important for increasing fish abundance and diversity in meadows. Seagrass-associated fish assemblages also benefit from adjacent habitats, especially mangroves, as they provide foraging grounds for fish that shelter in adjacent habitats (Gilby et al., 2018; Henderson et al., 2017a). Less structurally diverse habitats, such as unvegetated bare substrate, also play an important role in the wider seascape, as they can serve as foraging grounds for fish in adjacent habitats (Smith et al., 2010). Additionally, other habitat-forming benthic macroinvertebrates (BMI) such as sponges, soft corals, and hydroids, are less structurally complex than coral reefs, but still serve as vital areas of shelter and foraging for fish (Stoner and Titgen, 2003). While vastly understudied in tropical regions, these habitat-forming BMI may facilitate increased fish assemblage connectivity within a habitat mosaic.

Some fish also move between marine habitats and terrestrial and freshwater environments (Sheaves, 2009). For example, estuarine wetlands and river mouths function as nurseries for marine fish (Davis et al., 2012; Elliott and Whitfield, 2025; Sheaves et al., 2015). Fish recruitment to these habitats is often altered by freshwater flow, as increased riverine discharge both enhances connectivity channels and increases estuarine productivity (Burford and Faggetter, 2021; Davis et al., 2012). This is particularly important in tropical ecosystems, as discrete wet and dry seasons are often marked by structurally different fish communities (Davis et al., 2012). As further investigation into the significance of seascape connectivity occurs, it is evident that habitat characteristics and positioning within the seascape often work together to support healthy fish communities (Bradley et al., 2019; Henderson et al., 2017a; Mosman et al., 2020; Stoner and Titgen, 2003).

Sea level rise, ocean warming, extreme weather events, and mining developments pose major threats to benthic habitats and their ability to support dynamic ecosystems (Finnegan et al., 2015; Marra Traditional Owners, 2023; Reddin et al., 2022). These greatly contribute to habitat degradation and loss, which, in turn, have a significant negative impact on fish abundance, biomass, and diversity (Airoldi et al., 2008; Scapin et al., 2018). Thus, comprehensive monitoring is imperative for understanding changes in habitat and fish communities and informing long-term conservation planning. Marine ecology research in Australia is extensive, but it is mainly focused on the Great Barrier Reef and more populous areas. In contrast, there is relatively limited ecological, economic, or management information for tropical northern Australia, leading to significant gaps in our understanding. Increasing environmental threats, coupled with a lack of scientific knowledge in northern Australia, make continued research into marine ecosystem functioning imperative for adaptive management.

The Gulf of Carpentaria (the Gulf) is an ecologically and culturally diverse yet remote coastal area in northern Australia, spanning north-west Queensland and the Northern Territory (NT). It covers 330,000 km² of shallow waters, with depths reaching up to 70 m (Burford et al., 2009; Torgersen et al., 1983). Coastal waters are heavily influenced by riverine nutrient and sediment deposits, which create turbid yet highly productive ecosystems (Burford et al., 2009; Rothlisberg et al., 1994). The Gulf is home to diverse benthic and vegetated habitats including coral reefs, seagrass meadows, salt marshes, and mangroves (Collier et al., 2023). This diversity, in turn, supports significant megafauna populations of dugongs, turtles, and cetaceans as well as sea snakes, and diverse fish and invertebrate communities (Griffiths et al., 2020; Groom et al., 2017; Kyne et al., 2018; Plagányi et al., 2022). Unlike many other tropical areas, the Gulf has little coastal development, making it one of the least anthropogenically impacted marine environments worldwide (Burford et al., 2009; Halpern et al., 2008). This remoteness has resulted in a paucity of scientific research (Blaber et al., 1994, 1995) despite the wealth of Aboriginal knowledge and cultural history in the area. The Gulf is at

high risk for future environmental pressures caused by climate change, including sea level rise, increased rainfall and flooding, and increased temperatures (Duke et al., 2017; McMahon et al., 2022). As environmental and ecological pressures continue to increase, a comprehensive understanding of the Gulf's ecosystems and spatial context is required to inform robust management.

In this study, we conducted the first comprehensive survey of fish-benthic habitat associations in Marra Sea Country in the southwestern Gulf using baited remote underwater video (BRUV) stations. Our investigation had 2 aims: (1) to elucidate the role of four major habitats in shaping fish assemblages, (2) to assess the impact of site- and seascape-level variables in influencing fish species richness, relative abundance, and fish community composition.

2. Methods

2.1. Survey area

The study took place in Marra Sea Country (Fig. 1a), located in the NT's southwestern Gulf of Carpentaria between the Roper River to the northwest and Warrawarda (Rosie Creek) to the southeast. It encompasses the Australian mainland coast and the islands Kurrulinya (Maria Island) and Yumunkuni (Beatrice Island). Williyurru (Limmen Bight River) also flows into Marra Sea Country, meeting the Gulf across from Yumunkuni. These three rivers and other smaller waterways flow into the Gulf, connecting ecosystems and providing nutrients, and mangroves predominantly grow along these rivers and in the wetlands behind the shoreline. Habitat-forming seagrass is predominantly located along the coast, while BMI habitats are concentrated in deeper waters (Fig. 1b). Bare substrate is interspersed between these two habitats. Marra Sea Country encompasses two marine parks (Fig. 1b): the Limmen Bight Marine Park (LBMP; NT Government) and the Limmen Marine Park (LMP; Commonwealth of Australia). Created in 2012, the LBMP covers 884 km² of coastal waters that stretch from the shore to 3 nautical miles (5.5 km) offshore. It also includes 3 nautical miles of water around Kurrulinya. The LMP was established in 2013 in the deeper waters adjacent to the LBMP. It stretches between Williyurru and Warrawarda and covers an area of 1399 km². The LMP is zoned as habitat protection (IUCN Category IV) where all commercial fishing requires a permit, trawling and net fishing are banned, and recreational fishing is permitted (Commonwealth of Australia, 2018). Both marine parks were implemented to facilitate cooperative management between the Commonwealth and NT governments, Marra Traditional Owners, and scientific partners (Marra Traditional Owners, 2023; Parks and Wildlife Commission, 2019). The Marra Traditional Owners are the custodians of the Sea Country and have significant knowledge of the habitats and organisms that inhabit it. They manage Sea Country as the Marranbala Land and Sea Rangers, and provided vital cultural knowledge throughout the conception and undertaking of this project.

2.2. Fish surveys and data processing

Fish data were obtained using BRUVs in October 2023. All BRUVs were deployed in subtidal waters due to boat access restrictions, but intertidal and subtidal habitat data were used for seascape calculations. Each BRUV consisted of a metal frame and a GoPro in an underwater housing. A 1-m-long metal pole 0.25 m from the base of the BRUV was attached perpendicular to the frame with a mesh bag containing 500 g of pilchards at the end (Dorman et al., 2012). BRUV sites were pre-selected using a spatially balanced clustered design (Fig. 1a) using the *MBH design* package in R (Foster et al., 2023). *MBH design* generates spatially balanced designs using a generalization of Balanced Acceptance Sampling (Robertson and Duke, 1990), which selects sites via a quasi-random (Halton) sequence so that samples were spread evenly across the study area rather than clumped, while still allowing unequal inclusion probabilities across strata. Due to the varied spread of habitat

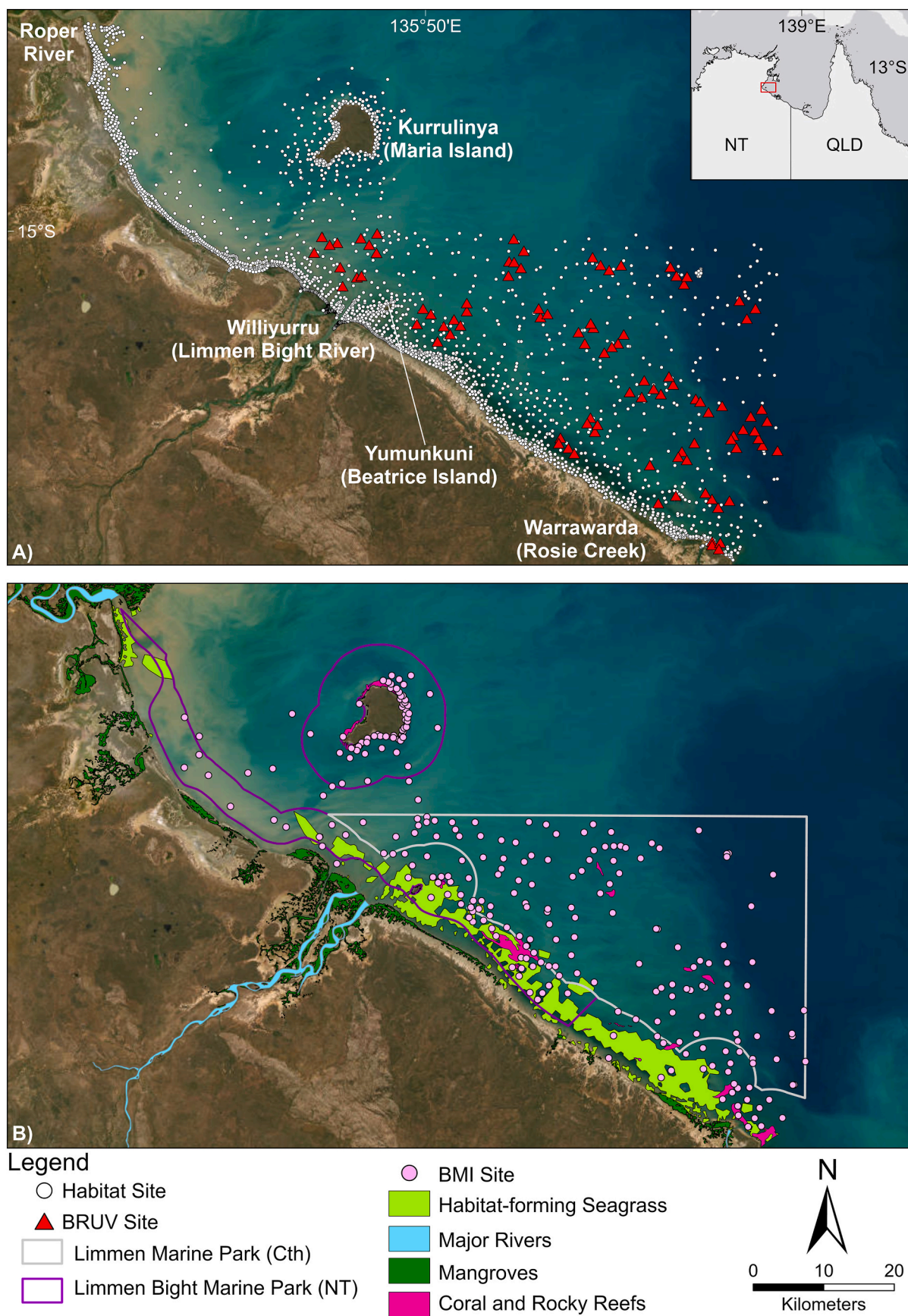


Fig. 1. Map of (a) habitat and baited remote underwater video survey sites and (b) location of marine parks and seascape features across Marra Sea Country. Cth = Commonwealth of Australia marine park; NT = Northern Territory government marine park; BMI Site = A site where benthic macroinvertebrates (hard coral, soft coral, sponge, or other BMI categories) were observed).

types across the seascape (Fig. 1b), habitat representation within the BRUV deployments was unequal. BRUVs were deployed >500 m apart to ensure site independence and for at least 70 min to allow sediment to settle before analysis. The BRUV footage length was standardized by watching for exactly 60 min from the time that the sediment was fully settled (Langlois et al., 2020).

A total of 95 BRUVs were analyzed by trained observers using *EventMeasure* (SeaGIS Pty Ltd). This software allows the observer to assign taxonomic information to each unique fish while analyzing BRUV footage. Fish family, genus, and species information is uploaded in predefined files of attributes that are able to be updated with additional species if necessary. Footage for each site was given a visibility score: very poor if the observer was unable to see either the bait arm or the bait bag, poor if the bait arm was visible but nothing past it, moderate if the bait arm and bag and some background habitat was visible, clear if the bait arm, bag, and background habitat were visible with very little suspended sediment, and very clear if all BRUV parts and habitat in the foreground and background were visible with no obstructions (Fig. S1). Sites were removed from analysis if visibility did not allow individuals to be identified at the family level or lower due to turbid water conditions or the camera being flipped upwards.

Each fish was identified to the lowest taxonomic level possible. Most fish were identified to the species level, but some were to the genus or family level due to constraints of identifying fish in imagery. Taxa identified to the family or genus level were only included in subsequent species richness or relative abundance calculations when no species from that family or genus was identified within the same BRUV deployment to avoid double-counting of taxa. Species richness was calculated as a minimum estimate of the total number of unique fish taxa observed over the 60-min analysis period. Relative abundance data for each fish species are represented as MaxN, or the maximum number of individuals of the same taxa seen in a single frame of the video (Whitmarsh et al., 2017). MaxN is preferable to measuring relative fish abundance as a raw count as it eliminates issues that arise from counting the same fish twice if it leaves and re-enters the frame (Schobernd et al., 2014). Thus, MaxN is a conservative estimate of relative fish abundance that does not account for temporal distribution of fish detections across the 60-min analysis period.

At the start of each BRUV video, a single image with the camera facing outwards and parallel with the seafloor was captured and uploaded into *CoralNet* software (<https://coralnet.ucsd.edu>), and the percentage of all benthic categories (seagrass, BMI, algae, and bare substrate) at each site was recorded (Table 1). The benthic categories were estimated using the point-count annotation method where the primary benthic category in each square equally spaced on the image was recorded and averaged across all drops for that site. After the *CoralNet* annotations were completed, each BRUV site was given a habitat type classification (seagrass, BMI, macroalgae, bare substrate) that corresponded with the dominant benthos.

2.3. Seascape predictors

The seascape variables we included in our models were distances from each BRUV site to habitat-forming seagrass cover, reef, Kurrulinya, the nearest major river mouth, the mainland, and mangroves (Table 1). Distances were calculated using the *sf* package in R (Pebesma, 2018; Pebesma and Bivand, 2023) and verified in ArcGIS Pro (ESRI). To determine the extent of habitat-forming seagrass, Thiessen polygons were created around each habitat survey site where habitat-forming seagrass was present in ArcGIS Pro, and adjacent polygons merged to create meadows. We defined habitat-forming seagrass as any strap-morphology species present: *Cymodocea serrulata*, *C. rotundata*, *Enhalus acoroides*, *Halodule uninervis*, and *Syringodium isoetifolium*. *Halophila* species characterized by small, oval- and oblong-shaped leaves were not classed as habitat forming (Kuo, 2020). More information about how habitat monitoring data were collected is included in Collier

Table 1

Site variables extracted from BRUV data and seascape variables used in analysis.

Site and Seascape Variables	Description	Data Source
BRUV Site Variables		
Seagrass % cover	The percent cover of seagrass at a BRUV site	BRUV habitat analysis – this study
Benthic macroinvertebrate % cover	The percent cover of BMI (hard coral, soft coral, sponges, bryozoa, hydroids, ascidians, and other BMI) at a BRUV site	BRUV habitat analysis – this study
Algae % cover	The percent cover of algae (erect macrophytes, erect calcareous, filamentous, turf algae, and encrusting algae) at a BRUV site	BRUV habitat analysis – this study
Depth (m)	The depth in meters at a BRUV site measured during field collection	Boat depth sounder during data collection – this study
Habitat type	The dominant cover type at each BRUV site. When there were no sessile organisms present, the habitat type is bare substrate	BRUV habitat analysis – this study
Visibility	Water clarity (very poor, poor, moderate, clear, very clear) at each BRUV site as determined by the amount of suspended sediment in the water and the observer's ability to identify fish	BRUV habitat analysis – this study
Latitude and longitude	The coordinates at each BRUV site	GPS during data collection – this study
Seascape Variables		
Distance to habitat-forming seagrass meadow (km)	The shortest straight-line distance in kilometers from a BRUV site to a habitat-forming seagrass meadow	2021 and 2023 habitat data (Carter et al., 2025; Collier et al., 2023; Smith et al., 2025)
Distance to reef (km)	The shortest straight-line distance in kilometers from a BRUV site to a coral or rocky reef	<i>Australian Tropical Reef Features – Boundaries of coral and rocky reefs</i> (Lawrey and Bycroft, 2025)
Distance to major river mouth (km)	The shortest straight-line distance in kilometers from a BRUV site to the mouth of Williyurru or Warrawarda	<i>Surface Hydrology Polygons (National)</i> (Crossman and Li, 2015)
Distance to Kurrulinya (km)	The shortest straight-line distance in kilometers from a BRUV site to the shore of Kurrulinya	<i>Australia's Land Borders</i> (Geoscience Australia, 2020)
Distance to mangroves (km)	The shortest straight-line distance in kilometers from a BRUV site to mangroves with canopy cover of 50% and above	<i>Geoscience Australia Mangrove Canopy Cover Collection 3</i> (Lymburner et al., 2021)
Distance to mainland (km)	The shortest straight-line distance in kilometers from a BRUV site to the shoreline of the Australian mainland. Excluded from analysis due to collinearity constraints	<i>Australia's Land Borders</i> (Geoscience Australia, 2020)
Management Zone	The management jurisdiction where a BRUV is located (LMP, LBMP, outside). Excluded from analysis due to redundancy with other variables	Commonwealth and Northern Territory governments

et al. (2023), Carter et al. (2025), and Smith et al. (2025).

2.4. Statistical analyses

2.4.1. Habitat effects on species richness and relative abundance

All statistical analyses were performed in R (R Core Team, 2025). To first elucidate differences in fish species richness and relative abundance among habitat types, generalized additive mixed models (GAMMs) were fit using the *mgcv* package (Wood, 2011). GAMMs were chosen over generalized linear mixed models due to their ability to estimate smooth, non-linear relationships from the data and, via random effects, account for non-independence in the data (Wood, 2017). A Poisson distribution was used for the species richness GAMMs while a negative binomial distribution was used in the relative abundance GAMMs due to over-dispersed count data. Latitude and longitude were included in the models as spatial smooths to account for spatial variation not captured by habitat type or large-scale spatial gradients. The equations were created as follows:

Species Richness ~ Habitat type
+ s(Latitude, Longitude, bs = "ds", k = 10) (1)

Relative Abundance ~ Habitat type
+ s(Latitude, Longitude, bs = "ds", k = 6) (2)

where bs = "ds" specifies that the smooth function was implemented using a Duchon spline (Wood, 2017), and k indicates the number of basis functions for the smooth terms used for fitting (Pedersen et al., 2019). Basis dimension diagnostics for species richness (k -index = 0.91, p = 0.14) and relative abundance (k -index = 0.87, p = 0.12) confirmed adequate smoothing. For significant categorical factors, pairwise comparisons were performed using the *emmeans* package (Lenth and Piaskowski, 2026) to identify which habitat types differed significantly in species richness and relative abundance.

2.4.2. Site and seascape effects on species richness and relative abundance

Data exploration was performed before fitting models. A Cleveland dotplot revealed two outliers in relative abundance data, likely due to large schools of *Clupidae* sp. observed near the surface, which were removed from subsequent relative abundance analysis. Collinearity among linear predictors was assessed using a pairwise comparison and Pearson correlation coefficients (PCC) in the *GGally* package (Fig. S2) (Schloerke et al., 2025). Any variables with a PCC value $> |0.7|$ were not included in models (Dormann et al., 2013). The comparison between distance to mangroves (km) and distance to mainland (km) generated a PCC of 1.0, so distance to mainland was removed from subsequent analysis. Distance to habitat-forming seagrass (km), distance to nearest major river mouth (km), and distance to mangroves (km) were all highly correlated with each other ($PCC > |0.7|$, Fig. 1b). As such, 3 model groups were created using the minimally correlated predictors (Table 2) for use in full-subset generalized additive mixed models (FSSGAMM) and distance-based redundancy analysis (dbRDA). The factor management zone was not included in the analysis because Kruskal-Wallis tests indicated it was redundant when including both site- and seascape-level predictors most likely as a result of the spatial imbalance of habitat types within each marine park ($p < 0.05$, Fig. 1b).

The influence of site- and seascape environmental variables on species richness and relative abundance was examined using full-subset GAMMs. Models were generated from combinations of 3-4 predictors from each model group to avoid overfitting (Table 2) (Fisher et al., 2018). Visibility was included as a random effect to account for potential underestimation of species richness and relative abundance, but to not make it the focus of the models. One hundred and forty models were generated for both species richness and relative abundance. Akaike Information Criterion (AIC) and R-squared (r^2) values for each model were

Table 2

The three model groups that were analyzed together in FSSGAMM and dbRDA analysis to avoid collinearity among predictors.

Group	Predictors (Full GAMM)	Predictors (dbRDA)
Group 1	Seagrass % cover at site, BMI % cover at site, algae % cover at site, distance to reef (km), distance to Kurrulinya (km), distance to major river mouth (km), depth at site (km)	Habitat type, distance to reef (km), distance to Kurrulinya (km), distance to major river mouth (km), depth at site (km)
Group 2	Seagrass % cover at site, BMI % cover at site, algae % cover at site (km), distance to reef (km), distance to Kurrulinya (km), distance to habitat-forming seagrass meadow (km)	Habitat type, distance to reef (km), distance to Kurrulinya (km), distance to habitat-forming seagrass meadow (km)
Group 3	Seagrass % cover at site, BMI % cover at site, algae % cover at site, distance to reef (km), distance to Kurrulinya (km), distance to mangroves (km)	Habitat type, distance to reef (km), distance to Kurrulinya (km), distance to mangroves (km)

compared simultaneously regardless of which model group they originated from. The model with lowest AIC was compared to all other models within <2 AIC, and the most parsimonious model was chosen (Table S1) (Burnham and Anderson, 2002). Residuals, dispersion statistics, and spatial autocorrelation for all GAMMs included in this analysis were checked using the *DHARMA* package (Hartig, 2025). All QQ plots indicated normal distribution of the residuals with non-significant Kolmogorov-Smirnov test, dispersion test, and outlier test results ($p > 0.05$). While all GAMMs also had non-significant combined adjusted quantile test results ($p > 0.05$), species richness versus habitat type and latitude and longitude had some quantile deviation at the 0.25 level. Because the overall adjusted quantile test was non-significant and the QQ plot was normally distributed, the model was retained in analysis. For each predictor, partial residual plots were created using *ggplot2* (Wickham, 2016) to visually assess the correspondence between the estimated effect of each predictor and the associated partial residuals (Fig. S3). Effect sizes for each significant smooth term were quantified on the response scale by generating model predictions between the 10th and 90th percentile of the predictor's observed values to avoid potential edge effects from sparse data at the extremes and values are reported as the raw difference in the predicted response and as a multiplicative fold-change. Given the number of candidate models and the correlated spatially structured nature of several seascape predictors, results from the FSSGAMM analysis should be interpreted as identifying plausible predictor sets rather than confirming a single causal driver. Variable importance across the full candidate set is reported alongside the best-fit model to reflect this (Table S2).

2.4.3. Fish community composition

The influence of habitat type and seascape predictors on fish assemblages was explored with dbRDA using the *vegan* package (Oksanen et al., 2025). Species that occurred at fewer than two sites were excluded from the analysis to minimize potential noise when investigating the main species gradients (Brasil et al., 2020; Poos and Jackson, 2012). A Bray-Curtis dissimilarity matrix was constructed. dbRDA models were run on the dissimilarity matrix testing the effects of habitat and seascape predictors from each of the 3 model groups (Table 2). The continuous predictors in each model group were scaled using z-score normalization. The model group with the highest adjusted r^2 value was chosen for further exploration. *Post hoc* pairwise Adonis tests were performed between each habitat type using the *pairwiseAdonis* package (Martinez Arbizu, 2020). Ordination axes were then calculated, and species with r^2 values over 0.3 and significant predictors ($p < 0.05$) are presented in the ordination plot.

3. Results

Of the 95 BRUV sites analyzed in Marra Sea Country, 61 sites were classified as bare substrate habitat, 19 were BMI habitat, 11 were seagrass habitat, and 4 were macroalgae habitat. Thirty-one sites had very clear visibility, 51 had clear visibility, 8 had moderate visibility, 4 had poor visibility, and 1 had very poor visibility. Across all sites, 88 fish species from 35 families were observed (Table S3). The most frequently observed families were trevallies (Carangidae, 75 sites), mackerels (Scombridae, 69 sites), emperors (Lethrinidae, 62 sites), and breams (Nemipteridae, 56 sites). The most diverse families were Carangidae (13 species), Lethrinidae (5 species), Nemipteridae (5 species), and Labridae (4 species) (Table S3). The most frequently observed species were Queensland school mackerel (*Scomberoides queenslandicus*, 66 sites), grass emperor (*Lethrinus laticaudis*, 53 sites), Australian remora (*Echeneis naucrates*, 40 sites), and yellowstripe scad (*Selaroides leptolepis*, 39 sites). There were 28 shark and ray species across 10 families, with half of those species coming from requiem sharks (Carcharhinidae) and whip-tail stingrays (Dasyatidae). Nine species of sharks and seven species of rays seen in the survey are classified as threatened (vulnerable, endangered, or critically endangered) by the International Union for Conservation of Nature (Table S3) (IUCN, 2012).

Habitat type significantly influenced both fish species richness and relative abundance. Fish species richness was 9.5 ± 0.8 species (mean $\pm$ 95% confidence interval) while relative fish abundance was 32.8 ± 5.5 MaxN. GAMMs revealed that species richness ($p < 0.01$) and relative abundance ($p < 0.01$) varied significantly among habitat types (Table S4). Species richness was significantly lower on bare substrate (8.2 ± 2.9 species) than in BMI habitats (11.1 ± 2.2 species) (pairwise comparison, $p < 0.05$; Fig. 2a). Relative fish abundance was significantly greater at seagrass habitats (70.9 ± 26.2 MaxN) than bare substrate (34.1 ± 8.6 MaxN, pairwise comparison, $p < 0.05$) (Fig. 2b).

3.1. Site and seascape effects on fish species richness and relative abundance

Both fish species richness and relative abundance were influenced by site-level habitat and seascape characteristics. The most parsimonious model from the FSSGAMM analysis retained BMI % cover, distance to habitat-forming seagrass meadow (km), and distance to reef (km) as predictors for fish species richness (Fig. 3, Table 3). Predicted species richness increased significantly by approximately 3.1 species (1.4-fold increase) across the range of BMI % cover until roughly 30% cover, where it then declined ($X^2 = 12.643$, $p < 0.01$). Sites with 0% BMI cover

encompassed several distinct substrate types (bare sediment, seagrass, macroalgae, mangrove-adjacent), which likely contributed to the high variability in species richness observed at low BMI cover. Confidence intervals also widen above ~50% BMI cover, reflecting the small number of high-cover sites ($n = 19$) rather than indicating a plateau in the relationship. Distance to habitat-forming seagrass meadow also showed a significant, non-linear relationship with species richness ($X^2 = 6.083$, $p < 0.05$), declining to a minimum approximately 8 km away before increasing at greater distances ($\Delta = 0.7$ species, 1.1-fold-change). Distance from reefs was retained in the best-fit model but did not significantly influence species richness ($X^2 = 4.667$, $p > 0.05$) (Table 3, Fig. S3). Visibility was significant in the best-fit model for species richness, indicating that it explains some residual variation in the model. Residual structure also showed weak spatial autocorrelation (Moran's $I = 0.041$, $p = 0.03$), suggesting a small impact on model inference. Relative fish abundance was influenced by BRUV site seagrass % cover, algae % cover, and distance to nearest major river mouth (Fig. 3, Table 3). Relative abundance rose significantly with seagrass % cover ($X^2 = 9.072$, $p < 0.01$), increasing by 15.8 individuals. As with BMI cover, high variability in sites with 0% seagrass cover may be attributed to the range of substrate types present at these sites. Confidence intervals also widen above ~60% seagrass cover due to the small number of high-cover sites ($n = 11$); this motivates the recommendation for a stratified sampling design below. Relative fish abundance also increased (16.1 individuals, 1.9-fold-change) with distance from the river mouth, to a maximum of around 25 km offshore ($X^2 = 10.676$, $p < 0.01$). Although algae % cover was retained in the best-fit model, it was not a significant predictor of relative abundance ($X^2 = 1.837$, $p > 0.05$).

3.2. Fish community composition

Model group 1, which included habitat type, distance to reef, distance to Kurrulinya, distance to major river mouth, and depth at site explained the most variation in Marra Sea Country fish communities (Adjusted $r^2 = 0.087$, Fig. 4, Table 4, Table S5). Habitat type was the strongest driver of fish communities ($r^2 = 0.092$, $p = 0.001$), followed by depth at site ($r^2 = 0.022$, $p < 0.01$), and distance to Kurrulinya ($r^2 = 0.026$, $p = 0.001$). Depth was closely associated with BMI habitats and the distribution of rainbow monacle bream (*Scolopsis regina*), reflecting the preference of this fish for deeper, structured reef environments. The significance of distance to Kurrulinya may represent a broader trend about spatial positioning, as all BRUVs were located to its east.

Fish communities differed significantly among habitat types in Marra

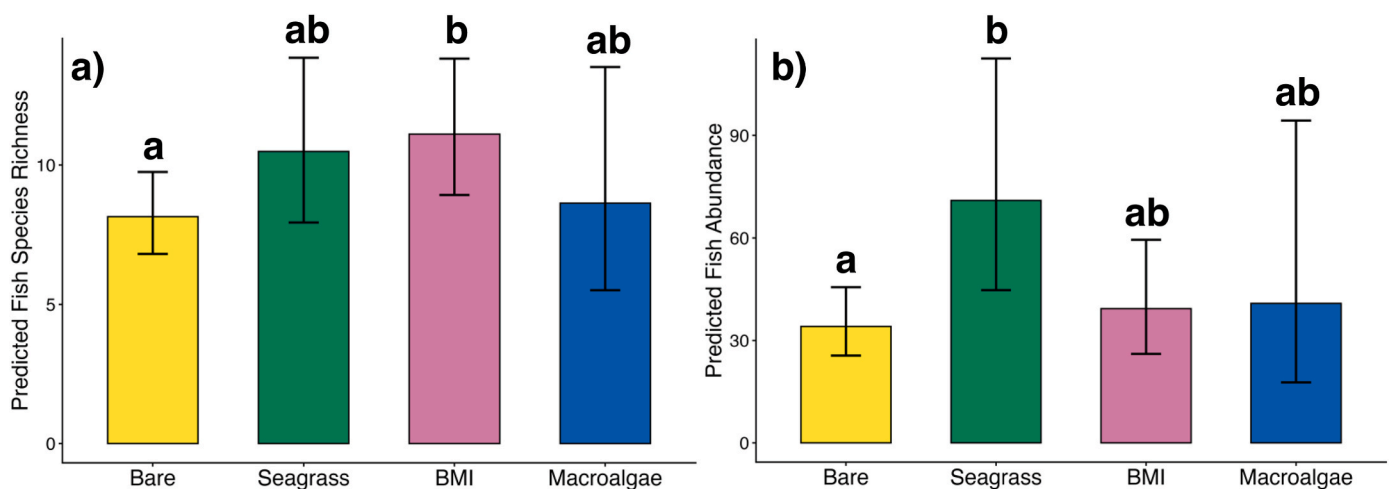


Fig. 2. Bar charts showing the predicted means and 95% confidence intervals from GAMM analysis for (a) species richness and (b) relative abundance across the four habitat types and spatial positioning. Letters above each bar indicate which habitats are significantly different from each other (pairwise comparison, $p < 0.05$).

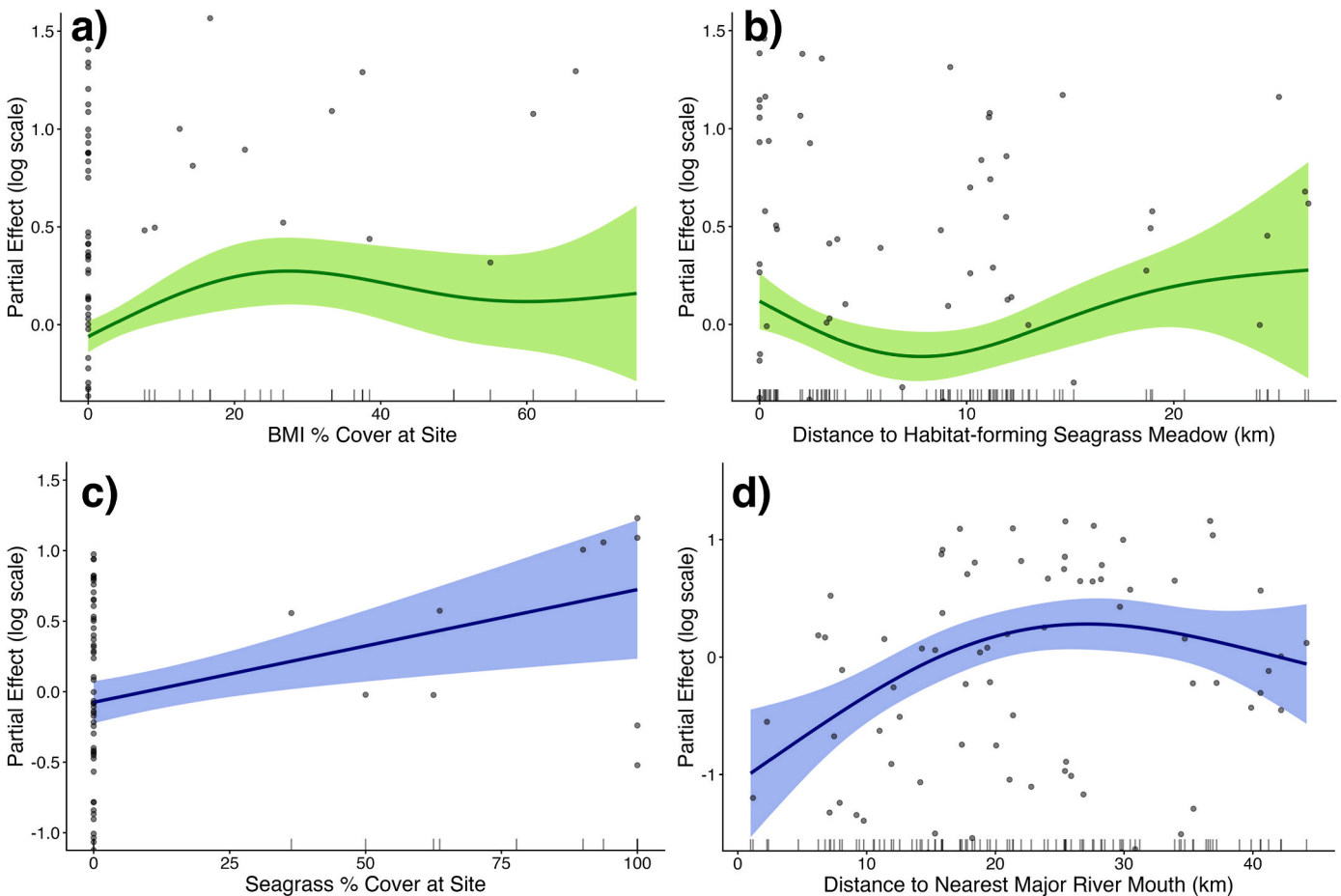


Fig. 3. Partial residual plots for (a) fish species richness and BMI % cover, (b) fish species richness and distance in kilometers to habitat-forming seagrass meadow, (c) relative fish abundance and seagrass % cover, and (d) relative fish abundance and distance in kilometers to nearest major river mouth from the best-fit FSSGAMM. Shaded area illustrates 95% confidence intervals, points represent partial residuals, and lines along the x-axis represent the distribution and density of observed data points.

Table 3
Best-fit FSSGAMM results for fish species richness and relative abundance. Bold font indicates a significant term ($p < 0.05$). Effect sizes are reported for significant fixed terms only.

Predictor	edf	X^2	p -value	Δ	Fold-change
Species Richness					
BMI % cover at site	2.336	12.643	$p < 0.01$	3.113	1.397
Distance to habitat-forming seagrass meadow (km)	2.466	6.083	$p < 0.05$	0.676	1.052
Distance to reef (km)	2.070	4.667	$p > 0.05$		
Visibility	3.235	21.688	$p < 0.001$		
Adjusted $r^2 = 0.294$					
Deviance explained = 37.5%					
Relative Abundance					
Seagrass % cover at site	1	9.209	$p < 0.01$	15.813	1.46
Distance to nearest major river mouth (km)	1.915	20.571	$p < 0.001$	16.053	1.896
Algae % cover at site	1.666	2.138	$p > 0.05$		
Visibility	0.0002	0	$p > 0.05$		
Adjusted $r^2 = 0.29$					
Deviance explained = 26.4%					

Sea Country, with pairwise comparisons confirming significant

differences between seagrass, BMI, and bare substrate (Adonis *post-hoc*, $p < 0.01$, Fig. 4, Table S6). Fish communities in macroalgae habitats were not significantly different from any other habitats (Adonis *post-hoc*, $p > 0.05$, Table S6). Seagrass habitats are oriented in the opposite direction to BMI habitats in the ordination space, indicating that their fish community compositions rarely overlap (Fig. 4). Seagrass communities are characterized by the golden trevally (*Gnathanodon speciosus*) ($r^2 = 0.361$). Conversely, the grass emperor (*Lethrinus laticaudis*) ($r^2 = 0.395$), rainbow monocle bream ($r^2 = 0.31$), and scribbled angelfish (*Chaetodontoplus duboulayi*) ($r^2 = 0.331$) are key species of BMI habitat fish community composition (Fig. 4). Bare substrate fish community composition was not driven by specific species, but rather the presence of fish from both seagrass and BMI habitats, indicating its role as a transitional habitat (Fig. 4). All r^2 and p -values for each significant species are included in the supplemental information (Table S7).

4. Discussion

Marra Sea Country in the Gulf of Carpentaria supports rich and diverse fish assemblages, with fish community distributions influenced by benthic habitat type and location within the larger seascape. In our study, we investigated the role of different benthic habitats in shaping these communities and explored how spatial proximity between habitat types and major seascape features further influenced fish assemblages. Both site and seascape factors were influential in shaping fish species richness and relative abundance, elucidating that habitat type and spatial configuration are important for fish assemblages. Furthermore,

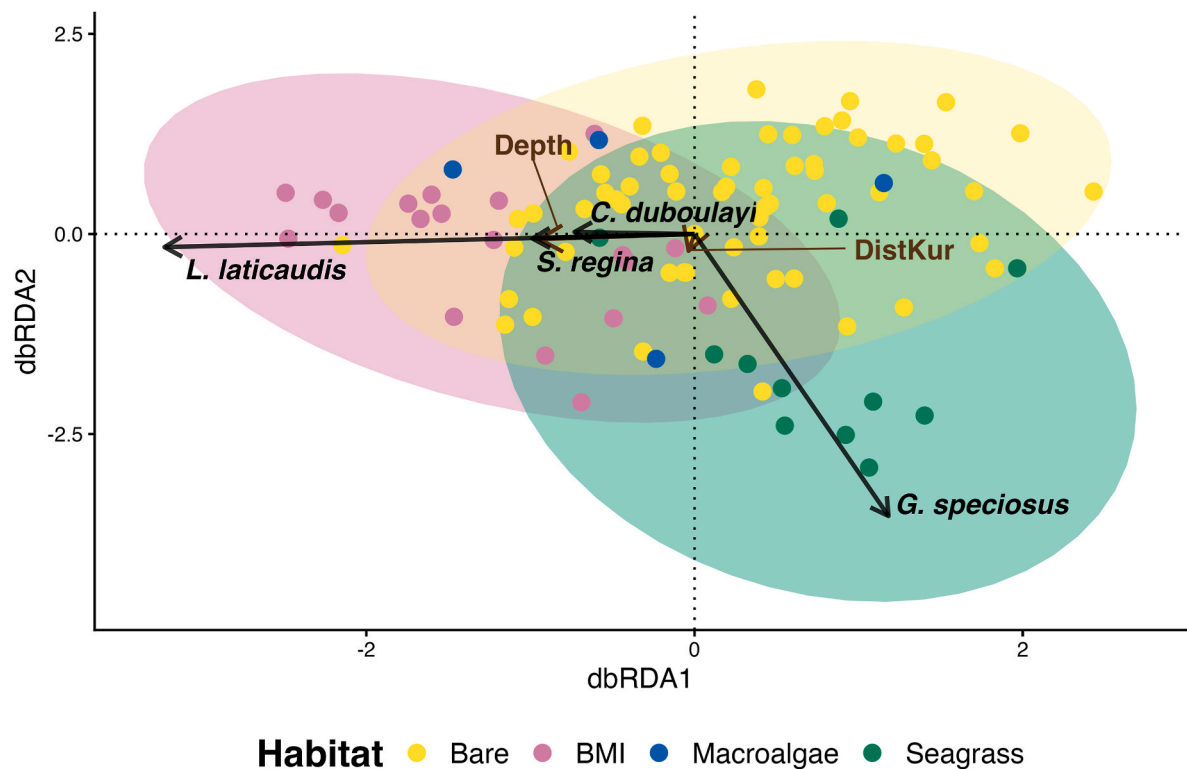


Fig. 4. dbRDA results illustrating the most influential fish species ($r^2 > 0.3$) and environmental predictors ($p < 0.05$) and which habitat types they are most closely associated with. Points represent each BRUV site and its corresponding habitat type, ellipses represent confidence intervals for the significant habitats, black arrows represent each species, and brown arrows represent predictors. DistKur = distance to Kurrulinya (km); Depth = depth at BRUV site (m). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Results and significance of a distance-based redundancy analysis comparing fish community composition and selected site and seascape predictors. Bold font indicates significant results ($p < 0.05$).

Predictor	Sum of Squares	F Statistic	p-value
Habitat type	3.125	2.96	$p = 0.001$
Depth at site (m)	0.751	2.132	$p = 0.001$
Distance to Kurrulinya (km)	0.882	2.505	$p = 0.001$
Distance to major river mouth (km)	0.486	1.381	$p > 0.05$
Distance to reef (km)	0.42	1.382	$p > 0.05$

unique habitats house statistically distinct fish communities, suggesting that habitat heterogeneity within the seascape is important in maintaining biodiversity (Hill et al., 2025; Messmer et al., 2011).
Habitat type is a main driver in shaping fish assemblages across Marra Sea Country. Specifically, species richness and relative abundance were significantly higher in BMI and seagrass habitats, respectively,

where structural complexity is relatively high, compared with bare substrate (Fig. 5). The positive effect of structural complexity is confirmed by other studies (Bradley et al., 2017; Hall and Kingsford, 2021; Moustaka et al., 2024; Nagelkerken and van der Velde, 2004), which show that species richness and abundance are higher in structured habitats such as coral reefs, mangroves, macroalgae, and seagrass than in unstructured habitats. Structured habitats, particularly those with high rugosity, diverse growth forms, and refuge holes, are often preferred by demersal fish, as they provide microhabitats and protection from predators (Gratwicke and Speight, 2005). Despite significant differences in species richness and relative abundance between bare and structured habitats in our study, the variation is much greater (Fig. 2a–b). The BMI habitats throughout the survey area were dominated by soft corals and sponges on soft substrate rather than the structurally complex hard coral reefs typical of studies reporting reef-associated fish communities, which likely contributes to the higher variability in BMI fish community composition observed here compared to other studies. Seagrass meadows also have less structural complexity

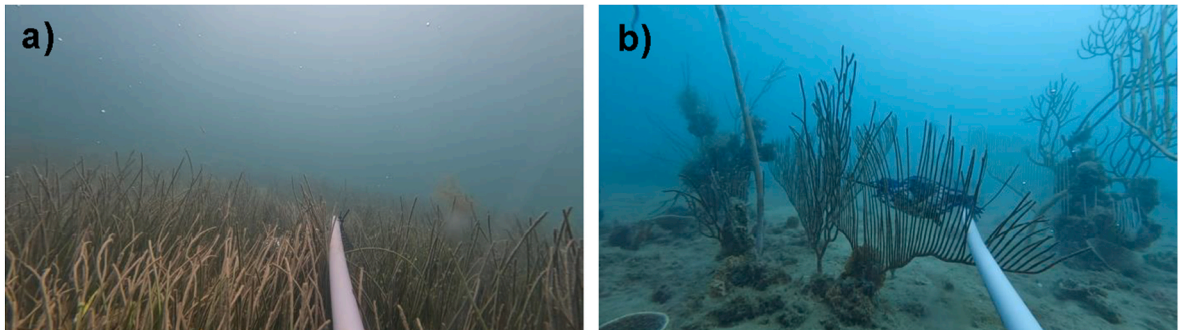


Fig. 5. Images from BRUVs that show examples of (a) high cover seagrass habitat and (b) high cover BMI habitat.

than coral reefs or mangroves. Decreasing structural complexity has been shown to increase variability in fish assemblages (Plass-Johnson et al., 2016), as this reduces access to food and shelter. It is also important to note that detectability assessments to calculate the probability of individual detections (Follana-Berná et al., 2019) were not undertaken in this study, which may further contribute to the variation in the results. To fully understand the effect of habitat complexity on fish communities across Marra Sea Country, future research should incorporate coral reef and mangrove habitats around Kurrulinya and Yumunkuni.

Bare substrate habitat supports a statistically unique fish community characterized by the presence of both seagrass- and BMI-associated species (Fig. 4), suggesting that bare sand in Marra Sea Country acts as a transition zone between adjacent areas of seagrass and BMI habitats, where species characteristic of each habitat overlap. Transitional habitats also support populations of habitat generalists (Dorenbosch et al., 2005) that may utilize these areas due to the lower competition with other species. This is consistent with the role of unvegetated substrates as foraging areas (Kulbicki et al., 2022) or migration corridors between different habitats (Berkström et al., 2012). Similar to our study, in a tropical rocky reef-sand transition habitat, fish species richness was lower than in the rocky reefs, but community composition was still distinct between the two (Otero-Ferrer et al., 2021). The co-occurrence of habitat-associated species from both seagrass and BMI species provides evidence that bare substrate may facilitate, rather than interrupt, seascape-scale fish movement in Marra Sea Country, highlighting that species richness and relative abundance metrics alone are insufficient for assessing habitat value in a seascape context. In a management context for Marra Sea Country, bare substrate should be considered as a functional and important component of the seascape.

The occurrence of distinct, specialist assemblages in seagrass and BMI habitats demonstrates that habitat heterogeneity underpins fish diversity across the seascape. Seagrass habitats are highly associated with *G. speciosus*, while *L. laticaudis*, *C. duboulayi*, and *S. regina* characterize BMI habitats (Fig. 4). The association of *G. speciosus* with seagrass habitats is consistent across tropical (Johan et al., 2020) and subtropical (Henderson et al., 2017b) ecosystems, as it is a predatory fish that may use these habitats as feeding areas (Hindell, 2006). *L. laticaudis* and *C. duboulayi* are strongly linked to reefs, using them as foraging grounds (Pratchett et al., 2008; Travers et al., 2010). There is little research on *S. regina*, but other members of its genus are associated with coral habitats (Hall and Kingsford, 2016). They have also been associated with increasing depth, which is consistent with the results from our study (Fig. 4) (Rainer and Munro, 1982). Despite the relatively lower structural complexity, these deeper water, isolated BMI habitats in Marra Sea Country supported coral reef-associated species, indicating their importance in facilitating diversity within the seascape. Thus, the combination of functionally different habitats that support different fish communities produces diversity across Marra Sea Country.

Species richness and relative abundance in Marra Sea Country were each influenced by both site- and seascape-level predictors, illustrating that both habitat characteristics and positioning within the seascape are influential in shaping fish assemblages. The predictors retained in the most parsimonious species richness model were BMI % cover, distance to habitat-forming seagrass meadow, and distance to reef, while the retained predictors for relative abundance were seagrass % cover, algae % cover, and distance to nearest major river mouth. Our finding that both site- and seascape-level predictors are important in structuring fish communities is supported by previous work (Eggertsen et al., 2020; Hill et al., 2025; Sievers et al., 2024), but the relative importance of local habitat variables versus seascape configuration on fish assemblages within tropical ecosystems may be context-dependent and vary across ecosystems (Bradley et al., 2019, 2020). Some studies (Moustaka et al., 2024; van Lier et al., 2018) found that habitat structural complexity characteristics, such as high benthic cover and canopy height were significant due to the microhabitats they create. Others determined that

position within a seascape and close proximity to other habitats and features is preferred to facilitate trophic exchanges and support ontogenetic shifts from one habitat to another (Goodridge Gaines et al., 2022; Olds et al., 2012). Due to the emphasis on a spatially balanced survey design, seascape distance predictors also covaried with geographic position because many of the habitats throughout Marra Sea Country are spatially structured, meaning that the seascape predictors are best interpreted as indices of position within the seascape rather than causally isolated drivers. Future surveys in the area should adopt an optimized stratified random design that focuses sampling efforts in and around the major habitats (coral reefs, BMI, seagrass, macroalgae, mangroves, and bare substrate) (Vilas et al., 2024). This experimental design ensures that the full range of habitats in the seascape is represented in the sampling effort and allows adequate replication within each habitat to determine the characteristics of the fish communities as well as less correlation between distance to different seascape features and geographic position (Vilas et al., 2024).

Seagrass cover and proximity to habitat-forming seagrass were retained in the best-fit GAMMs for relative abundance and species richness respectively, consistent with the well-established role of seagrass meadows in enhancing fish richness and abundance in the seascape (Inoue et al., 2021; Scapin et al., 2018; Smith et al., 2008). Seagrass supports fish communities in multiple ways, providing food sources (Davis et al., 2014), nursery habitats (Nagelkerken et al., 2002), and refuge from larger predators for smaller species (Wilson et al., 2013). The dense, habitat-forming seagrass in Marra Sea Country was dominated by *Syringodium isoetifolium*, a species characterized by long, cylindrical leaves that can reach 30 cm (Fig. 5a–Kuo and Den Hartog, 2001). The structural complexity created by these tall, dense seagrass shoots creates microhabitats for large numbers of small fish (Du et al., 2020), facilitating recruitment in large numbers to the seagrass meadows and providing protection from predators (Gullström et al., 2008; Riniatsih et al., 2021). Consistent with this, grunters (Terapontidae) - small fish highly associated with seagrass meadows in their juvenile stages (Sanchez-Jerez et al., 2002; Veale et al., 2015) - were exclusively found in seagrass habitats (Table S2). Predatory species, including sharks, trevallies, and mackerels, were also common in high-cover seagrass, suggesting dense meadows function as foraging grounds for larger species attracted from adjacent habitats to concentrated prey (Heithaus et al., 2002; Hindell, 2006). The concentration of small prey fish and large predators within and near dense, habitat-forming seagrass highlights that these meadows support fish communities across trophic levels, enhance seascape connectivity, and the importance of maintaining high-cover seagrass habitat in the management of Marra Sea Country.

The distance to the nearest major river mouth was the only seascape-level predictor retained in all of the top GAMMs for relative abundance. Relative fish abundance was low near the river mouth, increased to approximately 25 km offshore, and then decreased. Studies have shown that riverine discharge plumes into coastal waters are highly productive areas, as they enhance coastal primary productivity due to the influx of terrestrial- and freshwater-based nutrients (Gouveia et al., 2019; Grimes and Kingsford, 1996; Loneragan and Bunn, 1999). This, in turn, can enhance fish recruitment to the area by providing food sources (Leahy and Robins, 2021; Schweigert et al., 2013). The low relative abundance observed at the mouth of the river, however, could be a result of increased turbidity and currents that are not ideal for these fish communities (Leahy et al., 2011). Fish assemblage structures in estuarine ecosystems are also influenced by tides, salinity, rainfall, and temperature (Abrogueña et al., 2020; Barletta et al., 2005; Molina et al., 2020), which were not measured in this study and are outside the scope of this work.

The results from this work highlight the need for continued habitat and fish community research in the Gulf to better understand where different habitats are distributed and how fish communities interact with them. Due to its remoteness and low human population (Burford

et al., 2009; Halpern et al., 2008), there has been little research on fish communities. Surveys conducted in the 1990s focused on fisheries to examine the role of abiotic factors in shaping fish communities and fish distribution patterns across large areas of the Gulf (Blaber et al., 1994, 1995; Harris and Poiner, 1991). In this survey, we focused on links between fish communities and habitats in a seascape using BRUVs as a survey method. BRUVs were used due to their cost-effectiveness and efficiency (Langlois et al., 2010), but may introduce potential biases into measures of fish species richness and relative abundance and their ecological interpretations, as carnivorous fish may be overrepresented due to their attraction to the bait plume (Stobart et al., 2007), while crevice-dwelling fish may be underrepresented (Lowry et al., 2012). Furthermore, the combined effects of camera angle (perpendicular with the benthos) and structurally complex habitats may block fish from view that may be detectable in less complex habitats (Rhodes et al., 2020). Thus, the use of additional survey methods, such as unbaited remote underwater video stations (Jarrett et al., 2025) and non-visual methods in areas with low visibility (Baker et al., 2016), will more completely capture fish diversity across the seascape.

While the Gulf has been considered one of the least anthropogenically impacted ecosystems globally (Halpern et al., 2008), there is growing concern about its resilience to climate change (Marra Traditional Owners, 2023). In 2015, there was a massive mangrove dieback (Duke et al., 2017) driven by an extreme marine heatwave, severe drought, and a drop in water levels. Additionally, due to climate-related threats, including increases in temperature, precipitation, and sea levels, seagrass ecosystems across the Gulf are at high risk for future declines (Kenyon et al., 2026; McMahon et al., 2022). *Syringodium*, the primary habitat-forming seagrass across Marra Sea Country, is highly susceptible to disturbances caused by extreme weather events and flooding including increased freshwater discharge, sediment resuspension, and uprooting from swells (Cruz-Palacios and van Tussenbroek, 2005; Hanington et al., 2015). During the 2021 habitat surveys in Marra Sea Country, evidence of coral bleaching was also observed in soft coral communities in the LMP (Collier et al., 2023). Our study highlights the importance of both dense, habitat-forming seagrass and soft coral habitats for supporting fish communities across the seascape. As such, continued monitoring in Marra Sea Country and the wider Gulf is vital for tracking these changes and understanding fish responses.

Our findings have important implications for continued management in Marra Sea Country and the Gulf as a whole and contribute to the understanding of habitat and seascape for supporting diverse fish communities in tropical ecosystems. The BRUV surveys showed that the dense, habitat-forming seagrass and BMI habitats both support distinct fish communities. The benthic habitat surveys indicated that the distributions of these habitats are largely different, with habitat-forming seagrass being concentrated in the LBMP and BMI habitats being distributed in the LMP. These parks have different regulations in place regarding fishing and recreation (Collier et al., 2023), potentially exposing habitats to unequal threats and management challenges. Seagrass habitats were significant to fish species richness and relative abundance, underscoring its ecological role in supporting resilient tropical fish communities (Berkström et al., 2020). In heterogeneous seascapes, it is important to develop management schemes that preserve multiple habitat types to minimize threats to biodiversity and improve protected area function (Engelhard et al., 2017; Olds et al., 2016). Fish community analysis showed that bare substrate, seagrass, and BMI habitats support unique fish assemblages. However, the spatial relationships between habitats and seascape features were also vital for shaping these communities, indicating that a seascape management approach is integral for supporting fish community health. This work provides a baseline understanding of inter-habitat relationships across Marra Sea Country and identifies important areas within the seascape that fish communities use. These findings support management approaches that integrate ecological connectivity and cultural priorities

across Marra Sea Country and provide a transferable framework for conducting baseline surveys in support of conservation planning elsewhere in the Gulf.

CRediT authorship contribution statement

Sofi Forsman: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Alex Carter:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Catherine Collier:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Rachel Groom:** Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Emma Barrett:** Resources, Investigation, Funding acquisition, Conceptualization. **David Barrett:** Resources, Investigation, Funding acquisition, Conceptualization. **Shaun Evans:** Resources, Investigation, Funding acquisition, Conceptualization. **Kirsty Whitman:** Validation, Investigation, Formal analysis, Data curation. **Caitlin E. Smith:** Writing – review & editing, Methodology, Formal analysis. **Emma Lawrence:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Timothy M. Smith:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethics and permit approvals

All sampling was conducted in accordance with the relevant regulatory requirements, operating under the Australian Government Marine Park Activity Permit (#PA2023-00112-1), the Northern Land Council Permit (#136099), the Northern Territory Government Fisheries Permit (#S17-3570), the James Cook University Animal Ethics permit (#A2916), and the Charles Darwin Human Research Ethics permits (#H21046 and #H23079).

Declaration of generative AI use

During the preparation of this work, the authors used Claude AI for assistance in debugging R code used in statistical analyses. The authors reviewed and edited the output as needed and take full responsibility for the content of the published article.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alex Carter, Catherine Collier, Rachel Groom, and Timothy M. Smith received financial support was provided by Parks Australia and the Northern Territory Parks and Wildlife Commission. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2026.110330>.

Data availability

BRUV data from this project have been uploaded and are available on GlobalArchive (<https://globalarchive.org/geodata/explore/>). Raw survey data are also available as supplementary material.

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