Neglected biodiversity and ecological functioning – fish community structure associated with Antipatharia (black corals) on shallow reef ecosystems

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Abstract

Addressing anthropogenic threats compromising the persistence of tropical marine ecosystems requires an understanding of the fundamental ecological functions these organisms fulfil. Habitat provision is a major function of corals in tropical marine ecosystems, although most research in this area has concentrated on scleractinians (hard corals). Here, we provide one of the first empirical studies of fish communities on shallow tropical reefs associated with another, lesser-known hexacoral group – the antipatharians (black corals). We quantify i) the abundance, and taxonomic and functional diversity of fish communities associated with antipatharians, and ii) the type of associations between the fish and the antipatharian colonies. Surveys were conducted on an artificial reef (*SS Yongala* shipwreck) and on a coral reef (Orpheus Island) in the central Great Barrier Reef, Australia. We documented 28 different species of fish within seven trophic groups associating with antipatharians, predominantly using the colonies as shelter. At the functional group level, we found high similarity (~80%) in the fish community between the sites, and between antipatharians and scleractinians. However, antipatharians supported both taxonomically distinct fish assemblages (>40% of species) and unique types of associations with the fishes. Overall, our study provides empirical evidence of the important role of antipatharians in supporting fish functional and taxonomic diversity on shallow tropical reefs. Our results suggest that previously neglected hexacorals can play important ecological roles on shallow tropical reefs, where scleractinians are not the dominant coral taxa.

Introduction

Identifying, understanding and maintaining ecological functions is essential to sustaining ecosystems in the face of current anthropogenic stressors (Bellwood et al. 2004a, Hughes et al. 2017a, Brandl et al. 2019a). Traditionally, ecological studies have focussed on the taxonomic composition of assemblages. However, in recent years there has been an increasing focus on understanding the functional roles of species in recognition of the fact that relatively few taxa perform key ecological functions (Bellwood et al. 2004a, Naeem et al. 2012, Harborne et al. 2017). Consequently, the presence and abundance of functionally important species can be more relevant for ecosystem resilience than simply the number of different species (species richness) \ (McGill et al. 2006). For example, on coral reef ecosystems, a global analysis of unique trait combinations of fish showed that, in the Central Indo-Pacific, about one-third of ecological functions are provided by only one species (Mouillot et al. 2014).

Structural complexity is one of the most important ecological traits on reefs and has been associated with key coral taxa (Kerry and Bellwood 2015a, Darling et al. 2017, González-Barrios and Álvarez-Filip 2018). Three-dimensional habitat strongly influences the composition and diversity of a range of reef-associated taxa, particularly fishes (Jones and Syms 1998, Wilson et al. 2009). Reef complexity has been shown to influence species richness, abundance, biomass and trophic structure of fish assemblages (Behrents 1987, Beukers et al. 1997, Gratwicke and Speight 2005, Darling et al. 2017). The abundance and size of holes or cavities mediates predation dynamics and juvenile fish survivorship, thereby influencing the composition of fish communities at different levels (Almany 2004, Lingo and Szedlmayer 2006, Darling et al. 2017). Habitat complexity on coral reefs can be provided by both the underlying reef substrate and by habitat-forming sessile benthos, such as corals, algae and sponges. The loss of habitat-forming benthos and resulting loss of habitat complexity therefore compromises the ecological functioning of coral reefs (Graham and Nash 2013) and makes them less likely to recover from disturbances (Graham et al. 2015).

Most studies examining the importance of habitat-forming benthos on coral reefs have focussed on scleractinians (hard corals). For example, the abundance of scleractinians with complex growth forms (e.g. *Acropora* and *Pocillopora*) is often correlated with the composition of fish communities on shallow reefs (<30 m depth) \ (Beukers et al. 1997, Darling et al. 2012, Kerry and Bellwood 2015a). Similarly, a study in the Great Barrier Reef (GBR) showed that tabular *Acropora* spp. had disproportionate effects on the distribution of large reef fish communities, even when that morphology constituted a small fraction (4%) of the total benthic cover (Kerry and Bellwood 2015a). Moreover, a branching morphology can provide fine-scale structural complexity for small-bodied and/or juvenile fishes to refuge from predators (Beukers et al. 1997). Despite the importance of coral morphology and size (Zawada et al. 2019, Fisher 2023), most coral reef monitoring programs only document live coral cover, without considering structural complexity.

Structural complexity at reefscape scales can be estimated by visual scores (e.g. Gratwicke and Speight 2005), although these approaches can be easily influenced by surveyor perspectives. More recently, photogrammetry has enabled quantitative analysis of reef structural complexity (e.g. Friedman et al. 2012, Ferrari et al. 2016, Kornder et al. 2021). Moreover, photogrammetry has been used to quantify the total volume of shelter (habitat) provided by different scleractinian growth forms or 'shelter volumes'; and predictive models of shelter volume (a 3D metric) can be estimated based on 2D metrics (area or diameter) for each major growth form (Urbina-Barreto et al. 2021, Aston et al. 2022). Therefore, it is currently possible to quantify the shelter volume of different coral morphologies and investigate the link between coral complexity and reef fish abundance at finer spatial scales (Urbina-Barreto et al. 2022). To date, this research has focussed almost entirely on scleractinians, with no attempts to quantify the importance of other habitat-forming benthic groups in providing habitat complexity.

Antipatharians - commonly known as black corals – are a sister group to the scleractinians, within the class Hexacorallia. Antipatharians occur in all worlds' oceans except for the Arctic, at depths ranging from 1 to 8,900 m (Pasternak 1977, Molodtsova et al. 2008, Wagner et al. 2012). Unlike scleractinians, antipatharians do not produce a calcium carbonate skeleton but a thorny axial skeleton (brown or black in colouration) composed of different scleroproteins (Goldberg 1978, Goldberg et al. 1994). Antipatharians have a range of morphologies including flabellate (fan-like), whip-like, bottle-brush-like, and branching (which can be either small bush-like or large arborescent colonies) \ (Wagner et al. 2012). Despite limited studies on the topic, it is known that antipatharians provide important habitat complexity supporting an array of marine fauna. For example, Boland and Parrish (2005) examined the diversity and movement patterns of fish associated with branching antipatharians between 52 m and 73 m depth in Hawaii. While their study was conducted in a mesophotic coral ecosystem (MCEs; 30-150 m depth reefs), 95% of the fish recorded also occur on shallow reefs (Boland and Parrish 2005). Similarly, 90% of fish species inhabiting antipatharian forests (i.e. dense aggregations of branching antipatharian colonies) at mesophotic depths (>30 m) in the subtropical eastern Atlantic, were also found on shallow reefs, although the dominant species varied between shallow and mesophotic depths (Bosch et al. 2023). In temperate mesophotic ecosystems (TMEs) in the Mediterranean Sea, an array of fishes – including species of both conservation interest and high commercial value – were associated with antipatharian forests (Chimienti et al. 2022)

Despite the clear importance of antipatharians as habitat for a wide range of fish species across a range of habitats, there is currently little information on their role on shallow tropical reefs. Moreover, no studies have examined whether antipatharians host a different fish community to the one in association with neighbouring scleractinian corals. Here, we provide the first assessment of the fish community structure associated with antipatharians in shallow reef ecosystems, and explore how this previously overlooked benthic taxon influences fish communities on these reefs. We quantified the species richness, abundance and recorded the behaviour of fishes associated with both antipatharian and scleractinian colonies at two sites in the central Great Barrier Reef (GBR) to investigate: i) the fish community structure associated with antipatharians; and ii) the effects of coral taxon, coral area, coral shelter volume, and reef sites, on the fish communities. This information aims to improve our understanding of the role of antipatharians in supporting functional and taxonomic diversity on reefs.

Methods

Field sites: We conducted surveys at two locations on the central Great Barrier Reef, Queensland Australia, between May and October 2021: the *SS Yongala* wreck and Orpheus Island. The *Yongala* is located ~22 km from mainland (-19°18'16.20" S, 147°37'18.59" E), and sits between 14 m and 29 m depth. The wreck is a world-renowned dive-site for its high fish abundance; however, with the exception of one study of the fish species richness conducted in the late 1990's (Malcolm et al. 1999), scientific studies of the abundance and diversity of fish and benthic fauna are lacking. The wreck supports both antipatharian and scleractinian corals, and therefore represents a great opportunity to investigate the influence of both coral taxa on fish communities. Because the *Yongala* is in essence an 'artificial' reef, and to explore the generality of our results across shallow coral reefs, we also collected data on a well-studied shallow reef that supports a substantial population of antipatharians - Orpheus Island (18.6161° S, 146.4972° E, at Little Pioneer and Iris Point). All sites are within No-Take Marine Protected Areas (Marine Park zones), and *Yongala* is a Commonwealth Cultural Heritage Site.

Corals area and shelter volume: Photos with a scale were taken to estimate the planar area of each of the coral colonies using the software ImageJ (Bourne 2010). For scleractinians, we recorded the planar area as viewed from above, which is the traditional approach (Rogers et al. 1994) and also the method used by Urbina-Barreto et al. (2021) to develop predictive models of shelter volume. For antipatharians, planar area was calculated based on width (diameter) and height of the colonies as viewed from the side, which are considered the best estimators of surface area for non-scleractinian branching bushy-like coral colonies (Santavy et al. 2013). The shelter volume (dm^3) of all coral colonies was calculated using the predictive models (based on the colonies diameter) of Urbina-Barreto et al. (2021) for branching, massive and tabular colonies. No predictive models are available for encrusting and foliose growth forms, thus these two morphologies were treated as massive (Supplementary 1). Predictions of shelter volume were made using log-scale colony diameters, which were nearly identical to the predicted shelter volumes when using area (Supplementary 1).

Fish surveys: Four-minute long stationary videos of both antipatharian and scleractinian colonies were filmed on SCUBA during daylight hours (1100 - 1400). Coral colonies were filmed in pairs (one antipatharian and one scleractinian) - where the antipatharian and scleractinian were at the same depth,

≤10 m apart, and filmed at the same time or one immediately after the other. At *Yongala*, 17 coral pair videos were filmed (34 colonies) at two depth ranges: 14-20 m & 21-27 m (eight and nine colony pairs respectively). At Orpheus Island, scleractinians are not abundant beyond 14 m depth; therefore, six coral pair videos (12 colonies) were filmed at 14 m depth, where both coral taxa coexist, and to maintain a similar depth range to the other site.

Video analysis: We recorded the maximum number of fish species visible in a single video frame (MaxN) using EventMeasure (SeaGIS, Melbourne Australia), which allowed us to estimate the abundance of each fish species observed. We also recorded the 'behaviour' of each fish associating with coral colonies as follows:

- *HovA* - hovering around (<50 cm around the colonies)
- *HovH* - hovering around and hiding (hovering <50 cm around the colonies and seeking refuge among the coral structure)
- *Stat_next* – static (resting next to the coral colonies)
- *Stat_in* – static (static within or on the coral colonies)
- *Feed* - feeding on polyps (in the case of corallivores), or feeding on algae on top of coral (e.g. Scarus)
- *Clean* - being cleaned (by *Labroides dimidiatus*)
- *Pass* - passing by

No fishes were counted for the first ten seconds of the video to allow the fishes to resume 'normal behaviour'. While fishes passing by (*Pass*) were recorded, these were not considered for further analysis because of the uncertainty of their association with the corals. For instance, fish passing could have been foraging but were not observed consuming their prey.

Statistical analysis: All analyses were conducted in R 4.2.1 (R Core Team, 2022). The shelter volume (dm^3) of all coral colonies was calculated using the predictive models proposed by Urbina-Barreto et al. (2021) as described above. To standardise fish abundance and species richness, we used the area of the surveyed coral colonies (i.e. we used fish density m^{-2} and fish richness m^{-2}). Corals across two depth ranges were surveyed at *Yongala*; therefore, we explored the effect of depth on fish density m^{-2} and species richness m^{-2} for each of the coral taxa using generalised linear mixed-effects models (GLMMs) with a gamma distribution (log-link). The effect of depth on fish species richness m^{-2} for scleractinians did not meet the assumption of homogeneity of variance; therefore, it was examined using a generalised least squares (GLS) model with the variance function 'varIdent' to account for heteroscedasticity (i.e. unequal variances of species richness m^{-2} at each depth band). To investigate the effect of the different coral taxa and site on the fish abundance and species richness, we used GLMMs with gamma distributed errors and a log-link, and coral pair ID was included as a random effect to account for the paired antipatharian-scleractinian design of our study.

To explore the correlation between colony area and shelter volume of corals vs. the observed fish abundance and species richness, we fit GLMMs using the truncated poisson distribution (log-link) considering that our fish abundance and richness data did not contain zeros. Here, the colony ID was included as a random effect, and we used the total fish counts as abundance (i.e. the sum of MaxN of all fish species counted on each colony) and the total number of different fish species recorded for each colony. All GLMMs were fit using restricted maximum likelihood (REML) via the package "glmmTMB" (Brooks 2022) and model diagnostics (i.e., assumptions of normality, homogeneity or variances, no overdispersion) were assessed using the package "DHARMa" (Harting 2022). Post-hoc analysis, estimated marginal means, and pair-wise contrast were done using the package "emmeans" (Lenth et al. 2022); and predicted values were calculated with the function "predict" from the package "car" (Fox 2022) using 95% confidence intervals. All models formulas, results and summary statistics – marginal means, contrast estimates, 95% confidence intervals, and models Akaike's information criterion (AIC; Burman and Anderson 2002) – are available in Supplementary 2.

To visualise the overall significance of the different variables (site, coral taxa, area and shelter volume) on explaining the fish community structure, a constrained ordination using distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) was conducted with the variables overlaid as a vector. This was followed by a permutation-based multivariate ANOVA (PERMANOVA) of the dbRDA to identify significant (p <0.05) variables driving the fish community structure. Then, a one-way permutation-based multivariate ANOVA (PERMANOVA) was performed using the function ''adonis2'' in vegan (Oksanen 2022) to further assess findings. To validate our interpretation on the PERMANOVA, we performed a PERMDIST test ''betadisp'' (a multivariate equivalent to levene's test for homogeneity of variance).

Results

i) Fish community structure associated with antipatharians

A total of 28 fish species were recorded in close association with antipatharians (20 different species at *Yongala* and 13 at Orpheus, from 11 families and seven functional groups) \ (Figure 1; Appendix 1). The most common and abundant species were *Neopomacentrus azysron, Rhabdamia gracilis, Chromis nitida, N. bankieri, Verulux cypselurus, Ostorhinchus cladophilos, Cheilodipterus quinquelineatus,* and *N. cyanomos;* and HoH and HoA were the most common fish behaviours (Figure 2; Appendix 1). The marginal fish density at *Yongala* was 2.12 ± 0.5 (mean fish density m^{-2} ± SE), and 0.35 ± 0.5 m^{-2} at Orpheus (Figure 3a,b; Supplementary 2).

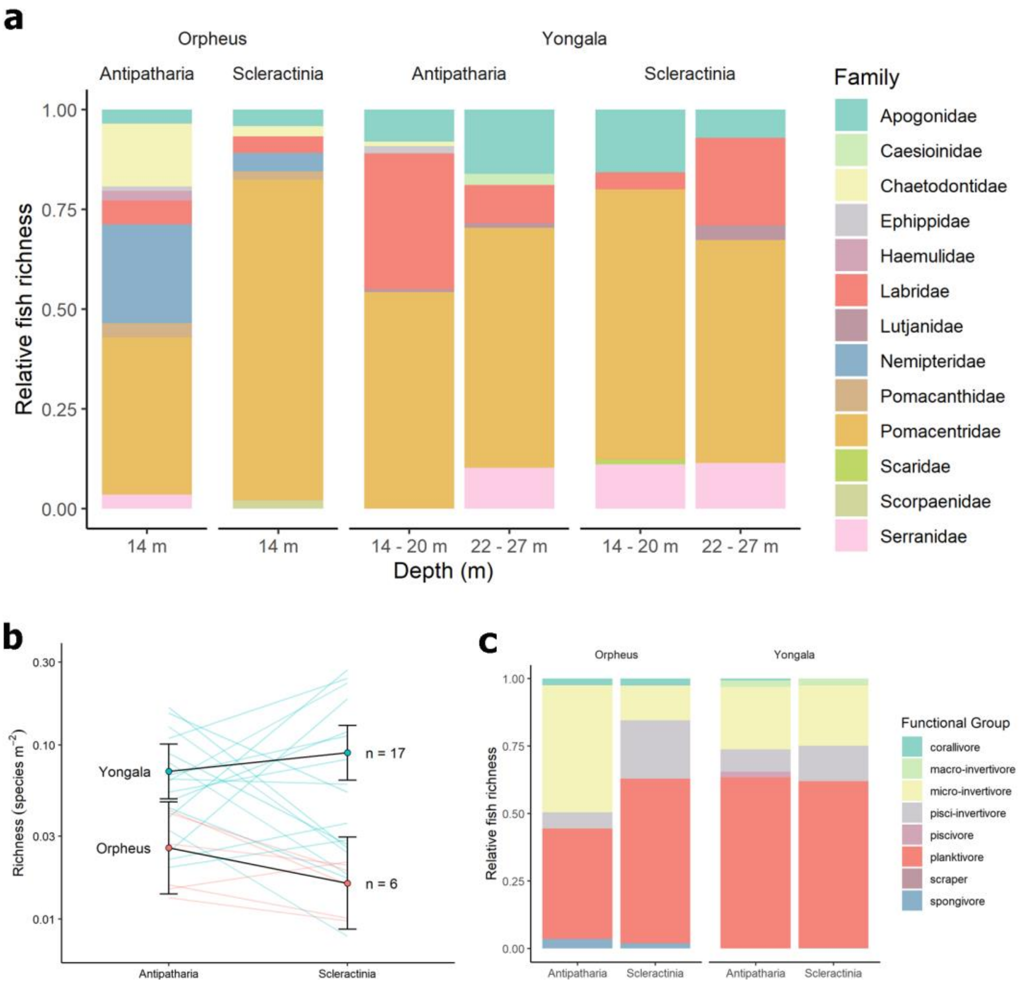

Figure 1 | Fish species richness associating with antipatharians and scleractinians at *Yongala* and Orpheus: **a)** Relative fish species richness m^{-2} for each fish family. **b)** Marginal effects plot of mean fish richness m^{-2} predicted for each coral taxa (Model 4 in Table 1). Coloured lines connect colony pairs (one antipatharian and one scleractinian) for each of the two sites: 34 colonies at *Yongala* (n = 17 colony pairs), and 12 colonies at Orpheus (n = 6 colony pairs) surveyed. **c)** Relative fish richness m^{-2} showing the proportional contribution of each functional group.

ii) Effects of the different variables on the fish community

Effect of depth on fish density m^{-2} and species richness m^{-2} at Yongala

We found no significant (p >0.05) differences between depths for either fish density m^{-2} or species richness m^{-2} (Table 1; Supplementary 2). Mean fish density m^{-2} for antipatharians in the shallower depth range (14–20 m) was 2.48 ± 0.81, and 0.86 ± 0.38 for scleractinians (Figure 3b). Species richness for antipatharians in the shallower depth range was 0.09 ± 0.05, and 0.06 ± 0.03 in the deeper range (mean n of fish species m^{-2}; Supplementary 2). For scleractinians species richness was 0.04 ± 0.01 (mean n of fish species m^{-2}) at the shallower depth range, increasing by 2.6% at the 22-27 depth range (0.07 ± 0.01, mean n of fish species m^{-2}); however, this was not significant (p >0.05; Table 1; Supplementary 2). Since depth had no effect at *Yongala*, we pooled the fish density m^{-2} and species richness m^{-2} across the two depth bands for subsequent analyses.

Effect of coral taxon and site on fish density m^{-2} and species richness m^{-2}

Fish density m^{-2} varied significantly between the coral taxa, although coral taxon did not have a significant effect on fish richness m^{-2}; and neither did the interaction between coral taxon and site (Table 1; Supplementary 2). Site did have a significant effect on fish richness m^{-2}, decreasing from 0.07 ± 0.01 m^{-2} at *Yongala* to 0.03 ± 0.008 m^{-2} at Orpheus for antipatharians (Figure 1b; Supplementary 2). For scleractinians, it varied from 0.09 ± 0.02 m^{-2} at *Yongala* to 0.02 ± 0.005 m^{-2} at Orpheus (Figure 1b; Supplementary 2). Site also had a significant effect on fish density, decreasing from 2.12 ± 0.5 m^{-2} at *Yongala*, to 0.35 ± 0.5 m^{-2} at Orpheus for antipatharians (Figure 3; Supplementary 2). Likewise, for scleractinians fish density decreased from 0.63 ± 0.2 m^{-2} at *Yongala*, to 0.09 ± 0.03 m^{-2}at Orpheus (Figure 3; Supplementary 2).

Effect of coral taxon and area (m^{-2}) or shelter volume (dm^{-3}) on fish abundance and species richness

Neither area, nor the shelter volume had a significant effect on fish abundance (Table 1; Supplementary 2). Likewise, the interaction between coral taxa and area or shelter volume did not have a significant effect on fish abundance (Table 1; Supplementary 2). In contrast, coral taxon had a significant effect on fish abundance in both models (Model 5a,b in Table 1; Supplementary 2). For species richness, both factors, coral taxon and area or shelter volume had a significant effect (Model 6a,b in Table 1; Supplementary 2); although the interaction between coral taxon and area or shelter volume did not significantly affect the species richness (Model 6a,b in Table 1; Supplementary 2).

Overall significance of the different variables driving the fish community structure

The dbRDA analysis (PERMANOVA; pseudo-F = 1.69, 999 permutations, p (perm) = 0.002) showed that coral taxon was the only variable that had a significant influence (p <0.05) on the fish community (Supplementary 2). For visualisation, the different variables added in the model (coral order, area, shelter volume, colony diameter, and sites) were plotted as vectors according to the magnitude and direction of the relationship, and overlaid on the fish community observed. Significant differences in the fish community between the coral taxa was also confirmed by the one-way permutation test (PERMANOVA; pseudo-F = 3.12, 999 permutations, p (perm) = 0.001). The PERMDISP test confirmed equal dispersion within the two coral taxa (F = 0.97, p = 0.302).

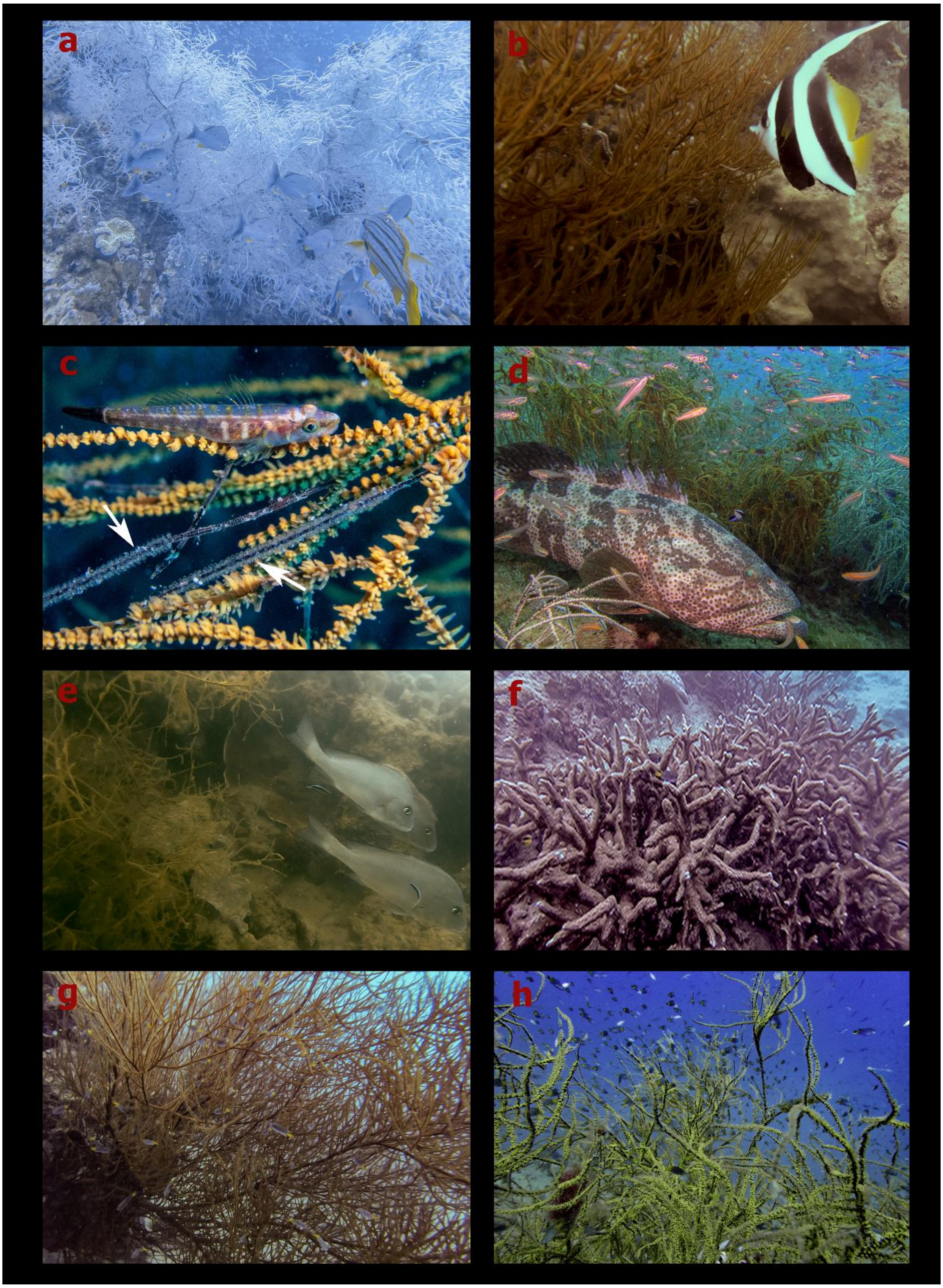

Figure 2 | Examples of interactions between fish and antipatharians and scleractinians in this study: **a)** *Lutjanus russellii* and *L. carponotatus* behind a white antipatharian colony sheltering from the current at *Yongala*. **b)** *Heniochus acuminatus* feeding on the polyps of an antipatharian colony at Orpheus. **c)** *Bryaninops tigris* residing on an antipatharian colony at *Yongala*; white arrows show its eggs deposited on the colony branches. **d)**

Epinephelus fuscoguttatus laying among antipatharian colonies at *Yongala*. **e)** *Diagramma pictum* being cleaned by *Labroides dimidiatus* while hovering next to an antipatharian colony at Orpheus. **f)** A range of fish species hiding among a branching scleractinian colony at Orpheus. **g)** A range of fish species hiding among a branching antipatharian colony at Orpheus. **h)** A range fish species hiding among a branching antipatharian at *Yongala*. (Photos: Erika Gress).

Discussion

The ongoing decline of reefs globally has prompted greater interest in the functional roles of different reef-associated taxa for preserving functional coral reef ecosystems (Bellwood et al. 2004a, Darling et al. 2012, McLean et al. 2021). Nonetheless, studies of key ecological functions in corals (e.g. reef accretion and habitat provision) have focused almost exclusively on scleractinians. While reef accretion is mainly attributable to scleractinians and calcifying algae, other benthic taxa provide important habitat complexity that supports coral reef biodiversity and ecosystem functioning. Our study represents one of the first to examine the role of antipatharians in supporting fish communities on shallow tropical reef ecosystems. We provide empirical evidence for the contribution of antipatharians for habitat provision in reefs where scleractinians are not the dominant benthic group. We found that antipatharians support overlapping fish species when compared to scleractinians, but also unique fish species and unique types of associations with fishes. Importantly, at the functional level, fish assemblages showed high similarity between the two coral taxa, suggesting that antipatharians may be able to support some redundancy of fish functional roles if scleractinians decline. Consequently, our findings highlight that antipatharians are important components of shallow tropical marine ecosystems that support a diverse range of fish species that utilise them for a range of different purposes.

Fish communities associated with antipatharians

Of the 28 different species (within seven functional groups) associated with antipatharians, the most common and abundant species were primarily using the colonies as shelter (HovH, HovA behaviours; Appendix 1). This is not surprising considering the ample shelter capacity that branching corals provide for small-bodied fish and/or juvenile fish (Beukers et al. 1997, Kerry and Bellwood 2015b), which is the most common morphology of antipatharians on both surveyed sites (Figure 2; Supplementary 1). This type of association (hovering around the colonies for protection) was not restricted to small-bodied fish – at both sites, we also recorded larger fish (e.g. *Lutjanus russellii*, *L. carponotatus*, *Platax pinnatus*) hovering behind antipatharian colonies (Figure 2a; Appendix 1). These larger fish may be using the antipatharian colonies to shelter from strong currents or to ambush prey. Additionally, we documented corallivorous fish (e.g. *Chaetodon rainfordi*, *Heniochus acuminatus*) feeding on antipatharian polyps (Figure 2b; Appendix 1). We also observed several *Gobiodon* species using antipatharians as habitat (Figure 2c; see also Allen et al. 2004), but we were not able to quantify the abundance of these cryptic fish using MaxN through video analysis. Nonetheless, further studies of cryptic reef fishes and their symbiosis with antipatharians deserves attention due to their important role in coral reef energy transfer (Brandl et al. 2019b).

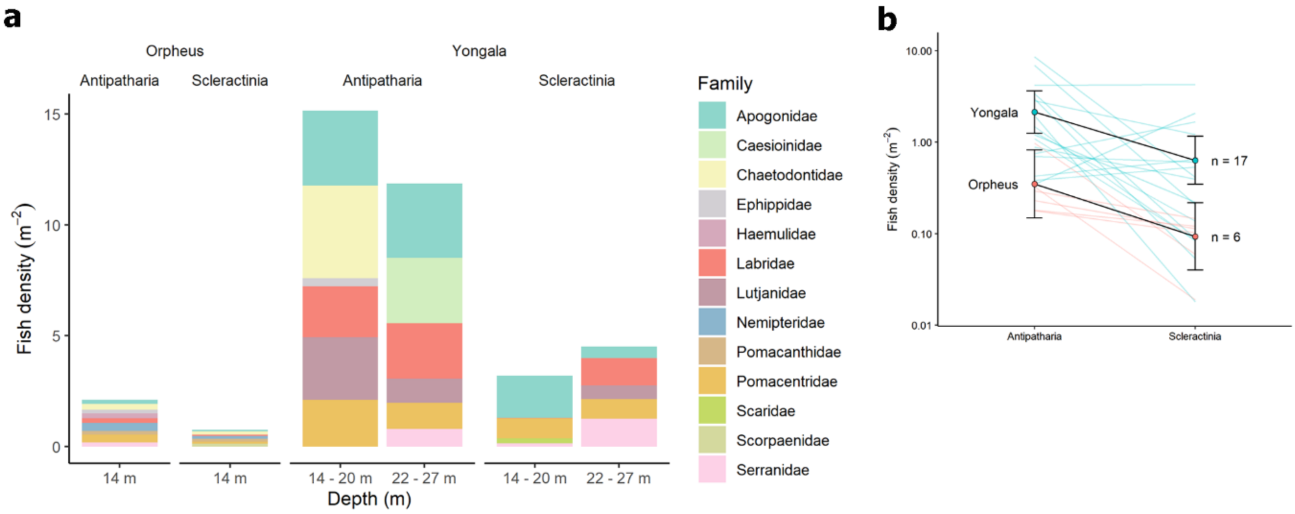

Figure 3 | Fish density associating with antipatharians and scleractinians at *Yongala* and Orpheus: **a)** Fish density m^{-2} showing the contribution of each family proportional to the average density of fish within the family. **b)** Marginal effects plot of mean fish density m^{-2} predicted for each coral taxa (Model 3 in Table 1). Coloured lines connect colony pairs (one antipatharian and one scleractinian) for each of the two sites: 34 colonies at *Yongala* (n = 17 colony pairs), and 12 colonies at Orpheus (n = 6 colony pairs) surveyed.

The use of antipatharians as nocturnal shelter by predator fishes has been reported from mesophotic reefs in Hawaii (Boland and Parrish 2005). In this current study conducted during daylight hours, we documented predator fishes (e.g. *Plectropomus leopardus*, *Cephalopholis boenak*) laying static next to or under antipatharian colonies (Stat_in behaviour; Appendix 1), which were potentially sheltering or waiting to ambush smaller fish. While not recorded on our stationary videos, we also observed other species of conservation interest and commercial value, such as the marble-grouper (*Epinephelus fuscoguttatus*), laying static among antipatharian colonies (Figure 2d). In addition, cleaner wrasse (*Labroides dimidiatus*) – which uses the antipatharians as habitat and refuge (Appendix 1) – attracted larger fish (e.g. *Diagramma pictum labiosum*, *Platax teira*) which hovered next to the coral colonies to get cleaned (Figure 2e; Appendix 1).

Several large predator fish (e.g. *Carangoides fulvoguttaus*, *Plectropomus maculatus*, *Lutjanus monostigma*, etc.) were observed passing by; and despite these fishes being likely foraging, we did not observed any actual predation events on the stationary cameras due to their limited field of view. Schools of the greater amberjack (*Seriola dumerili*), the bluefin tuna (*Tunnus thynnus*), and the yellowmouth barracuda (*Sphyraena viridensis*) have been documented searching for fish prey among antipatharian forests on TMEs in the Mediterranean (Chimienti et al. 2020). Consequently antipatharians are clearly important for a range of fish species, providing both protection for prey and foraging opportunities for predators. This highlights the role of antipatharians in one of the most fundamental ecological dynamics on coral reefs (Hixon and Beets 1993).

Influence of the different variables on the fish community observed

Site. We found site to have a significant effect on the fish density and richness m^{-2} (Table 1), which was not unexpected considering that fish communities on shipwrecks are known to differ to those found on natural reefs (Nieves-Ortiz et al. 2021, Sánchez-Caballero et al. 2021). Nonetheless, differences in fish richness and abundance are also evident from studies comparing both similar and distinct coral reef morphologies, and are often driven by site-level factors (Gilby et al. 2016, Galbraith et al. 2021). Despite fish density and richness being higher at *Yongala* (Figure 1 & 3), the diversity of fish functional groups was similar on both sites irrespectively of the coral taxon (five functional groups for all except for *Yongala* for antipatharians, which had six) \ (Figure 1c). The most dominant functional groups were micro-invertivore, planktivore and pisci-invertivore for both sites and for both coral taxa (Figure 1c), which suggest that, at the fish functional level, sites were less influential.

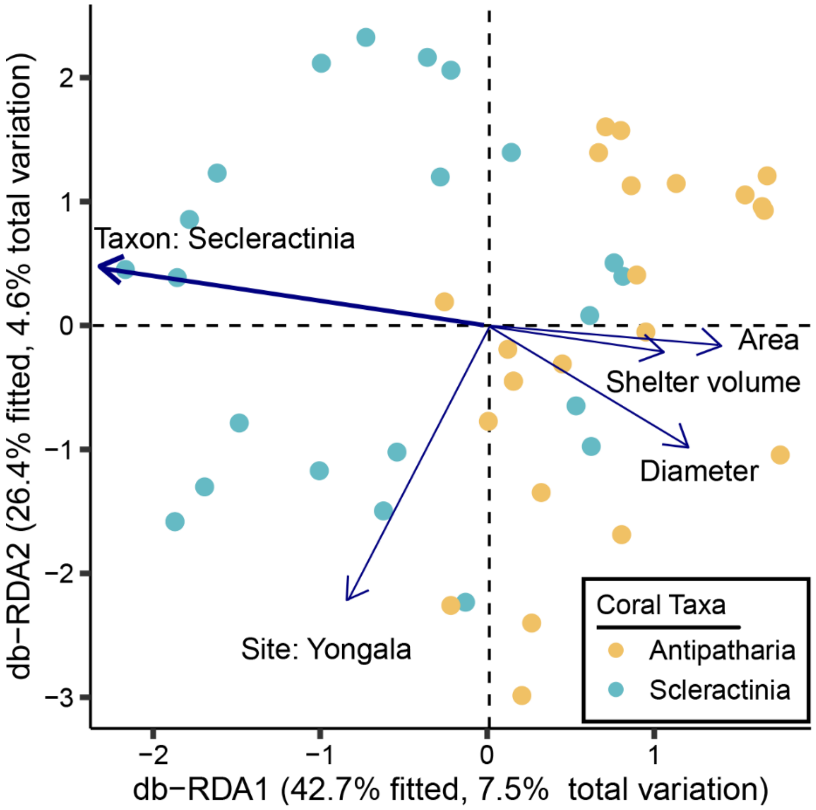

Figure 4 | Distance-based redundancy analysis (dbRDA) of fish communities associated to antipatharian (yellow dots) and scleractinian (blue dots) colonies. Vectors (arrows) represent the different variables tested on their significance as drivers of the fish community. The length and direction of the arrow represents the magnitude and direction of the relationship. Coral taxon (thicker arrow) was identified as the only significant variable (p <0.05) influencing the fish community (Supplementary 1).

At *Yongala*, depth did not have a significant effect on the fish community (Table 1), which is not surprising because most of the fish recorded occur across the depth gradient examined (<30 m depth). The one exception was *Ostorhinchus cladophilos*, which is not typically found above 20 m depth. Nonetheless, 62% of the fish recorded in this study inhabit mesophotic ecosystems (Froese & Pauly 2023). This is a similar result to a study from Hawaii, where 95% of the fish documented in association with antipatharians on mesophotic reefs are also found on shallow reefs (Boland and Parrish 2005). In contrast, in antipatharian forests from the eastern Atlantic, the most abundant species and functional entities (i.e. combination of fish traits) shifted, even when 90% of the fish functional entities were shared between shallow and mesophotic reefs (Bosch et al. 2023). Thus, antipatharians might promote specialisation of reef fishes along the reef depth gradient (Bosch et al. 2023), which is yet to be investigated on tropical reefs.

Table 1 | Summary table of the generalised linear mix-effect models (GLMMs). Model numbers (first column) correspond to the name given on Supplementary 2, which contains full model summaries, estimated marginal means and contrast analysis results. Significant factors in each model are in bold.

	Test - effects	**Formula**	**Parameters**	**p-value**	**Test statistic**
Model 1a	Depth on fish density m^{-2} - antipatharians at *Yongala*	Density m^{-2} ~ Depth range	Depth range	0.762	0.30
Model 1b	Depth on fish density m^{-2} - scleractinians at *Yongala*	Density m^{-2} ~ Depth range	Depth range	0.619	0.49
Model 2a	Depth on fish richness m^{-2} - antipatharians at *Yongala*	Richness m^{-2} ~ Depth range	Depth range	0.083	1.73

Model 2b	Depth on fish richness m^{-2} - scleractinians at *Yongala*	Richness m^{-2} ~ Depth range	Depth range	0.380	0.90
Model 3	Coral taxon and site on fish density m^{-2}	Density m^{-2} ~ Coral taxon * Site + (1 | Pair)	Intercept (Antipatharia-Oprheus) **Coral taxon** only effect (Scleractinia**)** **Site** only effect (Yongala**)** Interaction effect (Scleractinia: Yongala)	0.013 **0.019** **< 0.001** 0.871	2.47 2.33 3.6 0.16
Model 4	Coral taxon and site on fish richness m^{-2}	Richness m^{-2} ~ Coral taxon * Site + (1 | Pair)	Intercept (Antipatharia-Oprheus) Coral taxa only effect (Scleractinia**)** **Site** only effect (Yongala**)** Interaction effect (Scleractinia: Yongala)	< 0.001 0.273 **0.004** 0.149	12.1 1.09 2.87 1.44
Model 5a	Area m^2 and coral taxon on fish abundance	Abundance ~ Area m^2 * Coral taxa + (1 | Colony_ID)	Intercept (Antipatharia) Area m^2 only effect **Coral taxon** only effect **(**Scleractinia**)** Interaction effect (Area m^2: Scleractinia)	< 0.001 0.202 **< 0.001** 0.459	13.2 1.27 4.33 0.74
Model 5b	Shelter dm^3 and coral taxon on fish abundance	Abundance ~ Shelter dm^3 * Coral taxon + (1 | Colony_ID)	Intercept (Antipatharia) Shelter dm^3 only effect **Coral taxon** only effect **(**Scleractinia**)** Interaction effect (Shelter dm3:Scleractinia)	< 0.001 0.587 **< 0.001** 0.169	16.1 0.54 4.89 1.37
Model 6a	Area m^2 and coral taxon on fish richness	Richness ~ Area m^2 * Coral taxon + (1 | Colony_ID)	Intercept (Antipatharia) **Area m2** only effect **Coral taxon** only effect **(**Scleractinia**)** Interaction effect (Area m^2: Scleractinia)	< 0.001 **< 0.001** **0.024** 0.734	8.60 2.73 2.25 0.33
Model 6b	Shelter dm^3 and coral taxon on fish richness	Richness ~ Shelter dm^3 * Coral taxon + (1 | Colony_ID)	Intercept (Antipatharia) **Shelter dm^3** only effect **Coral taxon** only effect **(**Scleractinia**)** Interaction effect (Shelter dm^3:Scleractinia)	< 0.001 **0.013** **0.004** 0.055	11.2 2.47 2.85 1.91

Density m^{-2} refers to the standardised fish abundance m^{-2}; and *Abundance* is the sum of MaxN of all fish species counted on every coral colony, and then added for each coral taxa.

Area and Shelter volume. In addition to colony area (m^2), we used shelter volume (dm^{-3}) to quantify one of the most important ecological functions of corals – shelter provision (Urbina-Barreto et al. 2021, 2022). Importantly, shelter volume encompasses both the area of the coral and its morphology, both of which influence specific ecological functions (e.g. Lingo and Szedlmayer 2006; Kerry and Bellwood 2015a). In light of the lack of proxies to estimate shelter volume specifically for antipatharians, we use the ones developed for scleractinians (Urbina-Barreto et al. 2021). Our results suggest that these proxies adequately capture shelter volume in antipatharians (Supplementary 1). Nonetheless, dedicated proxies for antipatharians would be preferable for future studies. Notably, our models results were similar regardless of whether area or shelter volume was used (Table 1).

Structural complexity is a key predictor of both fish abundance and species richness on coral reefs (Graham and Nash 2013, Darling et al. 2017, Urbina-Barreto et al. 2022). However, in our study shelter volume influenced fish richness, but not abundance. Despite greater shelter volume comprising more habitat, niche space within a colony is more homogenous than at the colony perimeter (Robertson 1996, Holbrook and Schmitt 2002, Boström-Einarsson et al. 2014). Therefore, our results could be related to large colonies - with homogenous internal shelter volume - regulating fish abundance through competitive interactions. Additionally, nuanced relationships between patch habitat area and edge interactions with surrounding habitats are often associated to species richness, but not to abundance (Fonseca 2008, Hattori and Shibuno 2015). For instance, fish species richness may be enhanced around the colony perimeter where the habitat is more complex and where opportunities for interactions with surrounding habitat are optimised (Hattori and Shibuno 2015).

Coral taxon. The density, abundance and species richness of fish communities varied significantly between antipatharians and scleractinians (Table 1; Figure 4 & 5). The total number of species recorded in association with antipatharians was 28 (from 11 Families), and 21 with scleractinians (from 10 families) \ (Figure 1). Nonetheless, both coral taxa supported seven functional groups (Figure 1c). Almost one-third (32%) of the fish species associated with both coral taxa, and despite some species found in unique association with either scleractinians or antipatharians (Figure 5a), none of these species are considered as either antipatharian or scleractinian specialist (Appendix 1) \ (Froese & Pauly 2023). One potential explanation for the difference in fish richness among coral taxa is the type of association with the corals. For instance, while the most abundant families (Apogonidae, Pomacentridae, Labridae) were shared between both coral taxa, Lutjanidae was 80% more abundant for antipatharians (Figure 1). Within the family Lutjanidae, *L. russellii* and *L. carponotatus* were only recorded in association with antipatharians, and both fish species appeared to be using the colonies as shelter from currents (HovH behaviour; Figure 2a; Appendix 1). Similar specific interactions have been observed for scleractinians; for example, some fish use tabular *Acropora* colonies to protect themselves from solar irradiance (Kerry and Bellwood 2015b). Therefore, species-specific associations may contribute to dissimilarities in the fish species associating with antipatharians and scleractinians.

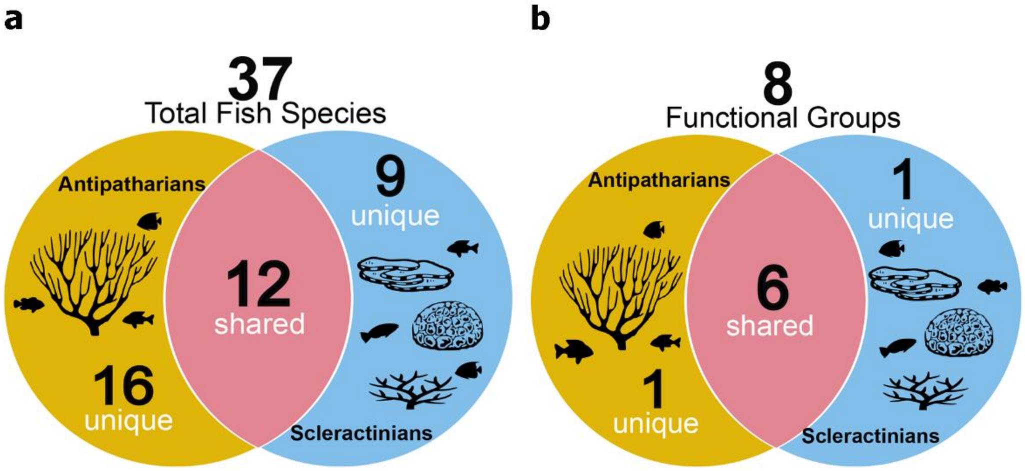

Figure 5 | a) Unique and shared fish species associated to each coral taxon. **b)** Unique and shared trophic groups associated to each coral taxon.

Variation in fish richness may also be attributable to intrinsic differences in morphological complexity between the two coral taxa. The differences in complexity and branching arrangement between antipatharians and scleractinians are shown in Figure 2 (f,g,h). Antipatharians do not grow as massive or encrusting colonies, and all growth forms extend vertically off the substrate, thereby increasing the exposed area available for habitat. Moreover, the canopy-like effect created by most antipatharian growth forms can enhance fine-scale hydrodynamic conditions (e.g. upwelling) that promote the retention of plankton and juvenile fish, which benefits planktivorous, intertivorous and piscivorous fish species (Guizien and Ghisalberti 2017). Additionally, habitat spaces provided by densely branched colonies might also influence fish density due to the schooling behaviour of most planktivore fishes, and the refuge availability and survivorship for juvenile and small-bodied fish. While shelter volume provides a quantitative measure of the space available for shelter, it is based on colony area or diameter (Urbina-Barreto et al. 2021); therefore, it does not capture the elevation from the substrate (colony height). This could explain why neither shelter volume nor area had a significant effect on fish abundance.

Numerous studies have identified colony height as a more influential factor driving fish assemblages than surface area or coral shape (Harborne et al. 2012, Fisher 2023). Therefore, future studies should quantify both shelter volume and colony height of corals when examining their correlation with fish assemblages. Additionally, the development of proxies specifically for antipatharians could enable finer-scale morphological differences to be captured. This information will enable trait-based approaches to understanding coral reef function to be extended to a wider range of benthos, rather than just scleractinians – an important approach considering scleractinians are not necessarily the dominant habitat-forming benthos in many shallow tropical ecosystems.

Implications for conservation

The importance of trait-based approaches to support and guide local and regional conservation strategies in light of the current coral reefs crisis is now well recognised (Bellwood et al. 2004b, Hughes et al. 2017a, McLean et al. 2021). However, most studies utilising trait-based approaches in coral reef ecology and the influence of benthic communities on fish assemblages focus on scleractinians (e.g. Harborne et al. 2012, Darling et al. 2017, Fisher 2023). Our study highlights that other coral taxa can significantly influence reef fish communities, playing an important role in providing three-dimensional habitat complexity on shallow tropical reefs. Other habitat-forming benthic groups have been previously considered (e.g. octocorals and sponges - Moynihan et al. 2022, González-Murcia et al. 2023); however, antipatharians are commonly neglected from coral reef monitoring programs and studies. A greater effort to quantify the abundance and ecological roles of the different benthic groups would lead to a more holistic understanding of how the different benthic taxa interact to support coral reef biodiversity.

While antipatharians are not abundant in the shallowest depths (<10 m), they are common in most other reef habitats from shallow and mesophotic depths (Wagner et al. 2012, Molodtsova et al. 2023). Importantly, antipatharians are less susceptible to the phenomenon known as bleaching (Gress et al. 2021), and other climate related stressors (Godefroid et al. 2023) than scleractinians. Given the impact of bleaching events on scleractinians (Hughes et al. 2017b, 2018), the importance of other coral taxa in supporting and maintaining reef ecological functions requires a greater understanding to account for in conservation strategies.

Human activities such as fisheries, mining, jewellery industry and pollution has led to some antipatharian species being listed as “near threatened” by the International Union for Conservation of Nature (IUCN) Red List of the Mediterranean (Bo et al. 2008, 2017). Nonetheless, the status of antipatharian species outside the Mediterranean remains unknown despite evidence of declines on some tropical reefs (Grigg 2004, Boland and Parrish 2005, Gress and Kaimuddin 2021). Considering the relevance of antipatharians in supporting reef biodiversity, we argue that a greater effort should be afforded to understanding the role of antipatharians and their status in a wider range of geographic locations.

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Data availability: The datasets generated during the current study are available via the following link: figshare.com/s/xxx (currently private-for-peer review).