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Ecological status of coral communities in Investigator Shoal of the Spratly Islands, South China Sea

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Abstract
The Spratly Islands in the South China Sea are renowned for their remarkable reefs and serve as critical habitats for diverse corals and marine life. These reefs also provide livelihood benefits through fisheries and tourism, although their accessibility is limited due to remote location and geopolitical disputes. Despite the combined impacts of rampant and unregulated artificial island construction, along with outbreaks of Crown-of-Thorns Starfish (COTS), many reefs in the region remain ecologically significant and warrant conservation efforts. Investigator Shoal, a remote atoll in the Spratlys holds great potential for scientific exploration of its coral communities. This study aimed to assess the ecological status of coral reefs in this atoll by examining the condition, diversity and abundance of corals. Surveys were conducted using the Coral Video Transect (CVT) method at two different depths (10 m and 20 m) across ten reef sites. The data were analysed using the Coral Point Count with Excel extension (CPCe) software. Overall, the reef assemblages showed a mean live coral cover of 46.4% ± 3.4, categorized as 'Fair' condition, with all reef sites had relatively high coral diversity. A total of 168 species from 64 genera and 22 families of hard and soft corals were identified. The soft coral *Xenia*, and the hard corals *Acropora* and *Porites* had the highest mean coverage and were abundant in the study area. Additionally, four rare and 19 vulnerable coral species were recorded, highlighting the ecological importance of these reefs despite the apparent impacts of land reclamation and COTS outbreak. The data presented in this study serve as baseline information for future conservation plans in the remote reefs of the Spratly Islands.

Keywords Spratly Islands · Anthropogenic stressor · Coral abundance · Hard coral · Scleractinia

1 Introduction

Coral reefs, often referred to as the "rainforest of the ocean", are known for their high productivity and immense biodiversity [1, 2]. They cover less than 0.1% of the ocean floor, yet are ecologically important habitats for roughly one-third of all marine species [3, 4]. The reefs serve as nurseries for various fish species, delivering substantial

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economic benefits to communities worldwide [5, 6, 7]. Globally, reef ecosystems support artisanal and commercial fisheries, ensuring food security for millions of people, particularly in Pacific Island countries where fishing is a primary source of food and income [8–10]. Moreover, the scleractinian reef structures protect coastlines by dissipating wave energy and preventing erosion [10]. Beyond these benefits, coral reefs contribute to marine productivity by facilitating nutrient cycling [11]. Their aesthetic appeal attracts tourists, generating revenue and employment for coastal communities [12]. While tourism offers untapped potential for citizen science [13, 14], coral reefs also serve as natural laboratories for understanding of marine ecology [15].

However, coral populations at local and regional scales face significant threats from human-driven activities associated with coastal urbanization [16]. These activities contribute to deforestation and increase nutrient and sediment runoff, which collectively compromise coral health and connected habitats [17, 18]. Land-based pollution, including agricultural runoff, industrial discharges and plastic waste suffocates corals and impairs their capacity for photosynthesis and growth [19–21]. Destructive fishing practices have further damaged reef structures and reduced fish populations [2]. Such pressures, combined with the effects of ocean warming and acidification have intensified coral bleaching and increased vulnerability to disease [22–25]. These challenges demand immediate conservation action, including community engagement and education on sustainable coastal development and fishing practices to prevent further reef degradation [26].

Remote islands are not spared from these threats. While isolated reefs are often considered resilient to direct human stressors due to their uninhabitability, they remain vulnerable to global climate change [27], destructive fishing practices [28] and geopolitical interests [29, 30]. The Spratly Islands, bordering the Coral Triangle are presumed to be rich in marine biodiversity [31, 32], supporting over 6500 marine species [33] and some 571 identified coral species in the South China Sea (SCS) [34]. Situated in the southern part of the SCS, the islands consist of over 150 coral formations, including reefs, banks, shoals, atolls, and small islets, serving as crucial breeding and stocking grounds for numerous marine organisms [35]. However, coral health in this region has faced increasing deterioration due to multiple stressors.

In the early 2000s, several offshore reefs in the Spratly Islands experienced a sharp decline in coral cover, from above 80% to below 6%, primarily due to destructive fishing practices and the effects of thermal anomalies [28]. While risks from marine-based pollution and sedimentation were considered low, the use of dynamite and cyanide [2, 36], along with destructive poaching of giant clams by Chinese fishermen using boat propellers, are of particular concern to some atolls [37, 38]. Additionally, large-scale dredging and land reclamation by multiple countries, competing for territorial and military bases have led to the destruction of nearby reef areas [29]. Global climate change, driven by elevated water temperatures has further shifted coral species composition [39], favouring thermally resistant species across 15 sites in the Spratly Islands [35]. Outbreaks of crown-of-thorns starfish (COTS) have also inflicted considerable damage. For instance, a survey at Layang-Layang Island recorded over a thousand COTS across a 7000 m^2 reef area, with extensive damage observed on the southwestern of the atoll [40]. Similar outbreaks were reported at four localities in the Spratly Islands between 2018 and 2021, along with the spread of the coral-killing sponge *Terpios hoshinota*, covering more than 50% of dead scleractinians on two surveyed reef slopes [41].

Despite the severity of these impacts, a lack of baseline data on coral health makes it challenging to identify factors affecting reef biodiversity and limits the ability to provide conservation strategies [42]. Documentation and monitoring efforts are essential to understand how coral communities respond to anthropogenic and climate change disturbances (e.g., [43–46]). While some studies documented species richness in the Spratly Islands, for example, Zhao et al. [47] identified 153 species from 56 genera of scleractinian corals in Nansha Islands, and Latypov [48] recorded 261 species from 71 genera in Vietnam Reefs, baseline data remain sparse for many remote sites, including Investigator Shoal. In May 2022, a scientific expedition was conducted by the Fisheries Research Institute (FRI) Sarawak to survey corals at 10 selected sites around Investigator Shoal using the Coral Video Transect (CVT) method. The primary objective was to assess the ecological status of coral communities by evaluating coral conditions and documenting patterns of species diversity and abundance across the reef sites. The findings provide baseline data into the current status of coral communities in Investigator Shoal that will support future studies and may contribute to evidence-based conservation and management strategies for coral reefs across the Spratly Islands Table 1.

Table 1 Localities of 10 reef sites and two depths (10 m & 20 m) around Investigator Shoal of the Spratly Islands, SCS

Reef site	Latitude (N)	Longitude (E)	Transect depth (m)	Survey date
S1	8.131325	114.5331	10	16/5/22
	8.131325	114.5331	20	16/5/22
S2	8.148494	114.6112	10	17/5/22
	8.148494	114.6112	20	17/5/22
S3	8.160908	114.6687	10	18/5/22
	8.160908	114.6687	20	18/5/22
S4	8.181347	114.7154	10	16/5/22
	8.181347	114.7154	20	16/5/22
S5	8.169389	114.7610	10	17/5/22
	8.169389	114.7610	20	17/5/22
S6	8.143842	114.7800	10	18/5/22
	8.143842	114.7800	20	18/5/22
S7	8.121544	114.8058	10	19/5/22
	8.121544	114.8058	20	19/5/22
S8	8.094492	114.7763	10	16/5/22
	8.094492	114.7763	20	16/5/22
S9	8.077019	114.7287	10	17/5/22
	8.077019	114.7287	20	17/5/22
S10	8.081231	114.6540	10	18/5/22
	8.081231	114.6540	20	18/5/22

2 Methods

2.1 Study area

The Spratly Islands are situated within an oval-shaped area between 6° and 12° N latitude and 109° and 117° E longitude, spanning an ocean expanse of approximately 160,000 to 500,000 km^2, depending on the defined maritime boundaries [50]. The Spratly Islands are partially or fully claimed by six countries, namely Brunei, China, Malaysia, the Philippines, Taiwan and Vietnam. Some coral islands and atolls, including the Spratlys and Paracels, are primarily used as military bases and strategic outposts [30]. This study focuses on the coral atoll known as Investigator shoal or *Terumbu Peninjau* in Malay (Fig. 1). Investigator shoal is one of several atolls within the Spratly Islands (alongside Erica Reef, Mariveles Reef and Swallow Reef), and is currently occupied by the Royal Malaysian Navy. Situated in the eastern part of the Spartly archipelago, the atoll spans an area of approximately 205 km^2. It is characterized by a distinctive club-shaped structure with a large central Sect. (1–2 km wide) and a narrow extension that stretches westward (1.5 m or less) [49]. This study was conducted at 10 selected reef sites around Investigator Shoal, where coral video recordings were carried out at 10 m and 20 m depths (Table 1). Depth selection was influenced by the morphology of the reef slope, as the northern side features a steep gradient of approximately 45°, while the southern side has a more gradual incline (FRI Sarawak, pers. comm.).

2.2 Underwater coral survey

The Coral Video Transect (CVT) method was used for coral surveys, following the procedures described by 51. [52]. At each reef site, a 100 m transect line was deployed and divided into four 20 m segments, separated by 5 m intervals. This segmentation allowed for the detection of small-scale spatial variability in benthic composition along the transect. The transect lines were laid parallel to the shoreline and aligned with the reef contour to ensure consistency in habitat orientation. A high-resolution 4 k GoPro Hero 12, protected in a waterproof casing was used to record the video footage. For each segment, four minutes of continuous video were captured to obtain high-quality and clear images for accurate coral identification. To maintain consistency in image quality and scale across sites, a reference bar was used to set the distance between the camera and substrate at 0.5 m. The camera was held at a perpendicular angle to the substrate throughout the survey.

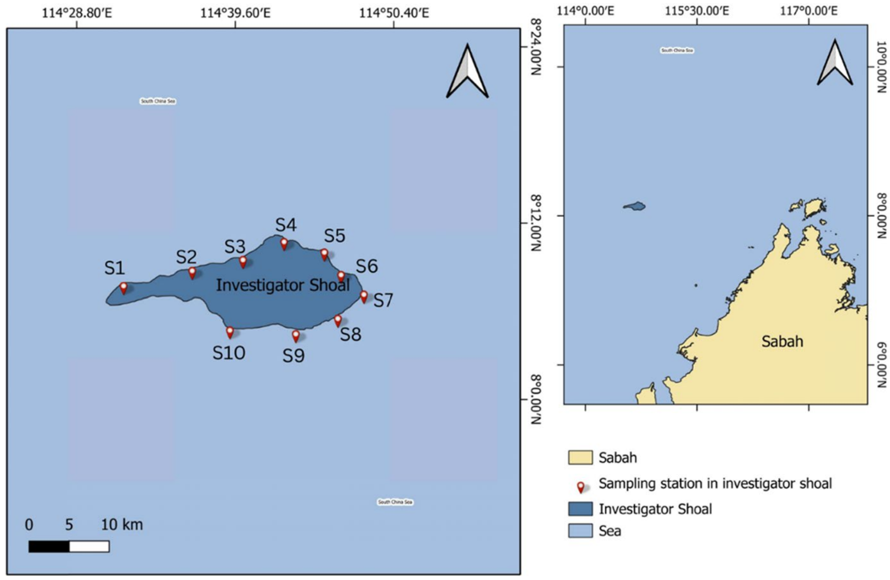

Fig. 1 Locations of 10 reef sites (S1–S10) around Investigator Shoal in the Spratly Islands, SCS

2.3 Video processing, image identification and data analysis

A total of 160 non-overlapping still images were extracted from the recorded videos at regular intervals (40 images per 20 m segment) to capture representative spatial coverage across each reef site. These images were further analyzed using Coral Point Count with Microsoft Excel extension (CPCe) software, version 4.1 [52], which enabled standardized quantification of benthic composition. A grid of 25 uniform quadrats was overlaid on each image, resulting in 4000 data points per 100 m transect line. The scleractinian hard corals were identified using the Indo Pacific Coral Finder Toolkit [53] and the online reference Corals of the World [54]. Meanwhile, soft corals and other benthic organisms were classified based on Fabricius & Alderslade [55] and Humann & DeLoach [56], respectively. A comprehensive species checklist of scleractinian corals was arranged alphabetically.

The data were summarized as the mean percentage cover for seven major benthic categories: hard corals (scleractinians and non-scleractinians), soft corals (including sea fans), dead corals (coral rubble and dead coral with or without algae overgrowth), coralline algae, other algae (various macroalgal species), other invertebrates (including sea anemones, sponges, echinoderms, and mollusks) and abiotic elements (sand, silt, and rock). The coral condition was categorized based on the mean percentage cover of live corals (hard and soft corals), following Chou et al. [57]. The classifications were defined as follows: excellent (> 75% live coral cover), good (51–75%), fair (26–50%) or poor (< 25%). The relative abundance of each coral genus was represented using a five-level rating scale, adapted from Fabricius & McCorry [58]: + = one or covering < 1% of coral colonies, + + = uncommon covering 1–5% of coral colonies, + + + = common covering 6–10% of coral colonies, + + + + = abundant covering 11–20% of coral colonies and + + + + + = dominant covering > 20% of coral colonies. The relative abundance and conservation status for each species were referred from Veron et al. [54] and IUCN Red List [59]. Abundance categories included: Not Evaluated (NE), Sometimes Common (SC), Common (C), Uncommon (UC) and Rare (R). Meanwhile, conservation status categories were Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU) and Endangered (EN).

2.4 Statistical analysis

Statistical comparisons were conducted to evaluate the mean percentage cover of seven benthic categories across different reef sites and depths. Normality tests, including the Kolmogorov–Smirnov test [60] and Shapiro–Wilk test [61] confirmed that the data followed a normal distribution. Hence, differences in the mean percentage cover of corals and other benthic categories between reef sites and depths were assessed using a One-way Analysis of Variance (ANOVA), followed by Post-hoc Tukey HSD tests. The cluster analysis was conducted to examine groups with similarity across reef sites, based on the mean percentage cover of coral genera. Prior to analysis, the data were normalized using a log (x + 1) transform function and analysed using the Bray Curtis method [62]. A non-metric multidimensional scale (nMDS) plot was then generated to visually represent similarity groupings among reef sites, based on interactions derived by the cluster analysis. In addition, a Similarity Percentage (SIMPER) analysis was conducted to estimate the mean similarity of dominant coral compositions between different groups, as illustrated in the nMDS plot. All univariate and multivariate statistical analyses were carried out using PAST software version 3 [63].

3 Results

3.1 Mean percentage cover of benthic categories and coral condition

The mean percentage cover of hard corals varied significantly across the 10 reef sites ($F_{9,70} = 2.82$, $p < 0.05$), as did the cover of soft corals ($F_{9,70} = 3.36$, $p < 0.01$), dead corals ($F_{9,70} = 10.63$, $p < 0.01$), coralline algae ($F_{9,70} = 49.05$, $p < 0.01$), other invertebrates ($F_{9,70} = 4.84$, $p < 0.01$) and abiotic elements ($F_{9,70} = 3.88$, $p < 0.01$). The post-hoc test indicated that the mean percentage cover of hard corals ranged from 21.2% to 53.2%, was the highest value recorded at S1 (53.2% ± 6.7) (Table 2). Meanwhile, a higher mean percentage cover of soft corals was recorded at S6 (19.9% ± 2.9) and S10 (18.1% ± 2.2). The mean percentage cover of dead corals ranged from 8.4% to 54.8%, with significantly higher values recorded at S7 (54.8% ± 8.2) and S2 (50.4% ± 6.3) compared to other sites. Significant differences were also observed for coralline algae, other invertebrates, and abiotic elements across reef sites, with the highest values recorded at S3 (31.8% ± 4.2), S10 (4.4% ± 1.1) and S5 (24.0% ± 10.1), respectively. No significant differences were found in the mean percentage cover of other algae, including *Padina*, *Halimeda* and turf algae, although the highest value was recorded at S2 (2.5% ± 1.1). When comparing depths, the mean percentage cover of hard corals ($F_{1,6} = 10.47$, $p < 0.05$), was significantly higher at 10 m (42.4% ± 2.6) than at 20 m (28.5 ± 2.3) (Fig. 2). Similarly, the mean percentage cover of dead corals was higher at 10 m (32.8 ± 3.7) compared to 20 m (28.6% ± 3.6), although the difference was not statistically significant. In contrast, other benthic categories, including soft corals (13.9% ± 1.1) ($F_{1,6} = 39.02$, $p < 0.01$), coralline algae (15.1% ± 2.4) ($F_{1,6} = 6.26$, $p < 0.05$), other invertebrates (2.5% ± 0.4) ($F_{1,6} = 138.80$, $p < 0.01$) and abiotic elements (10.3% ± 0.88) ($F_{1,6} = 41.25$, $p < 0.05$), were higher at 10 m compared to 5 m. Overall, the coral communities around Investigator Shoal were categorized as 'Fair' condition, with an average live coral cover of 46.4% ± 3.4. Four reef sites (S1, S3, S6, S10) were classified as 'Good' condition, while the remaining sites (S2, S4, S5, S7, S8, S9) were in 'Fair' condition (Table 2).

3.2 Mean percentage cover, diversity and abundance patterns of coral genera

A total of 64 coral genera from 22 families were recorded across 10 reef sites around Investigator Shoal (Table 3). Among these, 53 genera were identified as scleractinian hard corals, three as non-scleractinian hard corals and eight as soft corals. The soft coral genus *Xenia* exhibited the highest mean percentage cover at 18.3% ± 1.5, followed by *Acropora* (16.1% ± 2.1), *Porites* (11.4% ± 0.7), *Pocillopora* (4.8% ± 0.7), *Goniastrea* (3.9% ± 0.4), *Isopora* (3.7% ± 0.9) and *Dipsastraea* (3.6% ± 0.6). The remaining coral genera each accounted for less than 3% of the total cover. The relative abundance analysis revealed that the following coral genera were commonly observed across all reef sites: *Acropora*, *Astreopora*, *Isopora*, *Montipora*, *Pavona*, *Galaxea*, *Ctenactis*, *Fungia*, *Herpolitha*, *Pleuractis*, *Leptastrea*, *Lobophyllia*, *Coelastrea*, *Cyphastrea*, *Dipsastraea*, *Echinopora*, *Favites*, *Goniastrea*, *Hydnophora*, *Merulina*, *Pectinia*, *Platygyra*, *Pachyseris*, *Pocillopora*, *Seriatopora*, *Porites*, *Sarcophyton*, *Sinularia* and *Xenia*. Notably, several reef sites within Investigator Shoal were dominated by *Xenia* (S3, S6, S7) and *Acropora* (S3, S4, S7). These genera, along with *Porites* (S2, S3, S5, S7, S8, S9, S10) were particularly abundant across the study area.

3.3 Species checklist of scleractinian hard and soft corals

Based on the species checklist of hard and soft corals from Investigator Shoal, a total of 168 species belonging to 64 genera and 22 families were recorded (Table 4). S1 had the highest number of species (118), followed by S4 (112 species), S2 (106 species) and S8 (103 species). Meanwhile, the lowest species richness was observed at S6, with 75 recorded species. Among the 168 recorded species, 38 species were identified as the most common and recorded at all reef sites, while 27 species were recorded at only one site, thus considered the least common. The abundance and conservation categories of all 168 hard coral species from Investigator Shoal were also documented. Three percent of the recorded species (4 species) were classified as 'rare'. According to Veron et al. [54], the abundance of each species reflects a general global context, whereby a species may be common in a specific area but are globally rare. The majority of species were

Table 2 The mean percentage cover (% ± SE) of seven benthic categories at 10 reef sites around Investigator Shoal in the Spratly Islands, SCS

Reef site	Hard corals (%)	Soft corals (%)	Dead corals (%)	Coraline algae (%)	Other algae (%)	Other inverte-brates (%)	Abiotic element (%)	Coral condition
S1	53.2 ± 6.7^{a}	8.9 ± 2.7^{b}	35.2 ± 5.8	0.1 ± 0.0^{b}	0.8 ± 0.5	0.1 ± 0.1^{b}	1.7 ± 1.3^{b}	Good (62.1%)
S2	38.6 ± 4.9^{b}	5.2 ± 2.0^{b}	50.4 ± 6.3^{a}	0.3 ± 0.2^{b}	2.5 ± 1.1	1.8 ± 0.8	1.1 ± 0.5^{b}	Fair (43.8%)
S3	39.7 ± 6.2^{b}	14.7 ± 2.0	8.4 ± 1.3^{b}	31.8 ± 4.2^{a}	1.4 ± 0.3	2.9 ± 0.8	1.2 ± 0.3^{b}	Good (54.4%)
S4	34.0 ± 4.2^{b}	6.4 ± 2.6^{b}	46.4 ± 7.1	0.5 ± 0.3^{b}	0.3 ± 0.1	0.1 ± 0.0^{b}	12.4 ± 4.7	Fair (40.4%)
S5	28.1 ± 5.9^{b}	6.3 ± 3.3^{b}	38.2 ± 9.7	1.8 ± 1.0^{b}	0.3 ± 0.1	1.3 ± 0.6^{b}	24.0 ± 10.1^{a}	Fair (34.4%)
S6	44.7 ± 2.3	19.9 ± 2.9^{a}	8.4 ± 0.7^{b}	24.1 ± 2.2	1.4 ± 0.3	1.1 ± 0.2^{b}	0.4 ± 0.1^{b}	Good (64.6%)
S7	31.5 ± 9.7^{b}	5.9 ± 2.4^{b}	54.8 ± 8.2^{a}	1.0 ± 0.5^{b}	1.4 ± 0.4	2.0 ± 0.3	3.5 ± 0.7^{b}	Fair (37.3%)
S8	21.2 ± 4.8^{b}	10.5 ± 3.2^{b}	38.5 ± 3.4	23.3 ± 0.6	0.8 ± 0.6	1.0 ± 0.1^{b}	4.6 ± 1.9^{b}	Fair (31.8%)
S9	28.9 ± 2.2^{b}	13.4 ± 4.8	10.9 ± 2.0^{b}	31.8 ± 3.4	2.2 ± 0.8	1.7 ± 0.6	11.1 ± 4.5	Fair (42.3%)
S10	34.9 ± 2.6^{b}	18.1 ± 2.2^{a}	15.4 ± 2.9^{b}	25.5 ± 2.5	0.7 ± 0.3	4.4 ± 1.1^{a}	0.8 ± 0.3^{b}	Good (53.1%)
Mean	35.5 ± 4.9	10.9 ± 2.8	30.7 ± 4.7	14.0 ± 1.5	1.2 ± 0.5	1.6 ± 0.5	6.1 ± 1.7	Fair (46.4%)

Superscripts (^{a}) and (^{b}) indicate significant level ($p < 0.01$) based on Post-hoc Tukey HSD test

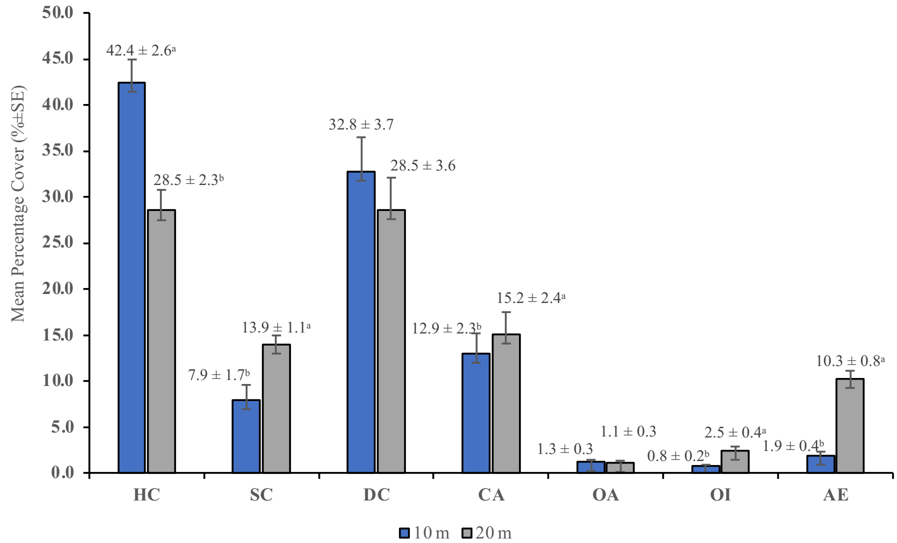

Fig. 2 The mean percentage cover (% ± SE) of seven benthic categories at two depths (10 m & 20 m). HC: Hard Corals; SC: Soft Corals; DC: Dead Corals; CA: Coralline Algae; OA: Other Algae; OI: Other Invertebrates; AE: Abiotic Elements. Superscripts ([a]) and ([b]) indicate significant level ($p < 0.01$) based on Post-hoc Tukey HSD test

also listed as Least Concern (56.3%; 90 species), Near Threatened (30.6%; 49 species) and Vulnerable (11.9%; 19 species). Only two species, *Pleuractis gravis* and *Pocillopora acuta* were categorized as Not Evaluated (1.3%; 2 species).

3.4 Coral genera composition in reef assemblages

Investigator Shoal exhibited different patterns of coral genera dominance across its reef assemblages. The cluster analysis and nMDS plot identified five similarity groups (G1–G5), each characterized by five dominant coral genera (Fig. 3). SIMPER analysis indicated that the soft coral *Xenia* was the most dominant genus in four out of the five groups: G1 (23.9% ± 1.5), G2 (15.3% ± 1.9), G3 (16.9% ± 1.9) and G4 (18.2% ± 1.6). In contrast, *Acropora* was the most dominant genus in G5, with a mean percentage cover of 12.6% ± 3.2 (Fig. 4). Other coral genera, such as *Porites* and *Goniastrea* also exhibited relatively high mean percentage cover across all groups. In summary, G1 (S8) was dominated by *Xenia*, *Porites*, *Pocillopora*, *Goniastrea* and *Acropora*. G2 (S3) was dominated by *Xenia*, *Porites*, *Acropora*, *Isopora* and *Pocillopora*. G3 (S9) was characterized by the dominance of *Xenia*, *Acropora*, *Porites*, *Seriatopora* and *Goniastrea*. G4 (S4, S5, S6, S10) was dominated by *Xenia*, *Acropora*, *Porites*, *Pocillopora* and *Goniastrea*. Whereas G5 (S1, S2, S7) was dominated by *Acropora*, *Xenia*, *Porites*, *Goniastrea*, and *Dipsastrea*.

4 Discussion

4.1 Coral communities in Investigator Shoal

The Spratly Islands represent an important reef ecosystem, forming part of a global marine biodiversity hotspots for corals, fishes and associated marine life [31, 32, 34]. However, coral communities in this region face immense pressure from direct and indirect anthropogenic activities [28, 30, 36]. These impacts are further exacerbated by global climate change, which continues to degrade reef health [3, 39]. Despite their ecological significance, data on coral reef conditions in the Spartly Islands remain scarce due to remote location, seasonal inaccessibility and geopolitical disputes among multiple countries. This study provides an updated assessment of coral communities at Investigator Shoal. The findings revealed that the reefs were categorized as 'Fair' condition, with an average live coral cover of 46.4%. Coral conditions varied across sites, ranging from 'Fair' to 'Good', with four sites (S1, S3, S6, S10) had relatively high coverage of hard corals (21.2 to 53.2%). However, some reef sites (e.g., S2, S4, S7) showed high dead coral cover exceeding 40%, which likely linked to localized stressors such as dredging and land reclamation related to military infrastructure. The extensive coral rubble at these sites further indicates mechanical damage and habitat degradation.

A comparative study by Tkachenko et al. [41] using photo transects across 15 sites at North Danger Reef, Tizard Bank, and Union Bank reported a mean hard coral cover of 36.6%, with site-specific values ranging from 3.7 to 69.2%. Their findings also revealed extensive coral rubble (> 30%), suggesting widespread reef degradation linked to destructive

Table 3 Mean percentage cover, diversity and abundance patterns of coral genera at 10 reef sites around Investigator Shoal in the Spratly Islands, SCS

	Reef Sites	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Mean (%)
No	Hard and soft corals											
	Scleractinian corals											
	Acroporidae											
1	*Acropora*[a]	++++	++++	+++++	+++++	++++	++	+++++	++++	++++	++++	**16.1 ± 2.1**
2	*Anacropora*	+	–	–	+	–	+	–	–	–	–	**0.1 ± 0.0**
3	*Astreopora*[a]	++	++	+	+	+	+	+	+	++	+	**0.9 ± 0.1**
4	*Isopora*	++	++	+++	++	++	–	+++	+++	++	++	**3.7 ± 0.9**
5	*Montipora*[a]	++	++	+	+	++	++	+	++	++	++	**1.9 ± 0.4**
	Agariciidae											
6	*Gardineroseris*	+	–	–	+	–	–	–	–	–	–	**0.0 ± 0.0**
7	*Leptoseris*	+	+	–	+	+	+	–	+	+	–	**0.3 ± 0.1**
8	*Pavona*[a]	+	++	++	+	++	++	++	++	+	++	**1.6 ± 0.3**
	Dendrophylliidae											
9	*Duncanopsammia*	–	–	+	–	–	–	–	–	–	–	**0.0 ± 0.0**
10	*Turbinaria*	+	–	+	+	–	+	+	+	+	+	**0.2 ± 0.1**
	Diploastraeidae											
11	*Diploastrea*	–	–	+	+	–	–	+	+	–	+	**0.2 ± 0.1**
	Euphylliidae											
12	*Coeloseris*	–	+	+	+	–	–	+	+	+	+	**0.3 ± 0.1**
13	*Euphyllia*	–	+	–	–	–	–	–	+	–	–	**0.1 ± 0.0**
14	*Galaxea*[a]	++	++	+	++	++	+	+	++	++	+	**1.3 ± 0.2**
	Fungiidae											
15	*Ctenactis*[a]	+	+	+	+	+	+	+	+	++	+	**0.7 ± 0.1**
16	*Danafungia*	+	+	+	+	+	–	+	+	+	+	**0.4 ± 0.1**
17	*Fungia*[a]	++	++	++	++	++	++	++	+	++	++	**2.3 ± 0.2**
18	*Halomitra*	+	+	–	+	–	+	–	+	+	+	**0.1 ± 0.0**
19	*Herpolitha*[a]	+	+	+	+	+	+	+	+	++	+	**0.5 ± 0.1**
20	*Lithophyllon*	–	+	++	+	+	++	++	+	+	+	**0.6 ± 0.1**
21	*Pleuractis*[a]	+	+	+	+	+	+	+	+	+	++	**0.7 ± 0.1**
22	*Polyphyllia*	–	+	–	+	+	–	–	–	–	–	**0.0 ± 0.0**
23	*Sandalolitha*	+	+	+	+	–	+	+	+	+	+	**0.3 ± 0.1**
	Leptastreidae											
24	*Leptastrea*[a]	+	+	+	+	+	+	+	+	+	++	**0.6 ± 0.1**
	Lobophylliidae											
25	*Acanthastrea*	+	+	+	+	+	–	+	+	–	+	**0.1 ± 0.0**
26	*Echinophyllia*	–	–	–	–	–	–	–	+	–	+	**0.1 ± 0.1**

Table 3 (continued)

	Reef Sites	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Mean (%)
27	*Homophyllia*	–	–	–	–	–	–	–	+	–	–	**0.0 ± 0.0**
28	*Lobophyllia*[a]	+ +	+ +	+	+ +	+ +	+ +	+	+ +	+ +	+ +	**2.2 ± 0.3**
29	*Oxypora*	–	–	–	–	–	+	–	+	+	+	**0.1 ± 0.0**
	Merulinidae											
30	*Astraeosmilia*	+	–	–	–	–	–	–	–	–	–	**0.0 ± 0.0**
31	*Astrea*	+ +	+	–	+ +	+ +	+ +	–	+	+ +	+	**1.1 ± 0.3**
32	*Caulastraea*	–	–	–	–	–	–	–	–	+ +	–	**0.0 ± 0.0**
33	*Coelastrea*[a]	+	+	+ +	+	+	+ +	+ +	+	+	+ +	**0.9 ± 0.1**
34	*Cyphastrea*[a]	+ +	+ +	+	+ +	+ +	+ +	+	+ +	+ +	+	**1.3 ± 0.2**
35	*Dipsastraea*[a]	+ +	+ +	+ +	+ +	+ +	+ + +	+ +	+ +	+ +	+ +	**3.6 ± 0.6**
36	*Echinopora*[a]	+ +	+	+ +	+	+ +	+ +	+ +	+	+ +	+	**1.3 ± 0.3**
37	*Favites*[a]	+ + +	+ +	+	+ +	+ +	+ +	+	+ +	+ +	+ +	**2.5 ± 0.6**
38	*Goniastrea*[a]	+ +	+ +	+ +	+ +	+ + +	+ +	+ +	+ +	+ +	+ +	**3.9 ± 0.4**
39	*Hydnophora*[a]	+	+	+	+ +	+ +	+	+	+	+	+	**0.8 ± 0.3**
40	*Leptoria*	+	+	–	+	+	+	–	+	+	+	**0.2 ± 0.1**
41	*Merulina*[a]	+	+	+ +	+	+ +	+ +	+ +	+ +	+	+	**1.2 ± 0.2**
42	*Mycedium*	–	–	+	+	–	–	+	+	–	+	**0.1 ± 0.0**
43	*Oulophyllia*	+	+	–	+	–	–	–	+	+	+	**0.1 ± 0.0**
44	*Paragoniastrea*	+	–	–	–	–	–	–	–	–	–	**0.0 ± 0.0**
45	*Pectinia*[a]	+ +	+	+ +	+	+	+	+ +	+	+ +	+	**0.8 ± 0.1**
46	*Platygyra*[a]	+ +	+ +	+	+ +	+ +	+ +	+	+ +	+ +	+ +	**1.8 ± 0.3**
	Pachyseridae											
47	*Pachyseris*[a]	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	**2.3 ± 0.2**
	Pocilloporidae											
48	*Pocillopora*[a]	+ +	+ + +	+ +	+ +	+ +	+ + +	+ +	+ + +	+ + +	+ +	**4.8 ± 0.7**
49	*Seriatopora*[a]	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+	+ +	+ +	**1.8 ± 0.3**
50	*Stylophora*	+	+	+	+ +	–	+	+	+	+	+	**0.5 ± 0.1**
	Poritidae											
51	*Goniopora*	+	–	–	–	–	–	–	–	–	–	**0.0 ± 0.0**
52	*Porites*[a]	+ + +	+ + + +	+ + + +	+ + +	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ + + +	**11.4 ± 0.7**
	Psammocoridae											
53	*Psammocora*		+	–	+	+	+	–	+	+	+	**0.2 ± 0.1**
	Non–scleractinian corals											
	Helioporidae											
54	*Heliopora*	+	–	–	+ +	+	+	–	+ +	+ +	–	**0.6 ± 0.2**
	Milleporidae											

Table 3 (continued)

	Reef Sites	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Mean (%)
55	*Millepora*	–	–	–	–	–	+	–	+	++	–	**0.1 ± 0.1**
	Tubiporidae											
56	*Tubipora*	+	–	–	–	+	–	–	+	–	–	**0.1 ± 0.0**
	Soft corals											
	Briareidae											
57	*Briareum*	–	–	–	+	–	–	–	–	–	–	**0.0 ± 0.0**
	Clavulariidae											
58	*Clavularia*	–	–	–	–	–	–	–	+	–	–	**0.0 ± 0.0**
	Nephtheidae											
59	*Dendronephthya*	–	+	–	+	–	+	–	+	–	+	**0.1 ± 0.0**
60	*Litophyton*	+	–	–	+	+	+	–	+	–	+	**0.3 ± 0.1**
	Sarcophytidae											
61	*Lobophytum*	++	++	–	++	++	++	–	++	++	++	**1.7 ± 0.4**
62	*Sarcophyton*[a]	++	++	+	++	++	++	+	++	++	++	**1.5 ± 0.3**
	Sinulariidae											
63	*Sinularia*[a]	+	+	+	++	+	++	+	++	+	++	**1.0 ± 0.3**
	Xeniidae											
64	*Xenia*[a]	++++	++++	+++++	++++	++++	+++++	+++++	++++	++++	++++	**18.3 ± 1.5**
	64 Genera and 22 Families	49	45	39	52	41	44	38	55	46	48	

Superscript ([a]) indicates the common genus recorded at all reef sites. The number of crosses (+) represents the relative abundance of coral genera based on the range of the mean percentage cover of an individual coral genus

+ = one or few covering < 1% of coral colonies

+ + = uncommon covering 1–5% of coral colonies

+ + + = common covering 6–10% of coral colonies

+ + + + = abundant covering 11–20% of coral colonies

+ + + + + = dominant covering > 20% of coral colonies

Table 4 Species checklist of scleractinian hard and soft coral corals at 10 reef sites around Investigator Shoal in the Spratly Islands, SCS

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
	Scleractinian corals													
	Acroporidae													
1	*Acropora*	*Acropora abrolhosensis*				x						x	C	VU
2		*Acropora cerealis*		x		x					x		C	LC
3		*Acropora clathrata*	x		x	x			x		x	x	C	LC
4		*Acropora cytherea*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
5		*Acropora digitifera*	x	x	x	x	x	x	x	x			SC	NT
6		*Acropora florida*	x	x		x	x			x		x	C	NT
7		*Acropora gemmifera*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
8		*Acropora granulosa*[b]	x										C	LC
9		*Acropora hyacinthus*	x	x		x	x				x	x	C	NT
10		*Acropora intermedia*	x	x	x	x	x		x	x	x	x	C	NT
11		*Acropora microphthalma*	x	x	x	x			x	x			C	LC
12		*Acropora muricata*	x	x	x	x	x		x	x	x	x	C	NT
13		*Acropora nasuta*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
14		*Acropora selago*	x	x		x	x			x		x	SC	NT
15		*Acropora speciosa*			x				x	x	x	x	UC	VU
16		*Acropora subglabra*	x	x	x	x	x		x				SC	LC
17		*Acropora tenuis*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
18		*Acropora valenciennesi*	x			x	x					x	C	LC
19	*Anacropora*	*Anacropora puertogalerae*	x			x		x					UC	VU
20	*Astreopora*	*Astreopora gracilis*[b]								x			SC	LC
21		*Astreopora myriophthalma*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
22	*Isopora*	*Isopora brueggemanni*	x	x	x	x			x	x	x	x	C	VU
23		Isopora cuneata		x		x				x			C	VU
24		*Isopora palifera*	x	x	x	x	x		x	x	x	x	C	NT
25	*Montipora*	*Montipora aequituberculata*	x		x		x		x	x			C	LC
26		*Montipora danae*		x						x			C	LC
27		*Montipora digitata*	x	x						x			C	LC
28		Montipora efflorescens[a]	x	x	x	x	x	x	x	x	x	x	C	NT
29		*Montipora informis*		x	x	x			x	x	x		C	LC
30		*Montipora peltiformis*[b]		x									UC	NT
31		*Montipora stellata*[b]		x									C	LC
32		*Montipora undata*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
33		*Montipora verrucosa*	x		x		x	x	x	x	x	x	SC	LC
	Agariciidae													

Table 4 (continued)

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
34	*Gardineroseris*	*Gardineroseris planulata*	x			x							UC	LC
35	*Leptoseris*	*Leptoseris explanata*[b]								x			UC	LC
36		*Leptoseris mycetoseroides*	x	x		x	x	x		x	x		SC	LC
37		*Leptoseris scabra*						x		x			UC	LC
38	*Pavona*	*Pavona cactus*	x		x				x				C	VU
39		*Pavona varians*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
40		*Pavona venosa*[a]	x	x	x	x	x	x	x	x	x	x	UC	VU
	Dendrophylliidae													
41	*Duncanopsammia*	*Duncanopsammia peltata*[b]			x								C	VU
42	*Turbinaria*	*Turbinaria mesenterina*[b]							x				C	VU
43		*Turbinaria patula*[b]			x								UC	VU
44		*Turbinaria stellulata*	x			x		x		x	x	x	UC	VU
	Diploastraeidae													
45	*Diploastrea*	*Diploastrea heliopora*			x	x			x	x		x	SC	NT
	Euphylliidae													
46	*Coeloseris*	*Coeloseris mayeri*		x	x	x			x	x	x	x	UC	LC
47	*Euphyllia*	*Euphyllia glabrescens*		x						x			UC	NT
48	*Galaxea*	*Galaxea astreata*[b]										x	C	VU
49		*Galaxea fascicularis*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
	Fungiidae													
50	*Ctenactis*	*Ctenactis albitentaculata*	x	x		x	x					x	SC	NT
51		*Ctenactis crassa*			x				x		x		UC	LC
52		*Ctenactis echinata*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
53	*Danafungia*	*Danafungia horrida*	x	x	x	x	x		x	x	x	x	C	LC
54		*Danafungia scruposa*	x				x						UC	LC
55	*Fungia*	*Fungia fungites*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
56	*Halomitra*	*Halomitra pileus*	x	x		x		x		x	x	x	C	LC
57	*Herpolitha*	*Herpolitha limax*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
58	*Lithophyllon*	*Lithophyllon concinna*		x	x		x	x	x	x	x	x	C	LC
59		*Lithophyllon undulatum*				x	x						UC	NT
60	*Pleuractis*	*Pleuractis granulosa*	x		x		x		x		x	x	UC	LC
61		*Pleuractis gravis*[b]		x									UC	NE
62		*Pleuractis paumotensis*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
63	*Polyphyllia*	*Polyphyllia talpina*		x			x						C	LC
64	*Sandalolitha*	*Sandalolitha dentata*[b]		x									UC	LC
65		*Sandalolitha robusta*	x	x	x	x		x	x	x	x	x	C	LC

Table 4 (continued)

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
	Leptastreidae													
66	*Leptastrea*	*Leptastrea purpurea*	x	x	x				x		x	x	C	LC
67		*Leptastrea transversa*[a]	x	x	x	x	x	x	x	x	x	x	UC	LC
	Lobophylliidae													
68	*Acanthastrea*	*Acanthastrea echinata*	x	x	x	x	x		x	x		x	C	LC
69		*Acanthastrea hemprichii*[b]	x										UC	VU
70	*Echinophyllia*	*Echinophyllia aspera*[b]										x	C	LC
71	*Homophyllia*	*Homophyllia australis*[b]								x			UC	LC
72	*Lobophyllia*	*Lobophyllia agaricia*[a]	x	x	x	x	x	x	x	x	x	x	UC	LC
73		*Lobophyllia corymbosa*		x			x					x	SC	LC
74		*Lobophyllia hemprichii*	x	x	x	x	x	x	x		x	x	C	LC
75		*Lobophyllia radians*	x	x		x				x	x	x	C	LC
76		*Lobophyllia recta*	x	x		x	x	x		x	x	x	C	LC
77		*Lobophyllia robusta*	x	x	x	x	x		x	x	x	x	UC	LC
78		*Lobophyllia valenciennesii*			x			x	x				UC	LC
79	*Oxypora*	*Oxypora crassispinosa*						x		x	x	x	UC	LC
	Merulinidae													
80	*Astraeosmilia*	*Astraeosmilia maxima*[b]	x										R	NT
81	*Astrea*	*Astrea curta*	x	x		x	x	x		x	x	x	C	LC
82	*Caulastraea*	*Caulastraea furcata*[b]									x		C	LC
83	*Coelastrea*	*Coelastrea aspera*[a]	x	x	x	x	x	x	x	x	x	x	SC	LC
84	*Cyphastrea*	*Cyphastrea chalcidicum*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
85		*Cyphastrea japonica*		x				x					UC	LC
86		*Cyphastrea microphthalma*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
87		*Cyphastrea serailia*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
88	*Dipsastraea*	*Dipsastraea amicorum*	x	x		x		x		x	x	x	UC	LC
89		*Dipsastraea matthaii*[b]					x						SC	NT
90		*Dipsastraea pallida*	x	x		x	x	x		x	x		C	LC
91		*Dipsastraea speciosa*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
92		*Dipsastraea truncata*	x									x	C	LC
93		*Dipsastraea vietnamensis*	x				x						R	NT
94		*Dipsastraea veroni*	x	x									R	NT
95	*Echinopora*	*Echinopora gemmacea*	x	x	x	x	x	x	x	x	x		UC	LC
96		*Echinopora horrida*[b]	x										UC	NT
97		*Echinopora lamellosa*	x	x	x	x	x		x		x	x	C	LC
98		*Echinopora pacifica*		x		x							UC	NT

Table 4 (continued)

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
99	*Favites*	*Favites abdita*	x		x	x	x	x	x	x	x	x	C	NT
100		*Favites chinensis*	x			x							UC	NT
101		*Favites colemani*	x	x		x		x				x	C	NT
102		*Favites complanata*	x	x		x	x				x		SC	NT
103		*Favites flexuosa*[b]	x										SC	NT
104		*Favites halicora*	x	x		x	x	x		x	x	x	UC	NT
105		*Favites micropentagonus*	x	x	x	x	x		x	x	x		UC	LC
106		*Favites pentagona*				x	x	x					UC	LC
107		*Favites rotundata*		x		x							SC	NT
108		*Favites valenciennesii*	x	x	x	x			x	x	x	x	UC	NT
109	*Goniastrea*	*Goniastrea edwardsi*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
110		*Goniastrea pectinata*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
111		*Goniastrea retiformis*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
112		*Goniastrea stelligera*	x			x	x	x		x		x	C	NT
113	*Hydnophora*	*Hydnophora exesa*	x	x		x	x	x		x			C	NT
114		*Hydnophora microconos*	x	x	x	x	x		x		x	x	UC	NT
115		*Hydnophora rigida*	x		x	x			x	x		x	SC	LC
116	*Leptoria*	*Leptoria irregularis*	x	x		x	x			x		x	UC	VU
117		*Leptoria phrygia*	x	x		x		x			x		C	NT
118	*Merulina*	*Merulina ampliata*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
119		*Merulina scabricula*	x	x	x	x		x	x	x	x	x	C	LC
120	*Mycedium*	*Mycedium elephantotus*			x	x			x	x		x	C	LC
121	*Oulophyllia*	*Oulophyllia bennettae*[b]	x										UC	NT
122		*Oulophyllia crispa*	x	x		x				x	x	x	UC	NT
123		*Paragoniastrea russelli*[b]	x										UC	NT
124	*Pectinia*	*Pectinia lactuca*[a]	x	x	x	x	x	x	x	x	x	x	C	VU
125		*Pectinia paeonia*	x		x	x			x				C	NT
126	*Platygyra*	*Platygyra contorta*	x	x			x			x		x	UC	LC
127		*Platygyra daedalea*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
128		*Platygyra lamellina*	x			x		x		x			UC	NT
129		*Platygyra pini*[a]	x	x	x	x	x	x	x	x	x	x	UC	LC
130		*Platygyra sinensis*	x	x	x	x	x		x	x		x	UC	LC
131		*Platygyra verweyi*	x	x			x					x	UC	NT
	Pachyseridae													

Table 4 (continued)

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
132	*Pachyseris*	*Pachyseris foliosa*			x				x				UC	LC
133		*Pachyseris gemmae*	x	x			x			x	x		R	NT
134		*Pachyseris rugosa*[a]	x	x	x	x	x	x	x	x	x	x	C	VU
135		*Pachyseris speciosa*	x	x	x	x		x	x	x	x	x	C	LC
	Pocilloporidae													
136	*Pocillopora*	*Pocillopora acuta*				x		x				x	C	NE
137		*Pocillopora damicornis*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
138		*Pocillopora meandrina*				x	x						UC	NT
139		*Pocillopora verrucosa*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
140	*Seriatopora*	*Seriatopora hystrix*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
141		*Seriatopora caliendrum*	x	x	x	x		x	x	x		x	UC	NT
142	*Stylophora*	*Stylophora pistillata*	x	x	x	x		x	x	x	x	x	C	NT
143		*Stylophora subseriata*[b]										x	C	LC
	Poritidae													
144	*Goniopora*	*Goniopora lobata*[b]	x										C	NT
145	*Porites*	*Porites cylindrica*	x	x	x	x	x		x	x	x	x	C	NT
146		*Porites horizontalata*		x						x			SC	VU
147		*Porites latistellata*[a]	x	x	x	x	x	x	x	x	x	x	UC	LC
148		*Porites lichen*				x					x		C	LC
149		*Porites lobata*[a]	x	x	x	x	x	x	x	x	x	x	C	NT
150		*Porites lutea*	x	x	x				x			x	C	LC
151		*Porites rus*[a]	x	x	x	x	x	x	x	x	x	x	C	LC
152		*Porites silimaniana*[b]	x										UC	VU
153		*Porites solida*	x			x						x	C	LC
	Psammocoridae													
154	*Psammocora*	*Psammocora collumna*					x	x					SC	LC
155		*Psammocora haimiana*		x		x							UC	LC
156		*Psammocora profundacella*				x				x	x	x	UC	LC
	Non-Scleractinian corals													
	Helioporidae													
157	*Heliopora*	*Heliopora coerulea*	x			x	x	x		x	x		–	VU
	Milleporidae													
158	*Millepora*	*Millepora exaesa*						x		x	x		–	LC
159		*Millepora platyphylla*[b]									x		–	LC
	Tubiporidae													
160	*Tubipora*	*Tubipora musica*	x				x			x			–	LC

Table 4 (continued)

No	Hard & soft corals	Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	Abundance status (sensu Veron, 2000)	IUCN status
	Soft Corals													
	Briareidae													
161	*Briareum*	*Briareum* sp.[b]				x							–	–
	Clavulariidae													
162	*Clavularia*	*Clavularia* sp.[b]								x			–	–
	Nephtheidae													
163	*Dendronephthya*	*Dendronephthya* sp.		x		x		x		x		x	–	–
164	*Litophyton*	*Litophyton* sp.	x			x	x	x		x		x	–	–
	Sarcophytidae													
165	*Lobophytum*	*Lobophytum* sp.	x	x		x	x	x		x	x	x	–	–
166	*Sarcophyton*	*Sarcophyton* sp.[a]	x	x	x	x	x	x	x	x	x	x	–	–
	Sinulariidae													
167	*Sinularia*	*Sinularia* sp.[a]	x	x	x	x	x	x	x	x	x	x	–	–
	Xeniidae													
168	*Xenia*	*Xenia* sp.[a]	x	x	x	x	x	x	x	x	x	x	–	–
	168 species, 64 genera and 22 families		118	106	82	112	88	75	81	103	88	99		

Species were identified following the current taxonomic revisions and descriptions on World Register of Marine Species (WoRMS). Symbol (x) indicates the species occurrence, while superscripts ([a]) indicates the most common species recorded at all reef sites and ([b]) as the least common species and recorded at only one site

Abundance categories: *SC* Sometimes Common, *UC* Uncommon, *C* Common, *R* Rare; Conservation categories: *NE* Not Evaluated, *DD* Data Deficient, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable, *EN* Endangered, *CR* Critically Endangered

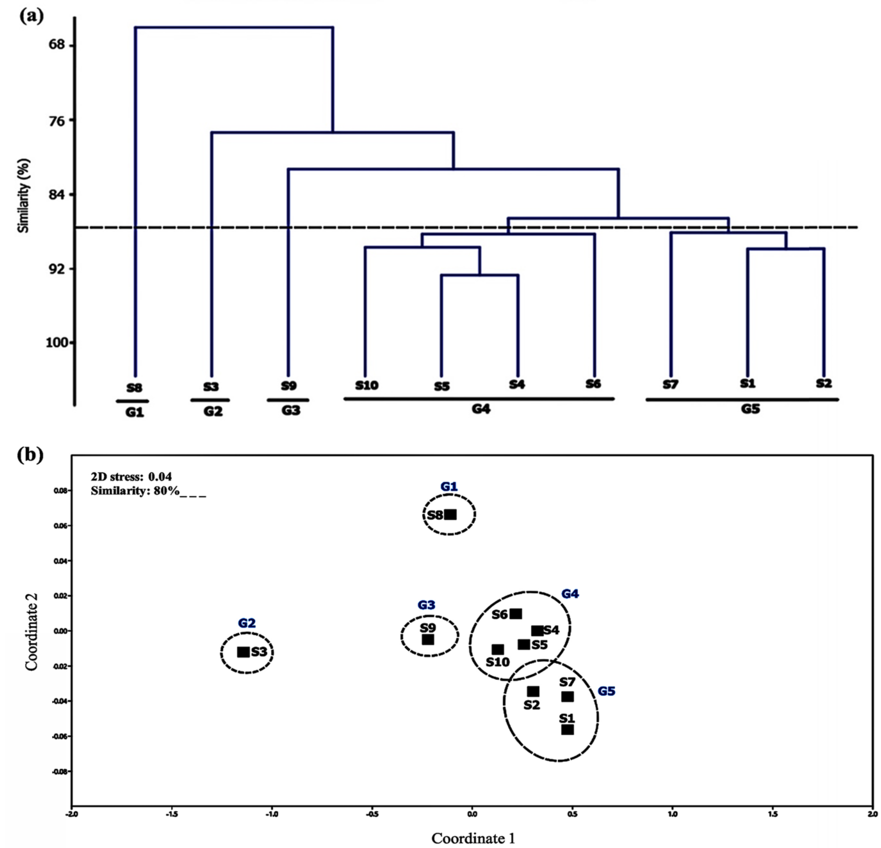

Fig. 3 Cluster (**a**) and nMDS plot (**b**) were clustered all reef sites within five groups (G1–G5) based on 60% similarity. All groups were separated based on mean percentage cover of coral genera around Investigator Shoal in the Spratly Islands, SCS

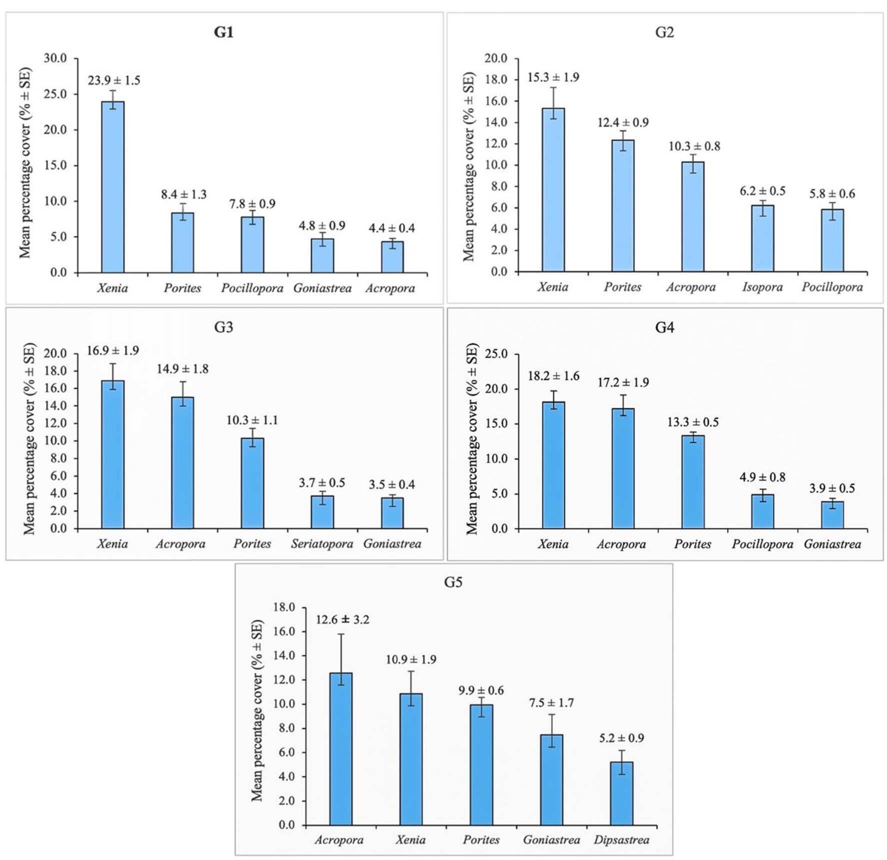

Fig. 4 Five groups (G1–G5) derived from cluster and nMDS plot. Each group consists of five different dominant coral genera and values are indicated based on their mean percentage cover (% ± SE)

fishing, dredging and reclamation. Between 2018 and 2021, surveys from Discovery Great Reef, Namyit Island, South Reef and Barque Canada Reef reported a similar mean hard coral cover of 35.6% (ranging from 8.4 to 69%), with declines attributed to thermal anomalies and COTS outbreaks [41]. Long-term records from Zhao et al. [64] and Xiao et al. [65] similarly reported severe reductions in hard coral cover, with losses reaching up to 80% driven by natural stressors and extensive human intervention, particularly due to the adverse effects of rapid conversion areas into military bases.

Mora et al. [29] also documented at least 20 atolls reclaimed for military use, including parts of the Paracel Islands. For instance, in the 1960s, dredging on Johnston Island (U.S.) destroyed 440 ha of reef and impacted another 2800 ha of nearby coral areas [66], while in 2006, coral cover loss extended up to 6 km from dredging activities at Hay Point, Australia [67]. Dredging and reclamation activities disturb benthic habitats and generate high sediment loads [68], which reduce coral resilience by impairing sediment-shedding ability, increasing susceptibility to disease, and degrading overall health [19, 69]. Such pressures underline the severe impacts of dredging and land clearing, which subsequently lead to further biodiversity loss [70].

In addition to mechanical impacts, coral reefs in the Spratly Islands have suffered mass bleaching events associated with El Niño thermal anomalies in 1998 and 2007 [28]. It further declines in 2010 and 2020 due to COTS outbreaks [40, 71] and the spread of *Terpios hoshinota*, a coral-killing cyanobacteriosponge [35]. Although no major COTS outbreaks were observed during this study, predation scars were evident particularly on *Acropora* colonies (*A. cytherea*, *A. hyacinthus*, *A. clathrata*), suggesting past disturbance events that contributed to high dead coral cover and 'Fair' condition at some reef sites.

Despite these stressors, certain sites (S1: 62%, S3: 54%, S6: 65%, S10: 53%) exhibited 'Good' coral condition, highlighting the resilience potential of reefs under favorable conditions. These findings align with Tkachenko et al. [41], who observed sites within the Spratly Islands maintaining coral cover above 50%. Such resilience may be attributed to reduced sedimentation and optimal environmental parameters [72, 73], as well as high hydrodynamic flow which enhances nutrient exchange and larval dispersal [74]. These environmental conditions likely provide thermal buffering, reduce sediment accumulation and further promoting conducive conditions to reef recovery [47, 65].

4.2 Coral communities at different depths

The composition of hard coral communities is primarily influenced by environmental factors such as depth gradients and light availability [75]. Physical parameters such as turbidity and sedimentation can further reduce light penetration as depth increases [19]. In fact, the light availability decreasing exponentially with depth [76]. In this study, significant differences in coral cover were observed between depths. Higher coverage of hard corals was recorded at 10 m, whereas soft corals (particularly *Xenia* spp.) and calcified algae (e.g., crustose coralline and *Halimeda*) were more abundant at 20 m. In the shallow waters of Investigator Shoal, branching and tabular *Acropora*, as well as massive and encrusting *Porites* were the dominant coral morphologies. This pattern is consistent with depth-related community structuring, as shallow reef zones typically host more diverse coral assemblages and dense coverage of various coral morphologies due to greater sunlight penetration [77]. Shallow-water environments provide high light intensity and full-spectrum light, which are essential for symbiotic zooxanthellae to carry out photosynthesis, thereby supporting the growth of hard corals [78, 79]. In contrast, soft corals and certain calcified algae are less dependent on light. These organisms rely more on heterotrophic feeding by capturing plankton and organic matter rather than solely on photosynthetic energy from symbionts. This adaptation allows them to thrive in deeper reef zones with reduced light availability [79]. Seasonal and daily changes in wave action and currents also play a role in shaping coral distribution, especially in [80, 81]. In deeper areas, the reduced exposure to hydrodynamic stress may enhance the survival of calcified algae by minimizing structural dislodgement [81, 82]. Notably, the findings also recorded high coverage of dead corals and coral rubble in shallow waters. This degradation is likely associated with land reclamation activities, which often involve dredging, excavation and dumping of materials. These activities can physically damage coral colonies, increase sedimentation levels and generate large quantities of rubble. Sediment generated by reclamation can smother live corals, leading to mortality and subsequent breakdown into rubble [19, 83].

4.3 Coral diversity and abundance patterns in Investigator Shoal

The Spratly Islands, located at the boundary of the Coral Triangle, are globally recognized for their remarkable coral diversity, with potentially up to 500 species [75]. While previous coral surveys in the Spratly Islands have reported various patterns of species richness, data scientific to Investigator Shoal remain scare due to its remoteness and limited seasonal accessibility. Over the past decades, only a few surveys have been conducted in the Spratlys. For example, 163 scleractinian species were identified in Taiping Island (Itu Aba Island) [84]. In other remote atolls of the Nansha Islands (the Chinese name for the Spratly Islands), 120 scleractinian species were documented, with *Acropora*, *Montipora* and *Porites* species being the most dominant [64].

Given this scarcity of data, the present study provides baseline information on coral diversity and abundance patterns at Investigator Shoal. A total of 168 coral species from 64 genera and 22 families were recorded, with site-specific richness ranging from 75 to 118 species. Of these, 154 species were scleractinians, four were non-scleractinian, and eight were soft coral genera. Compared to other reefs in the SCS, the number of scleractinian species recorded at Investigator Shoal exceeds those previously documented in the Xisha Islands (127 species) and the Nansha Islands (120 species) [64]. It is important to note that the species checklist in this study followed the current taxonomic classifications from the World Register of Marine Species (WoRMS). The findings also revealed 19 species listed as vulnerable under the IUCN Red List [59], along with four rare species (*Astraeosmilia maxima*, *Dipsastraea vietnamensis*, *Dipsastraea veroni*, *Pachyseris gemmae*) based on relative abundance reported by Veron [75]. These species are of particular concern due to their restricted distributions and highly vulnerable to environmental stressors. These results highlight the need for targeted conservation efforts and serve as a valuable baseline for future biodiversity monitoring in the remote reefs of the Spratly Islands.

The abundance pattern of coral communities at Investigator Shoal further showed that the soft coral *Xenia* sp. had the highest overall coverage and was recorded across all reef sites. It was found at both 10 m and 20 m depths, with higher abundance at deeper sites. This observation underscores with the detrimental effects of recent COTS outbreaks, as the disturbed reefs were rapidly colonized by fast-growing soft corals. This pattern aligns with findings from other reefs in the Spratly Islands, where COTS outbreaks were reported between 2018 and 2021 [41, 65, 71, 85]. Similar ecological shifts were noted by Koido et al. [86] in Kyushu Island, where *Xenia* sp. became dominant following reef damage caused by *Acanthaster planci* and the corallivorous gastropod *Drupella*. Similarly, Lalas et al. [87] found that soft corals often dominate reef areas around Okinawa Island that are exposed to recurrent anthropogenic and climate-related stress. These comparisons support the hypothesis that repeated COTS outbreaks have driven a community shift from hard to soft coral dominance in Investigator Shoal.

In addition to soft corals, this study also revealed the dominance of *Acropora* and *Porites* genera across multiple reef sites. The widespread occurrence of these genera reflects their natural abundance and ecological adaptability throughout Indo-Pacific coral reefs [75, 88]. Prior studies by Zhao et al. [64] also reported the dominance of *Acropora* and *Porites* corals at Zhubi Reef and Meiji Reef in the Spartly Islands. Comparable patterns were observed in the Paracel Islands [47] and Pratas Islands [89] around the SCS. In this study, tabular *Acropora* species, including *A. cytherea*, *A. hyacinthus* and *A. clathrata*, as well as massive *Porites lobata* and encrusting *P. rus* were found to dominate the reef flat and lagoon slope of the atoll. The dominance of these genera could be attributed to their contrasting yet complementary growth strategies. *Acropora* species are known for their rapid growth and effective reproduction through fragmentation, enabling them to occupy available space and outcompete slower-growing taxa [90, 91]. Conversely, *Porites* species are having structural resilience that can withstand to strong hydrodynamic forces and high sedimentation [92, 93]. Their ability to survive in turbid environments is facilitated by self-cleaning mechanisms such as mucus secretion and ciliary movement [94, 95]. These adaptive capacities help to ensure their long-term dominance in reef ecosystems [96]. As such, *Acropora* and *Porites* likely serve as key habitat-forming species in Investigator Shoal, creating habitats that support a diverse array of marine life.

5 Conclusion

The coral reefs at Investigator Shoal were generally categorized as 'fair' condition, with sites affected by dredging and land reclamation showed lower live coral cover. The reef surveys recorded a total of 168 coral species, representing 64 genera and 22 families of hard and soft corals, with *Xenia*, *Acropora* and *Porites* being the dominant genera across the reef assemblages. The presence of four rare and 19 vulnerable coral species further highlights the ecological significance of these reef ecosystems. The findings suggest that past large-scale land reclamation combined with the cumulative impacts of COTS outbreaks have likely influenced the current coral community structure in the region. These stressors have led to ecological shifts, including the proliferation of fast-growing soft corals and spatial variation in coral conditions. To ensure the long-term sustainability and biodiversity resilience of coral reefs in Investigator Shoal, it is important to adopt advanced monitoring tools such as drones, autonomous underwater vehicles (AUVs) and Landsat satellite imagery for large-scale reef assessments. Future research should incorporate photogrammetry and 3D reef mapping to improve the evaluation of structural complexity and habitat heterogeneity. Regular monitoring using both in situ surveys and satellite imagery is essential for early detection of coral stress indicators. Given the observed signs of COTS predation in this study, targeted control measures such as physical removal or biological control using natural predators should be implemented to reduce COTS populations. Additionally, effective reef management should take a holistic approach that addresses local stressors, including dredging and land reclamation, while also strengthening protection measures through intergovernmental collaboration. Failure to take timely and coordinated action may lead to further degradation and the potential extinction of vulnerable and rare coral species in the near future.

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Data availability All data generated or analyzed during this study are available within the manuscript. Additional information can be provided upon reasonable request.

Declarations

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Consent for publication Not applicable.

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