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The Status of the Coral Reefs of the Jaffna Peninsula (Northern Sri Lanka), with 36 Coral Species New to Sri Lanka Confirmed by DNA Bar-Coding

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Citation: Arulananthan, A.; Herath, V.; Kuganathan, S.; Upasanta, A.; Harishchandra, A. The Status of the Coral Reefs of the Jaffna Peninsula (Northern Sri Lanka), with 36 Coral Species New to Sri Lanka Confirmed by DNA Bar-Coding. *Oceans* **2021**, *2*, 509–529. <https://doi.org/10.3390/oceans2030029>

Academic Editor: Rupert Ormond

Received: 12 March 2021

Accepted: 16 July 2021

Published: 26 July 2021

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Abstract: Sri Lanka, an island nation located off the southeast coast of the Indian sub-continent, has an unappreciated diversity of corals and other reef organisms. In particular, knowledge of the status of coral reefs in its northern region has been limited due to 30 years of civil war. From March 2017 to August 2018, we carried out baseline surveys at selected sites on the northern coastline of the Jaffna Peninsula and around the four largest islands in Palk Bay. The mean percentage cover of live coral was $49 \pm 7.25\%$ along the northern coast and $27 \pm 5.3\%$ on the islands. Bleaching events and intense fishing activities have most likely resulted in the occurrence of dead corals at most sites (coral mortality index > 0.33). However, all sites were characterised by high values of diversity ($H' \geq 2.3$) and evenness ($E \geq 0.8$). The diversity index increased significantly with increasing coral cover on the northern coast but showed the opposite trend on the island sites. One hundred and thirteen species of scleractinian corals, representing 16 families and 39 genera, were recorded, as well as seven soft coral genera. Thirty-six of the scleractinian coral species were identified for the first time on the island of Sri Lanka. DNA barcoding using the mitochondrial *cytochrome oxidase subunit I* gene (*COI*) was employed to secure genetic confirmation of a few difficult-to-distinguish new records: *Acropora aspera*, *Acropora digitifera*, *Acropora gemmifera*, *Montipora flabellata*, and *Echinopora gemmacea*.

Keywords: Jaffna Peninsula; coral mortality index; DNA barcoding; phylogeny; biodiversity; conservation

1. Introduction

Corals are foundational species that appeared 425 million years ago and are responsible for creating the structural complexity and high productivity of coral reef ecosystems [1]. They have radiated into more than 1500 species and nearly 900 scleractinian corals. Almost all reef corals are hermatypic, that is, they contain in their tissues photosynthetic algae of the family Symbiodiniaceae [1–3], which, living in a symbiotic relationship with corals, are ultimately responsible for the high biomass and productivity of reef habitats [1,4]. The high species diversity of coral reefs has led to their designation as oceanic “rain forests” [5]. However, unprecedented declines in live coral cover and phase shifts in coral reef ecosystems have arisen from the impacts of anthropogenic activities. The most recent widespread degradation of coral reefs, involving coral bleaching and the consequent

death and loss of corals, is mostly due to climate change and ocean acidification [6,7]. Averting the effects of climate change will be a considerable challenge if we are to secure the ecological, economic, and social values of coral reefs in the marine biome.

Considering the global nature of these ongoing threats to coral reefs, we investigated the most neglected coral reef area on the Island of Sri Lanka (SL), which is located 40 km away from the southeast coast of the Indian mainland and has 1338 km of open coastline and 2791 km located within coastal lagoons [8]. Fringing-type coral reefs occupy about 2% of the coast and cover 475.70 sq km of Sri Lankan territorial waters [9], with more extensive and well-developed fringing reefs being present on the north-western and northern coasts than in the southern and eastern regions [10,11]. The first detailed records of these coral reefs date from the 19th century and were provided by Ridley (1883) and Ortmann (1889) [12,13]. Subsequently, further studies of Sri Lankan reefs were published through the 20th century [14–19], but most of these concerned the western, south-western, southern, and north-western parts of the country [20,21]. In contrast, the northern region of SL has, in the recent past, received very little attention, due to the decades of civil war. As a result, little is known about the distribution and diversity of corals in that area, yet the region includes the largest coral reef ecosystem in SL, located near the Gulf of Mannar and known as “Bar Reef”. It is recognised as a “High Regional Priority Area” by the International Union for the Conservation of Nature (IUCN)/National Oceanic and Atmospheric Administration (NOAA) USA “World Heritage Biodiversity” Project [22,23]. Further north lie Palk Strait and Palk Bay, which are highly productive shallow water areas containing coral reefs, seagrass beds, coastal lagoons, estuaries, mangroves, and salt marshes [22–27].

At the northernmost end of Sri Lanka is the Jaffna Peninsula, with around 293 km of coastline. Extensive fringing coral reefs are present along the northern coast of the peninsula and around the adjacent islands [28], many of which were previously unsurveyed. However, during and following the decades of civil war (which ended in 2009), these reefs were exposed to destructive fishing practices, such as the use of explosives, as well as over-fishing of many species, including ecologically important herbivorous fish and invertebrates, the loss of which has often been associated with a phase shift from coral dominated to algal dominated reefs [24–26]. Studying the ecology and biogeography of northern Sri Lanka represents a considerable challenge, since access presents problems and little information is available about the marine topography and substratum [29].

The present study aimed to report on the current status of reefs around the Jaffna Peninsula and to extend our knowledge of the understudied benthic community, including the diversity of coral species. To do so, we combined molecular tools and traditional morphometric approaches [30–32] and used DNA barcoding, which is known to have revolutionised the understanding of the evolution and systematics of scleractinian corals and resulted in an extensive taxonomic revision of the order [33–37]. Our surveys revealed that the coral reefs of the Jaffna Peninsula have a relatively high percentage of live coral cover and a greater diversity of scleractinian corals than other parts of the country.

2. Materials and Methods

2.1. Study Area

The Jaffna Peninsula (JP) and its islands surround an almost enclosed body of shallow water, located on the southern side of the 25–50 km wide Palk Strait. They form a reef and island complex (known as “Sethusamudram”) that lies at the south-eastern tip of the Indian mainland, partially enclosed off the Bay of Bengal (BOB) (Figure 1). The islands themselves are often referred to as the “Coral Islands Archipelago” and are believed to have been formed as a result of sea level rise since the late Holocene [8,24,38]. On the SL mainland, fossilised limestone rocks are present in the near-shore area, extending up to 50 m seawards, along the northern coast between Point Pedro and Keerimalai, while sandy to muddy seabed extends westwards from Keerimalai, as well as around the islands

of the JP. In contrast, the coastline along the south-eastern shore extending from Point Pedro towards the SL coastline is composed of sandy beaches.

Long stretches of the reef, called “paar” by local fishermen and made up mostly of fringing reef, extend along the northern coast and around the islands at depths between 1 and 8 m [24,27]. Typically, there is a reef flat, 15–20 m wide and 1 to 2 m deep, extending seawards from the shore, with a substrate mainly of dead coral rocks and coral gravel [24]. Beyond this, the reef front (including reef crest) and reef slope region are dominated by a mix of live coral and dead coral to a depth of nearly 6 m. The maximum depth of the reef base is no more than 8 m [24], so no surveys were undertaken beyond this depth.

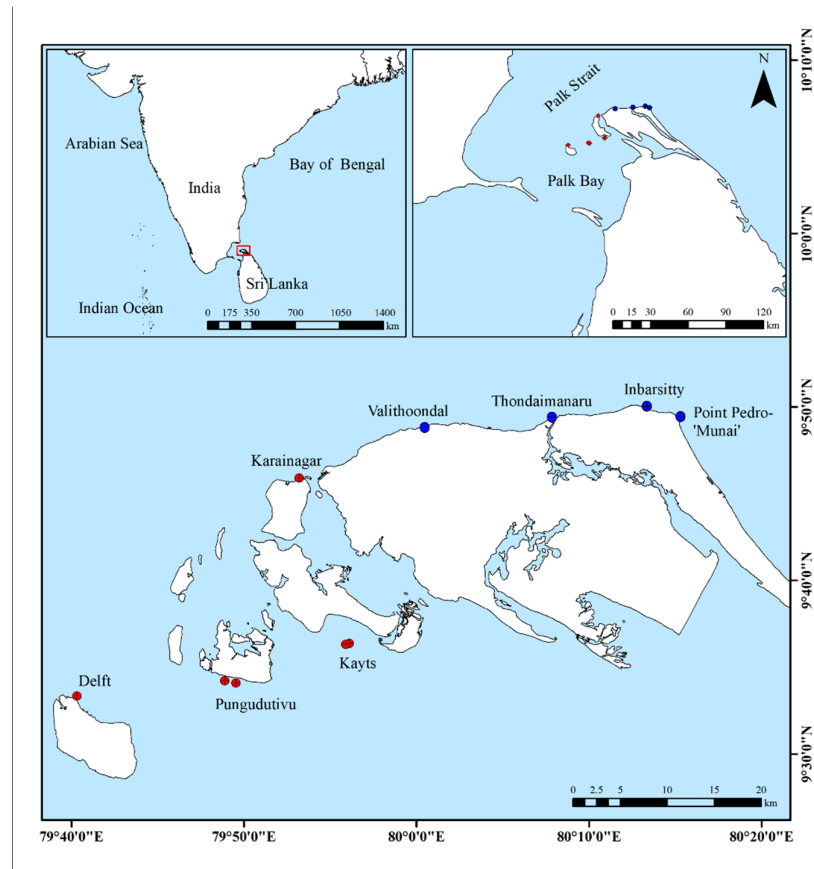


Figure 1. Maps showing (above left) the location of the Jaffna Peninsula (within the red rectangle) in relation to Sri Lanka and southern India, (above right) the relation of the Jaffna Peninsula to the Palk Strait and Palk Bay, and (below) the locations of the study sites (blue circles) on the northern side and the island sites (red circles) of the Jaffna Peninsula and its adjacent islands.

Study Sites

Eight reef areas were surveyed between March 2017 and August 2018. These can be divided into two groups, those on the island reefs located in the Palk Bay and those along the northern coast of the Palk Strait (Figure 1). Within these eight reef areas, ten actual sites were surveyed: the Delft reef front (Del), the Karainagar reef front (Knr), the Kayts outer reef slope (Kt1), the Kayts outer reef flat (Kt2), the Pungudutivu outer reef slope (Pu1), the Pungudutivu outer reef flat (Pu2), and the reef fronts at Point Pedro (Munai or Ptm), Inbarsitty (Inb), Thondaimanaru (Tho), and Valithoondal (Val) (Figure 1). These were either shallow, outer reef flat sites at 1 to 3 m depth, or reef front sites at 3 to 6 m depth. Visual inspections of the reef flats on the north coast revealed that all but the most protected sites supported very low, mostly nil, live coral cover; similarly, inner reef flats and reef lagoons at the island sites were mostly composed of seagrass beds and broken

coral rubbles. Given this, quantitative surveys were not carried out at these locations. In addition, the Delft, which is located in Palk Bay, is known as the island of dead corals, most pieces of which are believed to be of Miocene origin. In contrast, the islands of Pungudutivu and Kayts are well-known locally to have well-developed coral reefs extending to a depth of about 6 m.

2.2. Surveys and Sampling

Surveys were conducted using the standard Reef Check survey method (see http://reefcheck.org/ecoaction/Monitoring_Instruction.hp, accessed on 30 August 2018) [39]. A 100 m transect was divided into four 20 m long segments, each separated by a 5 m interval from the next one, so that the four segments could be considered as replicates. On each segment, substrate cover was recorded beneath the transect line at 0.5 m intervals, so that 40 data points were recorded per segment (160 per 100 m transect). The transect lines were laid down parallel to the shore, along the long axis of the reef. The work was undertaken using SCUBA at 2 to 6 m depth, and snorkel at 1 to 2 m depth. The substrate was recorded using the following categories (and codes): hard coral (HC), soft coral (SC), dead coral with macroalgae or nutrient indicating algae (NIA), recently killed coral (RKC), sponge (SP), coral rubble (RB), hard substrate of dead coral more than one year old covered by turf algae or encrusting coralline algae (RC), sand (SD), silt (SI), and others (including sea anemones, tunicates, gorgonians, or non-living substrate) (OT) [39]. Digital photography and videography were employed (using a GoPro Digital Hero 5 Black, GoPro Inc., (San Mateo, CA, United States of America) to provide a visual record of the reef habitats and coral assemblages along the transects. In addition, images of live coral specimens were recorded with a dedicated underwater camera (Canon PowerShot A620, Canon, United States of America).

2.3. Coral Reef Cover Analysis

The percentage cover of the substrates at the different study sites was compiled and processed using the Reef Check Substrate data entry sheet in the Microsoft Excel application [39]. To investigate differences in the benthic community between the study sites, Principal Component Analysis and Bray–Curtis Cluster Analysis were carried out using PAST version 3.22 (Øyvind Hammer, Oslo, Norway) [40]. The mean percentage covers of substrate categories were analysed using IBM SPSS Statistics (Version 27.0, IBM, Armonk, New York, United States of America). Mann–Whitney *U*-tests were used to test for differences in the substrate between the Palk Bay and Palk Strait reefs. Differences in proportions of main benthic categories (HC, SC, RC, NIA, RB) amongst sites were tested using a Kruskal–Wallis test. To assess the status of the reefs, a coral mortality index (CMI) was calculated by dividing the percentage values of dead coral cover by the combined value of live and dead coral cover. If the CMI was greater than 0.33, the reef was considered likely to have been impacted by natural or anthropogenic stressors [41]. Sites were also classified based on the amount of live coral cover as excellent (75–100% live coral), good (50–74.9% live coral), fair (25–49.9% live coral), or poor (0–24.9% live coral) [41].

2.4. Diversity of Coral Species

Underwater photographs were taken during the surveys at each site and were used to aid morphological taxonomic identification of coral species. In addition, as far as practicable, corals were identified in the field to genus level based on morphological characters following the Indo-Pacific Coral Finder Tool Kit [42]. Subsequently, traditional diagnostic features such as corallite wall structure, the presence of paliform lobes, verrucae, valleys, and columella, and other colony characters (as described in the Corals of the World by Veron [43]) were used for species discrimination. Species diversity, dominance, and evenness indices were calculated based on the numbers of species recorded along the transect lines [44].

2.5. DNA Extraction, Amplification, Sequencing, and Barcoding of Coral Species

A commercially available spin-column-based DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) was used for DNA extraction from coral tissues, according to the manufacturer's instructions. Small pieces of the coral samples were excised with sterile forceps, and 20–25 mg samples were placed in a sterile 1.5 mL microcentrifuge tube and subjected to extended lysis for 24 h or longer. The extracted DNA was stored at $-20\text{ }^{\circ}\text{C}$. A specific region of the 658 bp fragment of the cytochrome oxidase gene (subunit I) (COI) was amplified by polymerase chain reaction (PCR) using the universal primers LCO 1490 and HCO 2198 [45]. The PCR reaction mix consisted of 1 \times PCR colourless buffer (pH 8.3) (GoTaq, Promega), 4 mM MgCl_2 , 0.2 mM dNTPs, 0.25 μM of each primer, 0.01 mg mL^{-1} bovine serum albumin, 0.625 U Taq polymerase (GoTaq, Promega), and 50 $\text{ng } \mu\text{L}^{-1}$ genomic DNA in a 25 μL reaction volume. The PCR thermal regime consisted of one initial denaturation cycle for 2 min at $95\text{ }^{\circ}\text{C}$; five 1-minute denaturation cycles at $95\text{ }^{\circ}\text{C}$, annealing for 1.5 min at $45\text{ }^{\circ}\text{C}$ and an extension for 1.5 min at $72\text{ }^{\circ}\text{C}$; 35 1-minute denaturation cycles at $95\text{ }^{\circ}\text{C}$, annealing for 1.5 min at $50\text{ }^{\circ}\text{C}$ and an extension for 1 min at $72\text{ }^{\circ}\text{C}$, followed by a final extension for 5 min at $72\text{ }^{\circ}\text{C}$.

The PCR products were sequenced in both the forward and reverse directions by Macrogen Inc. (Seoul, Korea). All DNA sequence chromatograms were assembled and edited using Unipro (Novosibirsk, Russia), UGENE 1.29.0. The sequences were then aligned using ClustalW [46], and the aligned outputs queried to identify the species, along with the reference sequences of various coral species that were retrieved from the National Centre for Biotechnology Information (NCBI) (www.ncbi.nlm.nih.gov, accessed on 25 July 2021) [47], GenBank and Barcode of Life Data System (BOLD) databases, using the Basic Local Alignment Search Tool (BLAST).

2.6. Ethics Statement

Samples were collected with permits from, and in compliance with, the laws and regulations of the Sri Lanka Department of Wildlife Conservation.

3. Results

3.1. Benthic Substrate, Coral Distribution, and the Status of Reefs

The extent of the benthic categories varied significantly across the study sites (Figure 2). The mean percentage cover of benthic categories was compared between the sites on the Palk Bay islands and the sites on the northern coastal reefs in the Palk Strait. Nearly 50% of the substrate at the reef sites on the northern coast was composed of hard corals, while the remaining part was mostly composed of dead corals (RC and NIA).

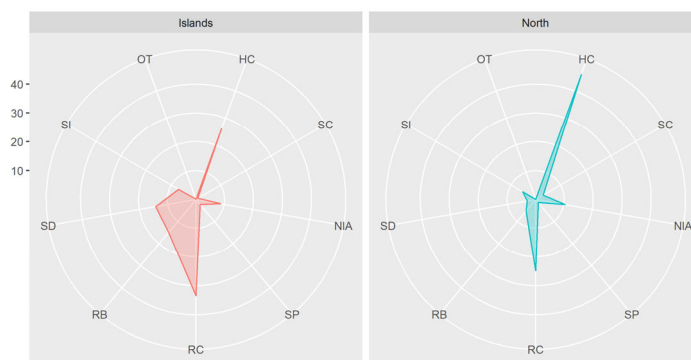


Figure 2. Radar plot giving an overview of benthic cover distribution on the coral reef sites on the Palk Bay islands (**left**) in comparison with those on the northern coast of the Jaffna Peninsula (**right**). (HC- hard coral, SC- soft coral, NIA- dead coral with macroalgae or nutrient indicating algae, SP- sponge, RB- coral rubble, RC- hard substrate of dead coral more than one year old covered by turf

algae or encrusting coralline algae, SD- sand, SI- silt, and OT- others (including sea anemones, tunicates, gorgonians, or non-living substrate)).

In contrast, the substrate cover at the island sites was composed principally of dead coral rocks covered with turf algae, with the rest mostly consisting of hard corals, rubbles, and fleshy macroalgae. There was a significant difference in mean percentage cover of hard corals (HC) between the northern coastal reefs ($n = 16$, median = 45.31 ± 10.0 range) and the island reefs ($n = 24$, median = 25.31 ± 25.62 range) (Mann–Whitney U -test, $p = 0.0001$). In addition, the mean percentage cover of soft corals (SC) was significantly higher on the northern coast compared to the islands (Mann–Whitney U -test, $p < 0.05$). In contrast, there were no significant differences in mean percentage cover of fleshy macroalgae (NIA), of coral rocks covered with turf algae (RC), or of coral rubble (RB) between the northern coast and island reef sites (Kruskal–Wallis test, $p > 0.05$).

Comparing individual sites, live coral cover was greatest at the Point Pedro (HC: $52\% \pm 7$; SC: $4\% \pm 3$), Inbarsitty (HC: $44\% \pm 3$; SC: $3\% \pm 2$), and Thondaimanaru (HC: $46\% \pm 6$; SC: $2\% \pm 1$) (\pm indicates SD) (Figure 3). The Valithoondal, Karainagar, Pungudutivu, and Kayts sites also had live coral cover of between 25% and 50%, corresponding to fair health status as defined here. Live coral cover was lowest (15–30%) at the five island sites Knr, Pu2, Kt1, Kt2, and Del (excluding Pu1). Pungkudutviu and Kayts islands were characterised by the highest mean percentage cover of dead coral ($61\% \pm 7$ and $58.5\% \pm 10.5$, respectively) followed by Delft reef front ($46\% \pm 6$) (Figure 3). Thus, a high live coral cover ($49\% \pm 7.25$) was observed on the northern coast and a low live coral cover (5%) on the island sites, except at Del (Figures 2 and 3). In all cases, the coral mortality index was greater than 0.33 (Figure 3), implying that all the reefs were stressed or impacted.

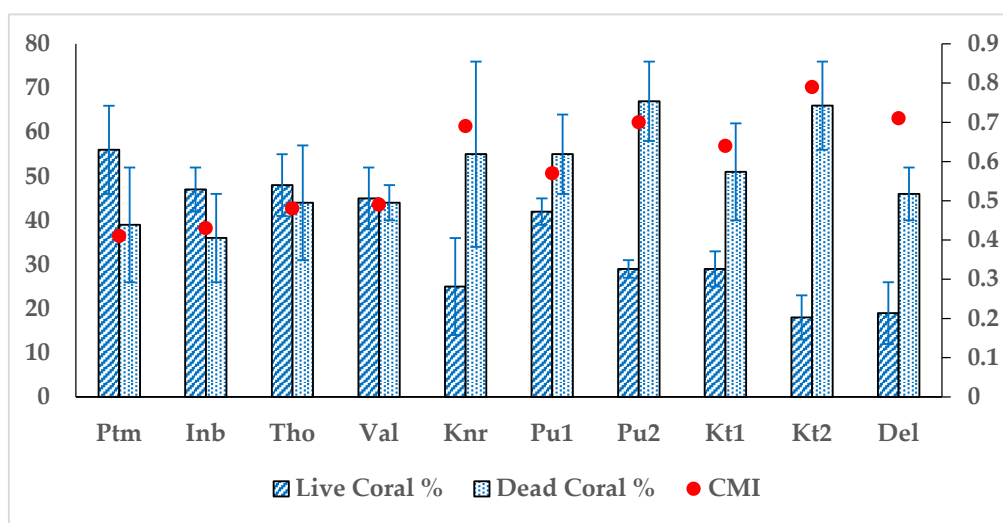


Figure 3. Percentages of live coral cover and dead coral cover, together with the values of the Coral Mortality Index (CMI) on coral reefs at each of the study sites.

Figure 4 revealed two major groups of sites that cluster at a 60% similarity level. Sites Knr, Val, Ptm, Tho, Inb, Pu1, and Pu2 fall into the upper group, and Kt1 and Kt2 into the lower group, within which the Delft reef front site (Del) appears to be an outlier. There were three sub-groups in the upper group of the dendrogram, consisting of Inb, Tho, and Ptm (showing >85% homogeneity), Pu1 and Pu2 (>80% homogeneity), and Val and Knr (>70% homogeneity). Thus, all of the north coast sites plus two of the island sites (Pu1 and Pu2) fall into the upper group and the remaining island sites into the lower group, so supporting the distinction made above based on coral cover alone.

Turf algae-dominated dead coral rocks (RC) were observed ubiquitously at the island reefs. The greatest extent of dead corals covered with turf algae ($48.5\% \pm 13$) occurred at

Kayts island and of coral rubble at Pungudutivu island ($31.5\% \pm 7$). The Delft reef front site (outlier group) in the dendrogram was distinguished from the other sites by the presence of a very low percentage of live hard coral cover ($16\% \pm 5$ SE) and a high percentage of abiotic substrates, such as sand ($31\% \pm 5$), although the highest proportion of abiotic forms were observed at Pungudutivu (mean of RB $31.5\% \pm 7$; SD $2.5\% \pm 2$).

Valithoondal and Karainagar reef sites had similar amounts of soft coral cover, and dead coral rocks covered with macroalgae such as *Turbinaria* sp., *Caulerpa* sp., and *Sargassum* sp. (Figure 5, Supplementary Table S1). Valithoondal reef region had the highest live coral cover ($45\% \pm 7$) of massive growth forms, including various species (Table 1). At Point Pedro, Valithoondal, and Karainagar, numbers of giant clams, sea cucumbers, tunicates, and sea anemones were present (documented as others, OT) (Supplementary Table S1). Soft corals were uncommon but were occasionally found on transects on the northern coast. No soft corals were recorded at Pungudutivu or Kayts islands, and only a few at Karianagar island.

Table 1. List of the coral families recorded, showing the total numbers of genera and species identified from the study area.

No.	Family	Jaffna	
		Genera	Species
1	Acroporidae Verrill, 1902	4	28
2	Agariciidae Gray, 1847	2	3
3	Dendrophylliidae Gray, 1847	1	5
4	Diploastraeidae Chevalier & Beauvais, 1987	1	1
5	Euphylliidae Alloiteau, 1952	1	2
6	Fungiidae Dana, 1846	2	3
7	Merulinidae Verrill, 1866	12	39
8	Leptastreidae Rowlett, 2020	2	3
9	Lobophylliidae Dai & Horng, 2009	5	8
10	Oulastreidae Vaughan, 1919	1	1
11	Plesiastreidae Dai & Horng, 2009	1	1
12	Pocilloporidae Gray, 1842	2	3
13	Poritidae Gray, 1842	2	13
14	Psammocoridae Chevalier & Beauvais, 1987	1	1
15	Siderastreidae Vaughan & Wells, 1943	1	2
16	Scleractinia incertae sedis (temporary name)	1	1
Total		39	113

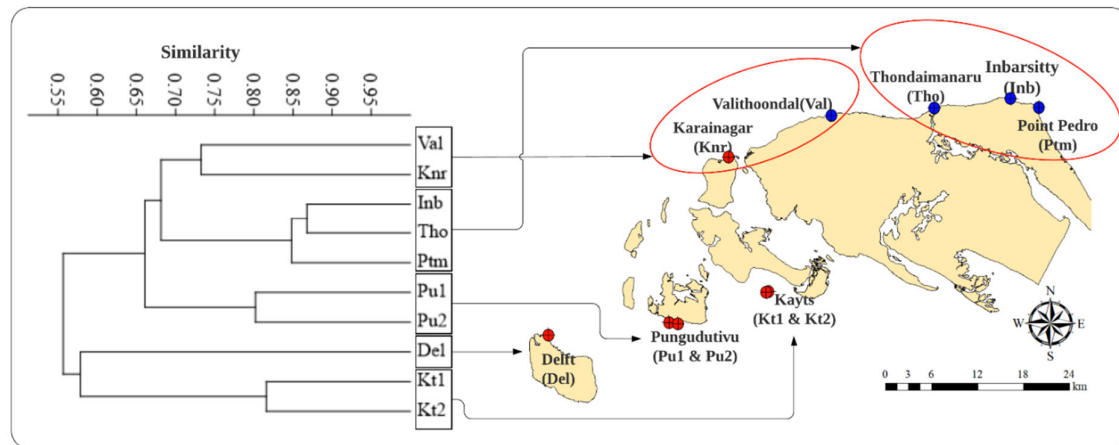


Figure 4. Bray–Curtis Cluster analysis based on differences in the benthic cover on the reefs of the Jaffna Peninsula, together with a map showing the locations of the sites. (Abbreviations as shown on the map.)

This distinction between reef areas was further explained by the principal component analysis (PCA) which illustrated the overall pattern of variation amongst sites and the dependence of this pattern on different benthic components (Figure 5). The analysis explains 58.8% of the total variance, of which principal component one (PC1) accounted for 32.3% of the variance and had a positive correlation ($PC1 > 0$) with the benthic substrates soft coral (SC), dead corals covered with macro algae (NIA), sponges (SP), sand (SD), and others (OT), while principal component two (PC2) accounted for 26.5% of the variance and showed a positive correlation ($PC2 > 0$) with the substrates rocks covered with turf algae (RC) and silt (SI). Accordingly, sites Pu1, Pu2, Tho, and Inb are assigned to the $PC1 < 0/PC2 < 0$ domain; sites Ptm, Val and Knr to the $PC1 > 0/PC2 < 0$ domain; sites Kt1 and Kt2 to the $PC1 < 0/PC2 > 0$ domain; and site Del to the $PC1 > 0/PC2 > 0$ (Figure 5).

The shallow areas (1 to 3 m depth) of reef front on the northern coast were dominated by macroalgae from October to April due to the Northwest Monsoon. The data were tested for any relationship between live coral cover (hard coral (HC) and soft coral (SC)) and algal cover (RC and NIA) across all sites, showing a significant negative correlation ($r = -0.73, p < 0.05$) between live coral cover and algal cover (Supplementary Figure S1).

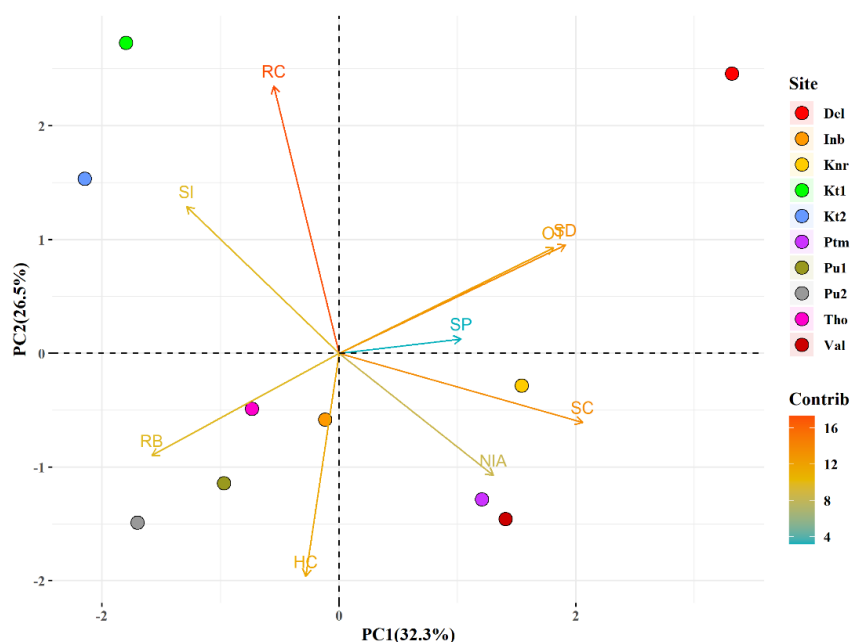


Figure 5. Principal component analysis (PCA) showing the pattern of differences between study sites and how they correlate with different benthic components (HC- hard coral, SC- soft coral, NIA- dead coral with macroalgae or nutrient indicating algae, SP- sponge, RB- coral rubble, RC- hard substrate of dead coral more than one year old covered by turf algae or encrusting coralline algae, SD- sand, SI- silt, and OT- others (including sea anemones, tunicates, gorgonians, or non-living substrate)).

3.2. Diversity, Taxonomic Composition, and Distribution of Coral Species

The taxonomic study across the eight reef areas surveyed revealed a total of 113 scleractinian coral species, from 39 genera and 16 families, together with seven soft coral genera (Table 1). Among these, 36 species of hard corals appear to be new records for Sri Lanka (Table 2), including species of the genera *Oulastrea*, *Coeloeris*, and *Siderastrea*, although all have been recorded in other parts of the Central Indian Ocean. The full species list (Table 1) includes 39 members of the family Merulinidae (44% of the total), 28 species of Acroporidae (32%), and 13 species of Poritidae (15%). The predominant genera present were *Acropora* (17 spp.), *Dipsastraea* (10), *Porites* (7), *Favites* (6), *Montipora* (6), *Goniopora* (6), *Turbinaria* (5), and *Platygyra* (5) (Supplementary Table S2).

Table 2. Numbers of families, genera, and species of scleractinian corals recorded in each of the eight reef areas studied around the Jaffna Peninsula, Sri Lanka.

	Ptm	Inb	Tho	Val	Knr	Pu1, Pu2	Kt1, Kt2	Del
Families	12	07	12	08	09	06	08	10
Genera	24	27	24	18	17	15	18	18
Species	49	30	44	25	36	34	33	37

The numbers of genera and species recorded differed between the study sites (Table 2). On the northern coast, massive coral growth forms were predominant and the principal genera present were *Dipsastraea* (6 spp.), *Porites* (6), *Montipora* (6), *Favites* (5), *Platygyra* (4), *Goniastrea* (3), and *Symphyllia* (3). Encrusting growth forms of the genera *Symphyllia*, *Lobophyllia* and *Acanthastrea* were also more common on the northern coast. In contrast, around the island sites, tabulate and branching *Acropora*, foliose *Montipora*, massive *Porites*, and smaller *Goniastrea* predominated, with branching and tabulate *Acropora* and foliose growth forms occupying large areas. The Pungudutivu and Kayts island sites, in

particular, were dominated by branching and tabulate *Acropora*, followed in substrate cover by *Porites*. The genus *Echinopora* was observed at Point Pedro, Thondaimanaru, Pungudutivu, and Kayts Islands. Only a single colony of *Pocillopora verrucosa* was documented, being at Point Pedro, while scattered *Pocillopora damicornis* were recorded on the Inabarsitty and Thondaimanaru reefs. The newly recorded species *Acropora gemmifera* was found at all the study sites, but *Acropora aspera*, *Acropora digitifera*, *Montipora flabellata*, and *Echinopora gemmacea* were uncommon, with only one colony recorded at any site.

Soft coral colonies representing the genera *Capnella*, *Cladiella*, *Clavalaria*, *Lobophyton*, *Subergorgia*, and *Sarcophyton* (Supplementary Table S1) were uncommon and made only a minor contribution (2–4%) to substrate cover, but they were found on the northern coast and on the islands of Karainagar and Delft.

A comparison of the number of species present at different sites showed that the northern coastal sites had higher richness and diversity than the island sites (Tables 3 and 4). Calculation of Shannon's diversity and evenness indices suggested that all the reefs, excluding Pungudutivu, had comparable diversity and evenness values ($H' \geq 2.5$; $E \geq 0.9$), with a low dominance index ($D \leq 0.1$). The Point Pedro reef front had nearly 50 hard coral species, followed by Thondaimanaru with 44 hard coral species (Table 3), but the Shannon–Weiner diversity index at Thondaimanaru was higher ($H' = 3.020$) than that at Point Pedro ($H' = 2.927$) (Table 4).

Table 3. List of the species newly recorded in Sri Lanka during the present study, showing whether they were recorded on the north coast at the Palk Strait sites (PS sites) or on the islands in Palk Bay (PB sites), together with their previously documented occurrence (indicated by ✓) in other South Asia, Indian Ocean and Arabian Sea regions (LWI—Lakshadweep Islands, GOM—Gulf of Mannar, ANI—Andaman and Nicobar islands, Arabian Sea (AS) (including Red Sea), CIO—central Indian Ocean region) [43].

No.	Family	Genus	Species	PS Sites	PB Sites	LWI	GOM	ANI	AS	CIO		
1	Acroporidae Verrill, 1901	<i>Acropora</i> Oken, 1815	<i>Acropora aspera</i> Dana, 1846	✓		✓		✓	✓	✓		
2			<i>Acropora digitifera</i> Dana, 1846	✓		✓	✓	✓	✓	✓		
3			<i>Acropora gemmifera</i> Brook, 1892	✓		✓		✓	✓	✓		
4			<i>Acropora latistella</i> Brook, 1891				✓		✓	✓		
5			<i>Acropora pulchra</i> Brook, 1891				✓		✓	✓		
6			<i>Alveopora</i> Blainville, 1830	<i>Alveopora allingi</i> Hoffmeister, 1925	✓	✓				✓	✓	
7			<i>Astreopora</i> Blainville, 1830	<i>Astreopora myriophthalma</i> Lamarck, 1816	✓	✓	✓	✓	✓	✓	✓	
8				<i>Astreopora listeri</i> Bernard, 1896	✓		✓		✓	✓	✓	
9				<i>Astreopora ocellata</i> Bernard, 1896	✓		✓				✓	
10				<i>Montipora</i> Blainville, 1830	<i>Montipora flabellata</i> Studer, 1901	✓					✓	
11					<i>Montipora informis</i> Bernard, 1897	✓	✓	✓	✓	✓	✓	
12	Merulinidae Verrill, 1865	<i>Goniastrea</i> Milne Edwards & Haime, 1848	<i>Goniastrea minuta</i> Veron, 2000		✓			✓		✓		
13			<i>Coelastrea</i> Verrill, 1866	<i>Coelastrea palauensis</i> Yabe & Sugiyama, 1936		✓					✓	
14			<i>Cyphastrea</i> Milne Edwards & Haime, 1848	<i>Cyphastrea japonica</i> Yabe & Sugiyama, 1936		✓					✓	
15				<i>Cyphastrea micropthalma</i> Lamarck, 1816		✓	✓	✓	✓	✓	✓	
16				<i>Platygyra</i> Ehrenberg, 1834	<i>Platygyra acuta</i> Veron, 2000	✓			✓	✓	✓	
17				<i>Echinopora</i> Lamarck, 1816	<i>Echinopora gemmacea</i> Lamarck, 1816	✓			✓	✓	✓	
18				<i>Dipsastraea</i> Blainville, 1830	<i>Dipsastraea amicornum</i> Milne Edwards & Haime, 1850		✓			✓	✓	
19					<i>Dipsastraea lizardensis</i> Veron, Pichon & Wijsman-Best, 1977	✓	✓			✓	✓	
20					<i>Dipsastraea rotumana</i> Gardiner, 1899		✓			✓	✓	
21			Scleractinia incertae sedis	<i>Pachyseris</i> Milne Edwards & Haime, 1849	<i>Pachyseris gemmae</i> Nemenzo, 1955	✓				✓	✓	
22			Oulastreidae Vaughan, 1919	<i>Oulastrea</i> Milne Edwards & Haime, 1848	<i>Oulastrea crispata</i> Lamarck, 1816	✓				✓	✓	
23	Poritidae Gray, 1842	<i>Porites</i> Link, 1807	<i>Porites evermanni</i> Vaughan, 1907	✓				✓		✓		
24			<i>Porites murrayensis</i> Vaughan, 1918	✓	✓			✓		✓		
25			<i>Porites pukoensis</i> Vaughan, 1907		✓					✓		
26			<i>Goniopora</i> de Blainville, 1830	<i>Goniopora lobata</i> Milne Edwards, 1860	✓	✓				✓	✓	
27				<i>Goniopora minor</i> Crossland, 1952	✓	✓	✓	✓		✓	✓	
28				<i>Goniopora somaliensis</i> Vaughan, 1907		✓				✓	✓	
29				<i>Goniopora tenuidens</i> Quelch, 1886		✓			✓	✓	✓	
30			Dendrophylliidae Gray, 1847	<i>Turbinaria</i> Oken, 1815	<i>Turbinaria frondens</i> Dana, 1846	✓					✓	
31					<i>Turbinaria reniformis</i> Bernard, 1896	✓	✓			✓	✓	
32					<i>Turbinaria stelluta</i> Lamarck, 1816	✓	✓	✓		✓	✓	
33			Lobophylliidae Dai & Horng, 2009	<i>Acanthastrea</i> Milne Edwards & Haime, 1848	<i>Acanthastrea ishigakiensis</i> Veron, 1990	✓				✓	✓	
34	<i>Micromussa</i> Veron, 2000	<i>Micromussa amakusensis</i> Veron, 1990			✓							
35	Agariciidae Gray, 1847	<i>Coelosseris</i> Vaughan, 1918	<i>Coelosseris mayeri</i> Vaughan, 1918		✓			✓		✓		
36	Siderastreidae Vaughan & Wells, 1943	<i>Siderastrea</i> Blainville, 1830	<i>Siderastrea savignyana</i> Milne Edwards & Haime, 1849	✓	✓		✓	✓	✓			

Table 4. The richness and values of diversity and evenness indices for hard corals at each of the study sites of the Jaffna Peninsula.

Reef Regions	Number of Species	Richness	Shannon's Diversity Index (H')	Simpson's Dominance Index (D)	Simpson's Diversity Index (D')	Evenness Index (E)
Point Pedro	49	3.429	2.927	0.066	0.934	0.921
Inbarsitty	30	2.921	2.61	0.084	0.916	0.900
Thondaimanaru	44	3.769	3.02	0.060	0.94	0.938
Valithoondal	25	3.470	2.752	0.069	0.931	0.971
Karainagar	35	2.704	2.575	0.089	0.911	0.929
Pungudutivu	32	2.475	2.323	0.127	0.873	0.880
Kayts	34	3.258	2.743	0.083	0.917	0.932
Delft	37	2.959	2.713	0.082	0.918	0.939

The relationships between mean values of live coral cover and the different diversity indices (Shannon's Diversity Index—H', Simpson's Dominance Index—D, and Evenness index—E) were investigated separately for each of the two parts of the study area, i.e., the island sites (Karainagar, Pungudutivu, Kayts, and Delft) and the northern coastline (Point Pedro, Inbarsitty, Thondaimanaru, Valithoondal). The relationship between these indices on the northern coast and on the island sites was further analysed with a Pearson correlation. On the northern coast, there was a moderate positive relationship between diversity and live coral cover (Pearson correlation: $r = 0.64$, $p > 0.05$). In contrast, among the island sites, there was a strong negative correlation between both diversity index (Pearson correlation: $r = -0.96$, $p < 0.05$) and evenness (Pearson correlation: $r = -0.98$, $p < 0.05$) on the one hand and live coral cover on the other. Similarly, there was a negative correlation (Pearson correlation: $r = -0.51$, $p > 0.05$) between the dominance index and mean live coral cover on the northern coast, but a strong positive correlation (Pearson correlation: $r = 0.96$, $p < 0.05$) between these variables among the island sites (Supplementary Figure S2).

3.3. DNA Barcoding of Selected Coral Species

Although most species could be identified from morphological characteristics alone, some that were difficult to distinguish morphologically and those considered rare were subjected to DNA barcoding to identify them with greater certainty. Based on the NCBI GenBank database sequences, the best match for each of the samples studied is shown in Table 5, together with the respective accession numbers. There were seven mitochondrial COI gene barcode sequences recorded that represented six new records for Sri Lanka: four species from the genus *Acropora*, including two samples of *A. gemmifera*, and one species each from the genera *Montipora* (*M. flabellata*) and *Echinopora* (*E. gemmacea*) (Figure 6, Table 5). The COI barcode sequences for all the samples showed a >99% similarity to the respective sequences recorded in GenBank.

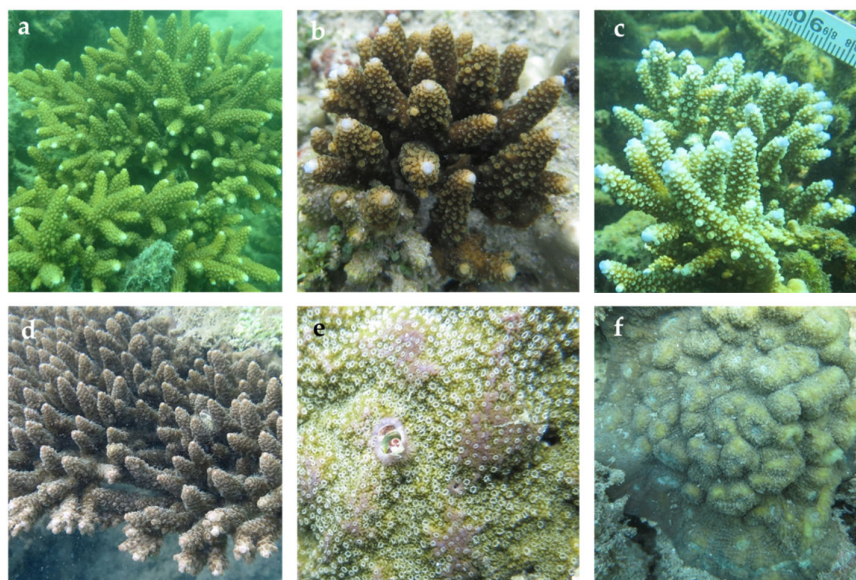


Figure 6. Species subjected to DNA barcoding: (a) *Acropora aspera*, (b) *Acropora digitifera*, (c) *Acropora gemmifera*, (d) *Acropora hyacinthus*, (e) *Montipora flabellata*, (f) *Echinopora gemmacea*.

Table 5. List of samples sequenced in this study and the most closely related barcodes found in GenBank, together with their accession numbers, and the publisher of the sequence.

Sample ID	Accession ID	Sequence Length	Molecular Identification (Closest Relative in GenBank)	Identity	Reference
COJP001	MN689059	709	<i>Acropora aspera</i> (KF448532.1)	99.69%	[48]
COJP002	MN689060	717	<i>Acropora gemmifera</i> (MG383839.1)	99.83%	[49]
COJP003	MN689061	721	<i>Acropora digitifera</i> (KR401100.1)	99.22%	[50]
COJP004	MN689062	711	<i>Acropora gemmifera</i> (MG383839.1)	99.83%	[49]
COJP006	MN689067	715	<i>Acropora hyacinthus</i> (LC326547.1)	99.85%	[51]
COJP007	MN689068	718	<i>Echinopora gemmacea</i> (HE654561.1)	99.84%	[52]
COJP009	MN689065	714	<i>Montipora flabellata</i> (HQ246603.1)	99.51%	[53]

4. Discussion

4.1. Status of Reefs and Extent of Impacts

Located close to the southern tip of the Indian sub-continent, Sri Lanka's coral reefs are surrounded by other well-developed reef areas in both the Western Indian Ocean and the Bay of Bengal. India has three coral reef regions, one of which, Palk Bay, lies adjacent to the present study area, on the opposite side of the Palk Strait. The others, lying much further away, are the Andaman and Nicobar Islands in the Bay of Bengal and the Lakshadweep islands located between the west coast of India and the Maldives. Further to the west lie the Maldives and the Chagos Archipelagoes [54,55]. According to Arthur [56], the reef faunas of the Gulf of Mannar and Palk Bay islands are closely related to those of other Sri Lankan coral reefs. However, the differences described here in benthic composition between islands in the Palk Bay and northern coast sites in the Palk Strait suggest that, in terms of coral cover and species present, the Palk Strait reefs may also be compared to those in the above-mentioned neighbouring regions (Figure 7).

To date, it was presumed that all the coral assemblages of Sri Lanka are less well-developed and diverse than those in these other regions. Due to the limited accessibility created by the civil war, previous surveys around the Jaffna Peninsula were essentially limited to confirmation of the presence of fringing coral reefs around the islands [10,27,28].

The first quantitative report was prepared only in 2005, as part of an environmental impact assessment of the Sethusamudram Ship Channel project [27]. Even then, only rapid surveys were conducted at four reef sites (Pungudutivu, Eluvaitivu, and two locations in Kankeasanthurai harbour), while two other fringing reefs, on Analaithivu and Karathivu islands, were inspected visually to assess their condition. The study reported live coral cover on the four reefs surveyed to be between 35% and 58% [24]. In contrast, this present study found that live coral cover at the majority of sites varied between 27% and 49%, with only the Point Pedro site having more than 50% live coral cover. While this difference might relate to differences in methodology or to the present study being restricted to shallow depths, an alternative explanation is that coral cover has declined since 2005 as a result of one or more impacts.

The structure of the benthic cover at the island sites in the Palk Bay is somewhat similar to reefs in nearby regions that have been similarly subject to climate-related coral bleaching and to fishing related impacts; thus, reports of findings on the Indian reefs may provide some understanding of the impacts likely to have affected the study area [56–60]. At most sites, turf algae growing over old corals appeared to be the predominant substrate and the contribution of coral rubble to the substrate was also noticeable, suggesting that coral cover may have been higher in the past. Algal-dominated reefs are often associated with post-bleaching impacts [60,61]. A more recent study has described the extent of bleaching in the region, with bleaching being much higher in Palk Bay (71.48%) at the depth of 2–3 m than towards the Gulf of Mannar (46.04%), where the coral communities are deeper than 6 m [60]. Quantitative studies in Lakshadweep, the Gulf of Mannar, and the Andaman and Nicobar Islands have described a reduction in live coral cover and declining reef health primarily due to bleaching events from 1998 to 2015 [56,58]. More than 70% of coral cover was bleached in the Andaman Islands, Gulf of Mannar, and Lakshadweep islands during the two global bleaching events in 1998 and 2010 [60,62–68]. The bleaching event of 1998 also caused extensive coral mortality in the southern, south-western, and north-western parts of Sri Lanka [69–71], but did not affect the coral reefs in the Pigeon Island, Northern Park, and Dutch Bay areas of eastern Sri Lanka [71]. The tsunami event of December 2004 is also known to have affected the eastern and southern coral reef regions of Sri Lanka [70,71].

On the other hand, coral reefs in the Andaman and Nicobar Islands, Lakshadweep, Gulf of Mannar, Chagos Archipelago, and Maldives have shown considerable recovery following past bleaching events [57–59,64–68]. Post-bleaching monitoring observations in Lakshadweep showed a reduction in the dead coral-algal substrate, coral recruitment, and an increase in live coral cover supporting a phase shift back from algal-dominated reefs to live coral-dominated substrates [58,61]. A similar scenario might have been experienced in the present study area by the Palk Bay islands, resulting in the observed high percentage cover of standing dead coral with turf algae and of coral rubble. In addition, another recent report on the biodiversity of northern Sri Lanka indicates a similar pattern of coral benthic composition on many of the islands in Palk Bay, including Pungudutivu [24].

However, it may be suggested that the recovery of corals in the Gulf of Mannar and Palk Bay has been severely hindered by illegal fishing by vessels. These vessels operate even in the shallowest areas, stirring up the bottom and causing sedimentation [58,61,69]; they are also involved in bottom trawling, which overturns corals and causes direct damage [24–26,72]. The area is also subject to illegal fishing practices such as blast fishing [72]. More generally, the inshore reefs, especially along the northern coast of JP, are subject to considerable fishing pressure, with 21 fish landing sites present within 48 km of coastline, and a higher number of fishing vessels operating than anywhere else in the nation [73]. These reefs have also been subject to other impacts, including increased terrestrial runoff and direct damage and sedimentation resulting from dredging and the creation of boat channels at Pungudutivu, Kayts, Point Pedro, and Valithoondal. Given the scarcity of available data, further detailed research will be required to elucidate the interacting effects

of environmental conditions, seasonal variation, local anthropogenic pressure, and global climate change on the community structure of these reefs.

4.2. Coral Species Diversity

This study has significantly improved knowledge of the coral species present in the study area. Previously, no comprehensive coral inventory had been produced for these reefs [11,20,21,27,28], which now appear to perhaps be some of the most biodiverse in Sri Lanka.

Ridley (1883) made the first note recording 49 coral species in Ceylon (Sri Lanka), his specimens being deposited in the British Museum [12]. Subsequent studies on coral species and their distribution were mostly undertaken in the more southern parts of Sri Lanka at sites including Galle, Hikkaduwa, the Kalpitiya Peninsula, Unawantuna, Weligama, Polhena, Tangalle, the Great and Little Basses, and Trincomalee [9–11,19–21,28]. In comparison, the coral reefs of northern Sri Lanka have been under-studied, except for those in the Gulf of Mannar (in north-west Sri Lanka). There was, however, some preliminary information on aspects of the coral fauna of the Jaffna area [24,27]. Initial rapid surveys by Rajasuriya [27] noted at least 43 species of hard corals belonging to 20 genera. He commented that the coral reefs on the north coast and around Pungudutivu Island were more diverse than those at other study sites in the area. In contrast, the present study recorded a total of 113 hard coral species belonging to 40 genera from just eight reef areas, with the highest number of species being recorded at Point Pedro reef front (50 spp.), followed by Thondaimanaru (44 spp.) (Table 2).

Several species recorded in the present study have also been found at other coral reef sites in Sri Lanka [9], while many were listed in the corals of India [74–77]. Thus, in terms of coral species diversity, the reefs appear more comparable to other Indian territorial reefs (Figure 7). According to Raghuraman et al., 2012 [76], the various reef areas of India support a total of 478 species, representing 19 families and 89 genera. Considering the coral species recorded, the closest faunistic relationship of the Jaffna Peninsula reefs is to the reefs of the Andaman and Nicobar Islands [12,16]. However, fewer species (133) were reported here than in the Andaman Islands, where around 400 species of corals have been recorded. Coral species diversity was also similar to the Gulf of Mannar, further to the west, which has about 100 species [75]. Of the 36 coral species reported here as new records for Sri Lanka, most appear to be widely but patchily distributed across the central Indian Ocean and the Arabian Sea (Table 3) [75], with the largest proportions of these also recorded from the Andaman and Nicobar Islands (23 spp.), the Arabian Sea (21 spp.), and the Central Indian Ocean (30 spp.) [61,74–76].

Since the ability of corals to survive and recover after a bleaching event varies between species, greater species richness may endow a habitat with greater community tolerance and a greater ability to adapt to sea surface temperature changes [78–81]. At the same time, species abundance and overall coral cover will also be influenced by natural environmental factors such as wave action, salinity, exposure to light, and sediment loading [82]. In the present study, thermally tolerant encrusting and massive coral growth forms such as *Porites*, *Favites*, *Goniastrea*, and *Dipsastraea* were found to have survived to a greater extent than branching species of the genera *Acropora*, *Pocillopora*, and *Stylophora*, which are more susceptible to thermal events in many Indo-Pacific regions [78,79]. Nevertheless, large colonies of tabulate and branching *Acropora* and tiered plates of *Echinopora* and *Montipora* dominated the islands, while massive coral colonies dominated the northern coast. Similar patterns of coral distribution have been described in earlier studies [24], with large domes of stress-tolerant *Dipsastraea*, *Favites*, *Goniastrea*, *Platygyra* and *Porites* [79,80,83] occupying shallow reef flats down to 6 m depth. Notably, there were only a few small colonies of *Pocillopora* and *Stylophora* observed during the present study; this may result from their susceptibility to past bleaching events.

Of the species recorded in the present study, three are listed as “vulnerable” by the International Union for the Conservation of Nature (IUCN): *Acropora aspera*, *Acropora specifera*, and *Acropora hemprichii*. These were found at the Punkudutivu, Kayts, and Karainagar island sites, respectively. In addition, “threatened” species of *Montipora flabellata*, *Turbinaria frondens*, *Turbinaria stellulata*, and a rare species of *Astreopora ocellata* were also recorded during this study.

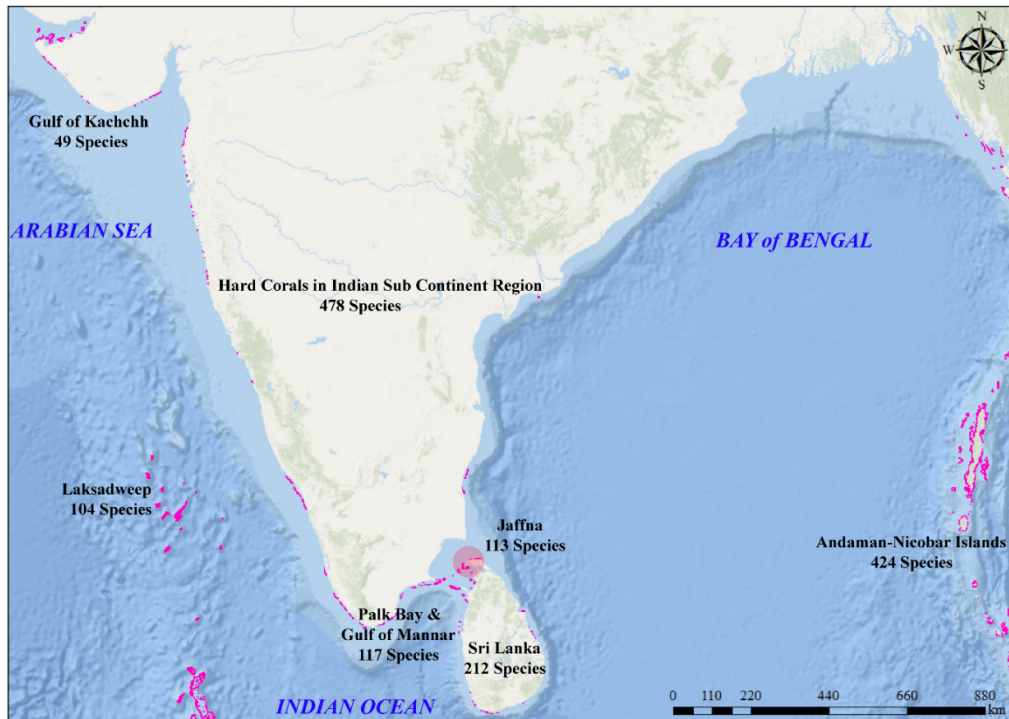


Figure 7. Comparison of the numbers of scleractinian corals recorded in different parts of India and Sri Lanka in relation to the Jaffna Peninsula and its islands. Pink colouring indicates the location of reef areas; the pink circle in the centre indicates the location of the present study areas at the northern end of Sri Lanka) [24,62,75,77].

4.3. DNA Confirmation of Selected Coral Species

The genus *Acropora*, belonging to the family Acroporidae, is the most diverse and widespread coral genus. The species show both enormous intraspecific morphological variability and striking similarities between species within a geographical region, making species identification a challenge [84]. Consequently, for several species whose growth patterns and corallite arrangements appeared atypical, DNA barcoding was employed in parallel with morphological analysis. Notably, *A. aspera*, *A. digitifera*, and *A. gemmifera* were confirmed as present in Sri Lanka for the first time, although they have been widely recorded elsewhere in the Indian Ocean. The mitochondrial *COI* gene sequence of each species was found to have more than 99% similarity with the published genome sequences (Table 5). Sample COJP001 has a 99.69% similarity with the genomic region of the *A. aspera* and the morphological features also confirmed this identification (Table 5). Based on the description provided by Veron [43], *A. aspera* is a branching species with scale-like radial corallites. It is often confused with the similar species *A. millepora*; however, the corymbose clumps of colonies with branches and the two various sizes of axial corallites serve to differentiate *A. aspera* from *A. millepora*. Samples COJP002 and COJP004 were matched to samples of *A. gemmifera*, with the closest similarity being to a Malaysian sample MG383839.1 [49]. COJP003 from the Valithoondal site was confirmed as *A. digitifera* and found to have the closest genetic relationship to a sample from the Egyptian coast of the

Red Sea, *A. digitifera*_KR401100.1 (Table 5) [50]. This species is widely distributed in the Indian Ocean, Red Sea, and eastern Pacific Ocean [43] (Supplementary Table S2).

The colonies of *M. flabellata*, one of the world's uncommon species, were recorded on the Point Pedro reef front. They had an encrusting form, were blue and pinkish to brown in colour, and had prominent thecal papillae covering the colony. Septa could not be observed, making species separation from *M. undata* difficult. However, sequences from this species had the closest match with reference sequences from the Hawaiian Islands, HQ246603.1 [53]. The sample COJP007, which was confirmed as being of *Echinopora gemmacea*, was found only at Point Pedro and Inbarsitty. According to [43], *E. gemmacea* is an uncommon species. This specimen has the closest kinship to *E. gemmacea* HE654561.1 from Yemen (Table 5) [52].

While the *COI* gene-based sequence relates to only a narrow portion of the genome, nevertheless, as found by others, it proved invaluable in confirming species-level identification of specimens from difficult to identify genera [33,85]. Apart from any intraspecific genetic variations, corals show a marked morphological plasticity that is considered to be largely adaptive [30]; molecular genetic studies are allowing a better understanding of this plasticity [86]. More generally, the use of DNA barcoding is enabling taxonomists to overcome the pitfalls of morphology-based identification and classification. In the present study, the use of barcoding has helped validate the finding of six scleractinian coral species new to Sri Lanka.

In summary, the northern coast of Jaffna Peninsula has the highest live coral cover among the regions of Sri Lanka; however, the reefs are prone to impacts from increasing fishing pressure and environmental pollution. These new insights into the coral biodiversity, distribution, and benthic biota of the coral reefs of the Jaffna Peninsula contribute knowledge required for future conservation and management. The present study indicates that the conservation of the coral reefs in Jaffna is critical, not only because of their direct ecological and economic importance, but because they may provide a reservoir of different coral species able to withstand the effects of future climate change.

Supplementary Materials: The following are available online at www.mdpi.com/article/10.3390/oceans2030029/s1.

Author Contributions: Conceptualisation, A.A. and V.H.; data curation, A.A., V.H. and S.K.; funding acquisition, A.A. and V.H.; investigation, A.A. and A.U.; methodology, A.A., V.H., A.U. and A.H.; project administration, V.H.; resources, V.H.; supervision, V.H. and S.K.; validation, A.U.; visualisation, A.A., A.U. and A.H.; writing—original draft, A.A.; writing—review and editing, V.H. and S.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research received funding from IDEAWILD and from the Research Facilitation Fund (RFF) of the Postgraduate Institute of Agriculture, University of Peradeniya.

Institutional Review Board Statement: Samples were collected with permits from, and in compliance with, the laws and regulations of the Sri Lanka Department of Wildlife Conservation.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We acknowledge the International Coral Reef Society (ICRS) for granting a graduate fellowship to the senior author. We also thank the Department of Agricultural Biology, Faculty of Agriculture, University of Peradeniya for providing molecular laboratory facilities, the Department of Fisheries Science, Faculty of Science, University of Jaffna for their technical support. We also thank the editor, Rupert Ormond, for extensive support in improving the text.

Conflicts of Interest: The authors declare that they have no known competing financial interest or personal relationship that could have appeared to influence the research studies presented in this paper.

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