

Article

Diversity of Coral Reef Fishes in the Western Indian Ocean: Implications for Conservation

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Abstract: Communities of coral reef fishes are changing due to global warming and overfishing. To understand these changes and inform conservation, knowledge of species diversity and distributions is needed. The western Indian Ocean (WIO) contains the second highest coral reef biodiversity hotspot globally, yet a detailed analysis of the diversity of coral reef fishes is lacking. This study developed a timed visual census method and recorded 356 species from 19 families across four countries in the WIO to examine patterns in species diversity. Species richness and composition differed most between the island countries of Madagascar and Comoros and both these locations differed from locations in Tanzania and Mozambique which were similar. These three regional groupings helped define WIO ecoregions for conservation planning. The highest species richness was found in Tanzania and Mozambique, and the lowest and most different species composition was found in Comoros. Biogeography explains these differences with naturally lower species diversity expected from the small, oceanic, and isolated islands of Comoros. Present day ocean currents maintain these diversity patterns and help explain the species composition in northeast Madagascar. Species distributions were driven by 46 of the 356 species; these provide guidance on important species for ongoing monitoring. The results provide a benchmark for testing future changes in reef fish species richness.

Keywords: coral reef fishes; species diversity; Indian Ocean; conservation; climate change



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1. Introduction

Species are the fundamental units of ecosystems and thus species inventories and their distributions provide a foundation for understanding coral reef communities and their conservation [1,2]. Communities of reef-associated fish species reflect their biogeography, and this includes evolutionary history, sea surface temperature, and larval recruitment patterns driven by ocean currents [1,3–5]. But these reef fish communities are changing due to global warming and overfishing, which are rapidly degrading coral reefs globally [6–8], driving declines in abundance and local extirpations of some species [9,10]. Understanding these changes and informing conservation knowledge about patterns in species diversity is needed.

Marine provinces, first defined over 150 years ago [11,12], along with barriers to species dispersal [13,14], provide a framework for understanding present day biogeographic patterns. The western Indian Ocean (WIO), is considered a distinct province of the Indo-Pacific region [15,16] and comprises 10 countries, all with coral reefs [17,18]. This province contains the second highest biodiversity hotspot in the Indo-Pacific, second to

the Coral Triangle in the western Pacific [19–21]. Ten biogeographic subregions within the WIO Province were defined using hermatypic corals [22], with the diversity hotspot centered in the northern Mozambique Channel on the coasts of northern Madagascar, the Comoros Archipelago, northern Mozambique, and southern Tanzania (Figure 1), an area considered likely to host the highest diversity and abundance of other marine fauna [23]. Veron and coauthors [24], based on zooxanthellate coral distributions, confirmed similar coral ecoregions in the WIO but delineated 12 subregions by separating Comoros from Mozambique and Madagascar. These ecoregions provide important conservation planning units [25].

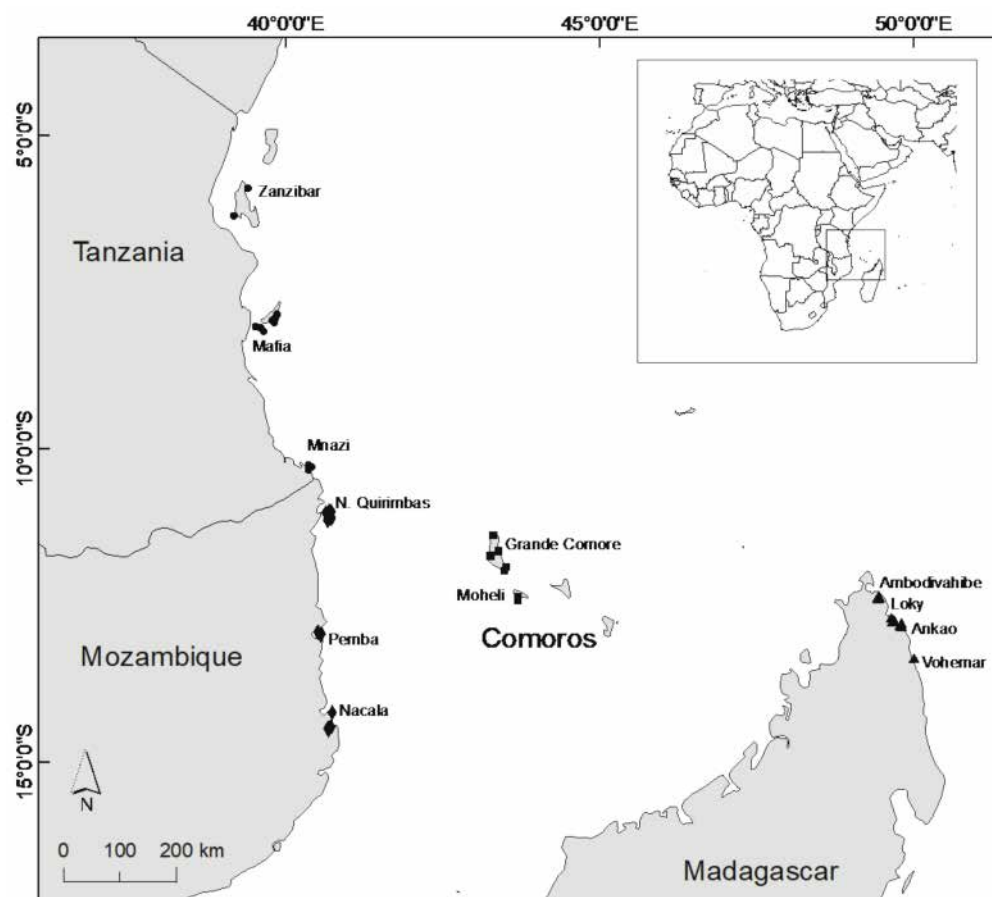


Figure 1. Map of study area showing countries and location of survey sites.

There are over 3000 tropical reef fish species found in the Indian Ocean, of which 74% range widely through the Indo–Pacific, thus giving ~850 species restricted to the Indian Ocean [5]. The WIO Province supports just over 2400 fish species, representing a second peak in fish diversity in the Indo–Pacific after the Coral Triangle [19]. The highest fish species richness is found to the west on the eastern African continental coastline, with ~600 to 960 species. The highest level of endemism in the WIO is found to the east in the Mascarene Islands of Reunion and Mauritius. High endemism is typical of peripheral biogeographic regions [15,26]. Reef fish species’ inventories in the WIO remain scattered and largely at a national level ranging from Madagascar [27,28], Comoros [29], Iles Eparses [30,31], to Reunion Island [32]. Therefore, data on species ranges are incomplete, though considerable early work established a sound base of identification sources [33,34]. However, a detailed regional analysis of the diversity of coral reef fishes in the WIO is lacking.

The present study developed a rapid underwater visual census method to compile reef fish species inventories across shallow reefs to examine biogeographic patterns in species assemblages across four countries. The study used the most diverse and/or most

numeric families that occur on coral reefs in the Indo-Pacific [35], representing potentially around 460 coral reef species from the WIO [3,27,34]. Families selected represented those reported as indicators of biogeographical patterns and coral reef health, such as Chaetodontidae [36,37]; of fishery importance [38]; of both wide-ranging and restricted range species; and of Tetraodontiformes, to expand the taxonomic diversity at the suborder level [3,39,40]. Two highly diverse families notably absent from this list are the Gobiidae and Blennidae, which are known to be excellent biodiversity indicators [41], however, they are too cryptic in their behavior and difficult to identify underwater while surveying a broad suite of species that range up to ~1 m in length. The final 19 families rank highly in importance as indicators on coral reefs (Table 1) and comprises a potential species list that represents ~50% of the putative total number of shallow coral reef species in the WIO [5]. This was therefore considered sufficiently broad and diverse to capture biogeographic patterns in the diversity of fishes within the region.

Table 1. Nineteen families surveyed for coral reef fish diversity analyses based on: (a) most speciose; (b) known indicators of aspects of fish communities; (c) fishery importance; (d) taxonomic diversity. Other rankings of coral reef fish families as indicators of diversity or importance on coral reefs are shown for comparison: Coral Reef Fish Diversity Index, CFDI^A (Allen and Werner 2002); numerical abundance^{C and B} (Choat and Bellwood 1991); consensus list of 10 characteristic coral reef families, B (Bellwood 1996); global comparison of most speciose families^{B and W} (Bellwood and Wainright 2002). These families are characteristic of coral reefs though not necessarily restricted to them and are among first 28 most speciose families of reef fish worldwide out of a possible 76 families (Bellwood and Wainright 2002).

Order	Suborder	Families	CFDI ^A	Abundance ^{C and B}	10 Coral Reef ^B	Most Speciose ^{B and W}
Perciformes (a)	Labroidei	Labridae (wrasse)	X	X	X	1
	Percoidei	Epinephelidae (groupers)				3
	Labroidei	Pomacentridae (damsel fishes)	X	X	X	2
Perciformes (b)	Percoidei	Chaetodontidae (butterfly fishes)	X	X	X	6
	Labroidei	Scarinae (parrot fishes) ¹	X		X	8
	Acanthuroidei	Acanthuridae (surgeon fishes)	X	X	X	7
	Percoidei	Lutjanidae (snappers)				10
	Percoidei	Pomacanthidae (angel fishes)	X			11
Perciformes (c)	Percoidei	Lethrinidae (emperors)				13
	Percoidei	Haemulidae (grunts)				23
	Percoidei	Mullidae (goat fishes)			X	19
	Acanthuroidei	Siganidae (rabbit fishes)				21
	Percoidei	Nemipteridae (bream)				24
	Percoidei	Carangidae (trevally)			X	N/A
Perciformes (d)	Percoidei	Caesionidae (fusiliers)				28
Tetraodontiformes	Tetraodontiformes	Balistidae (trigger fishes)				16
Tetraodontiformes	Tetraodontiformes	Monacanthidae (file fishes)				14
Tetraodontiformes	Tetraodontiformes	Ostraciidae (box fishes)				25
Tetraodontiformes	Tetraodontiformes	Tetraodontidae (puffer fishes)				18

¹ Scarinae are a subfamily within the Labridae (Bellwood et al. 2019) but for functional purposes are treated separately.

The current study aimed to examine patterns in species richness of reef fishes to contribute to our understanding of the biogeography of the less studied WIO province. It also aimed to assess how reef fish diversity patterns conform to known biodiversity hotspots and to delineate ecoregions in the WIO for coral reef conservation planning and threat assessments.

2. Materials and Methods

2.1. Study Sites

Coral reef fish species were recorded in 2009–2011 at 76 dive stations aligned to 45 sites which ranged from 1–33 m in depth (in the supplementary Table S1), spread across locations in four countries in the WIO: Madagascar, Comoros, Mozambique, and Tanzania (Figure 1) spanning latitude −5.84° (Zanzibar) to −14.47° (Nacala) and longitude 39.17 (Chumbe)

to 50.01 (Vohemar). Sites surveyed in Comoros were in Ngazidja (Grand Comore) and Mwali (Moheli), two of the three islands in the Union of Comoros, which are referred to hereafter as Comoros. The fourth southeastern island in the Comoros Archipelago, Mayotte, an overseas department of France, is a larger island with considerably more reef habitat, but was not surveyed here. Each country's dataset is a sample and cannot claim to be representative of the country as a whole. Sites were selected haphazardly and ranged from shallow, protected fringing reefs to deep, exposed forereefs (Table S1). Each location encompassed sites across a large depth range and were therefore broadly comparable, though this negated any analysis for habitat effects (Table S1). Forereefs and deep and shallow terraces were prioritized as these reef types tend to have higher coral cover and rugosity, and hence, higher fish species diversity.

2.2. Survey Method

Coral reef fish diversity was measured by recording presence/absence of species on a SCUBA based underwater visual census (UVC) survey, which involved a timed swim by one observer throughout (MS), recording all species within visibility (mean 14.1 m), supplemented with a few snorkel dives in shallow waters. The method was designed to provide sufficient breadth of species sampling, while remaining practically feasible for relatively rapid dive surveys across a large number of locations. The 19 families were selected based on those that are most speciose, are amenable to UVC (diurnal and not cryptic), have fishery importance, and included four Tetraodontiform families to extend the taxonomic diversity of the dataset (Table 1).

A complete species inventory of 19 families (Table 1) was recorded at each dive. Dive time and species richness were significantly correlated ($R^2 = 0.19$, slope = $0.27x + 91$, $p < 0.01$) though taxonomic diversity was not ($R^2 < 0.01$, slope = $-0.001x + 63$, $p < 0.86$). The species richness curve showed a species plateau at ≥ 75 min dive duration. Consequently, data from the two replicate dive stations at each site were combined to ensure that each reef site was represented by 75–85 min of underwater observations. This conforms to recommended dive times of 60–90 min [27].

Species identifications were checked using photographs, taxonomic references, and photographic guides (see Table S2 for species list and references). Species names were verified from the online Catalog of Fishes [42].

2.3. Data Analyses

To assess overall patterns of species diversity, the species presence/absence data per reef site was used to calculate the total number of species and the average taxonomic distinctness ($D+$). The average taxonomic distinctness is a measurement of the average taxonomic path length between two randomly chosen species in the assemblage [43] and was increasingly applied because it is considered a good proxy of biodiversity and it is relatively independent of sampling effort [44]. Species richness and taxonomic distinctness were tested for differences between areas within countries and dive time. Species accumulation curves derived from the Michaelis–Menten index using 9999 permutations [43] were utilized to predict maximum species richness for each country. The Michaelis–Menten equation was chosen because it is independent of the rarity of a species, being based solely on presence. Furthermore, on empirical considerations it was also found to be the least biased by the number of samples and the most stable statistic to use for estimated maximum species richness on previous biogeographic studies in the Indian Ocean [22]. Differences between the predicted maximum species richness from the Michaelis–Menten equation and actual number of species observed in each country were compared using Chi-Square.

To detect similarity patterns in the species assemblages on reefs across the region the Bray–Curtis similarity index was calculated among pairs of sites, and the similarity coefficients used to run two ordination techniques to detect similarity patterns between sites [43]: a cluster analysis and a nonmetric multidimensional scaling (MDS). Both methods were applied as they offer complementary information. The significance of the differences

between the geographical areas revealed in the cluster dendrogram and MDS plots was tested with an analysis of similarity (ANOSIM) based on randomization of the similarity matrix [43]. To investigate the main species that account for the observed patterns in species richness across the region, a similarity of percentage analysis (SIMPER) was used to detect the representative species of each geographical zone. Since the ANOSIM results showed significant country differences between Comoros and Madagascar, between these island countries and the mainland countries of Tanzania and Mozambique, and a marginal difference between the two mainland countries, the latter were combined as one, “mainland”, for the SIMPER analysis.

3. Results

A total of 356 species from the 19 families (Table S2) were recorded from 45 sites across the four countries. Of these, 15 could not be identified to species but were either recorded to genus (10) or to a species it closely resembled from the Pacific Ocean (5). In all cases these uncertain species could be reidentified on subsequent surveys at different sites by the same observer (MS), and therefore, all were used in the analyses of species diversity.

Overall, the predicted number of species did not differ statistically from the observed number (Figure 2; Chi-square = 0.602; $df = 3$; $p = 0.89$). However, on a country-by-country basis, there was a marginally significant difference for Comoros (Chi-square = 3.9; $df = 1$; $p = 0.049$). This suggests that surveys from all locations in all four countries were adequate in providing representative values of total species richness, but there was some indication that an increase in the number of surveys in Comoros would improve the data. The results show, based on the 19 families, a predicted mean total number of species of 321 for Mozambique and 319 species for Tanzania, both higher than Comoros (267) and Madagascar (294) (Figure 2). Note that these numbers refer to locations surveyed in each country, and not the country as a whole (see Methods). Mean species diversity per site was highest in Mozambique followed closely by Tanzania, and lowest from sites in Comoros (Figure 3a). In contrast, taxonomic distinctness was highest in Comoros (Figure 3b). However, variability within countries was very high, for example, the highest species richness was recorded at Vamizi lagoon (152) and the lowest at Neptunes (82), both in northern Quirimbas, Mozambique (Supplementary Material Figure S1).

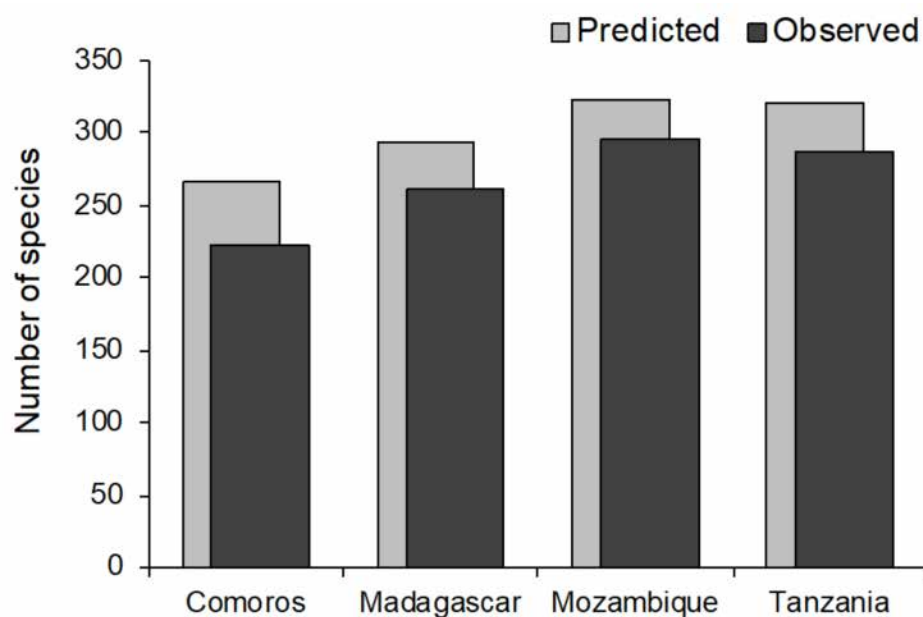


Figure 2. Total number of species observed (black) and predicted maximum species richness (grey) per country based on Michaelis–Menton permutations. Observed and predicted number did not differ significantly (Chi-square = 0.602; $p = 0.89$). Number of sites: Comoros: 7; Madagascar: 10; Mozambique: 16; Tanzania: 12; 76 dives in total, as detailed in Table S1.

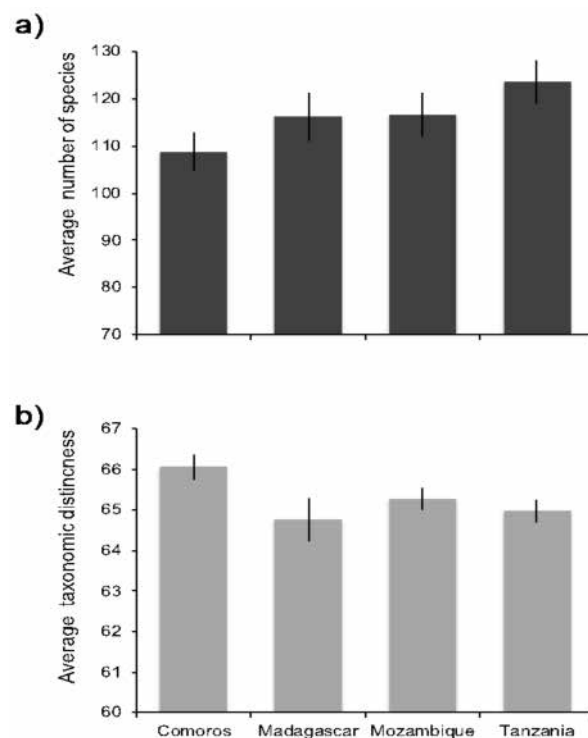


Figure 3. Mean fish species diversity: (a) mean total number of species observed per site (>75 min) in each country; (b) mean fish species diversity based on taxonomic distinctness (D+). Error bars are standard errors of mean. Sample sizes as in Figure 2.

Similarity in species' presence/absence between sites revealed four groupings at 54% similarity with all the Madagascar sites separate; the Comoros sites clustered separately; most of the sites from the African mainland, Tanzania, and Mozambique, clustered together in a complex set of smaller groups; and three extreme outliers of two sites from Mozambique and one from Tanzania (Figure 4). The same four groupings were confirmed in an MDS ordination though the stress level of 0.2 suggests country differences were not significant (Figure S2). The overall differences in species presence between the four countries were statistically different, with differences between sites in the two island countries, and between sites in island countries and mainland countries all highly significant, whereas differences between Tanzania and Mozambique were only marginally significant (Table 2).

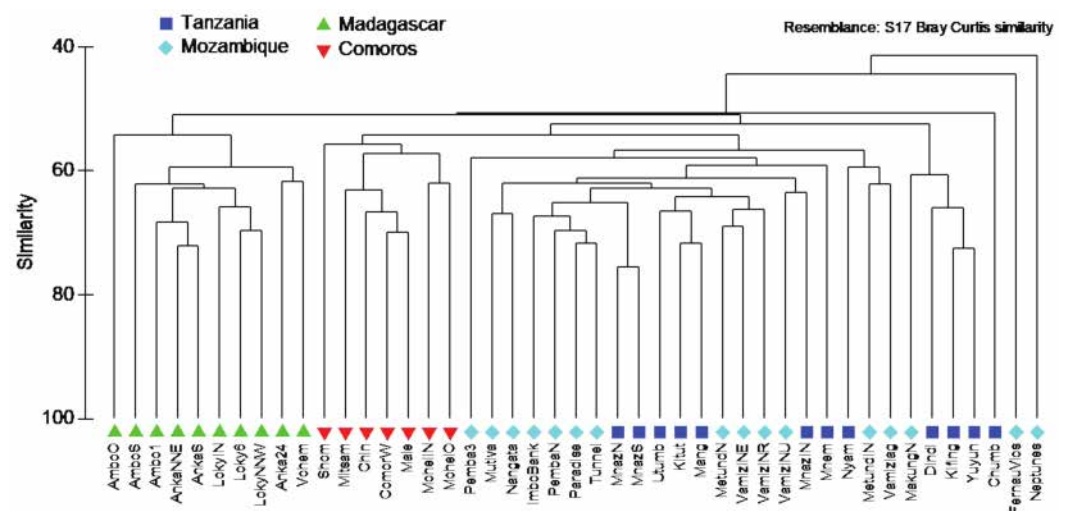


Figure 4. Bray Curtis cluster analysis showing similarity in species presence/absence between pairs of sites in western Indian Ocean (WIO).

Table 2. Results of ANOSIM based on 999 permutations for differences in species richness between (a) countries and (b) between areas within mainland countries, Tanzania, and Mozambique (based on 999 permutations). Areas within mainland countries that differed significantly are bolded. Pemba is in Cabo Delgado, Mozambique.

(a) Between Countries Global R = 0.405, $p = 0.001$		
Pairwise Tests—Groups	R Statistic	p
Madagascar, Comoros	0.864	0.001
Madagascar, Tanzania	0.592	0.001
Madagascar, Mozambique	0.483	0.001
Comoros, Tanzania	0.397	0.001
Comoros, Mozambique	0.354	0.007
Tanzania, Mozambique	0.103	0.048
(b) Between Areas within Mainland Countries Global R = 0.21; $p = 0.011$		
Pairwise Tests—Groups	R Statistic	p
Chumbe, Mafia	0.617	0.056
Chumbe, Nacala	0.321	0.200
Chumbe, Pemba	0.857	0.067
Chumbe, Vamizi	0.3	0.156
Chumbe, Mnazi	0.583	0.100
Mafia, Nacala	0.418	0.012
Mafia, Pemba	0.489	0.009
Mafia, Vamizi	0.131	0.061
Mafia, Mnazi	0.173	0.225
Nacala, Pemba	−0.01	0.571
Nacala, Vamizi	0.21	0.113
Nacala, Mnazi	0.148	0.229
Pemba, Vamizi	0.104	0.240
Pemba, Mnazi	0.5	0.029
Vamizi, Mnazi	−0.113	0.636

Fish species assemblages within the sites of the mainland countries, which ranged from -5° (Zanzibar—Mnemba) to -14° (Nacala sites with Fernau Vloso the southernmost), were different but similarity levels were relatively high, and there was no clear latitudinal or geographic pattern, though two outlier sites in Mozambique were apparent (Figures 4 and 5). None of these areas were statistically different from each other in terms of species presence except between two areas in Mozambique (Pemba, Nacala) and two areas in Tanzania (Mafia, Mnazi) (Table 2b). Though not statistically dissimilar (Figure 5), local scale differences in species richness suggested the following groupings (see Table S1 for reef types): (i) exposed forereefs at Mafia Island (Dindini, Yuyuni and Kifinge), similar to Makunga North, which had an exposed reef terrace, and a steeply sloping forereef in northern Mozambique; (ii) inner seas protected forereefs and lagoonal sites at Vamizi and Metundo islands in Mozambique; (iii) the largest group of similar reef sites ranging across the entire east African mainland with well-developed forereefs at ocean-exposed sites; (iv) outliers seen in Zanzibar: Chumbe, which is a narrow and relatively shallow (3–13 m) protected forereef with much sand and low rugosity; Mnemba, which is a relatively deep (to 18 m) exposed forereef; and Nyamlile, a large patch reef off Mafia island. The significantly

dissimilar extreme outliers in the whole plot (Figure 5) were two sites in Mozambique: Fernau Vlos in Nacala, a diffuse fringing forereef within the port channel with a few scattered corals on a sandy slope with some seagrass and little hard substrate, and Neptunes, which is an offshore deep terrace between Metundo and Vamizi islands with 90-degree walls dropping to around 500 m. The walls are broken in places with canyons, and the upper terrace ranges from ~7–12 m in depth.

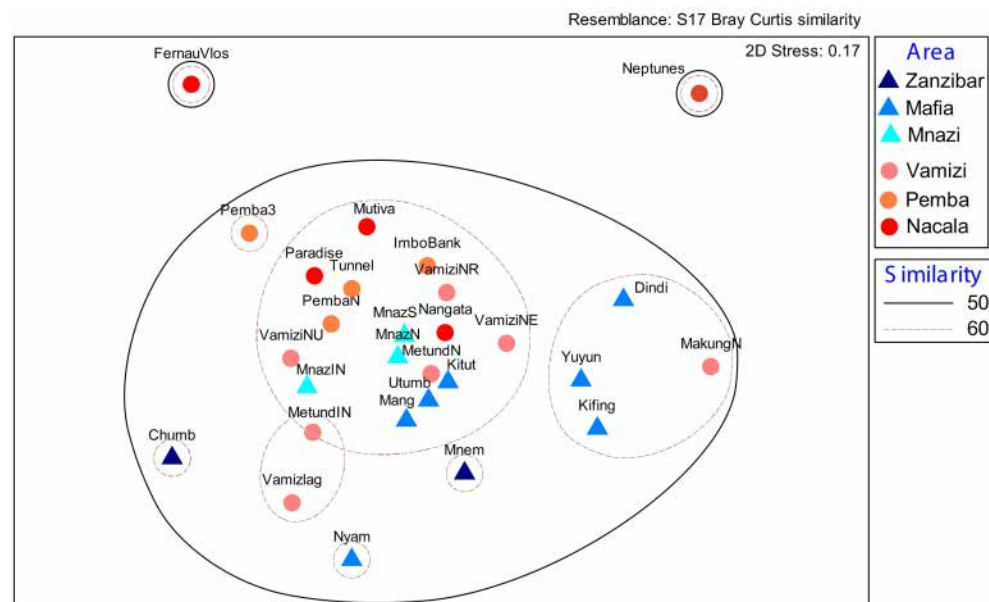


Figure 5. Multidimensional scaling (MDS) plot of mainland sites only, color coded with blues for northern sites (Tanzania) and reds for southern sites (Mozambique). Plot shows all sites are similar at 50%, but within this large group three groups were apparent, though with similarity at 60% these groups were not strongly dissimilar.

Fish species composition and homogeneity were most dissimilar between sites in NE Madagascar and Comoros: of the first 14 high ranking species that contributed to the dissimilarity between all three geographical zone comparisons, 11 contributed most to the differences between Madagascar and Comoros, while the other three high ranking species, *Pygoplites diacanthus*, *Heniochus acuminatus*, and *Cephalopholis argus*, were significant in the other geographic zone comparisons (Table 3). Thus, the SIMPER results of species' average dissimilarity values are ranked according to the top 30 species that most explain the differences between Madagascar and Comoros (Table 3). These cumulatively explain 19.74% of the dissimilarity in the species assemblages between these two geographic zones, and these species contributed between 56% (*Cheilinus trilobatus*) to 85% (*Plectropomus punctatus*) of the dissimilarity in this pairwise comparison (Table S3). The 10 most significant species in each of the three comparisons when combined gives 22 species in total. The average abundance shows that the species that ranked mostly highly had either, very high (0.9–1) relative abundance at sites (they were at most or all sites), or low or zero abundance (they were rare or absent at all sites) (Table 3).

The Madagascar—mainland pairwise comparison yielded many of the same species in explaining differences between assemblages as those seen in the Comoros–Madagascar comparison, but with three notable additions: *Chaetodon falcula*, *Cephalopholis argus*, and *Amphiprion allardi* (the latter two also significant in the Comoros–mainland comparison), as well as an additional eight species specific to Madagascar–mainland (*Acanthurus xanthopterus* to *Calotomus carolinus*, Table 3). In contrast, the Comoros–mainland comparison yielded several different species that did not rank highly in the other two SIMPER comparisons, notably *Heniochus acuminatus*, *Aprion viriscens* and *Ostracion meleagris*. Complete sets of all three pair-wise SIMPER geographic zone comparisons are provided in Table S3.

Table 3. SIMPER results for most significant 47 species, showing first 30 species (*Plectropomus punctatus* to *Cheilinus trilobatus*) that explain 19.74% of dissimilarity in species present at sites according to Madagascar–Comoros dissimilarity cumulative ranking (grey columns), and 17 additional species representing those within top 20 species in other comparisons (12–14% of cumulative mean dissimilarity /SD): (i) Madagascar–mainland comparison, and (ii) Comoros–mainland comparison. Rank AvDiss = Dissimilarity/SD averaged across all three group comparisons is presented as a metric for ranking species that contributed most to differences across all three pair-wise comparisons. Twenty-two species in bold represent top 10 most significant species in all three pair-wise comparisons. Ranges (Catalog of Fishes 2021): IP = Indo–Pacific (includes west coast of Americas); IWP = Indo–West Pacific; IO = Indian Ocean; WIO = western Indian Ocean (Somalia to Mauritius); RS = Red Sea; EA = East Africa (Kenya, Tanzania, Mozambique, Comoros, Madagascar); Mas= Mascarene islands (Reunion, Mauritius, Rodrigues).

Species	Family/Sub-Fam	Range	AVERAGE ABUNDANCE			Diss/SD			Cum.Av. Diss.Contrib %			Rank AvDiss/SD
			COMOROS	MAINLAND	MADAGAS	Comoros-Mainland	Madagascar-Mainland	Madagascar-Comoros	Comoros-Mainland	Madagascar-Mainland	Madagascar-Comoros	
<i>Plectropomus punctatus</i>	Epinephelidae	WIO	0	0.32	1	0.68	1.43	11.97	76.92	6.78	0.85	1
<i>Plectorhinchus gaterinus</i>	Haemulidae	WIO	0	0.57	0.9	1.14	0.88	2.89	13.62	59.79	1.63	5
<i>Hipposcarus harid</i>	Labridae	RS-IO ¹	0	0.54	0.9	1.06	0.93	2.88	27.36	49.69	2.4	6
<i>Epibulus insidiator</i>	Labridae	RS-IWP	0	0.79	0.9	1.87	0.61	2.88	0.73	82.37	3.16	3
<i>Chaetodon vagabundus</i>	Chaetodontidae	IWP	0	0.07	0.9	0.28	2.24	2.88	98.19	2.23	3.93	2
<i>Anampses twistii</i>	Labridae	RS-IWP	0.86	0.86	0	0.56	2.37	2.38	84.35	1.49	4.66	4
<i>Neoglyphidodon melas</i>	Pomacentridae	RS-IWP	0.14	0.75	1	1.43	0.57	2.37	2.76	85.29	5.4	8
<i>Scarus ghobban</i>	Scarinae	RS-IWP	0.14	0.61	1	1.15	0.8	2.37	12.01	66.81	6.12	9
<i>Cheilinus fasciatus</i>	Labridae	RS-IWP	0	0.61	0.8	1.23	0.87	1.95	7.58	62.1	6.8	11
<i>Acanthurus dussumieri</i>	Acanthuridae	IWP	0.14	0.21	0.9	0.64	1.6	1.87	80.63	5.57	7.48	10
<i>Chaetodon melannotus</i>	Chaetodontidae	RS-IWP	0.14	0.75	0.9	1.43	0.65	1.87	3.4	80.32	8.15	13
<i>Pomacanthus chrysurus</i>	Pomacanthidae	WIO	0.14	0.39	0.9	0.85	1.17	1.87	63.12	12.81	8.82	15
<i>Pomacentrus baenschi</i>	Pomacentridae	EA	0	0.36	0.8	0.74	1.17	1.96	74.43	14.88	9.49	16
<i>Mulloidichthys flavolineatus</i>	Mullidae	IWP	0.86	0.36	0.1	1.21	0.78	1.88	8.7	68.86	10.16	17
<i>Parupeneus trifasciatus</i>	Mullidae	IWP	0.86	0.46	0.1	1.04	0.93	1.87	24.89	54.24	10.83	18
<i>Lutjanus fulvoiflamma</i>	Lutjanidae	RS-IWP	0.14	0.64	0.8	1.22	0.83	1.55	9.82	63.6	11.45	23
<i>Pygoplites diacanthus</i>	Pomacanthidae	RS-IWP	0.71	0.86	0	0.72	2.36	1.55	75.08	0.75	12.06	7
<i>Chlorurus atrilunula</i>	Scarinae	WIO	0.14	0.43	0.8	0.89	1.07	1.55	57.87	20.73	12.67	25
<i>Thalassoma genivittatum</i>	Labridae	(WIO-Mas)	0.14	0.07	0.8	0.49	1.72	1.55	89.85	4.92	13.29	21
<i>Chromis ternatensis</i>	Pomacentridae	IWP	1	0.82	0.3	0.46	1.28	1.5	89.51	9.6	13.9	41
<i>Cheilinus oxycephalus</i>	Labridae	IWP	0.14	0.75	0.8	1.43	0.73	1.55	4.02	72.46	14.5	22
<i>Abudefduf vaigiensis</i>	Pomacentridae	RS-IWP	0.71	0.46	0	1.02	0.92	1.55	27.85	59.01	15.11	26
<i>Pomacentrus trichourus</i>	Pomacentridae	RS-WIO	0.14	0.54	0.8	1.04	0.95	1.56	26.37	50.95	15.72	24
<i>Pomacentrus caeruleopunctatus</i>	Pomacentridae	WIO-Mas	0.14	0.04	0.8	0.45	1.83	1.55	92.02	4.27	16.32	20
<i>Lutjanus ehrenbergi</i>	Lutjanidae	RS-IWP	0	0.11	0.7	0.34	1.36	1.5	96.48	7.35	16.9	47
<i>Pervagor janthinosoma</i>	Labridae	IWP	0.71	0.21	0.1	1.27	0.6	1.41	7.01	82.85	17.47	32
<i>Coris formosa</i>	Labridae	RS-WIO ²	0.71	0.11	0.1	1.4	0.47	1.4	4.64	90.14	18.04	38
<i>Variola louti</i>	Epinephelidae	RS-IWP	0.71	0.54	0.1	0.96	1.04	1.4	42.1	30.47	18.61	27
<i>Amblyglyphidodon indicus</i>	Pomacentridae	RS-IO	0.29	0.71	0.9	1.19	0.69	1.41	11.47	77.59	19.17	31
<i>Cheilinus trilobatus</i>	Labridae	IWP	0.29	0.75	0.9	1.23	0.65	1.4	9.26	79.26	19.74	36
Additional Significant Species (top 20) in Madagascar-Mainland Comparisons												
<i>Cephalopholis argus</i>	Epinephelidae	RS-IWP	0.29	0.86	0.1	1.35	1.87	0.69	5.25	3.6	81.16	14
<i>Chaetodon falcula</i>	Chaetodontidae	IO	0.43	0.86	0.1	1.09	1.87	0.88	16.25	2.91	67.67	19
<i>Amphiprion allardi</i>	Pomacentridae	WIO	0	0.71	0	1.55	1.55	Undefined	2.12	6.19	100	114
<i>Acanthurus xanthurus</i>	Acanthuridae	IWP	0.14	0.11	0.7	0.53	1.36	1.32	87.45	7.92	21.93	44
<i>Ctenochaetus binotatus</i>	Acanthuridae	IWP	0.71	0.36	1	1.12	1.32	0.63	15.2	8.48	85.38	64
<i>Pomacanthus semicirculatus</i>	Pomacanthidae	IWP	0.57	0.36	1	1.03	1.32	0.86	25.88	9.05	74.18	46

Table 3. Cont.

Species	Family/Sub-Fam	Range	AVERAGE ABUNDANCE			Diss/SD			Cum.Av. Diss.Contrib %			Rank AvDiss/SD
			COMOROS	MAINLAND	MADAGAS	Comoros-Mainland	Madagacar-Mainland	Madagascar-Comoros	Comoros-Mainland	Madagacar-Mainland	Madagascar-Comoros	
<i>Ctenochaetus truncatus</i>	Acanthuridae	IO	0.86	0.79	0.3	0.64	1.24	1.32	79.28	10.15	20.29	48
<i>Zebrasoma velifer</i>	Acanthuridae	IWP	0.71	0.36	0.9	1.12	1.24	0.69	14.68	10.69	80.58	69
<i>Pomacentrus caeruleus</i>	Pomacentridae	IO ³	0.71	0.39	1	1.08	1.22	0.63	17.28	11.23	88.06	>180
<i>Pterocaesio tile</i>	Caesionidae	IWP	0.86	0.79	0.3	0.64	1.24	1.32	79	11.77	20.84	49
<i>Calotomus carolinus</i>	Scarinae	IP	0.57	0.68	0.2	0.94	1.23	1.07	44.84	12.29	41.67	42
Additional Significant Species (Top 20) in Comoros–Mainland (Note <i>C. argus</i> and <i>A. allardi</i> , above, also Rank Here)												
<i>Heniochus acuminatus</i>	Chaetodontidae	IWP	0	0.79	0.6	1.88	0.88	1.2	1.45	60.56	27.75	12
<i>Aprion virescens</i>	Lutjanidae	IWP	0.71	0.21	0.5	1.27	0.99	0.99	6.43	46.28	47.41	40
<i>Ostracion meleagris</i>	Ostraciidae	IP	0.71	0.21	0.6	1.27	1.11	0.9	5.84	19.3	60.75	37
<i>Chromis lepidolepis</i>	Pomacentridae	IWP	0.29	0.75	0.5	1.23	0.99	0.99	8.14	32.72	55.92	45
<i>Chaetodon interruptus</i>	Chaetodontidae	IO	0.71	0.29	0.7	1.19	1.17	0.83	10.37	14.36	72.76	50
<i>Anampses lineatus</i>	Labridae	RS-IO	0.71	0.32	0.3	1.15	0.86	1.17	10.92	63.97	29.77	51

¹ In IO reported only from East Africa, Seychelles, Madagascar, Mascarenes, Maldives, Chagos Archipelago, Andaman Sea and Java (Fricke et al. 2021). ² and Sri Lanka, RFM pers.obs. ³ WIO to western Indonesia, RFM pers.obs.

Legend:

significant in Mada-Com and Mada-Main	only significant in Mada-Com	significant in Mada-Com and Com-main	significant in Mada-main and Com-main	only significant in Mada-main	only significant in Com-main
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The mean Dissimilarity/SD across all three pairwise comparisons provides a metric to rank species as most significant in all three SIMPER comparisons, with one representing the most highly ranked, *Plectropomus punctatus* (Table 3). The first 27 species (*Variola louti* is 27th) that ranked most highly out of the 356 observed species all appear in the Madagascar–Comoros comparisons, except for *Cephalopholis argus* and *Chaetodon falcula*, which explain differences between Madagascar and mainland countries, and *Heniochus acuminatus*, which explains differences between Comoros and mainland countries (Table 3).

Taking the top 20 species that most contributed to explaining differences (average cumulative dissimilarity of 12–14%) in species assemblages between the three geographic zones, the following broad patterns can be seen (Table 3):

- the five most significant species in explaining differences between Comoros and Madagascar were very common in Madagascar but not sighted in Comoros: *Plectropomus punctatus*, *Plectorhinchus gaterinus*, *Hipposcarus harid*, *Epibulus insidiator* and *Chaetodon vagabundus*. All were moderately common in mainland countries except *C. vagabundus*, which was rare;
- other species explained differences between Comoros and Madagascar but did not appear in the top 20 species in other paired geographic zone comparisons, such as *Pomacentrus baenschii* and *P. caeruleopunctatus*, or were species common in Madagascar (in 80% of sites) but either rare or absent in mainland;
- high ranking species in Comoros were not sighted in Madagascar, e.g., *Anampses twistii* and *Pygoplites diacanthus*. *Abudefduf vaigiensis*, though less significant, was also common in Comoros and not sighted in Madagascar. Other species common in Comoros but rare/absent in Madagascar included *Coris formosa*, *Mulloidichthys flavolineatus*, and *Parupeneus trifasciatus*;
- other species that contributed to both Madagascar–Comoros and Madagascar–mainland comparisons were common or relatively common across sites in Madagascar and mainland but were rare or absent in Comoros, such as *Neoglyphidodon melas*, *Scarus ghobban*, *Cheilinus fasciatus* and *Cheilinus oxycephalus*, and *Chaetodon melanotus*. With a similar distribution pattern though less significant was *Lutjanus fulviflamma* which was rare in Comoros. *Scarus ghobban*, (ranked 10th overall), was a key species distinguishing Comoros, where it was rare, from both Madagascar (8th rank) and mainland (20th rank, Table S3);
- species that were top ranking species contributing to the Comoros–mainland differences were not highly ranked in the other SIMPER results such as *Aprion virescens*, *Ostracion meleagris* and *Heniochus acuminatus*. The first two were more common in Comoros compared with mainland or Madagascar, whereas *H. acuminatus* was not sighted in Comoros. *Chaetodon interruptus* and *Anampses lineatus* were also common in Comoros and less common in mainland though were less significant in explaining differences;
- *Amphiprion allardi* and *Cephalopholis argus* were the only species significant in both island–mainland comparisons: *A. allardi* was only observed in mainland sites and *C. argus* was much more common in mainland sites.

In summary, the top 22 species that contributed most significantly to the differences in species occurrence and assemblage homogeneity between the three geographic zones (Table 3) were from 10 of the 19 families surveyed (where Scarinae are separated from Labridae): Labridae (six species), Chaetodontidae (4) Pomacentridae (3), Scarinae and Epinephelidae (two species of each), and one species in each of Acanthuridae, Lutjanidae, Haemulidae, Pomacanthidae, and Ostraciidae. Notably, very few larger bodied fishery species ranked highly in the dissimilarity rankings except *Plectropomus punctatus* and *Plectorhinchus gaterinus*. Five of the ten families ranked in the present study correspond to those most recommended as good indicators of reef fish diversity in other studies (Table 1). Notably absent from most of these other studies' recommendations are the Epinephelidae, Haemulidae and Ostraciidae.

4. Discussion

4.1. Biogeographic Patterns in Species Diversity

The designation of the WIO as one biogeographic marine Province [3,15,16] is supported by the species richness of coral reef fishes which was similar across the central WIO region surveyed, at ~55% similarity. However, within the study area, significant differences in species presence were found which separated locations in Comoros from northeast Madagascar and these both differed from mainland eastern Africa. The highest species richness was found in locations in Tanzania and northern Mozambique, with the lowest species richness and most different species composition in Comoros. A lower species richness of corals from Comoros is also reported [21]. These findings, based on a sample of 356 species, provide evidence for three ecoregions within this central region of the WIO: eastern Africa (Tanzania, including Zanzibar, and northern Mozambique); Comoros; and north-eastern Madagascar. These ecoregions can represent conservation planning units for Marine Spatial Planning [45] or the Red Listing of Ecosystems [46].

Biogeography is a primary driver of patterns in species richness of reef fishes [1,3,15,47]. Factors such as the island effect, reef area, coast length and sea surface temperature are significant elements of this biogeography [5,19,48,49]. The three islands of the Union of Comoros are small, oceanic and recent volcanic islands [50] isolated from other large coral reef systems: ~250 km from Mozambique and ~450 km from Madagascar. The total coastline length and reef area in Comoros are ~70–90% smaller than mainland east Africa or Madagascar [51]. These biogeographic factors therefore likely explain the naturally lower species richness and different assemblages in Comoros. Less diversity of habitats may also be a contributing factor, but this could not be tested with the current sampling design. However, taxonomic diversity was highest in Comoros, driven by the Tetradontiformes. Likely reasons can only be speculative currently, but they may relate to the unique steep bathymetry of these volcanic islands.

Present day ocean currents [19] that drive the dispersal of pelagic larvae also help maintain biogeographic patterns. Further evidence for the ecoregions of Comoros, northern Madagascar and mainland east Africa comes from modelling pelagic larval duration (PLD) which separated eastern Africa from Comoros and Northern Madagascar using a short PLD of 10 days [52], generally shorter than most reef fishes. However, at 50 PLD this area became one homogeneous region, a finding verified by the genetics of two species common in the present study, *Epinephelus merra* and *Lutjanus kasmira* [53,54]. This finding lends further weight to the delineation of the WIO as one biogeographic province.

4.2. Anthropogenic Influences

Reefs of the WIO are intensely fished in many locations [38,55,56], climate induced coral bleaching continues to degrade reefs [57] and both these impacts threaten some reef fish species [9] which could undermine studies examining patterns in species richness. However, fishing effects are largely seen in declines in biomass and fish size data [51,58,59], so with the species presence/absence data in the current study fishing effects will only manifest in zero values. Five species completely absent from Comoros and in the top 12 ranking species in the SIMPER analyses are species typically taken in WIO artisanal fisheries [38,60]. Two of these species, the grouper *Plectropomus punctatus* and the sweetlip *Plectorhinchus gaterinus*, are reported historically in Comoros [61] and at neighboring Mayotte the easternmost island in the Comoros Archipelago [62]. Both are widespread western Indian Ocean species and would be vulnerable to the coastal handline fisheries in Comoros [29] so their lack of sightings may indicate fishing effects. No confirmed sightings of *Plectropomus punctatus* in subsequent surveys in Moheli island in 2016 (B. Cowburn pers. comm.) and 2018 (M. Samoilys pers. obs.) further confirm this species is now very rare or locally extinct in these islands. *Plectorhinchus gaterinus* was also not sighted in surveys in Comoros in 2016 or 2018 and is reported as locally extinct in Reunion [32]. These two fishery species are therefore likely to have regional distribution patterns skewed by

fishing. The other fishery species absent in Comoros are more easily explained through range restrictions or habitat requirements (see below).

4.3. Species Level Differences

Knowledge of the diversity and distribution of coral reef fishes is important for conservation planning under future climate change scenarios [63], yet species level data are still lacking over large spatial scales [1]. The present study fills this gap revealing regional species distribution patterns with assemblages in Comoros less speciose compared with the other three countries. Several species not sighted in Comoros included wide ranging Indo-Pacific species, those widely reported in the WIO, as well as WIO endemics. For example, widely distributed Indo-Pacific species were *Epibulus insidiator*, *Chaetodon vagabundus*, and *Cheilinus fasciatus*. However, they were sighted in Comoros in subsequent surveys in 2016 (B. Cowburn pers. comm.) and *C. vagabundus* was also sighted in 2018 (M. Samoilys pers. obs.), suggesting the zero sightings in the current study reflect rarity not absence. The WIO endemic anemone fish *Amphiprion allardi* ranked highly in the SIMPER analysis because it is restricted to the mainland east African coast and is replaced by *A. latifasciatus* in Comoros and Madagascar [64]. Therefore, earlier records of *A. allardi* from Mayotte, Glorieuses and the Mascarene Islands [62,65,66] need updating. Other species not sighted in Comoros, *Hipposcarus harid* and *Lutjanus fulviflamma*, may be explained by restricted larval supply due to currents or habitat requirements. For example *H. harid* is reported from East Africa, western Madagascar [27], Mayotte island [62], and the French territories of Glorieuses and Geyser reef [67], but there are no records for Comoros in the Catalog of Fishes [42]. The reasons for this apparent disjunct distribution in the Comoros Archipelago require further study. *Lutjanus fulviflamma* is widely distributed in the WIO including Mayotte island [62]. Its absence in Comoros may be due to the juveniles' strong dependence on mangroves, which are uncommon in the islands of the Union of Comoros [51]. Only two species were common to Comoros but uncommon in the mainland countries and only moderately common in Madagascar: the snapper *Aprion virescens* and the boxfish *Ostracion meleagris*. This is possibly related to the predominantly steep narrow forereefs of these volcanic islands.

Principle species with restricted ranges that were driving regional differences include two Pomacentridae, *Pomacentrus baenschi* and *Pomacentrus caeruleopuntatus*, both reported as restricted to Madagascar and the Mascarene Plateau [65,68]. In the present study they were common in northeast Madagascar but sighted, though uncommon, in mainland (both species) and Comoros (*P. caeruleopuntatus*). These sightings require further investigation. In contrast, other species were ubiquitous in some locations and not in others, for example the parrotfish *Scarus ghobban*, with a wide Red Sea—Indo—West Pacific range [33], was sighted at every site in Madagascar, at just over half the mainland sites, but only 14% of the sites in Comoros. This pattern may reflect the small, isolated island effect (see above) and less diversity of habitats in Comoros.

Species missing from the northeast Madagascar sites are possibly explained by range restrictions due to ocean currents. *Pygoplites diacanthus* and *Anampses twistii* were not seen and *Cephalopholis argus* and *Chaetodon falcula* were rare, yet all are reported as widely distributed in the Indo—West Pacific [42] and in northwest Madagascar [27]. The South Equatorial Current (SEC) bifurcates east of Madagascar with the northern current flowing over the northern tip of Madagascar to continue to the Comoros and then the African continent, while the southern flow travels down the east coast of Madagascar to join the Agulhas current off South Africa [69]. The northeastern location of the present study may therefore represent Madagascan reefs where larval supply is weak because the SEC bifurcates further east, so self-recruitment is more prevalent [52]. Larval connectivity between the SEC, the west coast of Madagascar and the Comoros is likely to be strong due to the gyres in the north of the Mozambique Channel around the Comoros Archipelago [70]. Thus, species absent in northeast Madagascar are more likely explained by ocean currents

restricting larval supply rather than “near threatened” as reported for Reunion where there are greater human pressures [65].

The ranges of the 46 species that contributed most to the patterns in diversity of species across this central WIO region were largely (65%) highly wide ranging (Indo-Pacific, Red Sea—Indo-West Pacific) [42]. A further 30% were wide ranging within the Indian Ocean, including the WIO, or Red Sea—Indian Ocean [15]. Only 4.3% of species were highly restricted, to the Mascarene Plateau [27]. Of conservation interest are the two nominally Mascarene species (*Pomacentrus caeruleopuntatus* and *P. baenschi*) and the six species restricted to the WIO Province, two of which (*Plectropomus punctatus* and *Plectorhinchus gaterinus*) are in severe decline [51]. Species that are endemic to the WIO [71], yet not seen during these surveys, provide a list of species of potential concern that may be disappearing due to loss of habitats through coral mortality. Additional surveys are recommended for these species, to be considered for Red Listing by the Species Survival Commission [72]. One example is *Chaetodon blackburni*, last assessed in 2010 as Least Concern [72], only known to occur in East and southern Africa, from Kenya to 33° S, and Madagascar & Mauritius [42], but not sighted once in this study. The functional roles of reef fish species, their contributions to ecosystem processes, are never equal, and it is postulated that in tropical systems each species contributes relatively little compared with temperate systems, due to high diversity in the tropics [73]. Further study on the ecological role of the 46 most significant species driving the regional patterns in the current study may reveal functional attributes important in ecosystem processes on coral reefs.

4.4. Methods for Species Richness Surveys

The presence/absence of species from 19 families surveyed by the timed UVC method in this study recorded ~45% of the total putative number of reef species in the WIO [19] and was effective in detecting biogeographical patterns in assemblages and significant differences in species richness between locations. Further, total number of species per location were not different from predicted values, giving validity to the method and the total numbers of species observed. The biogeographical patterns span the central WIO across a latitudinal and longitudinal range of around eight and eleven degrees, respectively. Taxonomic distinctness also differed across this region suggesting it was valuable adding the Tetrodontiformes order (Trigger, Box, Puffer and File fish families) to the check list, in addition to the more commonly monitored Perciform families. These values and diversity patterns provide a benchmark for species assemblages prior to the 2016 mass coral bleaching event, which was widespread in the WIO causing significant coral mortality [74].

Ten of the nineteen families contributed the top 22 species that showed significant differences in species occurrence and assemblage homogeneity between the three geographic zones. Of these, the highest number of species were in the Labridae, Chaetodontidae, Pomacentridae, Scarinae and Epinephelidae. These match four of the six families in the widely used Coral Fish Diversity Index (CFDI) [75]. The other five significant families in the present study were Acanthuridae, Lutjanidae, Pomacanthidae, Haemulidae and Ostraciidae. Notably, many of the families important in local fisheries, such as Lethrinidae, Siganidae, Carangidae, did not rank, even in the top 46 species significant in explaining location differences. For rapid assessment surveys that have to address multiple issues and also need to collect density and fish size estimates, a reduced list of eight families would suffice, such as: Chaetodontidae, Scarinae, Epinephelidae, Acanthuridae, Lutjanidae, Pomacanthidae, Haemulidae and Ostraciidae. These families were significant in the present study and are either speciose, good reef fish indicators, or have fishery importance [37,39,76–78]. Pomacentridae and Labridae are important highly speciose families, but being small and often difficult to identify are often not counted to species level in standard monitoring programs, such as GCRMN [79]. However, they added valuable diversity data here and are recommended if species identifications are possible. For detailed conservation planning, species level data are preferable.

5. Conclusions

This study highlights that timed SCUBA surveys of reef fish species presence provide diversity metrics that are sensitive to change and can be used for conservation planning and to detect future impacts of conservation or reef degradation. For example, results indicate that conservation action in Comoros should prioritize protection of *Plectropomus punctatus* and *Plectorhynchus gaterinus*. The 22 most significant species that revealed patterns in diversity across the region came from the Scarinae, Chaetodontidae, Pomacentridae, Epinephelidae, Acanthuridae, Lutjanidae, Pomacanthidae, Haemulidae, and Ostraciidae suggesting these families should be considered for UVC surveys of reef fishes aiming to examine management, fishing effects and climate change on coral reefs. The current study provides a useful reference point for testing predictions of changes in reef fish species richness due to warming seas [63,80].

The study documents the occurrence of 356 species of reef associated fishes for locations in four countries in the WIO that lie across the northern Mozambique Channel area where the highest coral diversity in the WIO is found [21]. Testing that this region is a diversity hotspot for reef fish species will require comparable data from more peripheral sites such as in Kenya, Seychelles, Mauritius and Reunion. Our findings provide evidence that the WIO biogeographic province contains distinguished ecoregions: Comoros Archipelago; northeastern Madagascar; and northern Mozambique and Tanzania, including Zanzibar. This separation of Comoros from eastern Africa differs from the ecoregions based on hermatypic corals [22,24]. These intraregional differences are relevant in coral reef threat assessments and informed the recent IUCN Red Listing of Ecosystems process for the WIO's coral reefs [81].

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d14020102/s1>, Figure S1: Total number of species per survey site (n = 45) in >75 min of observations, Figure S2: MDS plot showing four distinct groupings of the sites in terms of their species richness with Comoros and Madagascar separated and different from each other and the two mainland countries, Tanzania and Mozambique grouped together, with two outlier sites; Table S1: Final list of 45 survey sites used in analyses, showing countries, locations, reef geomorphology and reef type; Table S2: Full species inventory from all sites with taxonomic authority and taxonomic references. Table S3: Full SIMPER for all 356 species showing average Abundance, Dissimilarity, Cumulative contributions to Dissimilarity, and rankings.

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