diversity

Article

The Role of Maximum Shelf Depth versus Distance from Shore in Explaining a Diversity Gradient of Mushroom Corals (Fungiidae) off Jakarta

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Abstract: Many coral reef systems are shelf-based and consist of reefs that are arranged in rows parallel to the coastline. They usually show an increase in species richness in the offshore direction, coinciding with decreasing terrigenous impact and a deeper seafloor. These two conditions usually concur, which makes it less easy to distinguish how each of them influences coral diversity separately. Since reefs off Jakarta (in the Thousand Islands archipelago) are arranged in an 80 km long string perpendicular to the coastline in south-to-north direction, with a maximum shelf depth halfway along (instead of at the end of) the string, this archipelago is very suitable for studies on inshore–offshore gradients. In the present study, mushroom corals (Fungiidae; n = 31) were used to examine diversity patterns on 38 reef sites along such a gradient, involving species richness over their entire depth range from reef flat to reef base (2–30 m) and separately at shallow depths (2–6 m). Total species diversity was highest in the central part of the archipelago, with unique species occurring in deep habitats. Diversity at shallow depths was only slightly higher here than at reefs located more nearshore and offshore, which both had less clear water. Therefore, shelf depth and distance from the mainland can be considered separate determinants of coral diversity off Jakarta.

Keywords: Scleractinia; Fungiidae; Indonesia; Java Sea; mega city; latitude; river outlets; water transparency; blast fishing

1. Introduction

Shelf-based reef systems are ideal model areas in which to study the influence of inshore-to-offshore environmental gradients on the diversity of reef coral assemblages. Reefs located closer to major shorelines (hereafter inshore or nearshore) are exposed to terrigenous and anthropogenic impact from nearby land mass [1] and to oceanic conditions at the offshore side, resulting in increasing water quality away from the coastline [2–7]. In addition, the seafloor of such shelf systems usually shows a gradually increasing depth in the same direction, up to the shelf ridge [8,9]. Nearshore reef zones receive sediment from river outlets, which keeps the seafloor shallow and water more turbid here [10]. In order to examine the effects of water quality and depth on species diversity, they should be analyzed separately. To serve as a model reef system and to enable the distinction of clear diversity patterns, the reefs should be abundant, evenly distributed, and be geomorphologically uniform. Most such reef systems are predominantly arranged alongside and parallel to the mainland shoreline, such as the Great Barrier Reef, located off the north-east Australian coast [11–15], and various smaller shelf-based reef complexes, such as the Spermonde Archipelago off Southwest Sulawesi [5,16–19], the

Padang shelf reef system off West Sumatra [20,21], the Berau Archipelago off eastern Borneo [22–24], the Semporna barrier reef at Northeast Borneo [25], the patch reefs off Brunei and Sarawak at Northwest Borneo [26–28], the barrier reef system along the coast of Belize [29,30], Madang Lagoon in northern Papua New Guinea [31,32], the southwestern lagoon of New Caledonia [33,34], and a few reef complexes along the Saudi Arabian coastline of the Red Sea [35–37]. Many of these examples are sheltered from deeper water (>200 m depth) by a chain of shallow barrier reefs, with the exception of West Sumatra, where reefs are separated from the ocean by a series of large islands [20,21].

In contrast, the Thousand Islands off Jakarta (locally known as Kepulauan Seribu) is a string of patch reefs (80 km long) oriented perpendicularly to the coastline from south to north in the shallow Java Sea, which is surrounded by the land masses of Java, Sumatra, and Borneo. The shelf is deepest in the middle of the archipelago (Figure 1). A river used to run here during Pleistocene low sea level stands, which now acts as a sunken channel with a predominantly westward current [38–42]. The islands are cay-crowned patch reefs [43,44], most of which are inhabited by fishermen or used for recreational purposes [45–49]. Some cays in Jakarta Bay have disappeared due to dredging and subsidence caused by groundwater extraction [50–53]. A large part of the bay within the present 10 m isobath will become reclaimed land, causing a few reefs to disappear and others to become situated closer to the coastline [54,55]. Consequently, nearshore reefs are exposed to sedimentation as a result of dredging activities, which is harmful to most corals [56]. Owing to the proximity of Jakarta, a large conurbation and a major port, reef communities here are also impacted by various kinds of pollution [1,57–60], much of which comes from river outlets inside and close to Jakarta Bay [51,61,62]. The reef communities here are threatened, because anthropogenic stresses have already been blamed for the disappearance of reef-dwelling species in Jakarta Bay during the last century [63,64]. On the positive side, the reefs off Jakarta have recovered from coral bleaching [65,66] and they survived attacks by the corallivorous crown-of-thorns sea star [67–69].

Since shelf depth in the Thousand Islands reef complex is largely independent of distance offshore, unlike the shelf-based reef complexes mentioned earlier, this archipelago is suitable for studies on the effect of seafloor depth on the diversity of reef-dwelling species. Reefs based on a deep seafloor have deep-ranging reef slopes and reef bases, offering habitats to many species that are absent in shallower water. Species dwelling on deeper reef parts receive less light and are less exposed to wave action than species dwelling on reef flats and upper reef slopes [70–72]. Thus, these reefs are expected to have a relatively rich coral fauna by also offering habitats to species that prefer deep reef conditions.

The Indo-Pacific mushroom coral family Fungiidae (Scleractinia) is an ideal model group in which to study cross-shelf diversity patterns because they are abundant from nearshore to offshore and from shallow to deep habitats [17,73,74], which include mesophotic depths [75–77]. Most species (80%) are free-living, which enables them to colonize unconsolidated substrates, such as sandy bottoms and rubble [71,78–80]. With over 50 valid species, this family forms a large taxon, representing about 8% of all Indo-Pacific reef-inhabiting scleractinians [81]. In addition to free-living mushroom corals, there are foliaceous species and encrusting ones [82,83]. Over 60% of all species represent solitary forms with a single mouth, most of which remain small, whereas the largest species can have more than one mouth [84–86]. During earlier studies in the Bay of Jakarta/Thousand Islands, 24 fungiid species were found at depths of 21 m or less [66,87–90]. Fungiidae do not show notably abnormal patterns in beta-diversity studies compared to other scleractinian families [3,88,91,92]. In biodiversity surveys off Borneo, Fungiidae showed similar species richness accumulation curves as the families Agariciidae and Euphylliidae [25,93,94]. Although the family Fungiidae has several species with the ability to live at depths >30 m [17,74–77], the same goes for staghorn corals of the family Acroporidae [94–97].

In the present study, Fungiidae are utilized as a model taxon to examine how coral diversity at shallow depths (2–6 m on reef flats and upper slopes) and over the whole reef profile (2–30 m from the reef flat down to the reef base) varies over an inshore–offshore gradient and over increasing depth on the seafloor off Jakarta. Previous coral diversity surveys in the same research area (in 1985 and 1995) were limited to shallow depths only (1–5 m) and thus excluded coral species possibly occurring at greater depths [88,89]. Distance from the mainland represents reach of terrigenous impact, which is most clearly visible through the presence of river plumes [24,64]. Shelf depth can influence wave-driven sediment resuspension [98,99], with relatively clear water expected above deep seafloors, and also on the maximum depth range of coral assemblages, including species that are specialized in deep-water habitats. A diversity gradient at shallow depths alone may also depend on abiotic parameters related to distance from the shoreline and to maximum shelf depth, for example by varying species concentrations that are partly determined by the distribution of rare species. The reef complex off Jakarta, with a shelf depth not linearly related to distance offshore, is therefore suitable for testing whether these two parameters can operate as distinct drivers of coral diversity.

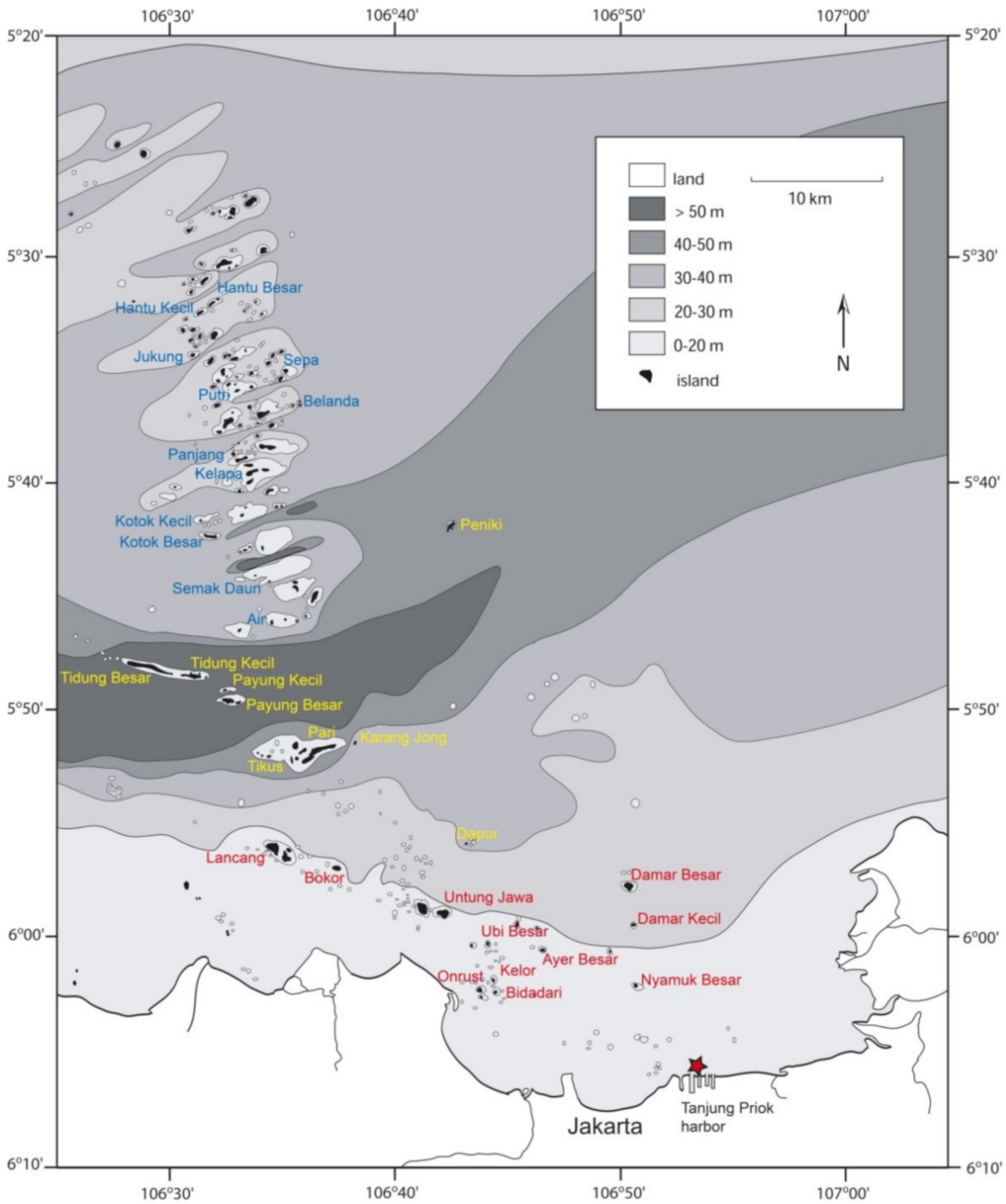

Figure 1. Map of Jakarta Bay and the Thousand Islands archipelago (Kepulauan Seribu) off Jakarta. Reefs surveyed in 2005 (Table 1) are indicated by their name in different colors to distinguish three shelf zones that vary in distance offshore and depth range: Red = Zone 1 (0–30 m), yellow = Zone 2 (30–60 m), blue = Zone 3 (20–40 m). The reference point for Tanjung Priok harbor is marked.

Table 1. Reef sites off Jakarta surveyed for Fungiidae with coordinates; shelf zone (Figure 1); shelf depth; secchi depth; and shortest distance to mainland, river outlet, and Tanjung Priok harbor (coordinates −6.0932, 106.8770).

Site	Coordinates, DD	Shelf Zone	Number of Species	Shallow Records	Shelf Depth, m	Secchi Depth, m	Nearest Mainland, km	Nearest River Outlet, km	Distance to Harbor, km
Onrust NW	−6.0334, 106.7328	1	0	0	9	1.5	2.3	2.3	17.3
Bidadari NW	−6.0321, 106.7463	1	5	5	11	1.5	3.6	3.7	16.0
Nyamuk Besar NW	−6.0291, 106.8523	1	2	2	18	3.5	7.6	12.9	7.6
Kelor NW	−6.0253, 106.7441	1	3	3	12	2.5	3.8	3.8	16.5
Ayer Besar NW	−6.0017, 106.7801	1	1	1	18	3.5	8.6	8.6	14.8
Ubi Besar NW	−5.9987, 106.7397	1	3	2	15	4.0	5.5	5.8	18.5
Damar Kecil NW	−5.9834, 106.8453	1	5	4	19	3.5	12.7	15.9	12.7
Untung Jawa NW	−5.9741, 106.7031	1	10	9	20	2.5	5.0	6.6	23.4
Damar Besar NW	−5.8547, 106.8409	1	10	10	28	8.0	15.4	15.4	15.9
Dapur NW	−5.9457, 106.7242	2	17	14	28	7.5	8.9	10.3	23.6
Bokor NW	−5.9430, 106.6271	1	10	9	20	5.0	6.7	6.7	32.2
Lancang NW	−5.9270, 106.5913	1	5	5	21	5.0	9.5	9.5	36.6
Pari S shoal	−5.8808, 106.6352	2	15	-	29	8.0	12.0	13.6	35.7
Tikus S	−5.8653, 106.5819	2	15	10	32	6.5	15.5	16.3	41.3
Tikus W	−5.8589, 106.5700	2	14	9	37	8.0	16.8	17.4	42.8
Pari E	−5.8544, 106.6389	2	17	8	37	12.5	14.8	16.6	37.4
Tikus N	−5.8536, 106.5786	2	17	12	43	11.0	16.9	17.6	42.4
Karang Jong E	−5.8522, 106.6486	2	20	11	34	11.5	15.0	16.9	36.8
Karang Jong NW	−5.8511, 106.6464	2	19	12	48	11.0	15.1	17.0	37.1
Tikus NE	−5.8501, 106.5848	2	18	11	34	8.5	16.9	17.8	42.1
Payung Besar E	−5.8219, 106.5631	2	15	11	54	10.5	19.4	21.5	46.0
Payung Kecil NW	−5.8134, 106.5492	2	19	11	54	15.5	20.1	23.0	47.8
Tidung Kecil NW	−5.7997, 106.5178	2	21	13	45	17.5	21.7	25.9	51.4
Tidung Besar NW	−5.7910, 106.4812	2	17	10	43	15.0	23.3	28.8	55.2
Air NW	−5.7606, 106.7456	3	15	11	29	12.0	27.3	28.9	39.7
Semak Daun NW	−5.7322, 106.5731	3	16	11	28	11.5	29.6	30.8	52.4
Kotok Besar NW	−5.6988, 106.5398	3	16	12	33	10.5	32.8	35.3	57.6

Table 1. *Cont*.

Site	Coordinates, DD	Shelf Zone	Number of Species	Shallow Records	Shelf Depth, m	Secchi Depth, m	Nearest Mainland, km	Nearest River Outlet, km	Distance to Harbor, km
Peniki NW	−5.6968, 106,7155	2	23	12	43	9.5	32.3	34.9	47.6
Peniki E	−5.6922, 106.7174	2	21	11	41	9.5	33.6	35.4	48.0
Kotok Kecil NW	−5.6888, 106.5336	3	19	15	25	10.0	33.9	36.6	58.9
Kelapa, NW	−5.6544, 106.5589	3	15	13	28	11.0	37.8	39.6	60.2
Panjang, NW	−5.6423, 106.5599	3	14	12	26	11.5	39.2	40.9	61.2
Belanda, NW	−5.6037, 106.6035	3	19	12	31	10.0	43.0	44.5	62.3
Putri, NW	−5.5904, 106.5673	3	15	11	26	10.5	45.0	46.4	65.6
Sepa, NW	−5.5755, 106.5799	3	15	13	29	11.0	46.4	47.9	66.3
Jukung, NW	−5.5669, 106.5272	3	11	10	30	9.5	47.5	49.9	70.2
Hantu Kecil, NW	−5.5354, 106.5319	3	19	15	31	10.0	51.0	53.2	72.3
Hantu Besar, NW	−5.5296, 106.5389	3	17	14	27	9.5	51.6	53.6	73.0

2. Materials and Methods

2.1. Research Area and Abiotic Parameters

Field data were sampled in September 2005 during a survey in Jakarta Bay and the Thousand Islands, together forming an 80 km long string of islands more or less perpendicular to the coastline in NNW direction (Figure 1). The expedition was organized by the Research Centre for Oceanography (Indonesian Institute of Sciences = LIPI) in Jakarta and by Naturalis Biodiversity Center, Leiden [100]. Thirty-eight reef sites were visited, mostly located at the northwestern side of each island, similar to expeditions in 1985 and 1995 [2,101–103] but now including three extra reefs: Karang Jong, Pulau Peniki, and an unnamed shoal south of Pulau Pari (Figure 1, Table 1).

The 38 reef sites were divided over three zones arranged from inshore to offshore, varying in shelf depth: 11 sites in Zone 1 (0–30 m), 15 sites in Zone 2 (30–60 m), 12 sites in Zone 3 (20–40 m). Seafloor depth was determined with the help of nautical charts (scale 1:20,000 or 1:50,000) issued by the Indonesian Navy [104–111]. Transparency of the water column was measured with a standard 30 cm wide secchi disc with maximum visibility depth marked in meters along a rope [111]. Site coordinates were determined with a GPS (Garmin eTrex). Coordinates of reference points on the coastline, representing possible sources of pollution (mainland, river outlets, and Tanjung Priok harbor), were found with Google Maps [112]. To convert coordinate units from DMS (degrees, minutes, seconds) to DD (decimal degrees) and to measure the distance from each reef site to reference points on the mainland, the program GPS Coordinates was used [113].

2.2. Coral Data

At each site a distinction was made between mushroom coral species recorded at 2–6 m depth only (reef flat and upper slope) and those over the whole reef profile, from 2 m depth down to the reef base at 30 m depth or less. These separate approaches (shallow vs. all depths) allow a distinction between coral diversity depending on water quality (distance offshore, turbidity) and diversity depending on bathymetrical reef range (limited by maximum shelf depth). The coral data from shallow depths were obtained from 30 m long, 1 m wide belt transects, three at 3 m and three at 5 m [100,114], within a depth range of 2–6 m, while records from deeper water were acquired by the roving diver technique [115]. Each data sample (one per reef site) is based on a single 60 min dive.

Representative specimens were photographed with a Ricoh Caplio RR30 camera in a Sea&Sea DX-3000 housing. Identifications were based on taxonomic revisions and faunistic works available in 2005 [90,116]; their present classifications follow subsequent species descriptions and taxonomic revisions [82,83,85,86,117]. Earlier records [66,90] and voucher specimens in the coral collection of Natural Biodiversity Center from the research area were reexamined to check for species that could have been missed during the 2005 survey.

2.3. Data Analysis

Abiotic parameters and diversity counts were correlated by linear and non-linear regressions and fitted line plots through quadratic and linear model functions in the Minitab package [118]. A quadratic model was preferred above a linear model when it resulted in a better correlation (higher r-value). The following abiotic relations were analyzed: Shelf depth–latitude, secchi depth–distance to mainland, and secchi depth–shelf depth. Total mushroom coral diversity was correlated with shelf depth, secchi depth, latitude, distance to mainland, distance to harbor, and distance to nearest river outlet. Because the last four functions were very similar in correlation, diversity in shallow water was only related to shelf depth, secchi depth, and latitude.

Species richness estimators were used to compare the total number of observed species (incidence data) for all 38 sites together with theoretically expected species numbers in order to determine whether the diversity data set is representative. The analyses were performed with the program EstimateS 9.1 [119]. The observed number of species (SObs) is presented as an asymptotic accumulation curve, which was constructed after the sample order was randomized and the values were averaged, resulting in a mean and standard deviation of the observed species number for each consecutive sample unit and for the estimators Chao2 and ICE (incidence coverage-based estimator), the latter of which is more sensitive to unique species. Therefore the number of uniques (species represented in a single sample) is also given.

3. Results

3.1. Abiotic Parameters

Shelf depth does not show a linear correlation with latitude ($r = 0.385$, $p > 0.05$). A deep channel (Zone 2) roughly runs in east-to-west direction and separates the two shallow shelf zones, Zone 1 and Zone 3 (Figure 1). This bathymetric variation is also reflected in the maximum shelf depth for each site, with 54 m depth records at Payung Besar and Payung Kecil (Figure 2a; Table 1).

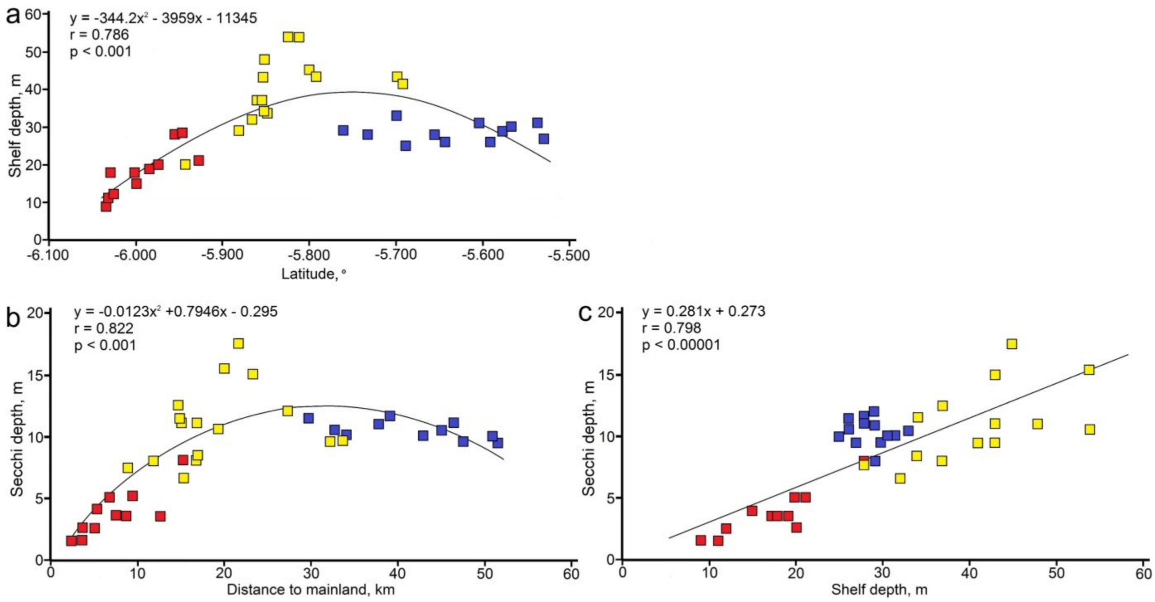

Figure 2. Significant relations between abiotic parameters off Jakarta: (**a**) Shelf depth in relation to latitude following quadratic model; (**b**) water transparency (secchi depth) in relation to distance from mainland, quadratic model; (**c**) secchi depth in relation to shelf depth, linear model. Color codes correspond with those of zones in Figure 1: Zone 1 (red), Zone 2 (yellow), Zone 3 (blue).

Secchi depth shows a similar relation, with the clearest water in the mid-section of the study area (Zone 2), where the seafloor is deepest (Figures 1b and 2b; Table 1). Therefore a quadratic model shows a stronger correlation between secchi depth and distance to mainland ($r = 0.822$) than a linear model ($r = 0.561$), meaning that water is less transparent north and south of the channel. Secchi depth shows a very significant linear relation with shelf depth ($p < 0.00001$), which is consistent with the clearest water occurring near reefs of Zone 2 (Figure 2c).

3.2. Species Diversity Patterns

3.2.1. Entire Depth Range

The number of mushroom coral species per site varied from 0 at Pulau Onrust (Bay of Jakarta) to 23 at Pulau Peniki in Zone 2 (Table S1; Figure 3a). The significant relation between species number and shelf depth fits better in a quadratic model ($r = 0.882$) than in a linear model ($r = 0.772$).

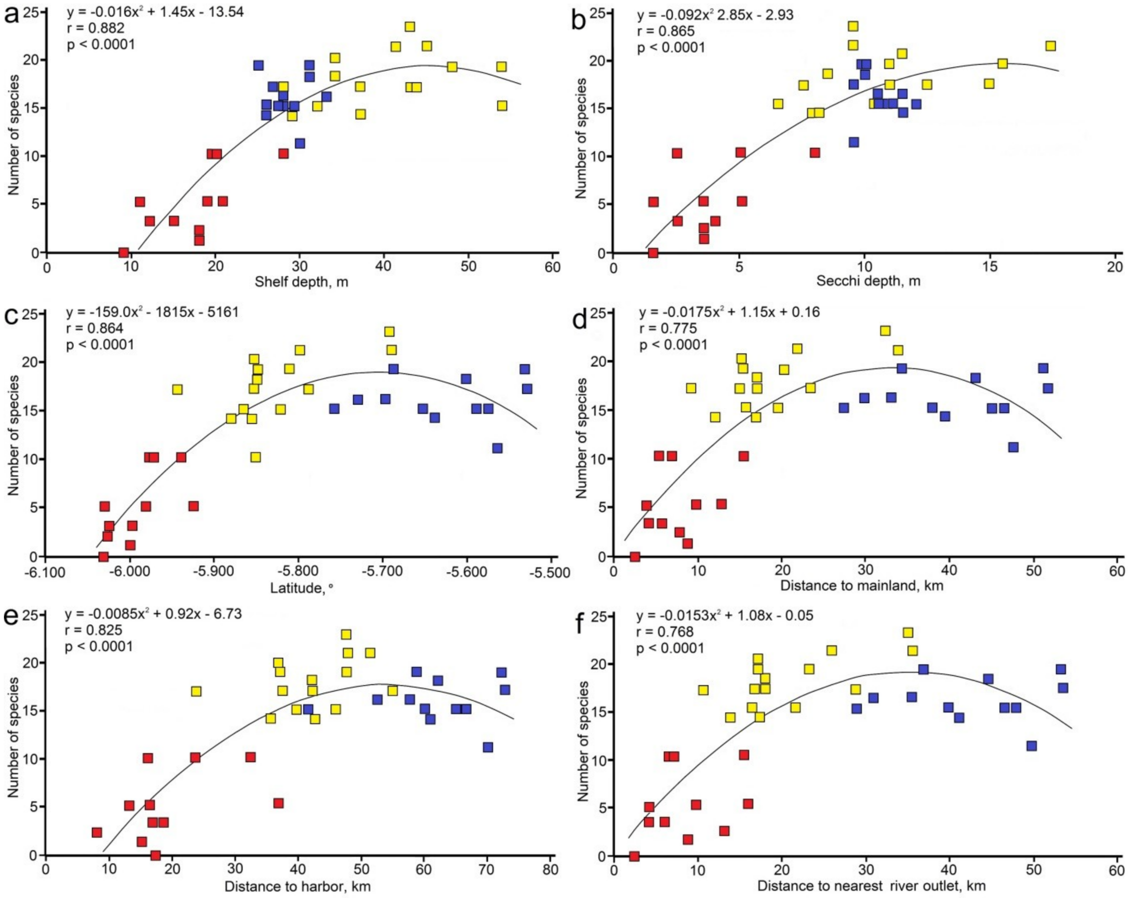

Figure 3. Significant relations (quadratic model) between mushroom coral diversity and abiotic parameters off Jakarta (2–30 m depth range): (**a**) shelf depth; (**b**) secchi depth; (**c**) latitude; (**d**) distance from mainland; (**e**) distance from harbor; (**f**) distance to nearest river outlet. Color codes correspond with those of zones in Figure 1: Zone 1 (red), Zone 2 (yellow), Zone 3 (blue).

The function approaches an asymptote, suggesting a saturation effect, meaning that over a shelf depth of ca. 42 m no higher numbers of observed species per sample unit can be expected. The number of species also depends on water transparency (secchi depth, Figure 3b), with a slightly stronger correlation for the quadratic model ($r = 0.865$) than the linear model (0.820) and a saturation point at ca. 16 m visibility depth. The quadratic relations between species diversity and distances of the reef sites from the mainland ($r = 0.775$), nearest river outlet ($r = 0.768$), and Tanjung Priok harbor ($r = 0.825$) are very similar to such a relation with latitude (r = 0.864), with the last being the strongest (Figure 3c–f). Their r-values do not differ significantly after Fisher r-to-z transformation ($p > 0.05$). All fit better than linear relations ($r = 0.559$, 0.574, 0.697, 0.655, respectively) and reflect a maximum species diversity in Zone 2.

A larger number of species in Zone 2 is also shown by the total number of all observed species in that zone ($n = 29$), as compared to nearshore Zone 1 ($n = 16$) and offshore Zone 3 ($n = 24$). With the addition of two historical records, the total numbers for Zone 2 and Zone 3 are each one species higher (Table 2; Figure 4d–f). Seven species represent new records for the research area (Table 2).

Table 2. Numbers of mushroom coral species (*n* = 31) encountered off Jakarta: 29 species recorded in 2005 and two additional ones observed in 1983 and 1995; # = new species record for the area. Shallow-water records (if any) are indicated by brackets.

Species	Zone 1 11 Sites	Zone 2 15 Sites	Zone 3 12 Sites	All Three Zones 38 Sites
Ctenactis albitentaculata (Hoeksema, 1989)	1 (1)	10 (2)	8 (5)	19 (8)
Ctenactis crassa (Dana, 1846)		8	9 (6)	17 (6)
Ctenactis echinata (Pallas, 1766)	4 (4)	14 (13)	12 (12)	30 (29)
Cycloseris boschmai (Hoeksema, 2014) #		2		2
Cycloseris costulata (Ortmann, 1889)	3 (2)	11	1	15 (2)
Cycloseris cyclolites (Lamarck, 1816) #		3		3
Cycloseris explanulata (van der Horst, 1922) #		3	1	4
Cycloseris fragilis (Alcock, 1893)		10	1	11
Cycloseris mokai (Hoeksema, 1989)		7	4	11
Cycloseris sinensis (Milne Edwards and Haime, 1851) #		1	2	3
Cycloseris tenuis (Dana, 1846) #		1		1
Cycloseris vaughani (Boschma, 1923) #		1		1
Danafungia horrida (Dana, 1846)	2 (2)	15 (14)	12 (12)	29 (28)
Danafungia scruposa (Klunzinger, 1879)	2 (2)	13 (12)	11 (11)	26 (25)
Fungia fungites (Linnaeus, 1758)	6 (6)	15 (14)	12 (12)	33 (32)
Halomitra pileus (Linnaeus, 1758)		2 (2)	2 (1)	4 (3)
Heliofungia actiniformis (Quoy and Gaimard, 1833)	2 (2)	10 (2)	8 (6)	20 (10)
Herpolitha limax (Esper, 1797)	3 (1)	15 (14)	12 (12)	30 (27)
Lithophyllon concinna (Verrill, 1864)	2 (2)	15 (14)	12 (12)	29 (28)
Lithophyllon repanda (Dana, 1846)	3 (3)	15 (14)	12 (12)	30 (29)
Lithophyllon scabra (Döderlein, 1901)		1 *		1 *
Lithophyllon undulatum Rehberg, 1892	5 (5)	7 (1)	5 (1)	17 (7)
Lobactis scutaria (Lamarck, 1801)		3 (1)		3 (1)
Pleuractis granulosa (Klunzinger, 1879)		10 (5)	6 (5)	16 (10)
Pleuractis moluccensis (van der Horst, 1919)	3 (2)	15 (1)	10	28 (3)
Pleuractis paumotensis (Stutchbury, 1833)	5 (5)	15 (14)	12 (12)	32 (31)
Podabacia crustacea (Pallas, 1766)	1 (1)	13 (8)	12 (12)	26 (21)
Podabacia kunzmanni (Hoeksema, 2009) #			(1)**	(1)**
Polyphyllia talpina (Lamarck, 1801)	4 (4)	11 (11)	7 (7)	22 (22)
Sandalolitha dentata Quelch, 1884		9	8 (1)	17 (1)
Sandalolitha robusta (Quelch, 1886)	8 (8)	14 (12)	12 (11)	34 (31)
Total number of species per zone/three zones	16 (16)	29 (18) + 1 *	24 (18) + 1 **	29 (21) + 2

* Record from Pulau Payung Besar in 1983; ** record from Pulau Panjang in 1995.

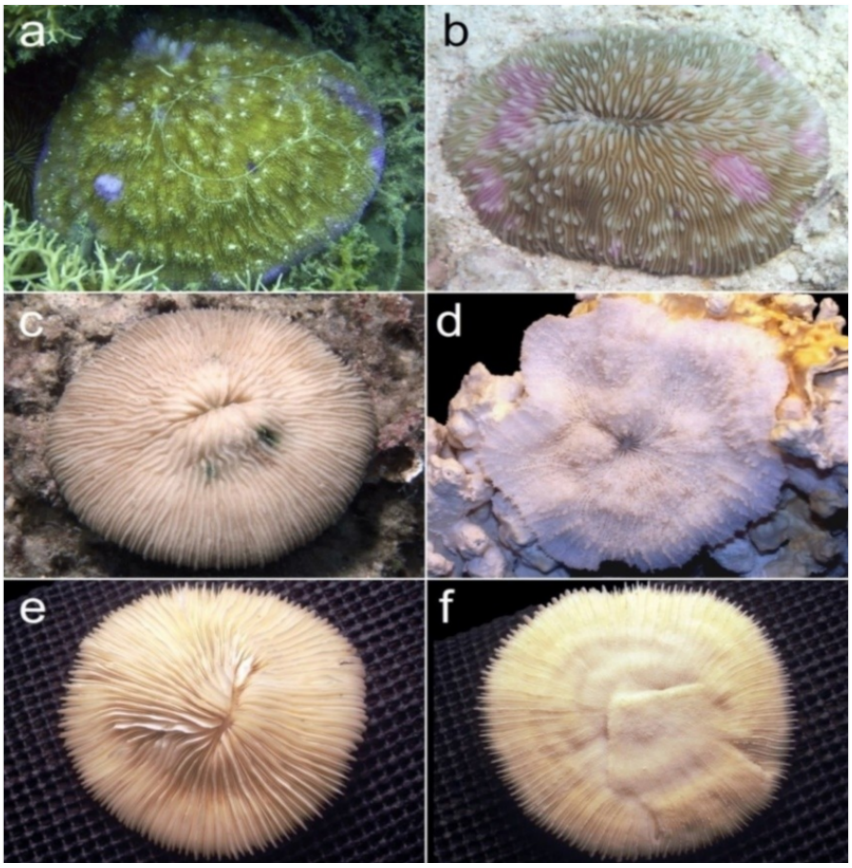

Figure 4. Shallow-water mushroom corals in zones 2–3: (**a**) *Halomitra pileus* at NW Pulau Peniki; (**b**) *Lobactis scutaria* at W Pulau Tikus; (**c**) *Pleuractis granulosa* at NW Pulau Kotok Kecil; (**d**) attached coral of *Podabacia kunzmanni* from N Pulau Panjang, 4 m depth (RMNH Coel. 24176, 18.ix.1995, coll. B.W.H.); (**e**) oral side of *Lithophyllon scabra* corallum from Pulau Tidung Besar (RMNH Coel. 16101, 12.v.1983, coll. B.W.H.); (**f**) aboral side of the same specimen.

Some species are common in all shelf zones, such as the free-living *Fungia fungites*, *Pleuractis paumotensis*, and *Sandalolitha robusta*, and the attached species *Lithophyllon undulatum* (Table 2). A few species with shallow-water records have only been encountered rarely in Zone 2 and Zone 3, such as the free-living species *Halomitra pileus*, *Lithophyllon scabra*, *Lobactis scutaria*, and *Pleuractis granulosa*, and the attached *Podabacia kunzmanni* (Table 2; Figure 4). Typical taxa for these two zones are the free-living *Ctenactis albitentaculata, Ctenactis crassa, Cycloseris boschmai*, *Cycloseris costulata, Cycloseris cyclolites*, and *Sandalolitha dentata* (Table 2; Figure 5). Deep-living species were found on lower reef slopes, such as the encrusting species *Cycloseris explanulata* and *Cycloseris mokai*, and on reef bases in both zones, such as the free-living *Cycloseris fragilis, Cycloseris sinensis*, and *Cycloseris vaughani* (Table 2; Figure 6). *Cycloseris fragilis* and *C. sinensis* were found in complete shape and in self-fragmenting mode (Figure 6c,d).

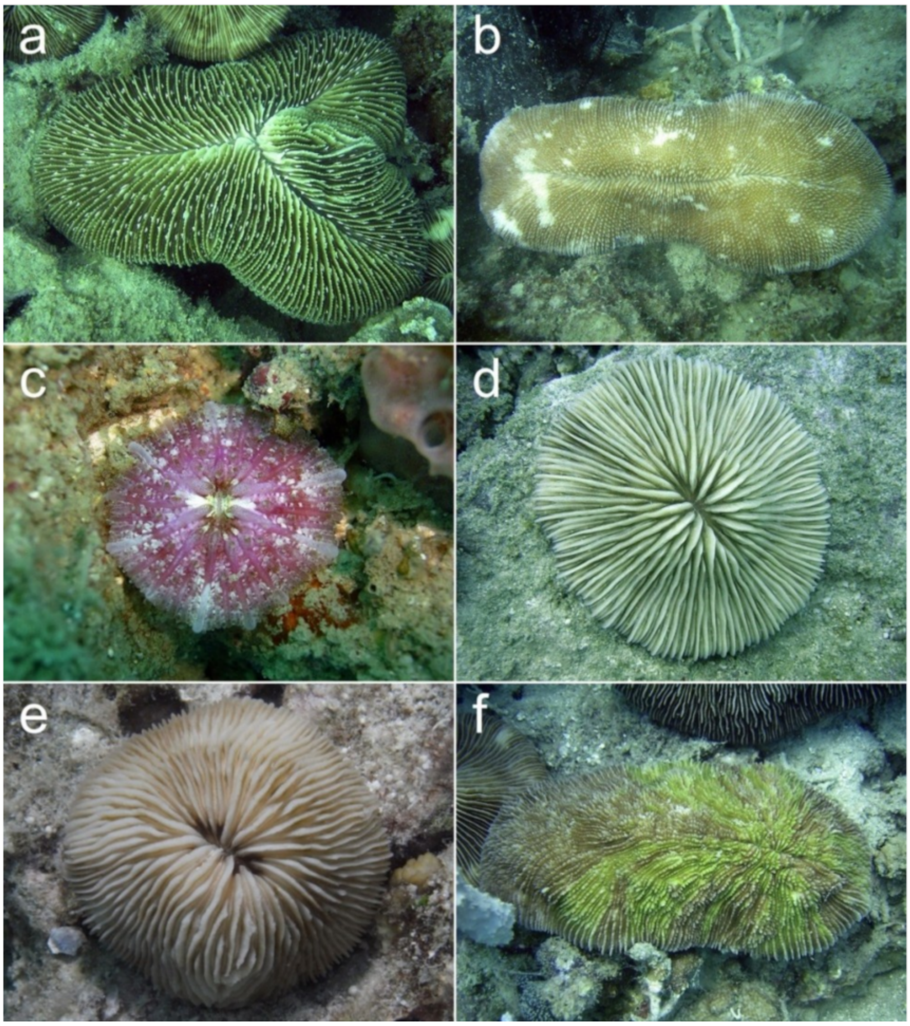

Figure 5. Free-living mid-slope mushroom corals at zones 2–3: (**a**) *Ctenactis albitentaculata* at NW Pulau Belanda; (**b**) *Ctenactis crassa* at S Pulau Tikus; (**c**) *Cycloseris boschmai* at E Karang Jong; (**d**) *C. cyclolites* at S Pulau Pari; (**e**) *C. tenuis* at E Pulau Peniki; (**f**) *Sandalolitha dentata* at S Pulau Kotok Kecil.

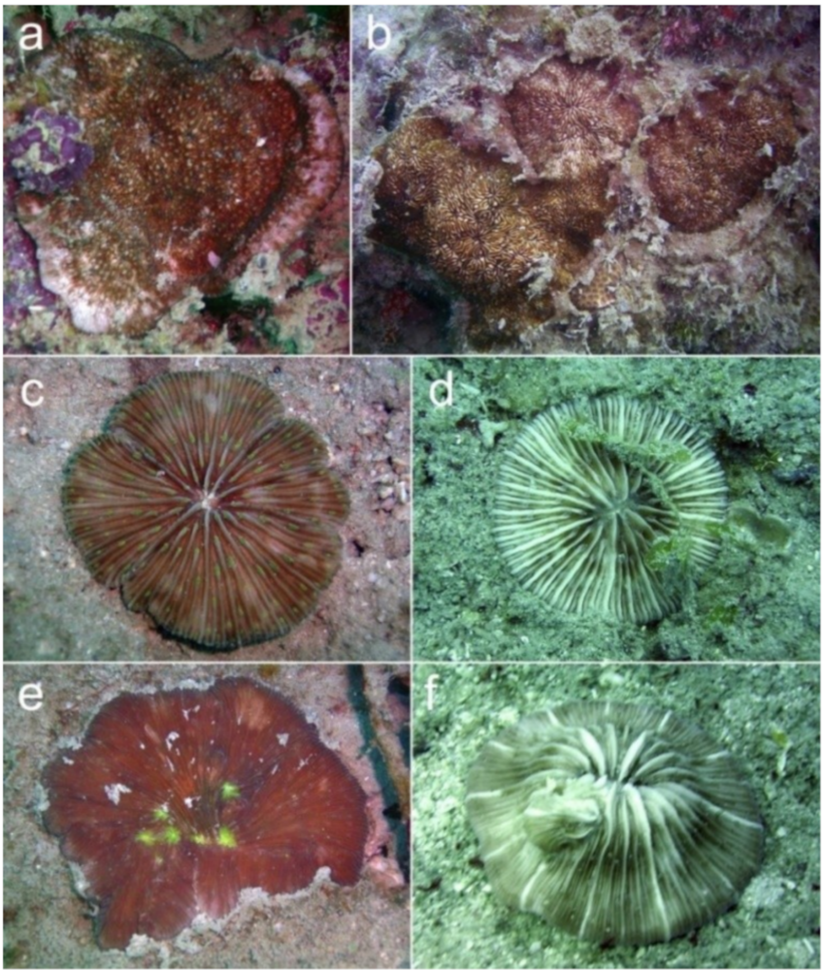

Figure 6. *Cycloseris* corals, encrusting on lower-slopes (**a**,**b**) and free-living on reef-bases (**c**–**f**) in zones 2–3: (**a**) *C. explanulata* at E Pulau Pari; (**b**) *C. mokai* at NW Pulau Hantu Kecil; (**c**) *C. fragilis* (self-fragmenting) at NW Pulau Peniki; (**d**) *C. fragilis* (complete) at NW Pulau Tidung Besar; (**e**) *C. sinensis* (self-fragmenting) at NW Pulau Peniki; (**f**) *C. vaughani* at E Karang Jong.

3.2.2. Shallow Depths

Species richness at 2–6 m depth excludes species only found on lower reef slopes and sandy reef bases. The relation between species number and shelf depth is represented better by a quadratic model (Figure 7a; r = 0.795) than a linear model (r = 0.614). The maximum values are found in Zone 3, while the plot reaches its maximum in Zone 2. A similar relation is found between species richness at 2–6 m depth and secchi depth, showing an increasing species richness with higher visibility from Zone 1 to Zone 2 (Figure 7b; quadratic r = 0.829, linear r = 0.735). The number of shallow species also increases in northward direction with distance offshore, approaching an asymptotic relation (Figure 7c; quadratic r = 0.852, linear r = 0.760). Totals of shallow-water records among the three zones vary little with values of 16, 18, and 17, respectively (Table 2).

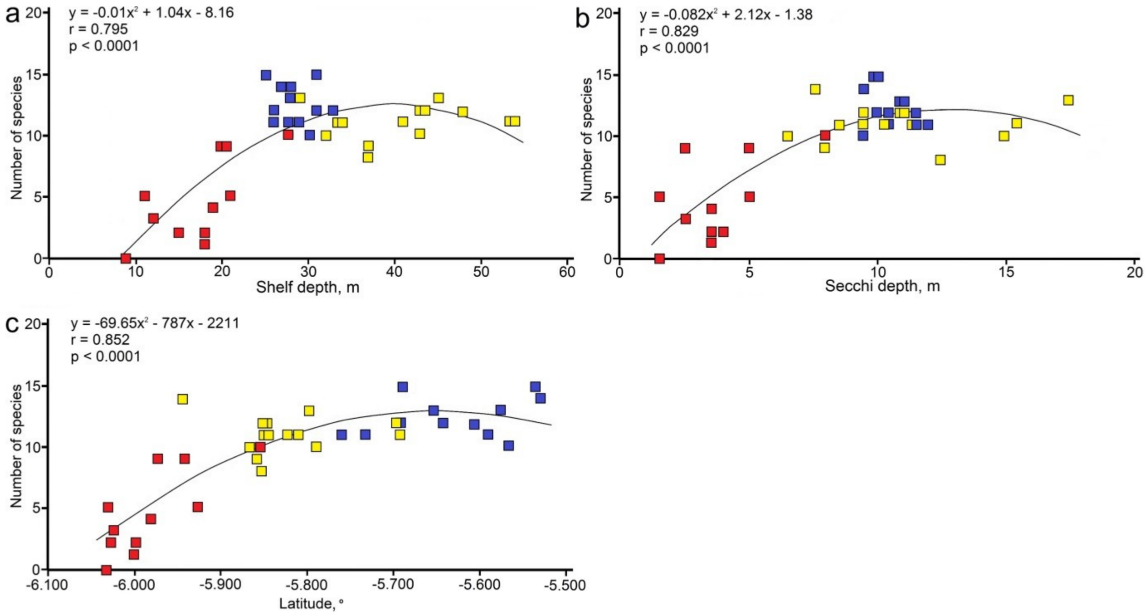

Figure 7. Significant relations between mushroom coral diversity and abiotic parameters off Jakarta for shallow reef depths (2–6 m): (**a**) shelf depth; (**b**) secchi depth; (**c**) latitude.

At some offshore localities, such as Pulau Putri in Zone 3, reefs were damaged at shallow depths because of blast fishing. Living mushroom corals were found in between dead and live coral fragments of other species (Figure 8).

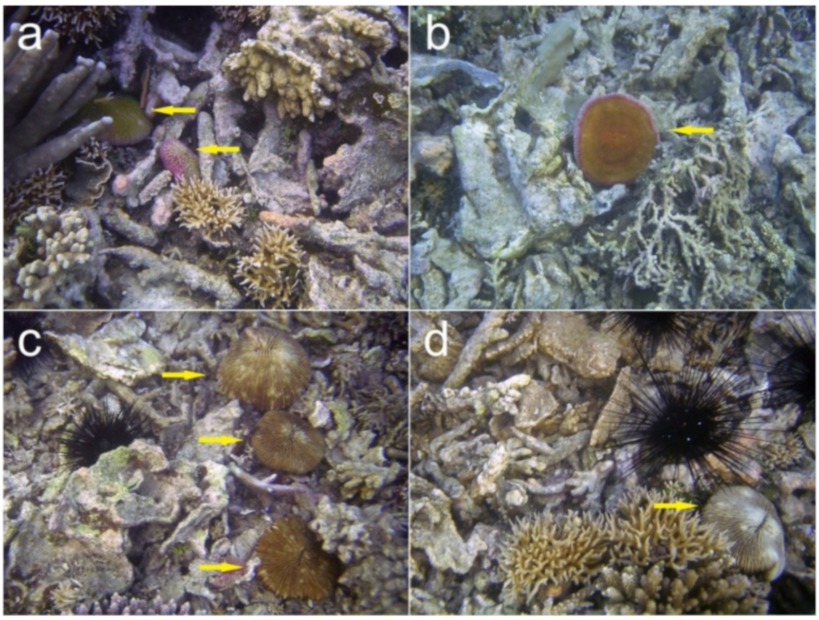

Figure 8. Reef flat of Pulau Putri at ca. 5 m depth (Zone 3), damaged by blast fishing. Free-living mushroom corals (arrows) are scattered among dead and live fragments of other corals: (**a**,**b**) *Fungia fungites*; (**c**,**d**) *Lithophyllon repanda*. Date: 14.ix.2005.

3.2.3. Species Richness Estimators

Application of species richness estimators (all reaching asymptotes) indicates that the total observed number of species (n = 29) is very similar to the estimated numbers Chao2 (n = 29) and ICE (n = 30) (Figure 9). The number of uniques (n = 2) is low. Two additional species observed in 1983 and 1995, respectively, were not taken into account.

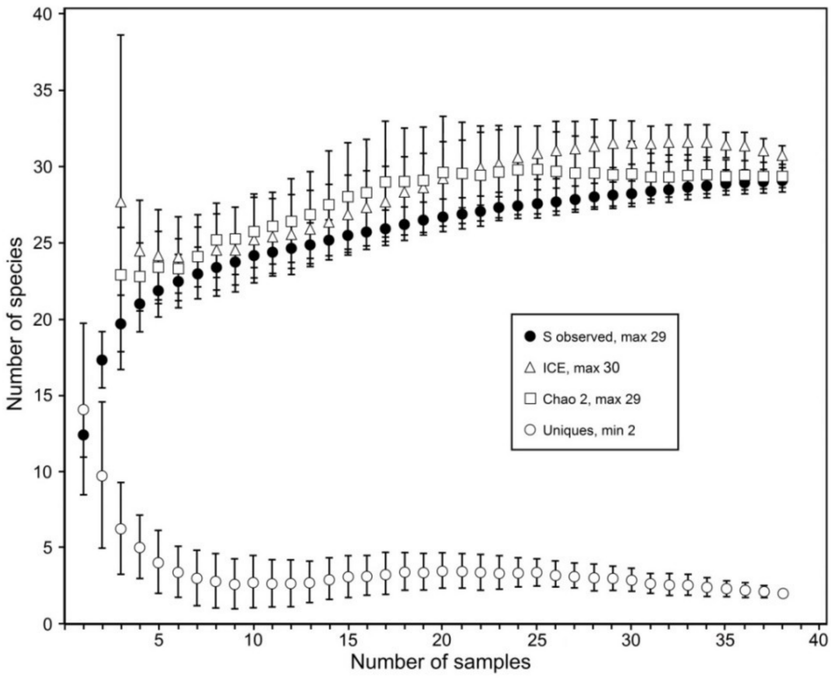

Figure 9. Species richness estimators covering 29 mushroom coral species observed in 38 reef sites based on incidence data.

4. Discussion

The arrangement of the reefs off Jakarta in an 80 km long string perpendicular to the coastline makes this archipelago suitable for a study of inshore–offshore diversity patterns. The present results show that the highest diversity of mushroom corals off Jakarta can be found on the reefs surrounded by a deep seafloor in the central section of the archipelago and not on the northernmost reefs, which are farthest away from the mainland. This concerns diversity at shallow depths, probably due to clear water in the central part, and over the entire reef profile, including a sandy base with sediment-tolerant species. The offshore reefs have shown a large reduction in water transparency since the 1920s, while the turbidity on the inshore reefs has not changed much until 2005, after which offshore reefs started to show a better visibility compared to inshore reefs [57,120–122]. Since the offshore reefs of Zone 3 are based on a shallow seafloor, sediment from the bottom may become resuspended more easily by wave action here than near reefs surrounded by deep water (Zone 2).

Lobactis scutaria, uniquely found in Zone 2 (Table 2; Figure 7b), is an example of a species that is common in clear water at shallow depths [16]. Other fungiids exclusively occurring in Zone 2 are free-living species found on reef slopes, such as *C. boschmai* and *C. cyclolites* (Figure 8c,d), and a single species living on a deep reef base, *C. vaughani* (Figure 6f), which is consistent with their distribution patterns at SW Sulawesi [17]. The latter species is also known to occur at mesophotic depths [77]. Encrusting species usually found on lower reef slopes, such as *C. explanulata* and *C. mokai*, were also most frequently observed in Zone 2. At SW Sulawesi, the outermost reefs are situated on a shallow barrier, which are less rich in fungiids than mid-shelf reefs surrounded by deeper reef slopes and reef bases [1,17,74], which is consistent with the depth-related diversity off Jakarta. Interestingly, mushroom corals in zones 2 and 3 may not be abundant at very shallow depths (<2 m), where families like Acroporidae and Poritidae are dominant [123].

Most previous coral studies on inshore–offshore gradients near Jakarta did not focus on diversity but on coral cover at shallow depths, generally finding highest values in Zone 2 and Zone 3 [2,57,58,114,124]. Reports dealing with coral diversity were limited to observations at shallow depths (5 m), and also with high numbers in Zone 2 and Zone 3 [88,89,102,125], thus discounting species that prefer greater depths. In a parallel study (in 2005) on algae down to 30 m depth, a maximum diversity was also found in the deeper part of the shelf (with the addition of some reefs more to the north) and a declining species number towards the north [126]. On the other hand, fish counts in shallow water (<10 m depth) resulted in an increase of species richness with distance offshore [127]. A similar relation was found for sponges collected from depths <20 m [128]. However, these studies did not distinguish between taxa that prefer shallow habitats and those that usually live deeper.

The present study did not reveal significant differences among species diversity gradients along a latitudinal gradient, distance offshore, distance from the nearest river outlet, and distance from Tanjung Priok harbor (Figure 2). There are multiple river outlets distributed along the coastline inside and outside Jakarta Bay, which together cause a diffuse influx of freshwater and contaminants along the shoreline [122,129], whereas reefs outside the Bay of Jakarta, in particular those farthest away from the mainland, show little difference in terrigenous impact [58].

A marine park has been designed to include only some of the most offshore reefs [45,47,130,131]. These remote reefs needed protection because illegal blast fishing was a very common practice here until the mid-1980s [132,133]. Its impact could still be witnessed in 2005 (Figure 8) and a recent study indicated that, until recently, blast fishing has still been going on [49]. Blast-generated craters and rubble fields may take decades to recover [133–136] and while it appears that free-living mushroom corals among the dead coral fragments have survived, they may also have arrived by migration [137]. Although the blast fishing predominantly took place at shallow depths, there are no signs that this affected species richness here in 2005.

The 2005 survey resulted in seven new records of reef coral species for Jakarta, including one from 4 m depth, the small attached *Podabacia kunzmanni*, which was described in 2009 and previously not recognized [82], and two small free-living species from deep (>20 m) sandy reef bases, *C. sinensis* and *C. vaughani* (Table 2). With a record of 31 fungiids, the islands of Jakarta are not as diverse as most areas studied in the adjacent Coral Triangle ($30 \leq n \leq 44$) [25,42,75,138] but they are more diverse than reef areas in the nearby Gulf of Thailand ($20 \leq n \leq 28$) [139].

Several corals of *C. fragilis* and *C. sinensis* were showing autotomy (self-fragmentation) and regeneration on the deep sandy reef bases as a mechanism of asexual reproduction (Figure 6c,e). This has not reported before from the Thousand Islands but it is common in similar habitats elsewhere [77,140,141]. On sandy substrates, this mechanism may replace sexual reproduction, for which a solid settlement substrate is needed before the corals become free-living [142,143]. Small, unattached mushroom corals can survive on sandy substrates because they are able to shed sediments [144,145] and they can move themselves away from direct threats [146–148]. Nevertheless, unattached fungiids are not unique as free-living and mobile corals on reefs worldwide and in the fossil record [78–80,149,150], which implies that the Fungiidae still constitute a suitable model taxon for Indo-Pacific coral diversity surveys.

Since many studies on reef condition focus on shallow reef zones, the present results indicate that more attention should be given to deeper reef parts. Recent research on reefs and reef zones > 20 m in depth has resulted in additional species records for other reef coral faunas, such as in the Persian Gulf [141], Taiwan [151], and the Great Barrier Reef [95]. Biodiversity surveys should therefore not be limited to shallow depths. There may be many other influences on species diversity, which have not been considered in the present study, such as salinity [24], dominant substrate type [17], and exposure to wave action and currents [1,17,91]. Future studies in the research area might focus on the impact of these natural factors on coral diversity and also on the effect of anthropogenic impact, such as land reclamation, pollutants, and worsening water quality [1,5,7].

Supplementary Materials: The following is available online at http://www.mdpi.com/1424-2818/11/3/46/s1, Table S1: Jakarta mushroom coral species records.

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