

## DISTRIBUTION PATTERNS OF MUSHROOM CORALS (SCLERACTINIA: FUNGIIDAE) ACROSS THE SPERMONDE SHELF, SOUTH SULAWESI

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**ABSTRACT.** — The distribution patterns of 37 mushroom coral species (Scleractinia: Fungiidae) were studied on 13 reefs in the Spermonde Archipelago (Makassar Strait, Indonesia) in 1984–1986. The studied reefs were either cay-crowned or submerged and were divided over four shelf zones varying in distance offshore. The species are compared with regard to their distributions (1) across the shelf in four zones parallel to the coastline, (2) around the reefs with orientation according to wind directions, and (3) along depth gradients over the reef flats, slopes, and bases. Most species showed their highest abundances on wave-exposed mid-shelf reef slopes. Within transects, species showed overlapping depth ranges, visible as multi-species assemblages with average densities in quadrats of up to 25 m<sup>-2</sup> composed of a maximum of 26 co-occurring species. Most species were concentrated on reef slopes, some mainly on shallow reef flats, and a few on deeper reef bases. Several species showed a downward shift in depth range with increasing distance offshore. A clustering of the reefs with respect to similarity in species composition appeared to be related to their distance offshore and to the presence or absence of shallow reef substrates important for recruitment. Use of the Fungiidae as a model taxon of phylogenetically closely related coral species in comparisons of their distribution patterns helps to gain insight with regard to their ecological differentiation along environmental gradients in coastal reef areas.

**KEY WORDS.** — depth, diversity, environmental gradients, onshore-offshore, wave exposure

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### INTRODUCTION

Ecological studies of onshore–offshore species richness patterns in coral reef areas usually concern shallow, tropical shelf seas, with most examples known from the Great Barrier Reef off eastern Australia (Done, 1982; Williams, 1982; Dinesen, 1983; Williams & Hatcher, 1983; Russ, 1984; Wilkinson & Trott, 1985; Preston & Doherty, 1990, 1994; DeVantier et al., 2006) and the Spermonde Archipelago in southwest Sulawesi (Moll, 1983; De Beer, 1990; Verheij & Prud'homme van Reine, 1993; Troelstra et al., 1996; De Voogd et al., 1999, 2006; Renema et al., 2001; Hoeksema & Kleemann, 2002; Kleemann & Hoeksema, 2002; Cleary et al., 2005; Becking et al., 2006; Hoeksema & Crowther, 2011). These studies either concern large species groups without enough detailed information to allow comparisons between closely related species, or they involve small groups of species that are cryptic and hard to find. The latter may be part of interspecific associations and rely on specific host organisms for their distributions, which therefore may not be independently related to abiotic factors (Stella et al., 2010, 2011). Hence, it is not yet certain how environmental gradients affect differentiation in distribution patterns in coastal reef systems among closely related coral species.

Recently, a molecularly based phylogeny reconstruction of 50 mushroom coral species (Scleractinia: Fungiidae) became available, which has enabled evolutionary studies of their life history traits and their role as hosts for associated fauna (Gittenberger et al., 2011; Hoeksema et al., 2012). This phylogenetic model may also help to gain insight pertaining to the evolution of the habitat preferences of mushroom coral species along environmental gradients, like depth, exposure to wave action, and distance offshore, for which extensive information from field surveys is required. Therefore, in the present study, cross-shelf bathymetric distribution patterns of 37 mushroom coral species on the Spermonde shelf (South Sulawesi, Indonesia) are presented and compared, which will be subject of a phylogenetic ecological analysis (Hoeksema, *subm.*).

Mushroom corals are very suitable for such studies because many species have an adult free-living (anthocyathus-) phase in their life history (Wells, 1966; Hoeksema, 1989), which enables them to survive on, and disperse over, various kinds of substrata, including deep sandy bottoms of reef bases (Goreau & Yonge, 1968; Fisk, 1983; Chadwick, 1988; Hoeksema, 1988; Chadwick-Furman & Loya, 1992; Hoeksema & De Voogd, 2012). Initially, all mushroom corals are attached to a hard substratum, but sooner or later individuals of free-living

species detach themselves (Yamashiro & Yamazato, 1987a, 1987b, 1996; Hoeksema, 1989; Hoeksema & Yeemin, 2011). A minority of the mushroom coral species remain attached after settlement (Hoeksema, 1989, 1993, 2009; Benzoni et al., in press).

Mushroom corals are restricted to the tropical Indo-Pacific (Wells, 1966; Hoeksema, 1989), where they can be found in mixed assemblages of various co-occurring species (Pichon, 1974; Claereboudt, 1988; Hoeksema & Moka, 1989; Hoeksema, 1991b; Latypov, 2007; Elahi, 2008; Hoeksema & Koh, 2009; Hoeksema & Matthews, 2011). These high concentrations of corals may not only be the result of sexual reproduction but can also be caused by cloning through budding (Gilmour, 2002, 2004b; Hoeksema, 2004a; Knittweis et al., 2009a; Hoeksema & Yeemin, 2011) or fragmentation (Nishihira & Pong-In, 1989; Yamashiro et al., 1989; Littler et al., 1997; Hoeksema & Gittenberger, 2010; Hoeksema & Waheed, 2011).

Detailed information about cross-shelf distribution patterns within a monophyletic group of sympatrically occurring species is rarely available, usually because of taxonomic problems involved with studies at species level. However, the taxonomic revision of the Fungiidae (Hoeksema, 1989), their recent phylogenetic analysis (Gittenberger et al., 2011), and the present information on their onshore-offshore distributions on the Spermonde shelf, make them ideal as a pilot group to study ecological differentiation in distribution patterns along cross-shelf environmental gradients.

## RESEARCH AREA

Fieldwork was carried out on the central part of the Spermonde shelf, which bears a large group of cay-crowned reefs and shoals known as the Spermonde Archipelago (Molengraaff, 1929). It is situated in the southern Makassar Strait, off the west coast of South Sulawesi (Fig. 1). The reefs at the outer edge of the shelf are situated on shallow banks, which were named the Spermonde Barrier Reefs (Niermeyer, 1911; Molengraaff,

1929; Umbgrove, 1947) or the Sangkarang Reefs (Van Vuuren, 1920a; De Nève, 1982). In addition to the barrier reefs, Van Vuuren (1920a, 1920b) distinguished rows of coral islands arranged parallel to the shore of SW Sulawesi. According to Umbgrove (1930, 1947) these reefs mark former protrusions along step-like shelf levels. Hutchinson (1945) subsequently divided the Spermonde Shelf into four zones arranged in N–S direction. These zones were also distinguished in later studies of the Spermonde Archipelago (De Klerk, 1983; Moll, 1983; Hoeksema & Moka, 1989; Hoeksema, 1990).

Off Makassar, the shelf is about 40 km wide (Figs. 2, 3). The first or innermost zone parallel to the shore is more or less bounded by the 20 m isobath and most of its reefs are crowned by unvegetated sand cays (Fig. 5A–C). The second zone ranges from 5 to 12.5 km off the coastline and the sea floor reaches a maximum depth of approximately 30 m. Most of its reefs are crowned by vegetated islets. The third zone ranges 12.5–30 km offshore where the depth of the sea floor varies roughly between 30 and 50 m. Most of its reefs are submarine shoals, with only a few having emerging cays (Fig. 5D). The outer rim, or barrier reef zone, ranges from 30 km offshore to the shelf edge, at about 40 km offshore. To the east, its depth reaches 40–50 m, while to the west its submarine contours drop immediately to below 100 m. Some of the reefs on the ridge that follows the outer shelf edge have islets on top of them.

The tidal range throughout the year is usually less than 1 m (Hutchinson, 1945). The predominant current direction in the southern Makassar Strait is towards the south, moderately constant throughout the year (Van der Stok, 1922; Soekarno, 1989). The wave generating monsoon winds are considered the main factor influencing the geomorphology and orientation of the reefs and their cays (Umbgrove, 1929, 1930). Most stronger winds occur during the northwest monsoon (Fig. 4) since those of the southeast monsoon are weakened by the inland mountains. In particular during the northwest monsoon (“the wet season”) fluvial discharge through river outlets, such as that of the Jeneberang River (Fig. 5A), causes freshwater inflow and the input of terrigenous sand and silt in the innermost shelf zone.

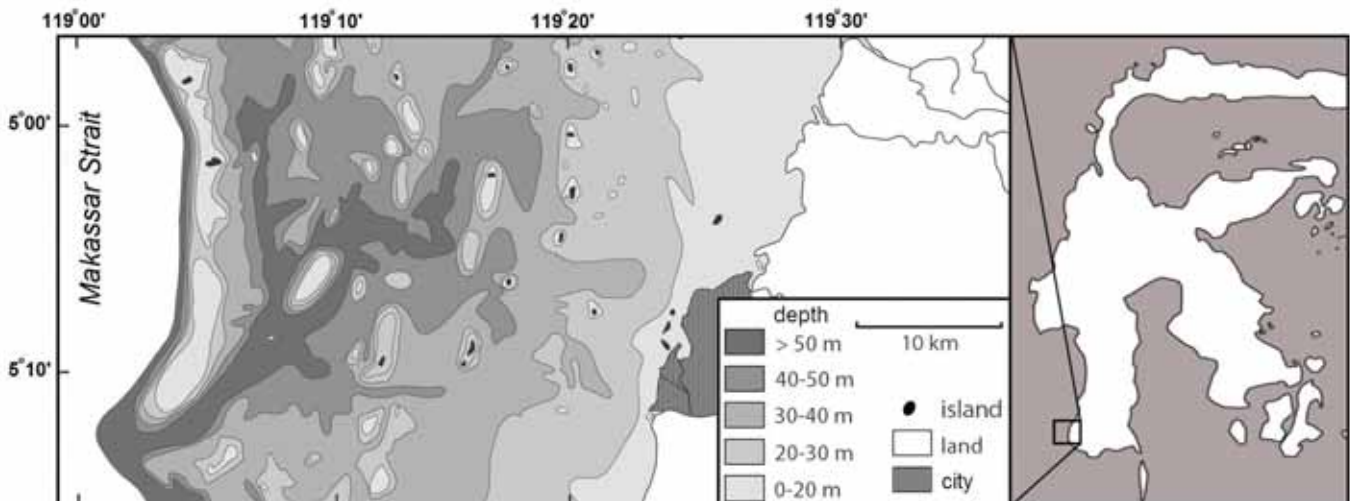


Fig. 1. Bathymetric map of the central section of the Spermonde Shelf (after De Klerk, 1983; Hoeksema, 1990), and its location at SW Sulawesi.

At the time of the survey, a sediment-loaded plume reaching Lae Lae (reef 1D in Fig. 5A) was common. A buoyant plume with most of its suspended load lost and with characteristic surface fronts of foam and detritus (see e.g. Hoekstra, 1989: Fig. 2b) was frequently observed reaching the E side of Kudingareng Keke (reef 3C in Fig. 2). From December to March (the wet season) silt and clay may be deposited far offshore due to maximal fluvial inflow, which also causes a low salinity and an enrichment of nutrients (Edinger et al., 1998; Cornils et al., 2011; Sawall et al., 2011). However, the river mouth of the Jeneberang delta has undergone much change (De Klerk, 1983) and dams have recently been constructed in the river bed to prevent sedimentation in Makassar Harbour, which may also

have an effect of the nearshore coral assemblages. The proximity of the city of Makassar and villages on some cays may have a polluting effect upon some reefs (Fig. 5A). Eutrophication is considered an important factor affecting the near-shore reefs (Edinger et al., 1998; Sawall et al., 2011). Salinity (‰) varies from 31.25 during the wet season to 34.48 during the dry season (Cornils et al., 2011). The southeast monsoon causes upwelling along the outer shelf rim, and consequently a decrease in water temperature and dissolved oxygen, and an increase in salinity and nitrate-nitrogen here (Ilahude, 1978). The vectorial cross-shelf environmental gradients are schematically indicated in an approximately E–W cross-section of the shelf, from Makassar on the mainland to Langkai Island on the barrier (Fig. 3).

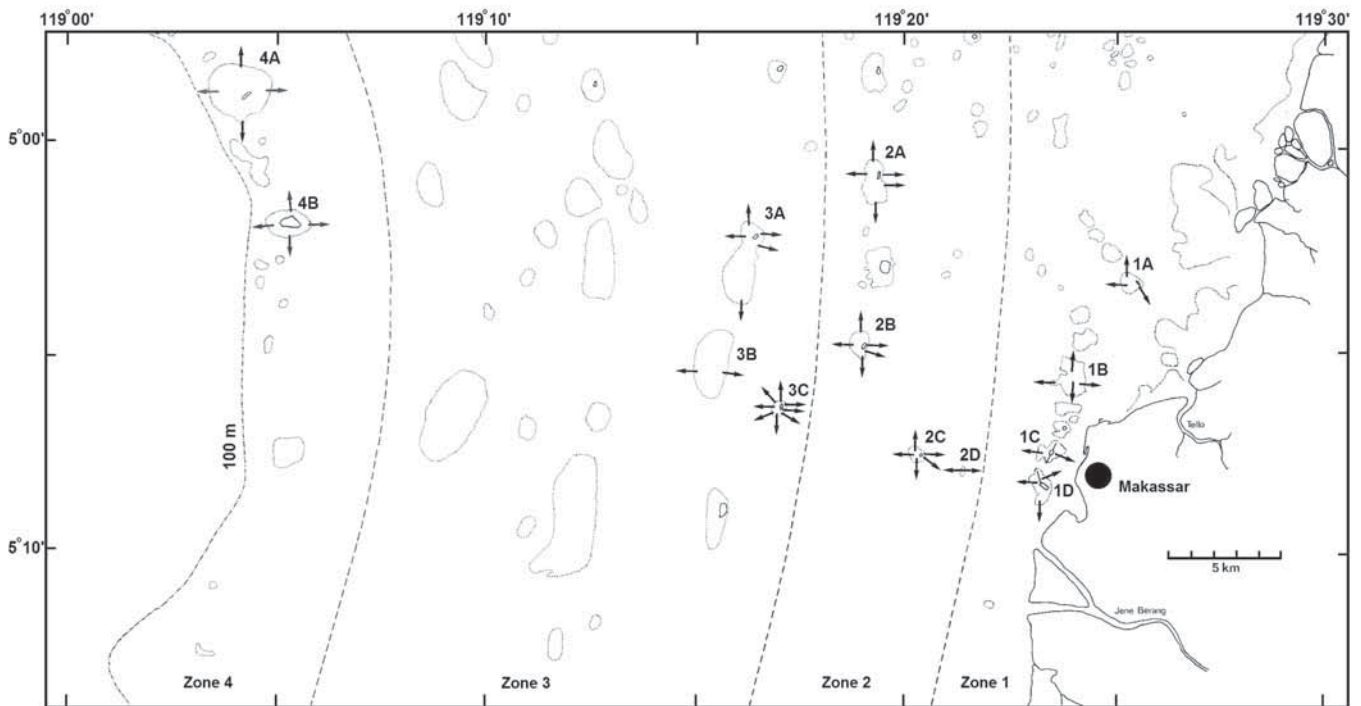


Fig. 2. The locations of 52 transects (arrows) around coral reefs on the central section of the Spermonde Shelf: 1A = Barang Baringang; 1B = Gusung Trabanusu (synonym Gusung Remanusu); 1C = Lae-Lae Keke (synonyms Lae-Lae Caddi and Gusung); 1D = Lae-Lae; 2A = Bone Batang; 2B = Barang Caddi (synonym Barang Keke); 2C = Samalona; 2D = Bone Baku; 3A = Bone Tambung; 3B = Kapodasang; 3C = Kudingareng Keke; 4A = Lanyukang; 4B = Langkai. Almost all reefs are cay-crowned (reefs 1B, 2D, 3B excluded); the cays of reefs 1A, 1C, 2A and 3C were not inhabited by people at the time of the survey.

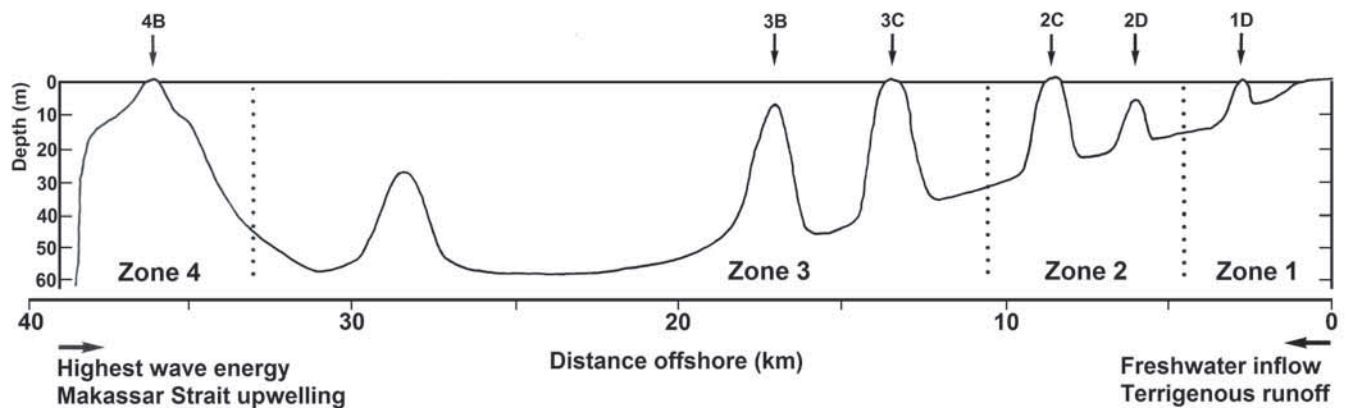


Fig. 3. Schematic cross-section of the central Spermonde Shelf (approximately W–E) from the Makassar Strait (off Langkai) to the mainland (at Makassar). The main cross-shelf environmental gradients are indicated (arrows). The positions of reefs 4B, 3B, 3C, 2C, 2D and 1D are indicated in Fig. 2.

**MATERIAL AND METHODS**

**Data sampling.** — The survey was conducted in 1984–1986 on 13 reefs on the central section of the Spermonde Shelf (Fig. 2). The investigated reefs have been divided over four parallel

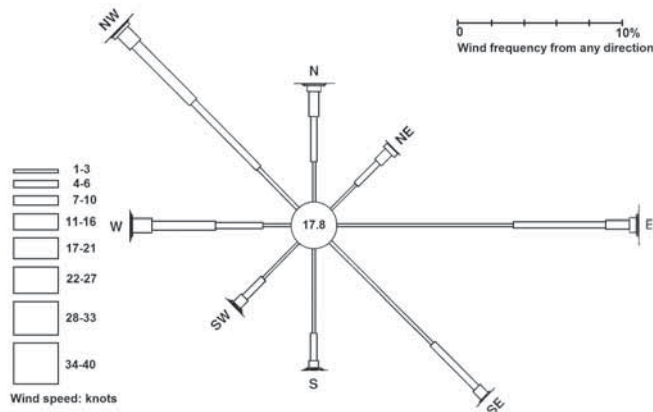


Fig. 4. The annual wind speed frequency distribution (elevation 14 m at Hasanuddin Airport, Ujung Pandang) registered over the years 1971–1979. The percentage of the frequency of variable winds below 1 knot is given in the centre of the rose. The wind rose is obtained by compiling data of monthly wind frequency distributions issued by Badan Meteorologi dan Geofisika, Jakarta.

zones varying in distance offshore and bathymetry (Fig. 3). Four of the selected reefs are located in the first or innermost zone along the shoreline. Four mid-shelf reefs are situated in the second zone and three in the third zone. Two reefs in the outermost (4<sup>th</sup>) shelf zone are based on shallow banks, which constitute the barrier on the outer rim. Three reefs have no cay or island on top of them: the shoal Gusung Trabanusu (reef 1B) remains about 1 m below sea level, whereas the submerged reefs Bone Baku (reef 2D) and Kapodasang (reef 3B) have their crests at 4 m depth. Cays on top of some reefs are usually situated close to the eastward slope (Fig. 5D). Bone Tambung (reef 3A), Lanyukang (reef 4A), and Langkai (reef 4B) are exceptions because of their wide eastward reef flats. Lae-Lae Keke (reef 1C) and Lae-Lae (reefs 1D) are enforced by breakwaters, which were constructed in the 1930s to shelter Makassar’s harbour against waves generated by the northwest monsoon (Fig. 5A–C). All reefs were visited by means of a small locally made wooden boat with an outboard engine.

To compare mushroom coral distributions with wind speed frequencies (Fig. 3), transect sites were selected around each reef, mainly at the N, W, S, and E side. Near E transects that contained relatively little or no coral cover (Wijsman-Best et al., 1981; De Klerk, 1983; Moll, 1983), a transect was added at the ESE side. To obtain a more complete image of the wind effect and in order to see whether the standard transects were

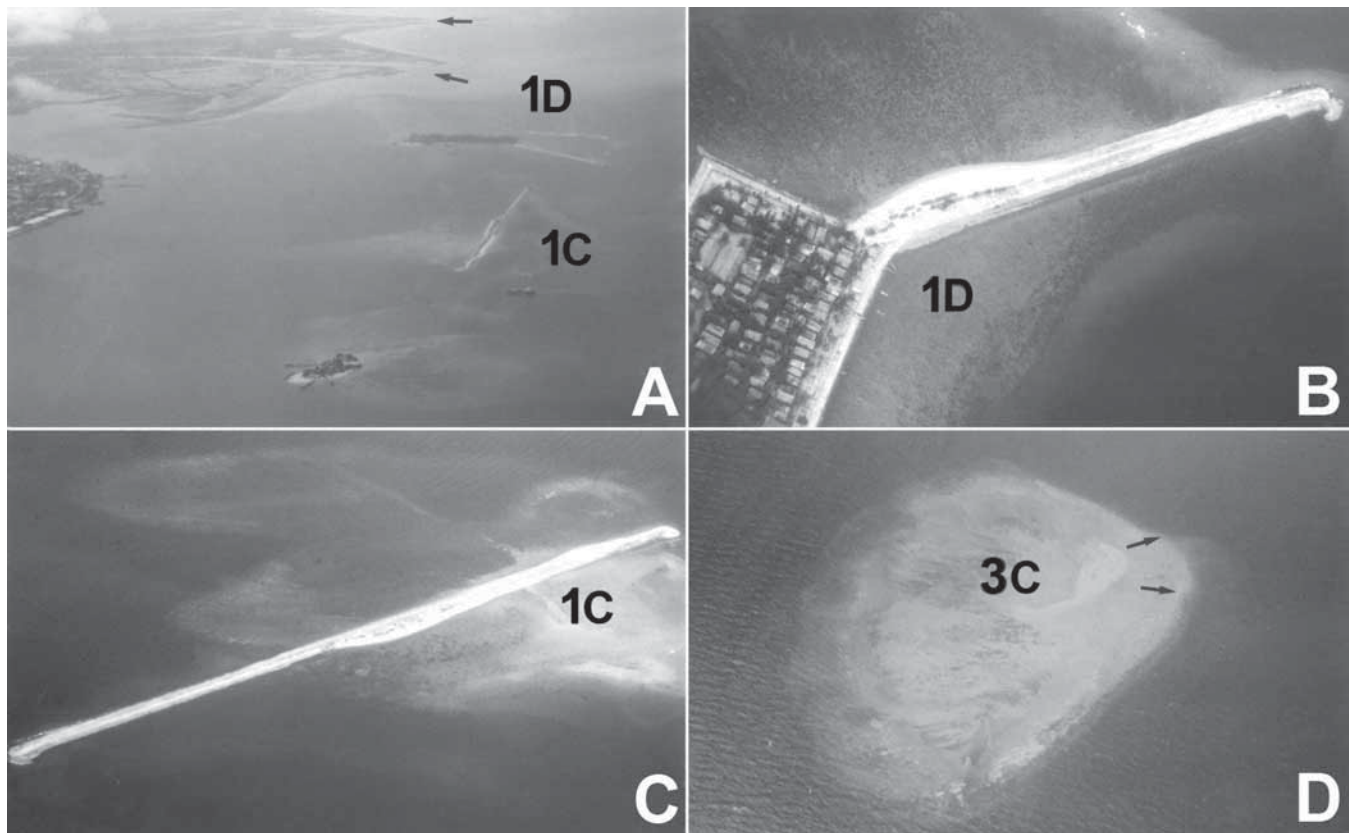


Fig. 5. A. Oblique aerial photo of the first shelf zone (view from the north, 8 Dec. 1987). Makassar’s port is at the left hand side. The Jeneberang Delta with two recent protruding river outlets (arrows) and a sediment loaded plume are visible in the south. In between the port and the northernmost river mouth there is a bay that extends a dammed previous northernmost river outlet (see Fig. 1). The displayed reefs are Lae Lae (1D), Lae-Lae Caddi (1C) and Kayangan. B. Perpendicular view on Lae-Lae showing the densely inhabited island with its reinforced rectangular outline and the NNW directed breakwater (12 Dec. 1987). C. Oblique aerial photo of Lae-Lae Keke (view from southeast) with an NNE-SSW oriented breakwater on top (12 Dec. 1987). D. Oblique aerial photo of reef 3C (Kudungareng Keke; view from southern direction) showing the sand cay and adjacent sandy slope (arrows) at its eastern side.

sufficient, three more transects were added as controls around Kudingareng Keke (reef 3C), at the NW, SW, and SE sides (Fig. 2). In each transect, species abundances were measured at various depths. On the reef flats, mushroom coral species inventories were conducted at 3 m depth and at 5, 10, 20, and 50 m distance away from the 3 m isobaths in the direction of the reef centre, at ca. 2.5, 2, 1.5, and 1 m depth, respectively (Fig. 6). On reef slopes and reef bases, inventories were made at 3 m depth intervals, from 6 m deep down to the depth at which the bottom became horizontal or no mushroom corals occurred anymore, with a maximum depth of 36 m (Fig. 6). To locate these depths, a diaphragm depth gauge with parabolic scale (0–80 m) and double needle revolution was used. At each survey depth, a  $50 \times 1$  m<sup>2</sup> belt quadrat was used as sample unit (SU) to measure the occurrence frequencies of mushroom coral species, for which a 50 m long fibreglass measuring tape was laid out, following the bottom contours parallel to the selected isobaths. By snorkeling or SCUBA diving, a 1.2 m long PVC tube (0.2 m at one end was used as handle) was moved alongside this tape to demarcate 1-m width. The were noted per 50 m<sup>2</sup> reef area used as sample unit (SU). A total of 565 belt quadrats in 52 transects resulted in 28,565 m<sup>2</sup> of reef bottom area surveyed (Table 1).

For each transect, three reef zones were distinguished in order to determine the substratum dominance order as observed in the belt quadrats, i.e., the reef flat, the reef slope, and the reef base (Fig. 7). The bottom inclination on the reef flats was under 15° and the substratum consisted predominantly of coral and rubble, except for E sides, which were sandy. The bottom inclination of the reef slopes usually varied between 15° and 45° and the substratum usually consisted of hard coral. Some westward slopes were partly covered by debris as a result of rubble avalanching and most eastward slopes consisted entirely of sand. At the reef base, the inclination was less than 15° and the sea floor itself consisted of sand or silt and contained little coral cover.

The species descriptions are given by Hoeksema (1989); their updated classification is according to Gittenberger et al. (2011). The present species names and their authorities are listed

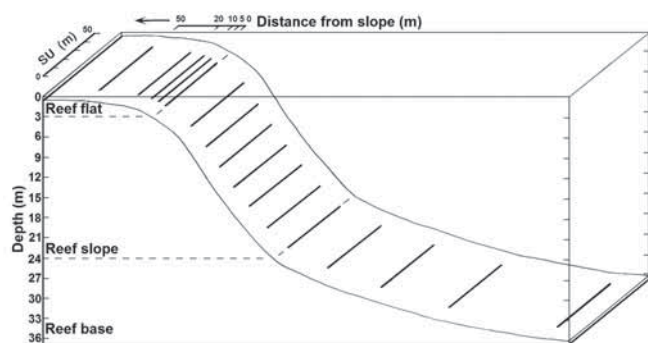


Fig. 6. Schematic cross-section of a transect profile (example: W transect of reef 3A) with the positions of the  $50 \times 1$  m<sup>2</sup> belt quadrats (SUs). The belt quadrats on the reef slope and base are indicated with 3 m depth intervals; those on the outer reef flat at 3 m depth and at 5, 10, 20, and 50 m distance from the 3 m isobaths in the direction of the island.

in Table 1. Corals that could not be directly identified in situ were collected for further examination and were deposited in the collection (RMNH Coel.) of NCB Naturalis.

**Reef fauna ordination.** — The CLUSTER.BAS program of Ludwig & Reynolds (1988) was employed to compute a Q-mode cluster analysis on the reefs with respect to their species compositions (based on presence-absence data; Table 2). The unweighted pair-group method using arithmetic averages (UPGMA) was applied and dissimilarities were measured as mean euclidean distance (MED). The UPGMA strategy is considered space conserving; the MED coefficient is sensitive to size displacement between data profiles (Romesburg, 2004), which means that similarity is greatest (MED = 0) when species compositions of two reefs are identical.

## RESULTS

**Mushroom coral densities.** — Three different distribution patterns were distinguished (Fig. 8): (1) a cross-shelf pattern between reefs varying in distance offshore, (2) a circum-reef pattern with variation around reefs depending on the dominant wind direction, (3) bathymetric patterns along depth gradients that vary around reefs and in distance offshore.

**Cross-shelf distributions:** Several Sample Units (SUs) showed dense mushroom coral concentrations (>500 individuals per 50 m<sup>2</sup>) in multi-species assemblages in shelf zones 1–3 (Figs. 8, 9). High numbers of specimens were recorded: 692 and 656 on reef 1D, 523 on reef 2A, 513 on reef 2B, and six SUs ranging from 539 to 752 on reef 3C. Mushroom coral abundance did not necessarily depend on species richness; the highest number counted in zone 4 was only 195 (reef 4B), in a single species aggregation (Fig. 9). Proximity to the mainland coastline did not limit mushroom coral abundance.

**Circum-reef distributions:** On most reefs, the highest mushroom coral concentrations were observed in W transects and in some N transects (Fig. 8). In addition, the NW and SW transects of reef 3C were also densely covered. These are the sides most strongly exposed to winds from the west (Fig. 4). Fungiids were absent from several E or ESE transects (reefs 1A, 1B, 2A, 3C), where the substrate mainly consisted of sand (Fig. 7), and sparse on some E sides, either shallow (reef 3A) or deep (reefs 2B, 2C). On the other hand, reefs 1C and 1D, with breakwaters on their top (Fig. 5A–C), had relatively high mushroom densities in their E transects, as did submerged reefs 2D and 3B, and reefs with wide eastward reef flats (reefs 3A, 4A, and 4B). Fungiids were absent from wide, wave-exposed westward reef flats in shelf zone 4, where waves generated by the northwest monsoon prevent coral settlement on dead rock and rubble. Fungiid presence was low on eastward reef slopes with a sand cay nearby where sand can be transported over the reef flat without being hindered by breakwaters.

**Bathymetric distributions:** The highest concentrations of mushroom corals were observed on reef slopes (Figs. 8, 10). Here the substratum is generally dominated by coral (living and dead), which is also the case for many reef flats in W

Table 1. Fungiidae (34 species) encountered in transects on the Spermonde Shelf. R, T and SU indicate the numbers of reefs ( $R_{\text{tot}} = 13$ ), transects ( $T_{\text{tot}} = 52$ ), and  $50 \times 1 \text{ m}^2$  belt quadrats or sample units ( $SU_{\text{tot}} = 565$ ) in which specimens were recorded per species. I is the total number of individual corals for all SUs together (28,250 m<sup>2</sup>). Three additional species were found outside SUs (*Halomitra clavator* Hoeksema, 1989, *Podabacia motuporensis* Veron, 2002, and *Cycloseris* sp. 1), bringing the total number of recorded Fungiidae to 37.

Species	R	T	SU	I
01. <i>Ctenactis albitentaculata</i> Hoeksema, 1989	8	20	41	66
02. <i>Ctenactis crassa</i> (Dana, 1846)	9	25	72	159
03. <i>Ctenactis echinata</i> (Pallas, 1766)	13	39	165	1509
04. <i>Cycloseris costulata</i> (Ortmann, 1889)	13	36	156	1051
05. <i>Cycloseris cyclolites</i> (Lamarck, 1816)	5	9	12	17
06. <i>Cycloseris distorta</i> (Michelin, 1842)	1	1	1	1
07. <i>Cycloseris fragilis</i> (Alcock, 1893)	8	16	38	424
08. <i>Cycloseris mokai</i> (Hoeksema, 1989)	7	23	62	254
09. <i>Cycloseris sinensis</i> (Milne Edwards & Haime, 1851)	7	19	40	471
10. <i>Cycloseris somervillei</i> (Gardiner, 1909)	6	12	19	38
11. <i>Cycloseris tenuis</i> (Dana, 1846)	9	34	176	938
12. <i>Cycloseris vaughani</i> (Boschma, 1923)	4	9	16	46
13. <i>Danafungia horrida</i> (Dana, 1846)	13	39	182	1256
14. <i>Danafungia scruposa</i> (Klunzinger, 1879)	13	39	169	1264
15. <i>Fungia fungites</i> (Linnaeus, 1758)	13	44	246	3909
16. <i>Halomitra pileus</i> (Linnaeus, 1758)	9	22	57	151
17. <i>Heliofungia actiniformis</i> (Quoy & Gaimard, 1833)	13	38	108	342
18. <i>Heliofungia fralinae</i> (Nemenzo, 1955)	8	24	75	625
19. <i>Herpolitha limax</i> (Esper, 1797)	13	45	241	1398
20. <i>Lithophyllon concinna</i> (Verrill, 1864)	13	38	159	2904
21. <i>Lithophyllon repanda</i> (Dana, 1846)	13	43	230	6588
22. <i>Lithophyllon scabra</i> (Döderlein, 1901)	12	39	159	556
23. <i>Lithophyllon spinifer</i> (Claereboudt & Hoeksema, 1987)	2	2	2	2
24. <i>Lithophyllon undulatum</i> Rehberg, 1892	9	31	84	148
25. <i>Lobactis scutaria</i> (Lamarck, 1801)	10	33	32	363
26. <i>Pleuractis granulosa</i> (Klunzinger, 1879)	9	39	133	828
27. <i>Pleuractis gravis</i> (Nemenzo, 1955)	10	29	84	254
28. <i>Pleuractis moluccensis</i> (Van der Horst, 1919)	13	40	168	1311
29. <i>Pleuractis paumotensis</i> (Stutchbury, 1833)	13	43	209	1907
30. <i>Podabacia crustacea</i> (Pallas, 1766)	11'	34	83	150
31. <i>Polyphyllia talpina</i> (Lamarck, 1801)	13	45	182	421
32. <i>Sandalolitha dentata</i> Quelch, 1884	7	18	40	63
33. <i>Sandalolitha robusta</i> (Quelch, 1886)	13	45	192	558
34. <i>Zoopilus echinatus</i> Dana, 1846	2	3	4	7

transects (Fig. 7). Reefs in zone 3 had the greatest vertical range of mushroom coral presence measured, down to 36 m. For the shallower reefs in shelf zones 2 and 1, mushroom corals extended down to 27 m and 15 m respectively. The zone 1 sea floor (15 m) consisted of fine silt (without any life cover) and mushroom corals were only observed down the reef slope as far as 12 m. On the submerged reefs 2D and 3B, the W slope quadrats had lower fungiid densities than those on adjacent reefs with a shallow reef flat. On zone 4 reefs, fungiids are relatively sparse where the reefs sit on top of the barrier, which is predominantly covered by sand. However fungiid depth ranges extend deeper in this zone at its western margin, where the reef slope merges into the Makassar Strait drop-off.

**Species distributions and abundances.** — In the transects 34 out of a total of 50 mushroom coral species were recorded (Table 1). Three additional species were observed outside transects, bringing the total for the Spermonde Shelf to 37. All, except three species, have a free-living anthocyathus phase. The three attached species were *Cycloseris mokai*, *Lithophyllon undulatum*, and *Podabacia crustacea*. An additional fixed species, *P. motuporensis*, was only recorded from outside a transect. *Cycloseris* species were present as both unbroken coralla and fragments (cf. Hoeksema & Waheed, 2011). The distributions of the 34 most common species are systematically described (Appendix 1) and schematically indicated in transect diagrams (Appendix 2; Figs. 12–45).

Table 2. Presence (1) absence (0) data of 34 Fungiidae at the 13 surveyed reefs on the Spermonde Shelf with total numbers per reef and per shelf zone. Three additional species were recorded from outside the SUs in zone 3 (Table 1).

Species	Reefs													
	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	4A	4B	
01. <i>Ctenactis albitentaculata</i>	0	0	0	0	1	1	1	0	1	1	1	1	1	
02. <i>Ctenactis crassa</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	
03. <i>Ctenactis echinata</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
04. <i>Cycloseris costulata</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
05. <i>Cycloseris cyclolites</i>	0	1	0	0	0	0	1	1	1	0	1	0	0	
06. <i>Cycloseris distorta</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	
07. <i>Cycloseris fragilis</i>	0	0	0	0	1	1	1	1	1	1	1	1	0	
08. <i>Cycloseris mokai</i>	0	0	0	0	1	1	1	1	1	1	1	0	0	
09. <i>Cycloseris sinensis</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	
10. <i>Cycloseris somervillei</i>	0	0	0	0	0	1	1	0	1	1	1	1	0	
11. <i>Cycloseris tenuis</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	
12. <i>Cycloseris vaughani</i>	0	0	0	0	0	0	1	0	1	0	1	1	0	
13. <i>Danafungia horrida</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
14. <i>Danafungia scruposa</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
15. <i>Fungia fungites</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
16. <i>Halomitra pileus</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	
17. <i>Heliofungia actiniformis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
18. <i>Heliofungia fralinae</i>	0	0	0	0	1	1	1	0	1	1	1	1	1	
19. <i>Herpolitha limax</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
20. <i>Lithophyllon concinna</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
21. <i>Lithophyllon repanda</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
22. <i>Lithophyllon scabra</i>	1	1	1	1	1	1	1	1	1	1	1	0	1	
23. <i>Lithophyllon spinifer</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	
24. <i>Lithophyllon undulatum</i>	0	1	0	0	1	1	1	0	1	1	1	1	1	
25. <i>Lobactis scutaria</i>	0	1	0	0	1	1	1	1	1	1	1	1	1	
26. <i>Pleuractis granulosa</i>	0	0	0	0	1	1	1	1	1	1	1	1	1	
27. <i>Pleuractis gravis</i>	0	0	1	0	1	1	1	1	1	1	1	1	1	
28. <i>Pleuractis moluccensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
29. <i>Pleuractis paumotensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
30. <i>Podabacia crustacea</i>	1	1	1	1	1	1	1	0	1	1	1	1	0	
31. <i>Polyphyllia talpina</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
32. <i>Sandalolitha dentata</i>	0	0	0	0	1	1	1	0	1	1	1	1	0	
33. <i>Sandalolitha robusta</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	
34. <i>Zoopilus echinatus</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	
Total nr.	19				31				34 (37)				30	

**Species richness patterns.** — The species richness pattern of Fungiidae along depth gradients across the Spermonde Shelf is very similar to the mushroom coral abundance pattern (Fig. 8): in general, the greater the abundance, the greater the richness, but in high mushroom coral concentrations species richness was not depending on mushroom coral abundance (Fig. 9). Overall, shelf zone 3 had the highest number of species ( $n = 34$ ), with zones 2, 4, and 1 having 31, 29, and 19 species, respectively. Across complete transects (Table 3), shelf zones 1 and 4 generally had lower species richness numbers compared to zones 2 and 3. Zone 3 transects had the highest species numbers (31–32 species), but in the E and ESE sectors, richness was extremely variable (0–26 species) and was comparable with the same sectors in zone 2. Around most other reefs, the

E and ESE transects were generally quite depauperate (0–14 species). The exceptions were reefs 1C and 1D (breakwaters on top) and submerged reefs 2D and 3D (without eastward sandy slopes) where species richness was not extraordinarily low in E transects. In shelf zones 2 and 3, almost all other transects had high species numbers (Table 3).

Within reef zones no distinct differences in fungiid species compositions can be noticed in N–S longshore direction (Table 2). There is no indication that Makassar is an anthropogenic source of eutrophication for the nearby reefs. Regarding fungiid species composition, reefs 1C and 1D show no visible impact with respect to sewage and possible pollution when compared to the more northward reefs (1A and 1B).

Table 3. The total number of fungiid species encountered in each of the 52 transects on the Spermonde shelf. The direction of transects around each of 13 investigated reefs (Fig. 2) is indicated.

Reef	Transect direction from reef centre							
	N	NW	W	SW	S	SE	ESE	E
1A	14		14				0	
1B	11		17		9			0
1C			14					14
1D			15		10			11
2A	27		28		21		13	0
2B	26		27		27		26	3
2C	23		25		25		22	7
2D			19					12
3A	32		31		31		22	5
3B			28					22
3C	23	32	30	31	31	27	27	0
4A	11		27		15			21
4B	14		21		10			16

Even inside Makassar Harbour (E-transects of reefs 1C and 1D) fungiids are abundantly present. There are also no clear indications that uninhabited reefs (1C, 2D, 3A, 4A) differ in species composition compared to the populated ones in the same shelf zone (Fig. 2).

**Indicator species.** — Classification of species assemblages and habitats by dominant species is a widely used approach in community ecology, which can be employed in the construction of strata or zones (Whittaker, 1975). It refers to the species occurring with the highest frequency of individuals (Greig-Smith, 1983). The dominant fungiid species (Table 4) contribute to the characterisation of the coral assemblages occurring on both hard and soft substrata (Fig. 7).

Shelf zone 1 showed little variation in dominant mushroom coral species (Table 4). *Polyphyllia talpina* was predominantly the most abundant species on the reef flats. *Lithophyllon scabra* was the dominant species on two reef flats and one slope. *Fungia fungites* was the most abundant species on three westward flats. *Pleuractis moluccensis* was the most abundant species on all reef bases inhabited by fungiids and on some of the reef slopes. Additional important species were *Lithophyllon repanda*, *Pleuractis paumotensis*, and *Herpolitha limax*. Whilst only seven species were dominant in the first zone, 13 species dominated habitats in the second shelf zone. *Fungia fungites* was the most abundant reef flat species in seven transects, followed by *Lithophyllon repanda* in two transects. *L. repanda* and *Pleuractis moluccensis* were the dominant reef slope species. This species was again the most abundant species on four reef bases, whereas *Cycloseris fragilis* and *C. sinensis* were dominant in two other sites. Shelf zone 3 showed some regularity in the composition of its most abundant species. *Fungia fungites* was dominant on seven transect flats and *Polyphyllia talpina* on two. *Lithophyllon repanda* was usually the most important species of the reef slopes. A total of five species dominated on the reef bases: *Cycloseris*

*fragilis*, *C. costulata*, *Pleuractis moluccensis*, *C. sinensis*, and *Herpolitha limax*. Zone 4 also showed little variation in its dominance patterns. *Fungia fungites* was dominant on most reef flats, *Lithophyllon repanda* on most reef slopes. The northern reef base of reef 4B was most densely covered by *C. sinensis* corals.

When the four shelf zones are compared, striking differences and similarities can be noticed (Table 4). *Lithophyllon scabra* was frequently the most abundant species in zone 1. More than in the other zones, *Polyphyllia talpina* was the most abundant species on the reef flats and *Pleuractis moluccensis* on the slopes, while the latter was also the most abundant species on the reef bases. In zones 2–4, *Fungia fungites* and *Lithophyllon repanda* were the most frequent dominators of the reef flats and the slopes, respectively. Three species were uniquely prevailing in zone 2, i.e., *Heliofungia fralinae* (N slope and base of reef 2C), *Pleuractis granulosa* (N slope of reef 2A) and *Heliofungia actiniformis* (W slope of reef 2D). Offshore reefs showed three dominant reef base species: *Cycloseris costulata*, *C. fragilis*, and *C. sinensis*. Within zones 2–4, especially on the reef flats, dominant species patterns around the southern reefs (2C, 3C, and 4B) showed more resemblance than those around the more northern reefs (2A, 3A, and 4A). Submerged reefs, 2D and 3B, showed a dominant species pattern that was abnormal within their respective shelf zones. Among the transects, those at the sheltered E and ESE sides were most exceptional in their dominance patterns, while some of the northern transects (e.g. those of reefs 2A, 2C and 3C) also showed relatively abnormal dominant species. Overall, the ten fungiid species most frequently counted were all represented by more than 1000 specimens in the total area surveyed (Table 1): (1) *Lithophyllon repanda*, (2) *Fungia fungites*, (3) *L. concinna*, (4) *Pleuractis paumotensis*, (5) *Ctenactis echinata*, (6) *Herpolitha limax*, (7) *P. moluccensis*, (8) *Danafungia scruposa*, (9) *D. horrida* and (10) *Cycloseris costulata*. This does not imply that all of these species were geographically the



Table 4. Dominant mushroom coral species on the reef flat (F), slope (S), and base (B) encountered in each of the 52 transects on the Spermonde shelf. The direction of the transects around each of the 13 investigated reefs is indicated (Fig. 2). Species are indicated by numbers as presented in Table 1. A dash represents no dominant species.

Reef	Zone	Transect direction from reef centre											
		N	NW	W	SW	S	SE	ESE	E				
1A	F	<i>P. talpina</i>		<i>P. paumotensis</i>									
	S	<i>F. fungites</i>		<i>L. repanda</i>									
	B	—		<i>P. moluccensis</i>									
1B	F	<i>P. talpina</i>		<i>F. fungites</i>									
	S	<i>H. limax</i>		<i>P. paumotensis</i>		<i>P. talpina</i>							
	B	<i>P. moluccensis</i>		<i>P. moluccensis</i>		<i>P. moluccensis</i>							<i>L. scabra</i> <i>P. moluccensis</i>
1C	F			<i>F. fungites</i>									
	S			<i>L. repanda</i>									
	B			—		<i>P. talpina</i>							<i>L. scabra</i>
1D	F			<i>F. fungites</i>									
	S			<i>P. moluccensis</i>		<i>P. talpina</i>							<i>L. scabra</i>
	B			<i>P. moluccensis</i>		<i>L. scabra</i>							
2A	F	<i>P. paumotensis</i>		<i>F. fungites</i>		<i>S. robusta</i>							
	S	<i>P. granulosa</i>		<i>L. repanda</i>		<i>P. moluccensis</i>		<i>P. talpina</i>					
	B	<i>C. sinensis</i>		<i>C. costulata</i>		<i>P. moluccensis</i>		<i>P. moluccensis</i>					
2B	F	<i>F. fungites</i>		<i>L. repanda</i>		<i>F. fungites</i>		<i>L. repanda</i>					
	S	<i>L. repanda</i>		<i>L. repanda</i>		<i>P. moluccensis</i>		<i>L. repanda</i>					
	B	<i>P. moluccensis</i>		<i>H. limax</i>		<i>C. sinensis</i>		—					<i>C. fragilis</i>
2C	F	<i>F. fungites</i>		<i>F. fungites</i>		<i>F. fungites</i>		<i>F. fungites</i>					
	S	<i>H. fralinae</i>		<i>L. repanda</i>		<i>P. paumotensis</i>		<i>L. repanda</i>					
	B	<i>H. fralinae</i>		<i>P. moluccensis</i>		<i>P. moluccensis</i>		—					<i>C. fragilis</i>
2D	F												
	S			<i>H. actiniformis</i>									<i>H. limax</i>
	B			—									
3A	F	<i>L. repanda</i>		<i>F. fungites</i>		<i>P. paumotensis</i>		<i>P. talpina</i>					<i>S. robusta</i>
	S	<i>L. repanda</i>		<i>L. repanda</i>		<i>L. repanda</i>		<i>L. repanda</i>					
	B	<i>P. moluccensis</i>		<i>C. fragilis</i>		<i>C. fragilis</i>		<i>C. costulata</i>					
3B	F												
	S			<i>L. concinna</i>									<i>P. moluccensis</i>
	B			<i>P. moluccensis</i>									
3C	F	<i>F. fungites</i>		<i>F. fungites</i>		<i>F. fungites</i>		<i>F. fungites</i>					
	S	<i>D. scruposa</i>		<i>L. repanda</i>		<i>L. repanda</i>		<i>L. repanda</i>					
	B	<i>H. limax</i>		<i>C. fragilis</i>		<i>C. sinensis</i>		<i>C. costulata</i>					
4A	F	<i>F. fungites</i>		—		<i>L. scutaria</i>		<i>L. repanda</i>					<i>F. fungites</i>
	S	—		<i>L. repanda</i>		<i>L. repanda</i>		—					<i>F. fungites</i>
	B	—		—		—		—					—
4B	F	<i>F. fungites</i>		—		<i>F. fungites</i>		<i>F. fungites</i>					<i>F. fungites</i>
	S	<i>L. repanda</i>		<i>L. repanda</i>		<i>L. repanda</i>		<i>L. repanda</i>					<i>C. tenuis</i>
	B	—		<i>L. repanda</i>		—		—					<i>C. sinensis</i>

Reef Zone	Transect direction								Substratum dominance ranks	
	N	NW	W	SW	S	SE	ESE	E		
1A	F	* ▲ ●		* ▲ ●			●			coral: * 1 * 2 * 3
	S	* ●		* ●			●			
	B	●		●			●			
1B	F	* ▲ ●		* ▲ ●		* ▲ ●			●	rubble: ▲ 1 ▲ 2 ▲ 3
	S	* ▲ ●		* ▲ ●		* ▲ ●			●	
	B	●		●		●			●	
1C	F			* ▲ ●					* ▲ ●	sand - silt: ● 1 ● 2 ● 3
	S			* ▲ ●					* ▲ ●	
	B			●					●	
1D	F			* ▲ ●		* ▲ ●			* ▲ ●	sand - silt: ● 1 ● 2 ● 3
	S			* ▲ ●		* ●			●	
	B			●		●			●	
2A	F	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	
	B	●		●		●		●	●	
2B	F	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	
	B	●		●		●		●	●	
2C	F	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	
	B	●		●		●		●	●	
2D	F									● 1 ● 2 ● 3
	S			* ▲ ●					* ▲ ●	
	B			●					●	
3A	F	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	* ▲ ●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●		* ▲ ●	●	
	B	●		▲ ●		●		●	●	
3B	F									● 1 ● 2 ● 3
	S			* ▲ ●					* ▲ ●	
	B			●					●	
3C	F	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	●	● 1 ● 2 ● 3
	S	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	* ▲ ●	●	
	B	●	▲ ●	●	●	●	●	●	●	
4A	F	* ▲ ●		* ▲ ●		* ▲ ●			* ▲ ●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●			* ▲ ●	
	B	●		●		●			●	
4B	F	* ▲ ●		* ▲ ●		* ▲ ●			* ▲ ●	● 1 ● 2 ● 3
	S	* ▲ ●		* ▲ ●		* ▲ ●			* ▲ ●	
	B	●		●		●			●	

Fig. 7. Substratum dominance order amongst coral (dead or alive), rubble and soft sediments on the flat (F), slope (S) and base (B) in each of the 52 examined reef transects (Fig. 2). The size of the symbols (coral, rubble, sand-silt) stands for the relative substratum dominance: the largest is the most important or the only substratum type available.

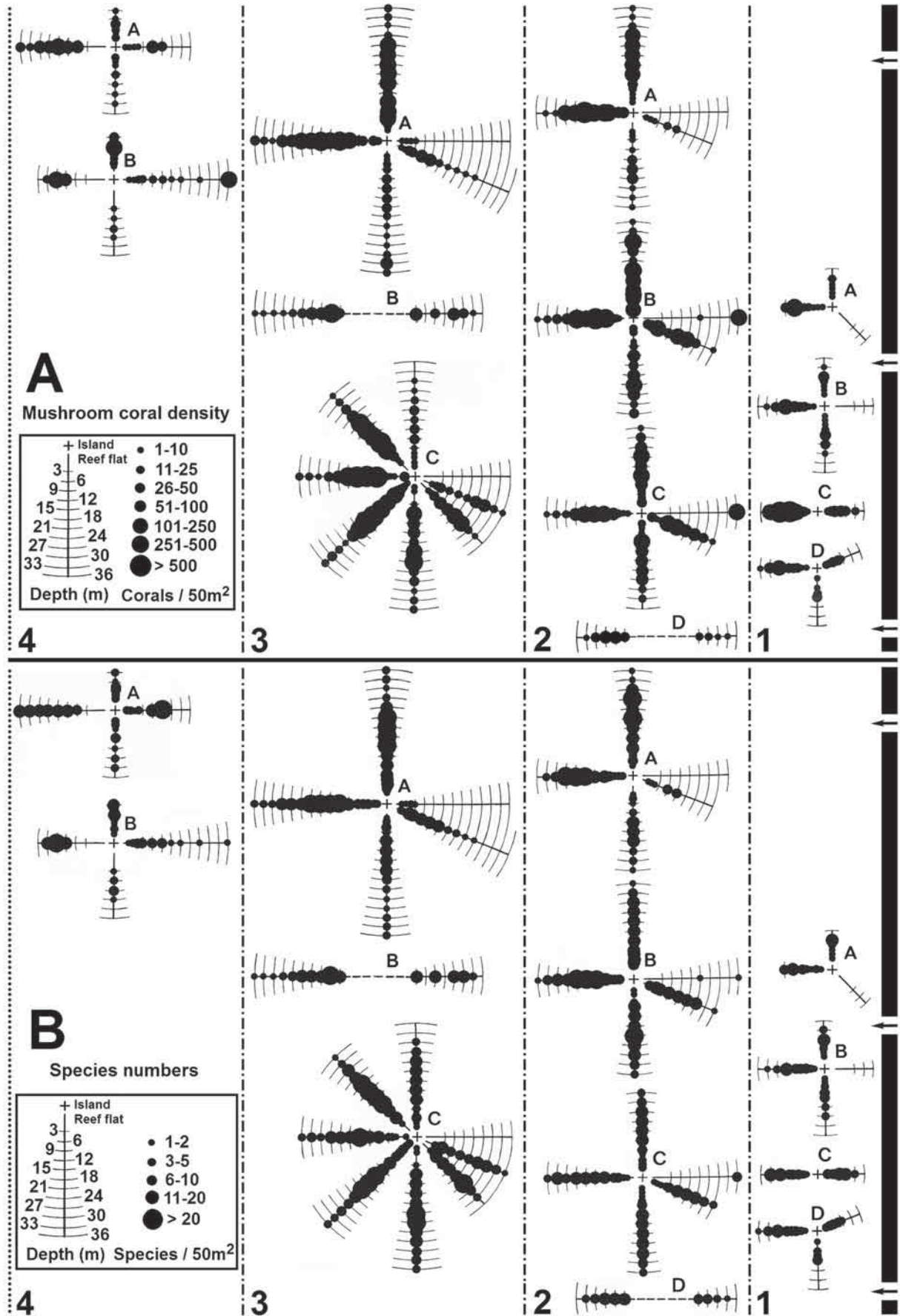


Fig. 8. Densities (A) and species richness (B) of mushroom corals indicated on isobathic projections of transects around 13 selected reefs on the Spermonde Shelf (Fig. 2). The depths ( $\geq 3$  m) of  $50 \times 1$  m<sup>2</sup> belt quadrats (SUs) are indicated around each reef (see legend). Three main river outlets are shown: the Maros (north), the Tello (central) and the Jeneberang (south). The position of Makassar city is east of reefs 1C and 1D.

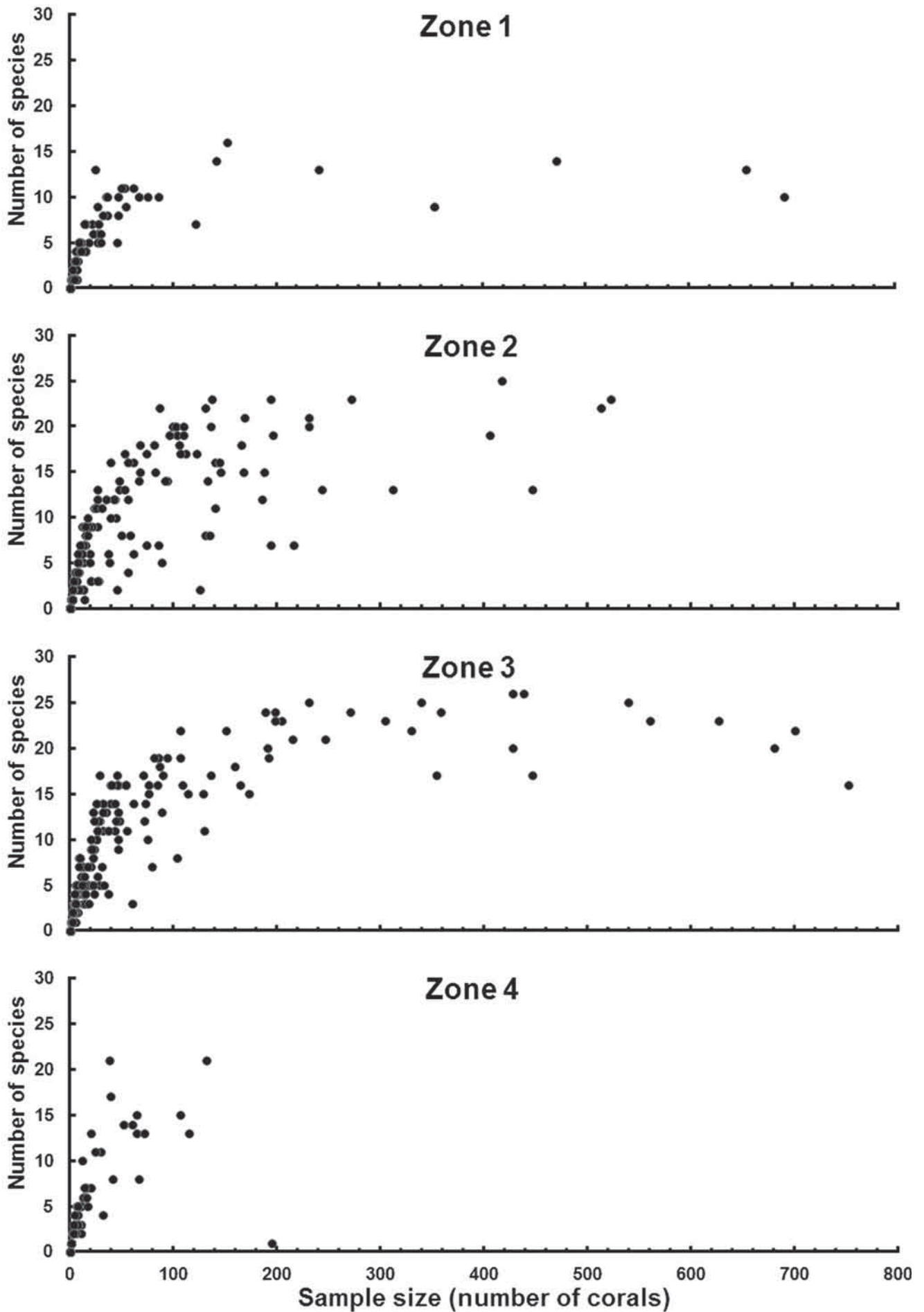


Fig. 9. Scatter diagrams of shelf zones 1–4 indicating mushroom coral sample sizes and number of species represented in 50 m<sup>2</sup> SUs.

most widely distributed over the Spermonde Shelf. Although they were observed on all 13 reefs, the ranking according to the number of transects in which they were found is different (Table 1): (1–3) *Herpolitha limax*, *Polyphyllia talpina*, and *Sandalolitha robusta*, (4) *Fungia fungites*, (5–6) *Lithophyllon repanda* and *Pleuractis paumotensis*, (7) *P. moluccensis*, and (8–12) *Ctenactis echinata*, *Danafungia horrida*, *D. scruposa*, *L. scabra*, and *Pleuractis granulosa*. Ranking according to the number of quadrats in which the species occurred (indicating an eurytopic, combined geographical and bathymetrical distribution) was different again (Table 1): (1) *Fungia fungites*, (2) *Herpolitha limax*, (3) *Lithophyllon repanda*, (4) *Pleuractis paumotensis*, (5) *Sandalolitha robusta*, (6–7) *Danafungia horrida* and *Polyphyllia talpina*, (8) *Cycloseris tenuis*, (9) *Danafungia scruposa*, and (10) *Pleuractis moluccensis*. Two of the most frequently counted species, *Ctenactis echinata* and *Lithophyllon concinna* (see above), are not listed here, which indicates that they had a clustered, stenotopic distribution.

**Reef fauna.** — The clustering according to species composition (Table 2) reflects the spatial arrangement of the reefs in the four shelf zones (Fig. 11). Some reefs had identical species compositions and were therefore clustered together (reefs 1A and 1D, reefs 2B and 3B). The reefs in zone 1 were most

similar in species composition, and were therefore grouped together. The N–S arrangement of the reefs (1A to 1D) is not reflected in the diagram. Reefs 2A and 2B with 3B displayed resemblance in fungiid fauna, whereas these reefs together were most affiliated with reef 2C. Within zone 3, reefs 3A and 3C were most similar in species composition. Each of the reefs of the outer rim (zone 4) was arranged separately in the dendrogram. It is striking that within shelf zones 2 and 3, the submerged reefs 2D and 3B were most dissimilar from the rest with respect to mushroom coral fauna.

The difference in fungiid species richness between onshore zone 1 and offshore zones 2–4, is partly reflected by the absence of deep-living *Cycloseris* species in zone 1, which are almost restricted to the reef bases (Tables 2, 4). The small difference in species number between zones 2 and 3 (Table 2) is related to the presence of some uncommon species in zone 3, such as *Cycloseris distorta*, *Halomitra clavator*, *Lithophyllon spinifer*, *Podabacia motuporensis*, and *Zoopilus echinatus*.

**Depth ranges.** — Most mushroom coral species had restricted depth ranges and did not occur over the complete depth gradient, as demonstrated by abundant species like *Ctenactis echinata*, *Fungia fungites*, *Lithophyllon concinna*, *L. repanda*, and *Pleuractis paumotensis* (Figs. 14, 26, 31, 32, 40). Some species occurring in all shelf zones appeared to shift to greater depths in offshore direction. like *P. moluccensis* (Fig. 39). On reefs with the deepest mushroom coral assemblages (zone 3), deep-living *Cycloseris* species were usually restricted to sandy substrates of the reef base, (Figs. 12, 18, 20, 21, 23), where they co-occurred with other free-living species, such as three *Heterocyathus* species and one *Heteropsammia* (Hoeksema & Best, 1991). Species with predominantly shallow distribution ranges were remarkably less abundant on reef slopes of submerged reefs. *Fungia fungites* showed relatively low densities at the westward slopes of submerged reefs 2D and 3B, where they lack shallow substrate for larval settlement, as compared to adjacent reefs in the same shelf zones (Fig. 26). Similar patterns were presented by several other species, like *Danafungia horrida*, *D. scruposa*, *Halomitra pileus*, *Lithophyllon concinna*, *L. repanda*, and *Lobactis scutaria* (Figs. 24, 25, 27, 31, 32, 36).

## DISCUSSION

**Taxonomic issues.** — The species were originally classified according to a taxonomic revision of the Fungiidae (Hoeksema, 1989), which was unpublished at the time of the survey. The present data was presented in a PhD thesis using that classification (Hoeksema, 1990). The advent of a new taxonomy based on a molecular analysis enables, for the first time, an interpretation of species distributions within the context of phylogenetic relations between fungiid species and to address problems raised in the earlier analysis (Hoeksema, 1990). For example, a molecular analysis revealed that two ecomorphs of *Cycloseris costulata* observed in the Spermonde Archipelago (Hoeksema, 1990) and other Indonesian localities (Hoeksema & Moka, 1989) belong to the same species, and that *C. costulata* is clearly distinct from the morphologically similar species *C. tenuis* (Gittenberger & Hoeksema, 2006), which co-occurred

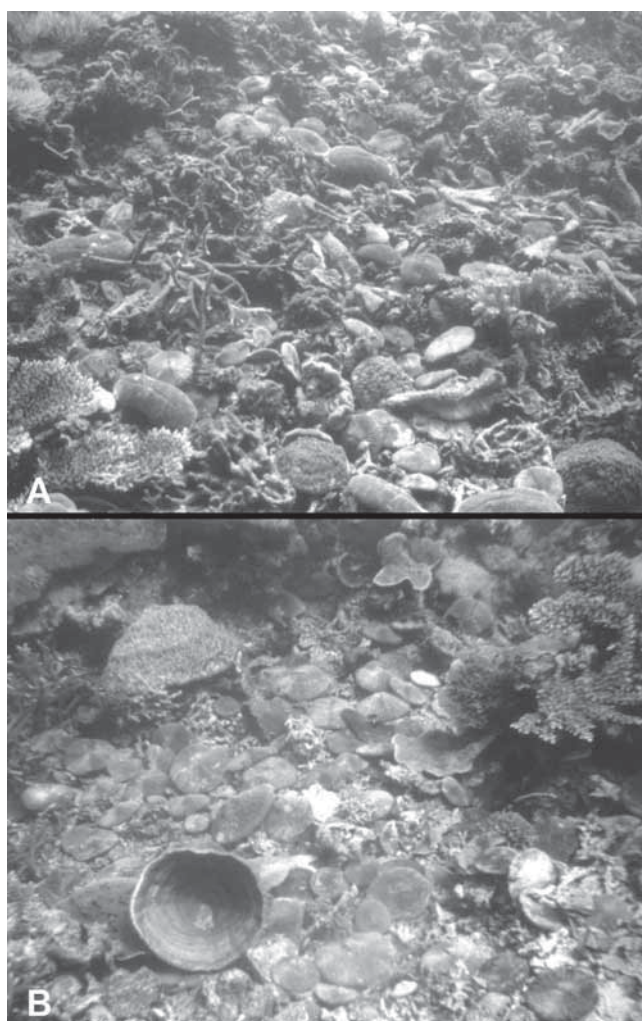


Fig. 10. Westward slope of reef 3C (Kudingareng Keke, May 28, 1986) with dense multi-species assemblage of mushroom corals mixed with coral fragments at 12 m (A) and 15 m depth (B).

commonly with *C. costulata* in shelf zones 2 and 3 (Fig. 12). Two species were excluded from the present analysis because they had not yet been formally recognised as fungiids at the time of the fieldwork, i.e., *Psammocora explanulata* Van der Horst, 1922, and *Coscinaraea wellsi* Veron & Pichon, 1980 (see Benzoni et al., 2007, in press). When the survey was conducted, specimens of both species were considered to belong to the Siderastreidae and as such were not recorded.

**Sampling design.** – The disadvantage of the belt quadrat method, compared to other benthic assessment methods, is that it is much more time consuming, whereas the time that can be spent per dive is limited (Loya, 1972, 1978). The advantage of its use is that it supplies direct information about species abundances, and that is why it appears to be more accurate than other methods (Weinberg, 1981; Dodge et al., 1982; Mingoa & Menez, 1988). In contrast to the line transect method,

which is currently much in use for estimating coral cover, the belt quadrat method is more suitable for counting individuals because it does not discriminate against the smallest corals. Due to their small surface areas, juvenile corals are easily missed by line transects (Marsh et al., 1984: Fig. 1). This is a serious shortcoming for the Fungiidae, in which individuals of most species are usually small in relation to other reef corals. Moreover, among the Fungiidae there are also great interspecific differences in maximum dimensions (Hoeksema, 1989, 1991a). By counting individuals within quadrats, one is less likely to overlook the smaller sized recruits, be they hidden underneath or between other corals or attached to an open substratum surface. Corals laying one on top of another are given equal weight in the counting. To minimise underwater time, a minimal area had to be determined for which a homogeneous sample plot should be selected (Scheer, 1978). However, homogeneity is not guaranteed for long strips of reef bottom parallel to isobaths

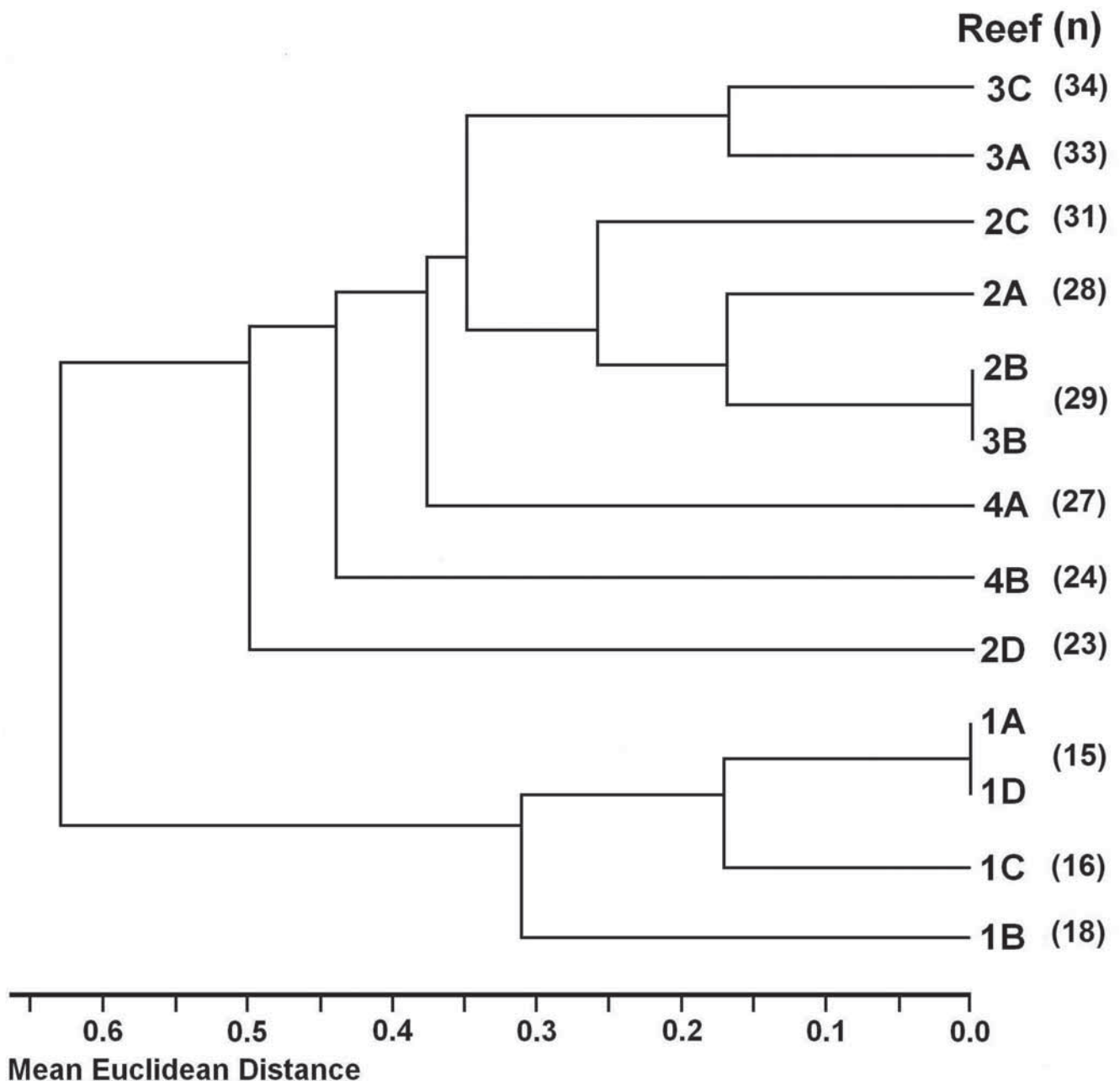


Fig. 11. UPGMA-dendrogram showing relations between the 13 surveyed reefs (Fig. 2) with respect to the fungioid species composition observed in the transects (Table 2). The species numbers (n) are given behind each reef (coded 1A-4B).

except at the sandy reef bases. Because representative and comparable transect data is needed, a minimum viable sample area is of little use, the more so since a maximum amount of information about rare species and sedentary recruits also had to be collected. Therefore, a greater than minimal area size was chosen, the  $50 \times 1 \text{ m}^2$  quadrat, which appeared fairly manageable in the available time underwater.

**Nearshore assemblages.** — Based on the present results on the spatial distribution of mushroom corals on the Spermonde Shelf, various species assemblages could be distinguished that were associated with three habitats: nearshore reefs, midshelf reefs, and the outer barrier reefs. The fungiid reef faunas in the near-shore reefs (zone 1) of are distinct from the rest (Fig. 11). Reefs in zone 1 are relatively shallow (deepest SU at 15 m) and the surrounding sea floor consists of fine sediment. Their fungiids are not nearshore specialists, but rather a subset of relatively few species ( $n = 19$ ) that are widely distributed across the shelf (Table 2). A similar observation with respect to the depauperation of the fungiid fauna with increasing terrigenous and fluvial influence was made in Bima Bay, Sumbawa (Hoeksema & Moka, 1989). These species can probably tolerate much sedimentation, relatively low salinity and poor illumination resulting from freshwater discharge and terrigenous runoff. Some common species, like *Lithophyllon scabra*, *Herpolitha limax*, *Pleuroactis paumotensis*, and *Polyphyllia talpina*, showed relatively high densities near the shore, reflected in their dominance in several reef zones (Table 4). Perhaps fungiids in the first zone benefit from primary and secondary production as a result of nutrient enrichment. Fluvial discharge and land-based pollution may cause eutrophication and stimulate organic production in tropical marine ecosystems, and near-shore reefs in particular (Skreslet, 1986; Edinger et al., 1998; Sawall et al., 2011). The high abundance of fungiids close to and inside Makassar Harbour and adjacent to heavily populated islands suggests that there is no visible effect of eutrophication in harbour and nearshore waters from discharges from the city and island populations.

**Mid-shelf assemblages.** — Species with more off-shore biased distributions are best represented in zone 3, and to a minor degree in zone 2. The sea floor surrounding the reefs in zones 2–3 is relatively deep, resulting in reef slopes and reef bases with the highest maximum depth limits (Fig. 3). The relatively clear water (remote from river discharge), the large depth gradient, low eutrophication, and moderate wave exposure (Fig. 3) may enable the occurrence of coral species that prefer oceanic conditions on the reefs here. For example deep-living *Cycloseris* species and *Lithophyllon spinifer* (absent in zone 1) are mostly restricted to the reef bases ( $> 20 \text{ m}$  deep) of zones 2–3 (Tables 2, 4). In zone 1, those depths do not exist and therefore species with predominant deep offshore distributions are most common in zones 2–3. *Halomitra clavator* and *Zoopilus echinatus* are examples of the largest free-living species known and they were only found on the most offshore mid-shelf reef slopes (zone 3). They are most common in clear water on exposed reef slopes with little sediment accumulation. Both species are also relatively thin and fragile and occur on the lower reef slopes, below the reach of wave action, a habitat that is most common in the more oceanic, offshore conditions of zone 3.

Zone 4 does not have such reef slopes, because its westernmost edge is too wind exposed and too close to the vertical Makassar Strait drop-off (Fig. 1).

**Barrier reef assemblages.** — Reefs in Shelf zone 4 were less rich in species than those in zone 3 because they sit upon a shallow sand ridge, the barrier. The sandy shallow reef bases at the N and S sides, as well as the sandy slopes at the E sides in zone 4 (Fig. 7) showed little or no coral cover. The absence of some mushroom coral species may be as a result of a high silt load. Upwelling during the southeast monsoon (Ilahude, 1978) and wave action during the northwest monsoon (Van der Stok, 1922) have most impact at the outer rim of the shelf (zone 4). The upwelling has a positive effect on primary production, and together with wave action it favours the abundant growth of calcareous algae at the exposed reef flats in zone 4 (De Nève, 1982). Calcareous algae belonging to *Halimeda* (Chlorophyceae) are also relatively abundant in oceanic environments (Drew, 1983). The physical breakdown of *Halimeda* segments produces aragonite dust (Folk & Robles, 1964; Orme, 1977; Drew, 1983), which, like the silt discharged by rivers, may exclude some species and/or hinder coral growth. Moll (1983) also found no distinct interzonal differences in scleractinian species composition overall between shelf zones 2 and 3, but there were differences between the outermost reefs (zone 4) rim and zones 2–3.

**Circum-reef distribution.** — Wave action appeared to have much influence on circum-reef mushroom coral distribution patterns. The westward sides of the Spermonde reefs showed the highest coral densities and species diversity (Fig. 8) and were generally also the most exposed to high wave energy (Fig. 4), whereas their sheltered eastward sides were under heavier sedimentation stress (Fig. 7). The relatively low abundance and richness and shallower depth range of fungiids in E and ESE transects were mainly due to the less solid bottom structure here (Fig. 4) and the accumulation of sand underneath the slopes. Some species, such as *Lithophyllon scabra* (Fig. 33) and *Cycloseris tenuis* (Fig. 22), were able to occur abundantly on the ESE-flats and upper slopes, whereas *Cycloseris fragilis* and *C. sinensis* had their highest densities on the eastward reef bases (Figs. 18, 20). The presence or absence of a sand cay seems to exert an important influence on the fungiid fauna. On both shoals 2B and 3D, the E transect was richer in species than in other reefs in the same shelf zones (Fig. 8). Corals in the E transect of reefs without cays exist in a lower sedimentation regime than nearby reefs with cays. The breakwaters on the two southernmost reefs in zone 1 (Fig. 5) probably protected the mushroom corals at the eastern sides against excessive sediment inflow from the flats (Fig. 7) because they hindered waves over and around the reefs. On the western reef flats in shelf zone 4 the wave impact may be too strong for mushroom coral occurrence (Fig. 8). Tidal currents may alter in direction but the predominant current direction in the Makassar Strait is from north to south and moderately constant during the year (Van der Stok, 1922; Soekarno, 1989). During the surveys these currents were noticed at the west and east sides of the reefs, but they did not have a clear impact on the circum-reef distribution patterns of mushroom coral species.

**Bathymetric distribution ranges.** — Mushroom corals clearly showed much interspecific variation in depth ranges. Reef coral zonation and diversity can be related to four stress factors: (1) diminishing light, (2) wave action, (3) sedimentation and (4) subaerial exposure (Chappell, 1980; Sheppard, 1982; Done, 1983b). Light intensity decreases with depth, especially at sites with much sediment suspension. Fricke & Schuhmacher (1983) recorded free-living fungiids from down to 100 m depth in the clear water of the Red Sea and Wells (1966) even reported a maximum depth of 120 m for *Cycloseris* without specified locality.

The suspended sediment load and light obstruction on the Spermonde Shelf decreases with increasing distance offshore, while the lower depth limit of most fungiid species also shifts downwards (together with that of scleractinians supplying hard substratum surface for juvenile mushroom corals). Therefore, the deepest limit of several mushroom coral species offshore is greater than onshore, where the sea floor is less deep and water is more turbid, hindering coral growth. This may be reflected in the preferred settlement depths of planula larvae regarding orientation and obscurity of settlement sites (compare Bak & Engel, 1979; Birkeland et al., 1981; Van Moorsel, 1989). Abe (1937) observed the swimming behaviour of *Heliofungia actiniformis* larvae and found that the majority of the planulae eventually displayed negative phototactic swimming behaviour. It is likely that the Fungiidae have different preferences regarding light conditions during settlement (Hoeksema, 1990), which may explain the diversification in species depth ranges in offshore direction.

Sediment that has settled on the reef bottom may become resuspended during storms. At the windward slopes, wave stress decreases with increasing depth. At the leeward east sides, sediment accumulation is high over the whole depth range (Fig. 7; Hoeksema, 1990) and the reef base is less deep than at the wind-exposed west sides (Fig. 3). This may explain why mushroom corals were less densely distributed and showed the shallowest maximum bathymetric range limits at the sheltered eastward sides of the reefs. Subaerial exposure during extreme low tides may affect mushroom corals in the shallowest reef zones, where they may be exposed to heat or to rain (Glynn, 1976; Chappell, 1980). Fungiid species richness is generally low here. *Fungia fungites* (Fig. 26) is an example of a species that may adapt to heat. During periods of elevated seawater temperatures, individuals on reef flats appeared relatively less affected by coral bleaching than those on the reef slopes (Hoeksema, 1991b; Hoeksema & Matthews, 2011).

Free-living fungiids may depend for a great part on waves and gravity for their downward dispersal (Hoeksema, 1988). Bak & Povel (1989), who studied physiognomic-structural attributes of Indonesian reefs, found fungiids to be closely related with structural reef variables, such as rubble, sediment/rubble and the abundance of loose coral fragments. Apparently free-living corals are closely associated with loose bottom elements (Hoeksema, 1988). Rubble avalanches were mostly observed on exposed upper reef slopes in the Spermonde Archipelago (Hoeksema, 1990). The impact of avalanching on coral zonation is mainly visible at these reef parts (see also Dollar, 1982).

Above the slopes, free-living fungiids can be swept away together with the rubble (Hoeksema, 1988), which may explain why some species show discontinuous depth ranges in some transects (e.g., *Fungia fungites*; Fig. 26).

While coral assemblage on the windward upper slopes may be most affected by wave action, sediment movement is considered a controlling factor on the lower slopes and below (Bak, 1977; Bak & Luckhurst, 1980; Sheppard, 1982; Done, 1983b). Some fungiid species are distinctly associated with soft substrata, such as most of the *Cycloseris* species and *Pleuractis moluccensis*. Some fungiids are known to show cleaning reactions after being covered by sediment (Marshall & Orr, 1931; Abe, 1939; Hubbard, 1972; Hubbard & Pocock, 1972; Gill & Coates, 1976; Schuhmacher, 1977, 1979; Bongaerts et al., 2012). Specimens of *P. moluccensis* may survive partial burial because of their protruding mouth (Schuhmacher, 1979). Corals of some *Cycloseris* species on the sandy reef bases can survive burial because of their domed shape or humped oral surface (Hoeksema & Moka, 1989), their mobility (Hubbard, 1972), or their capability of fragmentation (see below).

**Habitat heterogeneity of shelf-based coral reefs.** — Substantial environmental differences exist with regard to the physiography of coral reefs across tropical continental shelves (Hopley, 1982; De Klerk, 1983). More oceanic, peripheral habitats on a shelf differ physically and biologically from inshore habitats (Done, 1982) and together they provide a shelf-based coral reef system with much habitat diversity. The three major spatial units that are distinguished to study the environmental conditions considered important in fungiid distribution patterns over the Spermonde Shelf appear to be very much inter-related: bathymetric ranges vary around reefs depending on wave exposure whereas circum-reef distribution patterns vary with distance offshore. Although the central part of the Spermonde Shelf is only 40 km wide, it shows very similar cross-shelf species richness patterns with the Great Barrier Reef together with some reefs in Coral Sea, constituting a ca. 200 km onshore–offshore gradient. The faunas most onshore and most offshore of the GBR are usually depauperate compared to mid-shelf reefs; selected taxa for the comparisons have been taken from e.g. crustaceans (Preston & Doherty, 1990, 1994), fish (Williams, 1982; Williams & Hatcher, 1983; Russ, 1984), stony corals (Done, 1982, 1983a, 1983b; DeVantier et al., 2006), soft corals (Dinesen, 1983; Fabricius & De'ath, 2001), and sponges (Wilkinson & Trott, 1985). In the Spermonde Archipelago similar trends have been observed regarding species diversity in stony corals (Moll, 1983; Hoeksema, 1990) seaweeds (Verheij & Prud'homme van Reine, 1993), benthic foraminifera (Troelstra et al., 1996; Renema et al., 2001), sponges (De Voogd et al., 1999, 2006), echinoids (De Beer, 1990), multi-taxa assemblages (Cleary et al., 2005; Becking et al., 2006), and in morphotypes of sea anemones (Hoeksema & Crowther, 2011). On the 5 km wide shelf of Madang lagoon, Papua New Guinea, in the Bismarck Sea (36 species, 24 sites), there was a difference in species richness of Fungiidae between onshore (19 species) and offshore zones (28–29 species), but a distinctly richer mid-shelf zone could not be discerned. This pattern may be related to Madang's narrow shelf width (Hoeksema, 1993).



Foraminiferans showed a clearer cross-shelf zonation here (Langer & Lipps, 2003).

**Mushroom coral aggregations.** — Mushroom corals are able to cover large areas in high densities and dominate certain reef zones, especially reef bases but also shallower zones (Goreau & Yonge, 1968; Fisk, 1983; Hoeksema, 2004a; Hoeksema & Gittenberger, 2010; Hoeksema & Matthews, 2011). Because of their free mode of life, mushroom corals are perfect pioneers on soft substrates that cannot be inhabited by many other coral species. They are important for reef building, because their dead skeletons can serve as substrate for other corals to settle on, making soft substrates more inhabitable and suitable for colonization by other species, which may eventually help to increase reef surface area (Sheppard, 1981). On the Spermonde Shelf, some mushroom coral species showed aberrantly high density aggregations because of asexual reproduction by budding or fragmentation. Various mushroom coral species have incorporated fragmentation in their life histories and are therefore considered to be among the most successful coral species (Highsmith, 1982). Unattached fragments may undergo sessile dispersal over the reef bottom and spread the risk of mortality (Jackson, 1986). Well-documented examples of budding concern *Fungia fungites* (Boschma 1992, 1923a, 1923b; Hoeksema, 1989; Gilmour 2002, 2004a, 2004b; Hoeksema & Yeemin, 2011), *Heliofungia actiniformis* (Boschma 1992, 1923b; Hoeksema, 1989; Knittweis et al., 2009a), *H. fralinae* (Hoeksema, 2004a), and *Lobactis scutaria* (Krupp et al., 1992; Jokiel & Bigger, 1994; Kramarsky & Loya, 1996). Except for *L. scutaria*, these species also showed budding in the Spermonde Archipelago (Hoeksema, 1990; Knittweis et al., 2009b). *Heliofungia fralinae* showed high concentrations on the northern slope of reef 2C (Fig. 29), with many attached polyps attached to parent animals and many loose specimens around them (see Hoeksema, 2004a). After detachment and release, the larger corals apparently dispersed and had shifted or tumbled downward over the reef slope (cf. Hoeksema, 1988). A similar avalanche of corals of the same species was observed (outside transects) on the southwestern slope of the same reef. *F. fungites* occurred in high densities on reef flats (Fig. 26), which may result from sexual reproduction, after which the empty stalks regenerate asexually derived buds (Hoeksema & Yeemin, 2011). *Cycloseris fragilis* and *C. sinensis* were the only two species that used autotomy (self-fragmentation) to form aggregations on sandy reef bases (Figs. 18, 20). The impact of fragmentation and regeneration of mushroom coral fragments is well-known for *Cycloseris* species showing autotomy (Wells, 1966; Goreau & Yonge, 1969; Hoeksema, 1989; Fisk, 1983; Nishihira & Pong-In, 1989; Yamashiro et al., 1989; Yamashiro & Nishihira 1994, 1998; Colley et al., 2002; Hoeksema & Waheed, 2011). Mushroom coral species with large, thin skeletons, such as *Halomitra clavator*, *H. pileus*, and *Zoopilus echinata*, may also show high densities as a result of fragmentation (Pichon, 1974; Littler et al., 1997; Hoeksema & Gittenberger, 2010). This was not observed in the quadrats on the Spermonde Shelf, but occasionally regenerated fragments of these species were encountered outside transects, especially on westward (wave-exposed) reef slopes.

**Human impact.** — The proximity of a large city and the dense human populations on some of the islands may have impact on the coral fauna of the Spermonde reefs, as for instance on the reefs near Jakarta (Cleary et al., 2006, 2008). In shelf zones 2–4 reef dynamite blasting is a very popular fishing technique (Pet-Soede et al., 1999, 2001; Hoeksema, 2004b). Although its damage to the reefs may be considerable, it is expected to have little effect on fungiid species compositions. The blast craters occur mostly random near the reef edges (3–9 m depth). Mushroom corals are blown away or broken in pieces but may still survive the blasts. They are also usually the first corals to reoccupy the vacated substrate (Hoeksema, unpublished). Another anthropogenic disturbance to mushroom coral populations in the Spermonde Archipelago consists of coral harvesting for the aquarium industry. *Heliofungia actiniformis* appears to be one of the most popular species here and its population may be overexploited (Knittweis et al., 2009b; Knittweis & Wolff, 2010). At the time of the field survey for the present study (1984–1986), there were no signs of *H. actiniformis* fishing. The proximity of a large port and an airport may facilitate international aquarium trade and therefore also the overharvesting of mushroom corals.

In the 1990s, dams were constructed in the Jeneberang river and its delta to prevent flooding in Makassar city, which has restricted the flow of its discharge and likely also the transport of silt toward the nearshore reefs. This may have affected the coral fauna here. Historical coral collections may help to determine whether the proximity of large cities may have a negative effect on reef coral faunas over long time periods, as observed at Singapore and in the Bay of Jakarta (Hoeksema & Koh, 2009; Van der Meij et al., 2009, 2010; Hoeksema et al., 2011). Likewise, repetition of the surveys in the future may indicate whether mushroom corals assemblages on the Spermonde Shelf have changed over time.

**Prospects.** — The present study serves as a basis for consecutive studies on fungiid spatial distribution patterns on the Spermonde Shelf, for instance in relation to their recruitment or their associated fauna (see Hoeksema et al., 2012). Use of a phylogenetic reconstruction of the Fungiidae (Gittenberger et al., 2011) in interspecific comparisons of their distribution patterns will help to understand their ecological differentiation along environmental gradients (Hoeksema, *subm.*). The present results may also explain why mushroom coral species are present or absent in certain areas. This may form a factor in determining the geographic distribution ranges of mushroom corals, which predominantly overlap in the centre of maximum marine biodiversity, the so-called Coral Triangle (Hoeksema, 2007). Such factors may eventually be relevant for the conservation of corals, although mushroom corals are generally not among the most endangered species (Carpenter et al., 2008).

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### LITERATURE CITED

- Abe, N., 1937. Post-larval development of the coral *Fungia actiniformis* var. *palawensis* Döderlein. *Palao Tropical Biological Station Studies*, **1**: 73–93.
- Abe, N., 1939. Migration and righting reaction of the coral, *Fungia actiniformis* var. *palawensis* Döderlein. *Palao Tropical Biological Station Studies*, **4**: 671–694.
- Bak, R. P. M., 1977. Coral reefs and their zonation in Netherlands Antilles. *Studies in Geology*, **4**: 3–16.
- Bak, R. P. M. & M. S. Engel, 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology*, **54**: 341–352.
- Bak, R. P. M. & B. E. Luckhurst, 1980. Constancy and change in coral reef habitats along depth gradients at Curaçao. *Oecologia*, **47**: 145–155.
- Bak, R. P. M. & G. D. E. Povel, 1989. Ecological variables, including physiognomic- structural attributes, and classification of Indonesian coral reefs. *Netherlands Journal of Sea Research*, **23**: 95–106.
- Becking, L. E., D. F. R. Cleary, N. J. de Voogd, W. Renema, M. de Beer, R. W. M. van Soest & B. W. Hoeksema, 2006. Beta-diversity of tropical marine assemblages in the Spermonde Archipelago, Indonesia. *Marine Ecology*, **27**: 76–88.
- Benzoni, F., F. Stefani, J. Stolarski, M. Pichon, G. Mittra & P. Galli, 2007. Debating phylogenetic relationships of the scleractinian *Psammocora*: molecular and morphological evidences. *Contributions to Zoology*, **76**: 35–54.
- Benzoni, F., R. Arrigoni, F. Stefani, B. T. Reijnen, S. Montano & B. W. Hoeksema, in press. Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): Lost mushroom corals find their way home. *Contributions to Zoology*.
- Birkeland, C., D. Rowley & R. H. Randall, 1981. Coral recruitment patterns at Guam. *Proceedings of the 4th International Coral Reef Symposium, Manila*, **2**: 339–344.
- Bongaerts, P., B. W. Hoeksema, K. B. Hay & O. Hoegh-Guldberg, 2012. Mushroom corals overcome live burial through pulsed inflation. *Coral Reefs*, doi 10.1007/s00338-011-0862-z.
- Boschma, H., 1922. On budding and coalescence of buds in *Fungia fungites* and *Fungia actiniformis*. *Proceedings Koninklijke Nederlandse Akademie voor Wetenschappen, Amsterdam*, **24**: 257–268.
- Boschma, H., 1923a. Experimental budding in *Fungia fungites*. *Proceedings Koninklijke Nederlandse Akademie voor Wetenschappen, Amsterdam*, **26**: 88–96.
- Boschma, H., 1923b. Knospung und verwandte Erscheinungen bei *Fungia fungites* und *Fungia actiniformis*. *Treubia*, **3**: 149–179.
- Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzmán, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, E. Wood, 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, **321**: 560–563.
- Chadwick, N. E., 1988. Competition and locomotion in a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology*, **123**: 189–200.
- Chadwick-Furman, N. E. Y. Loya, 1992. Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. *Marine Biology*, **114**: 617–623.
- Chappell, J., 1980. Coral morphology, diversity and growth. *Nature*, **286**: 249–252.
- Claereboudt, M., 1988. Spatial distribution of fungiid coral population on exposed and sheltered reef slopes in Papua New Guinea. *Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia*, **2**: 715–720.
- Cleary, D. F. R., L. E. Becking, N. J. de Voogd, W. Renema, M. de Beer, R. W. M. van Soest & B. W. Hoeksema, 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. *Estuarine Coastal and Shelf Science*, **65**: 557–570.
- Cleary, D. F. R., Suharsono & B. W. Hoeksema, 2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. *Biodiversity and Conservation*, **15**: 3653–3674.
- Cleary, D. F. R., L. DeVantier, Giyanto, L. Vail, P. Manto, N. J. de Voogd, P. G. Rachello-Dolmen, Y. Tuti, A. Budiyanto, J. Wolstenholme, B. W. Hoeksema & Suharsono, 2008. Relating variation in species composition to environmental variables: a multi-taxon study in an Indonesian coral reef complex. *Aquatic Sciences*, **70**: 419–431.
- Colley, S. B., J. S. Feingold, J. Peña & P. W. Glynn, 2002. Reproductive ecology of *Diasteris distorta* (Michelin) (Fungiidae) in the Galápagos Islands, Ecuador. *Proceedings of the 9th International Coral Reef Symposium, Bali*, **1**: 373–379.
- Cornils, A., J. Schulz, P. Schmitt, M. Lanuru, C. Richter & S. B. Schnack-Schiel, 2011. Mesozooplankton distribution in the Spermonde Archipelago (Indonesia, Sulawesi) with special reference to the Calanoida (Copepoda). *Deep-Sea Research II*, **57**: 2076–2088.
- De Beer, M., 1990. Distribution patterns of regular sea urchins (Echinodermata: Echinoidea) across the Spermonde Shelf, SW Sulawesi (Indonesia). In: De Ridder, C., P. Dubois, M. C. Lahaye & M. Jangoux (eds.), *Echinoderm Research*. Balkema, Rotterdam. Pp. 165–169.
- De Klerk, L. G., 1983. Zeespiegels, riffen en kustvlakten in Zuidwest Sulawesi, Indonesië: een morphogenetisch-bodemkundige studie. *Utrechtse Geografische Studies*, **27**: 1–172.

- De Nève, G. A., 1982. Development and origin of the Sangkarang Reef Archipelago (South Sulawesi, Indonesia). *Proceedings 10th Annual Convention of the Indonesian Association of Geologists, Bandung*. Pp. 102–107, maps 1–5.
- DeVantier, L., G. De'ath, T. Done, E. Turak & K. Fabricius, 2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. *Coral Reefs*, **25**: 329–340.
- De Voogd, N. J., R. W. M. van Soest & B. W. Hoeksema, 1999. Cross-shelf distribution of SW Sulawesi reef sponges. *Memoirs of the Queensland Museum*, **44**: 147–154.
- De Voogd, N. J., D. F. R. Cleary, B. W. Hoeksema, A. Noor & R. W. M. van Soest, 2006. Sponge beta diversity in the Spermonde Archipelago, Indonesia. *Marine Ecology Progress Series*, **309**: 131–142.
- Dinesen, Z. D., 1983. Patterns in the distribution of soft corals across the Central Great Barrier Reef. *Coral Reefs*, **1**: 229–236.
- Dodge, R. E., A. Logan & A. Antonius, 1982. Quantitative reef assessment studies in Bermuda: A comparison of methods and preliminary results. *Bulletin of Marine Science*, **32**: 745–760.
- Dollar, S. J., 1982. Wave stress and coral community structure in Hawaii. *Coral Reefs*, **1**: 71–81.
- Done, T. J., 1982. Patterns in the distribution of coral communities across the Central Great Barrier Reef. *Coral Reefs*, **1**: 95–107.
- Done, T. J., 1983a. The distributions of coral communities on the Great Barrier Reef. In: Baker, J. T., R. M. Carter, P. W. Sammarco & K. P. Stark (eds.), *Proceedings of the Inaugural Great Barrier Reef Conference, Townsville*. James Cook University Press, Townsville. Pp. 83–88.
- Done, T. J., 1983b. Coral zonation: Its nature and significance. In: Barnes, D.J., (ed.), *Perspectives on Coral Reefs*. Manuka, Clouston Publisher, Manuka. Pp. 107–147.
- Drew, E. A., 1983. *Halimeda* biomass, growth rates and sediment generation on reefs in the Central Great Barrier Reef Province. *Coral Reefs*, **2**: 101–110.
- Edinger, E. N., J. Jompa, G. V. Limmon, W. Widjatmoko & M. J. Risk, 1998. Reef degradation and coral biodiversity in Indonesia: Effects of land based pollution, destructive fishing practices and changes over time. *Marine Pollution Bulletin*, **36**: 617–630.
- Elahi, R., 2008. Effects of aggregation and species identity on the growth and behavior of mushroom corals. *Coral Reefs*, **27**: 881–885.
- Fabricius, K. E. & G. De'ath, 2001. Biodiversity on the Great Barrier Reef: Large-scale patterns and turbidity-related local loss of soft coral taxa. In: Wolanski, E. (ed.), *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef*. CRC Press, London. Pp. 127–144.
- Fisk, D. A., 1983. Free-living corals: Distributions according to plant cover, sediments, hydrodynamics, depth and biological factors. *Marine Biology*, **74**: 287–294.
- Folk, R. L. R. Robles, 1964. Carbonate sands of Isla Perez, Alacran Reef Complex, Yucatan. *Journal of Geology*, **72**: 255–292.
- Fricke, H. W. & H. Schuhmacher, 1983. The depth limits of Red Sea stony corals: An ecophysiological problem (a deep diving survey by submersible). *Marine Ecology*, **4**: 163–194.
- Gill, G. A. & A. G. Coates, 1972. Mobility, growth patterns and substrate in some fossil and recent corals. *Lethaia*, **10**: 119–134.
- Gilmour, J. P., 2002. Substantial asexual recruitment of mushroom corals contributes little to population genetics of adults in conditions of chronic sedimentation. *Marine Ecology Progress Series*, **235**: 81–91.
- Gilmour, J. P., 2004a. Size-structures of populations of the mushroom coral *Fungia fungites*: The role of disturbance. *Coral Reefs*, **23**: 493–504.
- Gilmour, J. P., 2004b. Asexual budding in Fungiid corals. *Coral Reefs*, **23**: 595.
- Gittenberger, A. & B. W. Hoeksema, 2006. Phenotypic plasticity revealed by molecular studies on reef corals of *Fungia* (*Cycloseris*) spp. (Scleractinia: Fungiidae) near river outlets. *Contributions to Zoology*, **75**: 195–201.
- Gittenberger, A., B. T. Reijnen & B. W. Hoeksema, 2011. A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contributions to Zoology*, **80**: 107–132.
- Glynn, P. W., 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs*, **46**: 431–456.
- Goreau, T. F. & C. M Yonge, 1968. Coral community on muddy sand. *Nature*, **217**: 421–423.
- Greig-Smith, P., 1983. *Quantitative Plant Ecology*. 3<sup>rd</sup> Edition. Oxford, Blackwell. 359 pp.
- Highsmith, R. C., 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, **7**: 207–226.
- Hoeksema, B. W., 1988. Mobility of free-living fungiid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. *Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia*, **2**: 715–720.
- Hoeksema, B. W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen Leiden*, **254**: 1–295.
- Hoeksema, B. W., 1990. Systematics and ecology of mushroom corals (Scleractinia: Fungiidae). PhD Thesis Leiden University (Unpublished). 471 pp.
- Hoeksema, B. W., 1991a. Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Netherlands Journal of Zoology*, **41**: 122–139.
- Hoeksema, B. W., 1991b. Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: Stress tolerance and interference by life history strategy. *Marine Ecology Progress Series*, **74**: 225–237.
- Hoeksema, B. W., 1993. Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: An annotated checklist with the description of *Cantharellus jebbi* spec. nov. *Zoologische Mededelingen, Leiden*, **67**: 1–19.
- Hoeksema, B. W., 2004a. Impact of budding on free-living corals at East Kalimantan, Indonesia. *Coral Reefs*, **23**: 492.
- Hoeksema B. W., 2004b. Biodiversity and the natural resource management of coral reefs in Southeast Asia. In: Visser L. E. (ed), *Challenging Coasts: Transdisciplinary Excursions into Integrated Coastal Zone Development*. Amsterdam University Press, Amsterdam. Pp 49–71.
- Hoeksema, B. W., 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: The Coral Triangle. In: Renema, W. (ed.), *Biogeography, Time and Place: Distributions, Barriers and Islands*. Springer, Dordrecht. Pp 117–178.
- Hoeksema, B. W., 2009. Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singapore,

- including a new species and a new record. *Raffles Bulletin of Zoology, Supplement*, **22**: 81–90.
- Hoeksema, B. W., subm. Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). *Contributions to Zoology*.
- Hoeksema, B. W., M. B. Best, 1991. New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heteropsammia*. *Zoologische Mededelingen, Leiden*, **65**: 221–245.
- Hoeksema, B. W. & A. L. Crowther, 2011. Masquerade, mimicry and crypsis of the polymorphic sea anemone *Phyllodiscus semoni* and its aggregations in South Sulawesi. *Contributions to Zoology*, **80**: 251–268.
- Hoeksema, B. W. & N. J. de Voogd, 2012. On the run: Free-living mushroom corals avoiding interaction with sponges. *Coral Reefs*, doi 10.1007/s00338-011-0856-x.
- Hoeksema, B. W. & A. Gittenberger, 2010. High densities of mushroom coral fragments at West Halmahera, Indonesia. *Coral Reefs*, **29**: 691.
- Hoeksema, B. W. & K. Kleemann, 2002. New records of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae) boring in Indonesian mushroom corals (Scleractinia: Fungiidae). *Basteria*, **66**: 25–30.
- Hoeksema, B. W. & E. G. L. Koh, 2009. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. *Raffles Bulletin of Zoology, Supplement*, **22**: 91–101.
- Hoeksema, B. W. & J. L. Matthews, 2011. Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao, Gulf of Thailand. *Coral Reefs*, **30**: 95.
- Hoeksema, B. W. & W. Moka, 1989. Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. *Netherlands Journal of Sea Research*, **23**: 149–160.
- Hoeksema, B. W. & Z. Waheed, 2011. Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. *Coral Reefs*, **30**: 1087.
- Hoeksema, B. W. & T. Yeemin, 2011. Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. *Coral Reefs*, **30**: 975.
- Hoeksema, B. W., J. van der Land, S. E. T. van der Meij, L. P. van Ofwegen, B. T. Reijnen, R. W. M. van Soest & N. J. de Voogd, 2011. Unforeseen importance of historical collections as baselines to determine biotic change of coral reefs: The Saba Bank case. *Marine Ecology*, **32**: 135–141.
- Hoeksema, B. W., S. E. T. van der Meij & C. H. J. M. Franssen, 2012. The mushroom coral as a habitat. *Journal of the Marine Biological Association of the United Kingdom*. doi:10.1017/S0025315411001445.
- Hoekstra, P., 1989. Buoyant river plumes and mud deposition in a rapidly extending tropical delta. *Netherlands Journal of Sea Research*, **23**: 517–527.
- Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. Wiley, New York. 470 pp.
- Hubbard, J. A. E. B., 1972. *Diaseris distorta*, an “acrobatic” coral. *Nature*, **236**: 457–459.
- Hubbard, J. A. E. B., & Y. P. Pocock, 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geologische Rundschau*, **61**: 598–626.
- Hutchinson, D. R., 1945. Coral reefs and cays of the Makassar Straits. *HQ Allied Air Forces SW Pacific Area Intelligence Memoirs*, **50.2**: 1–30, Apps. I–III, maps 1–8, pls. 1–21.
- Ilahude, A. G., 1978. On the factors affecting the productivity of the southern Makassar Strait. *Marine Research in Indonesia*, **21**: 81–107.
- Jackson, J. B. C., 1986. Modes of dispersal of clonal benthic invertebrates: Consequences for species’ distributions and genetic structure of local populations. *Bulletin of Marine Science*, **39**: 588–606.
- Jokiel, P. L. & C. H. Bigger, 1994. Aspects of histocompatibility and regeneration in the solitary reef coral *Fungia scutaria*. *Biological Bulletin*, **186**: 72–80.
- Kleemann, K. & B. W. Hoeksema, 2002. *Lithophaga* (Bivalvia: Mytilidae), including a new species, boring in mushroom corals (Scleractinia: Fungiidae) at South Sulawesi, Indonesia. *Basteria*, **66**: 11–24.
- Knittweis, L., J. Jompa, C. Richter & M. Wolff, 2009a. Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia. *Coral Reefs*, **28**: 793–804.
- Knittweis, L., W. E. Kraemer, J. Timm & M. Kochzius, 2009b. Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: Implications for live coral trade management efforts. *Conservation Genetics*, **10**: 241–249.
- Knittweis, L. & M. Wolff, 2010. Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: Potential future management approaches. *Biological Conservation*, **143**: 2722–2729.
- Kramarsky-Winter, E. & Y. Loya, 1996. Regeneration versus budding in fungiid corals: A trade-off. *Marine Ecology Progress Series*, **134**: 179–185.
- Krupp, D. A., P. L. Jokiel & T. S. Chartrand, 1992. Asexual reproduction by the solitary scleractinian coral *Fungia scutaria* on dead parent coralla in Kanehoe Bay, Oahu, Hawaiian Island. *Proceedings of 7th International Symposium on Coral Reefs, Guam*, **1**: 527–534.
- Langer, M. R. & J. H. Lipps, 2003. Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. *Coral Reefs*, **22**: 143–154.
- Latypov, Y. Y., 2007. Free-living scleractinian corals on reefs of the Seychelles Islands. *Russian Journal of Marine Biology*, **33**: 222–226.
- Littler, M. M., D. D. Littler, B. L. Brooks & J. F. Koven JF, 1997. A unique coral reef formation discovered on the Great Astrolabe Reef, Fiji. *Coral Reefs*, **16**: 51–54.
- Loya, Y., 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology*, **13**: 100–123.
- Loya, Y., 1978. Plotless and transect methods. In: Stoddart, D. R. & R. E. Johannes (eds.), *Coral Reefs: Research Methods. UNESCO Monographs on Oceanographic Methodology*, **5**: 197–217.
- Ludwig, J. A. & J. R. Reynolds, 1988. *Statistical Ecology*. Wiley, New York. 337 pp.
- Marsh, L. M., R. H. Bradbury & R. E. Reichelt, 1984. Determination of the physical parameters of coral distributions using line transect data. *Coral Reefs*, **2**: 175–180.
- Marshall, S. M. & A. P. Orr, 1931. Sedimentation on Low Isles Reef and its relation to coral growth. III. The effect of sediment on corals. *Scientific Report of the Great Barrier Reef Expedition 1928–29*, **1**: 123–132, pls. 1–3.

- Mingoa, S. S. M. & L. A. B. Menez, 1988. A comparison of two benthic survey methods. *Marine Biology*, **99**: 133–135.
- Molengraaff, G. A. F., 1929. The coral reefs in the East Indian Archipelago their distribution and mode of development. *Proceedings of the 4th Pacific Science Congress, Batavia - Bandoeng*, **2A**: 55–89.
- Moll, H., 1983. *Zonation and diversity of Scleractinia on reefs off S.W. Sulawesi, Indonesia*. PhD Thesis Leiden University. 107 pp.
- Niermeyer, J. F., 1911. Barrière-riffen an atollen in de Oost-Indische Archipel. *Tijdschrift Koninklijk Nederlandsch Aardrijkskundig Genootschap* (Ser. 2), **28**: 877–894.
- Nishihira, M. & S. Pong-In, 1989. Distribution and population structure of a free-living coral, *Diastrea fragilis*, at Khang Khao Island in the Gulf of Thailand. *Galaxea*, **8**: 271–282.
- Orme, G. R., 1977. Aspects of sedimentation in the coral reef environment. In: Jones, O. A. & R. Endean (eds.), *Biology and Geology of Coral Reefs. Volume 4. Geology*, **2**: 129–182. Academic Press, New York.
- Pet-Soede, C., H. S. J. Cesar & J. S. Pet, 1999. An economic analysis of blast fishing on Indonesian coral reefs. *Environmental Conservation*, **26**: 83–93.
- Pet-Soede, C., W. L. T. van Densen, J. G. Hiddink, S. Kuyl & M. A. M. Machiels, 2001. Can fishermen allocate their fishing effort in space and time on the basis of their catch rates? An example from Spermonde Archipelago, S.W. Sulawesi, Indonesia. *Fisheries Management and Ecology*, **8**: 15–36.
- Pichon, M., 1974. Free living scleractinian coral communities in the coral reefs of Madagascar. *Proceedings of the 2<sup>nd</sup> International Coral Reef Symposium, Brisbane*, **2**: 173–181.
- Preston, N. P. & J. P. Doherty, 1990. Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. I. Agile shrimps. *Marine Ecology Progress Series*, **66**: 47–61.
- Preston, N. P. & J. P. Doherty, 1994. Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. *Marine Ecology Progress Series*, **104**: 27–38.
- Renema, W., B. W. Hoeksema & J. E. van Hinte, 2001. Larger benthic foraminifera and their distribution patterns on the Spermonde shelf, South Sulawesi. *Zoologische Verhandelingen, Leiden*, **334**: 115–149.
- Romesburg, H. C., 2004. *Cluster Analysis for Researchers*. Belmont, Lifetime Learning Publishers. 340 pp.
- Russ, G., 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series*, **20**: 23–34.
- Sawall, Y., M. Teichberg, J. Seemann, M. Litaay, J. Jompa & C. Richter, 2011. Nutritional status and metabolism of the coral *Stylophora subseriata* along a eutrophication gradient in Spermonde Archipelago (Indonesia). *Coral Reefs*, **30**: 841–853.
- Scheer, G., 1978. Application of phytosociologic methods. In: Stoddart, D. R. & R. E. Johannes (eds.), *Coral reefs: Research Methods. UNESCO Monographs on Oceanographic Methodology*, **5**: 175–196.
- Schuhmacher, H., 1977. Ability in fungiid corals to overcome sedimentation. *Proceedings of the 3<sup>rd</sup> International Coral Reef Symposium, Miami*, **1**: 503–509.
- Schuhmacher, H., 1979. Experimentelle Untersuchungen zur Anpassung von Fungiiden (Scleractinia, Fungiidae) an unterschiedliche Sedimentations- und Bodenverhältnisse. *Internationale Revue der Gesamten Hydrobiologie*, **64**: 207–243.
- Sheppard, C. R. C., 1981. The reef and soft-substrate coral fauna of Chagos, Indian Ocean. *Journal of Natural History*, **15**: 607–621.
- Sheppard, C. R. C., 1982. Coral populations on reef slopes and their major controls. *Marine Ecology Progress Series*, **7**: 83–115.
- Skreslet, S. (ed.), 1986. *The role of freshwater outflow in coastal marine ecosystems. NATO ASI Series G. Ecological Sciences 7*. Springer, Berlin. 451 pp.
- Soekarno, R., 1989. Comparative studies on the status of Indonesian coral reefs. *Netherlands Journal of Sea Research*, **23**: 215–222.
- Stella, J. S., G. P. Jones & M. S. Pratchett, 2010. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs*, **29**: 957–973.
- Stella, J. S., M. S. Pratchett, P. A. Hutchings & G. P. Jones, 2011. Coral-associated invertebrates: Diversity, ecology importance and vulnerability to disturbance. *Oceanography and Marine Biology: An Annual Review*, **49**: 43–104.
- Troelstra, S. R., H. M. Jonkers, S. de Rijk, 1996. Larger Foraminifera from the Spermonde Archipelago (Sulawesi, Indonesia). *Scripta Geologica*, **113**: 93–120.
- Umbgrove, J. H. F., 1929. The influence of the monsoons on the geomorphology of coral islands. *Proceedings of the 4th Pacific Science Congress, Batavia - Bandoeng (Java)*, **2A**: 49–54.
- Umbgrove, J. H. F., 1930. De koraalriffen van den Spermonde Archipel, S. Celebes. *Leidsche Geologische Mededelingen*, **3**: 227–247.
- Umbgrove, J. H. F., 1947. Coral reefs of the East Indies. *Bulletin of the Geological Society of America*, **58**: 729–778.
- Van der Meij, S. E. T., R. G. Moolenbeek & B. W. Hoeksema, 2009. Decline of the Jakarta Bay molluscan fauna linked to human impact. *Marine Pollution Bulletin*, **59**: 101–107.
- Van der Meij, S. E. T., Suharsono & B. W. Hoeksema, 2010. Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). *Marine Pollution Bulletin*, **60**: 1442–1454.
- Van der Stok, J. P., 1922. Maritieme meteorologie en getijden. In: Van der Stok, J. P. (ed.), *De zeeën van Nederlandsch Oost-Indië*. (with 4 tables and 22 maps, partly after p. 248). Koninklijk Nederlandsch Aardrijkskundig Genootschap, Amsterdam. Pp. 178–212.
- Van Moorsel, G. W. N. M., 1985. Disturbance and growth of juvenile corals (*Agaricia humilis* and *Agaricia agaricites*, Scleractinia) in natural habitats on the reef of Curaçao. *Marine Ecology Progress Series*, **24**: 99–112.
- Van Vuuren, L., 1920a. Barrière-riffen en atollen in den Ned. Indischen Archipel. *Handelingen 1ste Ned.-Indisch Natuurwetenschappelijk Congres, Batavia*. Pp. 186–198.
- Van Vuuren, L., 1920b. *Het Gouvernement Celebes. Monografie*, **1**: 1–535. Encyclopedisch Bureau, Weltevreden.
- Verheij, E. & W. F. Prud'homme van Reine, 1993. Seaweeds of the Spermonde Archipelago, SW Sulawesi, Indonesia. *Blumea*, **37**: 385–510.
- Weinberg, S., 1981. A comparison of coral reef survey methods. *Bijdragen tot de Dierkunde*, **51**: 199–218.
- Wells, J. W. 1966. Evolutionary development in the scleractinian family Fungiidae. In Rees, W. J. (ed.), *The Cnidaria and their Evolution. Symposium of the Zoological Society of London*, **16**: 223–246. Academic Press, London.

- Whittaker, R. H., 1975. *Communities and Ecosystems. 2<sup>nd</sup> Edition*. MacMillan, New York. 162 pp.
- Wijsman-Best, M., H. Moll & L. G. De Klerk, 1981. Present status of the coral reefs in the Spermonde Archipelago (South Sulawesi, Indonesia). *Proceedings of the 4th International Coral Reef Symposium, Manila*, **1**: 263–267.
- Wilkinson, C. R. & L. A. Trott, 1985. Light as a factor determining the distribution of sponges across the Central Great Barrier Reef. *Proceedings of the 5th International Coral Reef Congress, Tahiti*, **5**: 125–130.
- Williams, D. M. B., 1982. Patterns in the distribution of fish communities across the Great Barrier Reef. *Coral Reefs*, **1**: 35–43.
- Williams, D. M. B. & A. I. Hatcher, 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer-shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series*, **10**: 239–250.
- Yamashiro, H., M. Hidaka, M. Nishihira & S. Pong-In, 1989. Morphological studies on skeletons of *Diaseris fragilis*, a free-living coral which reproduces asexually by natural autotomy. *Galaxea*, **8**: 283–294.
- Yamashiro, H. & M. Nishihira, 1994. Radial skeletal dissolution to promote vegetative reproduction in a solitary coral *Diaseris distorta*. *Experientia*, **50**: 497–498.
- Yamashiro, H. & M. Nishihira, 1998. Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin 1843) a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology*, **225**: 253–267.
- Yamashiro, H. & K. Yamazato, 1987a. Studies on the detachment of the discs of the mushroom coral *Fungia fungites* with special reference to hard structural changes. *Galaxea*, **6**: 163–175.
- Yamashiro, H. & K. Yamazato, 1987b. Note on the detachment and post-detachment development of the polystomatous coral *Sandalolitha robusta* (Scleractinia, Cnidaria). *Galaxea*, **6**: 323–329.
- Yamashiro, H. & K. Yamazato, 1996. Morphological studies of the soft tissues involved in skeletal dissolution in the coral *Fungia fungites*. *Coral Reefs*, **15**: 177–180.

## Appendix 1. Systematic arrangement of 34 mushroom coral species distributions across the Spermonde Shelf.

*Ctenactis albitentaculata* (Fig. 12): Free-living, scattered in zones 2–4 (not present on reef 2D), mainly on deeper parts of reef slopes. Highest concentrations in W transects of reef 3B (5 per SU) and reef 3A (4 per SU).

*Ctenactis crassa* (Fig. 13): Free-living, fairly common in shelf zones 2–4, most abundant on reef slopes. Highest concentrations in W transects of reef 3A (8–10 per SU) and reef 1B (7 per SU).

*Ctenactis echinata* (Fig. 14): Free-living, abundant in all shelf zones, particularly on reef flats and slopes ( $\leq 18$  m). Highest concentrations in W transect of reef 3C (96–109 per SU) and SW transect of reef 3C (70–95 per SU).

*Cycloseris costulata* (Fig. 15): Free-living, common in all shelf zones; most abundant in zones 2–3; in zone 1 on reef flats and slopes and offshore mainly on lower slopes and on reef bases. Highest concentrations in W transect of reef 3A (53 per SU) and S transect of reef 3C (33 per SU).

*Cycloseris cyclolites* (Fig. 16): Free-living, rare, on reef slopes and reef bases in shelf zones 1–3,  $\geq 6$  m depth; in general most abundant around reef 3C but highest concentration on reef base (24-m depth) in E transect of reef 2C (5 per SU).

*Cycloseris distorta* (Fig. 17): Free-living, one specimen at reef 3C, SW transect, 18 m depth, on lower part of reef slope.

*Cycloseris fragilis* (Fig. 18): Free-living (also fragmenting), abundant in shelf zones 2–4, on reef slopes and reef bases,  $\geq 15$  m. Highest concentrations on reef base (24 m depth) in E transect of reef 2C (162 per SU) and on reef base (27-m depth) in E transect of reef 2B (77 per SU). Asexually reproduced fragments were most abundant on sandy bottoms of reef bases.

*Cycloseris mokai* (Fig. 19): Encrusting, common in shelf zones 2–3, attached, mainly on lower reef slopes and (only when overgrowing loose piece of rock) on upper reef bases. Highest concentrations in W transect of reef 3A (16–28 per SU) and N transect of reef 3A (17 per SU).

*Cycloseris sinensis* (Fig. 20): Free-living (also fragmenting), abundant in shelf zones 2–4 on reef slopes and bases ( $\geq 6$  m). Highest concentrations on reef base (30-m depth) in E transect of reef 4B (195 per SU) and on reef base (27-m depth) in E transect of reef 2B (48 per SU). Asexually reproduced fragments were most abundant on sandy bottoms of reef bases.

*Cycloseris somervillei* (Fig. 21): Free-living, rare in shelf zones 2–4, deeper than 15 m; most abundant at 21–36 m, on reef bases. Highest concentrations on reef base (24 m depth) in E transect of reef 2C (7 per SU) and on reef base (30 m depth) in W transect of reef 3C (5 per SU).

*Cycloseris tenuis* (Fig. 22): Free-living, common in shelf zones 2–4; mostly on slopes. Highest concentrations in SE transect of reef 3C (36 per SU) and in W transect of reef 3C (35 per SU).

*Cycloseris vaughani* (Fig. 23): Free-living, uncommon in shelf zones 2–4 (mainly zone 3), most abundant on deepest part of some reef bases. Highest concentrations on reef base (24 m depth) of reef 3C (10 per SU), base (33m depth) in N transect of reef 3A (4 per SU), base (33–36 m depth) in W transect of reef 3A (4 per SU), base (33 m depth) in SW transect of reef 3C (4 per SU), and base (33 m depth) in S transect of reef 3C (4 per SU).

*Cycloseris* sp. 1: Free-living, a few specimens were found outside transects on westward reef slopes in zone 3.

*Danafungia horrida* (Fig. 24): Free-living, common in all shelf zones; most common on reef slopes. Highest concentrations around reef 3C in NW transect (38–49 per SU), in SW transect (37–40 per SU), in W transect (35–36 per SU).

*Danafungia scruposa* (Fig. 25): Free-living, all shelf zones; most common on slopes. Highest concentrations around reef 3C in NW transect (40–49 per SU), SW transect (41–47 per SU), and W transect (36–40 per SU).

*Fungia fungites* (Fig. 26): Free-living, abundant in all zones, particularly on reef flats and upper reef slopes. Highest concentrations on reef flat (2.5–3 m) in W transect of reef 2A (137–285 per SU) and on upper reef slope (6-m depth) in W transect of reef 3C (124 per SU).

*Halomitra clavator*: Free-living, shelf zone 3. Three fragmented specimens were found on the W reef slope of reef 3A (15–21 m depth) and a single complete specimen was found 25 m deep at the West side of Pulau Badi (Hoeksema, 1989: Fig. 33).

*Halomitra pileus* (Fig. 27): Free-living, common in zones 2–4, on lower part of reef flats and on slopes; most common in N and W transects. Highest concentrations in W transect of reef 3C (14 per SU) and in NW and SW transects of reef 3C (both 13 per SU).

*Heliofungia actiniformis* (Fig. 28): Free-living, most common in zones 2–3; shallow in zone 1 (reef flats and slopes) and deeper in other zones (mainly slopes), particularly in W transects. Highest concentrations in W transect of reef 2D (15–16 per SU) and in N transect of reef 2B (11 per SU).

*Heliofungia fralinae* (Fig. 29): Free-living, locally common or aggregated in shelf zones 2–4 (most common in 2–3, absent on reef 2D). Highest concentrations on reef slopes in N transect of reef 2C (61–84 per SU), N transect of reef 3A (18–24 per SU), and W transect of reef 3A (18–23 per SU).

*Herpolitha limax* (Fig. 30): Free-living, common in all zones, common on reef flats, slopes and upper part of bases. Highest concentrations in W transect of reef 1A (53 per SU), NW transect of reef 3C (30 per SU) and SW transect of reef 3C (28 per SU).

*Lithophyllon concinna* (Fig. 31): Free-living, abundant in all zones; most common on reef flats and slopes at 3–15 m depth, especially in W transects. Highest concentrations in W transect of reef 2B (122 per SU) and in NW, W and SW transects of reef 3C (all 116 per SU).

*Lithophyllon repanda* (Fig. 32): Free-living, abundant in all zones; most common on reef flats and slopes at 3–15 m, especially in W transects. Highest concentrations in W transect (224–298 per SU), SW transect (192–251 per SU), and NW transect (224 per SU) of reef 3C.

*Lithophyllon scabra* (Fig. 33): Free-living, common in shelf zones 1–3 and rare in zone 4; deepest part of reef flats and on slopes. Highest concentrations in E transect of reef 1C (16–21 per SU) and in S transect of reef 1B (14 per SU).

*Lithophyllon spinifer* (Fig. 34): Free-living, shelf zone 3, on deeper part of westward reef slopes and upper part of reef bases (18–24 m). Besides two specimens in transects, several additional specimens were found at reefs 3A and 3C and the more northward Pulau Badi.

*Lithophyllon undulatum* (Fig. 35): Attached, scattered in zones 2–4 (one coral in zone 1), on lower part of reef flats and on slopes. Highest concentrations in N, S, and ESE transects of reef 2B (all 5 per SU).

*Lobactis scutaria* (Fig. 36): Free-living, common in shelf zones 2–4 (one coral from zone 1); most abundant on reef flats and slopes, rarely found on a reef base. Highest concentrations in S transect of reef 3C (11–14 per SU).

*Pleuractis granulosa* (Fig. 37): Free-living, common in shelf zones 2–4, usually on slopes with highest densities in N and W transects; absent on reef 2D and relatively rare on 2C. Highest concentrations in W transect of reef 2A (38 per SU), SW transect of reef 3C (36 per SU), and W transect of reef 2B (33 per SU).

*Pleuractis gravis* (Fig. 38): Free-living, common in shelf zones 2–4 (one coral from zone 1); most common on reef slopes and upper part of some reef bases. Highest concentrations in SW transect (14–18 per SU) and S transect (14 per SU) of reef 3C.

*Pleuractis moluccensis* (Fig. 39): Free-living, high densities in shelf zones 1–3 and rare in zone 4; in zone 1 shallow (flats and slopes), while further offshore deeper (on lower reef slopes and on reef bases). Highest concentrations on lower slopes in N transect of reef 3A (47 per SU) and S transect of reef 3C (43 per SU).

*Pleuractis paumotensis* (Fig. 40): Free-living, very common to abundant in all zones, on reef flats and slopes. Highest concentrations in W transect of reef 1A (84 per SU), W transect of reef 1C (83 per SU), and W transect of reef 1B (79 per SU).

*Podabacia crustacea* (Fig. 41): Attached, all shelf zones, on reef flats and most common on slopes. Highest concentrations in W transect of reef 1D and SW transect of reef 3C (both 7 per SU).

*Podabacia motuporensis*: Free-living, a few specimens were found outside transects on western slopes in zone 3.

*Polyphyllia talpina* (Fig. 42): Free-living, common in all shelf zones, common on reef flats, lower densities on reef slopes and reef bases. Highest concentrations in W transect of reef 3B (15 per SU), S transect of reef 1B (13 per SU), and S transect of reef 3C (10 per SU).

*Sandalolitha dentata* (Fig. 43): Free-living, scattered in shelf zones 2–4 (not on reefs 2D and 4B), on reef slopes and some upper reef bases, in low densities. Highest concentrations in NW transect of reef 3C (5 per SU) and W transect of reef 3A (4 per SU).

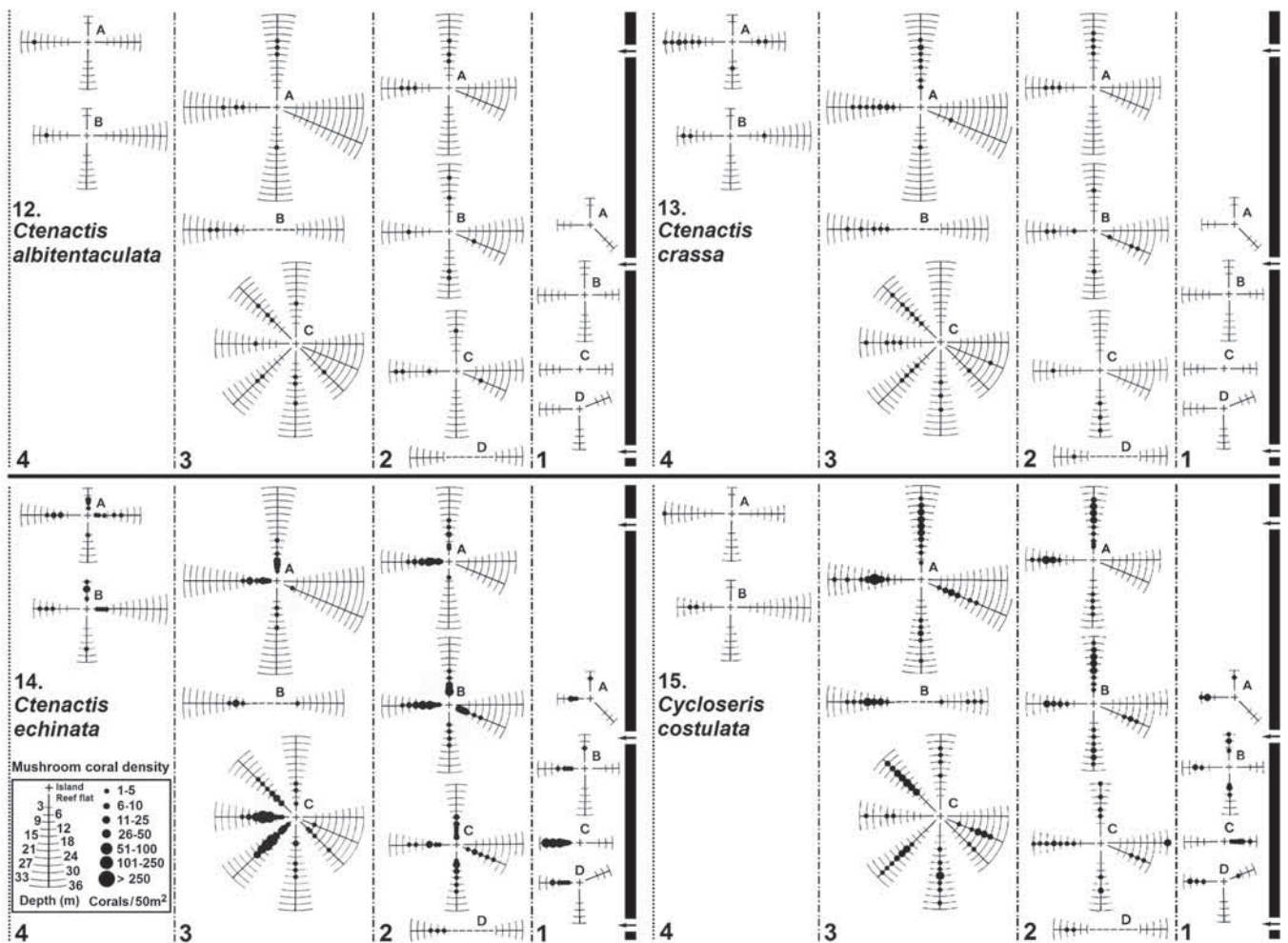
*Sandalolitha robusta* (Fig. 44): Free-living, common in all zones, on reef flats and slopes ( $\leq 21$  m depth). Highest concentrations in W transect of reef 3C (11–17 per SU) and W transect of reef 2A (13–15 per SU).

*Zoopilus echinatus* (Fig. 45): Free-living, rare in shelf zone 3, on slopes ( $\geq 12$  m depth). Highest concentrations in W transect of reef 3A (3 per SU) and NW transect of reef 3C (2 per SU).

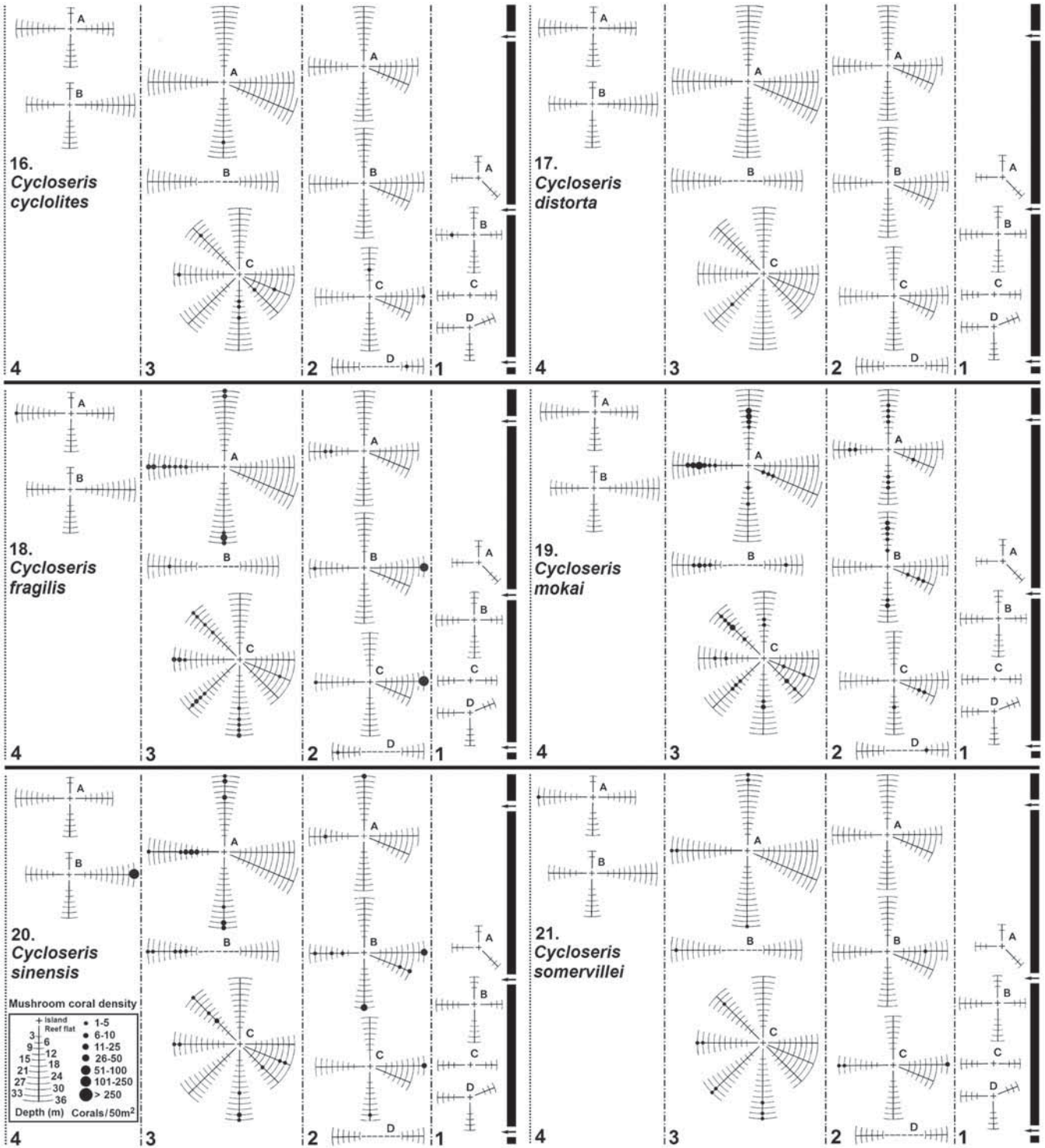


Appendix 2. Systematic arrangement of schematic transect diagrams.

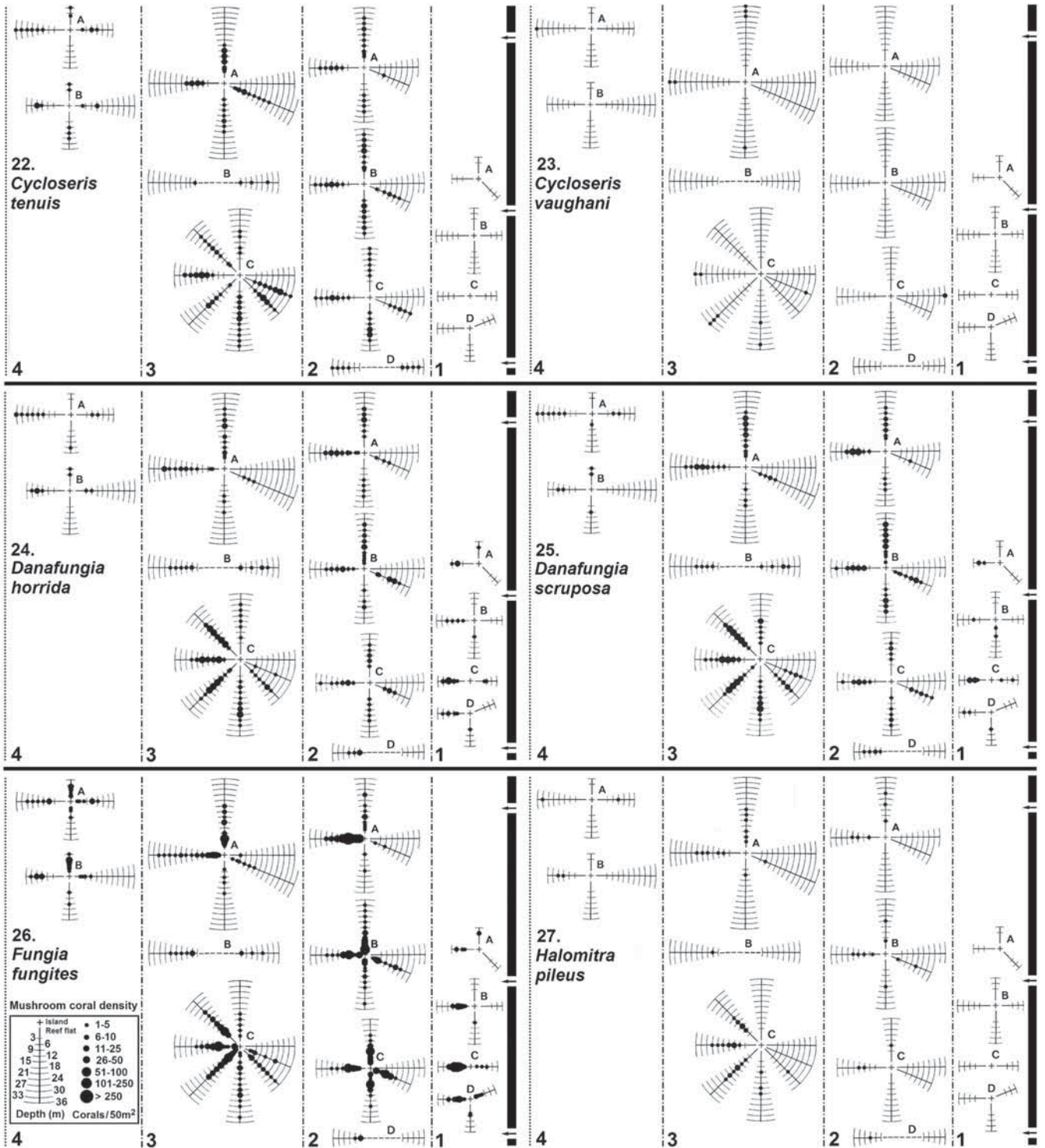
Figs. 12–45. Distribution and abundance patterns of Fungiidae on isobathic projections of transects around 13 reefs on the Spermonde Shelf (Fig. 2). Per reef, the position of 50 × 1 m<sup>2</sup> belt quadrats (SUs) are indicated with 3-m intervals (≥ 3 m depth). Three main river outlets are shown: the Maros (north), the Tello (central) and the Jeneberang (south). The position of Makassar city and harbour is east of reefs 1C and 1D.



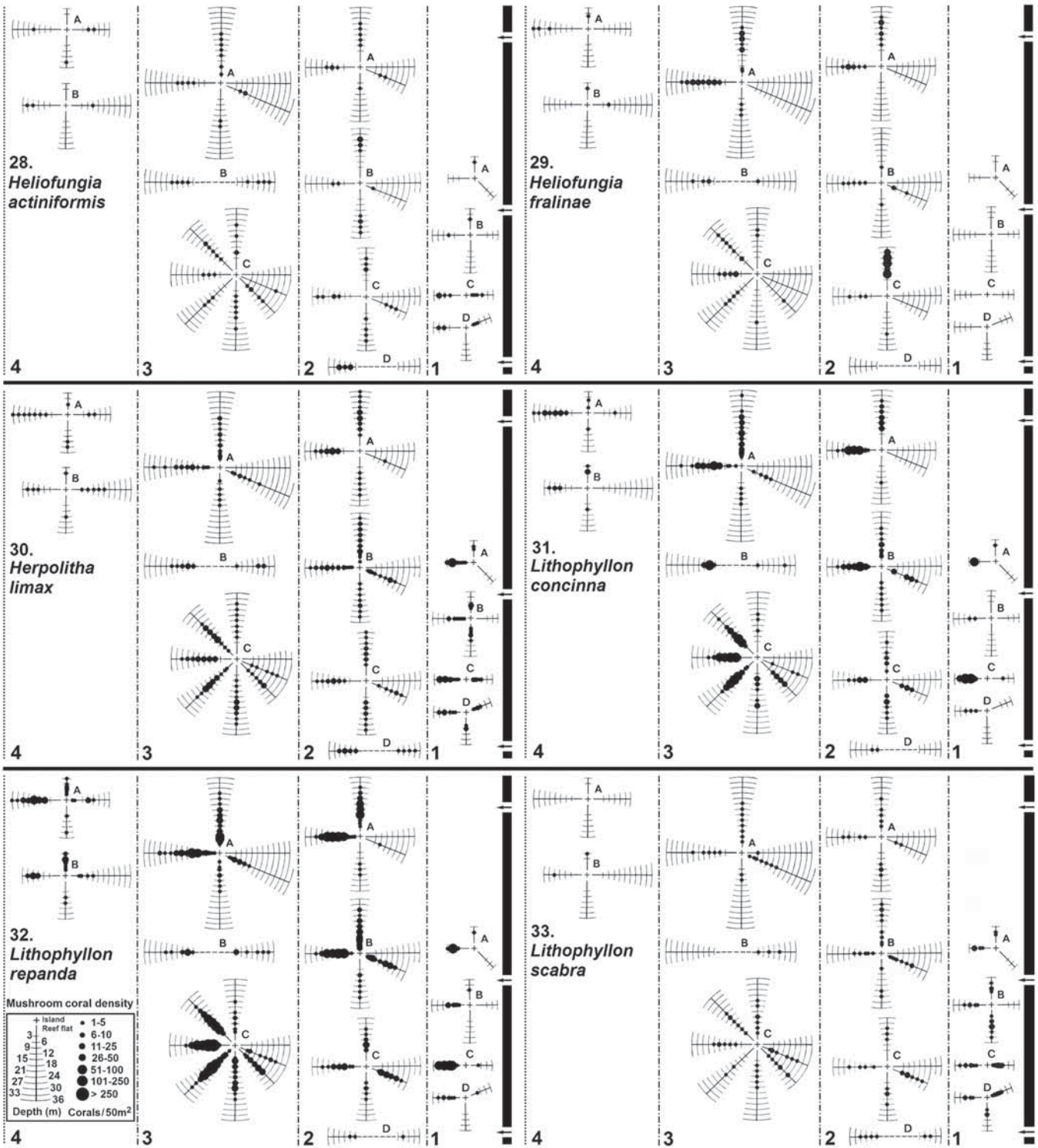
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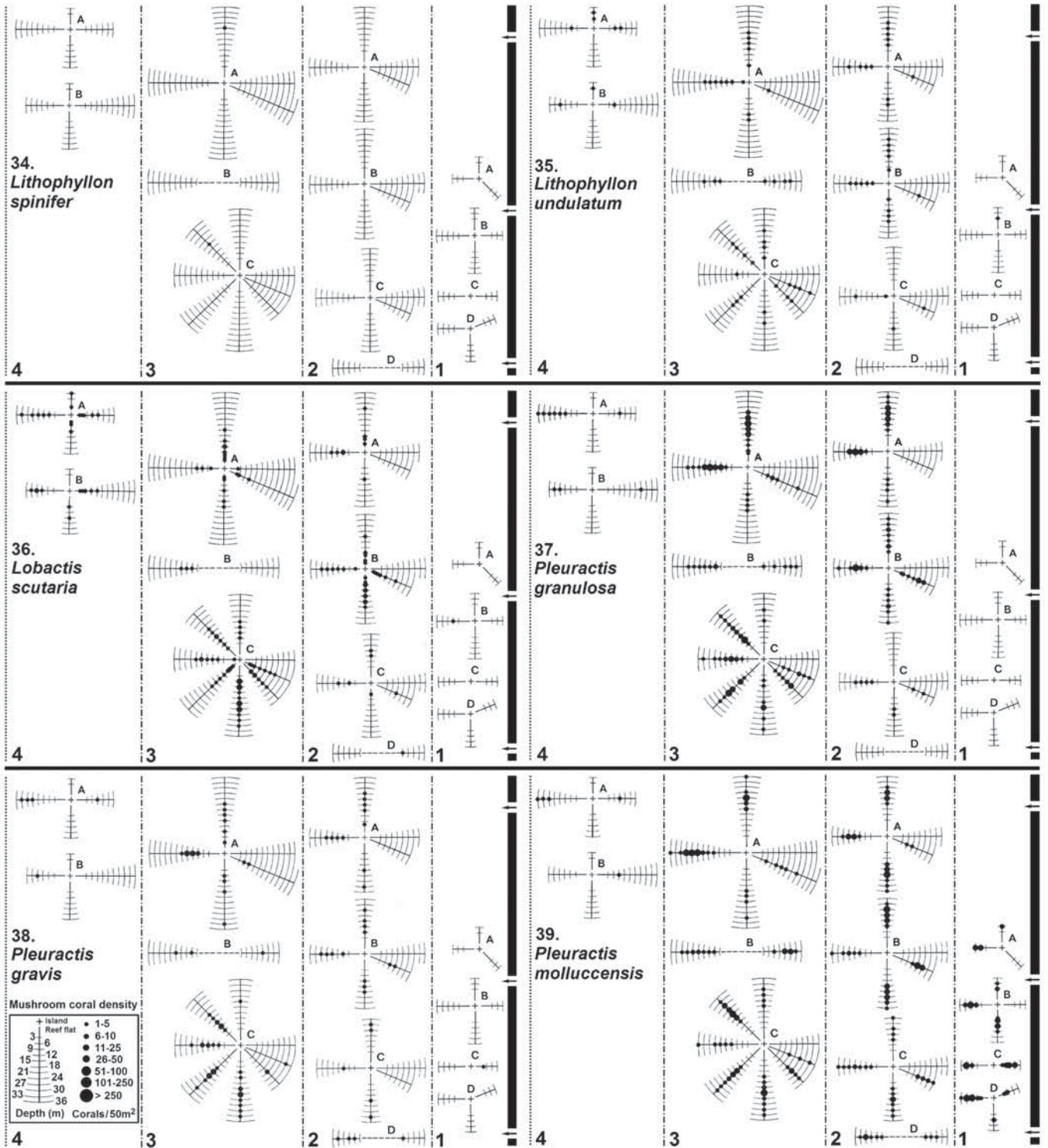
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