Patterns of coral species richness and reef connectivity in Malaysia

Waheed, Z.
Patterns of coral species richness and reef connectivity in Malaysia
PhD thesis, Leiden University

Cover design: Yee Wah Lau
Printed by: Gildeprint, Enschede
ISBN: 978 94 6233 460 1

FSC
www.fsc.org
MIX
Paper from
responsible sources
FSC® C012854

Funding. This thesis was accomplished with financial support from the Ministry of Higher Education Malaysia, with additional support from Universiti Malaysia Sabah, WWF-Malaysia, the A.M. Buitendijkfonds, and TREUB-maatschappij (Society for the Advancement of Research in the Tropics).

Disclaimer. Following the recommendation of Article 8.2 of the International Code of Zoological Nomenclature, I declare that this publication is not issued for public and permanent scientific record, or for purposes of zoological nomenclature, and therefore not published within the meaning of the Code.

Patterns of coral species richness and reef connectivity in Malaysia

Proefschrift

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van de Rector Magnificus prof. mr. C.J.J.M. Stolker,
volgens besluit van het College voor Promoties
te verdedigen op dinsdag 22 november 2016
klokke 13:45

door
Zarinah Waheed
geboren te Kota Kinabalu, Maleisië
in 1978

Promotiecommissie
Prof. dr. L.M. Chou (National University of Singapore, Singapore)
Prof. dr. M. Schilthuizen (Universiteit Leiden & Naturalis Biodiversity Center)
Prof. dr. H.P. Spaink (Universiteit Leiden)
Prof. dr. P.C. van Welzen (Universiteit Leiden & Naturalis Biodiversity Center)
Dr. F. Benzoni (University of Milano-Bicoca, Italy)
Dr. C.H.J.M. Fransen (Naturalis Biodiversity Center)

Promoter
Prof. dr. E. Gittenberger (Universiteit Leiden & Naturalis Biodiversity Center)

Copromoter
Dr. B.W. Hoeksema (Naturalis Biodiversity Center)

For my parents

Contents

Chapter 1 General Introduction 9

Chapter 2 A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia 29

Chapter 3 Coral reefs at the northernmost tip of Borneo: an assessment of scleractinian species richness patterns and reef benthos assemblages 49

Chapter 4 Diversity patterns of scleractinian corals at Kota Kinabalu, Malaysia, in relation to depth and exposure 77

Chapter 5 Scleractinian corals (Fungiidae, Agariciidae and Euphylliidae) of Pulau Layang-Layang, Spratly Islands, with a note on *Pavona maldivensis* (Gardiner, 1906) 97

Chapter 6 Reef coral species richness gradient across Malaysia 129

Chapter 7 Connectivity of reef invertebrate populations in Malaysia: perspectives of a mushroom coral, a blue seastar and a boring giant clam 161

References 193

Affiliation of co-authors 219

Summary 221

Nederlandse samenvatting 225

Ringkasan Bahasa Malaysia 229

Acknowledgements 233

Curriculum vitae 235

Publications 237

Chapter 1

General Introduction

Reef corals

Coral reefs are among the most productive ecosystems on earth. They provide goods and services to millions of people worldwide, directly or indirectly, in the form of food, coastline protection, tourism, pharmaceuticals, and other sources of income (Moberg and Folke 1999, Wilkinson 2008). They also have recreational and cultural importance for local communities. Shallow tropical coral reefs have much value as habitat, providing shelter to innumerable marine species, making them the most species-rich marine ecosystem in the world. Hard corals (Scleractinia) form the backbone of tropical coral reefs. They are the main builders in the reef ecosystem, which supports the wealth of marine biodiversity. Naturally, the corals themselves also contribute to this diversity.

Hard coral is composed of an individual polyp or a group of polyps that live together to form a coral colony. The ability of hard corals to build reefs stems from their symbiotic relationship with unicellular algae, zooxanthellae of the genus *Symbiodinium*. The photosynthesizing zooxanthellae, which live within the coral tissue, influence the growth rate and calcium carbonate ($CaCO_3$) deposition of corals. The success of building and maintaining the three-dimensional reef structures relies on environmental parameters such as light, temperature, and nutrient levels (Barnes and Chalker 1990; Falkowski et al. 1990; Atkinson 2011; Dubinsky and Falkowski 2011). Equally important is the coral resilience to competition, and disturbance or stress of natural or anthropogenic origin.

Most hard corals are colonial. Many coral species can easily be identified in situ, whereas others exhibit a wide range of morphological variation and plasticity, which makes their identification difficult (Veron 1995; Todd 2008). Such variation in coral appearance can be in the form of 1) corallite variation within a coral colony, usually in different parts of the colony, 2) colony growth form due to different environmental conditions such as depth or proximity to land, 3) coral colony variation between regions, most likely related to environmental gradients, genetic isolation, or a combination of these factors, and 4) soft tissue variation, such as in corals with fleshy polyp tissue, like *Euphyllia*, *Plerogyra* and *Physogyra* (see Veron 1995). In recent times, coral taxonomy has moved beyond using solely morphological characters for defining species boundaries. Increasingly frequent, molecular data and additional micro-morphological/microstructure traits are applied to support new species descriptions (Benzoni and Stefani 2012; Terraneo et al. 2014), and taxonomic classifications or revisions (Budd et al. 2012; Huang et al. 2014), while resolving problematic species or species complexes (Stefani et al. 2008, 2011; Benzoni et al. 2010, 2014; Gittenberger et al. 2011; Keshavmurthy et al. 2013; Forsman et al. 2015). At present, more than 800 species of scleractinian reef corals have been described (Paulay 1997, Veron et al. 2015).

The highest biodiversity in the marine world can be found in the Coral Triangle. This centre of maximum marine biodiversity spans across six countries (Indonesia, Malaysia the Philippines, Timor-Leste, Papua New Guinea, and the Solomon Islands), and is named after the somewhat triangular shape of the area (see Hoeksema 2007). It covers < 1.6% of the world's ocean area (Veron et al. 2011), yet it contains over 600 scleractinian reef coral species, accounting for almost 75% of the world's reef coral species (Veron et al. 2015). Marine diversity decreases along latitudinal and longitudinal gradients with increasing distance from this centre (e.g. Hoeksema 2007; Barber 2009; Bellwood and Meyer 2009; Carpenter et al. 2011). Several hypotheses have been proposed as explanatory models for this centre of maximum marine diversity (Rosen 1988; Hoeksema 2007; Bellwood et al. 2012). However, it is likely that a combination of factors may be at work to explain the patterns and species richness in the region (Hoeksema 2007; Halas and Winterbottom 2009; Cowman and Bellwood 2013).

Although famed for its astounding biodiversity, the reefs of the Coral Triangle are also known to be highly vulnerable, with more than 85% of the reefs threatened by unsustainable fisheries, coastal development and pollution, and this percentage increases to over 90% when thermal stress and coral bleaching is taken into account (Burke et al. 2012). Based on estimates of coral cover data, Indo-Pacific reefs had an average of only 22% cover in 2003, and coral cover loss was approximately 2% between 1997 and 2003 (Bruno and Selig 2007). Such numbers are worrying, and initiatives are being made to conserve and effectively manage coral reefs area through the establishments of marine protected areas (MPAs) or marine managed areas (e.g. Burke et al. 2012, White et al. 2014; Weeks at al. 2014).

Diversity measures and patterns

Documenting, mapping and explaining patterns of biodiversity are the essence of ecological studies (Magurran 2004). Understanding the current status of biodiversity is important in order to predict its response to environmental changes (Gaston 2000), and to identify systematic conservation planning and its sustainable use (Margules and Pressey 2000).

Biodiversity can be grouped into three main components: genetic diversity, species diversity and ecosystem diversity (Norse et al. 1986; Heywood and Baste 1996; Gaston and Spicer 2004; Gaston 2010). Genetic diversity reflects the variation of genes within a species, and species diversity refers to the different number of species in an area, whereas ecosystem diversity is the variation in ecosystems through its communities and habitats in a region. Aspects of the first two components of diversity are examined in this thesis.

Genes are the essence of a species. Genetic diversity can be measured by assessing and comparing DNA sequence data (Culver et al. 2011). Genetic data is increasingly being applied to resolve taxonomic uncertainties (as mentioned in the previous section). At the population level, genetic diversity is evaluated within and among populations to quantify the distribution and pattern of genetic variation of a species (Templeton 1998). Such population genetics studies have revealed various patterns of connectivity or disjunction among populations.

Species diversity is commonly quantified in terms of species counts to represent richness (McIntosh 1967; Magurran 2004), but it can be measured through other components such as species evenness, abundance, commonness, and rarity. Although species richness appears to be the simplest measure of diversity, the success of documenting species is highly dependent upon the species concepts of the chosen taxon, and the sampling regime (Magurran 2004; Bonar et al. 2011). Similar with genetic diversity, measures of species diversity can be made at the population or community level. Species diversity within a community or site is known as alpha diversity or local diversity, and the difference in species composition among communities or sites, such as along an environmental gradient, is referred to as beta diversity (Whittaker 1972; Whittaker et al. 2001).

Genetic diversity is critical in the evolution and adaptation of a species (and population) to environmental change (Templeton 1994). High genetic diversity ensures population fitness (Reed and Frankham 2003). In turn, greater species diversity enhances ecosystem functions (Harrison et al. 2014), and ensures greater ecosystem resilience to stresses and ability to recover from disturbances (Folke et al. 2004). Mapping of genetic diversity (Pope et al. 2016), and species diversity such as species richness in various spatial scales could reveal biodiversity patterns that can be useful for conservation prioritisations (Fleishman et al. 2006; Tittensor et al. 2010; Selig et al. 2014). Hence, all levels of diversity (and processes driving it) should be taken into account for conservation measures in order to ensure sustainability and resilience of biodiversity in general (Smith et al. 1993; Bowen 1999).

Reef-related studies in Malaysia

Malaysia is composed of two land areas: Peninsular Malaysia (also known as West Malaysia) on the Asian continent, and East Malaysia (the states of Sabah and Sarawak, and the Federal Territory of Labuan) on the island of Borneo. These two land areas are separated by the South China Sea. Malaysia's coral reefs have previously been reported to cover nearly 3,000 km^2 (Burke et al. 2012), but a recent estimate of reef coverage is approximately 1,687 km^2 (Cros et al. 2014a, b) (Fig. 1). A majority of the reefs are located at the northern and eastern coast of Sabah (Burke et al. 2011, 2012). In the demarcation of the Coral Triangle, only the east coast of Sabah along the Sulu Sea was included within the boundary (Veron et al. 2009, 2011). However, a recent review suggested the inclusion of the South China Sea overlying the Sunda Shelf within the Coral Triangle boundary, based on comprehensive coral distribution, diversity and affinity data (Veron et al. 2015), including a compilation of coral species records published by a team of scientists working in the South China Sea (Huang et al. 2015).

The reefs and coral fauna of Malaysia have been studied since the 1950s (e.g. Searle 1956; Purchon 1965; Dunn 1970; Morris 1978; Wood 1987; review in UNEP/IUCN 1988), with comparatively more literature from Peninsular Malaysia than East Malaysia (Meagher 1992). Some of these earlier studies include coral species list from various reefs of Malaysia (reviewed in Affendi and Rosman 2012 and Waheed et al. 2012). A recent update of reef coral species richness in the South China Sea across Malaysia, in part based on the dataset of these earlier studies, revealed 398 and 248 species for the east coast of Peninsular Malaysia and west coast of Sabah, respectively (Huang et al. 2015, 2016). Brunei Darussalam, which is situated in between Sabah and Sarawak, scored 391 species (Huang et al. 2015, 2016). Subsequently, coral species lists for the Strait of Malacca and the Sulu Sea were similarly updated and standardised with that of Huang et al. (2016). A total of 56 species was attained for the Strait of Malacca, and 382 species for the Sulu Sea, thus bringing the total number of reef corals to 501 species in Malaysia (Table S1). These numbers indicate that the reefs of Peninsular Malaysia (and Brunei) are more species-rich than those of East Malaysia. However, this result may very well be due to the lack of data from East Malaysia. As noted by Wells (1969) and quoted by Veron (1995), limitations to documenting species richness on reefs (of the Indo-Pacific) usually concern issues in species concepts and insufficient reef explorations.

Fig. 1. Distribution of coral reefs in Malaysia downloaded from the Coral Triangle Atlas, version 8 June 2011 (dataset from the UNEP-WCMC Biodiversity Map Library: Global Coral Reef Distribution). http://ctatlas.reefbase.org

In recent years, strides have been made in the field of phylogeography in the Indo-Pacific region including the Coral Triangle area, and some of these studies included parts of Malaysia. Such studies focused on various marine invertebrate species and elucidated the patterns of genetic breaks and the underlying processes for such patterns, which coincide with biogeographic boundaries in this region (e.g. Crandall et al. 2008b; DeBoer et al. 2008, 2014a; Kochzius et al. 2009; Nuryanto and Kochzius 2009; Carpenter et al. 2011, Huelsken et al. 2013). On a much smaller geographical scale, genetic diversity and population genetics studies in Malaysia on horseshoe crab (*Tachypleus gigas*) (Rozihan and Ismail 2012; Rozihan et al. 2013), and black scar oyster (*Crassostrea iredalei*) (Zainal Abidin et al. 2016) also found limited gene flow between Peninsular and East Malaysia, but this could be largely influenced by the life history traits of the species studied (see Leffler et al. 2012, Romiguier et al. 2014). Most population genetics studies in Malaysia are centred in Peninsular Malaysia (e.g. Yap et al. 2002; Ong et al. 2009; Rosly et al. 2013), which leaves an information gap to be filled for East Malaysia.

Thesis outline

The lack of information on the diversity of coral reefs in Malaysia, specifically from East Malaysia, triggered a series of investigations on the reef fauna in Malaysia. The position of Malaysia in the Indo-Malay Archipelago, and the border of the Coral Triangle, the area of maximum marine biodiversity, makes it an interesting backdrop for research on the coral fauna in general. This PhD thesis aims at obtaining a more profound insight into the patterns of scleractinian coral species richness and genetic population structure of model reef invertebrates across Malaysia. At the onset of this study in 2010, the northwestern boundary of the Coral Triangle was situated at the Sulu Sea margin in north Sabah. Two main focal points in this thesis are:

1) Is there a reef coral species richness gradient across Malaysia, and if so, does it decrease with increasing distance from the Coral Triangle?
2) Is there connectivity in the coral reefs of Malaysia?

This study was guided by two main hypotheses:

1) Reefs in Peninsular Malaysia and the west coast of Sabah are not as species-rich as the east coast of Sabah due to the low sea level stand during the Last Glacial Maximum, whereby the southern part of the South China Sea overlying the Sunda Shelf was dry and the reefs were emerged, whereas the Sulu Sea remained submerged (see Voris 2000; Hoeksema 2007).
2) Reefs on the east coast of Sabah are species-rich because the fringing reefs have been established along the slopes of the continental margin in the Sulu Sea since the Oligocene (see Von Fitch 1878; Weissel 1980; Potts 1983, 1984, 1985; McManus 1985; Wilson and Rosen 1998), which is consistent with a diverse zooxanthellate fossil coral collection from the same epoch (McMonangle et al. 2011; McMonangle 2012).

In order to address these questions, the goal was to collect data on coral species, and specimens of invertebrate model species from key coral reef areas in Malaysia. The lack of data from East Malaysia warranted further investigation of species richness patterns in several areas with high concentration of coral reefs around Sabah.

Model taxa

There is great challenge in measuring diversity of corals, particularly on reefs where species richness is overwhelmingly high. In order to tackle this daunting task, selected coral families with robust taxonomic framework can be targeted as model taxa for investigating species diversity (examples in Hoeksema 2007). In the present study, the taxonomically well-resolved and iconic mushroom coral family, the Fungiidae Dana, 1846 was selected as one of the model taxa. Two other families, viz. Agariciidae Gray, 1847 and Euphylliidae Alloiteau, 1952, though requiring taxonomic revision, were selected on the basis of their wide geographical distribution in the Indo-Pacific. Species of these three families and can be found in a large range of habitats from shallow coastal reefs to deep offshore environments. Species of these three families are also easily distinguishable from those of other coral families. Some members, especially of the Euphylliidae are conspicuous and easily detected on the reefs. These three coral families (~100 species) were used as proxy for all reef coral species (> 500 species) in Malaysia. Following recent phylogeny reconstructions, the classification of the families Agariciidae and Euphylliidae has been revised. Consequently the genus *Pachyseris*, which formerly belonged to the Agariciidae is now part of the Euphylliidae, and the genera *Catalaphyllia*, *Nemenzophyllia*, *Physogyra* and *Plerogyra*, which previously belonged to the Euphylliidae, are now classified as *incertae sedis* (Fukami et al. 2008, Kitahara et al. 2010, Benzoni et al. 2014). For clarity, the scleractinian species list given in Table S1 has been updated according to the current taxonomic framework. However, the old taxonomic framework of Agariciidae and Euphylliidae (sensu Veron 2000) remained the basis of this thesis (Chapters 2–6).

For genetic diversity studies, the life histories and geographical ranges of the model species are among the important factors to consider (Leffler et al. 2012), together with the molecular markers (mitochondrial or nuclear sequences, microsatellites, etc.) and the sampling range. In choosing the model species, we looked to existing genetic studies in the Coral Triangle, which lacked information from parts of Malaysia. As this study is centered on reef corals, we chose the mushroom coral *Heliofungia actiniformis* as a model species, using the same genetic marker as Knittweis et al. (2009). The blue seastar *Linckia laevigata* and the boring giant clam *Tridacna crocea* are popular candidates for population genetic studies (e.g. for *L. laevigata*: Crandall et al. 2008b; Kochzius et al. 2009; Williams and Benzie 1996; for *T. crocea*: DeBoer et al. 2008, 2014a; Kochzius and Nuryanto 2008). These two species are in the top five species with the highest number of locations sampled across the Indo-Pacific, including the Coral Triangle region (Keyse et al 2014). Genetic data from localities in Malaysia would increase the geographic scope of these species.

Chapters overview

Reef corals were examined at six localities across Malaysia and Layang-Layang in the disputed Spratly Islands in a range spanning the Sulu Sea, South China Sea and Strait of Malacca. Data collection and sampling took place during five separate fieldtrips, two of which were part of larger expeditions. By utilising presence/absence data of the model taxa, species richness patterns of corals were determined for Semporna (**Chapter 2**), Kudat (**Chapter 3**) and Kota Kinabalu (**Chapter 4**) in Sabah, East Malaysia. Environmental factors that can influence species composition such as reef depth and exposure were evaluated. Based on the coral composition data, reefs that were similar with or dissimilar from each other were determined, and distribution patterns of species were derived to identify aspects such as rarity (species that are common or rare in terms of occurrence of individuals). For the reefs of Kudat, benthic reef assemblages following the Reef Check substrate categories were also examined, and in addition to reef depth and exposure, proximity to mainland was evaluated in relation to coral species richness and benthic reef substrate (Chapter 3).

A coral checklist accompanied by images of each species of the model taxa was obtained from Layang-Layang (**Chapter 5**). During the surveys, an encrusting *Pavona* coral with small and extremely thin coralla was collected. Unexpectedly, molecular and morphological analyses revealed the coral as *Pavona maldivensis* (Gardiner, 1905). The morphological features, affinities with other closely resembling *Pavona* species, and status of *P. maldivensis* in Malaysia reefs are discussed.

In **Chapter 6**, the reef coral species richness patterns were explored across Malaysia, including Layang-Layang, by incorporating presence/absence data from the previous chapters (Chapters 2–5), and adding three sites from around Peninsular Malaysia, i.e. the Tioman and Redang group of islands, both on the east coast of the peninsula, and the Payar group of islands on the west coast of the peninsula in the Strait of Malacca near the Andaman Sea. The richness patterns were compared with those of other marine ecoregion delineations, i.e. Spalding et al. (2007) and Veron et al. (2015). Species distribution patterns indicate common and rare species (based on occurrence by locality), and potential endemics. At the end of Chapter 6, a species list of the model taxa is presented for all seven localities of this study.

Chapter 7 attempts to infer the connectivity patterns among reefs of Malaysia by examining the genetic diversity, demographic history and genetic population structure of three model species, viz. the mushroom coral *Heliofungia actiniformis* based on ribosomal ITS1, 5.8S and partial ITS2 sequences, and the blue seastar *Linckia laeviata* and the boring giant clam *Tridacna crocea* both based on partial mitochondrial cytochrome oxidase I sequences. Samples were obtained from five out of the seven localities in this study, excluding Payar and Redang where none of the model species were encountered. Factors to explain for the population structure and connectivity patterns across Malaysia are discussed.

Supporting Information

Table S1. Records of scleractinian reef corals in Malaysia. Species list of the South China Sea (east coast of Peninsular Malaysia and west coast of Sabah) was obtained from Huang et al. (2016), Supplementary Material 1. Species lists from the Strait of Malacca and the Sulu Sea (east of Sabah) were from Affendi and Rosman (2012) and Waheed et al. (2012), respectively, and updated and standardised accordingly. Records from Kudat were updated following the full coral species list of Fenner (2001).

No.	**Scleractinian reef coral species**	**Strait of Malacca**	**East coast Peninsular Malaysia (South China Sea)**	**West coast Sabah (South China Sea)**	**East coast Sabah (Sulu Sea)**
	Acroporidae Verrill, 1902				
1	*Acropora abrolhosensis* Veron, 1985	0	1	0	1
2	*Acropora abrotanoides* (Lamarck, 1816)	0	1	0	1
3	*Acropora aculeus* (Dana, 1846)	0	1	0	1
4	*Acropora acuminata* (Verrill, 1864)	0	1	0	1
5	*Acropora anthocercis* (Brook, 1893)	0	1	1	1
6	*Acropora appressa* (Ehrenberg, 1834)	0	1	0	0
7	*Acropora aspera* (Dana, 1846)	0	1	1	1
8	*Acropora austera* (Dana, 1846)	0	1	0	0
9	*Acropora awi* Wallace & Wolstenholme, 1998	0	1	0	1
10	*Acropora carduus* (Dana, 1846)	0	1	0	1
11	*Acropora caroliniana* Nemenzo, 1976	0	0	0	1
12	*Acropora cerealis* (Dana, 1846)	0	1	0	1
13	*Acropora clathrata* (Brook, 1891)	0	1	1	1
14	*Acropora cytherea* (Dana, 1846)	0	1	1	1
15	*Acropora dendrum* (Bassett-Smith, 1890)	0	1	0	0
16	*Acropora digitifera* (Dana, 1846)	0	1	1	1
17	*Acropora divaricata* (Dana, 1846)	1	1	1	1
18	*Acropora donei* Veron & Wallace, 1984	0	1	0	1
19	*Acropora echinata* (Dana, 1846)	0	0	0	1
20	*Acropora elegans* (Milne Edwards & Haime, 1860)	0	0	0	1
21	*Acropora elseyi* (Brook, 1892)	0	1	0	1
22	*Acropora exquisita* Nemenzo, 1971	0	0	0	1
23	*Acropora fastigata* Nemenzo, 1967	0	0	0	1
24	*Acropora florida* (Dana, 1846)	1	1	1	1
25	*Acropora gemmifera* (Brook, 1892)	0	1	1	1
26	*Acropora glauca* (Brook, 1893)	0	0	0	1
27	*Acropora globiceps* (Dana, 1846)	0	1	0	0
28	*Acropora grandis* (Brook, 1892)	0	1	0	1

29	*Acropora granulosa* (Milne Edwards & Haime, 1860)	0	0	0	1
30	*Acropora hemprichii* (Ehrenberg, 1834)	0	1	0	0
31	*Acropora hoeksemai* Wallace, 1997	0	1	0	1
32	*Acropora horrida* (Dana, 1846)	0	1	0	1
33	*Acropora humilis* (Dana, 1846)	0	1	0	1
34	*Acropora hyacinthus* (Dana, 1846)	0	1	1	1
35	*Acropora indonesia* Wallace, 1997	0	0	0	1
36	*Acropora insignis* Nemenzo, 1967	0	1	0	0
37	*Acropora intermedia* (Brook, 1891)	0	0	0	1
38	*Acropora jacquelineae* Wallace, 1994	0	0	0	1
39	*Acropora kirstyae* Veron & Wallace, 1984	0	1	0	0
40	*Acropora latistella* (Brook, 1892)	0	1	1	1
41	*Acropora listeri* (Brook, 1893)	0	1	0	1
42	*Acropora loisetteae* Wallace, 1994	0	0	0	1
43	*Acropora longicyathus* (Milne Edwards & Haime, 1860)	0	0	0	1
44	*Acropora loripes* (Brook, 1892)	0	1	1	1
45	*Acropora lutkeni* Crossland, 1952	0	1	0	1
46	*Acropora microclados* (Ehrenberg, 1834)	0	1	0	1
47	*Acropora microphthalma* (Verrill, 1869)	0	1	1	1
48	*Acropora millepora* (Ehrenberg, 1834)	0	1	1	1
49	*Acropora monticulosa* (Brüggemman, 1879)	0	1	0	0
50	*Acropora multiacuta* Nemenzo, 1967	0	0	1	1
51	*Acropora muricata* (Linnaeus, 1758)	1	1	1	1
52	*Acropora nana* (Studer, 1878)	0	1	0	1
53	*Acropora nasuta* (Dana, 1846)	0	1	1	1
54	*Acropora palmerae* Wells, 1954	0	1	0	0
55	*Acropora paniculata* Verrill, 1902	0	0	0	1
56	*Acropora papillare* Latypov, 1992	0	1	0	1
57	*Acropora plumosa* Wallace & Wolstenholme, 1998	0	0	0	1
58	*Acropora polystoma* (Brook, 1891)	0	0	1	1
59	*Acropora proximalis* Veron, 2000	0	1	0	0
60	*Acropora pruinosa* (Brook, 1893)	0	1	0	0
61	*Acropora pulchra* (Brook, 1891)	0	1	1	1
62	*Acropora retusa* (Dana, 1846)	0	1	0	0
63	*Acropora ridzwani* Ditlev, 2003	0	0	0	1
64	*Acropora robusta* (Dana, 1846)	1	1	1	1
65	*Acropora rosaria* (Dana, 1846)	0	1	0	0
66	*Acropora samoensis* (Brook, 1891)	0	1	0	1
67	*Acropora sarmentosa* (Brook, 1892)	0	1	0	1
68	*Acropora secale* (Studer, 1878)	1	1	0	1
69	*Acropora selago* (Studer, 1878)	0	1	1	1
70	*Acropora simplex* Wallace & Wolstenholme, 1998	0	0	0	1
71	*Acropora solitaryensis* Veron & Wallace, 1984	0	1	0	0
72	*Acropora speciosa* (Quelch, 1886)	0	1	0	1
73	*Acropora spicifera* (Dana, 1846)	0	1	0	0
74	*Acropora subglabra* (Brook, 1891)	0	0	0	1
75	*Acropora subulata* (Dana, 1846)	0	1	1	1
76	*Acropora tenuis* (Dana, 1846)	0	1	1	1
77	*Acropora teres* (Verrill, 1866)	0	0	0	1
78	*Acropora valenciennesi* (Milne Edwards & Haime, 1860)	0	1	1	1
79	*Acropora valida* (Dana, 1846)	0	1	1	1

80	*Acropora vaughani* Wells, 1954	0	1	0	1
81	*Acropora willisae* Veron & Wallace, 1984	0	0	0	1
82	*Acropora yongei* Veron & Wallace, 1984	0	1	0	1
83	*Alveopora allingi* Hoffmeister, 1925	0	1	0	1
84	*Alveopora catalai* Wells, 1968	0	0	0	1
85	*Alveopora daedalea* (Forskål, 1775)	0	1	0	0
86	*Alveopora excelsa* Verrill, 1863	1	1	0	0
87	*Alveopora marionensis* Veron & Pichon, 1982	0	1	0	0
88	*Alveopora minuta* Veron, 2000	0	1	0	0
89	*Alveopora spongiosa* Dana, 1846	0	1	1	1
90	*Alveopora tizardi* Bassett-Smith, 1890	0	0	1	1
91	*Alveopora verrilliana* Dana, 1872	0	0	1	1
92	*Anacropora forbesi* Ridley, 1884	0	1	0	1
93	*Anacropora matthai* Pillai, 1973	0	1	0	1
94	*Anacropora pillai* Veron, 2000	0	0	0	1
95	*Anacropora puertogalerae* Nemenzo, 1964	0	0	0	1
96	*Anacropora reticulata* Veron & Wallace, 1984	0	1	0	1
97	*Anacropora spinosa* Rehberg, 1892	0	0	0	1
98	*Astreopora cucullata* Lamberts, 1980	0	0	1	1
99	*Astreopora gracilis* Bernard, 1896	0	1	1	1
100	*Astreopora listeri* Bernard, 1896	0	1	0	1
101	*Astreopora myriophthalma* (Lamarck, 1816)	1	1	1	1
102	*Astreopora ocellata* Bernard, 1896	0	1	0	1
103	*Astreopora randalli* Lamberts, 1980	0	0	0	1
104	*Astreopora suggesta* Wells, 1954	0	0	0	1
105	*Enigmopora darveliensis* Ditlev, 2003	0	0	0	1
106	*Isopora brueggemanni* (Brook, 1893)	0	1	1	1
107	*Isopora crateriformis* (Gardiner, 1898)	0	1	0	0
108	*Isopora cuneata* (Dana, 1846)	0	1	1	1
109	*Isopora palifera* (Lamarck, 1816)	0	1	1	1
110	*Isopora togianensis* (Wallace, 1997)	0	1	0	0
111	*Montipora aequituberculata* Bernard, 1897	0	1	1	1
112	*Montipora altasepta* Nemenzo, 1967	0	1	0	1
113	*Montipora alveopora* Bernard, 1897	0	1	0	0
114	*Montipora angulata* (Lamarck, 1816)	0	1	1	0
115	*Montipora australiensis* Bernard, 1897	0	0	1	1
116	*Montipora cactus* Bernard, 1897	0	1	1	1
117	*Montipora calcarea* Bernard, 1897	0	1	0	0
118	*Montipora caliculata* (Dana, 1846)	0	1	0	1
119	*Montipora capitata* Dana, 1846	0	0	0	1
120	*Montipora capricornis* Veron, 1985	0	1	0	0
121	*Montipora cebuensis* Nemenzo, 1976	0	1	0	1
122	*Montipora cocosensis* Vaughan, 1918	0	1	0	0
123	*Montipora confusa* Nemenzo, 1967	0	1	0	1
124	*Montipora corbettensis* Veron & Wallace, 1984	0	1	1	1
125	*Montipora crassituberculata* Bernard, 1897	0	1	1	1
126	*Montipora danae* (Milne Edwards & Haime, 1851)	1	1	1	1
127	*Montipora delicatula* Veron, 2000	0	1	0	1
128	*Montipora digitata* (Dana, 1846)	1	1	1	1
129	*Montipora efflorescens* Bernard, 1897	0	0	1	1
130	*Montipora effusa* Dana, 1846	0	1	0	0

131	*Montipora elschneri* Vaughan, 1918	0	1	0	0
132	*Montipora florida* Nemenzo, 1967	0	1	1	1
133	*Montipora foliosa* (Pallas, 1766)	1	1	1	1
134	*Montipora foveolata* (Dana, 1846)	0	1	0	0
135	*Montipora friabilis* Bernard, 1897	0	1	0	0
136	*Montipora gaimardi* Bernard, 1897	0	1	0	0
137	*Montipora granulosa* Bernard, 1897	0	1	0	0
138	*Montipora grisea* Bernard, 1897	0	1	0	0
139	*Montipora hirsuta* Nemenzo, 1967	0	1	0	0
140	*Montipora hispida* (Dana, 1846)	1	1	1	1
141	*Montipora incrassata* (Dana, 1846)	0	1	0	1
142	*Montipora informis* Bernard, 1897	1	1	1	1
143	*Montipora mactanensis* Nemenzo, 1979	0	0	0	1
144	*Montipora malampaya* Nemenzo, 1967	0	1	0	1
145	*Montipora meandrina* (Ehrenberg, 1834)	0	1	0	0
146	*Montipora millepora* Crossland, 1952	0	1	0	1
147	*Montipora mollis* Bernard, 1897	0	1	1	0
148	*Montipora monasteriata* (Forskål, 1775)	0	1	1	1
149	*Montipora nodosa* (Dana, 1846)	0	1	0	0
150	*Montipora palawanensis* Veron, 2000	0	1	0	1
151	*Montipora peltiformis* Bernard, 1897	0	1	1	1
152	*Montipora solanderi* Bernard, 1897	0	1	1	0
153	*Montipora spongodes* Bernard, 1897	0	0	1	1
154	*Montipora spumosa* (Lamarck, 1816)	1	1	1	1
155	*Montipora stellata* Bernard, 1897	1	1	1	1
156	*Montipora tuberculosa* (Lamarck, 1816)	0	1	0	1
157	*Montipora turgescens* Bernard, 1897	0	0	0	1
158	*Montipora turtlensis* Veron & Wallace, 1984	0	1	1	0
159	*Montipora undata* Bernard, 1897	0	1	1	1
160	*Montipora venosa* (Ehrenberg, 1834)	1	1	0	1
161	*Montipora verrucosa* (Lamarck, 1816)	0	1	1	1
162	*Montipora verruculosa* Veron, 2000	0	1	0	1
163	*Montipora vietnamensis* Veron, 2000	0	1	0	1
	Agariciidae Gray, 1847				
164	*Coeloseris mayeri* Vaughan, 1918	0	0	1	1
165	*Gardineroseris planulata* (Dana, 1846)	0	1	1	1
166	*Leptoseris explanata* Yabe & Sugiyama, 1941	0	1	1	1
167	*Leptoseris foliosa* Dinesen, 1980	0	1	1	1
168	*Leptoseris fragilis* Milne Edwards & Haime, 1849	0	0	0	1
169	*Leptoseris gardineri* Van der Horst, 1921	0	1	1	1
170	*Leptoseris glabra* Dinesen, 1980	0	0	0	1
171	*Leptoseris hawaiiensis* Vaughan, 1907	0	1	1	1
172	*Leptoseris incrustans* (Quelch, 1886)	0	1	1	1
173	*Leptoseris mycetoseroides* Wells, 1954	0	1	1	1
174	*Leptoseris papyracea* (Dana, 1846)	0	1	1	1
175	*Leptoseris scabra* Vaughan, 1907	0	1	1	1
176	*Leptoseris solida* (Quelch, 1886)	0	0	1	1
177	*Leptoseris striata* Fenner & Veron, 2000	0	1	0	0

178	*Leptoseris tubulifera* Vaughan, 1907	0	1	1	1
179	*Leptoseris yabei* (Pillai & Scheer, 1976)	0	1	1	1
180	*Pavona bipartita* Nemenzo, 1979	0	1	0	1
181	*Pavona cactus* (Forskål, 1775)	0	1	1	1
182	*Pavona clavus* (Dana, 1846)	0	1	1	1
183	*Pavona danai* Milne Edwards & Haime, 1860	0	1	1	0
184	*Pavona decussata* (Dana, 1846)	1	1	1	1
185	*Pavona divaricata* Lamarck, 1816	1	0	0	1
186	*Pavona duerdeni* Vaughan, 1907	1	1	0	0
187	*Pavona explanulata* (Lamarck, 1816)	1	1	1	1
188	*Pavona frondifera* (Lamarck, 1816)	1	1	1	1
189	*Pavona maldivensis* (Gardiner, 1905)	0	1	1	1
190	*Pavona minuta* Wells, 1954	0	0	1	1
191	*Pavona varians* Verrill, 1864	1	1	1	1
192	*Pavona venosa* (Ehrenberg, 1834)	0	1	1	1
	Astrocoeniidae Koby, 1890				
193	*Madracis kirbyi* Veron & Pichon, 1976	0	1	1	1
194	*Palauastrea ramosa* Yabe & Sugiyama, 1941	0	1	1	1
195	*Stylocoeniella armata* (Ehrenberg, 1834)	0	0	0	1
196	*Stylocoeniella guentheri* (Bassett-Smith, 1890)	0	0	0	1
	Coscinaraeidae Benzoni, Arrigoni, Stefani & Stolarski, 2012				
197	*Coscinaraea columna* (Dana, 1846)	0	1	0	1
198	*Coscinaraea exesa* (Dana, 1846)	0	1	1	1
199	*Coscinaraea hahazimaensis* Yabe & Sugiyama, 1936	0	1	0	0
200	*Coscinaraea monile* (Forskål, 1775)	0	0	1	1
	Dendrophylliidae Gray, 1847				
201	*Turbinaria bifrons* Brüggermann, 1877	0	1	0	0
202	*Turbinaria crater* (Pallas, 1766)	0	1	0	0
203	*Turbinaria frondens* (Dana, 1846)	0	1	1	1
204	*Turbinaria heronensis* Wells, 1958	0	0	0	1
205	*Turbinaria irregularis* Bernard, 1896	0	1	0	1
206	*Turbinaria mesenterina* (Lamarck, 1816)	0	1	1	1
207	*Turbinaria mollis* Bernard, 1896	0	1	0	0
208	*Turbinaria patula* (Dana, 1846)	0	1	1	0
209	*Turbinaria peltata* (Esper, 1794)	1	1	1	1
210	*Turbinaria radicalis* Bernard, 1896	0	1	0	0
211	*Turbinaria reniformis* Bernard, 1896	0	1	1	1
212	*Turbinaria stellulata* (Lamarck, 1816)	0	1	1	1
	Diploastraeidae Chevalier & Beauvais, 1987				
213	*Diploastrea heliopora* (Lamarck, 1816)	1	1	1	1
	Euphylliidae Alloiteau, 1952				
214	*Catalaphyllia jardinei* (Saville-Kent, 1893)	0	0	0	1

215	*Euphyllia ancora* Veron & Pichon, 1980	0	1	1	1
216	*Euphyllia cristata* Chevalier, 1971	0	0	1	1
217	*Euphyllia divisa* Veron & Pichon, 1980	0	1	1	1
218	*Euphyllia fimbriata* (Splenger, 1799)	0	1	0	0
219	*Euphyllia glabrescens* (Chamisso & Eysenhardt, 1821)	0	1	1	1
220	*Euphyllia paraancora* Veron, 1990	0	0	1	1
221	*Euphyllia paradivisa* Veron, 1990	0	1	1	1
222	*Euphyllia paraglabrescens* Veron, 1990	0	1	0	0
223	*Euphyllia yaeyamaensis* (Shirai, 1980)	0	1	1	1
224	*Galaxea alta* Nemenzo, 1979	0	0	0	1
225	*Galaxea astreata* (Lamarck, 1816)	0	1	1	1
226	*Galaxea explanata* Quelch, 1886	0	1	0	0
227	*Galaxea fascicularis* (Linnaeus, 1767)	1	1	1	1
228	*Galaxea horrescens* (Dana, 1846)	0	1	0	1
229	*Galaxea paucisepta* Claereboudt, 1990	0	1	0	0
230	*Pachyseris foliosa* Veron, 1990	0	1	0	1
231	*Pachyseris gemmae* Nemenzo, 1955	0	1	1	1
232	*Pachyseris rugosa* (Lamarck, 1801)	0	1	1	1
233	*Pachyseris speciosa* (Dana, 1846)	1	1	1	1
	Fungiidae Dana, 1846				
234	*Ctenactis albitentaculata* Hoeksema, 1989	0	1	1	1
235	*Ctenactis crassa* (Dana, 1846)	0	1	1	1
236	*Ctenactis echinata* (Pallas, 1766)	0	1	1	1
237	*Cycloseris boschmai* Hoeksema, 2014	0	0	1	0
238	*Cycloseris costulata* (Ortmann, 1889)	0	1	1	1
239	*Cycloseris cyclolites* (Lamarck, 1816)	0	0	1	1
240	*Cycloseris explanulata* (Van der Horst, 1922)	0	1	0	1
241	*Cycloseris fragilis* (Alcock, 1893)	0	1	1	1
242	*Cycloseris mokai* (Hoeksema, 1989)	0	1	1	1
243	*Cycloseris sinensis* Milne Edwards & Haime, 1851	0	1	1	1
244	*Cycloseris somervillei* (Gardiner, 1909)	0	1	1	1
245	*Cycloseris tenuis* (Dana, 1846)	0	0	1	1
246	*Cycloseris vaughani* (Boschma, 1923)	0	0	1	1
247	*Cycloseris wellsi* (Veron & Pichon, 1980)	0	0	0	1
248	*Danafungia horrida* (Dana, 1846)	0	1	1	1
249	*Danafungia scruposa* (Klunzinger, 1879)	0	1	1	1
250	*Fungia fungites* (Linnaeus, 1758)	1	1	1	1
251	*Halomitra pileus* (Linnaeus, 1758)	0	0	1	1
252	*Heliofungia actiniformis* (Quoy & Gaimard, 1833)	0	1	1	1
253	*Heliofungia fralinae* (Nemenzo, 1955)	0	0	0	1
254	*Herpolitha limax* (Esper, 1797)	0	1	1	1
255	*Lithophyllon concinna* (Verrill, 1864)	0	1	1	1
256	*Lithophyllon ranjithi* Ditlev, 2003	0	0	0	1

257	*Lithophyllon repanda* (Dana, 1846)	0	1	1	1
258	*Lithophyllon scabra* (Döderlein, 1901)	0	1	1	1
259	*Lithophyllon spinifer* (Claereboudt & Hoeksema, 1987)	0	1	1	1
260	*Lithophyllon undulatum* Rehberg, 1892	0	1	1	1
261	*Lobactis scutaria* (Lamarck, 1801)	0	0	1	1
262	*Pleuractis granulosa* (Klunzinger, 1879)	0	1	1	1
263	*Pleuractis gravis (*Nemenzo, 1955)	0	1	1	1
264	*Pleuractis moluccensis* (Van der Horst, 1919)	0	1	1	1
265	*Pleuractis paumotensis* (Stutchbury, 1833)	0	1	1	1
266	*Pleuractis taiwanensis* (Hoeksema & Dai, 1991)	0	0	1	1
267	*Podabacia crustacea* (Pallas, 1766)	1	1	1	1
268	*Podabacia motuporensis* Veron, 1990	0	1	1	1
269	*Podabacia sinai* Veron, 2000	0	0	1	0
270	*Polyphyllia talpina* (Lamarck, 1801)	0	1	1	1
271	*Sandalolitha dentata* Quelch, 1884	0	1	1	1
272	*Sandalolitha robusta* (Quelch, 1886)	0	1	1	1
273	*Zoopilus echinatus* Dana, 1846	0	0	1	1
	Lobophylliidae Dai & Horng, 2009				
274	*Acanthastrea echinata* (Dana, 1846)	0	1	1	1
275	*Acanthastrea faviaformis* Veron, 2000	0	1	0	1
276	*Acanthastrea hemprichii* (Ehrenberg, 1834)	0	1	1	1
277	*Acanthastrea hillae* Wells, 1955	0	0	1	0
278	*Acanthastrea ishigakiensis* Veron, 1990	0	1	0	0
279	*Acanthastrea lordhowensis* Veron & Pichon, 1982	0	1	0	1
280	*Acanthastrea regularis* Veron, 2000	0	1	0	0
281	*Acanthastrea rotundoflora* Chevalier, 1975	0	1	0	1
282	*Acanthastrea subechinata* Veron, 2000	0	0	0	1
283	*Cynarina lacrymalis* (Milne Edwards & Haime, 1849)	0	1	1	1
284	*Echinomorpha nishihirai* (Veron, 1990)	0	0	0	1
285	*Echinophyllia aspera* (Eillis & Solander, 1786)	0	1	1	1
286	*Echinophyllia echinata* (Saville-Kent, 1871)	0	1	1	1
287	*Echinophyllia echinoporoides* Veron & Pichon, 1980	0	0	0	1
288	*Echinophyllia orpheensis* Veron & Pichon, 1980	0	1	1	1
289	*Echinophyllia patula* (Hodgson & Ross, 1981)	0	0	0	1
290	*Homophyllia australis* (Milne Edwards & Haime, 1849)	0	1	1	0
291	*Lobophyllia corymbosa* (Forskål, 1775)	0	1	1	1
292	*Lobophyllia dentata* Veron, 2000	0	1	0	0
293	*Lobophyllia diminuta* Veron, 1985	0	1	0	1
294	*Lobophyllia flabelliformis* Veron, 2000	0	1	1	1
295	*Lobophyllia hataii* Yabe, Sugiyama & Eguchi, 1936	0	1	1	1
296	*Lobophyllia hemprichii* (Ehrenberg, 1834)	1	1	1	1
297	*Lobophyllia pachysepta* Chevalier, 1975	0	1	0	1
298	*Lobophyllia robusta* Yabe & Sugiyama, 1936	0	1	0	1

299	*Micromussa minuta* (Moll & Best, 1984)	0	0	0	1
300	*Montastrea multipunctata* Hodgson, 1985	0	1	0	0
301	*Oxypora crassispinosa* Nemenzo, 1979	0	1	1	1
302	*Oxypora glabra* Nemenzo, 1959	0	1	0	1
303	*Oxypora lacera* (Verrill, 1864)	0	1	1	1
304	*Parascolymia vitiensis* (Brüggemann, 1877)	0	1	0	1
305	*Symphyllia agaricia* Milne Edwards & Haime, 1849	0	1	0	1
306	*Symphyllia hassi* Pillai & Scheer, 1976	0	1	0	1
307	*Symphyllia radians* Milne Edwards & Haime, 1849	0	1	1	1
308	*Symphyllia recta* (Dana, 1846)	1	1	1	1
309	*Symphyllia valenciennesii* Milne Edwards & Haime, 1849	0	1	0	1
	Merulinidae Verrill, 1865				
310	*Astrea annuligera* Milne Edwards & Haime, 1849	0	1	0	0
311	*Astrea curta* Dana, 1846	0	1	1	1
312	*Australogyra zelli* (Veron, Pichon & Wijsman-Best, 1977)	0	1	0	0
313	*Caulastraea curvata* Wijsman-Best, 1972	0	0	0	1
314	*Caulastraea echinulata* (Milne Edwards & Haime, 1849)	0	0	1	1
315	*Caulastraea furcata* Dana, 1846	0	0	1	1
316	*Caulastraea tumida* Matthai, 1928	0	1	0	1
317	*Coelastrea aspera* (Verrill, 1866)	0	1	1	1
318	*Coelastrea palauensis* (Yabe & Sugiyama, 1936)	0	1	0	1
319	*Cyphastrea agassizi* (Vaughan, 1907)	0	1	0	0
320	*Cyphastrea chalcidicum* (Forskål, 1775)	1	1	1	1
321	*Cyphastrea decadia* Moll & Best, 1984	0	0	0	1
322	*Cyphastrea japonica* Yabe & Sugiyama, 1932	0	1	0	1
323	*Cyphastrea microphthalma* (Lamarck, 1816)	0	1	1	1
324	*Cyphastrea ocellina* (Dana, 1846)	0	1	0	0
325	*Cyphastrea serailia* (Forskål, 1775)	0	1	1	1
326	*Dipsastraea albida* (Veron, 2000)	0	1	0	0
327	*Dipsastraea amicorum* (Milne Edwards & Haime, 1849)	0	1	1	1
328	*Dipsastraea danae* (Milne Edwards & Haime, 1857)	0	1	0	0
329	*Dipsastraea favus* (Forskål, 1775)	0	1	1	1
330	*Dipsastraea helianthoides* (Wells, 1954)	0	1	0	1
331	*Dipsastraea laxa* (Klunzinger, 1879)	0	1	0	1
332	*Dipsastraea lizardensis* (Veron, Pichon & Wijsman-Best, 1977)	0	1	1	1
333	*Dipsastraea maritima* (Nemenzo, 1971)	0	1	1	1
334	*Dipsastraea marshae* (Veron, 2000)	0	1	0	0
335	*Dipsastraea matthaii* (Vaughan, 1918)	0	1	1	1
336	*Dipsastraea maxima* (Veron, Pichon & Wijsman-Best, 1977)	0	1	1	1
337	*Dipsastraea pallida* (Dana, 1846)	0	1	1	1
338	*Dipsastraea rosaria* (Veron, 2000)	0	1	0	0
339	*Dipsastraea rotumana* (Gardiner, 1899)	0	1	1	1
340	*Dipsastraea speciosa* (Dana, 1846)	1	1	1	1

341	*Dipsastraea truncata* (Veron, 2000)	0	1	0	1
342	*Dipsastraea veroni* (Moll & Best, 1984)	0	1	1	1
343	*Dipsastraea vietnamensis* (Veron, 2000)	0	1	0	0
344	*Dipsastraea wisseli* (Scheer & Pillai, 1983)	0	0	0	1
345	*Echinopora gemmacea* (Lamarck, 1816)	0	1	1	1
346	*Echinopora hirsutissima* Milne Edwards & Haime, 1849	0	0	1	1
347	*Echinopora horrida* Dana, 1846	0	1	1	1
348	*Echinopora lamellosa* (Esper, 1795)	0	1	1	1
349	*Echinopora mammiformis* (Nemenzo, 1959)	0	1	1	1
350	*Echinopora pacificus* Veron, 1990	0	1	0	1
351	*Favites abdita* (Ellis & Solander, 1786)	1	1	1	1
352	*Favites acuticollis* (Ortmann, 1889)	0	1	0	0
353	*Favites chinensis* (Verrill, 1866)	0	1	0	1
354	*Favites colemani* (Veron, 2000)	0	1	0	1
355	*Favites complanata* (Ehrenberg, 1834)	0	1	0	1
356	*Favites flexuosa* (Dana, 1846)	0	1	1	1
357	*Favites halicora* (Ehrenberg, 1834)	0	1	1	1
358	*Favites magnistellata* (Chevalier, 1971)	0	1	1	1
359	*Favites melicerum* (Ehrenberg, 1834)	0	1	0	0
360	*Favites micropentagonus* Veron, 2000	0	1	0	0
361	*Favites paraflexuosus* Veron, 2000	0	1	0	1
362	*Favites pentagona* (Esper, 1794)	0	1	1	1
363	*Favites rotundata* Veron, Pichon & Wijsman-Best, 1977	0	1	1	1
364	*Favites russelli* (Wells, 1954)	0	1	0	0
365	*Favites spinosa* (Klunzinger, 1879)	0	1	0	0
366	*Favites stylifera* (Yabe & Sugiyama, 1937)	0	1	0	0
367	*Favites valenciennesi* (Milne Edwards & Haime, 1849)	0	1	1	1
368	*Goniastrea edwardsi* Chevalier, 1971	0	1	1	1
369	*Goniastrea favulus* (Dana, 1846)	0	1	0	0
370	*Goniastrea minuta* Veron, 2000	0	1	0	1
371	*Goniastrea pectinata* (Ehrenberg, 1834)	1	1	1	1
372	*Goniastrea retiformis* (Lamarck, 1816)	1	1	1	1
373	*Goniastrea stelligera* (Dana, 1846)	0	1	1	1
374	*Hydnophora exesa* (Pallas, 1766)	0	1	1	1
375	*Hydnophora grandis* Gardiner, 1904	0	1	0	1
376	*Hydnophora microconos* (Lamarck, 1816)	1	1	1	1
377	*Hydnophora pilosa* Veron, 1985	0	0	1	0
378	*Hydnophora rigida* (Dana, 1846)	1	1	1	1
379	*Leptoria irregularis* Veron, 1990	0	0	0	1
380	*Leptoria phrygia* (Ellis & Solander, 1786)	0	1	1	1
381	*Merulina ampliata* (Ellis & Solander, 1786)	1	1	1	1
382	*Merulina scabricula* Dana, 1846	0	1	0	1
383	*Mycedium elephantotus* (Pallas, 1766)	1	1	1	1
384	*Mycedium mancaoi* Nemenzo, 1979	0	0	0	1

385	*Mycedium robokaki* Moll & Best, 1984	0	1	0	1
386	*Mycedium spina* Ditlev, 2003	0	0	0	1
387	*Oulophyllia bennettae* (Veron, Pichon & Wijsman-Best, 1977)	0	1	0	1
388	*Oulophyllia crispa* (Lamarck, 1816)	0	1	0	1
389	*Oulophyllia levis* (Nemenzo, 1959)	0	1	0	0
390	*Paragoniastrea australensis* (Milne Edwards & Haime, 1857)	1	1	1	1
391	*Paragoniastrea russelli* (Wells, 1954)	0	0	0	1
392	*Paramontastraea salebrosa* (Nemenzo, 1959)	0	1	0	1
393	*Pectinia alcicornis* (Saville-Kent, 1871)	0	1	1	1
394	*Pectinia crassa* Ditlev, 2003	0	0	0	1
395	*Pectinia lactuca* (Pallas, 1766)	1	1	1	1
396	*Pectinia maxima* (Moll & Best, 1984)	0	1	1	1
397	*Pectinia paeonia* (Dana, 1846)	0	1	1	1
398	*Platygyra acuta* Veron, 2000	0	1	1	0
399	*Platygyra carnosa* Veron, 2000	0	1	0	0
400	*Platygyra contorta* Veron, 1990	0	0	0	1
401	*Platygyra crosslandi* Matthai, 1928	0	1	0	0
402	*Platygyra daedalea* (Ellis & Solander, 1786)	0	1	1	1
403	*Platygyra lamellina* (Ehrenberg, 1834)	1	1	1	1
404	*Platygyra pini* Chevalier, 1975	0	1	1	1
405	*Platygyra ryukyuensis* Yabe & Sugiyama, 1936	0	1	0	1
406	*Platygyra sinensis* (Milne Edwards & Haime, 1849)	0	1	1	1
407	*Platygyra verweyi* Wijsman-Best, 1976	0	1	0	0
408	*Platygyra yaeyamaensis* Eguchi & Shirai, 1977	0	1	0	0
409	*Scapophyllia cylindrica* Milne Edwards & Haime, 1849	0	1	1	1
410	*Trachyphyllia geoffroyi* (Audouin, 1826)	0	1	1	1
	Pocilloporidae Gray, 1842				
411	*Pocillopora damicornis* (Linnaeus, 1758)	1	1	1	1
412	*Pocillopora danae* Verrill, 1864	0	1	0	0
413	*Pocillopora grandis* Dana, 1846	1	1	1	1
414	*Pocillopora meandrina* Dana, 1846	0	1	0	1
415	*Pocillopora verrucosa* (Ellis & Solander, 1786)	1	1	1	1
416	*Pocillopora woodjonesi* Vaughan, 1918	0	0	1	0
417	*Seriatopora caliendrum* Ehrenberg, 1834	0	0	1	1
418	*Seriatopora hystrix* Dana, 1846	0	1	1	1
419	*Seriatopora stellata* Quelch, 1886	0	0	1	0
420	*Stylocoeniella armata* (Ehrenberg, 1834)	0	1	0	0
421	*Stylocoeniella cocosensis* Veron, 1990	0	1	0	0
422	*Stylocoeniella guentheri* Bassett-Smith, 1890	0	1	1	0
423	*Stylophora pistillata* Esper, 1797	0	1	1	1
424	*Stylophora subseriata* (Ehrenberg, 1834)	0	1	1	1
	Poritidae Gray, 1842				
425	*Goniopora cellulosa* Veron, 1990	0	0	0	1

426	*Goniopora ciliatus* Veron, 2000	0	1	0	0
427	*Goniopora columna* Dana, 1846	0	1	1	1
428	*Goniopora djiboutiensis* Vaughan, 1907	0	1	1	1
429	*Goniopora eclipsensis* Veron & Pichon, 1982	0	1	1	0
430	*Goniopora fruticosa* Saville-Kent, 1893	0	1	0	1
431	*Goniopora lobata* Milne Edwards & Haime, 1860	1	1	1	0
432	*Goniopora minor* Crossland, 1952	0	1	1	0
433	*Goniopora norfolkensis* Veron & Pichon, 1982	0	1	0	1
434	*Goniopora palmensis* Veron & Pichon, 1982	0	1	1	0
435	*Goniopora pandoraensis* Veron & Pichon, 1982	0	0	1	1
436	*Goniopora pedunculata* Quoy & Gaimard, 1833	0	0	0	1
437	*Goniopora pendulus* Veron, 1985	0	1	0	0
438	*Goniopora planulata* (Ehrenberg, 1834)	0	1	0	0
439	*Goniopora savignyi* Dana, 1846	0	1	0	0
440	*Goniopora somaliensis* Vaughan, 1907	0	1	0	1
441	*Goniopora stokesi* Milne Edwards & Haime, 1851	0	1	0	1
442	*Goniopora stutchburyi* Wells, 1955	0	0	0	1
443	*Goniopora tenella* (Quelch, 1886)	1	0	0	0
444	*Goniopora tenuidens* (Quelch, 1886)	0	1	1	1
445	*Porites annae* Crossland, 1952	0	1	1	1
446	*Porites aranetai* Nemenzo, 1955	0	1	0	0
447	*Porites attenuata* Nemenzo, 1955	0	1	0	1
448	*Porites australiensis* Vaughan, 1918	0	1	1	0
449	*Porites cocosensis* Wells, 1950	0	1	0	0
450	*Porites compressa* Dana, 1846	1	0	0	0
451	*Porites cumulatus* Nemenzo, 1955	0	1	0	0
452	*Porites cylindrica* Dana, 1846	0	1	1	1
453	*Porites densa* Vaughan, 1918	0	1	1	0
454	*Porites echinulata* Klunzinger, 1879	0	1	0	0
455	*Porites evermanni* Vaughan, 1907	0	1	0	1
456	*Porites horizontalata* Hoffmeister, 1925	0	1	0	1
457	*Porites latistellata* Quelch, 1886	0	1	0	1
458	*Porites lichen* Dana, 1846	1	1	1	1
459	*Porites lobata* Dana, 1846	0	1	1	1
460	*Porites lutea* Milne Edwards & Haime, 1851	1	1	1	1
461	*Porites mayeri* Vaughan, 1918	0	1	1	0
462	*Porites monticulosa* Dana, 1846	0	1	0	1
463	*Porites murrayensis* Vaughan, 1918	0	1	1	1
464	*Porites negrosensis* Veron, 1990	0	1	0	1
465	*Porites nigrescens* Dana, 1846	1	1	1	1
466	*Porites ornata* Nemenzo, 1971	0	0	0	1
467	*Porites pukoensis* Vaughan, 1907	0	0	0	1
468	*Porites rus* (Forskål, 1775)	1	1	1	1
469	*Porites sillimaniana* Nemenzo, 1976	0	0	0	1

470	*Porites solida* (Forskål, 1775)	0	1	1	1
471	*Porites stephensoni* Crossland, 1952	0	0	1	0
472	*Porites superfusa* Gardiner, 1898	1	0	0	0
473	*Porites tenuis* Verrill, 1866	1	1	0	0
474	*Porites vaughani* Crossland, 1952	0	0	0	1
475	*Poritipora paliformis* Veron, 2000	0	1	0	0
476	*Stylaraea punctata* (Linnaeus, 1758)	0	1	0	0
	Psammocoridae Chevalier & Beauvais, 1987				
477	*Psammocora contigua* (Esper, 1797)	1	1	1	1
478	*Psammocora digitata* Milne Edwards & Haime, 1851	0	1	1	1
479	*Psammocora haimiana* Milne Edwards & Haime, 1851	0	1	0	1
480	*Psammocora nierstraszi* Van der Horst, 1921	0	1	0	0
481	*Psammocora profundacella* Gardiner, 1898	0	1	0	1
482	*Psammocora superficialis* Gardiner, 1898	0	1	0	0
	Siderastreidae Vaughan & Wells, 1943				
483	*Pseudosiderastrea tayami* Yabe & Sugiyama, 1935	0	1	1	1
	Scleractinia Incertae sedis				
484	*Blastomussa merleti* (Wells, 1961)	0	1	0	0
485	*Blastomussa wellsi* Wijsman-Best, 1973	0	1	0	0
486	*Catalaphyllia jardinei* (Saville-Kent, 1893)	0	1	1	0
487	*Leptastrea aequalis* Veron, 2000	0	1	0	0
488	*Leptastrea bottae* (Milne Edwards & Haime, 1849)	0	0	0	1
489	*Leptastrea pruinosa* Crossland, 1952	0	1	1	1
490	*Leptastrea purpurea* (Dana, 1846)	0	1	1	1
491	*Leptastrea transversa* Klunzinger, 1879	1	1	0	1
492	*Nemenzophyllia turbida* Hodgson & Ross, 1981	0	0	0	1
493	*Oulastrea crispata* (Lamarck, 1816)	0	1	1	0
494	*Parasimplastrea omanensis* Sheppard, 1985	0	1	0	0
495	*Physogyra lichtensteini* (Milne Edwards & Haime, 1851)	0	1	1	1
496	*Plerogyra cauliformis* Ditlev, 2003	0	0	0	1
487	*Plerogyra diabolotus* Ditlev, 2003	0	0	0	1
498	*Plerogyra multilobata* Ditlev, 2003	0	0	1	1
499	*Plerogyra simplex* Rehberg, 1892	0	0	1	1
500	*Plerogyra sinuosa* (Dana, 1846)	1	1	1	1
501	*Plesiastrea versipora* (Lamarck, 1816)	0	1	0	1
	Total	**56**	**398**	**248**	**382**

Chapter 2

A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia

Zarinah Waheed and Bert W. Hoeksema

Abstract

The highest concentration of Malaysian coral reefs is found in the coastal area of Semporna, eastern Sabah, which is located just within the boundaries of the Coral Triangle, the area of maximum marine species diversity. The Semporna reefs consist of five major geomorphological reef types, which include lagoonal reefs inside a proto-atoll, fringing reefs, continental patch reefs, a barrier reef and a reef capping an oceanic island. Surveys were carried out in this area to compare the species richness patterns of the scleractinian coral families Agariciidae, Euphylliidae, and Fungiidae from nearshore to offshore reefs. In total, 44 species of Fungiidae, 31 Agariciidae and 15 Euphylliidae have been observed, including 12 new records for Sabah and four records that are so far considered endemic to northeast Borneo. Based on coral species compositions for each site, multivariate analyses suggest the distinction of two main groups that reflect a difference in reef exposure, with a gradient in increasing coral diversity from the relatively sheltered nearshore reefs to the exposed barrier reef. Some reefs have been damaged by blast fishing, a threat still prevalent in the area. Nevertheless, the high coral species diversity is remarkable and to date Semporna holds the record for the highest species richness of Fungiidae, which surpasses records from other areas in the Coral Triangle.

Marine Biodiversity (2013) 43: 37–51. doi:10.1007/s12526-012-0130-7

Introduction

Species richness of coral reefs is driven by an array of factors including geological history, ecological processes and physical environment (Hoeksema 2007; Veron et al. 2009), of which habitat heterogeneity is paramount (Hoeksema and Moka 1989; Cornell and Karlson 1996; Karlson, 1999; Karlson and Cornell 1999). High species diversity of scleractinian corals is usually found in habitats with distinct environmental gradients, such as exposure to wind, wave and terrestrial inputs (Cleary et al. 2005; Hoeksema 2007, 2012a). Several studies on the onshore-offshore species richness patterns of scleractinian corals have been carried out in tropical coral reef systems (Done 1982, 1983; Moll 1983; Moll and Suharsono 1986; Hoeksema 1993a, 2012a; Cleary et al. 2005, 2006; Becking et al 2006; DeVantier et al. 2006; Van der Meij et al. 2010). These studies conclude that different reef systems from onshore to offshore may have distinct coral composition and community structure. In Malaysia, few published studies on scleractinian species richness patterns and coral reefs in general have been conducted (Harborne et al. 2000; Toda et al. 2007). Consequently, in the eastern state of Sabah, the coral fauna is poorly investigated (but see Wood and Tan 1987; Fenner 2001; Ditlev 2003).

Sabah contains more than 75% of Malaysian reefs (Burke et al. 2002). High concentrations of reefs are found in the Banggi group of islands in the north and in the Semporna islands reef complex in the southeast of Sabah, both of which are within the Coral Triangle (Veron et al. 2009). The first mention of Semporna’s corals was in relation to using raised coral limestone as building materials (Fitch 1950; Roe 1951). Later, the presence of coral reefs was reported by Kirk (1962), with a further account in a note by Morris (1973). Subsequent studies covered larger areas, and described in detail the physical characteristics of the coral reefs (Morris 1978; Wood 1987), with information of the species diversity and distribution of scleractinian corals (Wood and Tan 1987), macro-invertebrates (George and George 1987), and fish (Wood and Wood 1987) of the Bodgaya Islands and Sipadan Island. Ekspedisi Galaxea ’98 reported the status of corals reefs and adjacent ecosystems in Darvel Bay, which is Sabah’s largest bay, situated to the north of Semporna (Ditlev et al. 1999). Since then, apart from a few Reef Check surveys that were carried out under the collaboration of Sabah Parks, Marine Conservation Society (MCS) and WWF-Malaysia, the reefs of Semporna and Darvel Bay have remained under-studied, with little published scientific information available (Wood et al. 2004; Wood and Dipper 2008; Ho and Kassem 2009; Affendi et al. 2012).

Wood (1977, 1978, 2001) indicated that although the reefs of Semporna were among the best in Sabah in terms of reef life diversity, there were signs of threats to the area. In addition to the natural threat of predation by *Acanthaster planci* (Linnaeus, 1758) (see Morris 1977; Wood 1978), blast fishing has been evident since the late 1970s and continues up to the present (Wood 1977, 1978; 2006a; Wood et al. 2008). Other unsustainable fishing practices in the area include cyanide fishing and muro ami (Pilcher and Cabanban 2000). Tourism, albeit not considered a threat, has caused some pressure on reefs that have been popular diving destinations since the 1980s, such as Sipadan and Mabul. Increasingly, other reefs in the Semporna area are being promoted for dive tourism, including those around Mataking, Pom Pom and all of the islands within the Tun Sakaran Marine Park (see Table 1, Fig. 1).

Information on the marine biodiversity of the Semporna region is fragmented because so far only parts of the area have been surveyed in various studies, each using different methods. The area features various geomorphological reef types, including lagoonal reefs inside a proto-atoll, fringing reefs, patch reefs, a barrier reef and a reef capping an oceanic island (Wood 1987, 1994). Together, they represent various different reef environments that may harbour a high diversity of coral reef species, some of which are considered rare or even endemic. Therefore, the area as a whole is suitable to study marine biodiversity patterns from nearshore to offshore reefs in which environmental variables can be taken into account, such as predominant wind direction (see e.g. Moll 1983; Cleary et al. 2005; Hoeksema 2012a). The purpose of the present study is to discern such diversity patterns for three scleractinian coral families, which were used as proxy for all scleractinian reef coral species. These patterns also include the distributions of rare species, and in particular endemics. Eventually, the results can be applied in planning conservation management strategies involving the use of natural resources relating to subsistence fisheries and dive tourism (see Wood 2001, 2006b).

Materials and methods

Research area

The barrier reef of the Semporna reef complex lies in the south of the Semporna peninsula and is composed of a chain of small islands and reefs referred to as the Ligitan group of islands and reefs (Wood 1978). The reefs facing the Ligitan Channel in the north are relatively shallow (< 20 m), while those facing the south extend deeper (> 50 m) and are exposed to oceanic elements (Fig. 1). These reefs are not well described with the exception of Sipadan Is. (Wood 1987; Wood and Tan 1987; Wood 1994; Isley et al. 2005) and Mabul Is. (Aw 2009). The oceanic island of Sipadan lies 12 km south of the barrier reef at the end of the continental shelf and has been proposed as a park. Towards the E–NE of the Semporna peninsula, at the entrance of Darvel Bay, is the Bodgaya reef complex gazetted as the Tun Sakaran Marine Park. There are eight islands in the park of which the two largest islands are part of a proto-atoll with a lagoon of 25 m depth (Wood 1987, 2001). Further to the east are several islands with Mataking Is. at the easternmost. The reefs in the N–NW of Semporna are situated in Darvel Bay and are composed of fringing and patch reefs. They are sheltered and characterised by turbid waters with high humic content, especially towards the inner part of the bay (Ditlev 2003).

There are several small rivers near the Semporna peninsula. The Kalumpang and Balung rivers flow southwards into the western part of the barrier reefs, while the Pegagau River flows northwards into the bay, but it is blocked by Pababag Is. Terrigenous input is possibly the cause of the relatively turbid waters on the nearshore reefs in the north and the islands within the bay.

The wet season is during the northeast monsoon that occurs from December to January while the southeast monsoon is during June and July. The transition periods bring variable wind patterns and rainfall (Wood 1994). The outer reefs of Darvel Bay and the Bodgaya reef complex are exposed to the northeast monsoon (Wood 1987; De Silva et al. 1999) and are sheltered from the southwesterly winds by the Semporna peninsula and Bum Bum Is. (Wood 1994). The barrier reefs are exposed to the winds from the south and the east (Wood 1987). Average wind distribution values throughout the year shows that the dominant wind direction is from the S–SE, although the predominant current direction is from north to south and remains moderately constant throughout the year (Wyrtki 1961). The tidal range varies between 1.2 and 2 m (Wood 1987).

Field sampling

The research study was carried out during the Semporna Marine Ecological Expedition (SMEE 2010) in Semporna, Sabah (5°57'–6°5' N, 115°59'–116°5' E) from 29 November to 18 December 2010. A total of 63 sites (1–40 m depth) were surveyed in a south-north direction, varying from nearshore to offshore reefs that are less than 50 km from mainland (Fig. 1). The sites were selected based on navigation charts (British Admiralty Charts nos. 1680 and 1681), reconnaissance dives in 2009, and local knowledge on popular tourist dive sites. The selection was designed to cover as much habitat diversity and geographical range as possible.

A species inventory of the coral families Fungiidae, Agariciidae and Euphylliidae was made at each site by employing the roving diver technique (Schmitt et al. 2002; Munro 2005; Hoeksema and Koh 2009). These three families were chosen for this study because they have a wide geographical distribution and are found in various reef habitats. They are also easily distinguishable from other coral families on the reef. All coral specimens were identified according to species concepts presented in taxonomic revisions and coral fauna descriptions: Dinesen 1980; Veron and Pichon 1980; Hoeksema 1989; Veron 2000; Ditlev 2003). The classification of the Fungiidae was adapted according to a recent phylogenetic construction of this family (Gittenberger et al. 2011). Photographs of each species encountered were taken and when in situ identification was not possible, specimens were collected for further examination. Collected specimens were deposited in the Borneo Marine Research Institute reference collection in Universiti Malaysia Sabah (UMS) in Kota Kinabalu. The species list was then compared to those of previous studies.

Data analysis

Data on the presence/absence of coral species per site surveyed were used for species richness analyses. For the coral families Agariciidae and Euphylliidae, data were collected at 59 sites, and for the Fungiidae at all 63 sites. The species richness estimators were calculated using the EstimateS 8.0 computer software (Colwell 2009), in which the sample order is randomized and the values are averaged. The mean and standard deviation of species richness at each sample number are calculated and the curves are extrapolated to estimate the total species richness in an area. The species accumulation curves show the rate at which additional species are found and more sampling will uncover more species, making the accumulation curves arch upwards (Magurran 2004). When the curves flatten out and reach an asymptote with minimal standard deviation, additional species are unlikely to be discovered. Indicators based on incidence (presence/absence) data are Chao 2, ICE, S Obs and Unique values (Colwell 2009).

Table 1. Sites, their proximity to shore or land (Off = offshore; Near = nearshore), and exposure to wind (S = exposed to the southern winds; N = exposed to the northern winds; I = intermediate reefs between the latter two; C = reefs along the coastline).

No.	Site	Proximity to shore/land	Exposure to wind
1	Roach Reef, Mid Rock	Off	S
2	NW Roach Reef, Second Reef	Off	S
3	SE of Tawau, Hand Rock	Off	S
4	SE of Tawau, Darby Rock	Off	S
5	SE of Tawau, Alert Patches 2	Off	S
6	SE of Tawau, Alert Patches 3	Off	S
7	Erzherzog Reef	Off	S
8	Horn Reef	Off	S
9	S Ligitan Reef, Yoshi Point	Off	S
9b	Mabul Is., N Ligitan Reef, Paradise 2	Off	S
10	Kapalai	Off	S
11	W Cust Reef	Off	S
12	Mabul Is., Eel garden	Off	S
13	Ligitan Is. 1	Off	S
14	Ligitan Is. 2	Off	S
15	Ligitan Is. 3	Off	S
16	Si Amil Is., Second beach	Off	S
17	Denawan Is.	Off	S
18	Ligitan Is. 4	Off	S
19	Cust Reef 2	Off	S
20	Creach Reef	Off	S
21	Sipanggau Is.	Near	S
22	W Bumbun Is. (channel)	Near	C
23	Pasalat Reef	Off	I
24	Bumbun Is., Tg. Pantau Pantau	Off	I
25	Batura Reef	Off	I
26	Bohayen Is.	Off	I
27	Timba Timba Is.	Off	I
28	Pandanan Is.	Off	I
29	Mataking Is.	Off	I
30	S Kulapuan Is.	Off	I
31	N Kulapuan Is.	Off	I
32	Pom pom Is.	Off	I
33	Kapikan Reef	Off	N
34	Mantabuan Is.	Off	N
35	Gaya Is.	Near	N
36	N Gaya Is.	Near	N
36b	NW Gaya Is.	Near	N
37	S Boheydulang Is., outer reef	Near	N
38	Boheydulang Is., outer reef lagoon	Near	N

Table 1 cont.

No.	Site	Proximity to shore/land	Exposure to wind
39	Tetagan Is., inner lagoon	Near	N
40	Ribbon Reef	Near	N
41	Maiga Is.	Off	N
42	Selakan Is.	Near	N
43	Sebangkat Is.	Near	N
43b	Singamata Pancang	Near	C
44	Sibuan Is.	Off	N
45	Church Reef 1	Off	N
46	Church Reef 2	Off	N
47	Larapan Is.	Near	C
48	Timbun Mata Is.	Near	N
49/49b	Balusuan Is.	Off	N
50	Batik Is.	Near	N
51	Tabawan Is.	Near	N
52	Silumpat Is.	Near	N
53	Batik Kulambu Is.	Near	N
54	Bakungan Is.	Off	N
55	Silawa Is.	Near	C
56	Mata Pahi Is.	Near	C
57	S Larapan Is. 2	Near	C
58	Semporna town, mangrove area	Near	C
59	Sipadan Is., Baracuda Point	Off	S
60	Sipadan Is., Hanging Gardens	Off	S

Multivariate analyses of the coral species composition were conducted for 59 sites (where data were collected for all families) using the Plymouth Routines in Multivariate Ecological Research (PRIMER) v.6 software (Clarke and Warwick 2001; Clarke and Gorley 2006). A resemblance matrix based on the Bray-Curtis similarity measure was used to determine the similarity between sites. The Bray-Curtis similarity index is equivalent to the Sorenson similarity index when used on presence/absence data (Clarke and Gorley 2006). A group-averaged hierarchical clustering dendrogram and multi-dimensional scaling (MDS) plots were generated from the Bray-Curtis resemblance matrix to show the grouping of sites based on the species composition. Similarity profiles (SIMPROF) were derived from the dendrogram and contours were applied to the MDS plots to show significant groupings of the sites. These groupings were then illustrated on the map to highlight the species richness and distribution patterns. The analysis of similarities (ANOSIM) was employed to test for differences among the a priori group classified by reef type based on proximity to shore and wind exposure (Table 1). Similarity percentages (SIMPER) analysis was attempted to determine whether characteristic species of each group, and species that contributed most to the dissimilarities among the groups could be discerned from presence/absence data.

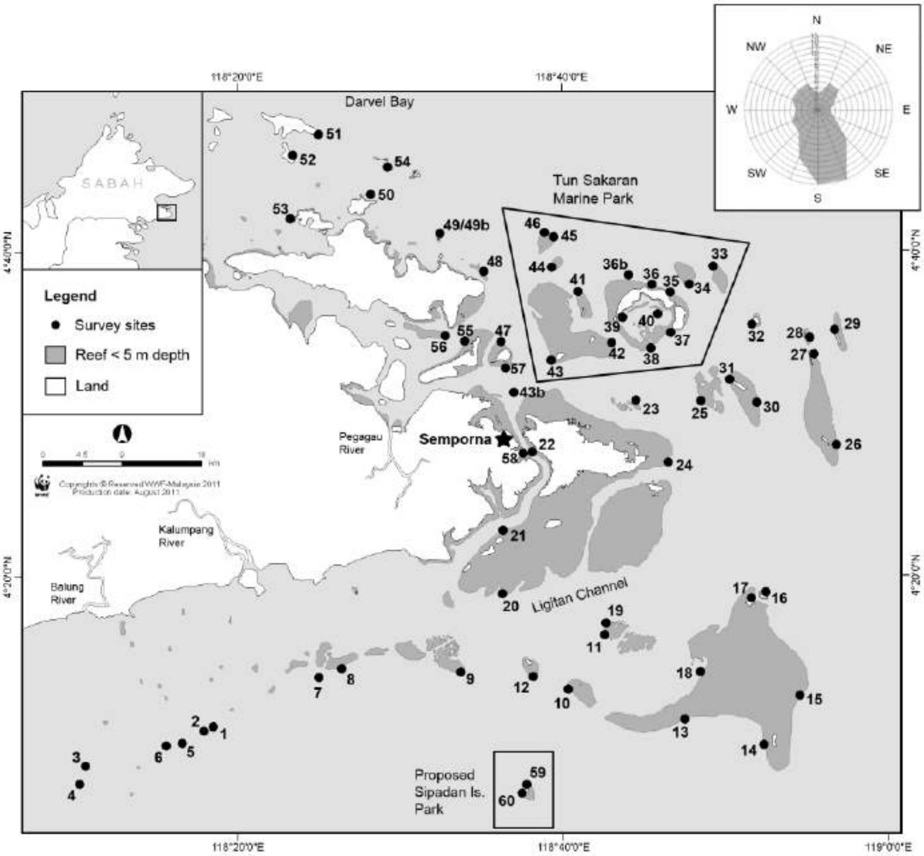


Fig. 1. The research area showing the 63 sampling sites with average wind distribution values from various directions year-round in 2011. The park boundaries are approximate. Dominant wind direction is from the S and SSE. Average wind speed is given in knots. Statistics are based on observations taken from the Tawau Airport between December 2010 to December 2011 from ©windfinder.com

Results

A total of 44 species of mushroom corals were recorded from 63 sites, whereas 31 species of agariciids and 15 species of euphylliids were documented from 59 sites (Table S1). Twelve species represent new records for Sabah: *Cantharellus jebbi*, *Cycloseris distorta*, *C. curvata*, *C. hexagonalis*, *Cycloseris* spec., *Lithophyllon spinifer*, the recently described *Sandalolitha boucheti* (see Hoeksema 2012b), *Halomitra clavator*, *Podabacia sinai*, *Leptoseris amitoriensis*, *Pavona danai* and *P. duerdeni*. Seven Agariciidae, two Euphylliidae and 15 Fungiidae have been added as new records for Semporna and Darvel Bay (Fig. 2, Table S2). Species richness estimators were applied to compare the observed and expected species richness. The species accumulation curves show that the estimated species numbers (ICE, Chao 2) for mushroom corals reached the observed species number very closely with an error of less than one. According to this model, additional sampling could reveal one more species (Fig. 3a). The species accumulation curves for agariciid and euphyliid corals show that the estimated species numbers (ICE, Chao 2) reached the observed species number asymptotically, therefore, sampling effort has been sufficient and additional sampling would not have resulted in more species (Fig. 3b, c).

Coral species composition of the sites varied with reef type, predominant wind direction and distance offshore. The number of species per site ranged from 24 at Ligitan Is. reef on the easternmost site of the barrier reef (site 15) to 55 at Batik Kulambu Is. in Darvel Bay (site 53). Species that were found at all sites are the mushroom corals *Herpolitha limax*, *Lithophyllon repanda, Pleuractis granulosa*, and *Podabacia crustacea*. Other coral species represented in at least 75% of the sites (n ≥ 45) were 12 Fungiidae (*Cycloseris costulata*, *Ctenactis echinata*, *C. crassa, Danafungia horrida, D. scruposa, Fungia fungites*, *Heliofungia actiniformis*, *Lithophyllon concinna*, *Pleuractis gravis, P. moluccensis, P. paumotensis*, and *Sandalolitha robusta*), three Agariciidae (*Leptoseris scabra*, *Pachyseris speciosa* and *Pavona varians*), and three Euphylliidae (*Euphyllia glabrescens*, *Physogyra lichtensteini*, and *Plerogyra sinuosa*).

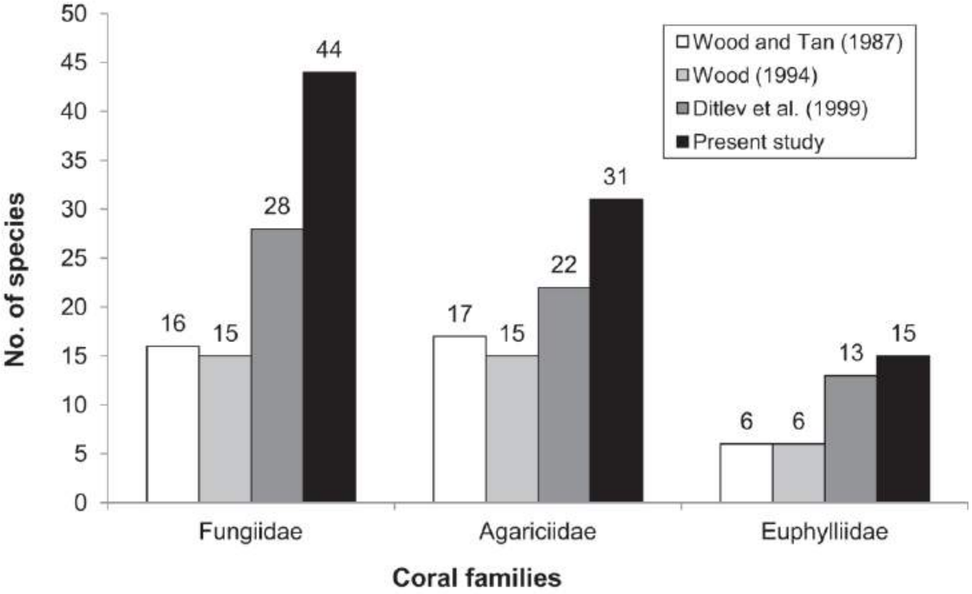


Fig. 2. Number of species of hard coral families Fungiidae, Agariciidae and Euphylliidae (from the largest to the smallest family) documented from Semporna and Darvel Bay. Note that the sampling intensity was not consistent in all these studies.

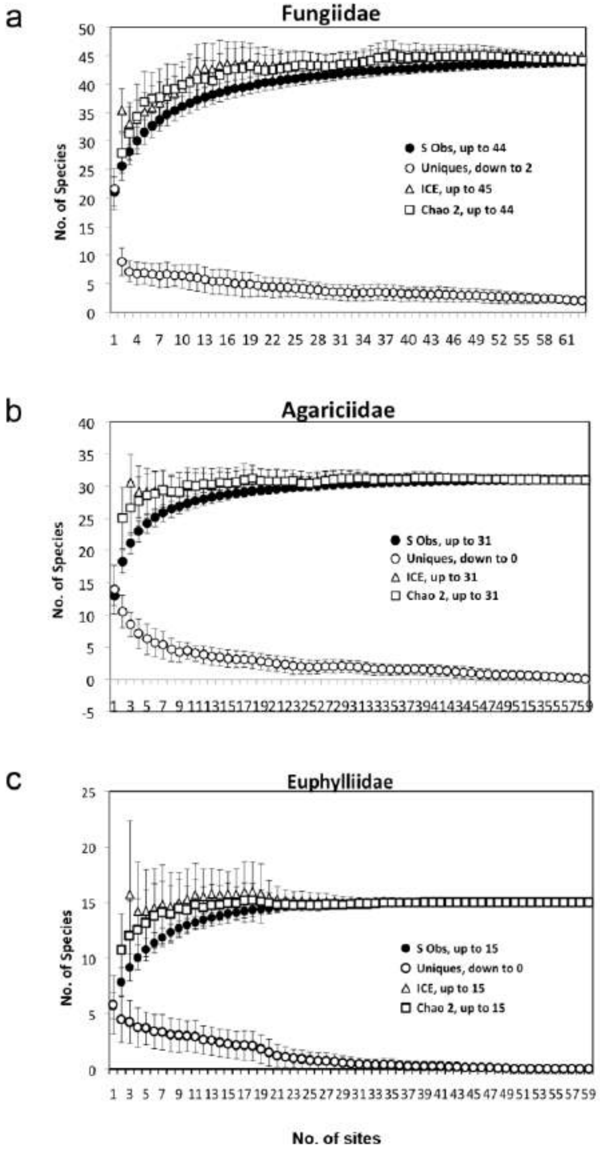


Fig. 3. Species accumulation curves for coral families **a** Fungiidae from 63 sites, **b** Agariciidae from 59 sites, and **c** Euphylliidae from 59 sites in Semporna. The curves appear to reach asymptotes, indicating that sampling efforts have been sufficient with the exception of the Fungiidae where the occurence of one additional species is possible.

Species that were encountered at only a few sites (n ≤ 3) appear to be limited to a certain environment based on the reef type, such as the mushroom corals *Cycloseris cyclolites*, *C. distorta, C. hexagonalis, C. vaughani, Podabacia sinai*, *Sandalolitha boucheti*, and the agariciids *Leptoseris amitoriensis, L. solida* and *Pavona minuta*. Some rare coral species only known from a few localities in the Coral Triangle are the mushroom corals *Lithophyllon ranjithi* (see Ditlev 2003; Hoeksema 2004) and *Halomitra clavator* (see Hoeksema 2004; Hoeksema and Gittenberger 2010), whereas some species only recorded from Semporna and Darvel Bay are the euphylliids *Plerogyra diabolotus*, *P. multilobata* and *P. cauliformis* (Ditlev 2003).

The dendrogram (using group-averaged hierarchical clustering) based on coral species composition suggested groups that reflect reef exposure (Fig. 4a). The SIMPROF test grouped the sites into six clusters with two singleton outliers, indicative of significant differences in species assemblages. At 70% similarity the MDS ordination showed two main groups, representing the exposed and sheltered reef sites plus two smaller clusters of exposed sites (Fig. 4b). The two main groups reflect sites exposed to different wind directions, but because the predominant wind direction is from the S–SE, the southern sites are referred to as the exposed reefs and the northern sites as the relatively sheltered reefs. When the clusters were plotted on the map, there appeared to be a clear distinction between the sites in the south and east of Semporna, and the neashore sites in the north and inner bay. Sites that had the highest species diversity (n > 50) were found at the sheltered neashore reefs (Fig. 5). However in contrast, all pairwise comparisons among the a priori groups were not statistically significant in terms of coral species composition for proximity to shore (ANOSIM Global R = 0.209, p = 0.1), and exposure to wind (Global R = 0.282, p = 0.1). There was also no significant difference in composition structure between proximity to shore and exposure to wind using the two-way crossed ANOSIM test.

Based on the SIMPER analysis, the average dissimilarity was highest between the groups South Exposed and the three sheltered areas, i.e. North Sheltered (46%), Inner Bay (46%) and North (44%) (Table 2). The groups that were most similar are North and North Sheltered (26%), followed by North Sheltered and Inner Bay (27%) and North and Inner Bay (27%). The latter three groups also showed the most similar species composition within the sites of its cluster. Because only presence/absence data was used to generate the results, each species contribution was very small, which resulted in a combination of too many species being characteristic of each group. As a result, it was difficult to ascertain the species that were indicators for the groups. Hence, the individual species distributions were compared in order to distinguish potential characteristic species.

The multivariate analysis identified two main groups based on reef exposure and this was supported by the distribution patterns of certain coral species: some were found in exposed reefs, i.e. *Lobactis scutaria*, *Pleuractis taiwanensis*, *Cycloseris somervillei*, *Pavona duerdeni* and *Leptoseris incrustans* (Fig. 6), while some others were found exclusively in sheltered nearshore reefs such as *Lithophyllon ranjithi*, *L. spinifer*, *Halomitra clavator*, *Leptoseris gardineri*, *Pavona frondifera*, *Nemenzophyllia turbida*, *Euphyllia paradivisa*, *Plerogyra diabolotus* and *P. cauliformis* (Fig. 7). The coral families

Fungiidae and Agarciidae had species representatives for both distribution patterns. Four euphyllid species showed a preference for nearshore reefs, whereas the others were widely distributed. *Plerogyra simplex* was the only euphylliid found primarily in exposed conditions, although it was also present in the Bodgaya lagoon (site 39).

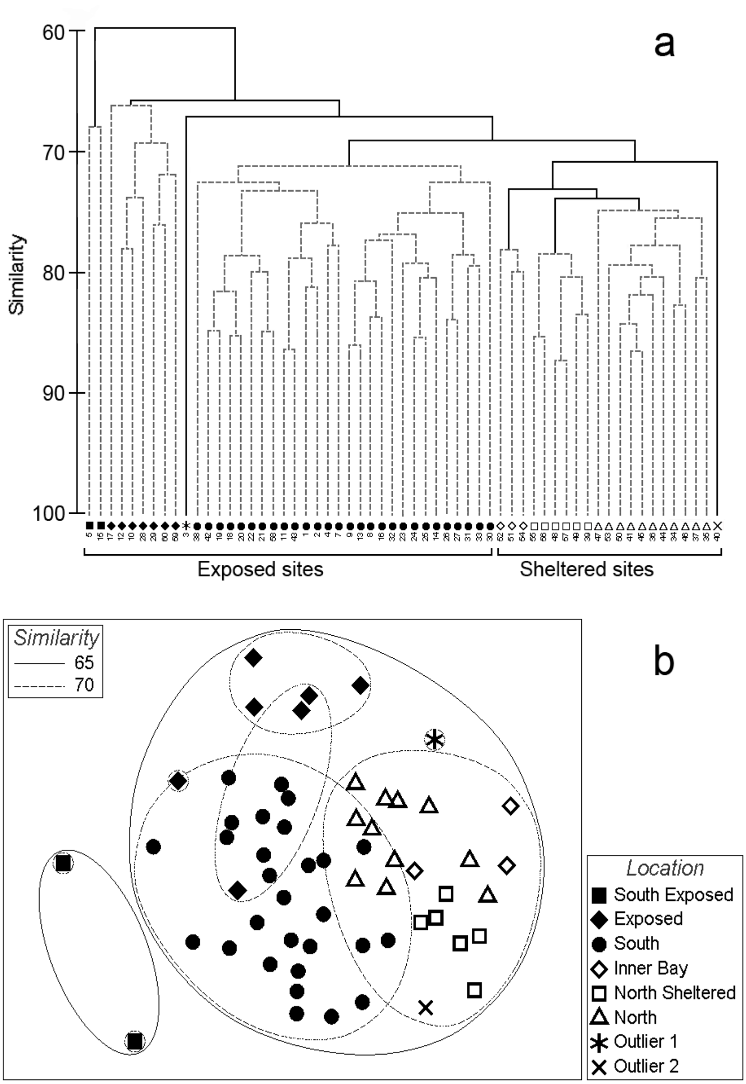


Fig. 4. **a** Dendrogram showing the group-averaged hierarchical clustering of 59 sites based on the species composition (presence/absence) of hard corals in Semporna. Significant clusters derived by SIMPROF are indicated by the solid black line, **b** Ordination of 59 sites in Semporna using multi-dimensional scaling (MDS) plots based on the significant clusters from 4a. The solid symbols represent exposed reef sites, while the open symbols denote sheltered reef sites.

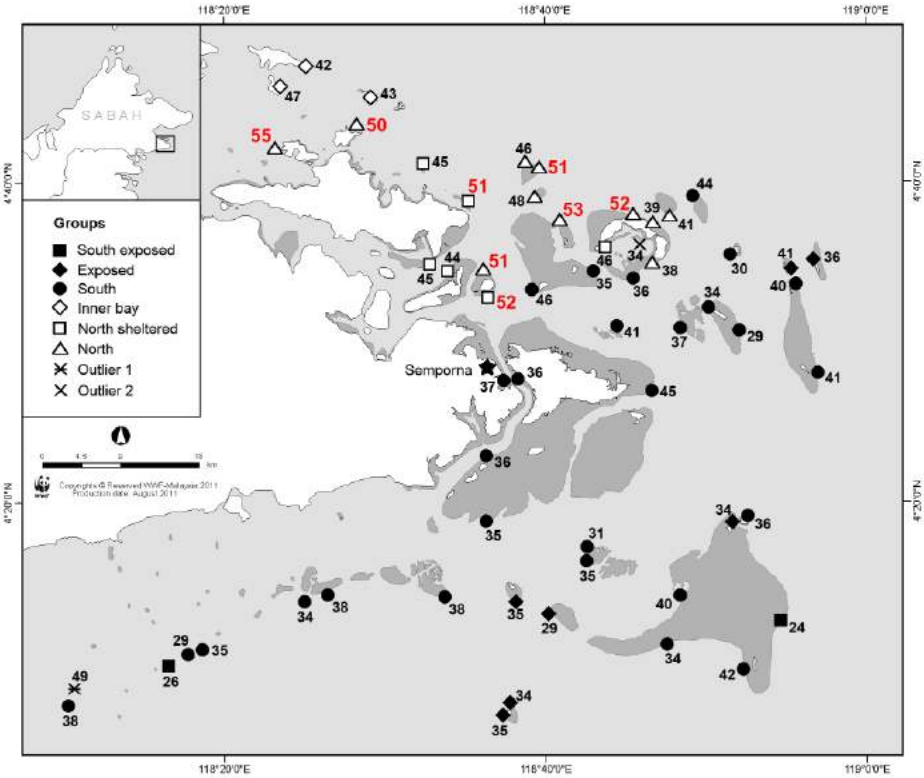


Fig. 5. Species richness patterns of the significant clusters from Fig. 4a. The numbers represent the combined species diversity of hard coral families Fungiidae, Agariciidae and Euphylliidae. Highlighted in a red, larger font are sites with the highest species richness (≥ 50 species).

Discussion

The combined number of scleractinian coral species for Semporna and Darvel Bay from the families Fungiidae, Agariciidae and Euphylliidae totals 90 species. This is approximately 17% of the overall predicted coral diversity for this region, which is expected to be between 540 to 550 species (Burke et al. 2002; Veron et al. 2009). When compared with previous studies (Wood 1987, 1994; Ditlev et al. 1999), the present study adds 24 new records to this area, 12 of which are new for the whole of Sabah. The reasons that previous studies documented fewer species may be three-fold: 1) the sheer number of scleractian species (> 500) makes identification difficult as the focus is too broad, 2) those studies were carried out to determine the condition of the reefs rather than concentrate solely on the coral species numbers, and 3) the sampling effort of those studies did not cover the entire range of habitats in Semporna and Darvel Bay. For these reasons, rare and inconspicuous species found in a limited locality range risk being overlooked.

The mushroom coral family is one of the taxonomically best-resolved scleractinian families with a phylogenetic analysis to support the classification (Gittenberger et al. 2011). In a recent study, *Psammocora explanulata* and *Coscinaraea wellsi* from the Siderastreidae have shown strong affinities with the Fungiidae (Benzoni et al. 2007, 2012a). These species were not included in the data collection because they were not yet formally recognised as fungiids during the fieldwork.

With regards to the Agariciidae, specimens of *Leptoseris hawaiiensis* and *L. scabra* that were encountered during the sampling appeared larger in size and had larger corallites and coarser septo-costae than the type specimens of these species (Vaughan, 1907). This variation could be related to the different locality, habitat type or depth range. Specimens of *L. fragilis* in the present study were identified by using the original species description by Milne-Edwards and Haime (1849) and an illustration of the type (Rousseau 1854). Similar specimens at the reference collection of the Borneo Marine Research Institute were identified by Ditlev et al. (1999). *Leptoseris fragilis* has not been given consideration in recent *Leptoseris* taxonomic revisions (Dinesen 1980; Veron and Pichon 1980) because the type specimen has been misplaced. Ditlev et al. (1999) recognised an additional species from Darvel Bay, *i.e*. *Pavona foliata*, which appears to be a *nomen nudum*. Since they did not provide descriptions or illustrations of this *Pavona* coral, its identity remains doubtful. He also reported on the presence of *P. divaricata* (Lamarck, 1816), which we did not recognise during the sampling. This species resembles *P. danai* or *P. frondifera*, depending on the reef environment. There are also some uncertainties regarding the status of some Euphylliidae such as the difficulty of recognising *Nemenzophyllia turbida* from *Plerogyra discus*. Both species have identical polyps and can only be distinguished by examining skeletal characters. During the present survey only *N. turbida* was encountered.

Table 2. Results of SIMPER analysis showing the percentages of similarities for each group and dissimilarities between groups based on coral species composition.

Groups	**South Exposed**	**Exposed**	**South**	**Inner Bay**	**North Sheltered**	**North**
Number of sites	2	7	28	3	6	11
Similarity (%) within group	68	70	74	79	80	78
Number of characteristic species[a]	16	31	33	34	39	39
Dissimilarity (%) between groups (number of distinguishing species)[a]						
South exposed	–	38 (40)	38 (43)	46 (43)	46 (45)	44 (49)
Exposed		–	33 (50)	38 (50)	38 (52)	32 (55)
South			–	34 (50)	32 (51)	29 (55)
Inner Bay				–	27 (40)	27 (43)
North sheltered					–	26 (48)

[a] The number of characteristic and distinguishing species were truncated when the cumulative contributions was ≥ 90%

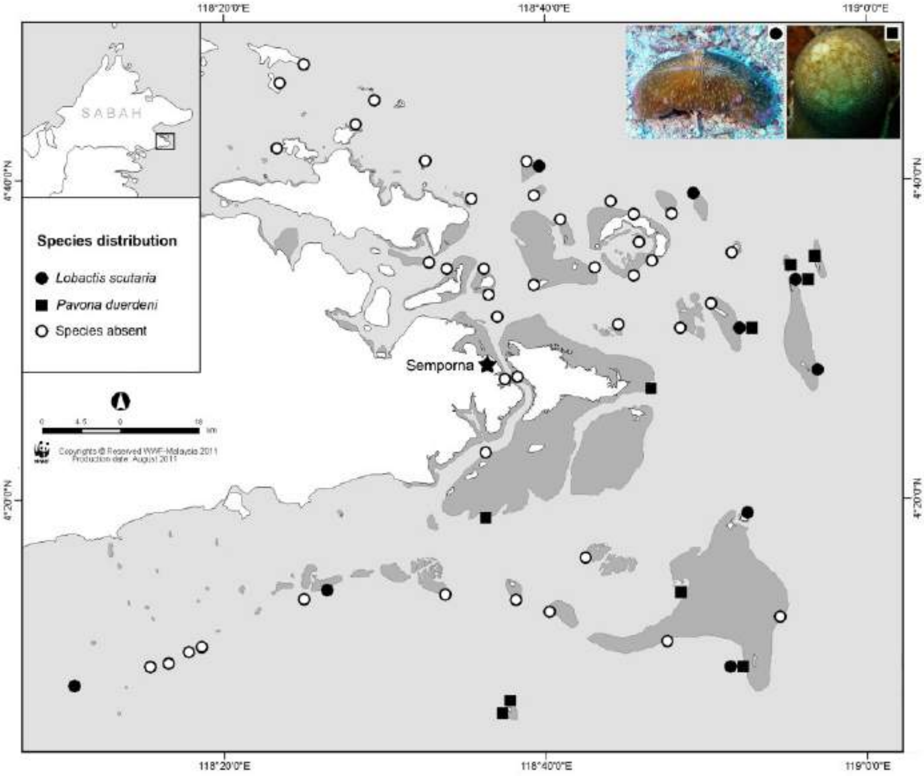


Fig. 6. Distribution patterns of some coral species with preference for exposed reefs

The cluster analysis and MDS ordination (Fig. 4a, b) indicate that the species composition differ between the exposed and sheltered reef sites. The first split of 60% separates sites 5 and 15 of the barrier reef from the main cluster. Both reef sites had the lowest species numbers among all the sites and were damaged from blast fishing or other factors such as storm surge, leaving some extensive rubble fields (Affendi et al. 2012). In addition to their low species diversity, this group is composed of only two sites, indicative of the small species contributions to its group pool, in contrast to the rest of the groups. The split differentiating the exposed and sheltered groups occurred at 70% suggesting that the reefs are not very dissimilar. Because of this, the SIMPER analysis showed that some indicator species were shared among the groups, especially those from the sheltered sites, which had 78–80% similar coral composition within its groups. Nevertheless, when the species distribution of each coral species was determined, several species exhibited distinct distribution patterns that corresponded with preferences for specific habitat type, which could indicate potential indicator species.

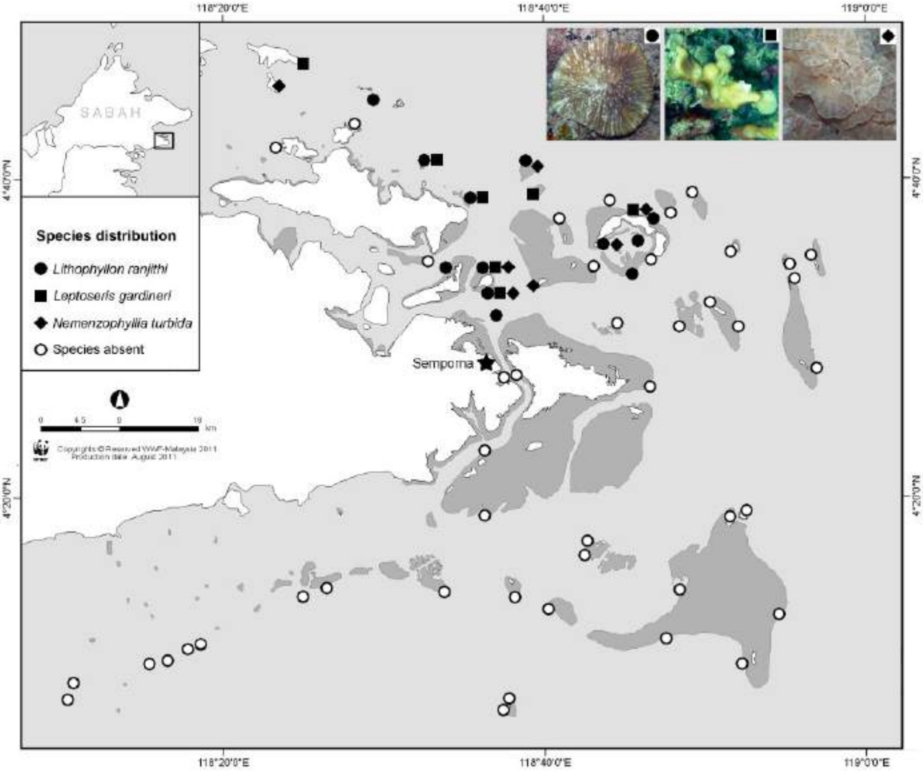


Fig. 7. Distribution patterns of some coral species with preference for nearshore northern reefs

There was an increase in species diversity from the exposed barrier reefs in the south to the relatively sheltered nearshore reefs in the north of Semporna and Darvel Bay. The barrier reef sites are characterised by deeper reefs that are exposed to the predominant wind direction from the S–SE. These conditions, as with oceanic islands that are distant from the coast, lack gentle reef slopes or variation in exposure to wave action that otherwise may contribute to habitat heterogeneity, hence, species diversity (Hoeksema 2007, 2012a). Wave-generating winds form one of the main factors influencing the geomorphology and coral species composition of coral reefs (Umbgrove 1929; Bradbury and Young 1981; Dollar 1982; Brown et al. 1983; Moll 1983; Hoeksema 2012a). Wave action is important for modeling the coral assemblage of the exposed upper reef slopes, while sediment movement is the controlling factor on the lower slopes and reef base (Sheppard 1982). Corals that thrive here usually belong to species that require clear waters that are able to withstand high wave energy. For example, the mushroom corals *Lobactis scutaria*, *Zoopilus echinata*, *Pleuractis taiwanensis* and *Cycloseris somervillei* were primarily found in the exposed outer reefs. While the former two are also common offshore species in other areas (Hoeksema et al. 2004, Hoeksema 2012a), the latter two species are usually associated with deeper and more sheltered parts of exposed reef slopes (Hoeksema and Dai 1991; Hoeksema 2010, 2012a). The agariciids *Pavona duerdeni* and

Leptoseris incrustans were only encountered in the exposed outer reefs. *Pavona duerdeni* has a massive growth form and is usually found on the mid-slope, while *L. incrustans* is an encrusting-type of coral and can be found along mid-slopes and shallower environments. *Leptoseris* corals have been reported to thrive at depths that are beyond the regular range of zooxanthellate corals (Kahng and Maragos 2006; Rooney et al. 2010; Dinesen et al. 2012). Some *Leptoseris* species have a preference for deep water or shady conditions such as crevices, caves and overhangs (Dinesen 1980; Hoeksema et al. 2010; Hoeksema 2012d), which are some of the features of the exposed reefs. So although the exposed reef sites may not have very high coral diversity, there are species that may preferentially be found under these reef conditions.

Highest coral species diversity is usually found in mid-shelf reefs (Done 1982, 1983; Moll 1983; De Vantier et al. 2006; Hoeksema 2012a). As for Semporna and Darvel Bay, there appears to be no clear mid-shelf zone, which was similar for Madang (Hoeksema 1993a). Here, the reef setting is around a peninsula and due to this, there is no clear pattern in species diversity from nearhore to offshore reefs. Instead, the pattern in species composition and diversity appeared to be driven by the exposure to wind frequencies. The highest diversity was found in the sheltered nearshore reefs as was reported for the reefs at the Flores Sea (Hoeksema and Moka 1989). A similar pattern was also observed in gall crabs (Brachyura: Cryptochiridae), whereby higher species richness of these obligate associates were found at sites with a higher number of host species in the sheltered northern reefs, and low occurrence sites were only found in the exposed southern reefs (Van der Meij and Hoeksema, 2013). Although the northern nearshore reefs were dubbed as sheltered reefs, they are also influenced by the northeast winds. These reefs had visibly more habitat heterogeneity as compared to the exposed reefs. Reefs at Tun Sakaran Marine Park had clear waters with little influence from sediments, except within the Bodgaya lagoon area, while the reefs towards the inner part of Darvel Bay had reduced water clarity with horizontal visibility of approximately 2–3 m at some reef sites. Under this turbid environment, Ditlev (2003) reported that some fungiid corals in the outer shoals of the bay reach enormous dimensions and form dense populations, although he did not specify their names. He also stated that *Leptoseris* and euphylliid corals were mostly found along the lower reef slopes of the bay. The present sampling sites only extended to the outer part of the bay, with Tabawan Is. at the northernmost site. Mushroom corals that were found at the nearshore reefs are *Halomitra clavator Lithophyllon ranjithi, L. spinifer* and *Heliofungia fralinae*. *Halomitra clavator* was confined to the northernmost sites of the bay that were facing the open sea while the latter three species had a larger distribution that extended to the reefs within the Park. Although these species are associated with sheltered reefs, they, except for *L. ranjithi*, have a preference for deep reefs with clear waters (Hoeksema 2012a). *Lithophyllon spinifer* has also been found on soft bottom substrates (Claereboudt and Hoeksema 1987; Hoeksema 1993a, 2012a).

Agariciid and euphylliid corals have not been as well studied as the fungiid coral family in terms of species distribution and richness patterns on a local scale. For agariciid corals, *Leptoseris gardineri* and *Pavona frondifera* were the only two species that exhibited a preference for sheltered reef conditions. Both species have foliose growth form but *L. gardineri* is usually found on the reef slope while *P. frondifera* is usually encountered in shallow reef parts. Euphylliid corals only found at sheltered sites are *Nemenzophyllia turbida*, *Euphyllia paradivisa*, *Plerogyra diabolotus* and *P. cauliformis*. Ditlev (2003) collected specimens of *P. diabolotus* and *P. cauliformis* from Mabul Is. (site 10). So, although in the present study these species were only observed at sheltered sites, they may also be found on the barrier reef, which was observed for *P. multilobata* (sites 18 and 19). *Nemenzophyllia turbida* is known to prefer turbid conditions. This species was first discovered on a reef with extremely high levels of suspended sediment, but with good water circulation at 15 m depth (Hodgson and Ross 1981). In the present study, *N. turbida* was found on the mid- and lower reefs slopes with sheltered conditions. Not much is known about *E. paradivisa* except that it is commonly found at shallow reef environments protected from strong waves (Veron 2000). The holotype was collected from 8 m depth at Bolinao, Philippines (Veron 1990).

Low species diversity at a few exposed sites may also result from blast fishing, as previously observed on the reefs of Si Amil Is. and Ligitan Is., with only 27 and 18.7% live coral cover, respectively (Pilcher and Cabanban 2000). Both islands are situated furthest from the coast, making law enforcement difficult. According to Pilcher and Oakley (1997), an average of four blasts were recorded every hour around the reefs of Mabul and Ligitan. In the present study, damage at Ligitan Is. (site 15) is reflected by the lowest coral species diversity (n = 24) with live coral cover between 8–15% over a very large area (Affendi et al. 2012). Several explosions were heard during dives (pers. obs.), and in addition to the reefs mentioned above, other sites appeared damaged by previous blasts including the reefs of the Tun Sakaran Marine Park (Wood 2006a). There is no evidence that blast fishing is more rampant at the exposed sites than the sheltered sites, except what can be inferred from the rubble fields at greater depths and the reef status data from Affendi et al. (2012). Regular monitoring is only carried out at reefs within the park area, and a phase shift from hard coral to soft coral cover has been reported for blasted reefs in the park (Wood and Dipper 2008).

Despite the above, the coral species diversity of Semporna and Darvel Bay is still remarkably high. The total of 44 species of mushroom corals that have been recorded from the present study surpasses other areas with very high biodiversity in the Coral Triangle that have been studied (Hoeksema et al. 2004; Hoeksema 2007, 2008). To date, Semporna holds the record for the highest species diversity of this coral family. There were also species that are endemic to northeastern Borneo, such as the fungiid *Lithophyllon ranjithi* and the euphylliids *Plerogyra multilobata*, *P. diabolotus* and *P. cauliformis* that have so far not been found elsewhere in the region. The fact that reefs in the research area were 70% similar in terms of species composition indicated that the whole area is generally species-rich, with only slight variations in species diversity among the sites that corresponded to the different habitat types of the exposed and sheltered reefs.

Investigations on the coral fauna of Semporna and Darvel Bay only began in the last 50 years and much remains to be discovered about the reefs in this area. Several studies have demonstrated the importance of determining changes in coral communities by using long-term monitoring data (Brown et al. 2002; Somerfield et al. 2008), or historical data as baselines for comparison (Hoeksema and Koh 2009; Van der Meij et al. 2010; Hoeksema et al. 2011; Van der Meij and Visser 2011). While it is important to focus on the immediate impact or disturbances on coral reefs, such as blast fishing in the case of Semporna and Darvel Bay, it is also imperative to detect the first signs of stress on the reef, or predict the response of the reef communities to disturbance. This would enable a better understanding of the processes involved in influencing changes on the reef communities (Hughes and Connell 1999).

Acknowledgments

This publication is a result of the Semporna Marine Ecological Expedition 2010 (SMEE 2010), co-organised by WWF-Malaysia, Universiti Malaysia Sabah and Universiti Malaya and Naturalis Biodiversity Center, the Netherlands. The expedition was funded through WWF-Malaysia. Research permission was granted by Sabah Parks, Department of Fisheries Sabah, and the Economic Planning Unit, Malaysia. Thanks are due to the crew of the Celebes Explorer for overseeing the logistics during SMEE 2010, Ms. Nina Ho who was invaluable to the expedition, and Mr. Sikula Magupin for producing maps of the research area. We also thank Dr. Elizabeth Wood and two anonymous reviewers for their helpful comments and suggestions.

Supporting Information

Supporting information are available at doi:10.1007/s12526-012-0130-7

Table S1. Hard coral species of families Fungiidae, Agariciidae and Euphylliidae observed at Semporna (as ESM 1 on Marine Biodiversity).

Table S2. Comparisons of hard coral species (families Fungiidae, Agariciidae and Euphylliidae) with previous studies in Semporna and Darvel Bay, Sabah (as ESM 2 on Marine Biodiversity).

Chapter 3

Coral reefs at the northernmost tip of Borneo: an assessment of scleractinian species richness patterns and benthic reef assemblages

Zarinah Waheed, Harald G.J. van Mil, Muhammad Ali Syed Hussein, Robecca Jumin,
Bobita Golam Ahad and Bert W. Hoeksema

Abstract

The coral reefs at the northernmost tip of Sabah, Borneo will be established under a marine protected area: the Tun Mustapha Park (TMP) by the end of 2015. This area is a passage where the Sulu Sea meets the South China Sea and it is situated at the border of the area of maximum marine biodiversity, the Coral Triangle. The TMP includes fringing and patch reefs established on a relatively shallow sea floor. Surveys were carried out to examine features of the coral reefs in terms of scleractinian species richness, and benthic reef assemblages following the Reef Check substrate categories, with emphasis on the hard coral cover. Variation in scleractinian diversity was based on the species composition of coral families Fungiidae (n = 39), Agariciidae (n = 30) and Euphylliidae (n = 15). The number of coral species was highest at reefs with a larger depth gradient i.e. at the periphery of the study area and in the deep South Banggi Channel. Average live hard coral cover across the sites was 49%. Only 7% of the examined reefs had > 75% hard coral cover, while the majority of the reef sites were rated fair (51%) and good (38%). Sites with low coral cover and high rubble fragments are evidence of blast fishing, although the observed damage appeared old. Depth was a dominant factor in influencing the coral species composition and benthic reef communities in the TMP. Besides filling in the information gaps regarding species richness and benthic cover for reef areas that were previously without any data, the results of this study together with information that is already available on the coral reefs of TMP will be used to make informed decisions on zoning plans for conservation priorities in the proposed park.

PLoS ONE (2015) 10(12): e0146006. doi:10.1371/journal.pone.0146006

Introduction

The second largest coral reef area in Sabah, Malaysia, is found at the northernmost tip of Borneo (Spalding et al. 2001) around the Kudat and Bengkoka peninsulas. Its position at the western boundary of the Coral Triangle, which has undergone some shifts over recent years (Green and Mous 2004, 2008; Hoeksema 2007; Veron et al. 2009), implies high marine biodiversity in the area. In addition to extensive coral reefs, large mangrove forests and seagrass beds, this area situated in between the South China Sea and the Sulu Sea functions as an important migratory route for pelagic fish, marine mammals and sea turtles, which also utilize these marine ecosystems as habitat, nesting and feeding grounds (Dumaup et al. 2003). Over 187 000 people live in the main towns of the peninsulas, with almost half of them depending on the marine resources for their livelihood (WWF factsheet 2013a; Weeks et al. 2014). Recognizing the importance of conserving and managing the coral reefs and other marine ecosystems, the Sabah State Government has approved to establish this area as a marine protected area (MPA) designated as the Tun Mustapha Park (referred as TMP hereafter) (Warta Kerajaan Negeri Sabah 2014).

Similar to other coral reefs in the region, the reefs of TMP face an array of threats, primarily from unsustainable and destructive fishing methods (Pilcher and Cabanban 2000; Burke et al. 2012). According to a profile of the ecological, socio-economic aspects and historical trends of reef fisheries at southern Banggi, the largest island in the proposed park (Teh et al. 2005, 2007), the reef fisheries are showing signs of early stage Malthusian overfishing, but the productivity of fisheries has not declined to a critical level (Teh and Sumaila 2007).

Descriptions of the coral reefs in the TMP mainly cover small parts of the islands and reefs (Wells 1977; Mathias and Langham 1978; Wood 1978). Hard coral cover ranged from 4 to 85% between 1996 and 1999 (Pilcher and Cabanban 2000), and in southeast Banggi more than 50% of the reefs had “poor” coral cover (< 25% cover) from 1999 to 2002 (Harding et al. 2001; Daw et al. 2002, 2003) following the criteria developed by the ASEAN-Australia Living Coastal Resources project (Chou et al. 1994). Along the east coast of Banggi and the reefs eastwards of Malawali Island, 86% of the reefs had “fair” or “good” coral cover (25–50% and 50–75% coral cover, respectively) (Koh et al. 2002; Lee and Chou 2003; Tanzil and Chou 2004; Waheed et al. 2009). At the west coast of the Kudat peninsula, mean hard coral cover was around 40% and a majority of the reef sites here were rated “fair” (Burns 2004; Murphy et al. 2005; Burns et al. 2005). In all these survey reports, blast fishing and overfishing were consistently mentioned as the main threats to the reefs within the TMP.

Very few surveys have been made to document the coral species richness in the TMP. From nine dives and along 28 transects, a total of 273 species of scleractinian corals have been reported around Banggi and the reefs southeast of Malawali (Fenner 2001; Waheed et al. 2009). This number seems to be quite low considering TMP’s position between the South China Sea and the Coral Triangle, both of which are large regions with over 550 reef coral species (Huang et al. 2015).

MPAs or marine reserves have been successful in enhancing the biomass and diversity of overexploited communities (Roberts and Polunin 1991; Russ and Alcala 1996; Roberts 1997; Halpern 2003). MPAs have also shown to be effective in preventing coral loss (Selig and Bruno 2010) and aiding in coral recovery (Mumby and Harborne 2010), though some studies have found otherwise (Huntington et al. 2011; Coelho and Manfrino 2007). Nevertheless, MPAs can only be successful if the design and function is in line with their goals (White et al. 2014). In the case of the proposed TMP, the management plans were established with three goals: 1) to eradicate poverty, 2) to ensure suitable development, and 3) to conserve its habitat and threatened species (WWF factsheet 2013a; Weeks et al. 2014). Using a set of MPA design principles developed by stakeholders (Lee and Jumin 2007; Green et al. 2014) and ecological and socio-economic data compiled from previous surveys and local knowledge, a series of multiple-use zoning plans was created. Data such as key species and habitat features were among other information that were applied to the conservation planning software Marxan with Zones (Watts et al. 2014), which then identified priority areas for three zones: 1) preservation zones, 2) community-managed zones, and 3) multiple-use zones (Weeks et al. 2014). The preservation zone is purely for habitat conservation where any form of extractive activities is prohibited, with the exception of permit-approved research. For this zone, the coral reef ecosystems were divided into four ecological regions based on their exposure to wind and currents. In each region, at least 30% of each ecosystem (coral reefs, seagrass and mangroves) and unique features (such as turtle and dugong habitats) required inclusion within the zone (WWF factsheet 2013a). The coral reefs were further categorized into eight reef habitat types defined by reef morphology and exposure (Weeks et al. 2014). As such, it is important to have information on the reef features and distribution within the TMP in order to optimise the selection process of the potential coral reef sites for the preservation zones.

While some information is available from previous surveys, there are areas within the proposed park that are without any data. In order to address this issue, as well as the need to identify potential reef habitats for the preservation zones, the Tun Mustapha Park Expedition (TMPE) 2012 was organized. The present study was carried out during the expedition and aimed to examine specific features of the coral reefs by focusing on hard coral species richness and benthic assemblages within the TMP. The main objective was to determine the species richness patterns of the scleractinian coral families Fungiidae, Agariciidae and Euphylliidae, which were used as proxy (~84 species) for all scleractinian reef corals (> 500 species) (Burke et al. 2002; Veron et al. 2009). These coral families were selected because they are common on reefs in the Coral Triangle, where they can be found from onshore to offshore reefs and over a wide depth range from shallow reef flats to the lower reef slopes (Moll 1983; Veron 2000; Hoeksema and Koh 2009; Hoeksema 2012a; Chapters 2, 4 and 5). The second objective was to examine the benthic assemblages as a proportion of the reef that is covered by benthos (hard coral, soft coral, sponge, nutrient indicator algae, recently killed coral, rock, rubble, sand, silt, and other substrate), particularly the hard coral component across the study sites. The species richness patterns and benthic communities were assessed in relation to environmental factors: 1) depth (between shallow and deep reef sites), 2) exposure (between sites that are sheltered and exposed to dominant wind-driven waves and currents), and 3) proximity from the mainland. These factors have been found to be important in structuring reef species composition and diversity across coral reef systems (e.g. Done 1982, 1983; Moll 1983; Moll and Suharsono 1986; Becking et al. 2006; Cleary et al. 2005, 2006; DeVantier et al. 2006; Hoeksema and Koh 2009; Hoeksema 2012a, b; Chapters 2 and 4) but with varying degrees of influence from one reef system to another. As the resolution of data collection for the coral families and the benthic assemblages were very different, both objectives were treated separately throughout this study.

Materials and methods

Physical setting

The proposed park is a corridor where the South China Sea meets the Sulu Sea through the Balabac Strait, which separates north Borneo from the Philippines. The eastern limit of the South China Sea begins at the tip of the Kudat peninsula, Tanjung Simpang Mengayau [variations in spelling= Tanjong Sampanmangio, Tanjung Simpangmangayau], towards the north along the west coast of Balambangan Island, Malaysia and the west coast of Balabac Island, the Philippines. The area to the east of this boundary is defined as the Sulu Sea (International Hydrographic Organization 1953).

The TMP will cover an area of approximately 8,987 km^2, comprising the coastal areas of the Kudat and Bengkoka peninsulas, and Marudu Bay, which is bounded by the two peninsulas (Warta Kerajaan Negeri Sabah 2014). Coral reefs in the TMP extend over 450 km^2 (WWF factsheet 2013b) and consist of fringing and patch reefs, with banks and shoals situated on a relatively shallow sea floor. Several extensive reef flats can also be found such as the Bankawan Reefs in the northeast of Banggi Island, covering over 100 km^2. Most of the reefs are established along a gradually sloping substrate before levelling into sandy sea floor. Reefs fringing the coastline are in turbid waters adjacent to a shallow seafloor (≤ 35 m) with gentle slopes that do not have much vertical incline (Wood 1978). Moderately steep reef slopes (~25–30 degree angle) are found near the Selat Banggi Selatan (referred as the South Banggi Channel hereafter) towards the south and southeast of the island. A few reef sites in the easternmost and northernmost part of the TMP are also in deeper waters, with much improved water visibility. Owing to the complex morphology of the coastline and islands, and generally shallow depth, there is no clear cross-shelf zonation pattern in the coral reef area.

The northeast monsoon lasts from November to March, and the southwest monsoon prevails from May to September. During the northeast monsoon, when rainfall is heaviest (Malaysian Meteorological Department 2013) water from the Pacific Ocean enters the Bohol Sea through the Surigao Strait and splits into two branches: one towards Mindoro and the other towards east Sabah. From the latter, the water passes through the Balabac Strait into the South China Sea. In contrast, currents from the South China Sea enter into the Sulu Sea from August to October (Wyrtki 1961).

Field sampling

Coral reefs were surveyed during TMPE 2012 in Kudat, Sabah (6°40'–7°30' N, 116°40’–117°40’ E) from 6 to 26 September 2012 at coastal and offshore reefs (1–35 m depth). Dives were made at 38 sites for coral species richness surveys and 36 sites for benthic community surveys, situated less than 60 km from the mainland (Fig. 1, S1 Table). Sites were selected based on navigation charts (Malaysia Nautical Chart MAL 871, British Admiralty Nautical Charts no. 948 and 1654), reconnaissance dives prior to the expedition, and local knowledge. The selection was intended to be representative of the TMP reef area and include as much habitat diversity as possible, but some areas were excluded from the surveys because of the presence of saltwater crocodiles (*Crocodylus porosus*), particularly at the east and southeast coast of Balambangan Island (Jumin 2009; Mohd. Firdaus 2013). Several areas were not accessible during the survey due to unfavourable weather conditions with strong winds from the west. Due to this, there was a sampling bias given that the reefs in the west along the coast of the Kudat peninsula were not as fully explored as the reef complex in the east. On several occasions, reefs could not be located due to bad surface visibility accompanied by strong surface currents and waves. Furthermore, only few surveys were possible south of the Kudat town in Marudu Bay owing to poor water visibility caused by wind-generated waves.

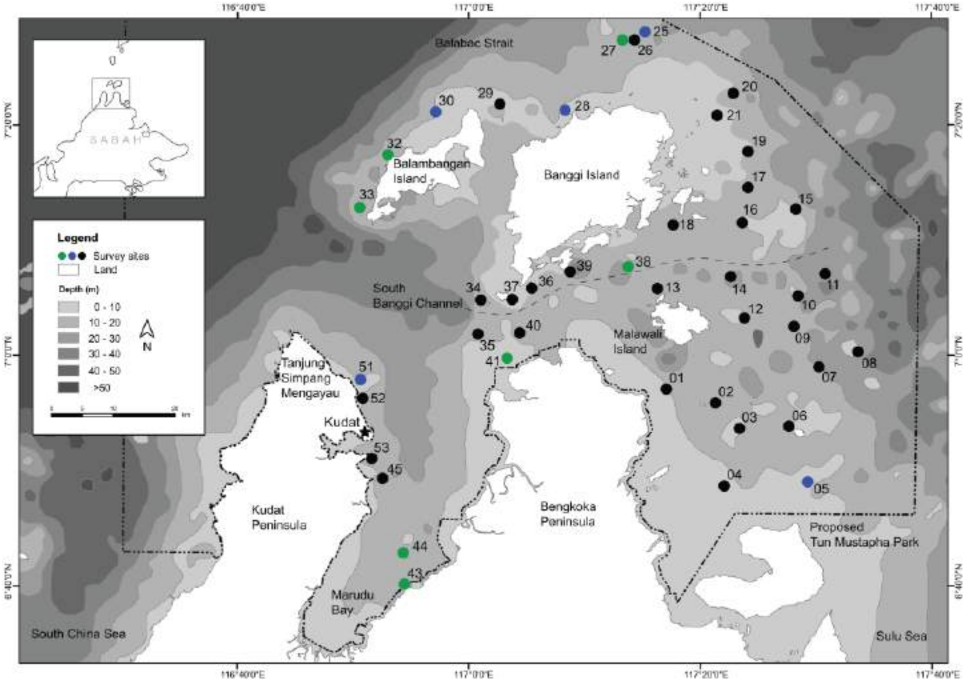


Fig. 1. Research area at the northern tip of Borneo. Symbols for data collected at survey sites; green: coral species richness only; blue: benthic community only: black: both. The sites indicated by the black symbol were plotted according to GPS coordinates of the coral species richness surveys (S1 Table). Labels (locality names excluding the proposed Tun Mustapha Park boundary) are given according to British Admiralty Nautical Charts no. 948 and 1654. Selat Banggi Selatan (South Banggi Channel) is indicated by the dashed grey line.

Coral species richness

Coral species incidence data was recorded at each site by adapting the roving diver technique (Schmitt et al. 2002; Munro 2005). This survey method involved diving along the reef for approximately 60 minutes from the reef base (≤ 35 m depth) to the reef crest or reef flat (~1 m depth) while recording target coral species on a slate board. This method gives a better overview of the coral fauna in terms of species presence/absence than the use of belt transects, which is depth-specific and aimed at obtaining species abundance data (Hoeksema and Koh 2009; Hoeksema 1991, 2012a). Each site was surveyed only once, hence no replicates were made. Photographs were taken for each coral species encountered at every site, and specimens that could not be identified in situ were collected for closer inspection and kept in the reference collection of the Borneo Marine Research Institute, Universiti Malaysia Sabah in Kota Kinabalu, Sabah.

Scleractinian coral families Fungiidae, Agariciidae and Euphylliidae were used as proxy for all reef coral species. The fungiids were surveyed at all sites during the present study (n = 38) and nine sites previously surveyed in 2005 (n = 2), 2007 (n = 2) and 2008 (n = 5) (S1 Fig.). The identification of this family was primarily based on Hoeksema (1989) and Gittenberger et al. (2011). For consistency in the comparisons with previous works, two new members of the Fungiidae, *Cycloseris explanulata* (Van der Horst, 1922) and *C. wellsi* (Veron and Pichon, 1980), previously classified as Siderastreidae (Benzoni et al. 2007, 2012a) were not included in the survey though both species were present in the area. Data on the Agariciidae and Euphylliidae (sensu Veron 2000) were collected at only 35 sites during the present study and identified based on the taxonomic criteria of Dinesen (1980), Veron and Pichon (1980), Veron (2000), and Ditlev (2003).

Benthic composition

Standard Reef Check methodology (Hodgson et al. 2006) was applied to assess the condition of the coral reefs in the TMP. However, data of only the benthic cover is presented here. The benthic communities were quantified at 36 sites and at two depth zones where possible (3–5 m and 8–10 m). In total, 55 transects were surveyed with 33 shallow and 22 deep (mid-reef) sites. For the substrate survey, Reef Check essentially uses the Point Intercept Transect (PIT) method (Hill and Wilkinson 2004), which involves recording the substrate type that lies directly below the transect line at 0.5 m intervals along four 20 m segments of a 100 m transect. A 5 m gap was left in between each segment to create replicates (of four segments) for each transect. The substrate is expressed as mean percentage cover for 10 substrate categories: hard coral, soft coral, sponge, nutrient indicator algae (all algae except coralline, calcareous and turf algae), recently killed coral, rock, rubble, sand, silt and others (substrate not indicated in the previous nine categories) (Hodgson et al. 2006).

Data analysis

In general, the study area was situated in relatively shallow depths, except for sites in the South Banggi Channel and the Mangsee Great Reef. The sites are exposed to winds from the northeast or the southwest, except for sites within Marudu Bay. Each site was in close proximity to an island (land mass), for example 70% of the sites were ≤ 5 km from an island, and only one site (site 15) was > 10 km away. As the distance to the nearest land mass was not variable, we examined the effect of distance from the mainland (Sabah coastline) to the sites. The a priori details for the depth, exposure and distance from the mainland of each site are given in S2 Table. The reef sites surveyed for coral species richness and benthic data from the transects ranged from 0.16 to 5 km apart. The benthic surveys were limited by depth (10 m maximum depth), while a greater depth range was necessary to record as many coral species as possible for the species richness surveys. The reefs are established on a gently sloping substratum, so the deeper slopes were at times a distance away from the shallow parts of the reef, hence creating some distance between both surveys. Thus, direct comparisons of both data types could not be made and the analyses for the coral species richness and benthic communities were made separately.

The coral species incidence data from 47 sites for the fungiids (38 sites from the present study and nines sites from previous surveys) and 35 sites for the agariciid and the euphylliid corals were used for species richness analyses. Species richness estimators were calculated using the software EstimateS (Colwell 2009) to indicate whether the sampling effort had been sufficient in representing the expected total coral species richness in the area (Magurran 2004). Multivariate analyses were used to examine the coral species richness patterns based on the coral species composition of 35 sites, where data was collected for all three coral families. Similarity profile analysis (SIMPROF) (Clarke et al. 2008) was used to identify the significant clusters of these sites based on the Bray-Curtis similarity measure (Bray and Curtis 1957). A group-averaged hierarchical clustering dendrogram was generated from 1,000 expected and simulated profiles using the R package *clustsig* (Whitaker and Christman 2014). The clusters are shown on the map to determine species richness patterns. To further interpret the coral species richness patterns in relation to the environmental conditions (as listed in S2 Table), data of the species richness were regressed across depth, exposure and distance from the mainland using a Generalised Linear Model (GLM) of the Poisson type in R (R Core Team 2013) and additional package *car* (Fox and Weisberg 2011) for model diagnostics.

For the benthic communities, the percentage cover of the substrate categories were averaged for all shallow and deep transects in order to get an overview of the benthic composition in the TMP. The benthic compositions were also visualised by transect and assessed by factors depth and distance from the mainland. Data was then transformed using the box cox transformation in order to meet the assumption of normality. Silt was excluded from subsequent analyses as the percentage cover was extremely low (0.4%, range = 0–4%). Two separate sets of regression analyses were performed to investigate the influence of depth and distance from mainland on the benthic communities. Reef exposure was not examined because the very few transects in the sheltered reef condition prevented any meaningful comparisons between the benthic communities. All statistical analyses were carried out in R and model diagnostics with the *car* package (Fox and Weisberg 2011; R Core Team 2013).

Results

Coral species composition and richness patterns

The species accumulation curves for the fungiid and the agariciid corals showed that the estimated number of species (ICE, Chao 2) is similar to the observed number of species; therefore the sampling has been sufficient (Fig. 2). In contrast, the species accumulation curve for the euphylliid corals appears to approach the asymptote, indicating that additional sampling may reveal more species.

Based on the target coral families, the total reef coral species count for the TMP is 84 species, represented by 39 Fungiidae, 30 Agariciidae and 15 Euphylliidae (S3 Table). A total of 18 new records for Kudat (e.g. Fenner 2001) include five fungiid species (*Cycloseris boschmai*, *C. curvata*, *C. distorta*, *Lithophyllon ranjithi*, *Sandalolitha boucheti*), seven agariciids (*Leptoseris fragilis*, *L. incrustans*, *L. solida*, *Pavona danai*, *P. duerdeni*, *Pavona* sp. 1, *Pavona* sp. 2) and six euphylliids (*Euphyllia cristata*, *E. paradivisa*, *Nemenzophyllia turbida*, *Plerogyra* cf. *cauliformis*, *Plerogyra* cf. *diabolotus* and *Plerogyra* cf. *multilobata*). In addition to the earlier reported total of 273 scleractinian species for TMP, the 18 new records add up to a new total of 291 species.

The number of coral species observed per site ranged from 13 in Marudu Bay (site 45) to 49 in four separate sites: Purukan Sibaliu (site 15), both sites at the Mangsee Great Reef (sites 26 and 27) and Molleangan Kecil (also known as Maliangin Kecil) at the southern tip of Banggi (site 34). Out of 35 sites, 19 (54%) had a total of ≥ 40 species. The common mushroom coral species *Fungia fungites* was found at all sites, while the mushroom coral *Danafungia fralinae*, and the euphylliid corals *Euphyllia cristata*, *E. paradivisa* and *Plerogyra* cf. *diabolotus* were each encountered only once (Table 1).

The SIMPROF test indicated four distinct clusters and an outlier (site 45) (Fig. 3). There was a distinction of two groups at similarity index of ~69: the larger of the two groups is further subdivided into two smaller groups (Groups 1 and 3) and one large group (Group 2) at similarity index ~70, and another small group (Group 4) that is composed of six sites. The species richness pattern that emerged when the clusters were overlaid on the map showed that sites with high species richness ($n \geq 45$) were located primarily at the periphery of the study site (Fig. 4). Reef sites that were adjacent to the mainland (Group 4) had noticeably lower species richness (except site 53, $n = 38$). These sites were among the shallowest sites during the survey.

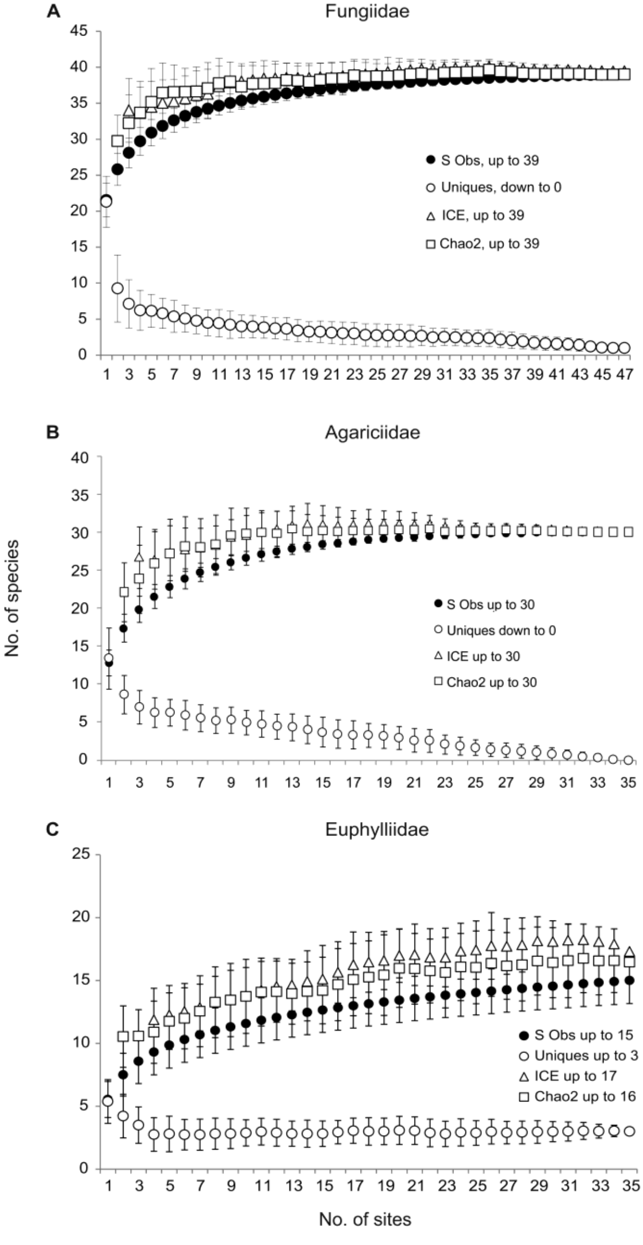


Fig. 2. Species richness accumulation curves (observed and estimated), A) Fungiidae at 47 sites, B) Agariciidae, and C) Euphylliidae, each at 35 sites.

Table 1. The occurrence of common and uncommon coral species in the proposed Tun Mustapha Park.

Common species	Frequency (n)[a]	Uncommon species	Frequency ($n \leq 3$)
Fungiidae			
Fungia fungites	47	*Cycloseris boschmai* [b]	3
Danafungia horrida	46	*Lithophyllon spinifer*	3
Danafungia scruposa	46	*Cycloseris curvata*	2
Herpolitha limax	46	*Cycloseris distorta*	2
Lithophyllon repanda	46	*Sandalolitha boucheti*	2
Pleuractis granulosa	46	*Heliofungia fralinae* [c]	1
Pleuractis paumotensis	46		
Ctenactis echinata	45		
Lithophyllon scabra	45		
Sandalolitha robusta	45		
Lithophyllon concinna	44		
Heliofungia actiniformis	44		
Cycloseris costulata	43		
Pleuractis moluccensis	43		
Ctenactis crassa	43		
Agariciidae			
Pachyseris speciosa	33	*Leptoseris fragilis*	3
Pavona explanulata	31	*Pavona duerdeni*	3
Pavona varians	31	*Pavona danai*	2
Leptoseris scabra	30	*Pavona* sp. 1	2
		Pavona sp. 2	2
Euphylliidae			
Plerogyra sinuosa	33	*Nemenzophyllia turbida*	3
Euphyllia ancora	30	*Plerogyra* cf.*cauliformis*	2
		Euphyllia cristata	1
		Euphyllia paradivisa	1
		Plerogyra cf. *diabolotus*	1

[a] represented at ≥ 85% of the reef sites: Fungiidae $n \geq 40$; Agariciidae, Euphylliidae $n \geq 30$

[b] from surveys in 2007 and 2008

[c] from a survey in 2008 only

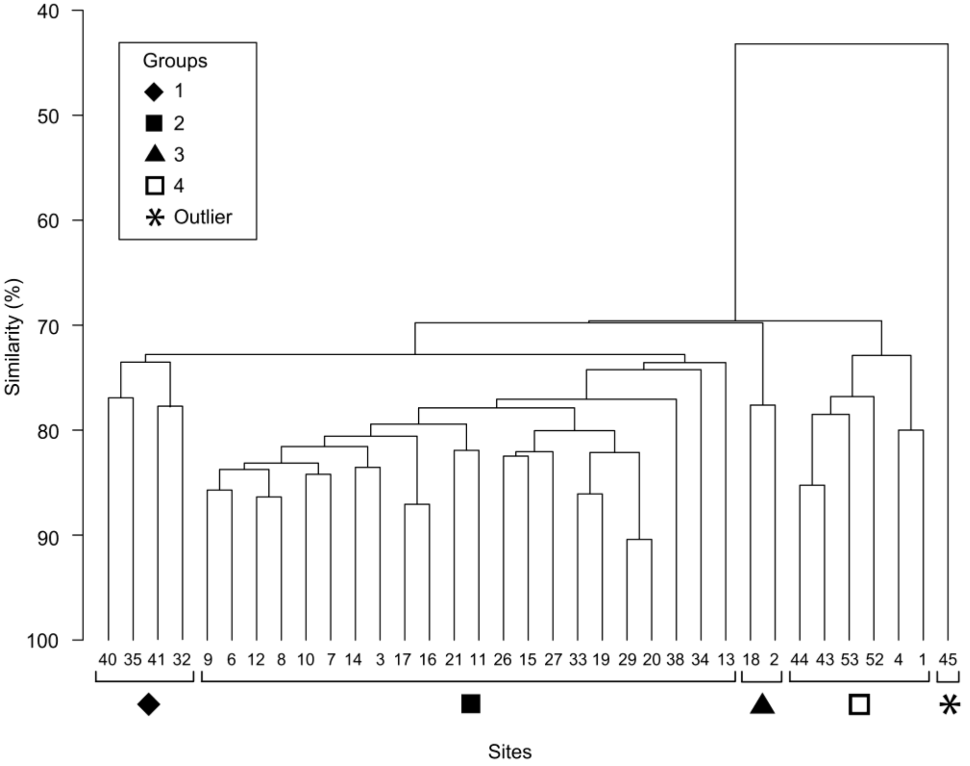


Fig. 3. Group-averaged hierarchical clustering dendrogram of coral composition based on the Bray-Curtis similarity index. Coral species composition was based on 35 sites where data was collected for all three coral families. Four significant clusters and one outlier (indicated by the symbols) were computed by the similarity profile (SIMPROF) analysis.

There was variability in the site conditions, i.e. there were more shallow sites (n = 27) than deep sites (n = 8), and more exposed sites (n = 30) than sheltered sites (n = 5). Approximately 62% of the sites were shallow and exposed. There were no sheltered sites that were deep. The coral species richness appeared to be higher at the deep sites and seemed to increase with distance from the mainland (S2 Fig.). Based on the regression analyses, only depth and exposure were significant factors influencing the coral species richness of the reef sites (Table 2, Model 1, S3 Fig.). When outlier site 45 was removed from the analyses, exposure became an insignificant factor and only depth had an effect on the species richness in the TMP (Table 2, Model 2). Even though Model 2 had underdispersion in the residuals, its AIC value was smaller and its model diagnostics were better than Model 1, hence Model 2 is a better model based on statistics (S4 Fig.).

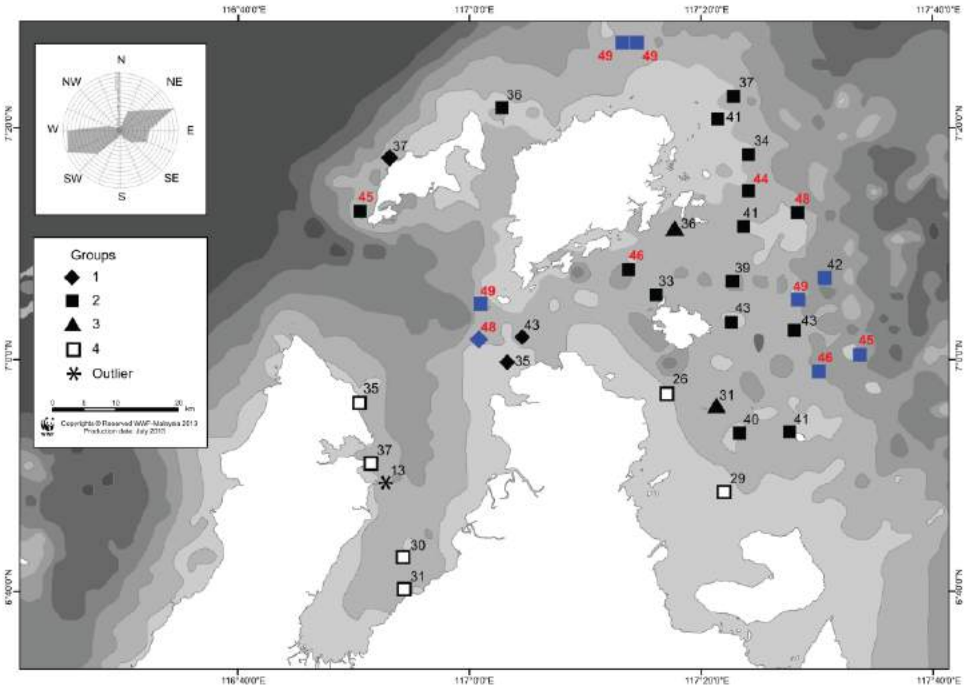


Fig. 4. Overlay of the significant clusters from Fig. 3 based on the SIMPROF analysis. Symbols in blue represent deep reef sites (> 20 m depth). Numbers indicate the total coral species for all three coral families. Sites with ≥ 45 species are shown in red bold font. Wind rose showing dominant wind directions is based on observations between January 2012 to November 2013 obtained from the Kudat Airport, Sabah from windfinder.com.

Benthic communities

The average hard coral cover of 55 transects in the TMP was 49% (Fig. 5). Following the criteria described by Chou et al. (1994), most reefs was rated either fair (51%) or good (38%) in terms of coral cover. Only 7% of the reefs had excellent coral cover, while 4% had poor coral cover. The coral cover ranged from 18% at Pancang Pukul (site 40D) to 77% at Mangsee Reef (site 26S) (S4 Table). Hard coral was the most dominant biotic component on the reef, accounting for almost half of the benthic substrate cover. Other functional biotic components were soft coral (3%, range: 0–31%) and nutrient indicator algae (5%, range: 0–29%). Major abiotic components (> 10% cover) that contributed to the benthic cover were rock (17%, range: 3–34%) and rubble (16%, range: 1–52%).

As the substrate cover adds up to 100% for each transect, correlations among the substrate categories are negatively related. At sites where hard coral cover was low, rubble was the dominant substrate in the shallow transects, and sand in the deep transects (Figs. 6, S5 and S6). In comparing the benthic components between both depths, there was a significant difference in nutrient indicator algae and sand cover, whereby both had higher cover in the deep transects (Figs. 7, S7, Table 3). Nutrient indicator algae was found in 21 deep transects (9%, range = 0–29%) and 17 shallow transects (2%, range = 0–15%), while sand was recorded from all deep transects (12%, range = 1–39%) and 28 shallow transects (6%, range = 0–29%). There seem to be no obvious difference in the structure of the benthic communities when the reef distance from the mainland was examined (Fig. 8). Nevertheless, rubble and sand cover decreased with distance from the mainland while hard coral cover increased slightly in both the shallow and deep transects (Table 3, S8 Fig.).

Table 2. The influence of depth, exposure and distance from the mainland on the coral species richness in the TMP.

Model description	Estimate	Std. error	z value	p
Model 1 – Depth + Exposure + Distance from mainland				
Intercept	3.7899	0.0825	45.9490	< 2e-16
Depth	-0.1852	0.0640	-2.8960	**0.0038**
Exposure	-0.2336	0.1003	-2.3290	**0.0199**
Distance from mainland	0.0019	0.0020	0.9850	0.3248
AIC = 232.76				
Residual deviance = 32.806, on 31 degrees of freedom				
Model 2 – Depth + Exposure + Distance from mainland (excluding site 45)				
Intercept	3.7920	0.0825	45.9910	< 2e-16
Depth	-0.1858	0.0640	-2.9040	**0.0037**
Exposure	-0.1056	0.1034	-1.0210	0.3072
Distance from mainland	0.0019	0.0020	0.9520	0.3411
AIC = 214.9				
Residual deviance = 19.359, on 30 degrees of freedom				

Significant values are indicated in bold.

Discussion

The new species records bring the total coral count to 291 species in the TMP. This number is higher than the range of 208–262 species found at five of the most diverse Coral Triangle localities in eastern Indonesia, each with nine to 50 dive stations (Best et al. 1989). A recent coral species count at western Sabah, to the southwest of TMP and just outside the Coral Triangle reached a slightly lower maximum of 248 species, taking recent taxonomic revisions into account (Huang et al. 2015). Hence, the TMP can be considered rich in coral species and based on the present study an even higher diversity can be expected when other coral families are included.

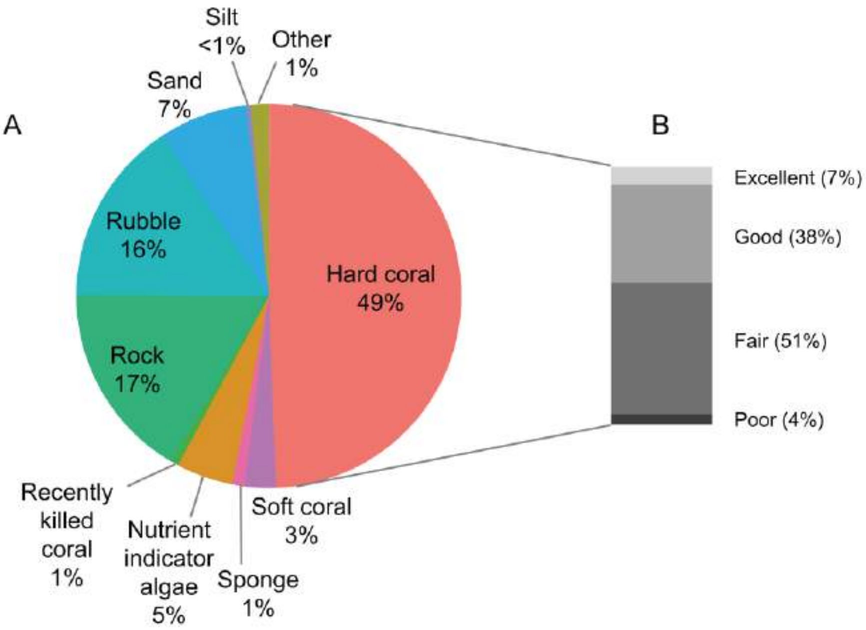


Fig. 5. Benthic composition in the proposed Tun Mustapha Park. A) Average percentage cover of benthic communities, B) Reef coral status following the criteria of Chou et al. (1994).

Absent, unusual and common coral species

Several species expected to be present based on previous records but not encountered in the present study were the mushroom corals *Heliofungia fralinae* and *Cycloseris boschmai* (from surveys in 2007 and 2008), and the agariciid *Pavona minuta* (Fenner 2001). The absent mushroom coral *Zoopilus echinatus* was also expected to occur in the area based on its presence in nearby localities in Sabah (Chapters 2 and 4) and Brunei (Turak and DeVantier 2011; Hoeksema and Lane 2014). All three mushroom coral species are predominantly found in offshore reefs (Hoeksema et al. 2004; Hoeksema 1993a, 2012a, c). *Pavona minuta* was uncommon and found encrusting on the reef substrate in shallow environments (Veron 2000), although in oceanic Sipadan Island on the east coast of Sabah, it was found at the opening of a small cave of a steep wall. Its very thin corallum, minute corallites and shallow calicular centres give it a smooth appearance (Wells 1954). Small colonies could appear inconspicuous making it easily overlooked on the reef. The absence of these species could imply that TMP lacks offshore reef conditions, or that depth is a limiting factor. In addition, the species accumulation curves for the euphylliids also indicate that more species ought to be found with more sampling effort, especially at sites that were not surveyed at the west coast of the Kudat peninsula, or areas less surveyed such as around Balambangan Island and the offshore Mangsee Reef.

Fig. 6. Benthic categories arranged by percentage hard coral cover in decreasing order for shallow and deep transects.

Some coral species exhibit explicit habitat preference and appear to be limited to a certain environment based on the reef type or depth (Hoeksema 1993a, 2012a; Bongaerts et al. 2013). Among the corals that are habitat specialist and uncommon in our study were the fungiids *Cycloseris curvata*, *C. distorta* and *Sandalolitha boucheti*, and the agariciids *Pavona duerdeni* and *Leptoseris fragilis*. These rare species, like *Heliofungia fralinae* and *Cycloseris boschmai*, are usually found in offshore reef habitats with clear waters (Hoeksema 2004, 2012a, b, 2014; Chapters 2 and 5). *Leptoseris* corals are also known to be deep-reef dwellers and are important components of mesophotic reefs (Kahng and Kelley 2007; Kahng et al. 2010; Rooney et al. 2010). Among species associated with shallow reefs, i.e. *Pavona danai*, *Euphyllia cristata* and *E. paradivisa*, the former two species were found near the Bankawan reef flat. Species with a preference for sheltered and occasional turbid conditions are *Lithophyllon spinifer*, *Nemenzophyllia turbida*, *Plerogyra* cf. *cauliformis* and *Plerogyra* cf. *diabolotus* (Ditlev 2003, Chapter 2). Coral species with known habitat preference can be useful indicators of environmental conditions in an area. Other endemic species such as the euphylliids *Plerogyra cauliformis*, and *P. diabolotus* have only been found in Semporna thus far (Ditlev 2003, Chapter 2). In Kudat, specimens that resembled these species and *P. multilobata* were not typically as described by Ditlev (2003), especially in their characteristic vesicle appearance. However, specimens of these species were not typical of the other closest species either, i.e. *Plerogyra simplex* (for *P. cauliformis*) and *Plerogyra sinuosa* (for *P. diabolotus* and *P. multilobata*).

There were two species of *Pavona* corals that were found in Kudat that do not fit the description of extant species from the Indo-Pacific. *Pavona* sp. 1 (labeled *Pavona* sp. in Chapter 4) superficially resembles *Pavona diffluens* (see Veron 2000) only known from the Red Sea, the Arabian Sea and the Persian Gulf. Only two specimens were found and both were from the sediment-laden waters of Marudu Bay (sites 52 and 53). There is a possibility that *Pavona* sp. 1 represents an ecophenotypic variation of *Pavona explanulata*, the closest resembling species, which has adapted to shallow, low-light and sandy substratum condition. Two specimens of *Pavona* sp. 2 (sites 3 and 10) have encrusting growth-form and appear to have very coarse corallites (S9 Fig.).

Common corals in the TMP are species that have widespread distributions and are ordinarily found on most western Indo-Pacific reef habitats (listed in Table 1). The mushroom coral *Fungia fungites* was the only species present at all sites. This species is usually common in shallow depths (Hoeksema 1991, 2012a; Hoeksema and Koh 2009), where it can reproduce asexually by budding (Hoeksema and Yeemin 2011). Other common coral species here have also been reported as dominant corals in the reefs of Sabah (Chapters 2 and 4) and other parts of the Indo-Pacific (Veron 2000).

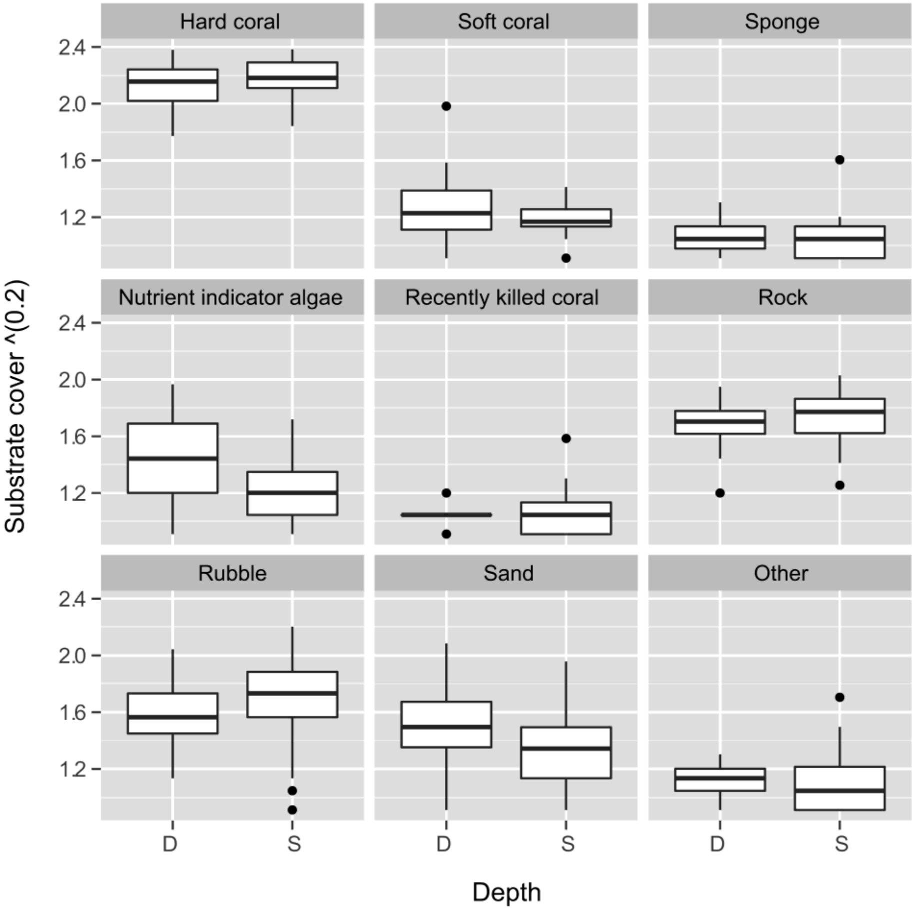


Fig. 7. Benthic categories based on shallow and deep transects. Silt was excluded from the analysis as the percentage coverage was very low.

Coral species richness patterns

Highest coral species richness is commonly found on mid-shelf reefs (Done 1982, 1983; Moll and Suharsono 1986; Hoeksema 1993a; DeVantier et al. 2006) but the reefs within the TMP did not exhibit a clear cross-shelf zonation pattern as most of the reefs are along gentle slopes across the study area before descending into greater depths at the border of the proposed park. The highest coral species richness was found on the reefs at the peripheral area of the study site away from the mainland (n = 8), and at reefs situated near the South Banggi Channel (n = 3). These reefs were among the deepest sites in the study area and exposed to strong currents that are most likely driving the coral composition on the reefs (e.g. Cleary et al. 2005). The deep reefs of the TMP also had a shallow reef zone, and this wider depth range could accommodate coral species with a preference for shallow as well as deep environments, therefore adding species richness to these reefs. Exposure was not significant in influencing the species richness patterns, but this could be due to the high variance in the dataset, as there were very few sites in the sheltered reef condition (approximately 15% of the surveyed reef area only). In comparison with reef studies elsewhere in Sabah, an almost similar pattern was observed for the reefs of Kota Kinabalu, whereby the deeper (and exposed) reefs had higher species richness (Chapter 4). In contrast to the reefs of Semporna, the highest species richness was noted on the sheltered nearshore reefs (Chapter 2).

Perceptibly lower species richness was seen at the reefs fringing the mainland, as indicated by the outlier site 45 and cluster of Group 4. For the latter, all six sites were shallow, of which only four sites were sheltered from the dominant winds, while two other sites were exposed reefs fringing the west coast of the Bengkoka peninsula, suggesting that this cluster was grouped based on its proximity to the mainland. These fringing reefs tend to be in turbid waters and the coral species here have presumably adapted to low light condition. Wood (1978) attributed the characteristics of the reef fauna and the lack of vertical reef development in the coastal reefs to the shallow depths and close proximity to shore. Although the proximity to the mainland was not as significant as depth in influencing the species richness patterns in the TMP, a difference in species composition could be discerned, as was also the case for reefs in Indonesia (Hoeksema 1993a; Cleary et al. 2005).

Approximately 85% of the surveyed reefs in the TMP were considered exposed reefs but they appear to be compositionally different in terms of coral species and hence clustered further into three groups (Fig. 3). Group 1 had three sites in the South Banggi Channel and one site at the west of Balambangan Island, which are characterized by very strong currents. The west coast of Balambangan had a different reefscape from the rest of the sites in the TMP by means of low-lying reefs with little profile development. These reef have been described as having a cyclic die-off and regrowth of alga-consolidated reefs (Wells 1977) caused by repetitive sediment-resuspension from strong current and wave force. Despite the lack in reef development, these reefs have been shown to have high coral diversity, as was also reported in other areas with non-reef-building coral environments (Perry and Larcombe 2003).

Reef benthos assemblages

Hard coral cover in the TMP (49%) exceeded the average values of other areas in the Indo-Pacific. Surveys in 2003 indicated that coral cover from 390 reefs in the region averaged only 22% (Bruno and Selig 2007). Looking at reefs closer to the TMP, the average coral cover in Tubbataha Reef, the Philippines some 320 km away was 36% in the deep sites and 40% in the shallow sites (Jontila et al. 2010). Elsewhere in Sabah, the average percentage cover was 41% in Lankayan Island, Sandakan (Reef Check Malaysia 2010) and 37% in Semporna (Affendi et al. 2012). The methods for collecting hard coral cover data were not necessarily the same, but were sufficiently similar so as to enable a general comparison across the region.

Table 3. The influence of depth and distance from the mainland on the benthic communities.

Model description	Estimate	Std. error	t value	p
Depth				
Hard coral	0.0446	0.0607	0.7350	0.4628
Nutrient indicator algae	-0.2860	0.0933	-3.0660	**0.0023**
Other	-0.0298	0.1040	-2.8700	0.7743
Recently killed coral	-0.0352	0.1290	-0.2730	0.7853
Rock	-0.0012	0.0858	-0.0140	0.9888
Rubble	0.0593	0.0858	0.6910	0.4900
Sand	-0.1910	0.0873	-2.1870	**0.0293**
Soft coral	-0.1333	0.0924	-1.4420	0.1501
Sponge	-0.0534	0.0967	-0.5530	0.5809
Adj. $R^2 = 0.7249$				
Distance from the mainland				
Hard coral	0.0030	0.0019	1.5720	0.1169
Nutrient indicator algae	-0.0007	0.0029	-0.2370	0.8125
Other	-0.0037	0.0028	-1.3170	0.1886
Recently killed coral	-0.0029	0.0037	-0.7720	0.4403
Rock	-0.0029	0.0027	-1.0630	0.2885
Rubble	-0.0093	0.0027	-3.4650	**0.0006**
Sand	-0.0086	0.0027	-3.1490	**0.0018**
Soft coral	-0.0018	0.0030	-0.5940	0.5528
Sponge	-0.0048	0.0032	-1.5170	0.1300
Adj. $R^2 = 0.7257$				

Significant values are indicated in bold.

Some earlier data on the reef status of the TMP is available for comparison, but cannot be used as baseline to measure changes in coral cover as different sites were surveyed. The Pulau Banggi Project for Coral Reef Biodiversity established permanent monitoring sites in the southeast of Banggi with a sampling series of three years from 1999 to 2002. There was no significant difference in mean coral cover in four permanent sites between the first two years (Daw et al. 2002). Other surveys were conducted at different reef sites in order to fill the information gap in the area. The findings from these surveys between 2002–2004 and 2009 showed that only 5% of the reefs had excellent coral cover and 9% had poor coral cover, while most were good (31%) or fair (55%) (Koh et al. 2002; Lee and Chou 2003; Tanzil and Chou 2004; Waheed et al. 2009). This is comparable with our results (reefs with 7% excellent, 38% good, 51% fair and 4% poor coral cover).

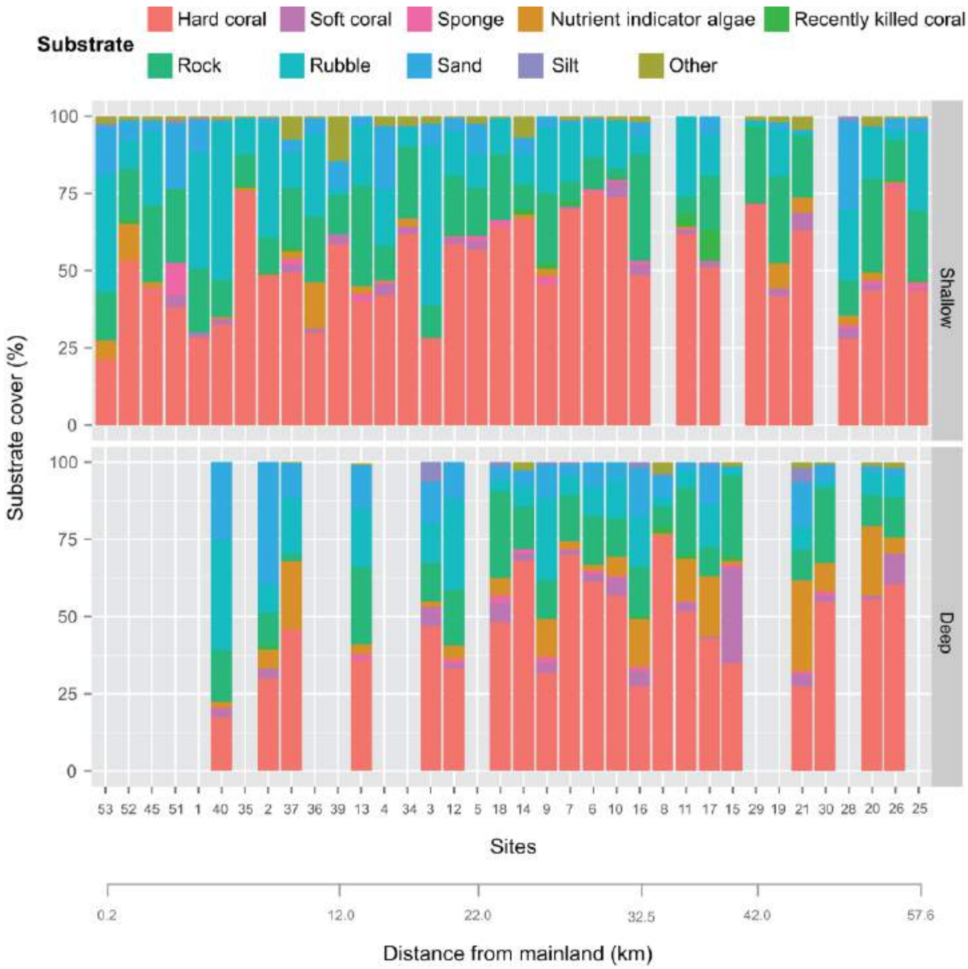


Fig. 8. Benthic categories arranged by percentage hard coral cover based on site proximity from the mainland for shallow and deep transects.

The comparison between the shallow and deep transects revealed a significant difference in the cover of nutrient indicator algae. Algae are commonly known to correspond with areas of high nutrient input or low grazers or herbivores (Hodgson 1999; McCook 1999; McClanahan et al. 2003). Input of nutrients is usually a concern for reefs near urban areas (Hodgson 1999), but our research site is considered remote with no major urban development nearby. Furthermore, proximity to the mainland had no effect on the algae cover (Fig. 8, Table 3). In previous surveys, algae cover was highly variable (0–49%) (Koh et al. 2002; Lee and Chou 2003; Tanzil and Chou 2004), but was usually more abundant in shallow depths (Harding et al. 2001; Daw et al. 2002). This is in contrast with our findings where algae cover was higher in the deep transect. Higher than average algal cover (between 13–29%) at some sites has been attributed to possible nutrient input from river mouths, (Koh et al. 2002) or shoreline vegetation (Lee and Chou 2003).

Sand cover was found to be high at the deep transects and decreased with distance from the mainland, which is consistent with the reef geomorphology of the TMP area. The fringing reefs are generally in shallow and turbid environments. It was common to find large stretches of sand among the patch reefs and reef flats. Moving further away from the mainland, most shallow reefs show a gentle incline before continuing into sandy substrate between 15–20 m depths.

Rubble cover was previously reported to be higher in the shallow reef sites (see Daw et al. 2002; Tanzil and Chou 2004; Waheed et al. 2009). A similar observation was made in the present study with an additional note that rubble cover appears to decrease with distance from the mainland. It is difficult to distinguish the main cause of high rubble cover as the differences between the effects from blast fishing and storm damage are subtle and can appear visually similar, especially in shallow reefs and areas where blast damage is old. The fact that blast fishing has been occurring in the area since the 1970s (Fisher 2000) and has been reported to be the primary threat to the reefs suggests that the presence of rubble in these reefs is most likely caused by this practice (Fox et al. 2003; Fox and Caldwell 2006). It is likely that blast fishing mostly occur at reefs closer to inhabited islands as it would take more effort to reach the more remote reefs, however, data is unavailable as evidence. Previously reported blast frequency was 0.8–1.3 incidences/hour in the Banggi region (Harding et al. 2001; Daw et al. 2003). Several reef sites had unconsolidated coral fragments as evidence of previous blast fishing (e.g. sites 3S and 10S), but the observed damage on the reef appeared old. Damage from blast fishing may have a long-lasting effect, especially when it occurs at a large scale and over a prolonged period of time (Fox et al. 2003; Fox and Caldwell 2006; Raymundo et al. 2007). Throughout the survey 15 blasts were heard with a maximum of six detonations in one dive. Signs of recent blast impact were also witnessed in the form of dead (and dying) fish at Kalutan Island (site 33) that most likely drifted there with the currents as the reef was intact and had one of the highest coral species richness in the TMP. Storm damage was mostly observed at the exposed reef flats of Bankawan and Carrington Reef (pers. obs.).

Although the Reef Check method is not able to indicate some ecological measures, such as the quality of the reefs, it is able to give snapshots of the reef status, hence shedding light to the reef condition of which very little is known of in the TMP. As a note, a reef with high coral cover does not give any indication to the health of the reef (see Wooldridge 2014). Nevertheless, an advantage of the Reef Check protocol is that its standard monitoring categories allows for comparison of data across large areas (Hodgson et al. 2006) in order to know the status of a particular reef in relation to other reefs. This is a useful start for the TMP where not much data is available from the area and monitoring protocols are not yet in place.

Conclusions

Plans are underway for the establishment of the Tun Mustapha Park by the end of 2015 and the park management will adopt a multiple use concept, whereby various zones will be identified for different uses, while at the same time ensuring conservation and sustainable use of natural resources (Jumin and Kassem 2009; Jumin et al. 2011). The present study showed that reefs with high species richness are found at the periphery of the TMP boundary away from the mainland and near the South Banggi Channel. Most of these reefs extend to deeper depths, as compared to the rest of the reefs within the proposed park. Depth is an important factor in influencing the coral species composition and some aspects of the benthic reef assemblages. The proximity to the mainland, though not significant as depth, also plays a part in structuring the coral species richness. Furthermore, reefs with good and poor coral cover have been identified. When these layers of information are overlaid on the TMP map, particular reefs stand out as being important from a conservation perspective and thus should be afforded protection under the preservation zones. A continuous monitoring programme should be established by setting up permanent monitoring sites within the TMP. Information collected from these sites would be crucial to evaluate temporal changes or assess impacts on the coral reefs (Burke et al. 2012).

Acknowledgments

This research was carried out during the Tun Mustapha Park Expedition (TMPE) 2012 that was jointly-organised by WWF-Malaysia, Universiti Malaysia Sabah, Sabah Parks, Malaysia and Naturalis Biodiversity Center, The Netherlands. Research permits were obtained from the Economic Planning Unit, Prime Minister’s Department Malaysia and the Sabah Biodiversity Centre. We thank the crew of the S/Y Raja Laut and M/Y Navorca of WWF-Phillipines for support during the fieldwork, Mohd Asri Barail and Irwanshah Mustapa for assistance in selecting dive sites in the field and Sikula Magupin for producing the map of the research area. We also thank the members of the Banggi Youth Club (BYC) who participated in the expedition. We appreciate the critical comments and suggestions from Dr. David Feary and three anonymous reviewers, which improved the manuscript tremendously.

Supporting Information

Supporting information are available at http://dx.doi.org/10.1371/journal.pone.0146006

S1 Fig. Additional sites surveyed for only Fungiidae between 2005 and 2008.

S2 Fig. Visual analysis. Exploring the coral species richness data.

S3 Fig. Model 1. Full model with all three environmental factors depth, exposure and distance to the mainland.

S4. **Fig.** Model 2. Model 1 excluding outlier site 45.

S5 Fig. Visual analysis. Exploring the benthic community data across all transects in accordance to the distance from the mainland.

S6 Fig. Correlation between hard corals and other dominant substrate components (rubble and sand).

S7 Fig. Model 3. Examining the effect of depth on the benthic communities.

S8 Fig. Model 4. Examining the effect of distance from the mainland on the benthic communities.

S9 Fig. *Pavona* spp. A) *Pavona* sp. 1 from site 53, B) *Pavona* sp. 2 from site 3 (see page 72).

S1 Table. Locality data of coral species diversity and benthic surveys in the proposed Tun Mustapha Park. The distance between the sites for both surveys ranged from 0.16 to 5.80 km apart of each other (see page 73).

S2 Table. Depth, exposure and distance from the mainland of sites for the coral diversity and benthic community surveys (see page 74).

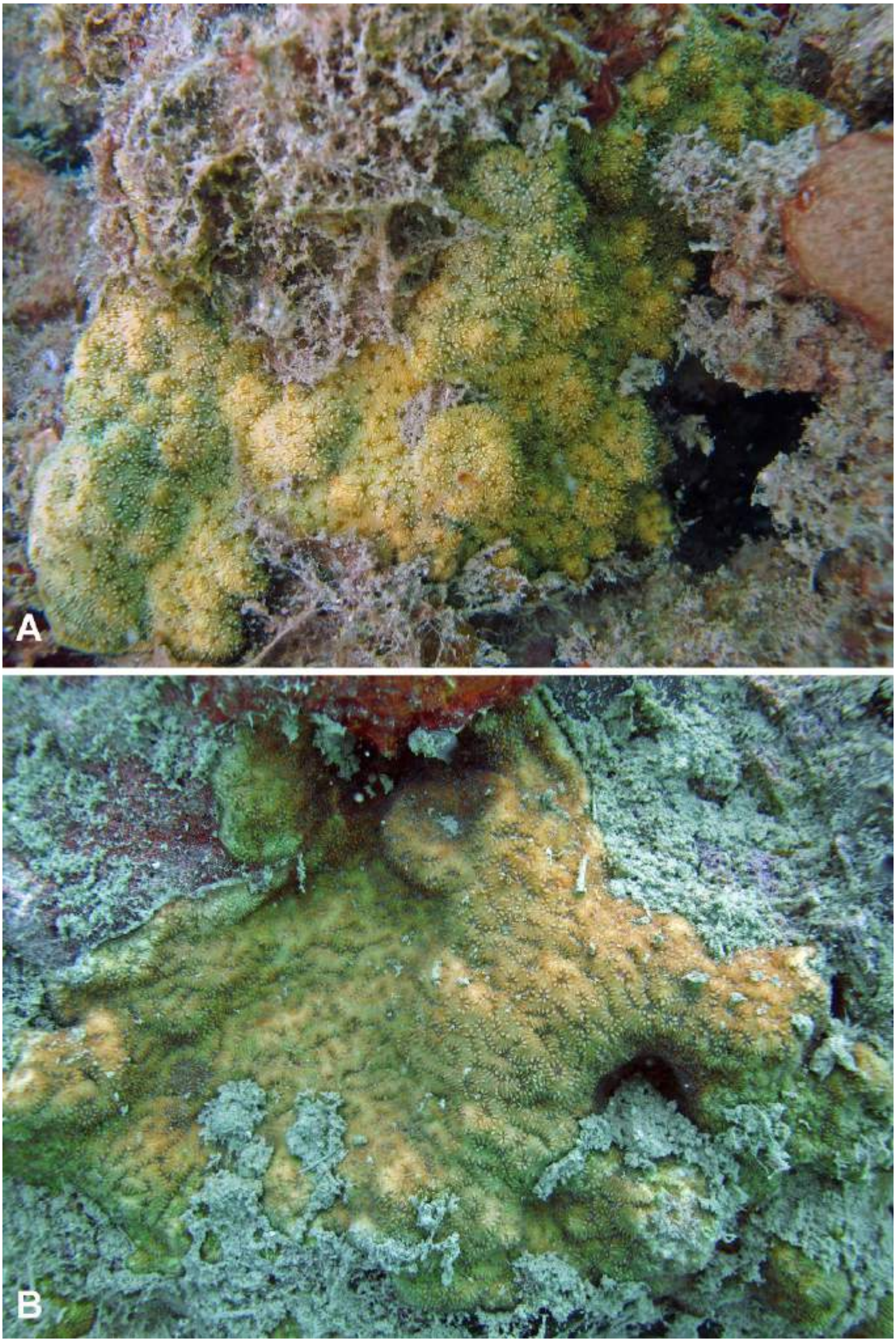
S3 Table. Fungiidae, Agariciidae and Euphylliidae species incidence. For Fungiidae, observations were made at 38 sites during the Tun Mustapha Park Expedition (TMPE) 2012 and nine sites from previous surveys in 2005, 2007 and 2008. For Agariciidae and Euphylliidae, observations were made at 35 sites during the Tun Mustapha Park Expedition (TMPE) 2012.

S4 Table. Reef substrate composition based on the benthic surveys in the proposed Tun Mustapha Park. Data was collected from 33 shallow and 22 deep reef sites.

S5 Table. Dataset for coral species richness analyses.

S6 Table. Dataset for benthic community analyses.

S9 Fig. *Pavona* spp. A) *Pavona* sp. 1 from site 53, B) *Pavona* sp. 2 from site 3.



S1 Table. Locality data of coral species diversity and benthic surveys in the proposed Tun Mustapha Park. The distance between the sites for both surveys ranged from 0.16 to 5.80 km apart of each other.

Site no.	Site name	Localities for diversity surveys		Localities for benthic surveys	
		Latitude (N)	Longitude (E)	Latitude (N)	Longitude (E)
1	Linggisan	6°57'08.9"	117°17'01.5"	6°57'17.5"	117°16'42.1"
2	Mandidarah Is.	6°55'56.7"	117°21'15.4"	6°55'54.5"	117°20'59.0"
3	Lubani Rock	6°53'45.0"	117°23'15.8"	6°53'13.3"	117°22'47.4"
4	Lundayang	6°48'39.4"	117°21'59.1"	6°48'44.2"	117°21'35.0"
5	Tigabu, S	6°49'05.9"	117°29'13.5"	6°49'16.2"	117°28'16.3"
6	Tigabu Is. / Tigabu, E	6°53'51.7"	117°27'36.1"	6°53'42.8"	117°30'45.1"
7	Buwaning	6°58'59.3"	117°30'11.2"	6°59'02.8"	117°29'55.1"
8	Buwaning. E	7°00'23.6"	117°33'37.4"	7°00'07.8"	117°33'30.2"
9	Simaggot	7°02'34.4"	117°27'58.5"	7°02'37.9"	117°27'54.6"
10	Straggler Is.	7°05'15.0"	117°28'21.8"	7°05'14.3"	117°28'13.7"
11	Fairway Shoal	7°07'06.3"	117°30'42.6"	7°07'09.3"	117°30'33.3"
12	Paliuk	7°03'17.4"	117°22'32.6"	7°03'07.1"	117°21'49.2"
13	Tanjung Is. / P. Mati	7°05'37.1"	117°16'07.8"	7°04'52.6"	117°14'52.3"
14	Sibaliu, S	7°06'50.0"	117°22'36.8"	7°06'58.2"	117°22'46.1"
15	Purukan Sibaliu	7°12'41.5"	117°28'13.7"	7°12'31.6"	117°28'09.0"
16	Sibaliu, N	7°11'33.4"	117°23'38.0"	7°11'42.8"	117°23'07.1"
17	East Banggi Patches / Bankawan Reef, E	7°14'37.2"	117°24'04.3"	7°14'06.3"	117°22'35.2"
18	Bankawan Reef, SW	7°11'21.8"	117°17'39.4"	7°11'05.9"	117°17'13.3"
19	Latoan Patch	7°17'43.3"	117°24'06.1"	7°17'34.7"	117°22'05.9"
20	Banggi Outer Reef, NE	7°22'53.7"	117°22'24.6"	7°23'27.5"	117°21'30.7"
21	Balundangan Besar Is., NE	7°20'50.5"	117°21'24.3"	7°20'57.6"	117°21'06.2"
25	Mangsee Great Reef, E	-	-	7°29'19.4"	117°16'50.8"
26	Mangsee Great Reef, S	7°27'25.7"	117°14'11.2"	7°27'47.3"	117°15'15.1"
27	Mangsee Great Reef, SW	7°27'24.8"	117°13'21.6"	-	-
28	Kapitangan	-	-	7°21'08.9"	117°08'22.0"
29	Tiga Is., N	7°21'47.7"	117°02'41.6"	7°21'22.8"	117°03'17.0"
30	Tanjung Siagut, W	-	-	7°21'26.5"	116°58'17.5"
32	Tanjung Timohing	7°17'27.3"	116°53'03.2"	-	-
33	Kalutan Is., N	7°12'52.7"	116°50'30.8"	-	-
34	Molleangan Kecil Is., NW	7°04'50.7"	117°00'58.5"	7°04'55.4"	117°01'05.9"
35	Belaruan	7°01'50.1"	117°00'41.7"	7°02'04.5"	117°00'11.2"
36	Patanunan Is., S	7°05'59.7"	117°05'21.1"	7°05'57.2"	117°05'13.3"
37	Molleangan Besar Is., E	7°05'07.2"	117°03'33.8"	7°05'09.5"	117°03'39.4"
38	Carrington Reef, SW	7°07'49.4"	117°13'41.9"	-	-
39	Balak-Balak Is., S	7°07'22.6"	117°08'36.0"	7°07'12.4"	117°08'25.0"
40	Pancang Pukul	7°02'01.6"	117°04'25.1"	7°02'01.6"	117°04'24.5"
41	Kalang	6°59'48.1"	117°03'13.4"	-	-
43	Rosob	6°40'12.5"	116°54'23.7"	-	-
44	Mempakad Reef	6°42'59.7"	116°54'17.8"	-	-
45	Limau-Limauan	6°49'21.0"	116°52'32.4"	6°49'24.2"	116°52'26.0"
51	Bak-Bak	6°59'36.4"	116°50'27.7"	6°57'38.6"	116°50'23.0"
52	Pantai Bahagia	6°56'21.7"	116°50'25.7"	6°55'07.1"	116°50'54.5"
53	Tanjung Tigasamil	6°51'07.1"	116°51'30.0"	6°51'18.8"	116°51'36.2"

S2 Table. Depth, exposure and distance from the mainland of sites for the coral diversity and benthic community surveys.

Sites for coral species richness data				**Sites for benthic community data**			
Site	Depth[a]	Exposure	Distance to mainland (km)[b]	Site	Depth[c]	Exposure	Distance to mainland (km)[b]
1	Shallow	Exposed	3.5	1S	Shallow	Exposed	3.1
2	Shallow	Exposed	11.1	2S	Shallow	Exposed	10.6
3	Shallow	Exposed	14.3	2D	Deep	Exposed	10.6
4	Shallow	Exposed	12.8	3S	Shallow	Exposed	13.4
6	Shallow	Exposed	22.2	3D	Deep	Exposed	13.4
7	Deep	Exposed	27.8	4S	Shallow	Exposed	12.4
8	Deep	Exposed	34.5	5S	Shallow	Exposed	22.0
9	Shallow	Exposed	25.8	6S	Shallow	Exposed	28.1
10	Deep	Exposed	29.0	6D	Deep	Exposed	28.1
11	Deep	Exposed	34.4	7S	Shallow	Exposed	27.4
12	Shallow	Exposed	18.4	7D	Deep	Exposed	27.4
13	Shallow	Exposed	14.8	8D	Deep	Exposed	34.4
14	Shallow	Exposed	24.3	9S	Shallow	Exposed	26.0
15	Shallow	Exposed	38.8	9D	Deep	Exposed	26.0
16	Shallow	Exposed	33.1	10S	Shallow	Exposed	28.9
17	Shallow	Exposed	37.0	10D	Deep	Exposed	28.9
18	Shallow	Exposed	25.0	11S	Shallow	Exposed	34.4
19	Shallow	Exposed	42.6	11D	Deep	Exposed	34.4
20	Shallow	Exposed	48.2	12S	Shallow	Exposed	17.2
21	Shallow	Exposed	43.7	12D	Deep	Exposed	17.2
26	Deep	Exposed	56.0	13S	Shallow	Exposed	12.3
27	Deep	Exposed	56.9	13D	Deep	Exposed	12.3
29	Shallow	Exposed	42.7	14S	Shallow	Exposed	24.5
32	Shallow	Exposed	31.6	14D	Deep	Exposed	24.5
33	Shallow	Exposed	22.0	15D	Deep	Exposed	38.4
34	Deep	Exposed	12.3	16S	Shallow	Exposed	32.5
35	Deep	Exposed	8.0	16D	Deep	Exposed	32.5
38	Shallow	Exposed	15.4	17S	Shallow	Exposed	35.2
40	Shallow	Exposed	4.8	17D	Deep	Exposed	35.2
41	Shallow	Exposed	2.4	18S	Shallow	Exposed	24.3
43	Shallow	Sheltered	0.9	18D	Deep	Exposed	24.3
44	Shallow	Sheltered	5.7	19S	Shallow	Exposed	42.1
45	Shallow	Sheltered	0.8	20S	Deep	Exposed	48.8
52	Shallow	Sheltered	0.4	20D	Deep	Exposed	48.8
53	Shallow	Sheltered	0.3	21S	Shallow	Exposed	43.6
				21D	Deep	Exposed	43.6
				25S	Shallow	Exposed	57.6
				26S	Shallow	Exposed	55.7
				26D	Deep	Exposed	55.7
				28S	Shallow	Exposed	46.9
				29S	Shallow	Exposed	42.0
				30D	Deep	Exposed	43.9
				34S	Shallow	Exposed	12.5
				35S	Shallow	Exposed	9.0
				36S	Shallow	Exposed	11.0
				36D	Deep	Exposed	11.0
				37S	Shallow	Exposed	10.7
				37D	Deep	Exposed	10.7
				39S	Shallow	Exposed	12.0
				40S	Shallow	Exposed	4.8
				40D	Deep	Exposed	4.8
				45S	Shallow	Sheltered	0.6
				51S	Shallow	Sheltered	0.8
				52S	Shallow	Sheltered	0.3
				53S	Shallow	Sheltered	0.2

[a] Depth: shallow sites are < 20 m, deep sites are > 20 m

[b] Distance to mainland is measured from each site to the nearest land point on the mainland (Sabah) following the shortest sea path on Google Earth

[c] Depth: shallow transects are between 3–5 m, deep transects are between 8–10 m

Chapter 4

Diversity patterns of scleractinian corals at Kota Kinabalu, Malaysia, in relation to exposure and depth

Zarinah Waheed and Bert W. Hoeksema

Abstract

A large part of the fringing and patch reefs of Kota Kinabalu is situated along the coastline of Sabah and around the islands of the Tunku Abdul Rahman Park (TARP). The park is composed of five islands and together with the surrounding sea it covers an area of ca. 50 km^2. Several studies have been carried out in the 1970s and 1980s to determine the status of the park's hard coral fauna, which serves as baseline information. The present study builds on previous ones by determining the species richness patterns of scleractinian coral families Fungiidae, Agariciidae and Euphylliidae observed at 28 reef sites within and outside the TARP boundary. Three additional sites were surveyed for mushroom coral species. The species diversity from this study is higher than those previously recorded. Based on the coral species composition for each site, results from multivariate analyses suggest two distinct groups of sites that reflect a difference in reef exposure, where the highest species numbers were observed at the exposed and deeper reefs. Findings of this study can provide a basis for future comparisons in order to detect changes in the coral communities around Kota Kinabalu and can be applied to developing conservation priorities for the park.

Raffles Bulletin of Zoology (2014) 62: 66–82.

Introduction

The coral reefs of Kota Kinabalu are part of a larger reef system along Borneo's west coast extending from Sulaman Bay in the north to Dinawan Island in the south with fringing reefs of approximately 54 km in length (Mathias and Langham 1978). Previous studies have documented the condition of Kota Kinabalu's coral reefs, mainly referring to their coral cover (Lulofs 1973; Lulofs et al. 1974; Wood 1977, 1978; Mathias and Langham 1978; Nyanti and Johnston 1992; Pilcher and Cabanban 2000), whereas only a few mentioned the coral fauna composition (Marsh 1992; Nyanti and Johnston 1992). Other references are listed in some of these studies, but most of these consist of unpublished reports and student dissertations that are difficult to access and not available for use as baseline.

One of the first documented studies on corals of Kota Kinabalu was about the use of corals as a limestone resource for construction purposes (Fitch 1950). By 1962, the main building materials produced in Sabah consisted of sand, stone, clay and coral. According to the Geological Survey Department (1963) the production of corals then was 44,000 m^3 with the approximate value of US$ 78,400.00. Approximately 450 tons of corals could be mined in a single day, which is estimated to be the equivalent of between 64 and 90 coral boulders. This report gave the first account of the condition of some Kota Kinabalu reefs, while specific aspects of reef damage were discussed in a subsequent report (Lulofs et al. 1974).

Very little literature appears to be available on the scleractinian coral diversity of Kota Kinabalu. Older studies reported on coral diversity to genus level only (Wood 1978; Nyanti 1984). During surveys carried out between 1984 and 1986, a total of 56 genera and 148 species of hard corals was recorded in the Tunku Abdul Rahman Park (TARP) of Kota Kinabalu (Nyanti and Johnston 1992). Marsh (1992) reported 53 genera and 131 species of hard corals from a survey of 10 days within the park area. A compilation of the coral species resulting from these reports comprised of 74 genera and 207 species of hard corals (Marine Research Unit of Sabah Parks 2005). However, 124 species among these were listed as "sp." and because they were based on different sources, it is difficult to verify the identity of these species. In addition, these sources did not include species descriptions or illustrations of the specimens. Furthermore, the identifications were made using various references following different coral species concepts. In studies concerning the offshore Mengalum Island, Wood (1978) found 28 genera, while Lee (1994) reported 64 genera of hard corals. These few studies have not presented a very clear coral diversity pattern of the Kota Kinabalu reefs.

Reefs in TARP that were surveyed every three to four years since 1987 showed a decline in live coral cover since 1994 (Woodman and Wilson 1994). However, the coral species diversity remained constant on most reefs (Mitchell 1999). On Manukan Island, there was a significant decrease in diversity and loss in coral cover between 1987 and 1999. There were changes in the coral fauna composition at generic level with increased abundance of *Acropora*, *Pocillopora* and *Seriatopora*, which are fast-growers. In turn, *Fungia* and

Porites had decreased in abundance. These changes were brought upon after a tropical storm in 1996 (Mitchell 1999).

A combination of anthropogenic impacts and natural events has affected the coral reefs in the vicinity of Kota Kinabalu. Reefs have been damaged by blast fishing (Lulofs 1973; Lulofs et al. 1974; Wood 1977, 1978; Mathias and Langham 1978), and to some extent by commercial collection of reef fauna for the aquarium and curio trade (Wood 1977, 1978; Phillips 1979). In 2002, a total of 13 blasts were recorded from nearby Sapangar Island (Woodman et al. 2004). Based on reef surveys conducted by Reef Check Malaysia in early 2010, a high cover of rubble was still evident on the reef of Malohom Bay (Gaya Island) resulting from previous blast fishing activities. Sedimentation has been inferred from land clearing in parts of Sapangar and Gaya bays (Mathias and Langham 1978). Wood (1978) observed intact but dead coral covered with either algae or silt. Reef conditions were better in shallow parts than on deeper slopes with horizontal visibility generally less than 7 m and considered sedimentation as a contributory factor in causing mortalities. A preliminary study on the sedimentation rates of the reefs in Gaya and Sapangar islands showed that the rates were < 10 mg cm^{-1} d^{-1} (Waheed et al. 2007) and within the acceptable threshold for coral reefs (Rogers 1990; Erftemeijer et al. 2012). However, the sedimentation rates were between 96–156 mg cm^{-1} d^{-1} on the reefs along the coastline near Sapangar Bay (Waheed et al. 2007).

Although Sabah lies outside the typhoon zone, severe storms have affected the shallow reefs in Kota Kinabalu. Stormy weather in January 1976 devastated the reef flat on the patch reefs off Gaya Island (Wood 1977, 1978). Tropical storm Greg, which occurred in December 1996, caused severe damage to the reefs on the windward sides of Manukan, Sapi, Gaya and Sulug islands (Pilcher and Cabanban 2000). An outbreak of 'red tide' caused by phytoplankton blooms is known to have occurred off the west coast of Sabah in 1976 (Roy 1977). Since this incident, red tide or harmful algal blooms (HABs) have occurred periodically and is a recurring problem in the west coast of Sabah, particularly in the coastal waters of Kota Kinabalu (Usup et al. 1989; Anton et al. 2008; Adam et al. 2011). Low densities of Crown-of-thorns starfish *Acanthaster planci* (Linnaeus, 1758) have been reported from Sapangar Island (Lulofs 1973) and the west coast islands (Wood 1977, 1978), but a significant outbreak was noted on Merangis reef of Gaya Island in 1991 and 1994 resulting in significant losses of branching corals such as *Acropora* spp. (Pilcher and Cabanban 2000).

The widespread coral bleaching event of 1997–1998 also affected the nearshore reefs of Kota Kinabalu (Wilkinson 1998). About 30–40% of the coral cover at Gaya Island adjacent to the Tunku Abdul Rahman Park was reported to show bleaching in May 1998 when the water temperature peaked at 32 °C. Within the park boundary, minor bleaching occurred only in Mamutik Island (Wilkinson 1998; Pilcher and Cabanban 2000). Another mass bleaching event occurred in 2010, when bleaching on the reefs of Sabah in general was rated as medium (25–50%) and extended down to 20–25 m depth (Tun et al. 2010). In 2012, the reefs of Kota Kinabalu had high bleaching rates (46 to 90 % of the coral cover), which affected the hard corals, soft corals and their associated fauna (Aw and Muhammad Ali 2012).

With the exception of coral mining, risks that stem from threats mentioned above still exist for the reefs of Kota Kinabalu. Much of what is known on the coral reefs of this area is entirely attributed to the few previous studies that reported on the general reef status and diversity. The present study aims to explore the coral fauna of the reefs, in particular its species diversity pattern across the coastal zone. The findings could add to the current knowledge of the area and perhaps be compared with what is known about the reefs to detect if there have been changes in the coral reef communities over time.

Materials and methods

Research area

Research was carried out on the west coast of Sabah, specifically in Kota Kinabalu, which includes seven islands: Suluq, Mamutik, Manukan, Sapi, Gaya, Sapangar and Udar Besar islands from Tanjung Aru to Sapangar Bay of the Kota Kinabalu coastline (Fig. 1). A large part of this area is within the Tunku Abdul Rahman Park (TARP).

TARP was established in 1974 and comprised of a large part of Gaya Island and the whole of Sapi Island, covering an area of 36.4 km^2. The inclusion of Manukan, Mamutik and Sulug islands in 1979 expanded the park area to 49.3 km^2 (Spait 2001). The eastern part of Gaya Island that faces Kota Kinabalu has been excluded (Wood 1978). The villages here comprise of houses on stilts all along the beach that extend out to the sea. Currently there are three resorts within the park area and one just outside its boundary. The number of visitors to TARP increased from approximately 136,000 in 1998 to nearly 300,000 in 2009 (Sabah Parks Visitor Statistics 2013). TARP is managed by Sabah Parks and the administrative centre is based on Manukan Island. Situated to the north of TARP are the islands Sapangar [variations in spelling = Sepangar, Sepanggar], Udar Besar, Udar Kecil and Peduk off Sapangar Bay. These islands are not tourist destinations. Similar to Gaya Island, the eastern shore of Sapangar Island is lined with houses on stilts. There is a road connecting Udar Kecil to the mainland, which is now part of the Sepanggar Naval Base. Udar Besar and Peduk islands are uninhabited.

Coral reefs fringe along most parts of these islands, and some parts of the coastline. Generally, the reefs in the north and west of the islands are often exposed to waves and sea swells, and hence characterised by predominantly rocky substratum and boulders interspersed with patches of rubble and coarse sand (Wood 1978). Reefs in the south and east of the islands that are facing the mainland are described to have sheltered conditions, where white-sandy beaches are found. Around Gaya Island, reefs have developed along the headland of both the north and south coast, but Wood (1978) remarked that the fauna here was different in some aspects. The condition of the reefs are varied, but the most extensive reef lies along the southern end of Sulug Island, which is rather exposed to strong currents. There are several patch reefs [= platform reefs; see Wood 1978] within the research area. Edgell Patches lie 1.6 km to the west of Sapi Island, just outside the park boundary. These reefs rise to about 12–13 m below the surface, and are rather flat with dense coral cover. The reef slopes down to 20 m and flattens out gradually before sloping down again. On the second tier of the reef flat, large barrel sponges *Xestospongia* sp. and whip corals have been encountered, indicating the possible occurrence of strong currents.

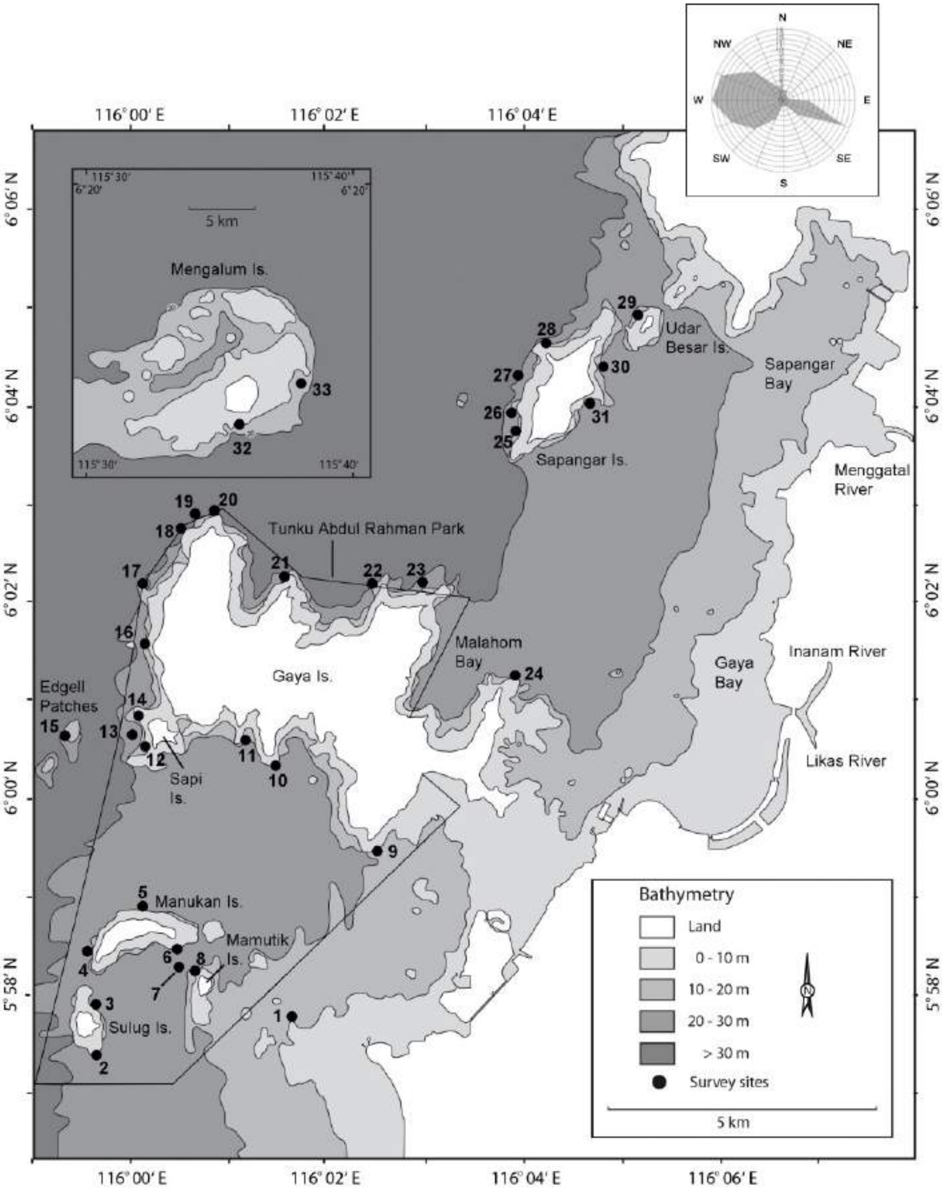


Fig 1. Survey sites (numbered 1–33) at Kota Kinabalu and Mengalum Island, Sabah, Malaysia. The boundary of the Tunku Abdul Rahman Park is indicated. The 2-year average wind distribution values show that the prevalent wind direction is from the west. Winds from the east-southeast is only dominant from December to January. Statistics were taken from wind speed measurements at Kota Kinabalu International Airport (November 2010–November 2012) from © Windfinder.com

Rivers in the vicinity of Kota Kinabalu are the Menggatal River that flows into Sapangar Bay and Inanam River that flows into Gaya Bay. The river systems in Sabah transport sediment to the coast during and after periods of rainfall. The sediment plume can reach between 5–10 km from the coastline to the South China Sea depending on the sediment load and water discharge, and areas with high sediment concentrations had either no coral reefs or only poor quality reefs (Jakobsen et al. 2007). The sediment plume from the Inanam River has been thought to be one of the main factors contributing to the degradation of reefs in the vicinity of Gaya Bay (Shoreline Management in the ICZM Context in Sabah 1999).

The northeast monsoon occurs from October to March and peaks in December to January while the southwest monsoon is from May to September and peaks in July to August (Wyrtki 1961), but yearly variations occur. The calmest conditions on the west coast reefs are from February to May (Wood 1978) although the area between the islands and the mainland is relatively sheltered year-round. Based on the average wind distribution values throughout the year, the prevalent wind direction is from the west (Fig. 1). From December to January, the wind from the east-southeast is rather dominant as well. During this period of the year, the water temperature is cooler. At the time of the survey high concentrations of slow-swimming salps (Thaliacea: Salpida: Salpidae) were observed in the water column and over the reefs, which were preyed on by mushroom corals (Hoeksema and Waheed 2012).

Field sampling

The survey was conducted between 16 and 28 July 2011 on 28 reef sites of Kota Kinabalu, Sabah (5°57'–6°5' N, 115°59'–116°5' E). Mushroom corals (Fungiidae) were previously monitored at three additional localities in July 2005. The reefs were surveyed from the reef base no deeper than 30 m to the reef flat, varying from sheltered to exposed conditions that were within 10 km from the coastline (Fig. 1, Table 1). Two additional sites were surveyed in Mengalum Island, situated approximately 56 km northwest of Kota Kinabalu, near the edge of the continental shelf. Both sites were not included in the data analysis because reef conditions appeared to differ from those more nearshore and weather conditions did not allow additional sampling, which would have given a better representation. Site selection was based on Malaysia Nautical Charts MAL 8608 and MAL 864 and Google Earth imagery.

Species incidence data were recorded at each site for the coral families Fungiidae, Agariciidae and Euphylliidae as proxy for all reef-dwelling Scleractinia by employing the roving diver technique (Schmitt et al. 2002). These coral families are found in various reef habitats and have a wide geographical distribution. A similar study was done in Semporna, Sabah (Chapter 2), and comparisons on the coral composition and species richness patterns of these families can be made. Coral specimens were identified following the species concepts from taxonomic revisions and coral fauna descriptions: Veron and Pichon (1980); Dinesen (1980); Hoeksema (1989); Veron (2000); and Ditlev (2003). The classification of the Fungiidae was adapted according to a recent phylogenetic construction of this family (Gittenberger et al. 2011), whereas for consistency in the comparisons, two recently added species (Benzoni et al. 2012a) were not included in the survey. Photographs of each species were taken and specimens were collected when in situ identification was not possible. These specimens were deposited in the Borneo Marine Research Institute reference collection in Universiti Malaysia Sabah (UMS) in Kota Kinabalu. Specimens of the target coral families already in the Sabah Parks reference collection at TARP, Manukan Island were examined and re-indentified.

Data analysis

Species of coral families Fungiidae, Agariciidae and Euphylliidae were listed and compared to previous studies undertaken in the same area. Species richness estimators were calculated using EstimateS 8.20 (Colwell 2009) to show the rate at which additional species were found in the course of consecutive dives, which indicates the expected total species richness in an area (Magurran 2004). For the coral families Agariciidae and Euphylliidae, data were collected at 28 sites and for the Fungiidae at 31 sites.

Multivariate analyses of the coral species composition were carried out for 28 sites (where data were collected for all families) using PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6 (Clarke and Warwick 2001; Clarke and Gorley 2006). Based on the Bray-Curtis resemblance matrix, sites that were most similar to each other were represented in a group-averaged hierarchical clustering dendrogram. The sites were also visualised in multidimensional scaling (MDS) plots, whereby the distance between each site represents their similarity or dissimilarity. Similarity profiles (SIMPROF) were derived from the dendrogram and contours were applied to the MDS plots to highlight the significant groupings of the sites, which were then plotted on the map to discern species richness patterns. The analysis of similarities (ANOSIM) was used to test for significant differences among the a priori groups classified by reef habitats influenced by exposure to wind-generated waves and depth. Sites that were exposed to the predominant wind from the west were labelled as exposed (20 sites), while sites at the leeward side of islands were labelled as sheltered (8 sites). Sites in the west and north of Gaya Island and west of Sapangar Island, where the seafloor extends beyond 30 m were considered deep (14 sites), while the rest of the sites that flattened out at around 20 m depth were considered shallow (14 sites, see Table 1).

Results

The biodiversity survey of Kota Kinabalu reefs resulted in records of 35 species of Fungiidae from 31 sites, and 26 species of Agariciidae and 11 species of Euphylliidae from 28 sites (Table 2, Appendix 1). In comparison to the species list that was compiled by Sabah Parks (Marine Research Unit of Sabah Parks 2005), 17 Fungiidae, 13 Agariciidae and 3 Euphylliidae in our survey represent new records for Kota Kinabalu. The two dives at Mengalum Island added two additional species to the list: *Pavona* sp. (Agariciidae) and *Plerogyra simplex* (Euphylliidae). Both were encountered only once and not found at any of the surveyed sites within Kota Kinabalu reefs. The total number of coral species per site ranged from 29 (site 1) to 55 (site 15) (see Fig. 1). Nineteen sites

(68%) had a total of ≥ 40 species, while five out of these 19 sites had ≥ 50 species. Some coral species were common and recorded for every site, while a few others were rare and found at only a few sites (Table 3).

Table 1. Locality data of the survey sites in Kota Kinabalu and Mengalum Island. Five sites (8, 12, 14, 32, and 33) were not included in the multivariate analyses as data were not collected for all three coral families. Exposure: exposed or sheltered in relation to the predominant wind from the west. Depth (maximum) of seafloor: shallow (≤ 30 m) or deep (≤ 30 m).

No.	Site	Latitute (N)	Longitude (E)	Exposure	Depth
1	Tanjung Aru reef	05°57’33.9”	116°01’44.6”	Sheltered	Shallow
2	S Sulug	05°57’23.3”	115°59’37.9”	Exposed	Shallow
3	N Sulug	05°57’47.5”	115°59’38.9”	Sheltered	Shallow
4	E Manukan Is.	05°58’26.4”	115°59’30.7”	Exposed	Shallow
5	N Manukan Is.	05°58’46.1”	116°00’10.6”	Exposed	Shallow
6	SE Manukan Is.	05°58’21.5”	116°00’32.3”	Sheltered	Shallow
7	NW Mamutik Is. 1	05°58’09.5”	116°00’34.1”	Sheltered	Shallow
8	NW Mamutik Is. 2	05°58’07.0”	116°00’45.0”	Sheltered	Shallow
9	SE Gaya Is., Tg. Wokong	05°59’25.6”	116°02’26.5”	Exposed	Shallow
10	S Gaya Is.	06°00’16.2”	116°01’29.1”	Exposed	Shallow
11	S Gaya Is., Batu Point	06°00’34.2”	116°01’11.6”	Exposed	Shallow
12	SW Sapi Is.	06°00’26.0”	116°00’13.0”	Exposed	Deep
13	W Sapi Is.	06°00’35.3”	116°00’01.3”	Exposed	Deep
14	NW Sapi Is.	06°00’45.0”	116°00’07.0”	Exposed	Deep
15	Edgell Patches	06°00’38.7”	115°59’22.2”	Exposed	Deep
16	W Gaya Is. 1	06°01’23.5”	116°00’14.9”	Exposed	Deep
17	W Gaya Is. 2	06°01’57.5”	116°00’16.1”	Exposed	Deep
18	NW Gaya Is., Tg. Bulijong 2	06°02’34.7”	116°00’32.8”	Exposed	Deep
19	NW Gaya Is., Tg. Bulijong 1	06°02’44.6”	116°00’40.5”	Exposed	Deep
20	NW Gaya Is., Tg. Bulijong 3	06°02’38.4”	116°00’52.9”	Exposed	Deep
21	N Gaya Is., Tg. Merangis	06°02’07.9”	116°01’29.2”	Sheltered	Deep
22	NE Gaya Is., Tg. Tavajun 2	06°01’58.8”	116°02’33.7”	Exposed	Deep
23	NE Gaya Is., Tg. Tavajun 1	06°01’55.9”	116°02’54.4”	Exposed	Deep
24	NE Gaya Is., Tg. Logong	06°01’05.7”	116°03’52.8”	Sheltered	Shallow
25	SW Sapangar 1	06°03’42.8”	116°04’03.5”	Exposed	Deep
26	SW Sapangar 2	06°03’50.1”	116°03’54.1”	Exposed	Deep
27	W Sapangar	06°04’11.3”	116°03’58.1”	Exposed	Deep
28	NW Sapangar	06°04’30.0”	116°04’18.2”	Exposed	Deep
29	Udar Besar Is.	06°04’49.1”	116°05’12.8”	Exposed	Shallow
30	NE Sapangar	06°04’26.0”	116°04’47.4”	Sheltered	Shallow
31	E Sapangar	06°03’58.5”	116°04’42.5”	Sheltered	Shallow
32	SW Mengalum Is.	06°11’10.4”	115°35’23.9”	Sheltered	Shallow
33	NE Mengalum Is.	06°12’42.1”	115°37’24.1”	Sheltered	Shallow

Table 2. Coral species of the families Fungiidae, Agariciidae, and Euphylliidae recorded from the Tunku Abdul Rahman Park and nearby islands in Kota Kinabalu during present and previous studies (Marine Research Unit of Sabah Parks 2005) and Sabah Parks reference collections. Six additional species from Nyanti and Johnston (1992) are each marked with an asterisk (*). All identifications have been updated to current revisions and descriptions.

	Sabah Parks list	**Sabah Parks ref. coll.**	**Present study**
Fungiidae			
Ctenactis albitentaculata Hoeksema, 1989			x
Ctenactis crassa (Dana, 1846)			x
Ctenactis echinata (Pallas, 1766)	x	x	x
Ctenactis sp.	x		
Cycloseris costulata (Ortmann, 1889)		x	x
Cycloseris cyclolites (Lamarck, 1815)	*		x
Cycloseris fragilis (Alcock, 1893)			x
Cycloseris mokai (Hoeksema, 1989)			x
Cycloseris sinensis Milne Edwards and Haime, 1851			x
Cycloseris somervillei (Gardiner, 1909)			x
Cycloseris tenuis (Dana, 1846)			x
Cycloseris cf. *vaughani* (Boschma, 1923)	*		
Cycloseris sp. 1			x
Cycloseris spp.	x		
Danafungia horrida (Dana, 1846)		x	x
Danafungia scruposa (Klunzinger, 1879)		x	x
Fungia fungites (Linnaeus, 1758)		x	x
Fungia spp.	x		
Halomitra pileus (Linnaeus, 1758)	x		x
Halomitra sp.	x		
Heliofungia actiniformis (Quoy and Gaimard, 1833)	x		x
Heliofungia sp.	x		
Herpolitha limax (Esper, 1797)	x	x	x
Herpolitha sp.	x		
Lithophyllon concinna (Verrill, 1864)	*		x
Lithophyllon repanda (Dana, 1846)		x	x
Lithophyllon scabra (Döderlein, 1901)			x
Lithophyllon spinifer (Claereboudt and Hoeksema, 1987)			x
Lithophyllon undulatum Rehberg, 1892	x		x
Lithophyllon sp.	x		
Lobactis scutaria (Lamarck, 1801)	*		x
Pleuractis granulosa (Klunzinger, 1879)			x
Pleuractis gravis (Nemenzo, 1955)			x
Pleuractis moluccensis (Van der Horst, 1919)			x
Pleuractis paumotensis (Stutchbury, 1833)		x	x
Pleuractis taiwanesis Hoeksema and Dai, 1991			x
Podabacia crustacea (Pallas, 1766)	x		x
Podabacia motuporensis Veron, 1990			x
Podabacia sinai Veron, 2002			x
Podabacia sp.	x		
Polyphyllia talpina (Lamarck, 1801)	x		x
Polyphyllia sp.	x		
Sandalolitha dentata Quelch, 1884			x

Table 2 cont.

	Sabah Parks list	Sabah Parks ref. coll	Present study
Sandalolitha robusta (Quelch, 1886)	x	x	x
Sandalolitha sp.	x		
Zoopilus echinatus Dana, 1846		x	x
Zoopilus sp.	x		
Agariciidae			
Coeloseris mayeri Vaughan, 1918	x		x
Coeloseris sp.	x		
Gardineroseris planulata (Dana, 1846)	x		x
Gardineroseris sp.	x		
Leptoseris explanata Yabe and Sugiyama, 1941	x		
Leptoseris foliosa Dinesen, 1980			x
Leptoseris fragilis Milne Edwards and Haime, 1849			x
Leptoseris gardineri Van der Horst, 1921			x
Leptoseris glabra Dinesen, 1980			x
Leptoseris hawaiiensis Vaughan, 1907			x
Leptoseris incrustans (Quelch, 1886)			x
Leptoseris mycetoseroides Wells, 1954	x		x
Leptoseris papyracea (Dana, 1846)		x	
Leptoseris scabra Vaughan 1907	x		x
Leptoseris cf. *solida*			x
Leptoseris tubulifera Vaughan 1907			x
Leptoseris yabei (Pillai and Scheer, 1976)	x		x
Leptoseris sp. 1	x		
Leptoseris spp.	x		
Pachyseris gemmae Nemenzo, 1955			x
Pachyseris rugosa (Lamarck, 1801)	x		x
Pachyseris speciosa (Dana, 1846)	x	x	x
Pachyseris sp.	x		
Pavona cactus (Forskål, 1775)	x		x
Pavona clavus (Dana, 1846)	x		x
Pavona decussata (Dana, 1846)	x	x	x
Pavona explanulata (Lamarck, 1816)	x		x
Pavona frondifera (Lamarck, 1816)	*		x
Pavona maldivensis (Gardiner, 1905)			x
Pavona minuta Wells, 1954			x
Pavona varians Verrill, 1864	x		x
Pavona venosa (Ehrenberg, 1834)			x
Pavona sp.	x		
Euphylliidae			
Catalaphyllia jardinei (Saville-Kent, 1893)	*		x
Euphyllia ancora Veron and Pichon, 1980	x		x
Euphyllia cristata Chevalier, 1971			x
Euphyllia divisa Veron and Pichon, 1980	x		x
Euphyllia glabrescens (Chamisso and Eysenhardt, 1821)	x		x
Euphyllia paraancora Veron, 1990			x
Euphyllia paradivisa Veron, 1990			x
Euphyllia yaeyamaensis (Shirai, 1980)			x
Euphyllia sp.	x		

Table 2 cont.

	Sabah Parks list	Sabah Parks ref. coll	Present study
Physogyra lichtensteini (Milne Edwards and Haime, 1851)	x		x
Physogyra sp.	x		
Plerogyra multilobata Ditlev, 2003		x	
Plerogyra sinuosa (Dana, 1846)	x		x
Plerogyra sp. 1	x		

Table 3. Coral species that were the most and least common during the survey (excluding Mengalum Island). A = Agariciidae, E = Euphylliidae, F = Fungiidae.

Coral species found at all sites		Least common coral species (n ≤ 3)	
Danafungia horrida	F	*Cycloseris somervillei*	F
D. scruposa	F	*Cycloseris* sp.	F
Fungia fungites	F	*Pleuractis taiwanensis*	F
Heliofungia actiniformis	F	*Podabacia motuporensis*	F
Herpolitha limax	F	*Zoopilus echinatus*	F
Lithophyllon concinna	F	*Leptoseris gardineri*	A
L. repanda	F	*Leptoseris* cf. *solida*	A
Pleuractis granulosa	F	*Pavona minuta*	A
P. moluccensis	F	*Euphyllia cristata*	E
P. paumotensis	F	*E. paradivisa*	E
Leptoseris glabra	A	*E. yaeyamaensis*	E
Leptoseris scabra	A	*Plerogyra multilobata*	E
Plerogyra sinuosa	E		

The species accumulation curves showed that the expected number of species (ICE, Chao 2) for Fungiidae is close to the observed number, and that with additional sampling, two more species are to be expected (Fig. 2a). For the families Agariciidae and Euphylliidae, the curves showed that the expected richness is identical to the observed, therefore more sampling is not expected to result in higher numbers (Figs. 2b, c).

The dendrogram derived from the cluster analysis comprised of three groups of sites and three singletons based on the SIMPROF test, which suggests that separations based on species richness were driven by either reef exposure or bathymetry. At 82% similarity the dendrogram and MDS plots showed two main groups that are represented by reefs exposed to- and sheltered from the predominant wind directions from the west, and a smaller group of two sites with relatively sheltered reefs (Figs. 3a, b). The exposed reefs, especially at Gaya and Sapangar islands, also extend to greater depths than the other reef sites (see Fig. 4). Based on the a priori groupings however, the ANOSIM test did not suggest a significant difference in coral species composition based on exposure to wind (ANOSIM Global R = 0.399, p = 0.1) and depth (Global R = 0.311, p = 0.1). There was also no significant difference in composition structure among the a priori groups using the two-way crossed ANOSIM test. This is most likely because the species composition of the reefs are about 80% similar. Nevertheless, it was clear that sites with the highest coral species diversity (n ≥ 50) were exposed with reef slopes extending to depths of at least 30 m (Fig. 4).

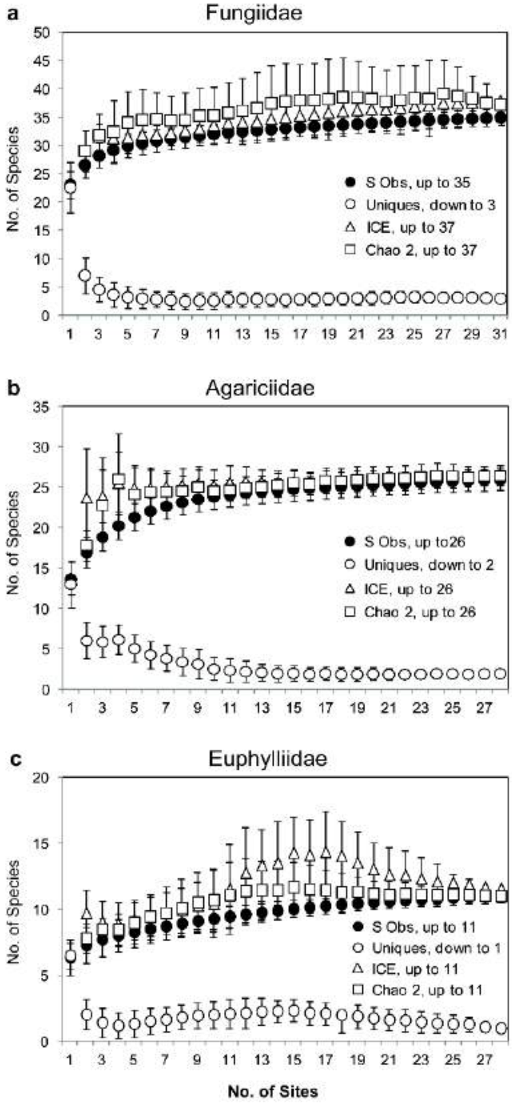


Fig 2. Species richness estimators for coral families: **a** Fungiidae (n = 35); **b** Agariciidae (n = 26); and **c** Euphylliidae (n = 11) observed at Kota Kinabalu. The curves indicate that the occurrence of two additional species is possible for the Fungiidae, but no extra species are expected for the Agariciidae and Euphylliidae.

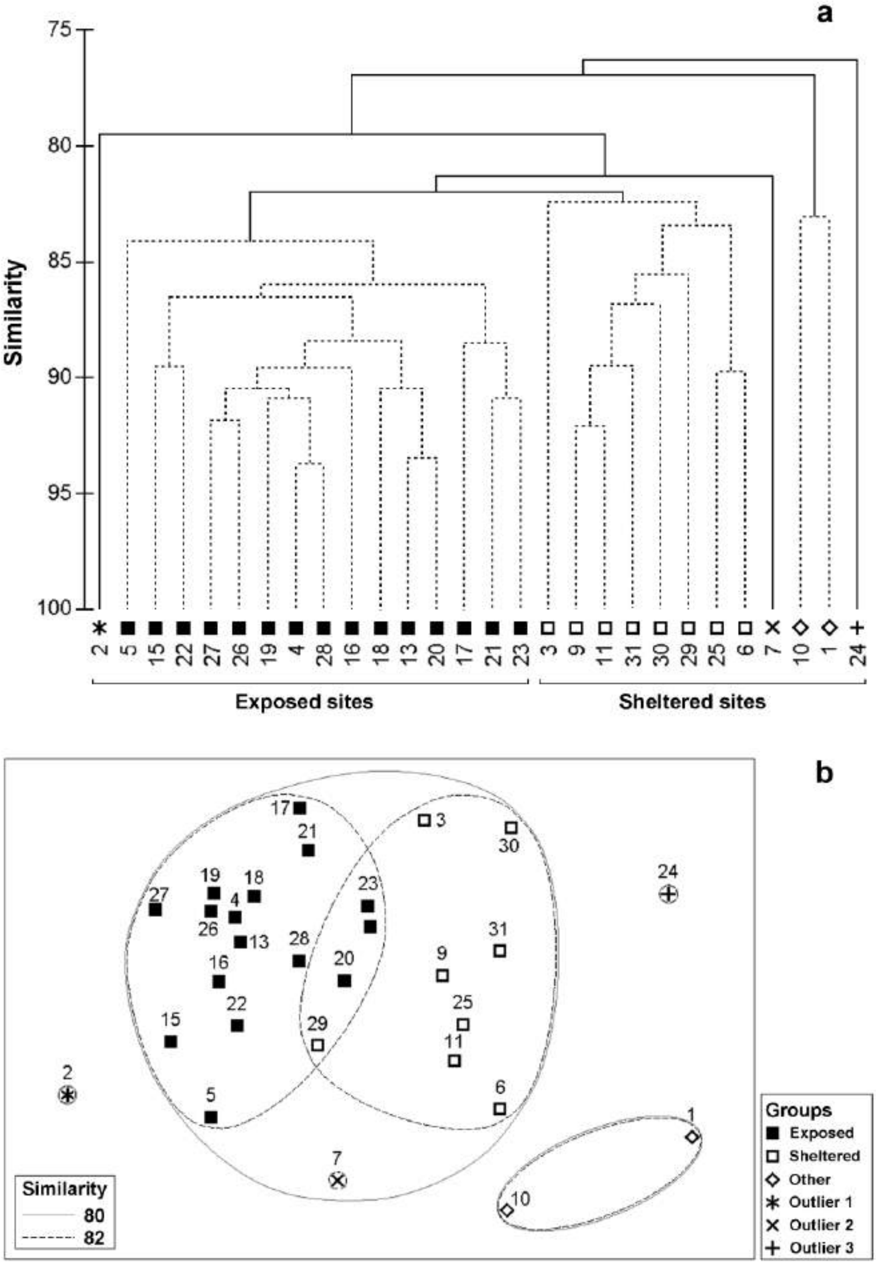


Fig. 3. a Dendrogram; and **b** multidimensional scaling (MDS) plots with significant clusters of 28 sites at Kota Kinabalu based on the Bray-Curtis resemblance matrix of coral species composition (presence/absence) of the families Fungiidae, Agariciidae, and Euphylliidae. The solid and open symbols represent exposed and sheltered reef sites, respectively.

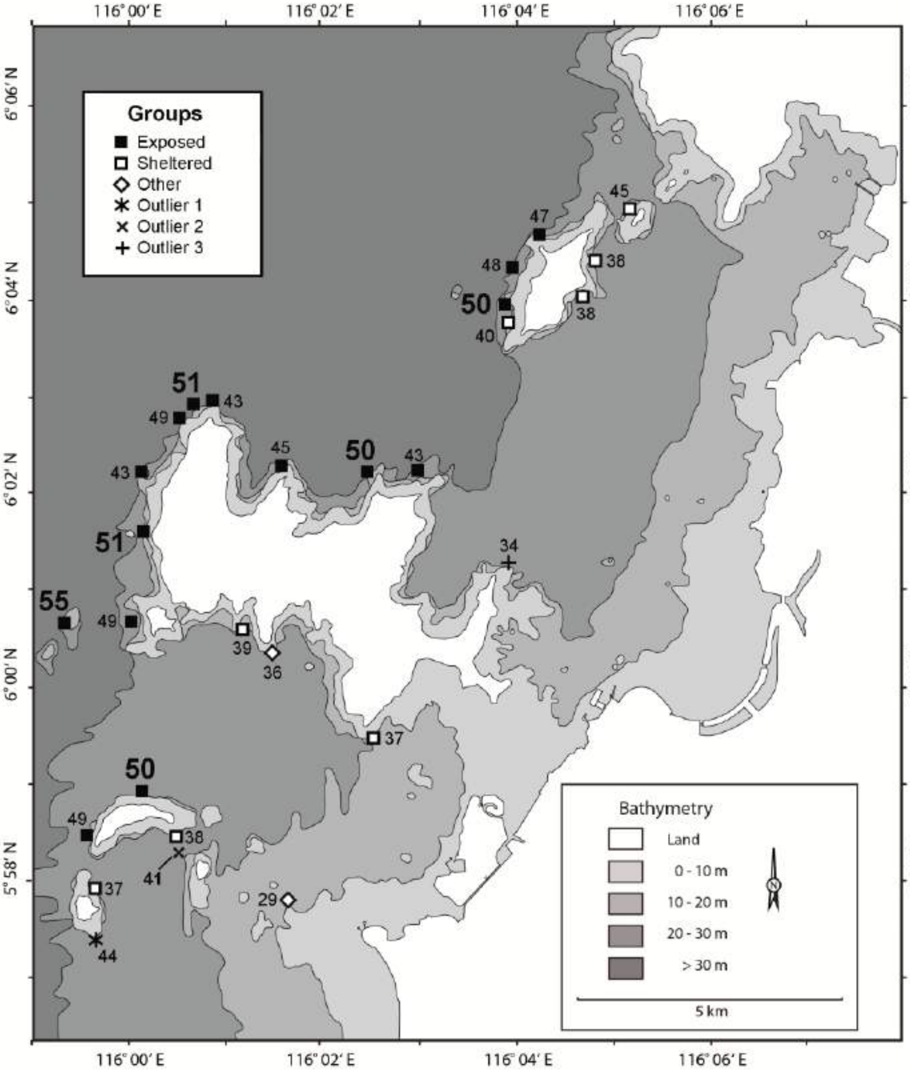


Fig. 4. Species richness patterns derived from the dendrogram and MDS plots in Fig. 3a, b. The numbers represent the combined species diversity of all three coral families Fungiidae, Agariciidae, and Euphylliidae. Sites with the highest species diversity (≥ 50 species) are shown in bold and larger fonts.

Discussion

Historical records

Only few studies on the reefs of Kota Kinabalu have been published despite their close proximity to the city's main jetty. Findings of other research may be present in the form of grey literature that has not been made available through online resources and therefore cannot easily be found. When comparing the present coral species list to those of previous studies and specimens in reference collections, it is difficult to draw conclusions as those earlier studies reported coral taxa mostly at genus level. However, the species listed by Sabah Parks were also found in the present study, except for the mushroom coral *Cycloseris* cf. *vaughani*. This species was reported in the checklist by Nyanti and Johnston (1992), but no description, illustrations or locality data were given, therefore it is difficult to verify the former presence of this species. Since this species is usually found on offshore reefs and at greater depths (Hoeksema 2012a, c), locality data in the earlier records could have supported the earlier identification. From the present study, 33 species are new records for Kota Kinabalu. This updated species list could serve as a baseline for future studies on the coral fauna of Kota Kinabalu.

Most of the coral specimens deposited in the Sabah Parks reference collection were free-living mushroom corals (Fungiidae) and staghorn corals (*Acropora* spp.). Fungiidae and Acroporidae are two iconic and commonly occurring coral taxa that can easily be found and sampled. Both taxa can cover large areas and may occur in dense multi-species aggregations or in monospecific stands (Wallace 1999; Hoeksema 2004, 2012a; Hoeksema and Gittenberger 2010; Hoeksema and Matthews 2011; Hoeksema and Benzoni 2013). Based on this reference collection, it appears that only common and shallow-living species were targeted and therefore these collections were not representative enough for comparison with the present data. Although reference material in museum collections can serve as baselines for studies of coral communities over time (e.g., Hoeksema and Koh 2009; Van der Meij et al. 2010; Hoeksema et al. 2011; Van der Meij and Visser 2011; Hoeksema and Wirtz 2013), this is only useful if the collections are extensive and sufficiently representative of the area by also including uncommon species.

Species occurrences

When comparing the coral species of the three target families between Kota Kinabalu and Semporna in the southeast coast of Sabah, the latter recorded 18 species more: nine fungiids (35 vs. 44), five agariciids (28 vs. 33), and four euphylliids (11 vs. 15). Some of these additional species are endemic to northeast Borneo such as *Lithophyllon ranjithi*, *Plerogyra diabolotus* and *P. cauliformis* (Chapter 2), while others have a limited distribution range, such as *Halomitra clavator* (Hoeksema and Gittenberger 2010). The total of 35 species of mushroom corals that was found in Kota Kinabalu is considered diverse and comparable to other areas that have been studied within the Coral Triangle (Hoeksema 2007, 2012a, c; Chapter 2). Mushroom coral species preferring offshore conditions were rare on the Kota Kinabalu reefs (as listed in Table 3 and includes

Lithophyllon spinifer and *Podabacia sinai*). *Cycloseris boschmai*, a relatively small species (Hoeksema 2014), was only encountered once (site 12) and has also been found in Semporna and Kudat (Chapters 2 and 3).

Agariciid corals that were considered rare in Kota Kinabalu were also uncommon in Semporna, such as *Pavona minuta*. An unusual *Leptoseris* specimen was encountered during the present study. It has irregular mounds (proximal cushions) protruding from its surface that is characteristic of *Leptoseris solida* (Quelch, 1886), but with several column-forms that are unlike *L. solida*'s. Its other characters closely resemble those of *L. solida*. As such, this specimen has been labeled *Leptoseris* cf. *solida* until further examination suggests differently. In a short note on the corals from the west coast of Sabah, *Leptoseris solida* was reported to be uncommon, usually found at reef edges and has a twisted and contorted growth form (Phillips 1979). The depicted specimen looked very much like some *Leptoseris tubulifera* specimens that were encountered during the present survey, which had larger corallites and coarser septocostae than the species' type specimen (Vaughan, 1907). The colony was also larger and generally more contorted than the typical *Leptoseris tubulifera* growth form. This variation could be related to a different locality or habitat type, as was observed for specimens of *Leptoseris hawaiiensis* and *L. scabra* from Semporna (Chapter 2).

The euphylliid coral *Plerogyra multilobata* Ditlev, 2003 has previously only been recorded from Semporna and Darvel Bay (Chapter 2) and Kudat-Banggi, Sabah (Chapter 3). This species was described solely by macro-morphological characters and is distinguishable from *P. diabolotus* only by its polyp structure (Ditlev 2003). The taxonomy of the Euphylliidae requires revision as molecular analyses have suggested that this family is polyphyletic (Fukami et al. 2008; Kitahara et al. 2010). The genera *Plerogyra*, *Physogyra* and *Nemenzophyllia* have close affinities with *Blastomussa*, which was originally classified with the family Mussidae (Huang 2012; Benzoni et al. 2014). Their present inclusion in the Euphylliidae is based on the current classification by Veron (2000), which is based on the macro-morphology of the polyps and the coral skeletons. *Plerogyra* species described by Ditlev (2003) need to be investigated further with the help of molecular methods to determine their taxonomic position.

The common occurring coral species of Kota Kinabalu are also similar with those in the other regions of Sabah as well as other areas within the Coral Triangle. The mushroom corals *Danafungia scruposa*, *Fungia fungites*, *Herpolitha limax*, *Lithophyllon repanda*, *Pleuractis granulosa* and *P. paumotensis* were common in Semporna and Kudat. *Fungia fungites*, *L. repanda* and *P. paumotensis* were also common in northwest Java, Berau, Raja Ampat, Ternate, and Makassar, Indonesia, while the other species mentioned above were considered dominant reef-dwelling species (Hoeksema 1991, 2008, 2010, 2012a; Hoeksema et al. 2004). These species have a widespread distribution and are found on many Indo-West Pacific reef habitats. Agariciid and euphylliid corals have not been as well studied as the fungiid corals, but in comparison with the other reefs of Sabah, it was found that common species include the euphylliid coral *Plerogyra sinuosa*, and the agariciid corals *Pavona varians* and *Pachyseris speciosa* (Chapters 2 and 3). Although these agariciid corals were not encountered at all survey sites in Kota Kinabalu, they were common on the reefs.

Due to weather constraints during the fieldwork, only two dives were made at Mengalum Island. Coral cover was rather poor, especially at site 32, which was close to the island. The reef was shallow (< 10 m) and patchy along a gradually declining sandy slope. However, it was here that specimens of *Pavona* sp. and *Plerogyra simplex* were encountered. The *Pavona* sp. specimen has deep corallites and exsert primary septa. It superficially resembles *Pavona diffluens* (Lamarck, 1816), a species only reported from the Red Sea, the Arabian Sea and the Persian Gulf (Veron 2000). Wood (1978) observed that several species of coral and fish that occur around the island were rarely seen on the west coast reefs (including Kota Kinabalu) and presumably reflected the offshore position of the island. She also noted that the slope around the island was gentle and sandy, and while the shallow reefs may be interesting, they are not striking. No account has been made on the bank reefs and shoals that lie closer to the edge of the continental shelf.

Species distributions

The cluster analysis and MDS ordination suggested a difference in coral species composition between the two main groups, which appears to be influenced by the exposed and sheltered conditions of the reefs. This is not supported by ANOSIM, most likely because the species compositions of the reefs in the area are about 80% similar as suggested by the dendrogram and MDS plots. Nevertheless, a difference in species composition was indicated by the SIMPROF test (Fig. 4). The exposed reefs extended down to 30 m depth and had better water clarity as compared to the sheltered reefs that did not exceed 20 m. The third group of the clusters, which is comprised of the relatively sheltered sites 1 and 10, had the lowest species diversity of all localities (with the exception of the outlier, site 24). In general, localities that were sheltered from the predominant winds and situated closer to the shoreline of the mainland had noticeably lower species diversity. A similar pattern was found for the mushroom coral faunas in the vicinity of river mouths near Madang, Papua New Guinea (Hoeksema 1993a), Berau, East Kalimantan (Hoeksema et al. 2004) and Makassar, South Sulawesi (Hoeksema 2012a, c). In contrast, highest species diversity of Semporna was found in the sheltered nearshore reefs (Chapter 2). In studies comparing species diversity at a larger scale, high species richness is usually found in areas showing high habitat heterogeneity (Best et al. 1989; Hoeksema and Moka 1989; Cornell and Karlson 1996; Karlson 1999; Karlson and Cornell 1999; Hoeksema 2007). By showing gradients in exposure and maximum depth from nearshore to offshore, the habitat diversity of the reefs of Kota Kinabalu may be considered high, although not as much as the reefs of the much larger Semporna, which also include a barrier reef system and lagoonal reefs (Chapter 2).

The reefs of Kota Kinabalu are fringing nearshore reefs predominantly along rocky shores, which may lack variation in habitat type, such as those found in the barrier reef system on the Spermonde shelf off Makassar, South Sulawesi (Moll 1983; Hoeksema 2012a, c). Such reefs contain sheltered and exposed sites in close proximity to each other at opposed sites of sand cays, and usually show much habitat heterogeneity along depth gradients from extensive shallow reef flats to moderately steep reef slopes and slowly declining sandy reef bases. The coral fauna of Kota Kinabalu included species that are restricted to certain habitat conditions, such as *Zoopilus echinatus*, which is a predominantly offshore species (Hoeksema 1993a, 2012a; Hoeksema et al. 2004). On the other hand, some species were absent while they should be present based on their known distribution ranges (see Veron 2000), such as the agariciid *Pavona duerdeni* and the euphylliid *Nemenzophyllia turbida*. Both species were found on the reefs of Brunei approximately 150 km southwest of Kota Kinabalu, albeit uncommon (Turak and DeVantier 2011). In Semporna, *P. duerdeni* was only encountered on exposed reefs while *N. turbida* had a preference for turbid and sheltered conditions. Both sheltered and exposed reef conditions are present in Kota Kinabalu, which implies that there may be other limiting factors at play.

Wave action generated by winds can influence the coral composition on the reefs (e.g. Bradbury and Young 1981; Dollar 1982; Brown et al. 1983; Moll 1983; Hoeksema, 2012a), especially on the exposed upper reef slopes, while sediment movement is the controlling factor on the lower slopes and reef base (Sheppard 1982). Reefs are also known to be limited by depth and light intensity (Chappell 1980; Done 1983). Sediment load can affect both mentioned factors by further decreasing light penetration reaching the reef. Wood (1978) stated that reef conditions in the shallower reef zones were generally better than on the deeper slopes and suggested sedimentation as the cause, in particular at several sites of Gaya and Sapi islands. Although the point source of sediments has not been determined, anthropogenic activities such as land clearing and reclamation for development, and nutrient enrichment from storm drains in Kota Kinabalu are possibly responsible (Pilcher and Cabanban 2000). There was no obvious difference in the water clarity ranging from the shallow to the deeper reef zones, but during the survey horizontal visibility was better in the exposed reef (~10 m) compared to the sheltered reef sites (5–7 m). In Jakarta Bay, various species of corals appeared to have disappeared from the reefs when a survey was done in 2005 and compared with scleractinian specimen collections from the 1920s (Van der Meij et al. 2010). Loss of some mushroom coral species from the reefs of Singapore has also been observed when the findings from a survey in 2006 were compared with old museum specimens that were collected since the 1860s (Hoeksema and Koh 2009). Both studies linked the loss of coral species with increased sediment load in the waters and reefs as a result of development.

The proximity of the TARP coral reefs to Kota Kinabalu makes it a popular tourist destination. In recent years, there has been an increase in the number of visitors to the park, and out of the five marine parks in Sabah, TARP receives the highest number of tourists (Sabah Parks Visitor Statistics 2013). Although the actual impact of tourism has not been measured, it has been suggested that tourist activities have contributed to the pressure on the reefs (Pilcher and Cabanban 2000). The park would be an ideal area for conducting research on the impacts of tourism, as well as the effects of sedimentation to the coral reef community in Kota Kinabalu (Cabanban and Nais 2003).

Conclusions

In summary, the present study gives an account of the coral species richness of the families Fungiidae, Agariciidae and Euphylliidae, which could serve as baseline for future studies on the coral reef ecosystem of Kota Kinabalu. These studies can either focus on other coral families, therefore adding more species to the current list, or to revisit the species richness of these three families in order to determine changes in the coral communities. There was a noticeable but statistically insignificant difference in the coral species composition between the sheltered shallow reefs and the exposed deeper reefs, with highest diversity in the latter. Presumably, the sheltered and shallow reefs offer less variety of habitats (shorter depth gradient), and may be influenced by nearshore processes such as sedimentation. Periodic monitoring is recommended in order to detect changes on the reef communities of Kota Kinabalu. For instance, very little is known about the effects of the 2010 coral bleaching event (Tun et al. 2010; Aw and Muhammad Ali 2012) in comparison to some other areas in Southeast Asia (e.g. Chavanich et al. 2012; Guest et al. 2012; Sutthacheep et al. 2012; Hoeksema et al. 2012a, 2013; Yeemin et al. 2013). Although the coral fauna of Kota Kinabalu is less diverse than Semporna, the area is deemed species-rich and from a mushroom coral standpoint, Kota Kinabalu should be considered part of the Coral Triangle (Hoeksema 2007).

Acknowledgments

Research permission was granted by Sabah Parks and the Economic Planning Unit, Malaysia. We thank Prof. Dr. Ridzwan Abdul Rahman of the Borneo Marine Research Institute, and the boat house crew of Universiti Malaysia Sabah for support during the fieldwork. Sabah Parks is also acknowledged for granting access to the coral collection at the Marine Research Unit at Manukan Island and the library at the Sabah Parks headquarters in Kota Kinabalu. Thanks are also due to Mr. Erik-Jan Bosch for producing the map of the research area. Critical comments and suggestions from two anonymous reviewers greatly improved the manuscript.

Supporting Information

Supporting information is available at
http://lkcnhm.nus.edu.sg/rbz/biblio/62/62rbz066-082.pdf

Appendix 1. Scleractinia species of families Fungiidae, Agariciidae, and Euphylliidae at Kota Kinabalu (Sites 1–31) and Mengalum Island (Sites 32 and 33).

Chapter 5

Scleractinian corals (Fungiidae, Agariciidae and Euphylliidae) of Pulau Layang-Layang, Spratly Islands, with a note on *Pavona maldivensis* (Gardiner, 1905)

Zarinah Waheed, Francesca Benzoni, Sancia E.T. van der Meij,
Tullia I. Terraneo and Bert W. Hoeksema

Abstract

Layang-Layang is a small island part of an oceanic atoll in the Spratly Islands off Sabah, Malaysia. As the reef coral fauna in this part of the South China Sea is poorly known, a survey was carried out in 2013 to study the species composition of the scleractinian coral families Fungiidae, Agariciidae and Euphylliidae. A total of 56 species was recorded. The addition of three previously reported coral species brings the total to 59, consisting of 32 Fungiidae, 22 Agariciidae, and five Euphylliidae. Out of these, 32 species are new records for Layang-Layang, which includes five rarely reported species, i.e., the fungiid *Lithophyllon ranjithi*, *Podabacia sinai*, *Sandalolitha boucheti*, and the agariciid *Leptoseris kalayaanensis* and *L. troglodyta*. The coral fauna of Layang-Layang is poor compared to other areas in Sabah, which may be related to its recovery from a crown-of-thorns seastar outbreak in 2010, and its low habitat diversity, which is dominated by reef slopes consisting of steep outer walls. Based on integrative molecular and morphological analyses, a *Pavona* variety with small and extremely thin coralla was revealed as *P. maldivensis*. Since specimens from Sabah previously identified as *P. maldivensis* were found to belong to *P. explanulata*, the affinities and distinctions of *P. maldivensis* and *P. explanulata* are discussed.

ZooKeys (2015) 517: 1–37. doi:10.3897/zookeys.517.9308

Introduction

Pulau [island] Layang-Layang is a small island standing 2 m high on the southeast rim of a reef known as Swallow Reef (Hancox and Prescott 1995). The reef is an atoll situated at the southern edge of the Spratly Islands in the South China Sea, approximately 300 km northwest of Kota Kinabalu, Sabah, Malaysia. Layang-Layang was reported to have one of the best reefs in East Malaysia in terms of coral cover and diversity and fish life (Ismail et al. 1998; Pilcher and Cabanban 2000).

Being remote, the reef was regarded to be in pristine condition (Pilcher et al. 1999; Pilcher and Cabanban 2000; Zainuddin et al. 2000), although it had experienced disturbances in the past years. In the 1980s, reclamation work was carried out to accommodate a military base, and in the 1990s the island was further extended to construct an airstrip, a resort and a seawall. For the latter developments, coral and sand were mined from the lagoon for building material. A comparative study in 1993 and 1998 showed that the impact of the development on the reef was most evident in the lagoon, with a reduction on live coral cover from 29% to 10% (Mohamed et al. 1994; Zakariah et al. 2007). The outer reefs were not affected by the construction development, except at sites immediate to the island. Here the coral cover averaged 48% at 5 m and 34% at 10 m depth in 1993 (Mohamed et al. 1994). At subsequent independent surveys from 1996 to 1999 in four outer reef sites, mean live coral cover was 73% at 5 m and 58% at 10 m depth (Pilcher and Cabanban 2000).

A massive coral bleaching event during the 1997–98 El Niño event had also affected the reefs of Layang-Layang. Up to 40% of the coral colonies at less than 10 m depth and 25% at 10–20 m depth were bleached at 55 monitoring sites, but by 1999 the corals had recovered or were overgrown with zoantharians and soft corals (Pilcher and Cabanban 2000).

A recent calamity to confront the reefs was an outbreak of the crown-of-thorns (COT) seastar, *Acanthaster planci* (Linnaeus, 1758), in July 2010. During a 3-day survey, densities of 1,011 COTs were counted in a 7,000 m^2 reef area over eight sites, which corresponds to over 1,400 individuals per ha with dominant size class of 21–30 cm (Nasrulhakim et al. 2010). During the time of the survey, reefs in the southwest of the atoll were badly damaged and had dead corals covered by algae. Although damage to the reefs was not quantified, it was noted that COT had started to infest the reefs in the northwest of the atoll and coral mortality was not as extensive as compared to the reefs in the southwest (Nasrulhakim et al. 2010).

While several short research expeditions and surveys have been carried out to collect baseline information on the marine biodiversity of Pulau Layang-Layang (Zakariah et al. 2007), only one checklist of hard coral species is available as reference, with over 140 species reported by Ridzuan et al (n.d.) cited in Pilcher and Cabanban (2000) (pp. 46–47, Appendix VI). In the present study, we aim to update the species list of the hard coral families Fungiidae, Agariciidae and Euphylliidae in Layang-Layang, as similarly done for the reefs of Sabah, Malaysia (Chapters 2–4). These families, together consisting of ~100 species, were selected as a proxy for scleractinian reef coral diversity, as they can be found in a variety of reef habitats and in a wide geographical range within the Indo-Pacific (Veron 2000). At the time of the survey, small, thin and encrusting corals thought to belong to an unknown *Pavona* species were encountered. Several specimens that were collected for closer inspection of corallite morphology appeared to match with *Pavona maldivensis* (Gardiner, 1905) despite the unusual growth form of the corallum. For verification, a comparison was made between these *P. maldivensis* specimens and those collected from other localities including its type locality in the Maldives. Samples of *P. explanulata* (Lamarck, 1816) closely resembling *P. maldivensis* were also examined in order to better define the boundaries between these two species.

Materials

Physical setting

Pulau Layang-Layang (7°22'20"N, 113°50'30"E) measures approximately 1,500 m x 200 m (Google Earth 2013). The only infrastructures on the island are buildings of the Royal Malaysian Navy base, the Marine Research Station Layang-Layang (MARSAL) of the Fisheries Department and the Avillion Layang-Layang Resort. An airstrip runs alongside these establishments. The atoll is somewhat oval in shape situated in a SW-NE axis and measures approximately 7 km long and 2 km wide. Its rim is formed by a ring of 13 shallow reefs, which covers an area of over 4 km^2 (Musa et al. 2006). The reef circumference is almost 17 km with a sandy cove at the western end and it encloses a shallow lagoon with a maximum depth of 20 m (Pilcher et al. 1999, Sahari et al. 2004, Svrcula 2008). The reefs rise to sea level from around 1,500 m depth forming steep outer reef walls (see Hutchison and Vijayan 2010). The north and northeast reef slopes have a more gradual profile to depths of 20–25 m before plunging down steeply, as compared to the reefs in the south and southwest where the reefs form vertical walls.

Water parameters were measured at 10 m depth of each survey site (Table S1). The water temperature ranged 28.4–30.0 °C, with a salinity range of 30.1–31.2 ppt. Temperature and salinity measurements were slightly higher in July 2002 (see Ku Yaacob and Ibrahim 2004) in comparison to our readings in March 2013.

Layang-Layang in the South China Sea is influenced by the monsoon system (see Wyrtki 1961). The northeast monsoon dominates between November to March and the southwest monsoon prevails from May to September (Saadon et al. 1998, Morton and Blackmore 2001, Ku Yaacob and Ibrahim 2004, Akhir 2012) while the transitional periods are in April and October (Saadon et al. 1998). The surface current patterns are characterised by the monsoonal system (Akhir 2012). The northeast monsoon causes an anticlockwise circulation pattern in the South China Sea, creating a southwesterly current from the northern rim of the sea, which either departs via the Karimata Straits or turns northeasterly along the west coast of Borneo (East Malaysia) and Palawan, whereas the southwest monsoon reverses the current direction, driving a northward current in the central South

China Sea while creating a clockwise gyre above the Spratly Islands (Wyrtki 1961, Morton and Blackmore 2001). The rainy season occurs during the northeast monsoon and due to unpredictable weather Layang-Layang is not accessible for diving. The diving season lasts from March to September annually.

Field sampling

Fieldwork was carried out 24–30 March 2013 on the reefs of Layang-Layang. Due to safety issues, surveys were confined to dive sites designated for tourism around the atoll. A total of 18 sites were surveyed on the outer slope of the reef wall from a maximum depth of 40 m to the shallow reef crest of 1 m using the roving diver technique (Schmitt et al. 2002) (Fig. 1, Table 1). An additional dive was made at the House Reef (10 m maximum depth) off the resort jetty (7°22'23"N, 113°50'37"E). A checklist of the coral families Fungiidae (sensu Gittenberger et al. 2011, Benzoni et al. 2012a), Agariciidae and Euphylliidae (sensu Veron 2000) was made for each site with photo documentation of each species. Specimens that could not be identified in situ were collected for further examination and are kept at the Borneo Marine Research Institute reference collection, Universiti Malaysia Sabah (UMS) in Kota Kinabalu.

Coral specimens were identified by referring to taxonomic literature (Dinesen 1980, Veron and Pichon 1980, Hoeksema 1989, 2012a, 2012b, 2014, Veron 2000, Ditlev 2003, Licuanan and Aliño 2009, Gittenberger et al. 2011, Benzoni et al. 2012a). Recent molecular studies have led to taxonomic revisions of many scleractinian corals, including the families Agariciidae and Euphylliidae (sensu Veron 2000). The genera *Coeloseris*, *Pachyseris*, *Catalaphyllia*, *Nemenzophyllia*, *Physogyra* and *Plerogyra* are now classified *incertae sedis* (Fukami et al. 2008, Kitahara et al. 2010, Benzoni et al. 2014). Nevertheless, these genera were included in the checklist for comparison with similar studies previously conducted around Sabah (Chapters 2–4).

Specimens of a thin morph of *P. maldivensis* were collected and small fragments were preserved in 95% absolute ethanol for molecular analyses. The specimens were bleached with sodium hypochlorite, rinsed, air-dried and small fragments were taken for morphological examination. The remaining coralla of these specimens are kept in the dry reference collection of the Borneo Marine Research Institute, UMS.

Further examination of *Pavona* corals

Seven samples of *P. maldivensis* corals collected from Layang-Layang and samples from Banggi, North Sabah (n = 1), Ternate, Indonesia (n = 1), New Caledonia (n = 2) and the Maldives (n = 2) were used for further molecular and morphological analyses. Samples of *P. explanulata* collected from Banggi, North Sabah (n = 1), Ternate, Indonesia (n = 2) and Redang, Peninsular Malaysia (n = 1) closely resembling *P. maldivensis* were also included. In total, 17 samples were used in the analyses (Table S2).

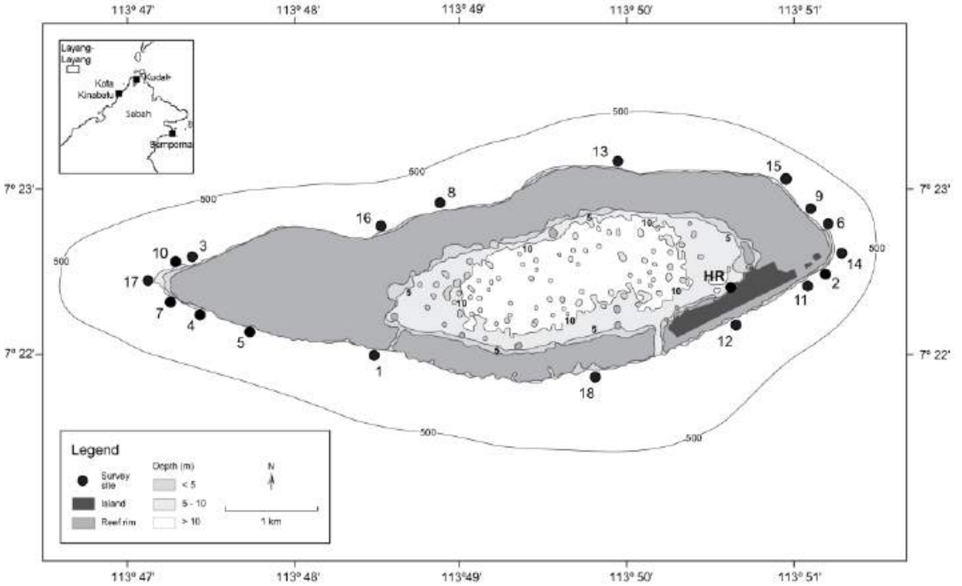


Fig. 1. Research area at Pulau Layang-Layang, Spratly Islands. Survey sites are numbered 1–18, and HR for the House Reef. Depth contours are indicated in metres (smaller font). For a complete georeferenced list of localities and depths of survey sites, see Table 1.

Table 1. Locality data of survey sites at Pulau Layang-Layang, Spratly Islands.

Site	Site name	Latitude (N)	Longitude (E)	Date	Max. depth (m)
1	Snapper Ledge	07^0 22.048	113^0 48.467	24/03/2013	31.8
2	Dogtooth Lair	07^0 22.470	113^0 51.100	24/03/2013	30.7
3	Wrasse Strip	07^0 22.557	113^0 47.397	25/03/2013	30.3
4	Shark Cave 1	07^0 22.279	113^0 47.457	25/03/2013	32.6
5	D'Wall	07^0 22.191	113^0 47.701	25/03/2013	33.8
6	Gorgonian Forest	07^0 22.710	113^0 51.218	26/03/2013	37.9
7	Shark Cave 2	07^0 22.323	113^0 47.321	26/03/2013	27.9
8	Crack Reef	07^0 22.876	113^0 48.910	26/03/2013	29.3
9	Coral Café	07^0 22.773	113^0 51.144	27/03/2013	38.5
10	Wrasse Strip 2	07^0 22.555	113^0 47.371	27/03/2013	33.5
11	Wreck Point	07^0 22.407	113^0 51.032	27/03/2013	33.3
12	Wreck Point 2	07^0 22.197	113^0 50.649	28/03/2013	40.4
13	Navigator Lane	07^0 23.110	113^0 49.979	28/03/2013	36.8
14	The Point	07^0 22.573	113^0 51.254	28/03/2013	34.2
15	Coral Café 2	07^0 23.013	113^0 50.912	29/03/2013	36.7
16	Mid Reef	07^0 22.725	113^0 48.539	29/03/2013	37.7
17	The Valley	07^0 22.447	113^0 47.180	29/03/2013	34.8
18	Runway	07^0 21.902	113^0 49.778	30/03/2013	40.3

Molecular analyses

Coral samples were sequenced for two markers, namely the mitochondrial intergenic spacer between CO1 and 16S-rRna (IGR for short; Terraneo et al. 2014) and the nuclear internal transcribed spacers 1 and 2 including the 5.8S region (ITS for short; White et al. 1990, Takabayashi et al. 1998). DNA extraction was performed using the DNeasy Blood and Tissue Kit (QIAGEN) following the manufacturer's protocol for animal tissue. The samples were left to incubate overnight. The extracts had concentrations of between 1 to 3 ng/µl for the PCR, quantified using a NanoDrop ND-1000 Spectrophotometer. The PCR mixture was composed of 2.5 µl CoralLoad Buffer (containing 15 mM $MgCl_2$), 1.0 µl of each primer (10 pmol), 0.5 µl dNTPs (2.5 mM), 0.5 µl Taq polymerase (15 units/ µl), 18.5 µl of extra pure water and 1.0 µl DNA extract. The primer sequences and PCR amplification details are provided in Table 2. The PCR cycles consisted of an initial denaturation step of 95 °C for 2 min, followed by 39 cycles of 95 °C for 30 s, annealing temperature for 1 min, extension step of 72 °C for 1 min and a final elongation step of 72 °C for 5 min. The PCR products were run on a 1% agarose gel electrophoresis, stained with ethidium bromide and visualized on a Red^{TM} Personal Imaging System. Successfully amplified samples were sent to Macrogen Europe for bidirectional sequencing on an ABI Automated Sequencher 3730xl. The sequences were edited and assembled with Sequencher 4.10.1 and the consensus sequences were blasted against GenBank to check for specific amplification or contamination.

Sequences were aligned on the GUIDANCE server using PRANK algorithm (Penn et al. 2010a, b) and pruned in BioEdit 7.2.5 (Hall 1999). Gaps were treated as missing data. Pairwise genetic differences were calculated as uncorrected p-distance in MEGA 6.06 (Tamura et al. 2013). The most appropriate model of nucleotide substitution based on the Akaike Information Criterion (AIC) as determined in jModelTest 2.1.6 (Darriba et al. 2012) was a three-parameter model a proportion of invariant sites (TPM3uf+I) for IGR and a Kimura two-parameter model with a proportion of invariant sites and gamma distributed rates (K80+I+G) for ITS. Phylogenies were reconstructed separately for each marker and for the concatenated dataset partitioned by genes based on three optimality criteria.

Maximum Likelihood (ML) analyses were carried out in Garli 2.0 (Zwickl 2006) with the default configuration settings. Separate runs were made for searching the ML tree (100 replicates of random addition) and bootstrapping (1000 replicates). The bootstrap consensus tree was visualised with SumTrees 3.3.1 of the DendroPy 3.12.0 package (Sukumaran and Holder 2010) with a majority rule consensus that includes branch length information. Maximum Parsimony (MP) analyses were conducted in PAUP* 4.0a136 (Swofford 2002) using heuristic searches with 100 replicates of random addition with a Tree Bisection and Reconnection (TBR) branch swapping method. Branch support was obtained with 1000 bootstrap replicates to produce a majority rule consensus tree. Bayesian Inferences (BI) were made in MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003, Ronquist et al. 2012), whereby four Markov Chain Monte Carlo (MCMC) of 10 million generations were applied in two runs, saving one tree every 100 generations and discarding the initial 25% of the total trees as burnin. The average standard deviation of split frequencies after 10 million generations was 0.001615 for IGR, 0.001679 for ITS and 0.001840 for the concatenated dataset in the Bayesian analyses. For the mtDNA phylogeny, sequences of *P. maldivensis* and *P. explanulata* available on GenBank (Luck et al. 2013) were included in the analyses. In order to root the trees, the closely related species *Leptoseris foliosa* was selected as outgroup (Benzoni et al. 2012b, Terraneo et al. 2014). Novel sequences were submitted to GenBank (accession numbers KR706116– KR706143).

Table 2. Primer pairs, gene region, fragment size, annealing temperature and references of the molecular markers used in this study.

Name	Primer	Gene region	Fragment size	Annealing temp.	Reference
AGAH	GCT TGA CAG GGT TTC CAA GA	COI-1-rRNA intron	~1200	54 °C	Terraneo et al. (2014)
AGAL	CGC ATT GAA ACA CGA GCT TA	COI-1-rRNA intron	~1200	54 °C	Terraneo et al. (2014)
ITS4	CCT CCG CTT ATT GAT ATG C	ITS1-5.8S-ITS2	~700	55 °C	White et al. (1990)
A18S	GAT CGA ACG GTT TAG TGA GG	ITS1-5.8S-ITS2	~700	55 °C	Takabayashi et al. (1998)

Morphological analyses

A subset of the *Pavona* corals was examined under a Leica MZ16 microscope and analysed using scanning electron microscope (SEM). Coral fragments were mounted on SEM stubs using blu-tack and coated with Pd/Au for 8 minutes. Images were taken with a JEOL JSM6490LV scanning electron microscope. Distinguishing characters for species identification include macromorphological features of the corallum and calices as well as micromorphological features of the septocostae, columella and radial elements (terminology according to Dinesen 1980, Budd et al. 2012, Benzoni et al. 2012b). Original species descriptions of *P. maldivensis* and *P. explanulata* as well as descriptions by Wells (1954), Pillai and Scheer (1976), Scheer and Pillai (1983), Veron and Pichon (1980) were used as references.

Results

Coral checklist

The number of scleractinian corals recorded in the study area is 56 species with 31 Fungiidae, 22 Agariciidae and three Euphylliidae (Table 3, Figs. 2–8, Table S3). Thirty-two species were not documented from Layang-Layang before and are considered new records (17 Fungiidae, 14 Agariciidae, and one Euphylliidae). Most coral colonies were small in size, making identification difficult for some specimens. Specimens that could not be identified to species level in situ include corals of three *Leptoseris* spp. (Fig. 9). All were encountered once, except *Leptoseris* sp. 1 at two sites. The House Reef within the lagoon was species-poor in terms of Scleractinia and only one fungiid species, *Danafungia horrida*, was encountered.

Other coral species recorded at Layang-Layang during earlier studies, but not encountered during the present survey are the fungiids *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and *Podabacia crustacea* (Pallas, 1766), the agariciids *Pavona cactus* (Forskål, 1775) and *P. decussata* (Dana, 1846), and the euphylliids *Euphyllia ancora* Veron and Pichon, 1980 and *Plerogyra sinuosa* (Dana, 1846) (Pilcher et al. 1999, Pilcher and Cabanban 2000). The presence of *H. actiniformis* and both euphylliids was verified by images in Pilcher et al. (1999), thus bringing the total species count to 59 (Table 4).

Table 3. Checklist of hard coral families Fungiidae, Agariciidae and Euphylliidae from 18 sites at Layang-Layang. Species marked with an asterisk (*) are now considered *incertae sedis*. The number of sites indicate the species occurrence frequencies and the figure number corresponds with photos in Figs. 2 to 8. Previous records are indicated as follows: a = Pilcher and Cabanban (2000), b = Abdullah (2005), dash (-) = species not reported before, therefore are considered new records for Layang-Layang.

Family	No.	Species	No. of sites	Figure no.	Previous records
Fungiidae	1	*Ctenactis albitentaculata* Hoeksema, 1989	1	2a	b
	2	*Ctenactis crassa* (Dana, 1846)	15	-	b
	3	*Ctenactis echinata* (Pallas, 1766)	12	-	a
	4	*Cycloseris boschmai* Hoeksema, 2014	6	2b	-
	5	*Cycloseris costulata* (Ortmann, 1889)	12	2c	-
	6	*Cycloseris cyclolites* (Lamarck, 1815)	1	-	-
	7	*Cycloseris explanulata* (Van der Horst, 1922)	2	2d	-
	8	*Cycloseris mokai* (Hoeksema, 1989)	6	2e	-
	9	*Cycloseris sinensis* Milne Edwards and Haime, 1851	1	-	-
	10	*Cycloseris tenuis* (Dana, 1846)	11	2f	-
	11	*Danafungia horrida* (Dana, 1846)	13	2g	a
	12	*Danafungia scruposa* (Klunzinger, 1879)	13	2h	a
	13	*Fungia fungites* (Linnaeus, 1758)	15	3a	a, b
	14	*Halomitra pileus* (Linnaeus, 1758)	5	3b	a
	15	*Herpolitha limax* (Esper, 1797)	15	3c	a, b
	16	*Lithophyllon concinna* (Verrill, 1864)	13	-	-
	17	*Lithophyllon ranjithi* Ditlev, 2003	7	3d	-
	18	*Lithophyllon repanda* (Dana, 1846)	17	3e	b
	19	*Lithophyllon scabra* (Döderlein, 1901)	12	3f	-
	20	*Lithophyllon undulatum* Rehberg, 1892	4	3g	a
	21	*Lobactis scutaria* (Lamarck, 1801)	15	3h	b
	22	*Pleuractis granulosa* (Klunzinger, 1879)	12	4a	-
	23	*Pleuractis gravis* (Nemenzo, 1955)	5	4b	-

Table 3 cont.

Family	**No.**	**Species**	**No. of sites**	**Figure no.**	**Previous records**
	24	*Pleuractis moluccensis* (Van der Horst, 1919)	6	4c	a
	25	*Pleuractis paumotensis* (Stutchbury, 1833)	16	-	-
	26	*Podabacia motuporensis* Veron, 1990	1	-	-
	27	*Podabacia sinai* Veron, 2000	1	4d	-
	28	*Polyphyllia talpina* (Lamarck, 1801)	1	4e	a, b
	29	*Sandalolitha boucheti* Hoeksema, 2012	2	4f	-
	30	*Sandalolitha dentata* Quelch, 1884	12	4g	-
	31	*Sandalolitha robusta* (Quelch, 1886)	9	4h	a, b
Agariciidae	32	*Coeloseris mayeri* Vaughan, 1918*	3	5a	-
	33	*Gardineroseris planulata* (Dana, 1846)	7	5b	a
	34	*Leptoseris foliosa* Dinesen, 1980	5	5c	-
	35	*Leptoseris glabra* Dinesen, 1980	17	5d	-
	36	*Leptoseris hawaiiensis* Vaughan, 1907	12	5e	-
	37	*Leptoseris incrustans* (Quelch, 1886)	9	5f	-
	38	*Leptoseris kalayaanensis* Licuanan and Aliño, 2009	13	5g	-
	39	*Leptoseris mycetoseroides* Wells, 1954	18	5h	a
	40	*Leptoseris scabra* Vaughan, 1907	12	6a	-
	41	*Leptoseris solida* (Quelch, 1886)	6	6b	-
	42	*Leptoseris troglodyta* Hoeksema, 2012	1	6c	-
	43	*Leptoseris yabei* (Pillai and Sheer, 1976)	1	6d	-
	44	*Pachyseris rugosa* (Lamarck, 1801)*	8	6e	a
	45	*Pacyhseris speciosa* (Dana, 1846)*	6	6f	a
	46	*Pavona bipartita* Nemenzo, 1980	3	6g	-
	47	*Pavona clavus* (Dana, 1846)	3	6h	a
	48	*Pavona duerdeni* Vaughan, 1907	5	7a	-
	49	*Pavona explanulata* (Lamarck, 1816)	6	7b	a
	50	*Pavona maldivensis* (Gardiner, 1905)	4	7c	-
	51	*Pavona minuta* Wells, 1954	6	7d	a
	52	*Pavona varians* Verrill, 1864	14	7e	a
	53	*Pavona venosa* (Ehrenberg, 1834)	9	7f	-
Euphylliidae	54	*Euphyllia glabrescens* (Chamisso and Eysenhardt, 1821)	1	8a	a
	55	*Euphyllia paraancora* Veron, 1990	1	8b	-
	56	*Physogyra lichtensteini* Milne Edwards and Haime, 1851*	1	8c	a

Fig. 2. Fungiidae recorded at Pulau Layang-Layang in this study. **a** *Ctenactis albitentaculata* **b** *Cycloseris boschmai* **c** *C. costulata* **d** *C. explanulata* **e** *C. mokai* **f** *C. tenuis* **g** *Danafungia horrida* **h** *D. scruposa*.

Fig. 3. Fungiidae recorded at Pulau Layang-Layang in this study. **a** *Fungia fungites* b *Halomitra pileus* **c** *Herpolitha limax* **d** *Lithophyllon ranjithi* **e** *L. repanda* **f** *L. scabra* **g** *L. undulatum* **h** *Lobactis scutaria*.

Fig. 4. Fungiidae recorded at Pulau Layang-Layang in this study. **a** *Pleuractis granulosa* **b** *P. gravis* **c** *P. moluccensis* **d** *Podabacia sinai* **e** *Polyphyllia talpina* **f** *Sandalolitha boucheti* **g** *S. dentata* **h** *S. robusta*.

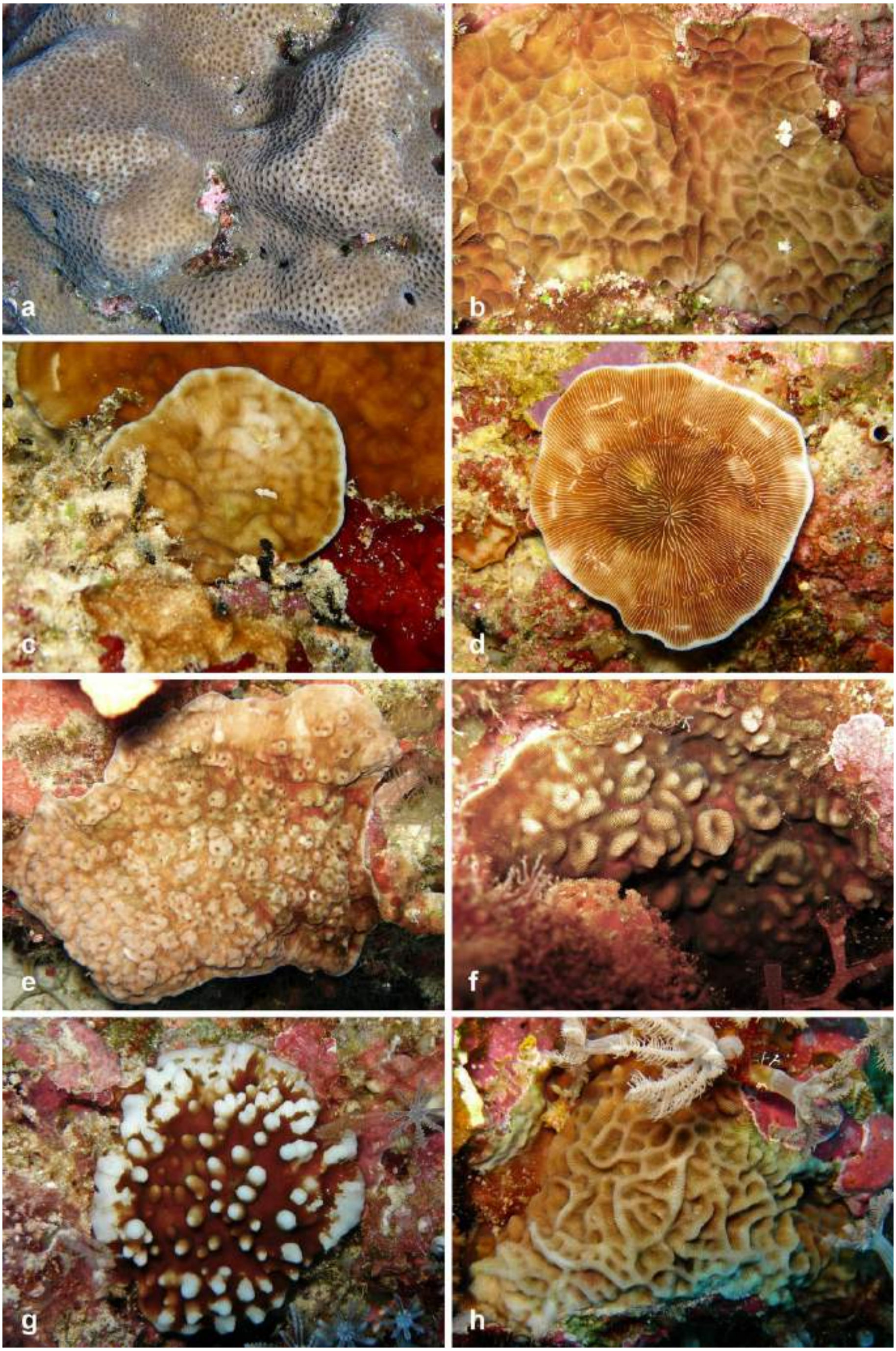


Fig. 5. Agariciidae recorded at Pulau Layang-Layang in this study. **a** *Coeloseris mayeri* **b** *Gardineroseris planulata* **c** *Leptoseris foliosa* **d** *L. glabra* **e** *L. hawaiiensis* **f** *L. incrustans* **g** *L. kalayaanensis* **h** *L. mycetoseroides*.

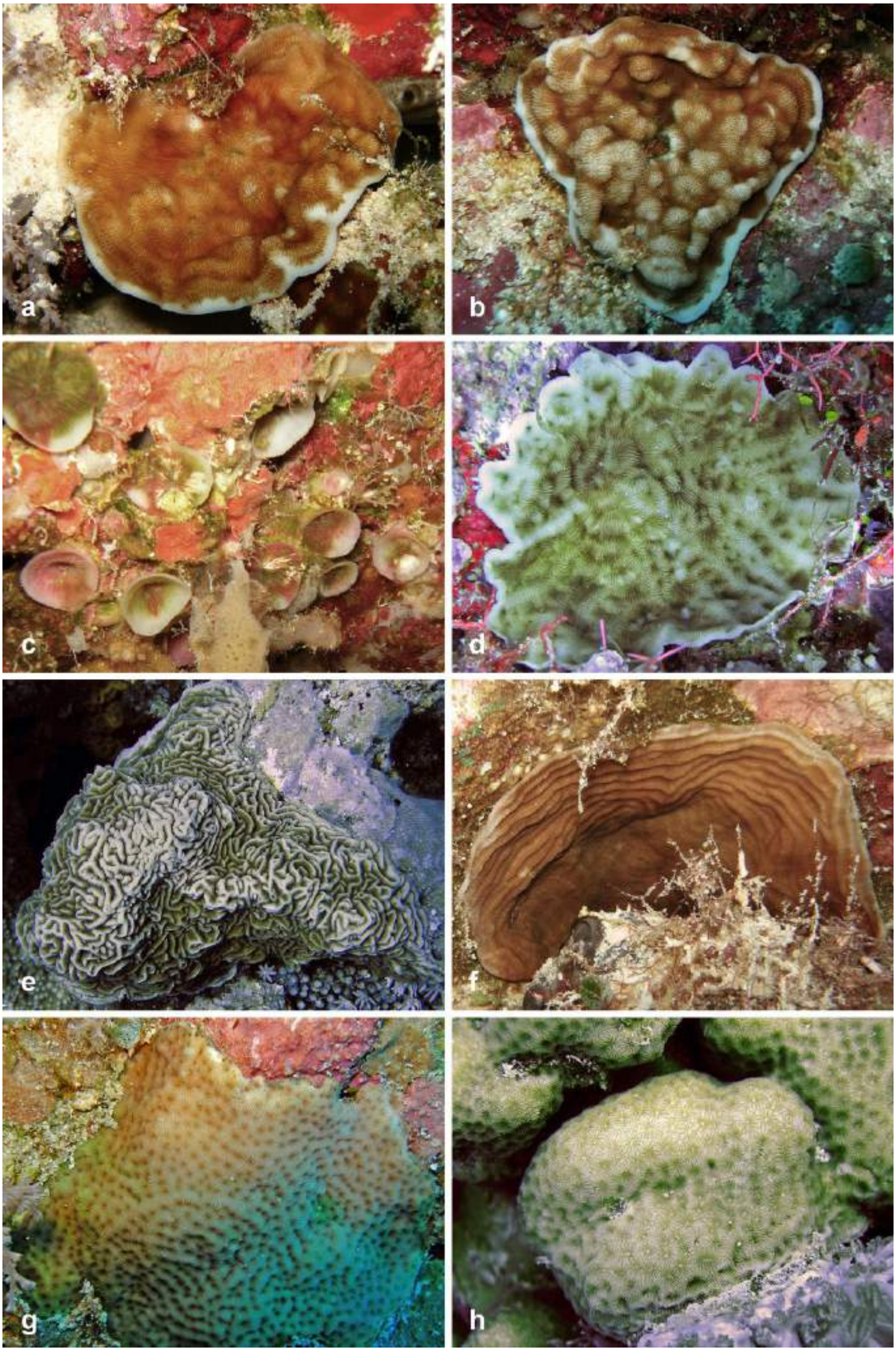


Fig. 6. Agariciidae recorded at Pulau Layang-Layang in this study. **a** *Leptoseris scabra* **b** *L. solida* **c** *L. troglodyta* **d** *L. yabei* **e** *Pachyseris rugosa* **f** *P. speciosa* **g** *Pavona bipartita* **h** *P. clavus*.

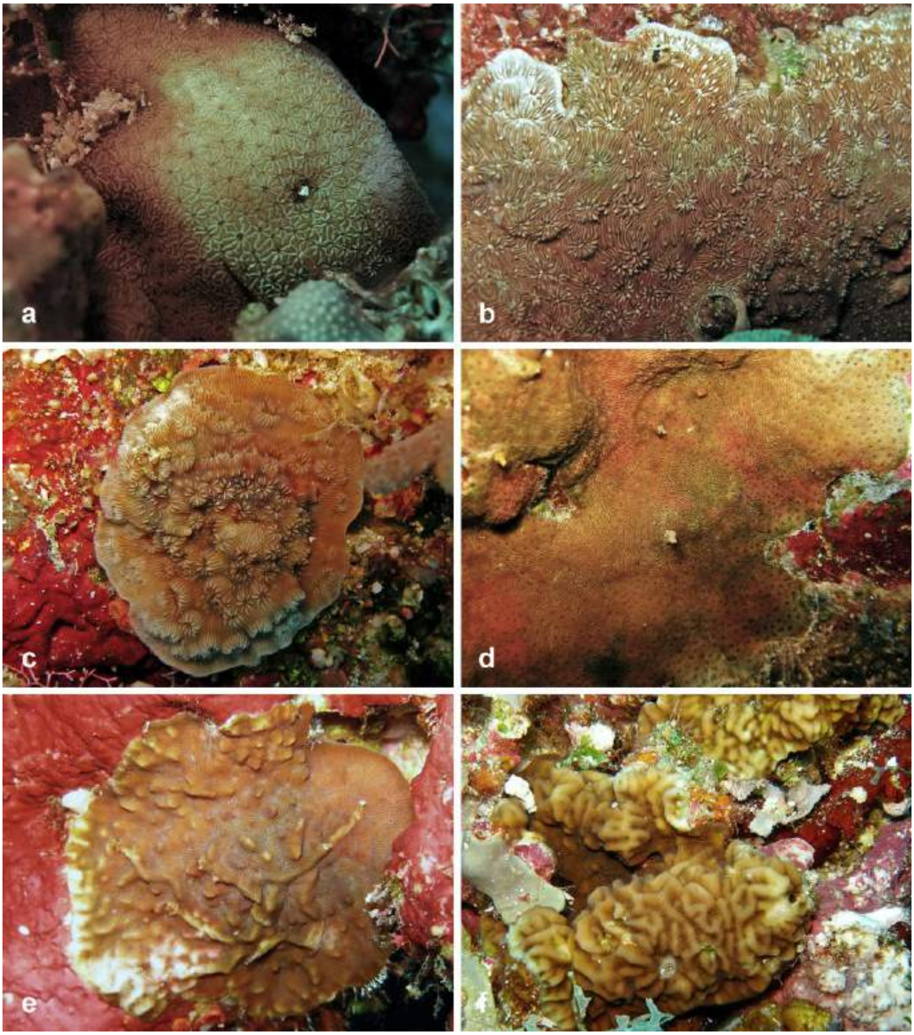


Fig. 7. Agariciidae recorded at Pulau Layang-Layang in this study. **a** *Pavona duerdeni* **b** *P. explanulata* **c** *P. maldivensis* (registration no. IPMB-C 13.00007) **d** *P. minuta* **e** *P. varians* **f** *P. venosa*.

Pavona corals – molecular perspective

Sequences were obtained from 11 and 17 *Pavona* samples for the IGR and ITS markers, respectively. Amplification success for the IGR marker was rather low and the length of the sequences ranged between 432 and 887 bp, shorter than the expected length of ~1200 bp (Terraneo et al. 2014). Tree topologies obtained from the ML, MP and BI analyses for each gene and the concatenated dataset were comparable so only the ML phylogram is shown. There were some differences in the topology between the IGR and ITS phylogeny trees, but the ITS tree was less resolved and has lower support values (Figure S1).

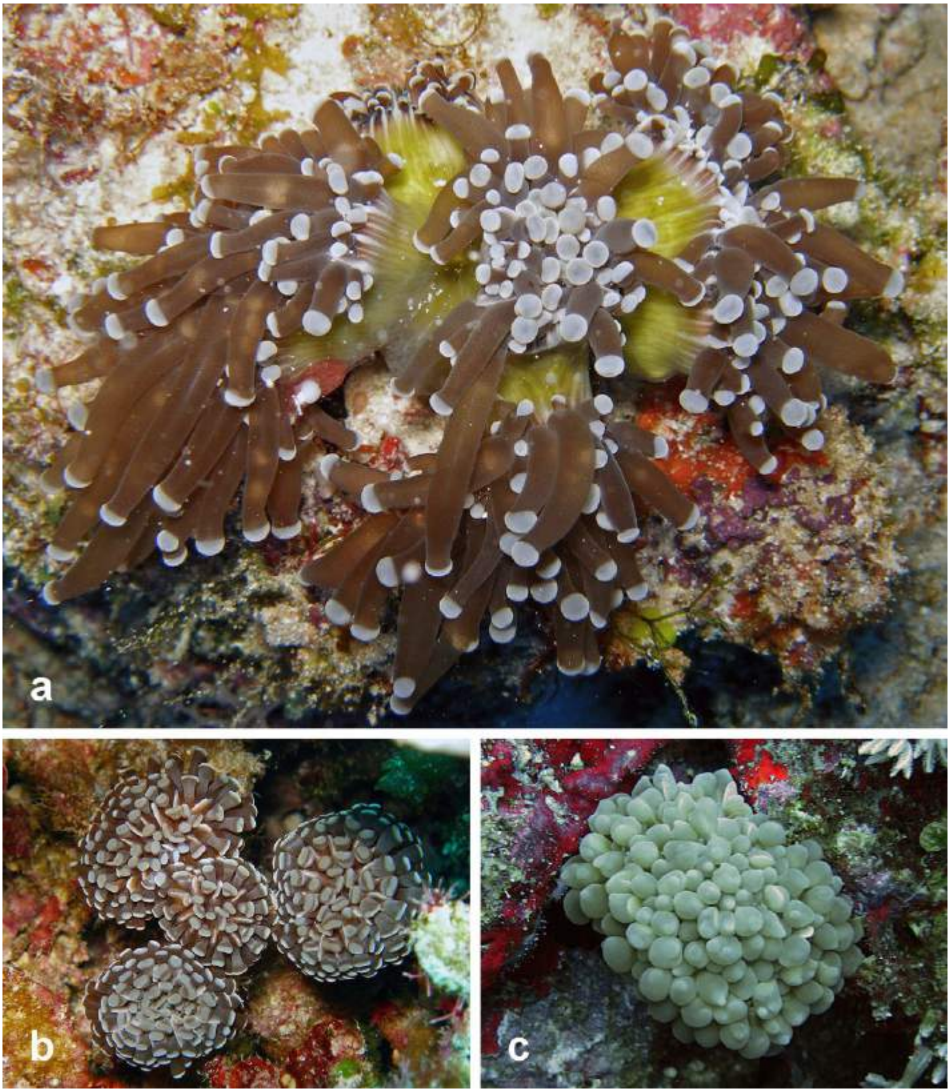


Fig. 8. Euphylliidae recorded at Pulau Layang-Layang in this study. **a** *Euphyllia glabrescens* **b** *E. paraancora* **c** *Physogyra lichtensteini*.

The topology of the IGR tree is almost similar with the concatenated sequences tree and has well-supported basal clades, hence we focus on the latter. The final alignment of the concatenated sequences consisted of 1360 characters with 1243 constant, 35 variable and 82 parsimony informative characters. The phylogram consists of four clades (Fig. 10). Samples of the *Pavona maldivensis* from Layang-Layang (samples with LAC labels) clustered with those of *P. maldivensis* from other areas (clade I). Clade II consists of a single specimen of *Pavona* cf. *explanulata* from Hawaii (Luck et al. 2013). Samples BAN02 from Banggi, North Borneo and TER28 from Ternate, Indonesia, initially identified as *P. maldivensis* during in situ observations from previous studies clustered together with *P. explanulata* samples (clade III). *Pavona* cf. *explanulata* from Redang, Peninsular Malaysia formed clade IV. The pairwise genetic difference between clades, although considerably low, were highest between clade II and clade IV (0.073 ± 0.011), followed by clade II and clade III (0.066 ± 0.011) and clade I and clade IV (0.047 ± 0.005). The intraspecific genetic distance within the clades was also very low: 0.004 ± 0.001 for clade I and 0.008 ± 0.002 for clade III.

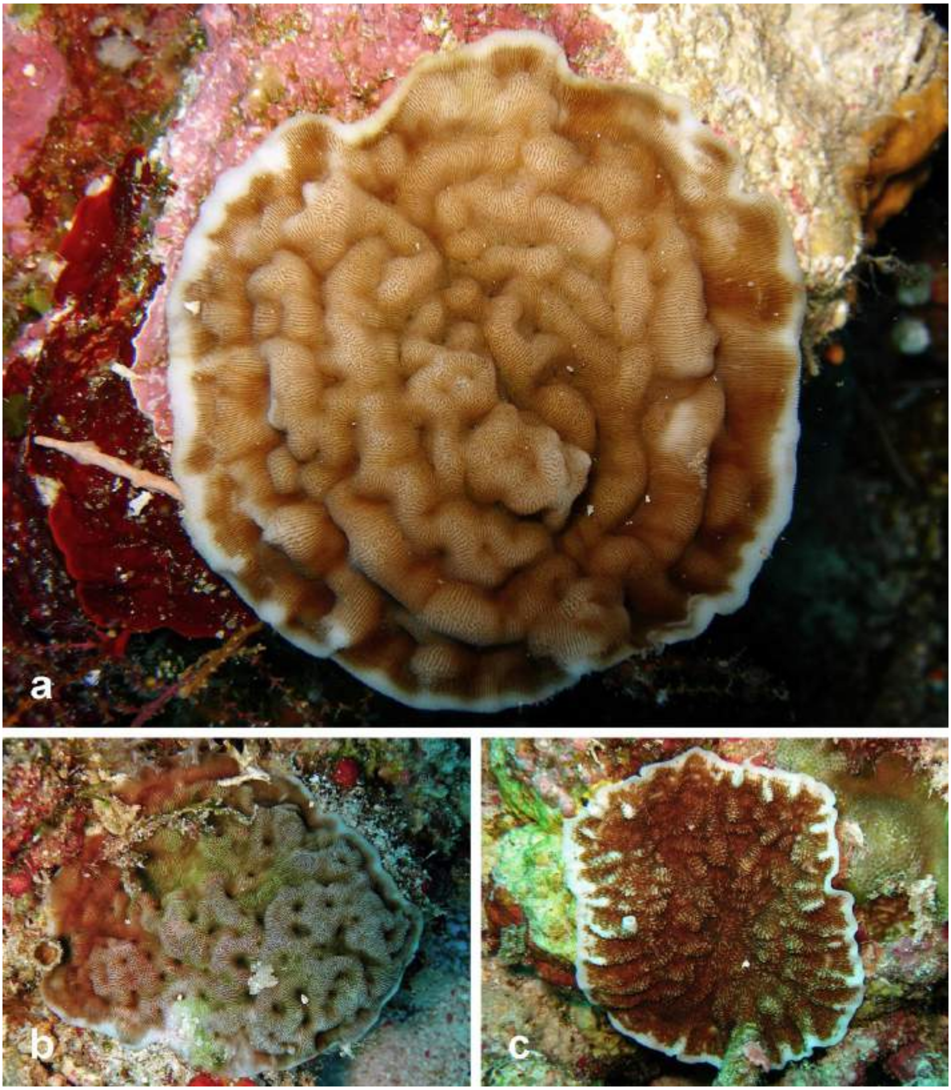


Fig. 9. Undetermined *Leptoseris* coral species recorded at Pulau Layang-Layang in this study **a** *Leptoseris* sp. 1 (registration no. IPMB-C 13.00009) **b** *Leptoseris* sp. 2 **c** *Leptoseris* sp. 3.

Table 4. Hard coral species that were not encountered in the present study. Species marked with an asterisk (*) is now considered *incertae sedis*. Previous records are indicated as follows: a = Pilcher et al. (1999), b = Pilcher and Cabanban (2000). The presence of *Heliofungia actiniformis*, *Euphyllia ancora* and *Plerogyra sinuosa* are verified by images in Pilcher et al. (1999).

Family	No.	Species	Previous records	Status
Fungiidae	1	*Heliofungia actiniformis* (Quoy and Gaimard, 1833)	a, b	Verified
	2	*Podabacia crustacea* (Pallas, 1766)	b	Unverified
Agariciidae	3	*Pavona cactus* (Forskål, 1775)	b	Unverified
	4	*Pavona decussata* (Dana, 1846)	b	Unverified
Euphylliidae	5	*Euphyllia ancora* Veron and Pichon, 1980	a, b	Verified
	6	*Plerogyra sinuosa* (Dana, 1846)*	a, b	Verified

Pavona corals – morphology

Macro- and micromorphology features of the *Pavona* corals support the clades of the molecular analyses (Fig. 10a–l, Figure S2). In general, the *P. maldivensis* specimens from Layang-Layang were small in size, the largest measured 11 cm x 8 cm while the smallest was 3.5 cm x 3 cm. All *P. maldivensis* specimens from Layang-Layang had paper-thin coralla (≤ 1 mm) and were found encrusting the reef wall (e.g. Fig. 7c). Several specimens had knobs or rounded columns protruding from the corallum (Fig. 10a). The specimen from the Maldives has a columnar or club-shaped growth form (Fig. 10e). The corallite morphology is variable within the same specimen, largely depending on the position of the corallites in the corallum. Calices at the top of the knobs or columns are small and compact and become larger and widely spaced towards the base or on horizontal plates (see Gardiner 1905). Calices vary from circular, distinctly raised edges (plocoid) (Fig. 10d) to broad, flattened edges particularly at the base of the colony (Fig. 10f), or a combination of both features (Fig. 10b) when inclined towards the margin. Calices with raised walls protrude up to 2–4 mm. The columella is well-developed in the form of a peg (Fig. 10b) or a single, rounded or twisted rod (Fig. 10d, f).

Specimens of *P. explanulata* were either encrusting (Fig. 10g, i), submassive (Fig. 10k) or a combination of submassive with plate margins. Corallites may have irregular arrangements and shapes and mostly lack any form of wall (theca), giving the corallum a smooth surface appearance. Veron and Pichon (1980) described the thecae as "synapticulothecate", if present, which is defined as rod-or bar-like structures extending between the septa (Budd et al. 2012). In plate colonies, the corallites are inclined towards the margin and usually in parallel rows. The columella consists of several fused processes that extend from the radial elements into the fossa (Fig. 10h) or a single process, which appears as a twisted rod (Fig. 10j, l). Synapticular rings may be visible in this species (Fig. 10j, l). The specimen from Redang, Peninsular Malaysia looks superficially like *P. explanulata*, but the morphology differs from the rest of the *P. explanulata* specimens by the deeply seated columella and the widely spaced septa (Fig. 11). This specimen resembles *Pavona* cf. *explanulata* in Veron and Pichon (1980: Fig. 31).

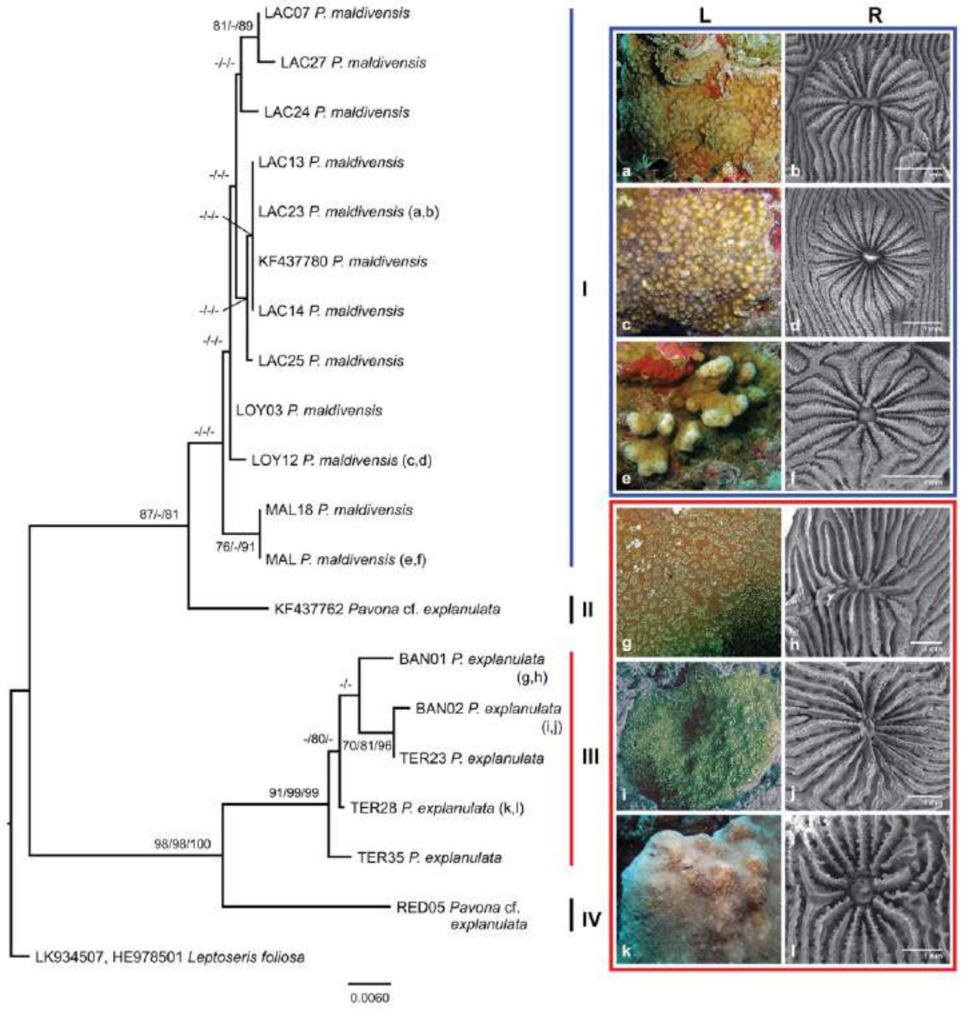


Fig. 10. Maximum likelihood phylogram of *Pavona maldivensis* and *P. explanulata* based on combined mitochondrial intergenic spacer between CO1 and 16S-rRna and nuclear marker ITS1-5.8S-ITS2 sequences. Support values for maximum likelihood, maximum parsimony (> 70) and bayesian posterior probabilities (> 80) are given at the nodes. Dashes (-) indicate nodes without statistical support. Letters in parentheses correspond to images a–l in rows L and R. L: coral colonies in situ, R: SEM images of calices. Locality for the coral samples are: LAC = Layang-Layang, LOY = Loyalty Islands, MAL = the Maldives, BAN = Banggi, East Malaysia, TER = Ternate, Indonesia, RED = Redang, Peninsular Malaysia. **a–b** *P. maldivensis* from Layang-Layang **c–d** *P. maldivensis* from Loyalty Islands **e–f** *P. maldivensis* from the Maldives **g–h** *P. explanulata* from Banggi, Sabah **i–j** *P. explanulata* from Banggi, Sabah **k–l** *P. explanulata* from Ternate, Indonesia. Additional samples KF437780 *Pavona maldivensis* and KF 437762 *Pavona* cf. *explanulata* are from Pearl and Hermes Atoll, the northwest Hawaiian Islands and O’ahu, Hawaii, respectively (Luck et al. 2013). Outgroup LK934507, HE978501 *Leptoseris foliosa* is from Prony Bay, New Caledonia (Benzoni et al. 2012b, Terraneo et al. 2014).

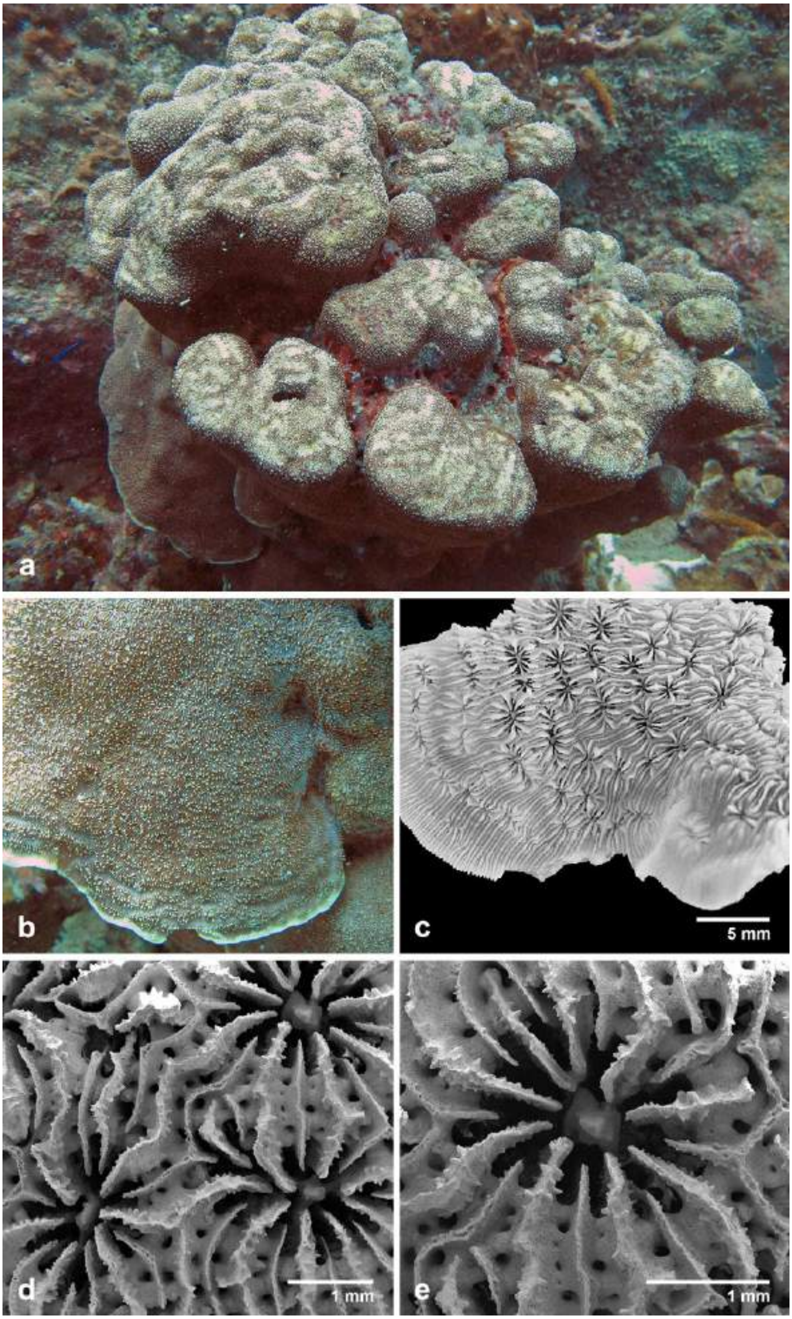


Fig. 11. Specimen RED05 *Pavona* cf. *explanulata* from Pulau Redang, Peninsular Malaysia. **a** coral colony in situ at 13 m depth **b** corallites detail at the plate margin **c** coral fragment preserved in ethanol **d**, **e** SEM images showing calices.

Septocostae of both *Pavona* species are closely compacted, but in *P. maldivensis* they have denser granulated sides (Fig. 12). In *P. explanulata*, the order of septa may alternate between thin with rows of fine granules and thick with prominent spines. The upper margin of the septa (forming radial elements) consist of beaded granules in *P. maldivensis*, and in *P. explanulata* it appears to taper into a somewhat straight ridge. The side walls or lateral faces of the septa are covered with granules either in rows or scattered on the surface (e.g. Fig. 12a, d). Aligned granulations alongside the lateral faces also known as menianae (Kitahara et al. 2010, Benzoni et al. 2012b, Terraneo et al. 2014), or menianes (Kitahara et al. 2012, Hoeksema 2012b), are more obvious in *P. explanulata* (Fig. 12b, d) as compared with *P. maldivensis*, which has short series of menianae, if formed (Fig. 12c). Radial elements of *P. explanulata* can have almost smooth margins (e.g. Fig. 12b), and this has been described by Veron and Pichon (1980) for the second order septa of this species. A summary of the variation in morphological characters between *P. maldivensis* and *P. explanulata* is given in Table 5.

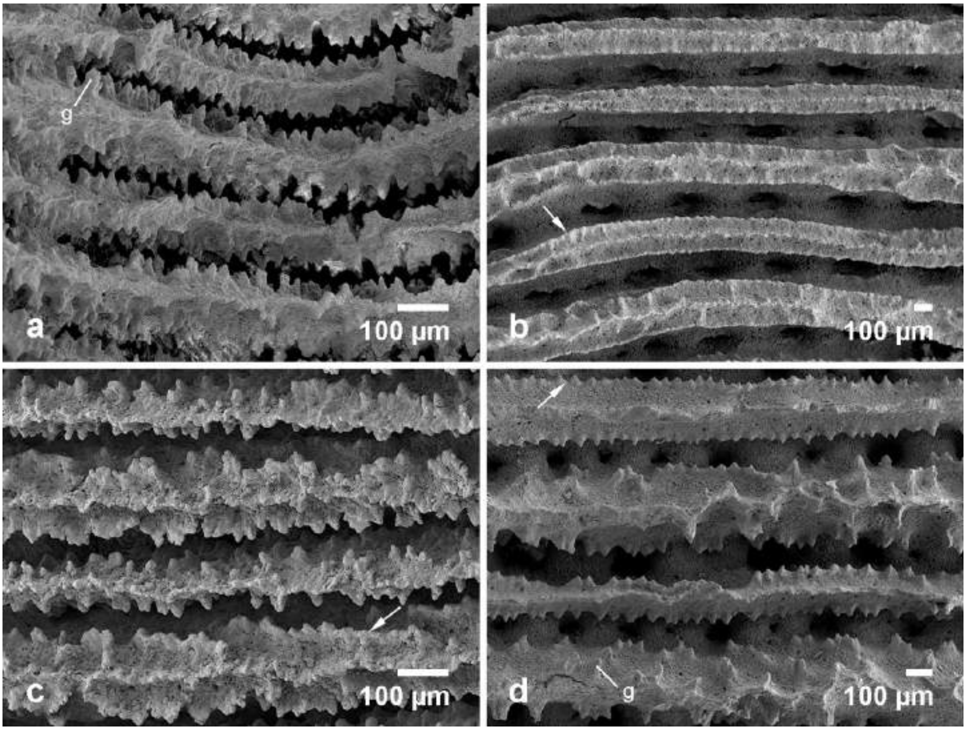


Fig. 12. Variation of radial elements in *Pavona maldivensis* (**a**, **c**) and *P. explanulata* (**b**, **d**). **a** specimen LAC23 from Layang-Layang, **b** specimen BAN02 from Banggi, North Borneo, **c** specimen LOY12 from Loyalty Islands, and **d** specimen TER28 from Ternate, Indonesia. Lateral faces of septa are covered with granules (g) as indicated in **a** and **d**. Aligned granulations along the lateral faces of septa (menianae) are indicated by white arrows in **b**, **c**, and **d**.

Table 5. Summary of variation in morphological characters between *Pavona maldivensis* and *P. explanulata*

Morphological characters	***Pavona maldivensis***	***Pavona explanulata***
Growth form	Encrusting; paper-thin coralla, club-shaped (specimen from the Maldives)	Encrusting, submassive; may have plate margins
Corallite (arrangement)	Small and compact (top of the colony), widely spaced (base of the colony)	Irregular spacing and arrangement, in parallel rows towards the margin
Corallite (shape)	Circular, plocoid, flattened edges when inclined towards the margin	Irregular shape, but may be somewhat circular
Theca	Distinct; plocoid	Mostly lacking, synapticulothecate if present
Columella	Well-developed; peg-like, single, rounded or twisted rod	Several fused processes
Septo-costae	Compact, dense granulated sides	Compact, septa alternate between thin with fine granules and thick with spines
Radial elements	Beaded granules	Tapers into straight ridge, may have smooth margins
Lateral faces	Granules in rows or scattered on the surface, may form short series of menianae	With granules and meaninae

Discussion

Species occurrence

The total number of coral species noted at Layang-Layang is less than that of other localities in Sabah where similar surveys have been conducted. Nevertheless, the overall species diversity is considered high even for fungiid corals, despite the fact that steep reef walls are hostile environments for free-living mushroom corals, as they can get dislodged from these drop-offs (Hoeksema and Moka 1989). In contrast, agariciid corals of the genus *Leptoseris* are known to flourish at greater depths (Kahng and Maragos 2006, Rooney et al. 2010, Dinesen et al. 2012, Luck et al. 2013). Based on the three target coral families, there is a decrease in the number of species from the east to the west coast of Sabah, from Semporna (90 species: 44 Fungiidae, 31 Agariciidae, 15 Euphylliidae; Chapter 2) to Kudat (84 species: 39 Fungiidae, 30 Agariciidae, 15 Euphylliidae; Chapter 3), then Kota Kinabalu (72 species: 35 Fungiidae, 26 Agariciidae, 11 Euphylliidae; Chapter 4), and finally offshore Layang-Layang (59 species: 32 Fungiidae, 22 Agariciidae, 5 Euphylliidae) (see inset of Fig. 1). This is concordant with the general pattern of decreasing diversity away from the designated centre of maximum marine biodiversity (Briggs 1974, Hoeksema 2007, 2013, 2015, Bellwood and Meyer 2009), also known as the Coral Triangle, with its present western border at the Sulu Sea (Veron et al. 2009, 2011). However, Huang et al. (2014b) demonstrated that there is no significant structure in species diversity on a larger scale from the eastern to the western reefs of the South China Sea, and suggested that local dynamics are at play in driving the species richness and distribution patterns in the area. Based on their coral species composition, the Spratly Islands clustered together with southern Vietnam rather than closer continental localities such as Sabah, Brunei or Palawan, the Philippines (Huang et al. 2014b), which implies that the former two localities may have similar reef attributes. For oceanic Layang-Layang with its steep reefs walls, an additional factor for its lower species richness as compared to nearby continental reef areas such as Kota Kinabalu and Kudat could be the lack of habitat heterogeneity, which would be important for supporting species diversity (Done 1982, Best et al. 1989; Cornell and Karlson 1996, 2000, Karlson and Cornell, 1998, Hoeksema 2007, 2012c).

Among the new coral records for Layang-Layang are five rarely documented species, i.e., *Lithophyllon ranjithi* (Fig. 3d), *Podabacia sinai* (Fig. 4d), *Sandalolitha boucheti* (Fig. 4f), *Leptoseris kalayaanensis* (Fig. 5g) and *L. troglodyta* (Fig. 6c). *Lithophyllon ranjithi*, a mushroom coral previously thought to be endemic to northeast Borneo was encountered at seven sites. The first mention of this species from the South China Sea was from Brunei (Turak and DeVantier 2011), although this record could not be confirmed in a later review (Hoeksema and Lane 2014). This species is usually found on nearshore or coastal reefs (Chapter 2) so it was surprising to find it at an offshore and oceanic locality. Conversely, *L. kalayaanensis* was anticipated to be present in Layang-Layang. In fact, its type locality, the Kalayaan Islands in the Philippines is located ~350 km northeast from the atoll and this species has been reported from three other localities in the South China Sea, two with rather similar reef conditions (Licuanan and Aliño 2009) and one from the coastal area of Nha Trang, Vietnam (Hoeksema et al. 2010). Specimens of *L. kalayaanensis* were found at 13 sites along steep reef walls and considered rather common in Layang-Layang. *Leptoseris troglodyta*, a cavernicolous and azooxanthellate species was encountered only once during the dives. A cluster of about 12 small calices was found on the ceiling of a small cave in a reef wall at 30 m depth (Site 1). This species is widely distributed in the West Pacific (Hoeksema 2012b) and this account is the first record for the South China Sea. *Podabacia sinai* was previously recorded from the Red Sea (Veron 2000) but meanwhile it has also been found in various other Indo-Pacific localities (Hoeksema unpubl.). *Sandalolitha boucheti* has been observed in Vanuatu (Hoeksema 2012a) and Semporna, East Sabah (Chapter 2). This species was represented on the Layang-Layang reefs by two specimens. The largest of these (Ø ~6 cm; Fig. 4f) was still attached by a very wide stalk while the other was free-living and showed a large detachment scar. It is abnormal for free-living mushroom corals to maintain a long-lasting fixed growth form (Hoeksema and Yeemin 2011), which may hinder their identification.

Corals of three *Leptoseris* spp. could not be identified to species level. Two specimens of encrusting *Leptoseris* sp. 1 had free margins and small corallites (≤ 1.5 mm in size). One of these corals (Fig. 9a) has calices in rows somewhat concentric and parallel with the margin and a central corallite can be discerned. Corallites appear sunken because of the high and continuous carinae. This specimen measures Ø 5 cm, and it is possibly a juvenile

L. mycetoseroides. Further examination of these specimens is required for certainty. Unfortunately, specimens of *Leptoseris* sp. 2 and 3 were not collected; nevertheless photos have been included for visual record (Fig. 9b, c).

Three coral species that have been reported from Layang-Layang but were not observed in the present study are the fungiid *Podabacia crustacea* and the agariciids *Pavona cactus* and *P. decussata* (Pilcher and Cabanban 2000). Since there is no photographic evidence or other supporting information to support the presence of these species on the atoll, they have not been included in the current species list. Still, it is very likely that these three species are present on the reef as they are common Indo-Pacific species and their distribution ranges certainly cover across the South China Sea, including the Spratly Islands (see Huang et al. 2014b). As a note, *P. cactus* is usually found in turbid and sheltered reef conditions (Veron and Pichon 1980, Veron 2000). However, *P. cactus* and *P. decussata* can also be found in shallow reef environments such as upper reef slopes and lagoons. It is possible that these species are present in the lagoon reefs, which were underexplored in our study, as surveys were only possible around the reef walls of the atoll.

Many coral colonies in Layang-Layang appeared small in size, and most were juveniles. This was consistent across the reef sites for most coral families including those targeted in our study. For example, the largest collected *L. kalayaanensis* specimen measured 7.5 cm x 5 cm while the smallest was 4 cm x 3 cm. Also, the initial uncertainty in identifying *P. maldivensis* most likely stemmed from the fact that the specimens were very small in size (collected colonies were between 11 cm x 8 cm and 3.5 cm x 3 cm). This puzzling find can be explained by the fact that corals in the study area are recolonizing after the outbreak of the corallivorous crown-of-thorns (COT) seastar. Surveys during the COT outbreak in July 2010 were conducted down to 10 m depth only (Nasrulhakim et al. 2010), but the damage extends deeper based on our surveys (~20 m depth). Preceding this event there was also a COT outbreak on the nearby reefs of Brunei in April-May 2010, and at the same time a report of large numbers of COT at the reefs of the Tunku Abdul Rahman Park in Kota Kinabalu, Sabah on the northwest coast of Borneo (Lane 2012). Following this outbreak, Brunei and Kota Kinabalu reported to have thermally induced bleaching episodes in June-July 2010 (Lane 2011, Aw and Muhammad Ali 2012). There is no account on whether the reefs of Layang-Layang were also affected by this bleaching event, and based on our observations, we are unable to determine if a bleaching episode did occur.

There is no information on the extent of damage caused to the reefs and the rate of recovery from the COT outbreak in 2010, as the reefs of Layang-Layang are not monitored regularly. Many studies have reported the effects of COTs to reefs in terms of coral cover loss and changes in coral assemblage (e.g. Lourey et al. 2000, Pratchett 2010, Lane 2011, 2012, Baird et al. 2013, Bos et al. 2013, Osborne et al. 2014, Saponari et al. 2014). While COTs are known to have a feeding preference for *Acropora* (De'ath and Moran 1998, Pratchett 2007), they have also been found to feed on many different coral taxa (Glynn 1974, Ormond et al. 1976, Colgan 1987, De'ath and Moran 1998, Pratchett 2007, 2009), which includes fungiids (De'ath and Moran 1998, Prachett 2007, 2009, 2010, Scott et al. 2015) and agariciids (Colgan 1987, Prachett 2007, 2009, 2010) particularly during an outbreak or when food becomes scarce (Moran 1986). Similarly for Layang-Layang, it appears that the COT outbreak resulted in high coral mortality (E Foo, J Bell, R Wahab, Avillon Layang-Layang Resort, pers. comm.). Our study was carried out almost three years after the outbreak and from our observations, the high frequency of coral recruits and small-sized colonies indicate an ongoing recovery of corals. We question whether all coral species (as prior to the outbreak) have re-established on the reefs as coral species such as *Euphyllia ancora* and *Plerogyra sinuosa*, both reported as common from previous surveys (NJ Pilcher, pers. comm.), were not observed during the present study. We are unable to draw a conclusion that the absence of certain species previously reported for Layang-Layang is caused by the 2010 COT event. While some baseline data is available for comparison (e.g. Pilcher et al. 1999, Pilcher and Cabanban 2000), there is no specific locality data of species occurrences to refer to. As far as we know, the reefs of Layang-Layang were monitored between 1996 and 1999 (see Pilcher et al. 1999, Pilcher and Cabanban 2000) and since then and prior to that, reef surveys were conducted intermittently. As several studies have impressed upon the importance of utilising long-term monitoring data in order to assess changes to the coral communities (e.g. Brown et al. 2002, Somerfield et al. 2008), there is a need to establish a coral reef monitoring plan for Layang-Layang. With a monitoring plan in place, any changes or disturbance can be detected at the onset so that mitigation measures can be taken if necessary.

***Pavona* species boundaries**

The IGR marker has proven to be successful in resolving species boundaries in the family Agariciidae and the genus *Pachyseris* (Terraneo et al. 2014). In our small dataset, the IGR marker gave better resolution than the ITS marker in resolving species-level relationships for two *Pavona* species. Both the IGR and the concatenated gene tree supported two main groups, one of *P. maldivensis*, including specimens from Layang-Layang, and the other of *P. explanulata*.

For all specimens in the *P. maldivensis* clade, the calice size is smaller, the calice walls are raised and distinct, the septocostae spacing is more compact and there is more surface ornamentation on the radial elements as compared to *P. explanulata*. They share some similar features in colony growth form, but *P. explanulata* does not form club-shaped branches. *Pavona explanulata* specimens also tend to have a smooth surface appearance due to the absent calice wall, but exceptions do occur. The columella is well-developed as a single, rounded or twisted rod for both species, peg-like for *P. maldivensis* and as fused processes in *P. explanulata*. Lastly, synapticular rings are obvious in *P. explanulata* but not so in *P. maldivensis*, though Veron and Pichon (1980) have described them to be obvious on the branch ends.

Upon re-examining the morphological characters of the *Pavona* specimens identified as *P. maldivensis* in our previous studies (Chapters 2 and 4), it was clear that the specimens were similar to *P. explanulata* instead. However, these specimens have calices with somewhat distinct walls, a feature that is more typical of *P. maldivensis*. This is most likely one of the factors that prompted the misidentification of these specimens. Adding to this, *P. maldivensis* has a wide distribution range in the Indo-Pacific (e.g. Veron and Pichon 1980, Scheer and Pillai 1983, Maragos and Jokiel 1986, Dai and Lin 1992, Nishihira and Veron 1995, Glynn et al. 2007, Pichon 2007, Pichon and Benzoni 2007), and has been reported from the Bodgaya and Sipadan islands in Semporna, Sabah (Wood and Tan 1987). Hence, we had expected to find this species in our previous study areas (i.e. Semporna and Kota Kinabalu).

Although *P. maldivensis* and *P. explanulata* may not be considered the most problematic species within *Pavona*, specimens that closely resemble these species have been collected and analysed. For example, sample KF437762 *Pavona* cf. *explanulata* (Luck et al. 2013) clusters basally to *P. maldivensis* rather than with its conspecifics, while sample RED05 *Pavona* cf. *explanulata* from Redang clusters basally to the other samples of *P. explanulata*. For the latter, the macro- and micromorphology of this specimen was noticeably different from the rest of the *P. explanulata* samples. These cases indicate that the identity of *P. explanulata* should be carefully re-examined in the future through a larger morpho-molecular study including several specimens from various localities.

Implication of misidentified *Pavona maldivensis*

Based on the findings of this study, the "true" *P. maldivensis* has only been found in Layang-Layang out of the other localities previously visited in Sabah, Malaysia, i.e. Semporna and Kota Kinabalu (Chapters 2 and 4), and the status of this species in those localities remains ambiguous until future data is available. It is highly likely that the misidentified specimens from those previous studies are *P. explanulata*, as was discovered for specimens from Banggi and Ternate utilised in this study, or a variety closely resembling it.

The name *Pavona explanulata*, like *P. maldivensis*, has been mistakenly used in the past (examples given by Veron and Pichon 1980: pp. 17-36). Furthermore, the type specimen of *P. explanulata* appears to be missing and the original species description is rather vague, so taxonomic literature of this species since when it was first described needs to be re-examined in order to better define its species boundaries.

Conclusions

The coral species list for the families Fungiidae, Agariciidae and Euphylliidae in the present study added 32 new records for Layang-Layang and includes rarely recorded species such as *Leptoseris kalayaanensis*, which is thus far a South China Sea endemic. The mushroom coral *Lithophyllon ranjithi* has a wider distribution range than previously thought and can no longer be considered endemic to northeastern Borneo. This is the first record of this species from an oceanic and offshore reef habitat, in contrast to its previously reported habitat preference for coastal and sheltered reef conditions.

An integrative molecular and morphological approach was utilised to determine that specimens identified as *P. maldivensis* from previous surveys are in fact *P. explanulata*. The combination of both techniques have proven to be powerful in addressing species complexes in scleractinians (e.g. Benzoni et al. 2007, 2011, 2014, Kitahara et al. 2012, Arrigoni et al. 2014a, b, c, Kitano et al. 2014), particularly if type specimens and coral samples from the type locality are included in the analyses (Huang et al. 2014a), and taxonomic descriptions are consolidated (Benzoni et al. 2010). While the species boundaries between *P. maldivensis* and *P. explanulata* may already be distinct based on morphological descriptions and images in current taxonomic literature, the present study has included SEM images of calices and radial elements of specimens of both species for the first time to further illustrate the previous descriptions. In addition, a specimen closely resembling but dissimilar from *P. explanulata* was also shown. As such, this finding may serve as a stepping stone for further investigations of *Pavona*.

Acknowledgments

Research permits for Layang-Layang were granted by the Economic Planning Unit and the National Security Council of the Prime Minister's Department, Malaysia, and the Sabah Biodiversity Council. Travel expenses for Z. Waheed was funded by the A.M. Buitendijkfonds, The Netherlands. We acknowledge the Marine Research Station Layang-Layang (MARSAL) for the visit to the field station at Layang-Layang. We thank the team at Avillon Layang-Layang Resort for living and diving logistics, the managing director Eugene Foo and divemasters Jasper Bell, Rozlan Wahab and Amanda La Brooy for fruitful discussions. Loyalty Island data was collected during the BIBELOT campaign in 2014 onboard RV Alis of IRD at Nouméa. Sampling permits were granted by the Loyalty Islands Province, New Caledonia. BW Hoeksema is grateful to Cecile Fauvelot and Claude Payri for the invitation to join this expedition, and to Francesca Benzoni and Paola Galli for allowing him to participate in the Maldives International Reef Biodiversity Workshop in 2014, which enabled him to obtain data on *P. maldivensis.* Sampling of *P. explanulata* in Ternate, Indonesia was done under Ekspedisi Widya Nusantara (E-Win) co-organised by Naturalis and the Indonesian Institute of Sciences (LIPI) with research permits from LIPI and RISTEK. We highly appreciate the constructive comments from Bastian T. Reijnen, Nadiezhda Santodomingo and one anonymous reviewer, which greatly improved the manuscript.

Supporting Information

Figure S1. Maximum likelihood phylogram of *Pavona maldivensis* and *P. explanulata*. **a** mitochondrial intergenic spacer between CO1 and 16S-rRna. The sequence alignment consisted of 680 characters with 593 constant, 23 variable and 64 parsimony informative characters, **b** nuclear marker ITS1-5.8S-ITS2, with 680 characters of 649 constant, 14 variable and 17 parsimony informative characters. Support values for maximum likelihood, maximum parsimony (> 70) and bayesian posterior probabilities (> 80) are given at the nodes. Dashes (-) indicate nodes without statistical support.

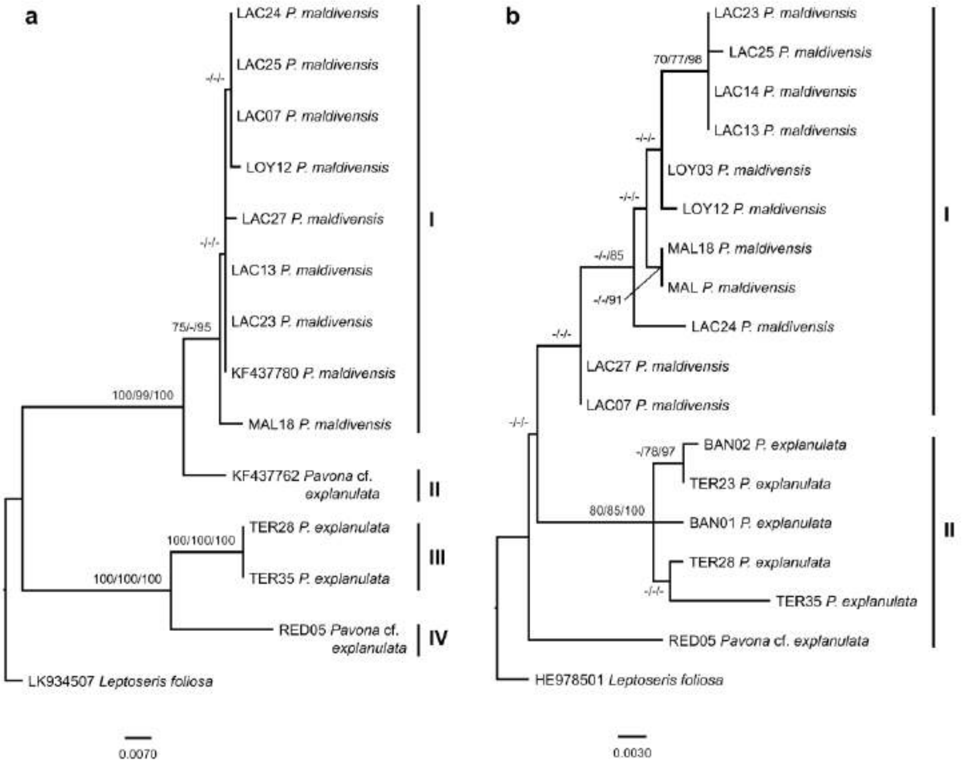
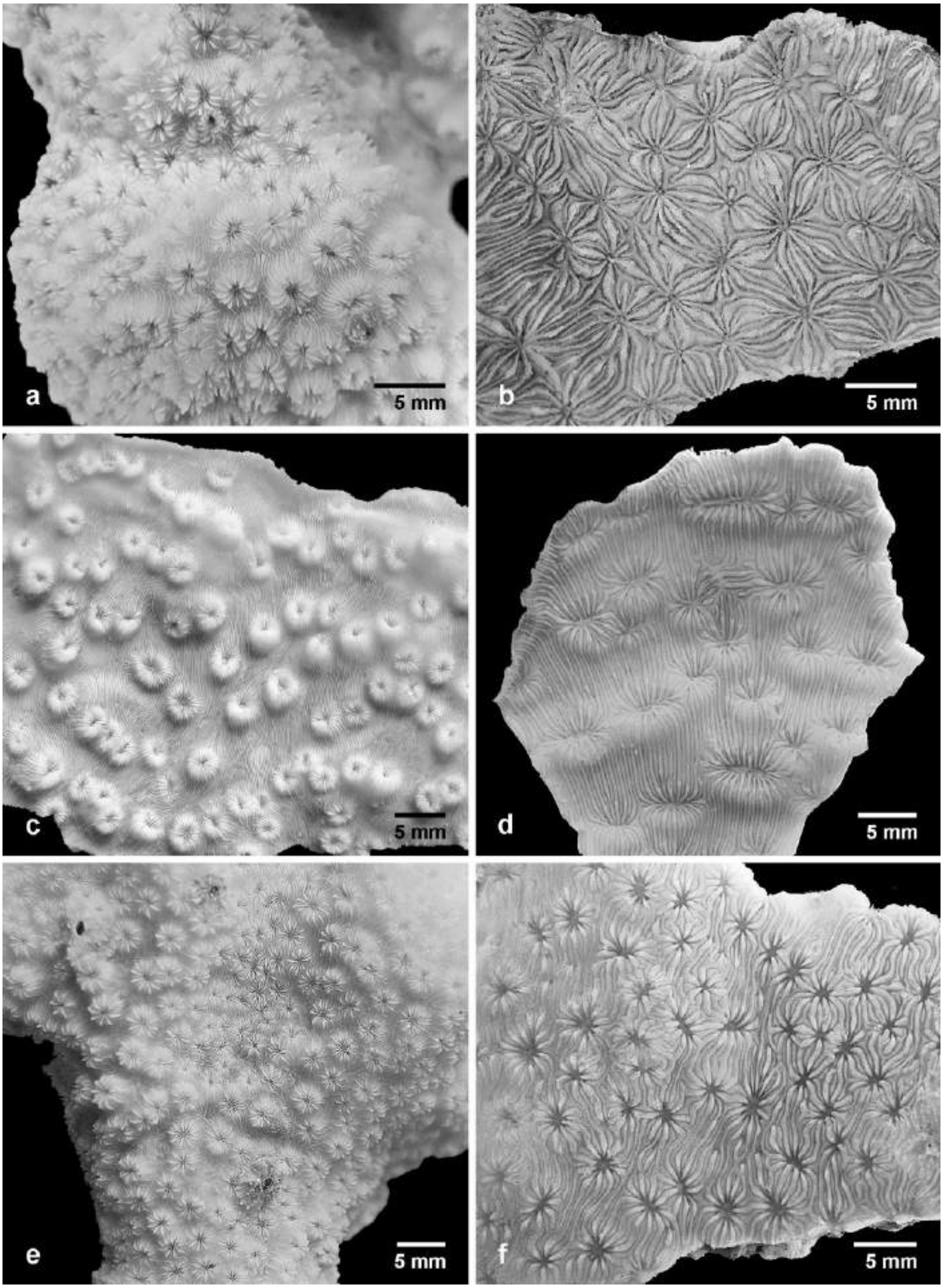


Figure S2. Variation of corallite form and structure in *Pavona maldivensis* (**a**, **c**, **e**), and *P. explanulata* (**b**, **d**, **f**). **a** specimen LAC23 from Layang-Layang, **b** specimen BAN01 from Banggi, North Borneo, **c** specimen LOY12 from Loyalty Islands, **d** specimen BAN02 from Banggi, North Borneo, **e** specimen MAL from the Maldives, and **f** specimen TER28 from Ternate, Indonesia.



Other supporting information are available at doi:10.3897/zookeys.517.9308

Table S1. Physical properties of seawater at Pulau Layang-Layang.

Table S2. Coral samples included in the molecular analyses with supporting collection and locality data (see page 127)

Table S3. Species occurrence of hard coral families Fungiidae, Agariciidae and Euphylliidae at Pulau Layang-Layang.

Table S2. Coral samples included in the molecular analyses with supporting collection and locality data

Specimen details									GenBank Accession No.	
Field Col. No.	**Registration No.**	**In situ ID**	**Specimen ID**	**Collector**	**Date**	**Locality**	**Lat (N)**	**Long (E)**	**IGR**	**ITS**
BAN01	RMNH Coel. 41654	*Pavona explanulata*	*Pavona explanulata*	Z. Waheed	19/09/08	Banggi, North Sabah, Malaysia	07° 05'16.0"	117° 01'31.0"	–	KR706127
BAN02	RMNH Coel. 41655	*Pavona maldivensis*	*Pavona explanulata*	Z. Waheed	19/09/08	Banggi, North Sabah, Malaysia	07° 04'27.0"	117° 01'38.0"	–	KR706128
TER23	RMNH Coel. 41656	*Pavona maldivensis*	*Pavona explanulata*	SET van der Meij	06/11/09	Ternate, Indonesia	0° 52' 2.0"	127° 19 45.8"	–	KR706129
TER28	RMNH Coel. 41657	*Pavona explanulata*	*Pavona explanulata*	SET van der Meij	09/11/09	Gura Ici, Indonesia	0° 01' 51.9"	127° 14' 1.8"	KR706116	KR706130
TER35	RMNH Coel. 41658	*Pavona explanulata*	*Pavona explanulata*	SET van der Meij	12/11/09	Tidore, Indonesia	0° 42' 44.1"	127° 28' 47.3"	KR706117	KR706131
LAC07	RMNH Coel. 41659	*Pavona* sp.	*Pavona maldivensis*	Z. Waheed	26/03/13	Layang-Layang, Spratly Islands	07° 22.191	113° 47.701	KR706118	KR706132
LAC13	IPMB-C 13.00010	*Pavona* sp.	*Pavona maldivensis*	B.W. Hoeksema	26/03/13	Layang-Layang, Spratly Islands	07° 22.876	113° 48.910	KR706119	KR706133
LAC14	IPMB-C 13.00011	*Pavona* sp.	*Pavona maldivensis*	B.W. Hoeksema	26/03/13	Layang-Layang, Spratly Islands	07° 22.876	113° 48.910	–	KR706134
LAC23	IPMB-C 13.00017	*Pavona* sp.	*Pavona maldivensis*	Z. Waheed	29/03/13	Layang-Layang, Spratly Islands	07° 23.013	113° 50.912	KR706120	KR706135
LAC24	IPMB-C 13.00018	*Pavona* sp.	*Pavona maldivensis*	Z. Waheed	29/03/13	Layang-Layang, Spratly Islands	07° 23.013	113° 50.912	KR706121	KR706136
LAC25	IPMB-C 13.00019	*Pavona* sp.	*Pavona maldivensis*	Z. Waheed	30/03/13	Layang-Layang, Spratly Islands	07° 21.902	113° 49.778	KR706122	KR706137
LAC27	IPMB-C 13.00020	*Pavona* sp.	*Pavona maldivensis*	Z. Waheed	30/03/13	Layang-Layang, Spratly Islands	07° 21.902	113° 49.778	KR706123	KR706138
RED05	IPMB-C 14.00010	*Pavona* cf. *explanulata*	*Pavona* cf. *explanulata*	Z. Waheed	01/07/13	Redang, Terengganu,	05° 45' 36.7"	103° 02' 10.4"	KR706124	KR706139
LOY03	RMNH Coel. 41662	*Pavona maldivensis*	*Pavona maldivensis*	B.W. Hoeksema	16/02/14	Loyalty Islands, New Caledonia	21° 29.204' S	168° 07.164'	–	KR706140
LOY12	RMNH Coel. 41663	*Pavona maldivensis*	*Pavona maldivensis*	B.W. Hoeksema	20/02/14	Loyalty Islands, New Caledonia	20° 55.067' S	167° 04.311'	KR706125	KR706141
MAL18	RMNH Coel. 41664	*Pavona maldivensis*	*Pavona maldivensis*	B.W. Hoeksema	17/05/14	Maaga, Maldives	03° 07' 11.5"	72° 56' 21.7"	KR706126	KR706142
MAL	RMNH Coel. 41665	*Pavona maldivensis*	*Pavona maldivensis*	F. Benzoni	08/05/14	Biledhdhoo, Faafu Atoll, Maldives	03° 07' 14.2"	72° 58' 46.9"	–	KR706143
–	(GenBank)	-	*Pavona maldivensis*	–	–	–	–	–	KF437780	–
–	(GenBank)	-	*Pavona* cf. *explanulata*	–	–	–	–	–	KF437762	–
HS2854	(GenBank)	-	*Leptoseris foliosa*	–	–	–	–	–	LK934507	–
HS2854	(GenBank)	-	*Leptoseris foliosa*	–	–	–	–	–	–	HE978501

Chapter 6

Reef coral species richness gradient across Malaysia

Zarinah Waheed, Affendi Yang Amri and Bert W. Hoeksema

Abstract

Biodiversity components such as species richness are commonly used for conservation prioritisations. In this study, the reef coral species richness patterns were examined across Malaysia from east to west spanning the Sulu Sea, South China Sea and Strait of Malacca: Semporna, Kudat, Kota Kinabalu, Layang-Layang in the Spratly Islands, Tioman, Redang and Payar. Three reef coral families i.e. Fungiidae, Agariciidae and Euphylliidae, with a total of ~94 species were used as model taxa to represent all scleractinian reef corals (> 500 species). There was a decrease in species richness from east to west Malaysia with longitude being a major factor in structuring species richness composition. A similarity profile analysis revealed clusters than were concordant with earlier recognized marine ecoregion delineations. Most species were widespread. Several species with a central Indo-Pacific distribution showed limited geographical range, not extending westward beyond Sabah, East Malaysia, while others were restricted to a single locality. Patterns of species richness and geographical distribution are most likely influenced by environmental heterogeneity, seasonal current circulation patterns and the geological history of the Sunda Shelf. The present results may be relevant for the conservation and management of coral reef areas in Malaysia and support that the northwestern boundary of the Coral Triangle may have to be moved westward.

Manuscript in preparation

Introduction

In recent times, the centre of maximum marine biodiversity or the Coral Triangle, has been identified within the Indo-Australian Archipelago (Briggs 1987; Hoeksema 2007; Bellwood and Meyer 2009; Veron 2009). Species diversity decreases across latitudinal and longitudinal gradients away from this epicentre (e.g. Ekman 1934; Briggs 1974; Hughes et al. 2002; Barber 2009; Bellwood and Meyer 2009; Carpenter et al. 2011), but not necessarily at equal rates (Veron et al. 2015). The Coral Triangle extends southward from the Philippines (including the east coast of Sabah, Malaysia in the Sulu Sea) to the Solomon Islands (Veron et al. 2009). However, a recent review based on comprehensive coral distributions, diversity and affinity data has suggested the inclusion of the Sunda Shelf (part of the South China Sea across Malaysia) within the boundary of the Coral Triangle (Veron et al. 2015). Indeed, the South China Sea has proven to be unexpectedly species-rich (Hoeksema and Lane 2014; Huang et al. 2015; 2016, Lane and Hoeksema 2016), and contains coral fauna that is nearly similar to that of the Coral Triangle albeit with slightly lower species diversity: 571 vs. 627, respectively (Huang et al. 2015; Veron et al. 2015).

Estimating species richness numbers in a defined area is one of the fundamental objectives in many ecological studies (Boulinier et al. 1998) and an analysis of species richness data may reveal diversity patterns that could be crucial for conservation and management plans (e.g. Fleishman et al. 2006; Tittensor et al. 2010; Selig et al. 2014). In Malaysia, publications on coral species lists began appearing in 1950s (reviewed in Affendi and Rosman 2012). The first study on coral richness patterns (by genera) for Peninsular Malaysia was carried out by Toda et al. (2007). Recently, the coral species richness pattern for the South China Sea was explored by Huang et al. (2015, 2016). Interestingly, the coral species composition across the South China Sea is structured by latitude and not longitude, which suggests that on a longitudinal scale, species compositional pattern may be driven by local factors, such as environmental heterogeneity and current circulation patterns (Huang et al. 2015).

The present study has a similar purpose as Huang et al. (2015), but on a smaller geographical scale, confining our study area to Malaysia, and with fewer model species. Malaysia is divided into land areas, Peninsular Malaysia (also known as West Malaysia) and East Malaysia (part of Borneo), and it is bordered by three seas: the Strait of Malacca, the South China Sea, and the Sulu Sea. This entails the inclusion of localities in the Strait of Malacca and the Sulu Sea, thus slightly expanding the longitudinal range, but reducing the latitudinal range of our study area as compared to that in Huang et al. (2015).

The reef coral species richness patterns were explored by utilizing data collected from around Sabah, i.e. Semporna, Kudat and Kota Kinabalu (Chapters 2, 3, 4, respectively), and from Layang-Layang, the Spratly Islands (Chapter 5), and incorporating newly collected data from around Peninsular Malaysia, i.e. the islands of Tioman, Redang and Payar. Three scleractinian families were used as model taxa, i.e. Fungiidae (sensu Gittenberger et al. 2011, Benzoni et al. 2012a), Agariciidae and Euphylliidae (sensu

Veron 2000), as similarly done in the previous studies. While a comprehensive coral species list is given by Huang et al. (2015, 2016), the present analysis is limited to the data collected by the first and the senior authors (ZW, BWH) to reduce observer bias. The role of longitude in structuring the species compositions were investigated from the eastern to the westernmost sites. Additionally, the species richness patterns of the three coral families in the present study area were compared with different definitions of marine ecoregion boundaries (Spalding et al. 2007 vs. Veron et al. 2015). Finally, species that are common (present in all localities) and rare (with a restricted distribution range) were noted, as both are contributing components in determining species richness patterns (Lennon et al. 2004).

Materials and methods

Study area

Surveys were carried out in six localities across Malaysia in a westward direction, with three reef areas each in east and west Malaysia, and Layang-Layang in the group of Spratly Islands (Table 1, Fig. 1a). In East Malaysia (north Borneo), data was collected from the reefs of Semporna and south of Darvel Bay (15 sites within the Tun Sakaran Marine Park and two sites at Sipadan Island Park), the Banggi group of islands in Kudat and Marudu (recently gazetted as the Tun Mustapha Park), and the Tunku Abdul Rahman Park (TARP) and adjacent reefs in Kota Kinabalu. In Peninsular Malaysia, data collection was made in the marine parks of Pulau Tioman, Pulau Redang and Pulau Payar to represent the east and west coast of the peninsula. Sampling effort varied from 12 sites in Payar to 59 sites in Semporna (Chapters 2–5: Fig. 1, Fig. S1). In total, 194 sites were surveyed (with 19 additional sites for mushroom coral surveys only).

Table 1. Sampling localities from east to west Malaysia

Locality	Sea basin	Code	Latitude	Longitude
Semporna, East Malaysia	Sulu Sea	SEM	04°06′ – 04°48′	118°10′ – 118°57′
Kudat, East Malaysia	Sulu Sea	TMP	06°40' – 07°28'	116°50' – 117°34'
Kota Kinabalu, East Malaysia	South China Sea	KK	05°57' – 06°12'	115°59' – 116°05'
Layang-Layang, Spratly Is.	South China Sea	LAC	07°22' – 07°23'	113°47' – 113°52'
Tioman, Pen. Malaysia	South China Sea	TIO	02°42' – 02°56'	104°03' – 104°13'
Redang, Pen. Malaysia	South China Sea	RED	05°43' – 05°49'	102°59' – 103°04'
Payar, Pen. Malaysia	Strait of Malacca	PAY	06°03' – 06°05'	100°02' – 100°03'

Coral species incidence data were collected at each site for the coral families Fungiidae (sensu Gittenberger et al. 2011), Agariciidae, and Euphylliidae (sensu Veron 2000) as proxy for all reef coral by adapting the roving diver technique (Schmitt et al. 2002; Munro

2005; Hoeksema and Koh 2009). Dive time for data collection was maintained at 60 minutes per site and the maximum depth varied by locality depending on the seafloor bathymetry (Semporna and Layang-Layang = 40 m, Kudat = 35 m, Kota Kinabalu, Tioman and Redang = 30 m, Payar = 20 m). Specimens were identified based on taxonomic literature and coral fauna descriptions of Dinesen (1980), Veron and Pichon (1980), Hoeksema (1989, 2012b, d, 2014), Veron (2000), Ditlev (2003), Licuanan and Aliño (2009), Gittenberger et al. (2011), Benzoni et al. (2012). Recent taxonomic revisions have classified the Euphylliidae (sensu Veron 2000) genera *Catalaphyllia*, *Nemenzophyllia*, *Physogyra* and *Plerogyra* as Scleractinia *incertae sedis* (Fukami et al. 2008; Kitahara et al. 2010; Benzoni et al. 2014). Nevertheless we continue to include these genera in our study for consistency in the comparisons with previous works (Chapters 2–5).

Data analysis

Coral species with confirmed identifications were used for further analyses. The species lists of Semporna and Kota Kinabalu were edited based on new insights regarding the identities of *Pavona maldivensis* and *P. explanulata* (Chapter 5). At present, *P. maldivensis* has only been observed in Layang-Layang out of all the reef areas surveyed in the present study. Total number of species per site were tabulated for each locality and compared across the seven localities. Species accumulation curves were estimated by plotting the species richness against the number of sites in each locality using the R package *vegan* (Oksanen et al. 2015).

Multivariate analyses were used to investigate the coral species richness patterns across the localities based on the species presence/absence data. Similarity profile analysis (SIMPROF) was used to determine significant clusters without imposing any a priori groups based on the Bray-Curtis similarity measure (Bray and Curtis 1957). A cluster analysis was implemented in the R package *clustsig* (Whitaker and Christman 2014) in accordance to Clarke et al. (2008), which produced a group-averaged hierarchical clustering dendrogram generated from 1,000 expected and simulated profiles. To further examine the species richness patterns, non-metric multidimensional scaling (NMDS) was attempted on the R package *vegan* (Oksanen et al. 2015), however the NMDS analysis returned solutions with nearly zero stress level and no convergent solution, or two convergent solutions after > 400 tries. Such low stress values are typical of small datasets with very few observations, and metric methods are suggested to be more suitable (Oksanen et al. 2015). Therefore, a classical metric multidimensional scaling, also known as principal coordinates analysis (Gower 1966) was applied in R (R Core Team 2013).

To evaluate the role of longitude in structuring the coral species composition and distribution, the Mantel test of matrix correlation was used (Mantel 1967; Legendre and Legendre 2012) in the R package *vegan* (Oksanen et al. 2015). A Bray-Curtis distance matrix was calculated for the species richness data and plotted against the longitude data constructed with a Euclidian distance matrix. Mantel test was used to calculate a Spearman’s rank correlation coefficient with 10,000 permutations. The obtained species richness structure was compared with existing groupings reflecting marine ecoregions as proposed by 1) Spalding et al. (2007) by dividing our study area into four: South China Sea oceanic islands, Sunda Shelf, Malacca Strait, and North Borneo (see Spalding et al. 2007: Figure 3, Box 1), and by 2) Veron et al. (2015) in their revised definition of the Coral Triangle, extending the boundary from the Sulu Sea to include the Sunda Shelf, separate from the Spratly Islands and the Strait of Malacca (see Veron et al. 2015: Figure 6). A visual comparison was made without performing any statistical analysis as the localities within the present study covers only parts of the ecoregions outlined above, and would not be representative of each region. For example, based on Spalding et al. (2007), the Sunda Shelf region includes the Java Sea, yet we only have two localities from this region, both in the South China Sea along the east coast of Peninsular Malaysia. Finally, coral species that were widespread and occurred in all locations and species with limited geographic distribution were noted.

Results

Species richness

The total number of sclerctinian coral species for families Fungiidae, Agariciidae and Euphylliidae was 106 species, with 94 confirmed identifications, five unidentified agariciids (three *Leptoseris* and two *Pavona* species), and seven species labeled with cf., still considered unidentified separate species (Table S1 and references to figures therein). Since there is evidence that *Pavona* cf. *explanulata* is distinct from *P. explanulata* based on morpho-molecular analyses (Chapter 5), it was considered a positive identification and included as such for further analyses. Nine species were new records for Malaysia (Fungiidae: *Cantherellus jebbi*, *Cycloseris curvata*, *C. distorta*, *C. hexagonalis*, *Halomitra clavator*, *Podabacia kunzmanni* and *Sandalolitha boucheti*; Agariciidae: *Leptoseris amitoriensis* and *Pavona* cf. *explanulata*). There was a gradient in species richness from Payar in the Strait of Malacca (n = 33) in eastward direction towards Semporna in the Sulu Sea (n = 89), except for Layang-Layang with slightly less number of species than Tioman (58 vs. 60 species, respectively) (Fig. 1b). There was a general pattern of higher species richness per site in Sabah, East Malaysia than in Peninsular Malaysia and Layang-Layang (Fig. 1c). Sempona recorded the highest number of species per site (n = 55), but Kota Kinabalu had a higher average number of species per site (43 ± 6.2) as compared to Semporna (39 ± 7.1) and Kudat (39 ± 7.9). Layang-Layang had an average number of species per site that was comparable to Tioman and Redang (24 ± 7.2, 27 ± 4.3, and 30 ± 4.3, respectively). The sites in east Malaysia and Layang-Layang had a larger range in terms of number of species per site, whereas in Peninsular Malaysia the number of species per site were less variable (Fig. 1c).

Based on a comparison between our results and previous reports for east coast Peninsular Malaysia, the species list of the present study does not include ten species previously recorded from there (Huang et al. 2015): *Leptoseris gardineri*, *L. striata*, *L. yabei*, *Pavona bipartita*, *P. maldivensis*, *Pachyseris gemmae*, *Euphyllia fimbriata*, *E. paradivisa*, *E. paraglabrescens* and *Physogyra lichtensteini*. On the other hand, three new records were added for this area: *Leptoseris solida*, *Pavona minuta* and *Euphyllia cristata*.

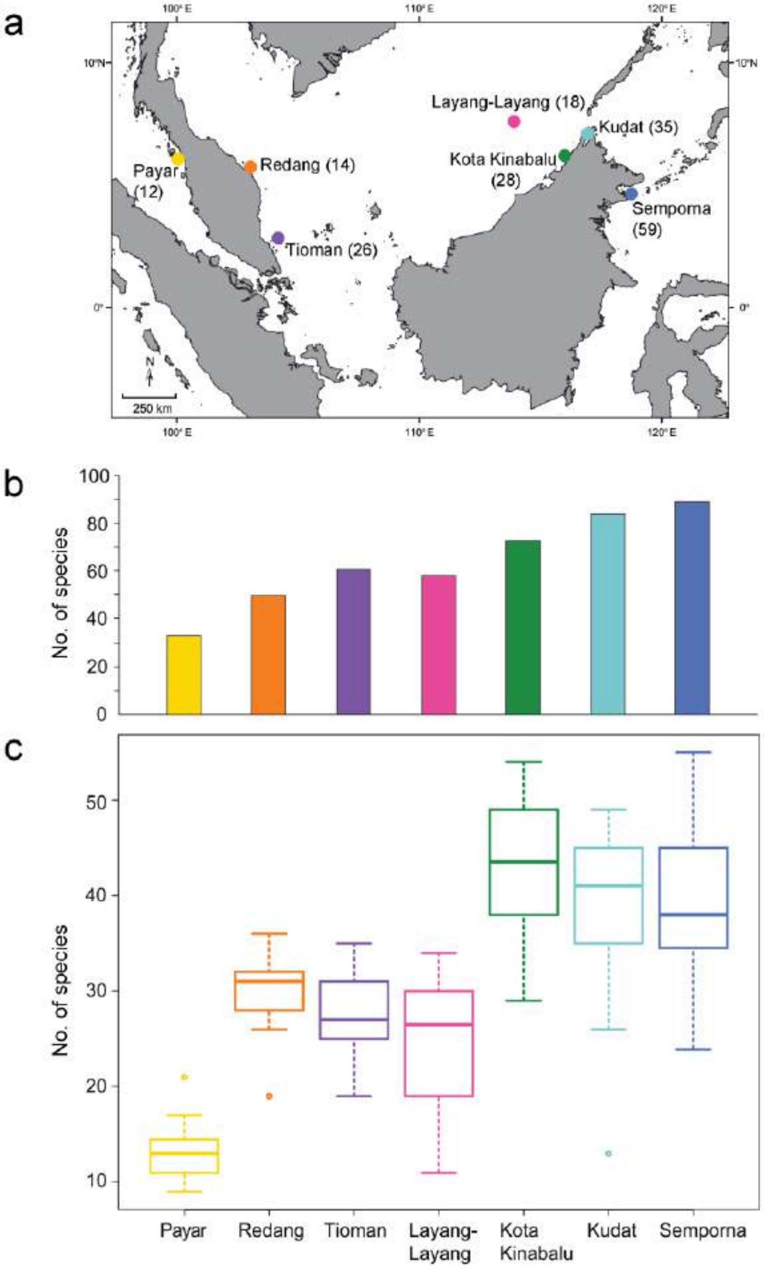


Fig. 1. a Map of the study area in Malaysia, with three localities in Peninsular Malaysia: Payar, Redang and Tioman, three localities in Sabah, East Malaysia: Kota Kinabalu, Kudat and Semporna, and Layang-Layang atoll in the Spratly Islands. The number in brackets represents the number of sites surveyed for each locality, **b** Gradient in total number of coral species from west to east Malaysia: Payar (33), Redang (50), Tioman (60), Layang-Layang (58), Kota Kinabalu (73), Kudat (83) and Semporna (89), **c** Range of coral species by sites at each locality.

Species accumulation curves level out for Semporna, Kudat and Kota Kinabalu indicating adequate sampling effort (Fig. 2). However, other localities may require additional sampling in order to ascertain that all species have been documented (see also Fig. S9).

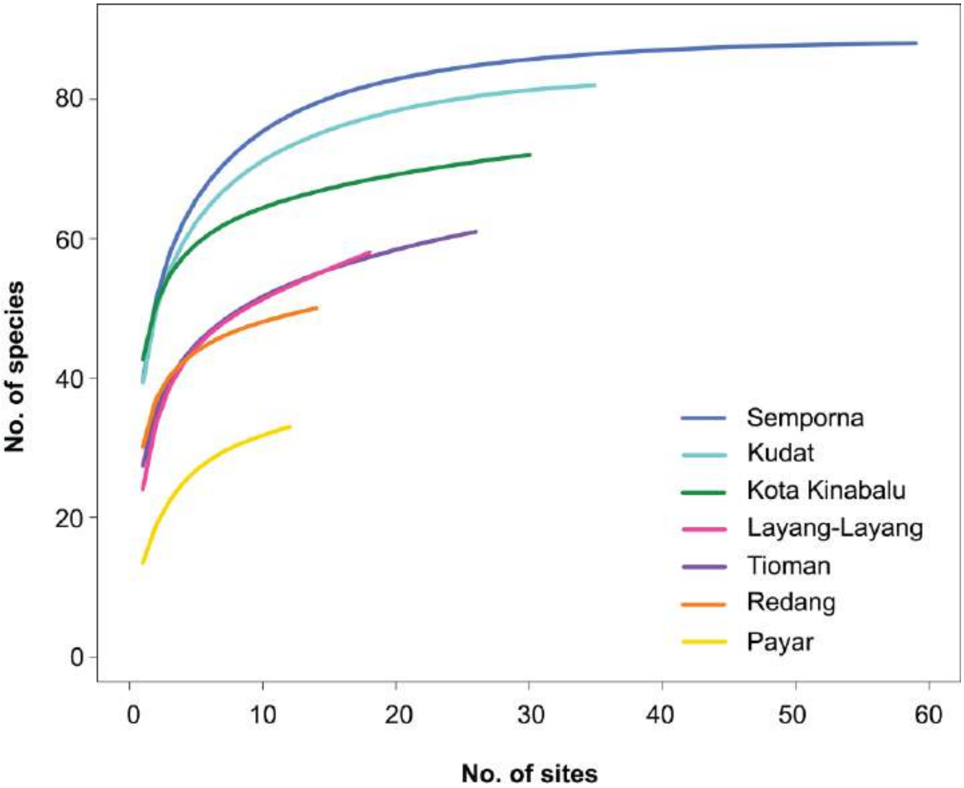
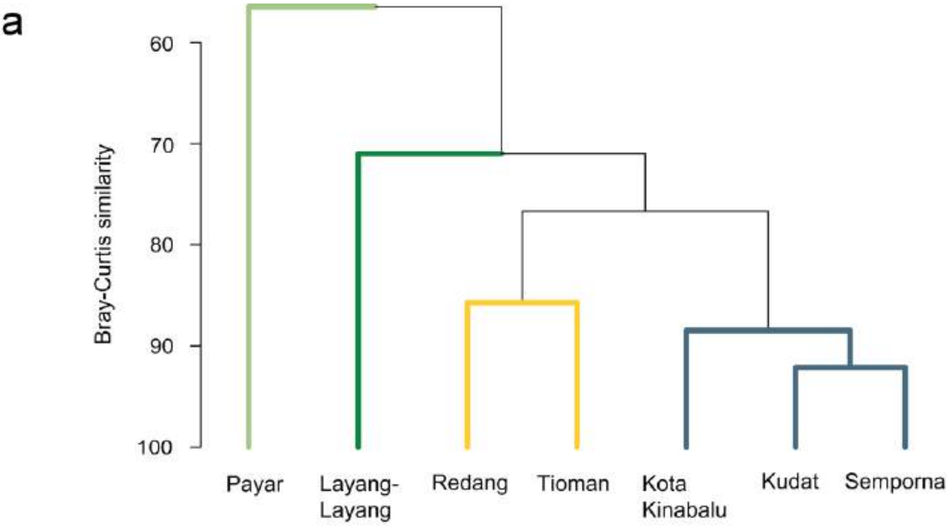


Fig. 2. Species accumulation curves of the seven localities indicate that for some localities, such as Layang-Layang, Tioman, Redang and Payar, additional sampling may be required.

Species richness patterns and structure

The cluster analysis of the seven localities across Malaysia identified four distinct groups ($p < 0.05$), with two significant clusters (Fig. 3a). Semporna, Kudat and Kota Kinabalu in north Borneo clustered together, whereas Tioman and Redang on the east coast of Peninsular Malaysia formed a group. The relatively species-poor Payar was most dissimilar from the rest of the localities (~56 similarity index). Layang-Layang stands alone most likely for the occurrence of endemic or rare species that were absent from neighbouring localities. Metric MDS ordination returned a similar pattern as the SIMPROF analysis with a good fit to the data (~0.86) (Fig. S10).



b

Spalding et al. (2007)	118	114	117	117	126	126	126
Veron et al. (2015)	-	3	4	4	4	7	7

Fig. 3. a Group-averaged hierarchical clustering dendrogram of coral species composition based on three coral families for seven reef localities in Malaysia, **b** Classification by marine ecoregions according to numbering by Spalding et al. (2007: Figure 3), and Veron et al. (2015: Figure 6).

There was a correlation between coral species richness and longitudinal gradients (Spearman's rho = 0.631, p = 0.001) indicating structure in coral species assemblages by localities. A comparison of the present species richness patterns with the definitions of marine ecoregions or boundaries sensu Spalding et al. (2007) and Veron et al. (2015) is visualised in Fig. 3b. The structuring of the present results based on the SIMPROF and ordination analyses was concordant with the demarcation of the four marine ecoregions by Spalding et al. (2007): 1) north Borneo (Semporna, Kudat and Kota Kinabalu, 2) Oceanic South China Sea islands (Layang-Layang), 3) Sunda Shelf/east coast Peninsular Malaysia (Tioman and Redang) and Strait of Malacca (Payar). The clustering differed with the one presented by Veron et al. (2015) in that Kota Kinabalu grouped together with Kudat and Semporna, and that Tioman and Redang were dissimilar from Kota Kinabalu.

Species distribution and geographic range limitation

Based on a listing of coral species by localities, various species (with positive identifications) appeared to be common and present in all localities, whereas other species were unique to certain areas (Table 2). Five coral species occurred exclusively in Semporna, three fungiids *Cantharellus jebbi*, *Cycloseris hexagonalis* and *Halomitra clavator*, one agariciid *Leptoseris amitoriensis*, and one euphylliid *Plerogyra diabolotus.* Regarding the latter, a closely resembling species has been noted from Kudat, Kota

Kinabalu and Tioman, which was labelled *Plerogyra* cf. *diabolotus*. Coral species occurring only in the Sulu Sea (Kudat and Semporna) were four fungiids *Cycloseris costulata*, *C. distorta*, *C. vaughani* and *Heliofungia fralinae*, and two euphylliids *Nemenzophyllia turbida*, and *Plerogyra cauliformis*. A closely resembling species to the latter observed from Kota Kinabalu was labelled as *Plerogyra* cf. *cauliformis.*

Despite being less diverse than the adjacent localities in the South China Sea and Sulu Sea, Layang-Layang harboured rare agariciid species, *Leptoseris kalayaanensis* and *L. troglodyta*. Three unidentified *Leptoseris* specimens were also encountered. In addition, *Pavona maldivensis*, a species with a wide distribution range (Chapter 5 and references therein) was only positively identified from Layang-Layang out of all sampled localities.

A species resembling but separate from the agariciid *Pavona explanulata* was collected from Redang (Chapter 5). Corals of this species (labelled as *Pavona* cf. *explanulata*) were also noted in Tioman and thus far only found in the east coast of Peninsular Malaysia. The mushroom coral *Podabacia kunzmanni* was only encountered in Payar, the Strait of Malacca, relatively close to Singapore and its type locality off West Sumatra (Hoeksema 2009).

Table 2. Coral species with widespread and restricted distribution range

Locality	**Species occurrence**
All localities	Fungiidae: *Ctenactis crassa*, *Danafungia scruposa*, *Fungia fungites*, *Herpolitha limax*, *Lithophyllon undulatum*, *Pleuractis granulosa*, *P. moluccensis*, *P. paumotensis*, *Polyphyllia talpina* Agariciidae: *Gardineroseris planulata, Leptoseris glabra*, *L. mycetoseroides*, *L. scabra*, *Pachyseris rugosa*, *P. speciosa*, *Pavona clavus*, *P. explanulata*, *P. varians*, *P. venosa* Euphylliidae: *Euphyllia glabrescens*
Semporna (Sulu Sea)	Fungiidae: *Cantharellus jebbi*, *Cycloseris hexagonalis*, *Halomitra clavator* Agariciidae: *Leptoseris amitoriensis* Euphylliidae: *Plerogyra diabolotus*
Kudat & Semporna (Sulu Sea)	Fungiidae: *Cycloseris costulata, C. distorta, C. vaughani, Heliofungia fralinae* Euphylliidae: *Nemenzophyllia turbida, Plerogyra cauliformis*
Kota Kinabalu, Kudat & Semporna (north Borneo)	Fungiidae: *Pleuractis taiwanensis* Agariciidae: *Leptoseris fragilis*, *L. gardineri*, *Pachyseris gemmae* Euphylliidae: *Euphyllia paradivisa*
Layang-Layang, Spratly Is.	Agariciidae: *Leptoseris kalayaanensis, L. troglodyta, Pavona maldivensis*
Tioman & Redang (East coast Peninsular Malaysia)	Agariciidae: *Pavona* cf. *explanulata*
Payar (Strait of Malacca)	Fungiidae: *Podabacia kunzmanni*

Discussion

Sampling effort varied by localities, but mostly proportional to the concentration of accessible coral reefs. However, the species accumulation curves indicate that data collection is not yet saturated for Layang-Layang and localities in Peninsular Malaysia. Indeed, the number of sites for Semporna are double to that of Kota Kinabalu and Tioman, but this is due to the high concentration of reefs and diverse habitat types around the Semporna peninsula and Darvel Bay. In contrast, reefs of Kota Kinabalu and Tioman displayed almost similar reef types, i.e. fringing, patch and several deep submerged reefs. For Layang-Layang and Redang, only the exposed reefs were visited (Chapter 5: Fig. 1 Fig. S1), both due to diving logistics. Additional surveys should be made in the lagoon of Layang-Layang atoll, and reefs in the north and west of Redang Is. (the latter on the leeward side of the island). As for the Payar group of islands, the sites appeared to be representative of the windward and leeward reef areas but additional surveys would indicate the completeness of the data collection.

Decreasing coral species richness from east to west Malaysia

It is well known that marine diversity decreases with increasing distance from the Coral Triangle (e.g. Hoeksema 2007; Barber 2009; Bellwood and Meyer 2009; Carpenter et al. 2011), as was also evident in the results of the present study with less model species on a small-scale longitudinal gradient. But the processes driving and maintaining the exceptional biodiversity in this region remain indefinite (e.g. Avise et al. 1987; Palumbi 1997; Barber and Bellwood 2005). It may be easy to explain for a latitudinal gradient in species diversity, e.g. decrease in temperature (Veron 1995; Chen 1999; Hoeksema 2015), whereas in longitudinal gradients, variation is driven by different factors. Several hypotheses have been proposed as explanatory models for the patterns of species richness decreasing from the centre of maximum marine biodiversity (reviewed in Hoeksema 2007; Bellwood et al. 2012). There is increasing consensus that most likely a combination of hypotheses may be at work to explain the patterns of species richness in the region (Halas and Winterbottom 2009; Cowman and Bellwood 2013) and that these hypotheses may not be mutually exclusive (Bellwood and Hughes 2001; Hoeksema 2007; Bellwood and Meyer 2009; Bowen et al. 2013; Briggs and Bowen 2013).

Several factors have been proposed as drivers to the distribution and species richness patterns of the Coral Triangle. These factors include geological history, habitat heterogeneity, and current circulation patterns, which then influences larval dispersal and reef connectivity (Hoeksema 2007, see also Keith et al. 2013). These factors are also not mutually exclusive, and can be applied to explain for the patterns in our results, as was also discussed by Huang et al. (2015) for the South China Sea.

Since the Pleistocene, coral reefs remained along the margin of the Sunda Shelf (Moolengraaff 1929; Umbgrove 1947). At the Last Glacial Maximum, approximately 17,000 before present (BP), the sea level was 120 m lower (Fairbanks 1989). West Borneo (present day Sarawak and west Kalimantan) was connected to Peninsular Malaysia (and the Southeast Asian mainland) and Sumatra, but Borneo was separate from Palawan and Sulawesi (Voris 2000). The reefs of north Borneo (presumably such as reefs of Semporna) were able to establish in the Sulu Sea as fringing reefs along steep slopes of the continental margin (Potts 1984), evidenced by fossil corals from north Borneo dating to the Oligocene in the Kinabatangan (McMonagle et al. 2011) and to the Early Miocene from East Kalimantan (Santodomingo et al. 2016). Large rivers draining into the South China Sea may have caused turbid and hyposaline conditions along the northwest coast of Borneo and hindered reef development (Molengraaff and Weber 1921). The Spratly Islands, which includes Layang-Layang, were once part of eastern Sundaland before rifting, but the reefs were able to build up and keep pace with subsidence up to present day (Hutchison and Vijayan 2010). The Sunda Shelf most likely became flooded 9,000–10,000 BP, hence present day coral reefs of the South China Sea over the shelf are possibly younger than 10,000 BP, and the sea only reached its present level approximately 5,000–6,000 BP (Hoeksema 2007). Moolengraaff (1922, 1929) hypothesized that the shelf is relatively species-poor in corals because recruitment is still ongoing as species are being dispersed from surrounding species-rich area. Nevertheless, Huang et al. (2015, 2016) have shown that the shelf is more diverse than previously thought, with Peninsular Malaysia scoring almost 400 coral species.

Circulatory patterns in the South China Sea, Sulu Sea and Strait of Malacca are influenced by the monsoonal system and the Pacific and Indian Ocean tides (Wyrtki 1961). Water from the western Pacific enters the South China Sea via the Luzon Strait, and the Sulu Sea via the Dipolog Strait. The South China Sea and the Sulu China Sea is connected through the Mindoro and Balabac straits. The current patterns reverses in direction between the northeast (NE: November–March) and southwest (SW: May–September) monsoons (see Chapter 7: Fig. 1) along the coastlines of Peninsular Malaysia and west Borneo (Wyrtki 1961; Saadon et al. 1999; Morton and Blackmore 2001; Xu and Malanotte-Rizzoli 2013), as well as between the South China Sea and Sulu Sea (Cai et al. 2005, 2008, 2009, Cai and He 2010). This seasonal reversing circulation pattern creates a complex system of eddies and gyres in the South China Sea (Qu 2000; Morton and Blackmore 2001; Camerlengo and Demmler 2007; Liu et al. 2008; Tangang et al. 2011; Xu and Malanotte-Rizzoli 2013), and the Sulu Sea (Cai et al. 2008), which could aid in retaining or dispersing larvae, thereby facilitating connectivity across the reef systems and influencing the composition and range expansion of coral species (McManus 1994). The Strait of Malacca receives water mass from the South China Sea (NE) and the Java Sea (SW) (Rizal et al. 2012), with a prevalent northwest flow into the Andaman Sea (Wrytki 1961; Rizal et al. 2010; but see Chen et al. 2014).

Habitat availability and heterogeneity is vital in shaping species richness and community structure (Done 1982; Best et al. 1989; Veron 1995; Cornell and Karlson 1996, 2000; Cleary et al. 2005; Sanciango et al. 2013). There was a gradient in species richness of our localities on a longitudinal scale, but this pattern was not consistent evidenced by Layang-Layang having less number of species than Tioman. This is most likely reflected by the homogenous habitat of the atoll. This was also noticeable for the oceanic island of Sipadan, with less number of species than nearby fringing reefs of Semporna (Chapter 2). There was also compositional differences among the sites of each locality and across the localities, which is strongly influenced by habitat diversity, coupled with other localised factors such as current patterns (see Wood et al. 2014), competition and disturbance (Cornell and Karlson 2000). Compositional variability and gradients along longitudinal scales have also been reported by others (e.g. Ekman 1953; Rosen 1988; Paulay 1997, Huang et al. 2015).

The clustering of the seven localities in the present study follows the marine ecoregion delineation of Spalding et al. (2007). Each ecoregion is deemed to have similar species composition, influenced by evolutionary history and patterns of dispersal and isolation, shaped by ecosystems of similar oceanographic factors or topographic features, which can be differentiated from adjacent systems (Spalding et al. 2007). However, our localities are constrained to the boundaries of Malaysia and our data do not represent the areal span of each ecoregion. Nevertheless, from the perspective of Malaysia, there are four distinct ecoregions. In the following sections, these ecoregions are discussed in terms of environmental heterogeneity or other local factors, with notes on coral species showing limited geographical ranges.

East side story – Semporna, Kudat and Kota Kinabalu

At the eastern end of Malaysia (Sabah), situated well within the Coral Triangle region, the Semporna peninsula and the adjacent Darvel Bay harboured the highest number of coral species among all localities. The reefs here are among the deepest in our research area. Semporna is unique because it has high habitat heterogeneity, containing various geomorphological reef types, from deep offshore barrier reefs and an oceanic island to shallow fringing and turbid nearshore reefs (Wood 1987, 1994), creating habitat diversity that can cater for high diversity of coral species with varied habitat preferences (Chapter 2). Darvel Bay with its turbid reef conditions contained unusual species. Ditlev (2003) hypothesized that some species in the bay are relicts or “local specialist” that have adapted to the bay’s conditions and would not be able to survive in more open conditions, and thus have not spread to other localities. Darvel Bay appears to share similar characteristics as reefs in the Kutai Basin in East Kalimantan. According to Santodomingo et al. (2016), the regime of turbid conditions with high coral species richness have been present since the Miocene in the Kutai Basin. Turbid reef habitats may have played a key role in the early diversification in the Coral Triangle, whereby corals that lived under this condition may have emerged to be more resilient to environmental changes (Santodomingo et al. 2016).

Rare species include the euphylliid *Plerogyra diabolotus*, collected by Ditlev (2003) from several islands in Semporna and Darvel Bay. We observed this species mostly from the latter, but we noted a rather similar looking species in Kudat, Tioman and Redang with polyps in the shape of ear-like lobe, though with not much of a “pointed outgrowth resembling a devil’s ear” (see Ditlev 2003). Based on an account by Fenner (2014), *P. diabolotus* has been observed in Chagos, which is the first record outside of Borneo. Ditlev (2003) remarked on a Red Sea *Plerogyra*, which is close to *P. diabolotus* in terms of skeletal details, but with less elaborate polyp development. This description fits our *Plerogyra* cf. *diabolotus* specimens though we are unable to confirm this without images of the Red Sea *Plerogyra* and the coral specimens. Another rare species is the agariciid

Leptoseris amitoriensis, which was observed at only two sites (< 20 m depth), both within the Tun Sakaran Marine Park. This species was first reported from deep waters of Iriomote Is. in the Ryukyu Islands, Japan (Veron 1990) and it has been found in eastern Indonesia, the Philippines and part of the South China Sea (Veron 2000).

At the more westward localities of Kudat and Kota Kinabalu, the number of coral species is slightly less. The reefs of both localities are situated on shallower seafloor as compared to Semporna. Reef depth and exposure were important in structuring the coral species richness, whereby sites that were deep and exposed (to dominant wind directions) were most species-rich (Chapter 3 and 4). There was more habitat diversity in Kudat as compared to Kota Kinabalu (deep channels, gentle slopes, exposed to very strong wave action, near mangroves, and shallow, sheltered and turbid bay) but some reefs were unexplored due to the presence and known habitats of saltwater crocodiles (*Crocodylus porosus*), or due to bad weather during the data collection (Chapter 3). Despite the decrease in total species richness, the average number of species per site was high in Kota Kinabalu. The reef environment is rather similar among the sites (similarity index ~80), and there was more exposed and deep sites rather than sheltered and shallow sites, which maintained a high number of species at each site (Chapter 4).

Some species did not occur westwards from Kudat, such as *Nemenzophyllia turbida* and *Plerogyra cauliformis*, which were first described from the Cebu Strait (Hodgson and Ross 1982) and the adjacent Sulu Sea (Ditlev 2003), respectively. For the former, its geographic range has been reported to be throughout the central Indo-Pacific, but excluding the east coast of Peninsular Malaysia (Turak et al. 2008b). This species was not observed in the Strait of Malacca, even though the reefs of Payar fit the habitat preference of this species, and that is turbid or sheltered environments. Previously only found in east Sabah, *P. cauliformis* and *P. multilobata* have been reported from northern Palawan (Huang et al. 2016). Few species did not occur westwards from Kota Kinabalu, such as *Leptoseris gardineri* and *Euphyllia paradivisa*, but both have been reported from the east coast of Peninsular Malaysia (Affendi and Rosman 2012). Based on known geographic ranges, *L. gardineri* is widely distributed across the Indo-Pacific from the northern Indian Ocean to the oceanic West Pacific including Eastern Australia (Veron 2000). *Euphyllia paradivisa* is widespread in the Indo-Pacific (Veron 2000; Turak et al. 2008a), including the Gulf of Eilat/Aqaba (Eyal et al. 2016).

Layang-Layang

Reefs of the Spratly Islands are distinct in species richness and composition from the adjacent reef areas (Huang et al. 2015). The vertical reefs of the Layang-Layang atoll plunge to depths of 1,500 m (Hutchison and Vijayan 2010). Such oceanic conditions lack environmental heterogeneity to accommodate a wide range of coral species, especially those with preference for slopes or shallow environments, e.g. *Pavona cactus* and *P. decussata*, and they are hostile for free-living mushroom corals (Hoeksema and Moka 1989). However, a few coral species here were absent from reefs elsewhere in our study area, particularly the agariciids, which are known to be deep reef dwellers (Kahng and Maragos 2006; Kahng et al. 2007, 2010; Rooney et al. 2010; Dinesen et al. 2012; Luck et al. 2013; Hoeksema et al. 2016), such as *Leptoseris kalayaanensis* and *L. troglodyta*, and from oceanic conditions, *Pavona maldivensis* (Chapter 5). At the time of our data collection, reefs of Layang-Layang were recovering from a serious crown-of-thorns (COT) seastar outbreak in 2010 (Nasrulhakim et al. 2010). A high frequency of coral recruits and juveniles were encountered, which made identification of several corals difficult. A few species that were present at the atoll prior to the outbreak were not found during our surveys (Chapter 5). Consequently, the total species richness may be higher than reported, and the reefs should be revisited for further observations in the near future.

West side story – Tioman, Redang and Payar

The present results show a decrease in species richness from east to west Malaysia for the three model families, but total diversity of reef corals for the east coast of Peninsular Malaysia exceeds that of west coast Sabah, and is comparable with some of the most diverse localities in the South China Sea (Huang et al. 2015). Harborne et al. (2000) reported fewer species but with high number of species per site in Redang, consistent with our results. Geomorphology of reefs along the east coast of Peninsular Malaysia is rather consistent: shallow and fringing reefs bordering islands, with a somewhat similar reef zonation pattern, but with some habitat diversity that results in species diversity (Harbourne et al. 2000). Ng et al. (1999) remarked that the flora and fauna taxa of Tioman resembled that of Borneo rather than Peninsular Malaysia, suggesting that Tioman was likely connected with both land-masses during the Last Glacial Maximum (Stubbs 1961; Ng 1988; Kottelat 1990).

Although the reef of Payar is dissimilar from the rest of the localities (similarity index ~56), the results under this section are discussed together with those of the other Peninsular Malaysia reefs. Coral diversity is lower in the west coast of the peninsula compared to the east coast (Harborne et al. 2007; Toda et al. 2007), due to turbid conditions and muddy bottom substrates (Chua and Charles 1980) caused by heavy sedimentation (Chua and Ross 2002). The accumulation of settling particles showed similar results, with average accumulation rates of 49.8 mg/cm^2/day on the west coast reefs (1–3 m depth) versus 3.5 mg/cm^2/day on the east coast reefs (1–12 m depth) (Lee and Mohamed 2011). Many rivers along the east coast of Sumatra and west coast of Peninsular Malaysia transport tons of sediment into the strait (Soegiarto 2000) bringing along silt and other particulate matter (Chua et al. 2007), which inhibits reef development.

Purely by observation, there were subtle differences in the morphology of some agariciid species in comparison to their counterparts in the east, but not so much that these corals were unrecognisable. Indeed, intraspecific phenotypic variation and coral plasticity are well known among scleractinians, depending on differences in sedimentation and light penetration with increasing depth and distance offshore (Hoeksema 1993b; Gittenberger and Hoeksema 2006; Todd 2008). On the contrary, the morphology of some species appears to show little geographic variation across the seas.

Only two coral species were unique to Peninsular Malaysia: *Pavona* cf. *explanulata* at Tioman and Redang, and *Podabacia kunzmanni* only at Payar. There is a strong possibility that the former may be present in reefs elsewhere, but not recognised as distinct from *P. explanulata*. The latter has only been reported from Western Indonesia and Singapore, usually from dead corals and rubble areas (Hoeksema 2009; Hoeksema and Koh 2009). We confirm that the distribution of this species extends to the Strait of Malacca.

Conservation implications

Classification of coral reef areas (and other adjacent ecosystems) by regions can be a useful tool for conservation and management planning (Spalding et al. 2007). Based on our analysis by using three reef coral families as model taxa, the coral reefs of Malaysia can be divided into four groupings, similar with the ecoregion classification of Spalding et al. (2007). The cluster of sites with the highest species richness include Semporna, Kudat and Kota Kinabalu, which suggest that the northwestern boundary of the Coral Triangle should be extended westward to include Kota Kinabalu and the west coast of north Borneo. Future studies should include other reef coral families in order to verify this classification pattern.

Undoubtedly, species richness is not the only important factor for consideration in conservation planning. Other components of biodiversity should also be considered (United Nations 1992), including endemic or rare species either in terms of abundance or distribution range, and phylogenetic diversity (Huang 2012; Selig et al. 2014; Winter et al. 2013; Curnick et al. 2015; Huang et al. 2016; Mouillot et al. 2016). Genetic information and biophysical models are important for conservation prioritisation as both can provide insights to population connectivity and potential dispersal barriers (e.g. Kool et al. 2011; Dorman et al. 2014; Beger et al. 2014; von der Heyden et al. 2014; Wood et al. 2014; Juinio-Menez 2015).

Data collection of the present study was carried out within marine park areas, except for Layang-Layang and several sites in Semporna. The gazettement of the proposed Tun Mustapa Park in Kudat was made in May 2016, and launched in July 2016. Layang-Layang in the Spratly Islands, which is a small part of the fourth ecoregion, remains unprotected. Reefs of Layang-Layang, Tioman, Redang and Payar should be revisited in order to verify that the current species list is representative of the reefs in the respective localities. Additional sites should be surveyed in the Strait of Malacca and the east coast of Peninsular Malaysia. Very little data is available on the reefs of Sarawak (e.g. reefs off Kuching and Miri, Sarawak), and information of the coral species richness would be important to get a complete picture of the richness patterns and reef connectivity across Malaysia.

Acknowledgments

Permit for research in Malaysia was granted to ZW by the Economic Planning Unit of the Prime Minister's Department, Malaysia (UPE: 40/200/19/2642). Additional permits for data collection were granted by various departments: Sabah Parks and the Sabah Biodiversity Council for marine parks in Sabah, the National Security Council of the Prime Minister's Department for Sipadan Island and Layang-Layang Island, and the Department of Marine Parks Malaysia for marine parks in Peninsular Malaysia. Fieldwork in Semporna was during the Semporna Marine Ecological Expedition (SMEE) 2010, whereas in Kudat during the Tun Mustapha Park Expedition (TMPE) 2012. Both expeditions were co-organised by WWF-Malaysia, Universiti Malaysia Sabah and Naturalis Biodiversity Centre, The Netherlands (and University Malaya for SMEE 2010). Travel expenses for ZW was funded by the A.M. Buitendijkfonds and Treub-Maatschappij, the Society for the Advancement of Research in the Tropics, The Netherlands for fieldwork in Layang-Layang and Peninsular Malaysia, respectively. We are grateful to the various dive operators, dive masters and crew for diving logistics throughout this research: Avillion Layang-Layang, East Marine Holidays Sdn Bhd, Tioman Dive Centre, East Divers Tioman and Redang Kalong Resort. We highly appreciate the comments and suggestions from Nadia Santodomingo and Liew Thor Seng in the onset of the manuscript.

Supporting Information

Table S1. Species absence/presence of hard coral families Fungiidae, Agariciidae and Euphylliidae from seven localities in Malaysia. Locality abbreviation: SEM = Semporna, TMP = Kudat, KK = Kota Kinabalu, LAC = Layang-Layang, TI) = Tioman, RED = Redang, PAY = Payar. Figures (Fig. No.) correspond with photo Fig.s in the present chapter, or figures in other chapters of this thesis. Species marked with asterisk (*) are now considered *incertae sedis*.

No.	Species	SEM	TMP	KK	LAC	TIO	RED	PAY	Total	Fig. No.
	Fungiidae									
1	*Cantherellus jebbi* Hoeksema, 1993	1	0	0	0	0	0	0	1	Fig. S2a
2	*Ctenactis albitentaculata* Hoeksema, 1989	1	1	1	1	1	0	0	5	Chapter 5 Fig. 2a
3	*Ctenactis crassa* (Dana, 1846)	1	1	1	1	1	1	1	7	Fig. S2b
4	*Ctenactis echinata* (Pallas, 1766)	1	1	1	1	1	1	0	6	Fig. S2c
5	*Cycloseris boschmai* Hoeksema, 2014	1	1	1	1	0	0	0	4	Chapter 5 Fig. 2b
6	*Cycloseris costulata* (Ortmann, 1889)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 2c
7	*Cycloseris curvata* (Hoeksema, 1989)	1	1	0	0	0	0	0	2	Fig. S2d
8	*Cycloseris cyclolites* (Lamarck, 1815)	1	1	1	1	0	0	0	4	Fig. S2e
9	*Cycloseris distorta* (Michelin, 1842)	1	1	0	0	0	0	0	2	Fig. S2f
10	*Cycloseris fragilis* (Alcock, 1893)	1	1	1	0	1	1	0	5	Fig. S2g
11	*Cycloseris hexagonalis* (Milne Edwards and Haime, 1851)	1	0	0	0	0	0	0	1	Fig. S2h
12	*Cycloseris mokai* (Hoeksema, 1989)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 2e
13	*Cycloseris sinensis* Milne Edwards and Haime, 1851	1	1	1	1	1	1	0	6	Fig. S3a
14	*Cycloseris somervillei* (Gardiner, 1909)	1	1	1	0	0	1	0	4	Fig. S3b
15	*Cycloseris tenuis* (Dana, 1846)	1	1	1	1	0	0	0	4	Chapter 5 Fig. 2f
16	*Cycloseris vaughani* (Boschma, 1923)	1	1	0	0	0	0	0	2	Fig. S3c
17	*Danafungia horrida* (Dana, 1846)	1	1	1	1	1	0	1	6	Chapter 5 Fig. 2g
18	*Danafungia scruposa* (Klunzinger, 1879)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 2h
19	*Fungia fungites* (Linnaeus, 1758)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 3a
20	*Halomitra clavator* Hoeksema, 1989	1	0	0	0	0	0	0	1	Fig. S3d
21	*Halomitra pileus* (Linnaeus, 1758)	1	1	1	1	0	0	0	4	Chapter 5 Fig. 3b
22	*Heliofungia actiniformis* (Quoy and Gaimard, 1833)	1	1	1	0	1	0	0	4	Fig. S3e
23	*Heliofungia fralinae* (Nemenzo, 1955)	1	1	0	0	0	0	0	2	Fig. S3f
24	*Herpolitha limax* (Esper, 1797)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 3c

Table S1 cont.

25	*Lithophyllon concinna* *(Verrill, 1864)*	1	1	1	1	1	1	0	6	Fig. S3g
26	*Lithophyllon ranjithi* *Ditlev, 2003*	1	1	0	1	0	0	0	3	Chapter 5 Fig. 3d
27	*Lithophyllon repanda* (Dana, 1846)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 3e
28	*Lithophyllon scabra* (Döderlein, 1901)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 3f
29	*Lithophyllon spinifer* (Claereboudt and Hoeksema, 1987)	1	1	1	0	1	0	0	4	Fig. S3h
30	*Lithophyllon undulatum* Rehberg, 1892	1	1	1	1	1	1	1	7	Chapter 5 Fig. 3g
31	*Lobactis scutaria* (Lamarck, 1801)	1	1	1	1	0	0	0	4	Chapter 5 Fig. 3h
32	*Pleuractis granulosa* (Klunzinger, 1879)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 4a
33	*Pleuractis gravis* (Nemenzo, 1955)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 4b
34	*Pleuractis moluccensis* (Van der Horst, 1919)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 4c
35	*Pleuractis paumotensis* (Stutchbury, 1833)	1	1	1	1	1	1	1	7	Fig. S4a
36	*Pleuractis taiwanensis* (Hoeksema and Dai, 1991)	1	1	1	0	0	0	0	3	Fig. S4b
37	*Podabacia crustacea* (Pallas, 1766)	1	1	1	0	1	1	0	5	Fig. S4c
38	*Podabacia kunzmanni* Hoeksema, 2009	0	0	0	0	0	0	1	1	Fig. S4d
39	*Podabacia motuporensis* Veron, 1990	1	1	1	1	1	1	0	6	Fig. S4e
40	*Podabacia sinai* Veron, 2000	1	0	1	1	0	0	0	3	Chapter 5 Fig. 4d
41	*Polyphyllia talpina* (Lamarck, 1801)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 4e
42	*Sandalolitha boucheti* Hoeksema, 2012	1	1	0	1	0	0	0	3	Chapter 5 Fig. 4f
43	*Sandalolitha dentata* Quelch, 1884	1	1	1	1	1	1	0	6	Chapter 5 Fig. 4g
44	*Sandalolitha robusta* (Quelch, 1886)	1	1	1	1	1	1	0	6	Chapter 5 Fig. 4h
45	*Zoopilus echinatus* Dana, 1846	1	0	1	0	0	0	0	2	Fig. S4f
	Agariciidae									
46	*Coeloseris mayeri* Vaughan, 1918*	1	1	1	1	0	0	1	5	Chapter 5 Fig. 5a
47	*Gardineroseris planulata* (Dana, 1846)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 5b
48	*Leptoseris amitoriensis* Veron, 1990	1	0	0	0	0	0	0	1	Fig. S5a
49	*Leptoseris foliosa* Dinesen, 1980	1	1	1	1	1	0	0	5	Chapter 5 Fig. 5c
50	*Leptoseris fragilis* Milne Edwards and Haime, 1849	1	1	1	0	0	0	0	3	Fig. S5b
51	*Leptoseris gardineri* Van der Horst, 1921	1	1	1	0	0	0	0	3	Fig. S5c
52	*Leptoseris glabra* Dinesen, 1980	1	1	1	1	1	1	1	7	Chapter 5 Fig. 5d
53	*Leptoseris hawaiiensis* Vaughan, 1907	1	1	1	1	1	0	1	6	Chapter 5 Fig. 5e

Table S1 cont.

54	*Leptoseris incrustans* *(Quelch, 1886)*	1	1	1	1	0	1	0	5	Chapter 5 Fig. 5f
55	*Leptoseris kalayaanensis* *Licuanan and Aliño, 2009*	0	0	0	1	0	0	0	1	Chapter 5 Fig. 5g
56	*Leptoseris mycetoseroides* Wells, 1954	1	1	1	1	1	1	1	7	Chapter 5 Fig. 5h
57	*Leptoseris* cf. *mycetoseroides*	0	0	0	0	0	0	1	1	Fig. S5d
58	*Leptoseris.papyracea* (Dana, 1846)	1	1	1	0	1	1	0	5	Fig. S5e
59	*Leptoseris scabra* Vaughan, 1907	1	1	1	1	1	1	1	7	Chapter 5 Fig. 6a
60	*Leptoseris solida* (Quelch, 1886)	1	1	0	1	1	1	0	5	Chapter 5 Fig. 6b
61	*Leptoseris* cf. *solida*	0	0	1	0	0	1	0	2	Fig. S5f
62	*Leptoseris troglodyta* Hoeksema, 2012	0	0	0	1	0	0	0	1	Chapter 5 Fig. 6c
63	*Leptoseris tubulifera* Vaughan, 1907	1	1	1	0	1	1	0	5	Fig. S5g,h
64	*Leptoseris yabei* (Pillai and Sheer, 1976)	1	1	1	1	0	0	0	4	Chapter 5 Fig. 6d
65	*Leptoseris* sp. 1	0	0	0	1	0	0	0	1	Chapter 5 Fig. 9a
66	*Leptoseris* sp. 2	0	0	0	1	0	0	0	1	Chapter 5 Fig. 9b
67	*Leptoseris* sp. 3	0	0	0	1	0	0	0	1	Chapter 5 Fig. 9c
68	*Pachyseris foliosa* Veron, 1990*	1	1	0	0	1	0	0	3	Fig. S6a
69	*Pachyseris gemmae* Nemenzo, 1955*	1	1	1	0	0	0	0	3	Fig. S6b
70	*Pachyseris rugosa* (Lamarck, 1801)*	1	1	1	1	1	1	1	7	Chapter 5 Fig. 6e
71	*Pacyhseris speciosa* (Dana, 1846)*	1	1	1	1	1	1	1	7	Chapter 5 Fig. 6f
72	*Pavona bipartita* Nemenzo, 1979	1	1	0	1	0	0	0	3	Chapter 5 Fig. 6g
73	*Pavona cactus* (Forskål, 1775)	1	1	1	0	1	1	0	5	Fig. S6c
74	*Pavona clavus* (Dana, 1846)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 6h
75	*Pavona danai* Milne Edwards, 1860	1	1	0	0	1	0	1	4	Fig. S6d
76	*Pavona decussata* (Dana, 1846)	1	1	1	0	1	1	1	6	Fig. S6e
77	*Pavona duerdeni* Vaughan, 1907	1	1	0	1	1	0	1	5	Chapter 5 Fig. 7a
78	*Pavona explanulata* (Lamarck, 1816)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 7b
79	*Pavona* cf. *explanulata*	0	0	0	0	1	1	0	2	Chapter 5 Fig. 11
80	*Pavona frondifera* (Lamarck, 1816)	1	1	1	0	1	1	1	6	Fig. S6f
81	*Pavona* cf. *frondifera*	0	0	0	0	1	0	1	2	Fig. S6g
82	*Pavona maldivensis* (Gardiner, 1905)	0	0	0	1	0	0	0	1	Chapter 5 Fig. 7c
83	*Pavona minuta* Wells, 1954	1	0	1	1	1	0	0	4	Chapter 5 Fig. 7d
84	*Pavona varians* Verrill, 1864	1	1	1	1	1	1	1	7	Chapter 5 Fig. 7e
85	*Pavona venosa* (Ehrenberg, 1834)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 7f

Table S1 cont.

86	*Pavona cf. venosa*	0	0	0	0	1	0	0	1	Fig. S6h
87	*Pavona sp. 1*	0	1	1	0	1	1	1	5	Chapter 3 S9 Fig.
88	*Pavona* sp. 2	0	1	0	0	0	0	0	1	Chapter 3 S9 Fig.
	Euphylliidae									
89	*Catalaphyllia jardinei* (Saville-Kent, 1893)	1	1	1	0	1	1	0	5	Fig. S7a
90	*Euphyllia ancora* Veron and Pichon, 1980	1	1	1	0	1	1	0	5	Fig. S7b
91	*Euphyllia cristata* Chevalier, 1971	1	1	1	0	1	1	0	5	Fig. S7c
92	*Euphyllia divisa* Veron and Pichon, 1980	1	1	1	0	1	1	0	5	Fig. S7d
93	*Euphyllia glabrescens* (Chamisso and Eysenhardt, 1821)	1	1	1	1	1	1	1	7	Chapter 5 Fig. 8a
94	*Euphyllia paraancora* Veron, 1990	1	1	1	1	0	0	0	4	Chapter 5 Fig. 8b
95	*Euphyllia paradivisa* Veron and Pichon, 1980	1	1	1	0	0	0	0	3	Fig. S7e,f
96	*Euphyllia yaeyamaensis* (Shirai, 1980)	1	1	1	0	1	0	0	4	Fig. S7g
97	*Nemenzophyllia turbida* Hodgson and Ross, 1982*	1	1	0	0	0	0	0	2	Fig. S7h
98	*Physogyra lichtensteini* (Milne Edwards and Haime, 1851)*	1	1	1	1	0	0	1	6	Chapter 5 Fig. 8c
99	*Plerogyra cauliformis* Ditlev, 2003*	1	1	0	0	0	0	0	2	Fig. S8a
100	*Plerogyra* cf. *cauliformis*	0	1	0	0	0	0	0	1	Fig. S8b
101	*Plerogyra diabolotus* Ditlev, 2003*	1	0	0	0	0	0	0	1	Fig. S8c
102	*Plerogyra* cf. *diabolotus*	0	1	0	0	1	1	0	3	Fig. S8d
103	*Plerogyra multilobata* Ditlev, 2003*	1	0	1	0	0	0	0	2	Fig. S8e
104	*Plerogyra* cf. *multilobata*	0	1	0	0	0	0	0	1	Fig. S8f
105	*Plerogyra simplex* Rehberg, 1892*	1	0	1	0	0	0	0	2	Fig. S8g
106	*Plerogyra sinuosa* (Dana, 1846)*	1	1	1	0	1	1	1	6	Fig. S8h

Fig. S1. Sites at Peninsular Malaysia (E-W: Tioman, Redang and Payar group of islands)

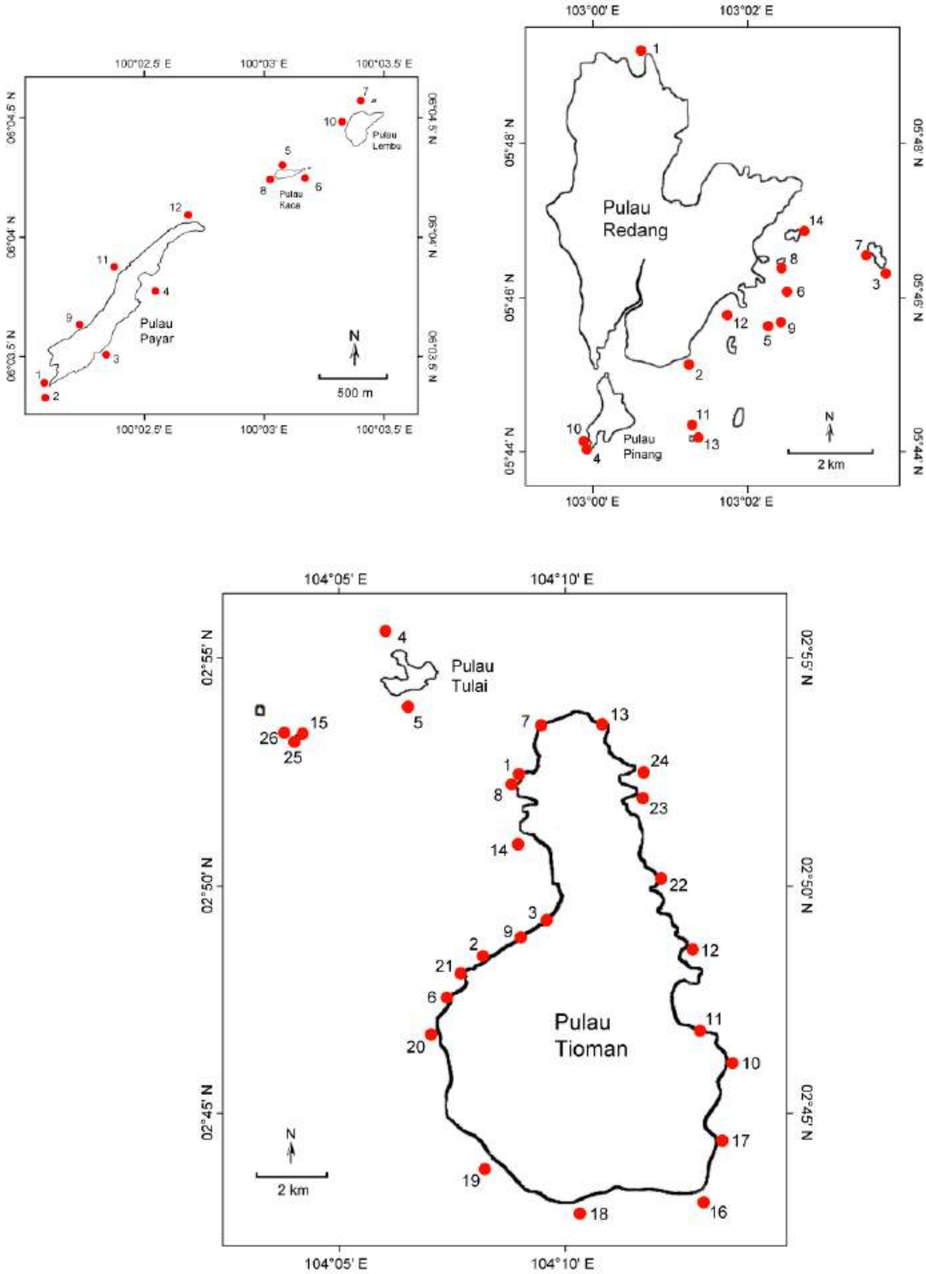


Fig. S2. Fungiidae recorded from this study. **a** *Cantherellus jebbi* **b** *Ctenactis crassa* **c** *C. echinata* **d** *Cycloseris curvata* **e** *C. cyclolites* **f** *C. distorta* **g** *C. fragilis* **h** *C. hexagonalis*.

Fig. S3. Fungiidae recorded from this study. **a** *Cycloseris sinensis* **b** *C. somervillei* **c** *C. vaughani* **d** *Halomitra clavator* **e** *Heliofungia actiniformis* **f** *H. fralinae* **g** *Lithophyllon concinna* **h** *L. spinifer*.

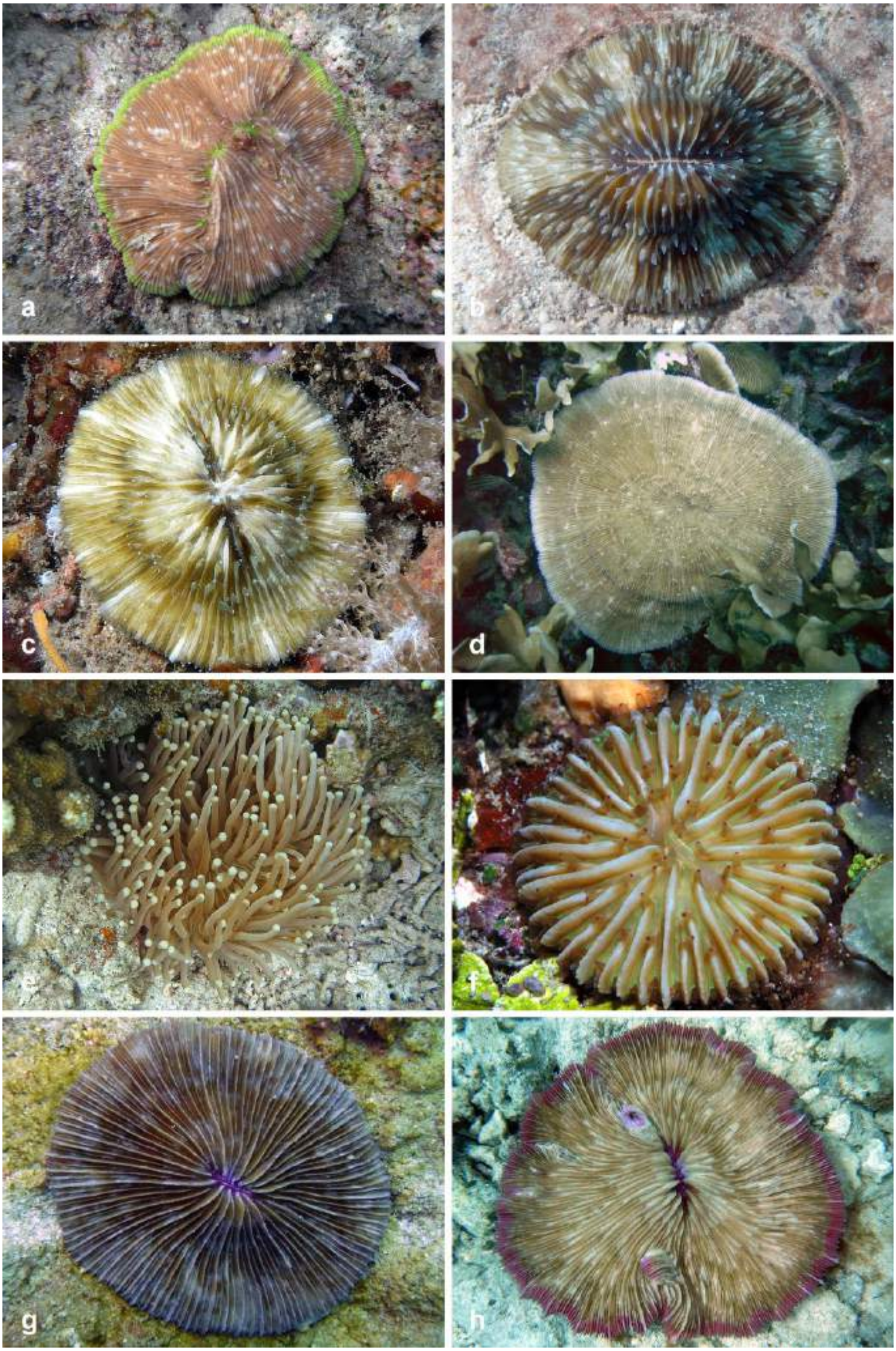


Fig. S4. Fungiidae recorded from this study. **a** *Pleuractis paumotensis* **b** *P. taiwanensis* **c** *Podabacia crustacea* **d** *P. kunzmanni* **e** *P. motuporensis* **f** *Zoopilus echinatus*.

Fig. S5. Agariciidae recorded from this study. **a** *Leptoseris amitoriensis* **b** *L. fragilis* **c** *L. gardineri* **d** *Leptoseris* cf. *mycetoseroides* **e** *L. papyracea* **f** *Leptoseris* cf. *solida* **g–h** variation of *L. tubulifera*.

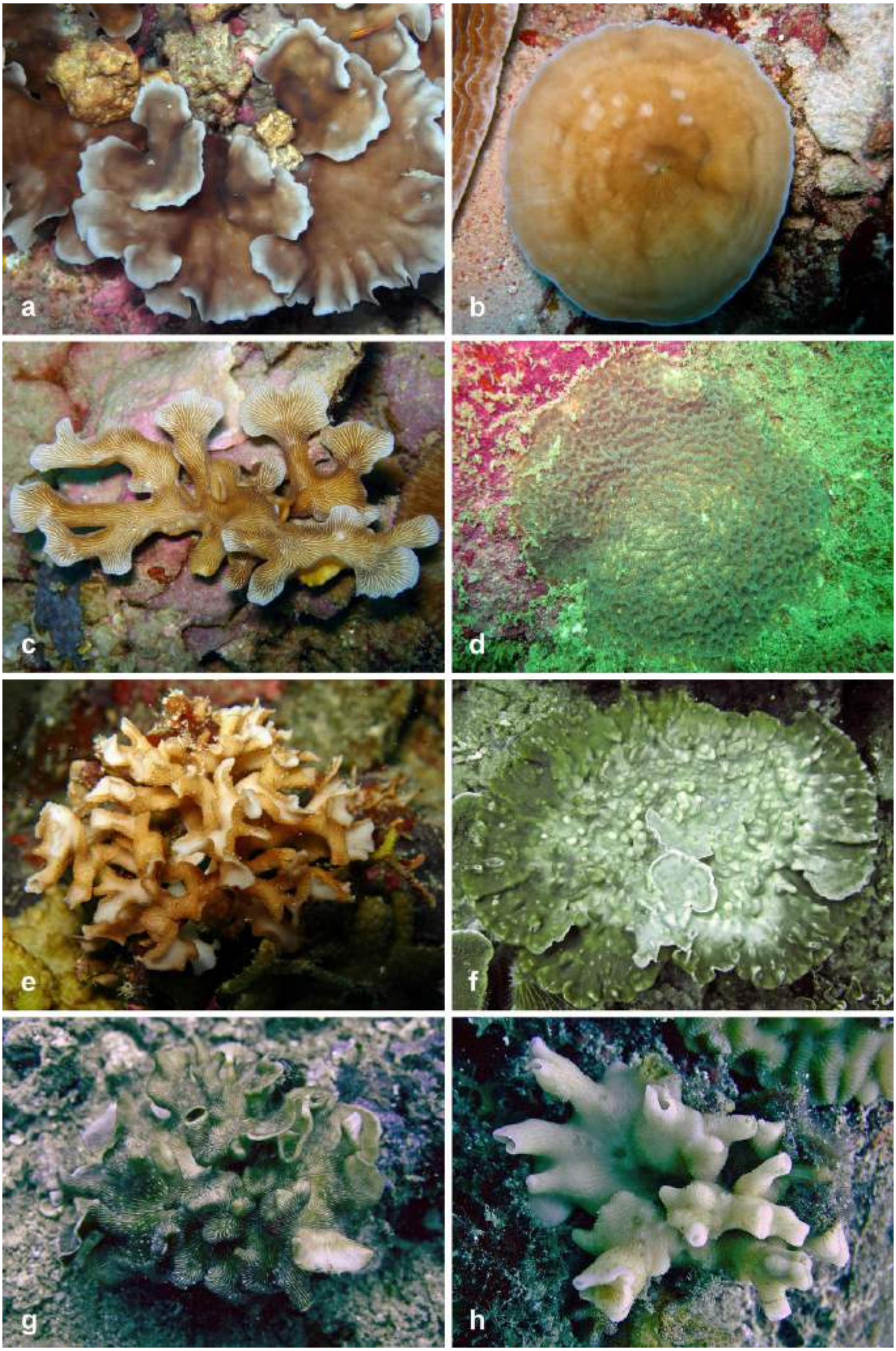


Fig. S6. Agariciidae recorded from this study. **a** *Pachyseris foliosa* **b** *P. gemmae* **c** *Pavona cactus* **d** *P.danai* **e** *P. decussata* **f** *P. frondifera* **g** *Pavona* cf. *frondifera* **h** *Pavona* cf. *venosa*.

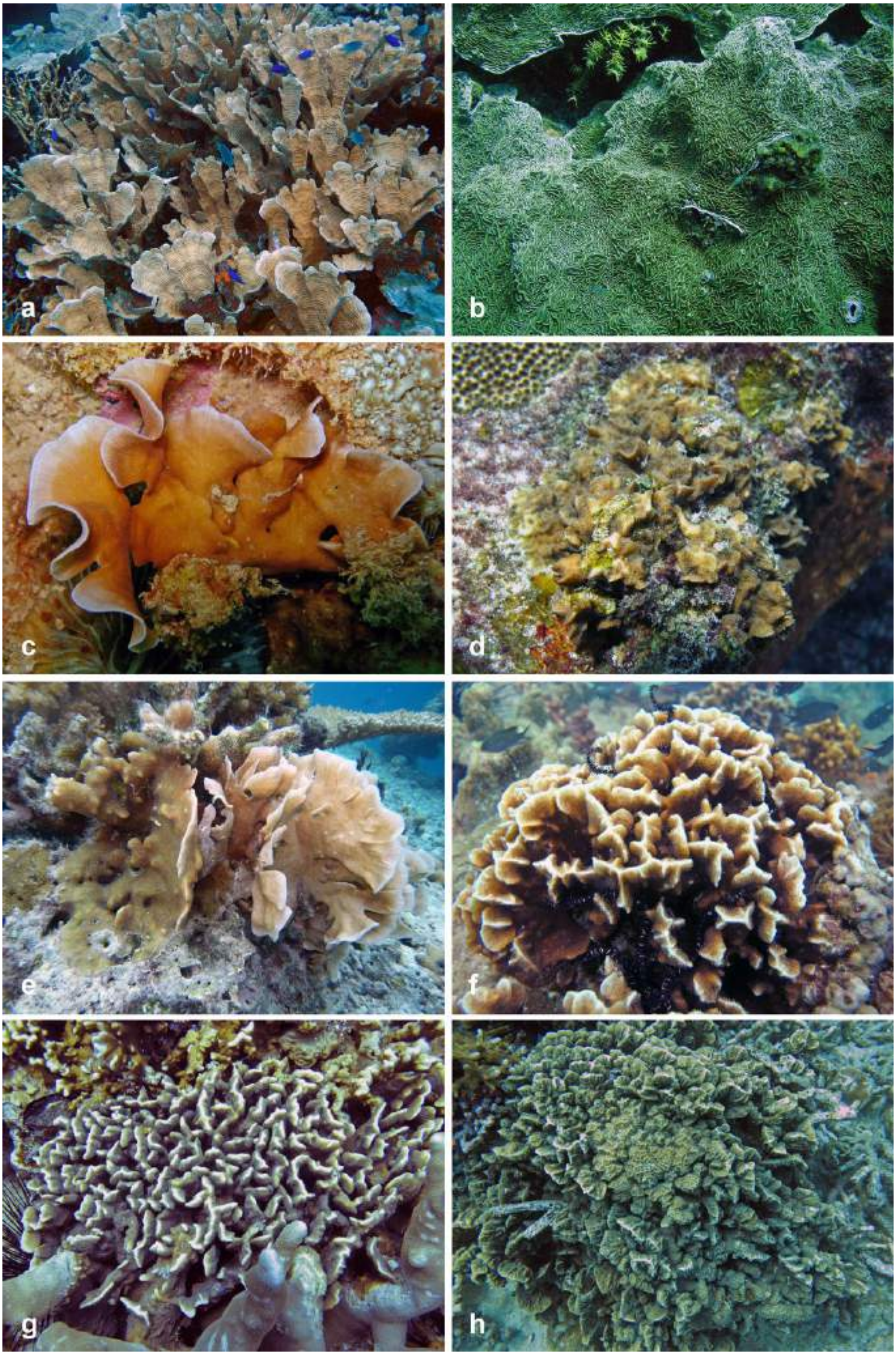


Fig. S7. Euphylliidae recorded from this study. **a** *Catalaphyllia jardinei* **b** *Euphyllia ancora* **c** *E. cristata* **d** *E. divisa* **e**-**f** *E. paradivisa* **g** *E. yaeyamaensis* **h** *Nemenzophyllia turbida*.

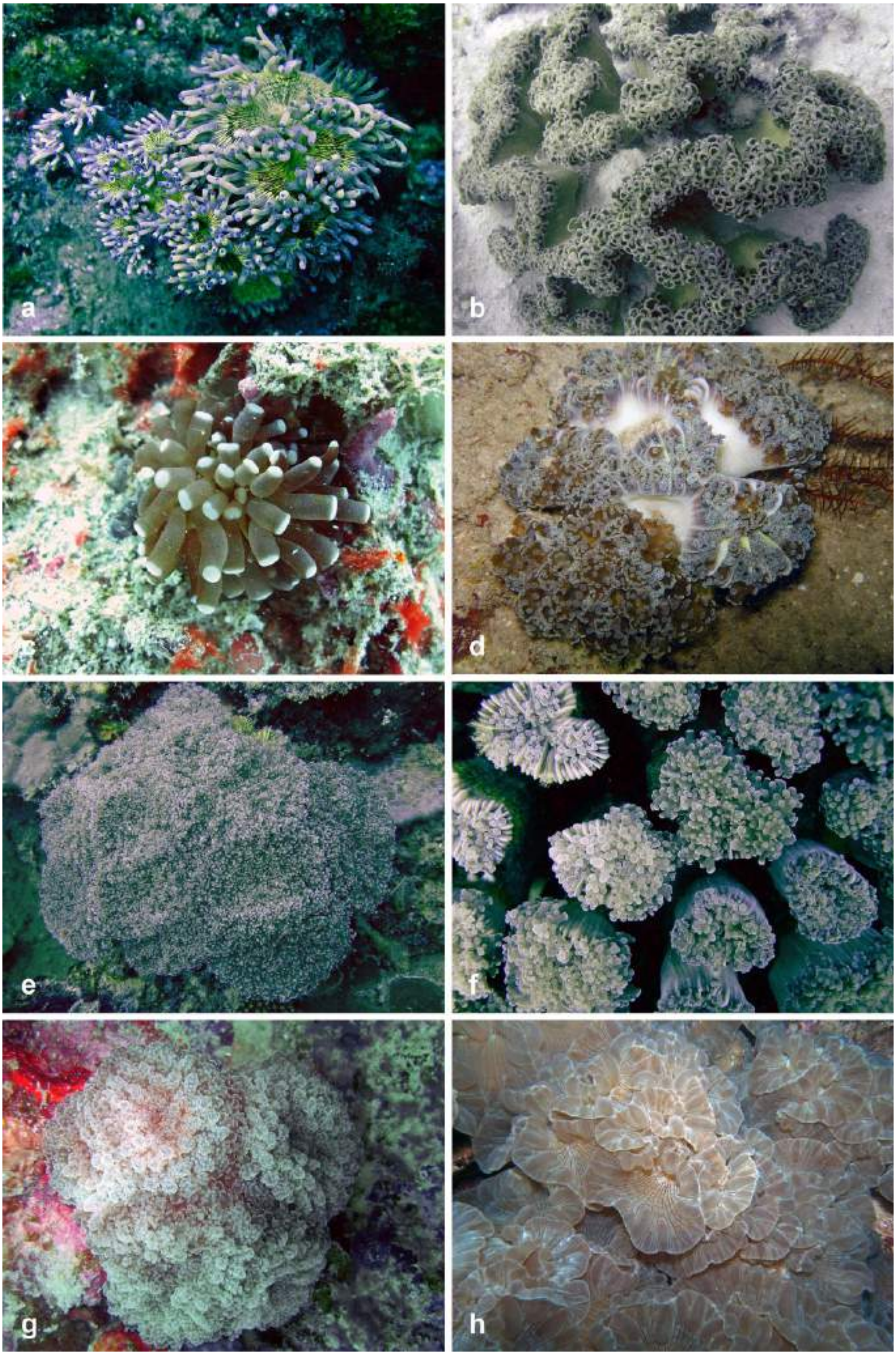


Fig. S8. Euphylliidae recorded from this study. **a** *Plerogyra cauliformis* **b** *Plerogyra* cf. *cauliformis* **c** *P. diabolotus* **d** *Plerogyra* cf. *diabolotus* **e** *P. multilobata* **f** *Plerogyra* cf. *multilobata* **g** *Plerogyra simplex* **h** *Plerogyra sinuosa*.

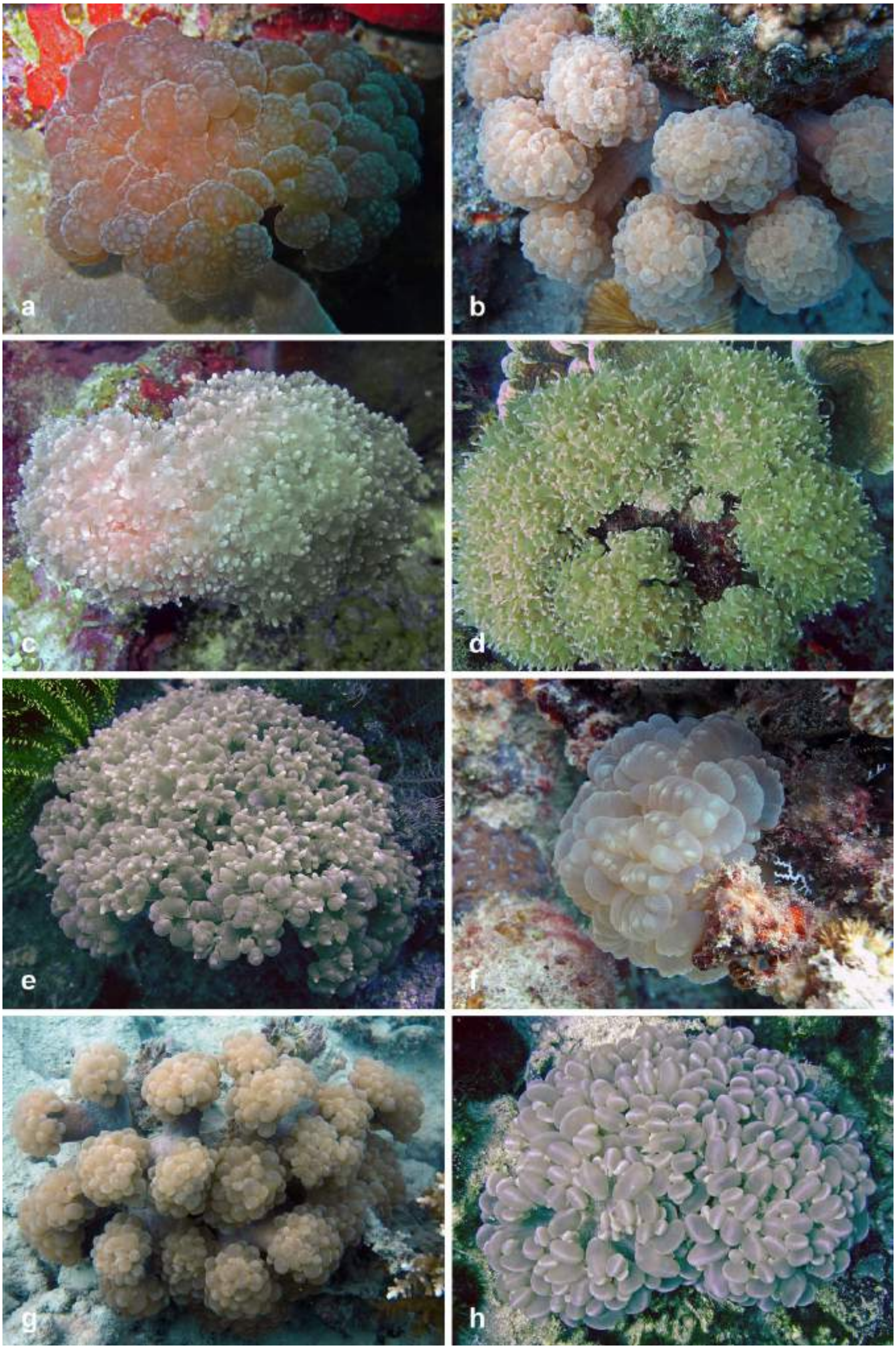


Fig. S9. Species accumulation curves of each locality based on three coral families (Fungiidae, Agariciidae and Euphylliidae). The grey shaded area indicates the standard deviation.

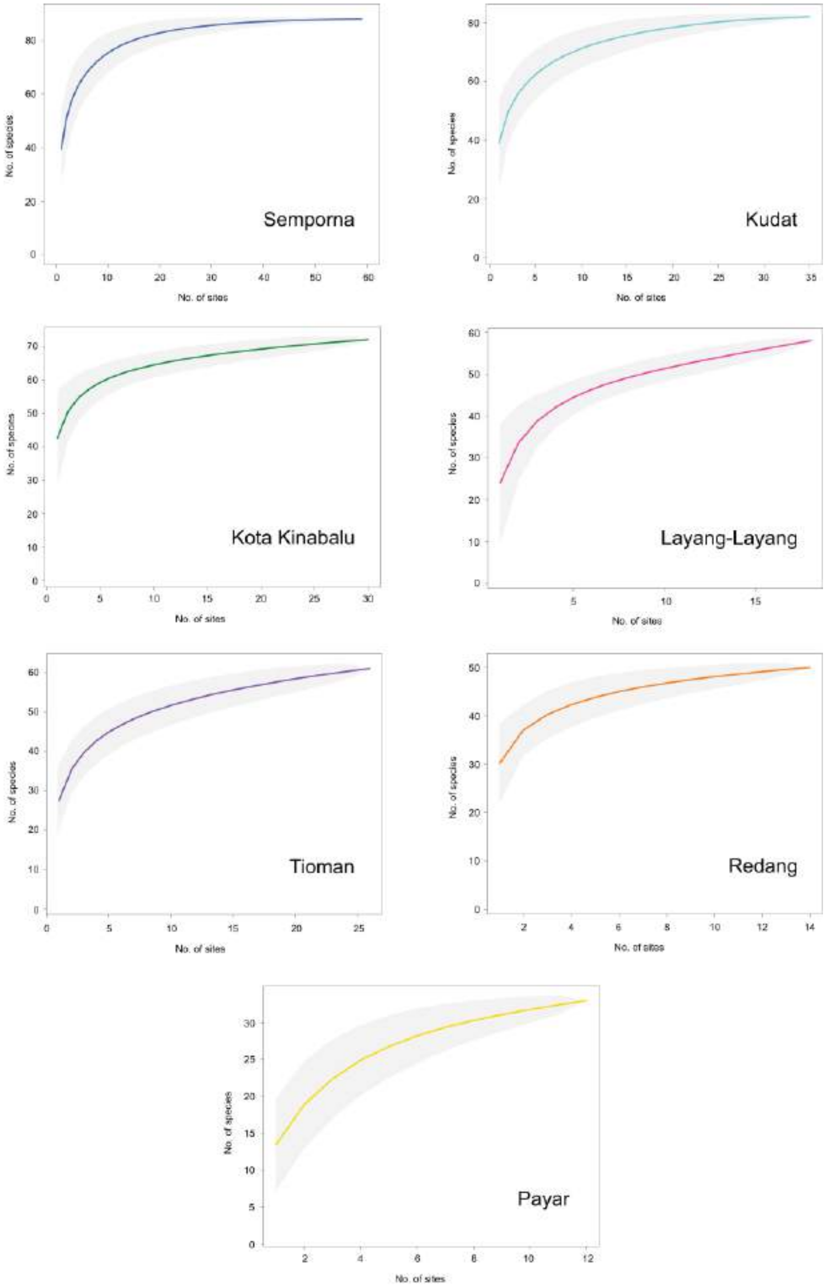
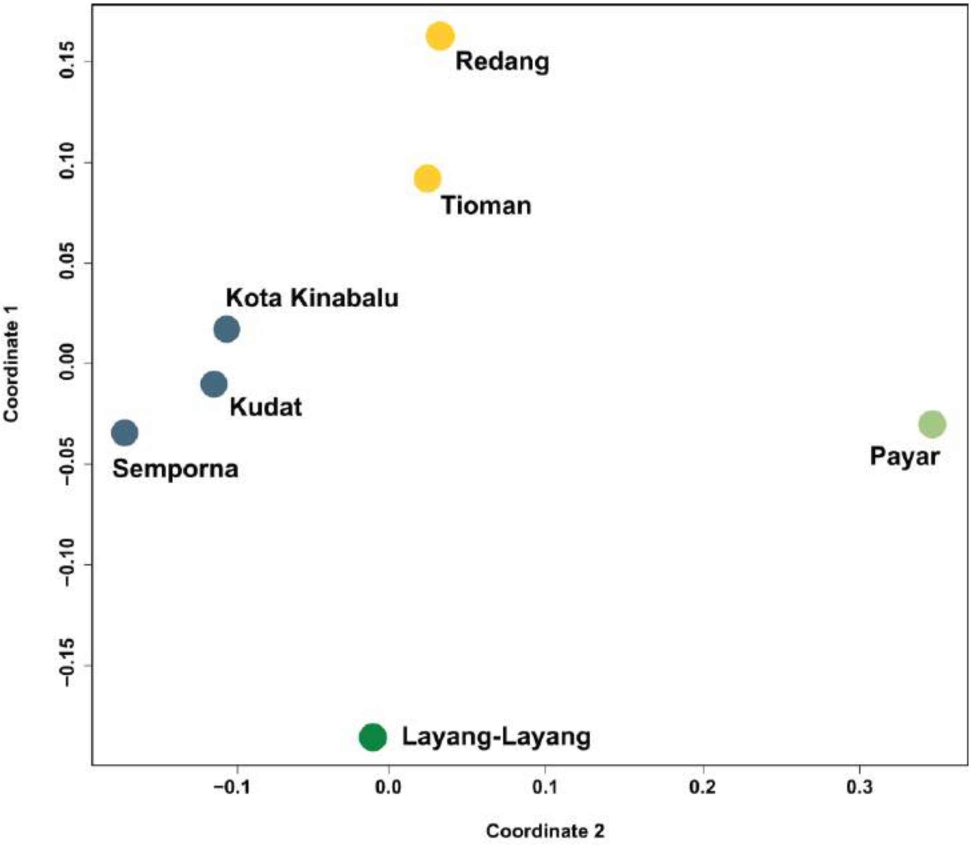


Fig. S10. Metric MDS ordination of seven reef localities in Malaysia based on coral species composition of three coral families.



Chapter 7

Connectivity of reef invertebrate populations in Malaysia: perspectives of a mushroom coral, a blue seastar and a boring giant clam

Zarinah Waheed, Bastian T. Reijnen, Bert W. Hoeksema and Marc Kochzius

Abstract

Numerous studies on population genetics in the Indo-Pacific region that include the Coral Triangle have revealed phylogeographic patterns in marine species populations. Very few of these studies extend into Malaysia and the South China Sea. Consequently, little is known about the population structure and connectivity pattern among the coral reefs in Malaysia, at both sides of the South China Sea. In view of this, we examined the genetic population structure of three model species: the mushroom coral *Heliofungia actiniformis*, the blue seastar *Linckia laeviata*, and the boring clam *Tridacna crocea* from seven localities across Malaysia, and Layang-Layang in the Spratly Islands. Additional samples of *H. actiniformis* and *L. laevigata* were obtained from Davao, the Philippines, and for the former also from Brunei and New Caledonia. The analyses were based on ribosomal ITS1, 5.8S and partial ITS2 sequences of *H. actiniformis*, and partial mitochondrial cytochrome oxidase I sequences of *L. laevigata* and *T. crocea*. Populations of *H. actiniformis* appeared to be constant-size, while *L. laevigata* and *T. crocea* showed departure from neutrality, indicating population expansion. There was genetic structuring in populations of *H. actiniformis* ($\Phi_{ST} = 0.143$, $P < 0.0001$), with support for three main groupings: 1) west South China Sea 2) east South China Sea, and 3) Sulu-Sulawesi Seas, suggesting restricted gene flow among these groups. Lack of population structure in *L. laevigata* implies connectivity among the sampled reef sites. There was subtle genetic structuring in populations of *T. crocea* ($\Phi_{ST} = 0.031$, $P < 0.0001$), but AMOVA did not detect any structure in the a priori groupings. These differing genetic population structure and scale in connectivity are most likely attributed to the life history traits of the model species, geological history and seasonal current patterns in the South China Sea and Sulu Sea.

Manuscript in preparation

Introduction

The Coral Triangle region encompasses much of eastern Indonesia, East Malaysia, the Philippines, Papua New Guinea, East Timor and the Solomon Islands (Veron et al. 2009). The concept of a triangular centre was first referred to by Kohn (1967) and illustrated by Briggs (1974), though Ekman (1934) recognized that the Indo-West Pacific was separate from the East Pacific and the Atlantic. Since then other authors have presented their own terminology, definition and boundaries for this centre (reviewed in Hoeksema 2007). Paramount for its diverse marine habitats and species, this area is also faced with various threats, making it high priority for conservation (Burke et al. 2011, 2012). Studies on population genetics and phylogeographic patterns in the Indo-Pacific region including the Coral Triangle area (reviewed by Crandall et al. 2008a; Carpenter et al. 2011; Keyse et al. 2014; Bowen et al. 2014) have been conducted to understand the processes driving and maintaining the extraordinary biodiversity in this region (Avise et al. 1987; Palumbi 1997; Barber and Bellwood 2005), and infer the connectivity among coral reefs. Information on population connectivity is essential in formulating effective management plans or designing MPA networks (Cowen et al. 2007; review by Cowen and Sponaugle 2009). Different scales of restricted gene flow or barrier to dispersal have been discovered in the Indo-Pacific region (e.g. Barber et al. 2002; Ravago-Gotanco et al. 2007; Gaither et al. 2011) and populations that are potentially isolated or dependant on other reef populations may be vulnerable, and thus would need protection status tailored to the unique requirements of these reef areas.

Malaysia is composed of Peninsular Malaysia and East Malaysia separated by the South China Sea. East Malaysia makes up the north-northwest of Borneo, and is bounded by the South China Sea in the west and the Sulu Sea in the east. The Sulu Sea on the east coast of Sabah (or the east of north Borneo) marks the boundary of the Coral Triangle for Malaysia (see Veron et al. 2009), but a recent review suggested an extension of the boundary to include the South China Sea overlying the Sunda Shelf (Veron et al. 2015). Few reef areas have been sampled in Malaysia (Gaither and Rocha 2013) and very little is known about the connectivity patterns across the South China Sea. In this study we aim to explore the degree of connectivity among the coral reefs of Malaysia, by examining the genetic population structure of three model species with differing life history traits, i.e. the mushroom coral *Heliofungia actiniformis*, the blue seastar *Linckia laevigata* and the boring giant clam or crocus clam *Tridacna crocea*.

For population genetic studies, *L. laevigata* and *T. crocea* are two of the top five species with the highest number of locations sampled across the Indian and Pacific Ocean including the Coral Triangle region (Keyse et al. 2014 and references therein). Further studies on these two species was recommended to include mtDNA COI markers to address the gap in sampling localities in order to increase the geographic scope and enable comparable data for further analysis (Keyse et al. 2014). The population dynamics and the genetic population structure of *H. actiniformis* have been examined in Indonesia and across the Indo-Malay Archipelago (Knittweiss et al. 2009a, 2009b; Knittweis and Wolff 2010). While some species distribution data is available on *H. actiniformis*, very little is known about the genetic population structure of this species in Malaysia. Use of the similar genetic marker by Knittweis et al. (2009a), i.e. the nuclear internal transcribed spacers 1 and 2 including the 5.8S region will allow for future combined analyses.

Model species

Heliofungia actiniformis (Quoy and Gaimard, 1833) is a conspicuous free-living and solitary mushroom coral species with long tentacles extended continuously, which make them suitable habitat for cryptobenthic invertebrates and fish (Hoeksema and Fransen 2011; Bos 2012; Hoeksema et al. 2012b; Bos and Hoeksema 2015) and attractive for the aquarium industry (Knittweis et al. 2009b; Knittweis and Wolff 2010). It can be found in a wide range of reef habitats from shallow lagoons to deep reef bases, down to 24 m (Hoeksema 2012a) and has a distribution range predominantly in the West Pacific (Hoeksema 1989; Veron 2000). A laboratory study on *H. actinifomis* reported the release of brooded larvae from parent polyps and settlement after three days (Abe 1937). However, coral larvae are able to prolong their settlement timing in the absence of suitable habitat (Graham et al. 2008), and brooded larvae are equipped with energy reserves to sustain their planktonic duration if necessary (Wilson and Harrison 1998). Adult mushroom corals are also able to reproduce asexually by budding and fragmentation (Gilmour 2004; Hoeksema 2004; Hoeksema and Gittenberger 2010; Hoeksema and Waheed 2011; Hoeksema and Yeemin 2011).

Linckia laevigata (Linnaeus, 1758) is a seastar with striking blue colouration, which is common in most coral reef environments from the western Indian Ocean to southeastern Polynesia (Clark and Rowe 1971; Marsh 1974; Yamaguchi 1977). It also occurs in other colour variations that may differ by locality (Williams and Benzie 1997; Williams 2000; Crandall et al. 2014). Crandall et al. (2008b) reported that populations in the Indian Ocean are predominantly orange, while populations in the Pacific are predominantly blue in colour. In Malaysia, the brilliant blue morph is common, but a salmon-orange morph was often encountered, and has been reported from Japan and the Philippines (Williams and Benzie 1997). *Linckia* reproduce by broadcast spawning. They reproduce sexually by releasing gametes into the water column for external fertilization (Yamaguchi 1973) and its larvae has a long pelagic duration of 22–28 days (Yamaguchi 1977).

Tridacna crocea Lamarck, 1819 is the smallest giant clam in the genus *Tridacna*. It can be found in shallow reef environments and is distributed from the eastern Indian Ocean to the West Pacific (Othman et al. 2010). Similar to *L. laevigata*, *Tridacna* reproduce by broadcast spawning, but has a pelagic larval duration of 7–14 days (Lucas 1988; Shokita et al. 1991), and are able to settle on the reef in approximately 10 days (Copland and Lucas 1988) by boring into the reef substrate.

All three model species are popular marine ornamental species. According to CITES data, *H. actiniformis* is in the top ten species of corals imported into the United States, the European Union and Japan between 1997–2001, whereas *L. laevigata* is the most commonly imported seastar, accounting for 3% of the total trade in invertebrates (Wabnitz et al. 2003). *Tridacna crocea* clams are not only harvested for the aquarium trade, but also for subsistence (DeBoer et al. 2008 and review in Copeland and Lucas 1988). Overharvesting of giant clam species and decline of populations due to anthropogenic activities (Othman et al. 2010; Neo and Todd 2012a, b; DeBoer et al. 2014a) have prompted the protection of all giant clam species under Appendix II of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES; UNEP-WCMC 2013). Seven out of eight giant clam species are also on the IUCN RED LIST of Threatened Species (Mollusc Specialist Group 1996).

Materials and methods

Study area and sample collection

Heliofungia actiniformis, *L. laevigata* and *T. crocea* were sampled from seven localities across Malaysia and Layang-Layang in the Spratly Islands (Fig. 1, Table 1). Sampling was carried out within marine parks, except for 44 out of 59 sites in Semporna and sites in Layang-Layang (Chapters 2–5). Additional samples of *L. laevigata* and *H. actiniformis* were obtained from Davao, the Philippines, and for the latter also from Brunei and New Caledonia. Samples were collected in the form of tentacle tissue for *H. actiniformis*, a piece of arm cutting (~2–3 cm) for *L. laevigata* and some mantle tissue for *T. crocea*. All samples were stored in 95% absolute ethanol prior to DNA extraction.

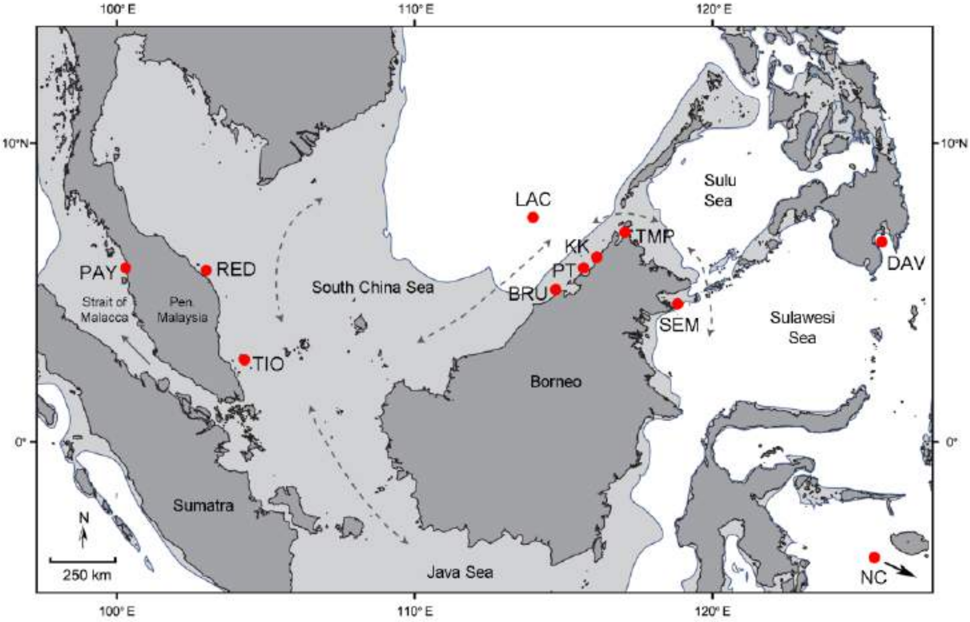


Fig. 1. Sampling sites across Malaysia (PAY, RED, TIO, PT, KK, TMP, SEM). Other localities include Layang-Layang, Spratly Islands (LAC), Brunei (BRU), Davao, the Philippines (DAV), and Nouméa, New Caledonia (NC). Locality data is given in Table 1. Dark gray shading are present-day land formations; whereas light gray shading are areas exposed during the last glacial maxima (17,000 – 18,000 years ago) when sea-level stand was 120 m lower than at present (Voris 2000). Dashed arrows indicate seasonal reversing current patterns.

Table 1. Sampling localities, codes and coordinates

Site	Location	Code	Latitude (N)	Longitude (E)
Semporna, Malaysia	Sulu Sea	SEM	04°06′ – 04°48′	118°10′ – 118°57′
Kudat, Malaysia	Sulu Sea	TMP	06°40' – 07°28'	116°50' – 117°34'
Kota Kinabalu, Malaysia	South China Sea	KK	05°57' – 06°12'	115°59' – 116°05'
Pulau Tiga, Malaysia	South China Sea	PT	05°41' – 05°51'	115°37' – 115°41'
Brunei Darussalam	South China Sea	BRU	05°06'27"	114°45'36"
Layang-Layang, Spratly Islands	South China Sea	LAC	07°22' – 07°23'	113°47' – 113°52'
Tioman, Peninsular Malaysia	South China Sea	TIO	02°42' – 02°56'	104°03' – 104°13'
Redang, Peninsular Malaysia	South China Sea	RED	05°43' – 05°49'	102°59' – 103°04'
Payar, Peninsular Malaysia	Strait of Malacca	PAY	06°03' – 06°05'	100°02' – 100°03'
Davao, the Philippines	Sulawesi Sea	DAV	06°29' – 07°01'	125°34' – 125°44'
Nouméa, New Caledonia	Coral Sea	NC	21°16'– 21°27' S	165°40' – 125°58'

DNA extraction, amplification and sequencing

DNA was isolated from *H. actiniformis* tentacle tissue using the DNeasy Blood and Tissue Kit (QIAGEN) following the standard protocol for animal tissue (version 07/2006). The nuclear internal transcribed spacers 1 and 2 including the 5.8S region (ITS for short) were amplified using primers A18S (Takabayashi et al. 1998b) and ITS-4 (White et al. 1990). For *L. laevigata* and *T. crocea,* the mitochondrial COI gene was amplified using primers HCO2198 and LCO1490 (Folmer et al. 1994) for the former, and primers COI-Tricro-Frwd and COI-Tricro-Rev (Kochzius and Nuryanto 2008) for the latter.

The PCR amplification was carried out in a 25 µl reaction volume, which contained 2.5 µl PCR CoralLoad Buffer (containing 15 mM $MgCl_2$) (QIAGEN), 1.0 µl of each primer (10 pmol), 0.5 µl dNTPs (2.5 mM), 0.5 µl Taq polymerase (15 units/µl) (QIAGEN), 5 µl Q-solution (QIAGEN) (only for ITS, otherwise it was replaced with extra pure PCR water), 13.5 µl of extra pure PCR water and 1.0 µl diluted DNA extract. The PCR cycles consisted of an initial denaturation step of 94 °C for 3 min, followed by 39 cycles of 94 °C for 1 min, annealing temperature of 55 °C for 1 min (COI: 45 °C), an extension step of 72 °C for 1 min and a final elongation step of 72 °C for 5 min. The amplicons were analysed on a 1% agarose gel electrophoresis, stained with ethidium bromide and visualized on a Red^{TM} Personal Imaging System. Successfully amplified samples were sent to Macrogen Europe for PCR cleaning and bidirectional sequencing on an ABI Automated Sequencher 3730xl.

Sequence alignment and phasing

Sequences were assembled and edited with Sequencher 4.10.1 (Gene Codes Corporation), aligned on the GUIDANCE server using MAFFT algorithm (Penn et al. 2010a, b) and trimmed in BioEdit 7.2.5 (Hall 1999). Heterozygous positions in the ITS gene were observed as double peaks in chromatograms. Sequences with haplotypes that could not be determined from chromatograms based on distinct peak sizes were resolved with PHASE 2.1 using the default settings (Stephens et al. 2001; Stephens and Donnelly 2003). Input files for PHASE were generated using SeqPHASE (Flot 2010). Sequences with unresolved positions were eventually excluded from the analyses. The COI sequences did not contain any gaps or ambiguous positions between base pairs. Protein translations were made in MEGA 6 (Tamura et al. 2013) to ensure that stop codons were not present.

Genetic diversity and historical demography

Genetic diversity indices such as haplotype diversity (*h*) and nucleotide diversity (π) (Nei and Li 1979; Nei 1987) were determined for all populations using Arlequin 3.5.1.3 (Excoffier and Lischer 2010). Population demographic changes were examined with Tajima's *D* (Tajima 1989) and Fu's *Fs* (Fu 1997) to assess the population deviation from neutrality. Significant negative values could indicate recent population expansion or selection sweep, while positive values could reflect population bottleneck or balancing selection (Tajima 1989, 1993; Fu and Li 1993). Fu's F is more sensitive in detecting population growth (Fu 1997). To further investigate the demographic changes of each species, mismatch distributions were analysed to test the model of sudden population expansion (Slatkin and Hudson 1991; Rogers and Harpending 1992; Rogers 1995). Populations that have undergone growth or expansion are expected to have unimodal and smooth distributions, whereas populations in demographic equilibrium are expected to have multimodal and ragged distributions. Sum of squared deviation (SSD) tests the fit between the observed and expected distribution (Schneider and Excoffier 1999), whereas Harpending's raggedness index (*r*) evaluates the smoothness of the distributions (Harpending 1994). Non-significant SSD and Harpending's *r* values support a sudden population expansion (Harpending 1994). In order to obtain accurate estimates of the demographic analyses, only locations with more than five samples were included in the analyses, which then excluded New Caledonia for *H. actiniformis* and Layang-Layang and Tioman for *L. laevigata*. All demographic analyses were tested for statistical soundness with 10,000 permutations in Arlequin 3.5.1.3 (Excoffier and Lischer 2010) with the final significance level determined by sequential Bonferroni corrections (Rice 1989).

Phylogenetics, population structure and gene flow

Population genetic structuring was examined by employing four techniques: first by creating phylogentic trees, multidimensional scaling (MDS) plots and haplotype networks to visualise the relationships among the unique haplotype, second by calculating Φ statistics and conducting analysis of variance (AMOVA) to determine the degree of population differentiation among the locations, third by performing hierarchical AMOVA to identify potential population groupings based on geographical affinities, and finally by determining the association between genetic distance and geographical distance implemented with Mantel tests to infer patterns of isolation by distance and gene flow among the populations.

Prior to running the phylogenetic analysis, the most appropriate model of nucleotide substitution was determined in jModelTest 2.1.6 (Darriba et al. 2012) based on Akaike Information Criterion (Akaike 1974). The best fit of model was a transition model TIM3+I for H. *actiniformis* and TIM1+G for *L. laevigata*, and a three-parameter model TPM3uf+I for *T. crocea*. Phylogenies were reconstructed based on Bayesian Inferences (BI) in MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist et al. 2012). Gaps were treated as missing data. Four Markov Chain Monte Carlo (MCMC) of 10 million generations were applied in two runs, saving one tree every 100 generations and discarding the initial 25% of the total trees as burnin. The average standard deviation of split frequencies after 10 million generations was 0.007927 for *H. actiniformis,* 0.009375 for *L. laevigata* and 0.004710 for *T. crocea*. *Psammocora contigua* (Genbank accession number AY722782), *Linckia guildingi* (Genbank accession number AF187940) and *Tridacna maxima* from North Sabah (unpublished) were selected as outgroups for *H. actiniformis, L. laevigata* and *T. crocea*, respectively.

To further visualise representations of the sequence clustering, metric multidimensional scaling (MDS) analysis was performed in R using the bios2mds package (Pelé et al. 2012). A distance matrix was calculated based on the pairwise differences between each sequence, and then mapped onto a 2-dimensional space.

A haplotype network for each species was constructed based on unique haplotype difference using statistical parsimony principle (Templeton et al. 1992) as implemented in TCS version 1.21 (Clement et al. 2000). All haplotypes (of *H. actiniformis*, *L. laevigata* and *T. crocea*) were included in this analysis. Gaps in the *H. actiniformis* sequence alignment were treated as a fifth nucleotide state. Clades were defined as clusters of haplotype separated by the highest number of mutational steps (e.g. Knittweis et al. 2009a; Kochzius et al. 2009). A clade composed of a single haplotype is considered an outlier. The clades were depicted as pie charts and overlaid onto the map of the study area.

AMOVA was employed to calculate pairwise Φ_{ST} between all locations (excluding populations with less than five samples, i.e. New Caledonia, and Layang-Layang and Tioman for *L. laevigata*). Hierarchical groupings were done manually by taking into account the significant Φ_{ST} between locations. Hierarchical AMOVA was conducted to calculate Φ_{ST}, Φ_{SC} and Φ_{CT} values in order to assess genetic variation of each grouping and determine the grouping with the most probable partitioning (largest Φ_{CT} difference). Statistical significance was assessed with 10,000 permutations in Arlequin and significance level was Bonferroni adjusted. The analyses were run using the Tamura and Nei model of nucleotide substitution, which is the best approximation of the TIM3, TIM1 and TPM3uf models available in Arlequin 3.5.1.3 (Excoffier and Lischer 2010). For *L. laevigata*, a gamma distribution (0.108) was applied based on the results obtained from jModelTest.

For the Isolation by Distance (IBD) analysis, correlation between genetic (pairwise Φ_{ST}) and geographical distance (km) was evaluated using Mantel test (Manly 1994) and reduced major axis (RMA) regression in Isolation by Distance Web Service (IBDWS) version 3.23 (Jensen et al. 2005) with 10,000 randomisations. Geographical distance was measured as the shortest path between two populations by sea, estimated on Goole Earth version 7.1.5.1557.

Results

Sampling efforts were performed at 176 sites in six localities in Malaysia, and 18 sites in Layang-Layang. The three model species were absent from two localities: Pulau Payar in the Strait of Malacca, and Pulau Redang, Peninsular Malaysia in the South China Sea. *H. actiniformis* was not encountered in Layang-Layang. Six *Tridacna* samples that were collected from Redang turned out to be juvenile *T. maxima*, a species that can also be found boring into the substrate (Neo et al. 2015). *Tridacna crocea* was also absent from Kota Kinabalu and Pulau Tiga at the time of the sampling.

Sequence data was obtained for 557 individuals from all three species throughout nine sampling localities. Approximately 627 bp of nuclear ITS sequences from 226 *H. actiniformis* yielded 19 haplotpes. Mitochondrial COI fragments of 601 bp from 233 *L. laevigata* and 439 bp from 98 *T. crocea* resulted in 120 and 51 haplotypes, respectively. All unique haplotypes will be deposited in GenBank (Table S1).

Genetic diversity and historical demography

Haplotype and nucleotide diversities of *H. actiniformis* were quite variable across all population (Table 2). Haplotype diversity ranged from 0.604 in Kota Kinabalu to 1.000 in New Caledonia, whereas nucleotide diversity ranged between 0.004 in Kota Kinabalu and 0.009 in Kudat, Pulau Tiga and Tioman ($h = 0.72$, $\pi = 0.008$). The haplotype and genetic diversity was notably lowest at Kota Kinabalu. Genetic diversity within populations of *L. laevigata* and *T. crocea* was higher than *H. actiniformis*, and almost similar to each other, albeit slightly higher in *L. laevigata*. In *L. laevigata*, haplotype diversity ranged between 0.978 in Davao and 1.000 in Layang-Layang, whereas nucleotide diversity ranged between 0.006 in Layang-Layang and 0.020 in Kota Kinabalu and Pulau Tiga ($h = 0.98$, $\pi = 0.018$). For *T. crocea*, haplotype diversity ranged from 0.900 in Tioman to 0.978 in Kudat. Average nucleotide diversity ranged from 0.009 in Semporna and Layang-Layang to 0.015 in Kudat ($h = 0.96$, $\pi = 0.011$).

Tajima's D values were negative for all *L. laevigata* and *T. crocea* populations, and for Kota Kinabalu and Brunei populations in *H. actiniformis*, but all values were statistically not significant (Table 3). Fu's F values were positive for all *H. actiniformis* populations, and negative for all *L. laevigata* and *T. crocea* populations, but only significant in Semporna, Kudat and Kota Kinabalu populations of *L. laevigata* and Semporna and Layang-Layang populations of *T. crocea* ($p < 0.0001$). Positive Tajima D and Fu's Fs values could indicate a population bottleneck, however for *H. actiniformis*, the positive values were statistically not significant. The overall negative values for *L. laevigata* and *T. crocea* indicate an excess of rare haplotypes compared to what would be expected under neutrality, suggesting population size expansion or selection (Fu 1997) especially for populations with supporting statistical significance in Fu's Fs test.

Table 2. Summary statistics of *Heliofungia actiniformis*, *Linckia. laevigata* and *Tridacna crocea* at each locality (as in Fig. 1). *N* = number of samples, *H* = number of haplotypes, *h* = haplotype diversity, π = nucleotide diversity.

	Heliofungia actiniformis				*Linckia laevigata*				*Tridacna crocea*			
Site	*N*	*H*	*h*	π	*N*	*H*	*h*	π	*N*	*H*	*h*	π
Semporna (SEM)	57	10	0.771	0.008	89	57	0.984	0.017	45	30	0.972	0.009
Kudat (TMP)	70	10	0.782	0.009	54	45	0.991	0.019	14	12	0.978	0.015
Kota Kinabalu (KK)	47	8	0.604	0.004	49	36	0.981	0.020	–	–	–	–
Pulau Tiga (PT)	20	5	0.800	0.009	20	17	0.984	0.020	–	–	–	–
Brunei (BRU)	8	4	0.821	0.007	–	–	–	–	–	–	–	–
Layang-Layang (LAC)	–	–	–	–	3	3	1.000	0.006	18	15	0.974	0.009
Tioman (TIO)	9	3	0.639	0.009	1	1	–	–	21	9	0.900	0.011
Davao (DAV)	13	4	0.654	0.007	17	14	0.978	0.017	–	–	–	–
New Caledonia (NC)	2	2	1.000	0.008	–	–	–	–	–	–	–	–

The mismatch distributions showed multimodal patterns (Fig. S1) with relatively high raggedness values for *H. actiniformis* (r = 0.11–0.45), which were not significant except for Semporna and Kudat populations ($p < 0.002$) (Table 3). Large values of Harpending's *r* suggest that the model does not provide a good fit to the data (Harpending et al. 1998). Sum of squared deviations (SSD) between the observed and expected mismatch were high and statistically significant for Kota Kinabalu and Tioman populations (0.45 and 0.26, respectively, $p < 0.002$). These results indicate that these four populations may be in demographic equilibrium or population decline. While a non-significant raggedness index usually denotes a good fit for population expansion, as was shown for populations of Davao, Pulau Tiga and Brunei, the distributions of these populations were multimodal and ragged-shaped, which do not support population expansion. For *L. laevigata*, multimodal mismatch distributions were obtained for all locations (Fig. S2), with a significant SSD for the Semporna population (SSD = 0.119, $p < 0.002$), which indicates a constant population size or a declining population size. The non-significant values of the raggedness index and SSD test for the Kudat, Kota Kinabalu, Pulau Tiga and Davao populations did not match the mismatch distributions under the population expansion model. For *T. crocea*, raggedness indices from the mismatch distributions were all non-significant. Unimodal curves were observed for Semporna and Layang-Layang populations, supporting the population expansion model for these two locations (Fig. S3).

Phylogenetics, population structure and gene flow

Phylogenetic analyses resulted in tree topologies with low support values in the basal clades, especially for *L. laevigata* and *T. crocea* (Fig. 2). The mtDNA COI marker is most likely not providing enough resolution for the basal clades. Furthermore, none of the clades correspond to the locality or the defined populations of each model species.

Table 3. Neutrality tests Tajima's D and Fu's Fs, as well as Sum of squared deviations (SSD) and Harpending's raggedness index (*r*) for *Heliofungia actiniformis*, *Linckia. laevigata* and *Tridacna crocea* at each locality

	Heliofungia actiniformis				*Linckia laevigata*				*Tridacna crocea*			
Site	D	Fs	SSD	*r*	D	Fs	SSD	*r*	D	Fs	SSD	*r*
SEM	1.76	6.11	0.09	**0.14**	-1.52	**-24.75**	**0.119**	0.010	-1.69	**-24.59**	0.004	0.03
TMP	2.92	8.44	0.07	**0.12**	-1.18	**-24.72**	0.018	0.009	-1.26	-4.35	0.02	0.08
KK	-0.75	2.58	**0.45**	0.11	-0.85	**-18.90**	0.019	0.016	-	-	-	-
PT	2.09	7.65	0.08	0.13	-0.45	-5.86	0.016	0.017	-	-	-	-
BRU	-0.95	3.03	0.10	0.15	-	-	-	-	-	-	-	-
LAC	-	-	-	-	-	-	-	-	-1.53	**-9.83**	0.01	0.05
TIO	2.37	7.05	**0.26**	0.35	-	-	-	-	-0.97	-0.21	0.03	0.04
DAV	1.44	5.98	0.22	0.45	-0.19	-4.13	0.024	0.024	-	-	-	-

Significant P values after Bonferroni correction are in bold and underlined.

The *H. actiniformis* tree recovered three well-supported basal clades (Fig. 2a), and one 'clade' of a single sample from New Caledonia (which we consider an outlier). This structure was also recovered in the MDS plot (Fig. 3a) and haplotype network (Fig. 4a). In the latter, the clades were separated by five or more steps. Haplotypes from clades A and B were found in all localities (apart from New Caledonia) (Fig. 5a). Clade C was represented by populations of north Borneo and one individual from New Caledonia. The outlier haplotype was from New Caledonia. A summary of the haplotype frequency percentage is given in Table 4.

For *L. laevigata*, two main clusters and one small cluster were retrieved from the MDS plot and haplotype network (Figs. 3b and 4b). The clades distribution exhibited an almost similar pattern as *H. actiniformis*, and was also separated by five or more steps. Haplotypes from clade A were shared by all populations, and clade B was only from north Borneo and Davao populations, whereas clade C occurred exclusively in north Borneo populations, with a higher frequency in the west coast of Sabah (Fig. 5b).

In *T. crocea*, there appears to be two main subdivisions from the MDS plot (Fig. 3c), however, an additional two outliers were discerned from the haplotype network (Fig. 4c). The two main clades were separated by three steps. The distribution of the clades on the map showed no clear pattern of subdivision; all sampled populations contained clades A and B, whereas the two outlier individuals were from Tioman (C), and Semporna (D) (Fig. 5c).

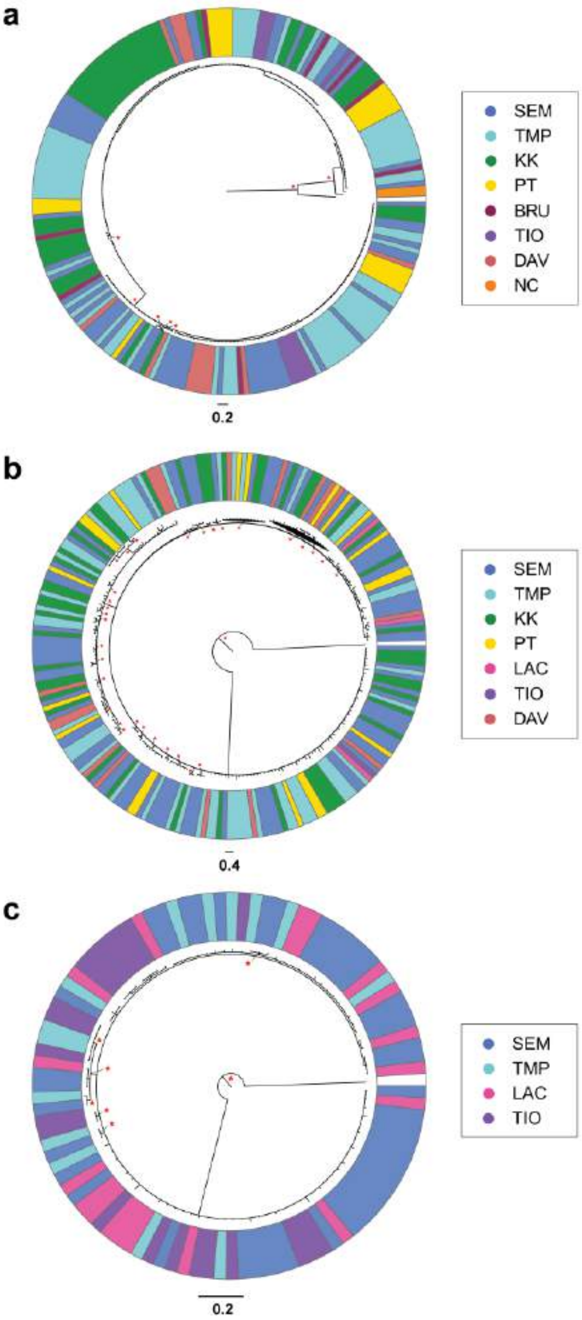


Fig. 2. Phylogram of **a** *H. actiniformis* based on nITS marker, **b** *L. laevigata*, and **c** *T. crocea* based on mtCOI marker inferred in MrBayes 3.2.2. Support values (> 80) for bayesian posterior probabilities are indicated with a star. Colours at the branch tips indicate population origin of each sequence.

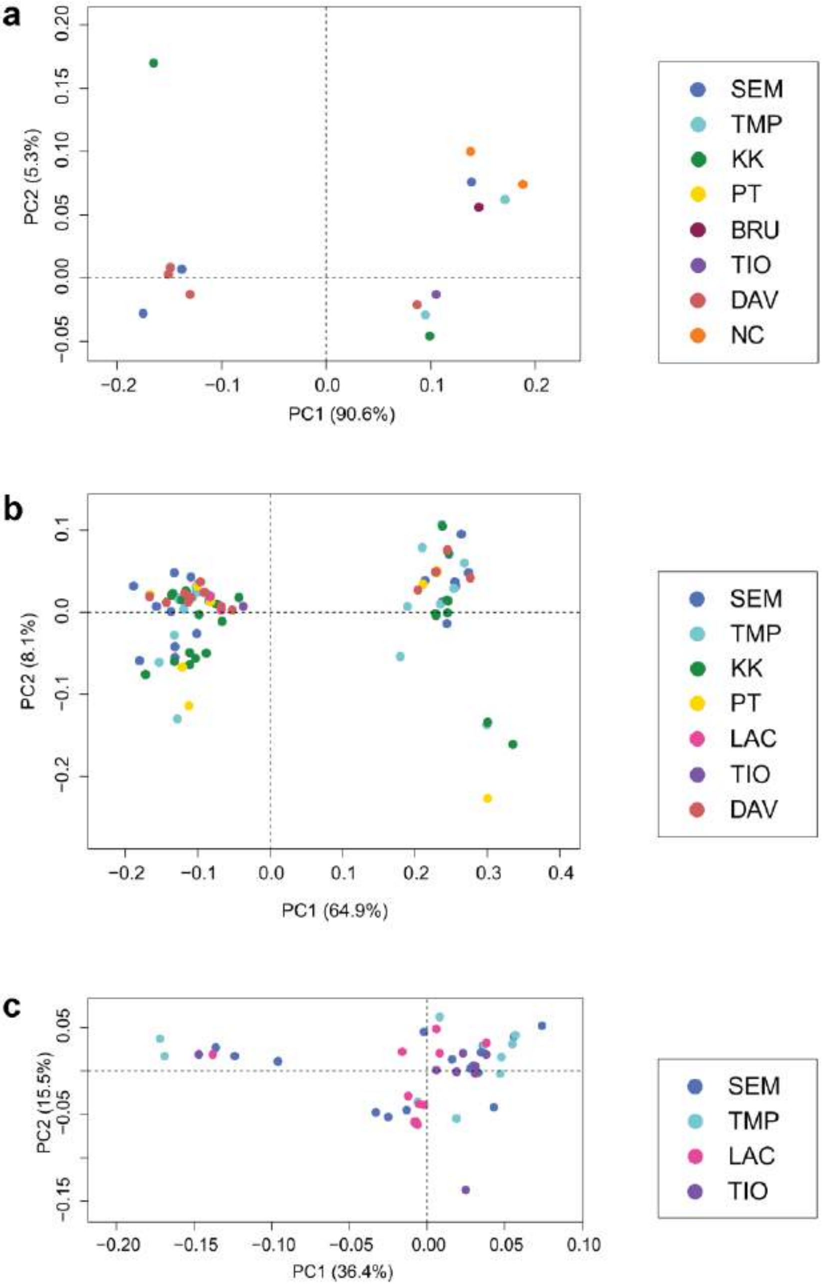


Fig. 3. Multidimensional scaling plots of **a** *H. actiniformis*, **b** *L. laevigata*, and **c** *T. crocea*.

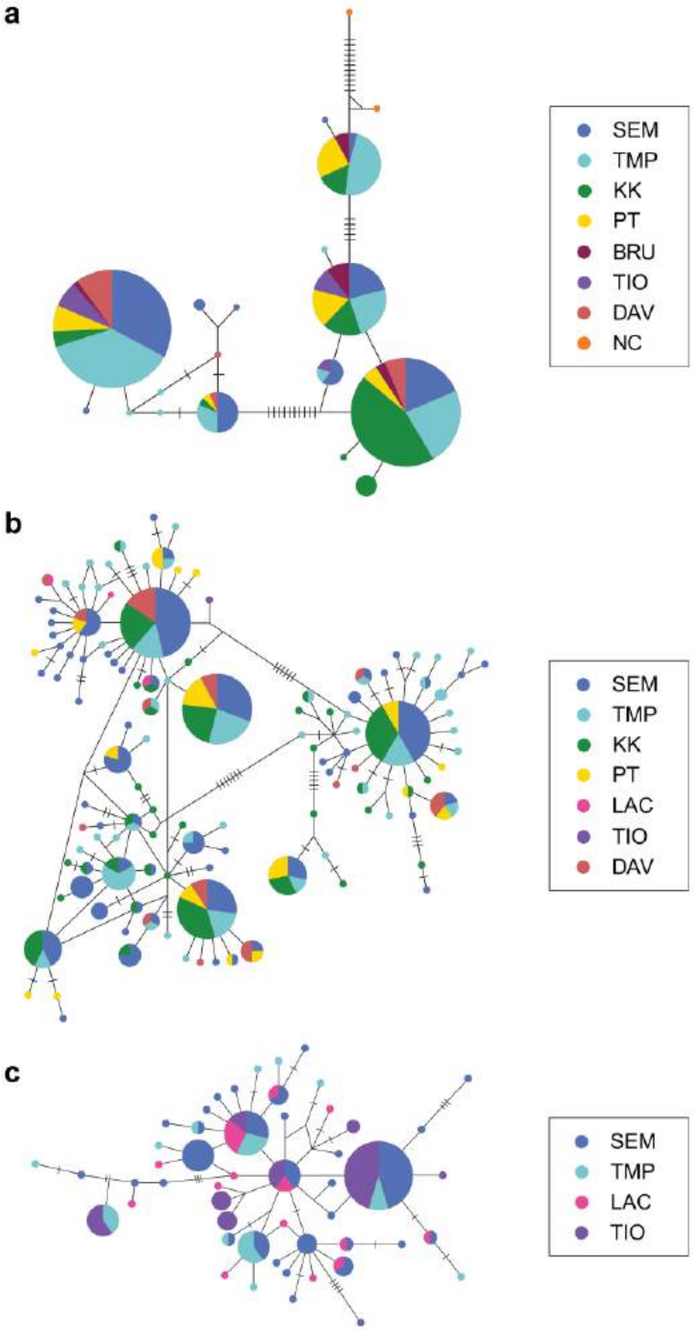


Fig. 4. Haplotype networks of **a** *H. actiniformis*, **b** *L. laevigata*, and **c** *T. crocea*. Each circle is a unique haplotype. The size of the circle is proportional to the haplotype frequency. The line between the circles represents one mutational step, and hatches represent additional mutational steps.

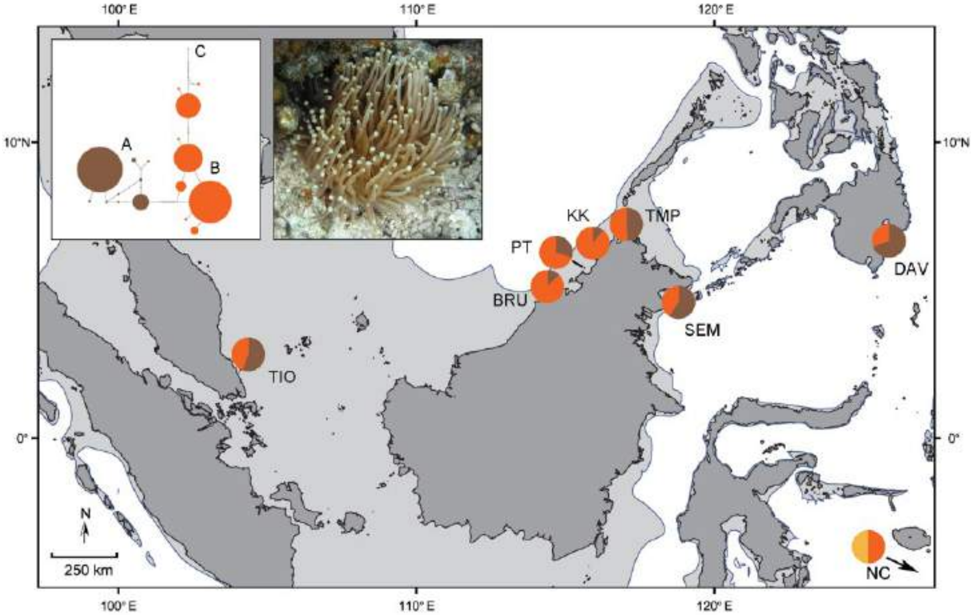


Fig. 5a. Distribution of clades across *H. actiniformis* populations.

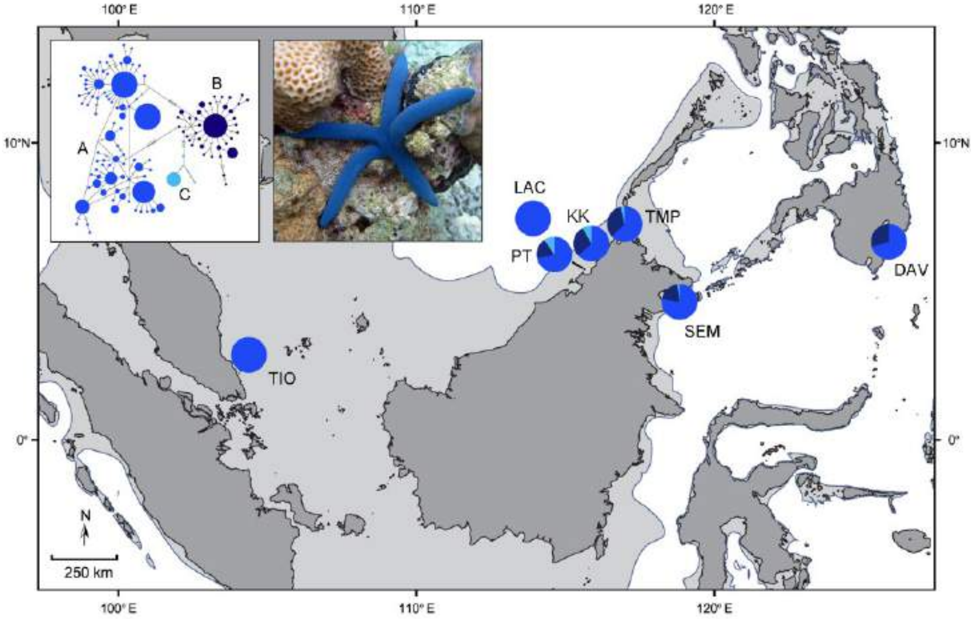


Fig. 5b. Distribution of clades across *L. laevigata* populations.

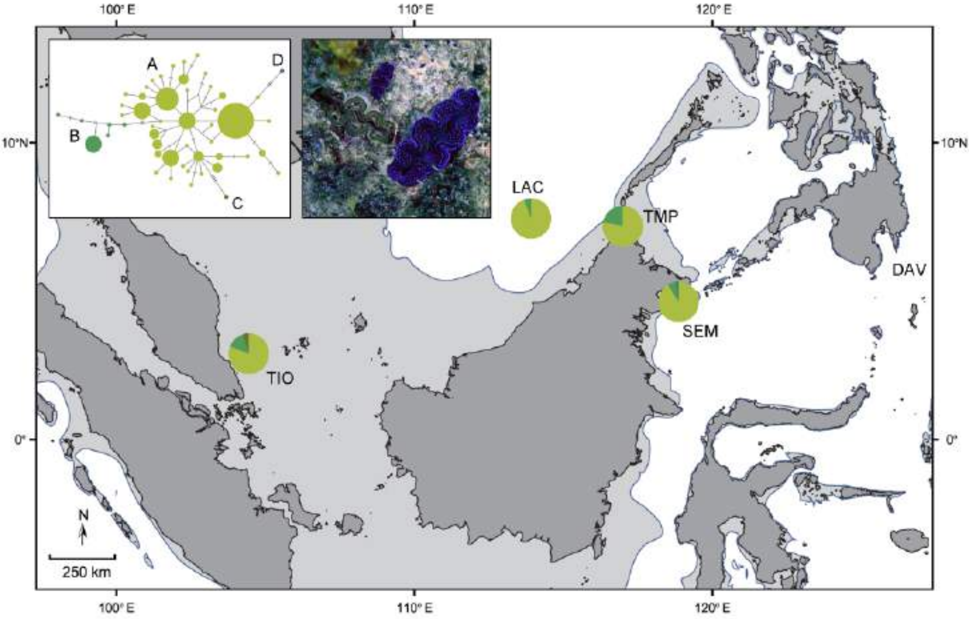


Fig. 5c. Distribution of clades across *T. crocea* populations.

Table 4. Haplotype frequency (total number of sequences and percentage) of each clade and outlier.

Heliofungia actiniformis

Clade A		Clade B		Clade C		Clade D	
Total	%	Total	%	Total	%	Total	%
94	41.2	104	45.6	29	12.7	1	0.4

Linckia laevigata

Clade A		Clade B		Clade C	
Total	%	Total	%	Total	%
163	70	60	26	10	4

Tridacna crocea

Clade A		Clade B		Clade C		Outlier	
Total	%	Total	%	Total	%	Total	%
86	88	10	10	1	1	1	1

There was weak but significant genetic population structure in *H. actiniformis* (Φ_{ST} = 0.143, P < 0.0001) and *T. crocea* (Φ_{ST} = 0.031, P < 0.0001) and no genetic population structure in *L. laevigata* (Φ_{ST} = 0.001, P = 0.394) in the study area. Most of the pairwise Φ_{ST} values between populations were non-significant (Table 5). However, significant population subdivision was detected in *H. actiniformis*. Nine out of 21 pairwise comparisons were significant at P < 0.05 and five comparisons remained significant after Bonferroni correction with Φ_{ST} values of 0.254 – 0.484. The highest level of population differentiation was observed when comparing Kota Kinabalu with other populations except nearby populations of Brunei and Pulau Tiga (but the latter was significant at P < 0.05). Significant genetic structure was also found between populations of Semporna and Brunei (Φ_{ST} = 0.265, P = 0.007). The pairwise Φ_{ST} values between populations of *L. laevigata* were very low, suggesting very little to no population differentiation. In *T. crocea*, significant genetic structure was detected between populations of Tioman and Semporna (Φ_{ST} = 0.053, P = 0.005), and Tioman and Layang-Layang (Φ_{ST} = 0.074, P = 0.006).

Table 5. Pairwise Φ_{ST} values between populations of *Heliofungia actiniformis*, *Linckia laevigata* and *Tridacna crocea*.

Heliofungia actiniformis

	DAV	SEM	TMP	KK	PT	BRU
SEM	-0.020					
TMP	0.049	0.012				
KK	<u>**0.484**</u>	<u>**0.327**</u>	<u>**0.207**</u>			
PT	**0.230**	**0.140**	0.036	**0.113**		
BRU	**0.405**	<u>**0.265**</u>	0.129	0.019	-0.037	
TIO	-0.022	-0.047	-0.034	<u>**0.355**</u>	0.071	0.213

Linckia laevigata

	DAV	SEM	TMP	KK
SEM	-0.007			
TMP	-0.012	0.013		
KK	-0.006	0.016	-0.012	
PT	-0.025	-0.009	-0.015	-0.018

Tridacna crocea

	SEM	TMP	LAC
TMP	0.010		
LAC	0.010	0.016	
TIO	<u>**0.053**</u>	0.031	<u>**0.074**</u>

Significant at P < 0.05 are indicated in bold
Significant P values after Bonferroni correction are underlined

Hierarchical AMOVA yielded very low support values in all a priori groupings and none were significant after Bonferroni correction (Table 6). In all model species, the percentage of variation within populations was much higher than the variation among populations within regions and among region groupings (Table S2). For *H. actiniformis*, the highest percentage of variation among the groups and largest fixation index were found for the assigned grouping of 1) Tioman (west South China Sea), 2) Brunei, Pulau Tiga, Kota Kinabalu (east South China Sea), and 3) Kudat, Semporna, Davao (Coral Triangle region) (% var. = 17.47%, $\Phi_{CT} = 0.17$, $P = 0.029$). AMOVA confirmed no significant structure in *L. laevigata* in the region. Furthermore, AMOVA did not detect structure in our assigned groupings for *T. crocea*, despite the significant pairwise Φ_{ST} values between populations of Tioman and Semporna, and populations of Tioman and Layang-Layang.

Table 6. Hierarchical analyses of molecular variance (AMOVA) for populations of *Heliofungia actiniformis*, *Linckia laevigata* and *Tridacna crocea*. Populations were partitioned according to haplotype distributions, significant Φ_{CT} values between populations and different seas. Generic labels were given to certain groupings: SCS = South China Sea, SS = Sulu Sea, CT = Coral Triangle.

Groupings	% Var. among groups	Φ_{CT}	P-value
Heliofungia actiniformis			
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. CT (TMP, SEM, DAV)	**17.47**	**0.17**	**0.029**
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. SS (TMP, SEM) vs. DAV	**15.82**	**0.16**	**0.049**
SCS (TIO, BRU, PT, KK) vs. CT (TMP, SEM, DAV)	14.75	0.15	0.055
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. North Sabah (TMP) vs. East Sabah. (SEM) vs. DAV	11.06	0.11	0.231
Linckia laevigata			
West and north Sabah (PT, KK, TMP) vs. SEM and DAV	1.81	0.0181	0.102
West and north Sabah (PT, KK, TMP) vs. East Sabah (SEM) vs. DAV	1.78	0.0178	0.106
West Sabah (PT, KK) vs. North Sabah (TMP) vs. East Sabah (SEM) vs. DAV	1.78	0.0178	0.198
Tridacna crocea			
TIO vs. (LAC, TMP, SEM)	4.24	0.04	0.249
West SCS (TIO) vs. LAC vs. SS (TMP, SEM)	2.52	0.03	0.336

Significant at $P < 0.05$ are indicated in bold

There was no correlation between genetic and geographical distance across all populations for all three model species, as indicated by Mantel test (Fig. 6). This was not surprising for populations of *L. laevigata*, but unexpected for *H. actiniformis* and *T. crocea*, whereby both of which have recovered weak but significant genetic structure among populations and significant pairwise differences between certain localities across the study area. An overview of the results is given in Table 7.

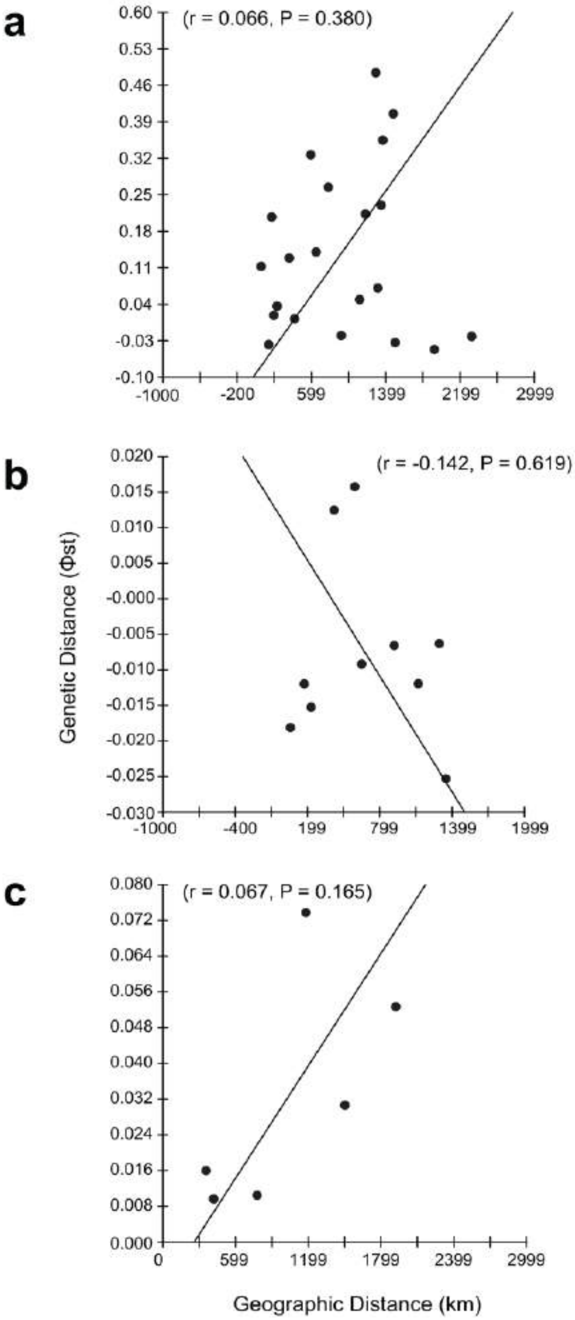


Fig. 6. Isolation by distance plots showing the relationship between genetic and geographical distance using Mantel test and Reduced Major Axis (RMA) for **a** *H. actiniformis*, **b** *L. laevigata*, and **c** *T. crocea*.

Table 7. Summary of results

	H. actiniformis	***L. laevigata***	***T. crocea***
Haplotype	19	120	53
Haplotype (*h*) and genetic (π) diversity	*h*: 0.604 – 1.000 π: 0.004 – 0.009 Lowest *h* and π in Kota Kinabalu	*h*: 0.978 – 1.000 π: 0.006 – 0.020	*h*: 0.900 – 0.978 π: 0.009 – 0.015
Neutrality test • Tajima's D • Fu's F (Fs) Positive values could indicate bottleneck. Negative values could indicate expansion.	• D negative in Kota Kinabalu and Brunei • Fs positive in all populations	• D negative in all populations • Fs negative in all populations and P-values significant for Semporna, Kudat and Kota Kinabalu	• D negative in all populations • Fs negative in all populations and P-values significant for Semporna and Layang-Layang
Mismatch distribution • Distribution (graph) • Harpending's *r* • SSD Multimodal could indicate equilibrium. Unimodal could indicate expansion. Significant *r* and SSD values could indicate bottleneck. Non-significant *r* and SSD values could indicate expansion.	• Multimodal • *r* significant in Semporna and Kudat • SSD significant in Kota Kinabalu and Tioman	• Multimodal • *r* non-significant • SSD significant in Semporna	• Unimodal in Semporna and Layang-Layang, multimodal in Kudat and Tioman • *r* non-significant • SSD non-significant
Phylogenetic inference	3 clades, 1 outlier (from New Caledonia)	No clear distinction	No clear distinction
MDS plot	3 clusters, 1 outlier (from Kota Kinabalu)	2 main clusters, 1 small cluster	2 clusters, possible 1 outlier (from Tioman)
Haplotype network	3 clades, 1 outlier (from New Caledonia)	3 clades	2 clades, 2 outliers (from Tioman and Semporna)
Genetic structure in populations	Significant genetic structure between population of Kota Kinabalu and other populations (except Brunei and Pulau Tiga), and Semporna and Brunei	Non-significant population subdivision	Significant genetic structure between populations of Tioman and Semporna, and Tioman and Layang-Layang
Hierarchical AMOVA	1) Tioman (west South China Sea), 2) Brunei, Pulau Tiga, Kota Kinabalu (east South China Sea), and 3) Kudat, Semporna, Davao (Coral Triangle region)	Non-significant structure in a priori groupings	Non-significant structure in a priori groupings
Isolation by Distance	No correlation between genetic and geographical distance	No correlation between genetic and geographical distance	No correlation between genetic and geographical distance

Discussion

In this study, sampling efforts were performed at seven localities. For two of these localities: Redang and Payar, sampling was made at 14 and 12 sites, respectively, but all three model species were not encountered at both localities. *H. actiniformis* has been reported from the east coast of Peninsular Malaysia (Harbourne et al. 2000; Affendi and Rosman 2012) and Singapore (Purchon 1956; Hoeksema and Koh 2009). Based on literature, no records have been found from the Strait of Malacca. It was also absent from Layang-Layang at the time of the sampling (Chapter 5). There have been anecdotal reports of *L. laevigata* from Redang, but no information is available for the Strait of Malacca. Nevertheless, this species has been found in the Andaman Sea (Putchakarn and Sonchaeng 2004). Populations of *T. crocea* have been reported from the east coast of Peninsular Malaysia (Harborne et al. 2000; Wong and Arshad 2011) in Tioman (Tan et al. 1998; Kee Alfian et al. 2005; Neo et al. 2015) and Redang (Lee et al. 2012), however specimens were only encountered and collected from Tioman. Based on its known distribution range (see Lucas 1988; Othman et al. 2010), it was expected to be present at Payar. This species has also been reported from Lee Pae Island (Koh Lipe) and Mu Ko Surin Marine Park in Thailand (Chantrapornsyl et al. 1996), north of Payar. *Tridacna crocea* was also curiously absent from Kota Kinabalu and Pulau Tiga along the west coast of Sabah, although samples of this species have been collected from Kota Kinabalu previously (Kochzius and Nuryanto 2008). We have no explanation as to why we did not find all target species in each of the localities mentioned above.

Genetic variability

Genetic variability of *H. actiniformis* was higher than the average nucleotide diversity of other populations of the Indo-Malay Archipelago apart from Adi in West Papua (see Knittweis et al. 2009a). Higher variability is expected at areas with high connectivity or at areas with larvae input from neighbouring populations (Knittweis et al. 2009a). The genetic variability of *L. laevigata* and *T. crocea* were comparable with other populations in the Indo-Malay Archipelago (*L. laevigata*: Crandall et al. 2008b; Kochzius et al. 2009; Alcazar and Kochzius 2016, *T. crocea*: Kochzius and Nuryanto 2008; Neo and Todd 2012b; DeBoer et al. 2008, 2014b; Hui et al. 2016), which could suggest a similar demographic history among these population (e.g. Duda and Palumbi 1999).

Population structure across the South China Sea and Sulu Sea

An almost similar pattern of clades was retrieved for all three model species (Fig. 5). Without taking into account the haplotypes of *H. actiniformis* from New Caledonia (n = 2), and *L. laevigata* from Layang-Layang (n = 3) and Tioman (n = 1) as it is difficult to draw conclusions based on very few samples, all three species had two main clades (A and B) with shared haplotypes among all sampled populations. A smaller clade (C) was primarily found in north Borneo for *H. actiniformis* and *L. laevigata*. As the population structure and connectivity patterns of the three model species vary from each other to some degree, each species is discussed separately.

Population subdivision in H. actiniformis

For *H. actiniformis*, genetic differentiation between populations of Kota Kinabalu and other populations (Semporna, Kudat, Tioman and Davao) was further supported by the hierarchical analysis grouping of sites in the west South China Sea (Tioman), east South China Sea (Brunei, Pulau Tiga, Kota Kinabalu) and Coral Triangle or Sulu-Sulawesi Seas (Kudat, Semporna, Davao). Limited larval exchange among the populations was further strengthened by the fact that the neutrality tests were not rejected and the demographic history analyses indicated constant population size (or possibly selection or bottleneck). With a short pelagic larval duration of 2–3 days, it is not unexpected to have population subdivision from neighbouring reefs (Knittweis et al. 2009a). Restricted gene flow was also observed in populations of *H. actiniformis* in the Spermonde Archipelago, Indonesia and across the Indo-Malay Archipelago, which were not located along or near the path of the Indonesian Throughflow to aid larval dispersal (Knittweis et al. 2009a).

There was no genetic differentiation between populations of Kota Kinabalu, Pulau Tiga and Brunei, with a maximum distance of approximately 190 km between these populations along the west coast of Sabah, which point towards small-scale larval exchange facilitated by local current patterns. The current patterns in the South China Sea are influenced by the monsoonal system (Wyrtki 1961), with the northeast monsoon prevailing from November to March and the Southwest monsoon from May to September (Saadon et al. 1999; Morton and Blackmore 2001; Ku Yaacob and Ibrahim 2004; Akhir 2012), while April and October are the inter-monsoon months (Saadon et al. 1999). Along the northwest coast of Borneo, northeasterly currents run along the coast during the northeast monsoon, which reverses in direction during the southwest monsoon (Wyrtki 1961; Morton and Blackmore 2001). This seasonal reversing current is most likely facilitating the larval connectivity among populations of *H. actiniformis* along the northwest coast of Borneo.

Connectivity in populations of L. laevigata

Exclusion of haplotypes from Tioman and Layang-Layang limits the discussion to the populations in north Borneo and Davao, the Philippines. No significant genetic population structure was detected for *L. laevigata*. The neutrality tests indicated possible expansion in populations of Semporna, Kudat and Kota Kinabalu, and supported by the Rogers' test of sudden population expansion (Rogers 1995), despite the multimodal distributions. Population expansion after a bottleneck has also been observed in populations of *L. lae*vigata in the Indo-Malay Archipelago (Crandall et al. 2008b; Kochzius et al. 2009) including the Visayas, the Philippines (Alcazar and Kochzius 2016).

Populations from north Borneo and Davao, spanning across the South China Sea, Sulu Sea and Sulawesi Sea were not significantly different from each other, indicating unrestricted gene flow. Connectivity between the seas are facilitated by northeasterly currents from the South China Sea entering the Sulu Sea through the Balabac Strait during the southwest monsoon between August and October, and the southward currents from the Sulu Sea into the Sulawesi Sea in October. Conversely, currents from the Sulu Sea enter the South China Sea during the northeast monsoon (Wyrtki 1961). Similar to the populations of *H. actiniformis* along the northwest coast of Borneo, the seasonal changing currents, possibly coupled with the long pelagic larval duration in *L. laevigata*, may be enabling larval dispersal across the reef communities of these seas. In addition, the series of reefs between these two seas may act as stepping stones for larval dispersal (Kimura and Weiss 1964; Junio-Menez et al. 2003).

Previous studies of *L. laevigata* on various geographical scales across the Indo-West Pacific region using different markers showed divergence among populations of the Pacific and Indian Ocean (e.g. Williams and Benzie 1997, 1998; Benzie 1998; Williams et al. 2002), and with only moderate genetic structuring (Crandall et al. 2008b). An overlap between these two ocean populations was suggested in the Indo-Malay or northwest Pacific region (Williams 2000), or considered as a genetic break in the Indo-Malay Archipelago in the Sunda Strait (Crandall et al. 2008b; Kochzius et al. 2009). A more comprehensive analysis with newly added localities found the strongest genetic differentiation to the east of Cenderawasih Bay along northeast New Guinea, thus segregating populations between the west: Cenderawasih Bay, Central Indonesia and Indian Ocean, with the east: Western and Central Pacific (Crandall et al. 2014). As all our sampling localities fall to the west of Cenderawasih Bay and the Sunda Strait, it corresponds to the large population of the 'west', and hence exhibited a homogenous population, consistent with the previous findings.

A distinct clade for Borneo?

Clade C of *H. actiniformis* and *L. laevigata* was only present in populations of north Borneo (except for one haplotype of *H. actiniformis* from New Caledonia). Distinct haplotypes or clades occurring in only a few localities have also been noted in *H. actiniformis* from nearshore populations in the Spermonde Archipelago (referred to as private haplotypes by Knittweis et al. 2009a), indicating isolation and limited larval exchange with other populations (Barber et al. 2006). These haplotypes are considered 'young' and have not had the opportunity for widespread dispersal (Palumbi 1997). Distinct group of haplotypes have also been observed in the mantis shrimp *Haptosquilla pulchella* in Sulawesi and West Papua (Barber et al. 2002, 2006), and even in populations with disjunctive locations over a wide geographic range for the mantis shrimp *Gonodactylellus viridis* (Barber et al. 2006). For *L. laevigata*, it is not possible to conclude that Clade C is exclusively found in north Borneo, as the only other population to compare with is from Davao, the Philippines. Coincidentally, a clade exclusive to the eastern part of the Visayas, separate from the central Visayas, was detected in the Philippines (Alcazar and Kochzius 2016). Further analyses and more samples from other localities in the South China Sea and Sulu Sea are needed in order to determine the presence of a distinct clade in north Borneo.

Equivocal results in populations of T. crocea

Weak but significant genetic population structure was detected in *T. crocea*, but there was no significant structure in the a priori groupings. The neutrality tests indicated expansion in all populations, particularly for Semporna and Layang-Layang (as determined by the significant Fu's F test). This was further supported by the test of sudden population expansion (Rogers 1995), as well as by the unimodal distribution for populations of Semporna and Tioman. Strong population structures have been shown across the Indo-Malay Archipelago including parts of the Coral Triangle (DeBoer et al. 2008; Kochzius and Nuryanto 2008), with a partitioning of three phylogeographic regions, i.e. Western Indonesia, Central Indonesia and Eastern Indonesia (DeBoer et al. 2008, 2014b). On a larger scale, genetic division was detected in the East Indian Ocean, Indo-Malay Archipelago and West Pacific (Huelsken et al. 2013; Hui et al. 2016), with a distinct lineage to the east of Cenderawasih Bay (Huelsken et al. 2013), which is almost similar with the genetic break in populations of *L. laevigata* (see Crandall et al. 2014). Our analyses suggested some structure in the populations we examined, but did not point towards a clear partition in the region. Furthermore, the scale of our sampling is much smaller as compared to these previous studies, with a maximum distance of approximately 1190 km between Semporna and Tioman. It is very likely that there is connectivity between populations from Layang-Layang, Kudat and Semporna, as was found for populations of *L. laevigata*.

The lack of conclusive results makes it difficult to confirm that the population of Tioman is genetically differentiated from the populations of north Borneo. The water circulation pattern along the east coast of Peninsular Malaysia reverses between the two monsoon seasons (Xu and Malanotte-Rizzoli 2013). During the northeast monsoon a southwesterly current from the northern rim of the sea passes the Vietnam coast and splits into a small branch that turns northwestwards into the Gulf of Thailand, and a major current that flows southwards through the Karimata Strait into the Java Sea (Xu and Malanotte-Rizzoli 2013), or turns northeasterly along the northwest coast of Borneo (Wyrtki 1961; Morton and Blackmore 2001). The current circulation pattern reverses in direction during the southwest monsoon, driving a northward current from the Karimata Strait through the central South China Sea towards the northern rim of the sea (Wyrtki 1961; Morton and Blackmore 2001; Xu and Malanotte-Rizzoli 2013). This seasonal reversal circulation pattern creates a complex system of eddies and gyres in the South China Sea (Qu 2000; Tangang et al. 2011; Xu and Malanotte-Rizzoli 2013), which could aid in retaining or dispersing larvae across the reef systems in this shallow sea, thereby connecting the reef populations between north Borneo and the east coast of Peninsular Malaysia.

Populations of *T. crocea* from the Philippines have strong genetic affinities with populations from Central Indonesia possibly as a result of the Indonesian Throughflow or the Sulu Sea Troughflow (DeBoer et al. 2014b). Kochzius and Nuryanto (2008) also distinguished connectivity between populations of Kota Kinabalu and Pulau Seribu in the Java Sea. In contrast, studies using allozyme markers found genetic differentiations among populations of the Kalayaan Island group in the South China Sea, the Tubbataha reefs in the Sulu Sea, North Palawan and South Palawan (Juinio-Meñez et al. 2003), but these results cannot be compared with ours due to the different markers.

Distance is not an issue?

Approximately 17,000 years ago, when the sea level was 120 m lower than the present day level, Borneo and Palawan were separated by the Balabac Strait with a width of only 12 km, while Borneo and Sulawesi were separated by a narrow, deep oceanic trench (Voris 2000). These narrow pathways may have allowed gene flow between these seas (but see McManus 1985 for review on the intermittent isolation between the South China Sea and Sulu Sea). At sea level 30 m lower than present day level, land mass between Borneo and Sumatra (including Peninsular Malaysia) were very likely separated (Umbgrove 1949; Emery et al. 1972; Ben-Avraham and Emery 1973; Voris 2000). At present sea level, approximately 10-fold increase in shallow water habitat since the Last Glacial Maximum around 18,000 years ago has allowed dispersal of marine species across the Sunda Shelf and between the Pacific and Indian Ocean (Bellwood and Wainwright 2002; Crandall et al. 2012; Gaither and Rocha 2013). This allows for marine species with moderate to long pelagic larval duration to establish in the Sunda Shelf, such as *T. crocea* and *L. laevigata*, albeit at a slower rate in the former than the latter (see Junio-Menez 2003, and for other examples see Crandall et al. 2012), and disperse under the influence of prevailing monsoonal current patterns.

Isolation by distance analyses revealed no consistent pattern of geographic variation in genetic diversity of the three model species. For *H. actiniformis,* hierarchical AMOVA showed differentiation in the grouping of the west South China Sea (Tioman), east South China Sea (Brunei, Pulau Tiga, Kota Kinabalu) and the Coral Triangle or Sulu-Sulawesi Seas (Kudat, Semporna, Davao), but this restricted gene flow among the grouped populations cannot be attributed to geographical distances among the populations, but possibly the life history trait of this species or local current patterns. This is in contrast with the results of Knittweis et al. (2009a), whereby geographical separation is an important factor in the connectivity among populations in the Spermonde and the Indo-Malay Archipelago.

The lack in pattern of isolation by distance for *L. laevigata* and *T. crocea* in our results is somewhat consistent with the pattern of genetic break for these two species as shown by studies on a larger scale across the Indo-Malay Archipelago. Population of these species can be divided into three general regions, 1) Eastern Indian Ocean, 2) central Indo-Malay Archipelago, and 3) Western Pacific (Kochzius et al. 2009), or 1) Western Indonesia, 2) the Philippines and central Indonesia, and 3) Eastern Indonesia (DeBoer 2014b), with distinct divergence between the Indian and Pacific Ocean (Crandall et al. 2008b). Our sampling localities within the South China Sea and Sulu Sea are nested within the central Indo-Malay Archipelago, or the Philippines and Central Indonesia region, hence congruent with the broad pattern of regional structure in the Indo-West Pacific. Simulation models of connectivity structure distinguished the Spratly Islands (South China Sea), Palawan, the Philippines and the Sulu Archipelago as a region with high levels of connectivity, with the Spratly Islands as an upstream source of larvae for the Sulu Archipelago and the Coral Triangle (Kool et al. 2011) as well as other reefs areas within the South China Sea (Dorman et al. 2015). This underscores the importance of the Spratly Islands and the need to designate a conservation zone or have a concerted effort to establish a management regime for these groups of islands (McManus 1994; Oakley and Pilcher 1996; Ablan et al. 2002).

Conclusions and future direction

Our results on the genetic population structure of *H. actiniformis, L. laevigata* and *T. crocea* in the South China Sea and the Sulu Sea inferred different scales of connectivity, which are most likely attributed to the geological history, contemporary current patterns driven by seasonal monsoon winds and life history trait of the model species (e.g. pelagic larval duration). There was subtle genetic structuring in populations of *H. actiniformis*, with limited larval exchange among three main groupings: 1) west South China Sea (Tioman), 2) east South China Sea (Brunei, Pulau Tiga, Kota Kinabalu), and 3) Coral Triangle or Sulu-Sulawesi Seas (Kudat, Semporna, Davao). The lack of genetic structuring in populations of *L. laevigata* and *T. crocea* suggest connectivity among the sampled reef populations, which is influenced by seasonal circulation patterns in the seas.

Samples for this study were collected from marine park areas except for 44 out of 59 sites in Semporna, which are outside of the Tun Sakaran Marine Park boundary, and sites in Layang-Layang, the Spratly Islands. Semporna has the largest concentration of coral reefs in Malaysia and is known to have high species richness of hard coral, including a few endemic species (Chapter 2). In spite of this, only small areas have been gazetted as the Tun Sakaran Marine Park, and the Sipadan Island Park. Reefs in Semporna should be assessed in order to determine appropriate conservation or management measures tailored to address the issues confronting these reefs (e.g. blast fishing). Layang-Layang together with the other islands and reefs in the Spratly Islands is very likely an important source of larvae for other populations in the South China Sea, the Sulu Sea and the Coral Triangle, and as yet no protection is afforded to these group of islands and reefs.

Acknowledgments

Research permit for Malaysia was granted by the Economic Planning Unit of the Prime Minister's Department, Malaysia (UPE: 40/200/19/2642). Additional permits for sampling were granted by various departments: Sabah Parks and the Sabah Biodiversity Council for marine parks in Sabah, the National Security Council of the Prime Minister's Department for Sipadan and Layang-Layang, and the Department of Marine Parks, Malaysia for marine parks in Peninsular Malaysia. Samples from Semporna were collected during the Semporna Marine Ecological Expedition (SMEE) 2010, whereas samples from Kudat were collected during the Tun Mustapha Park Expedition (TMPE) 2012. Both expeditions were co-organised by WWF-Malaysia, Universiti Malaysia Sabah and Naturalis Biodiversity Center, The Netherlands. Travel expenses for Z. Waheed were funded by the A.M. Buitendijkfonds and Treub-Maatschappij, the Society for the Advancement of Research in the Tropics, The Netherlands for fieldwork in Layang-Layang and Peninsular Malaysia, respectively. We are grateful to the various dive operators for diving logistics throughout this research: Avillion Layang-Layang, East Marine Holidays Sdn Bhd, Tioman Dive Centre, East Divers Tioman and Redang Kalong Resort. We thank Dr. Arthur Bos for samples from Davao, the Philippines. B.W. Hoeksema is grateful to Dr. David Lane for providing logistic support for sampling in Brunei. Samples from New Caledonia were obtained during the mission CORALCAL 4 in 2012 onboard RV Alis of IRD at Nouméa. B.W. Hoeksema would like to thank Dr. Claude Payri and Dr. Francesca Benzoni of IRD for their invitation to join this cruise. Provinces Sud and Nord of New Caledonia provided sampling permits.

Supporting Information

Fig. S1. Mismatch distribution for populations of *Heliofungia actiniformis*

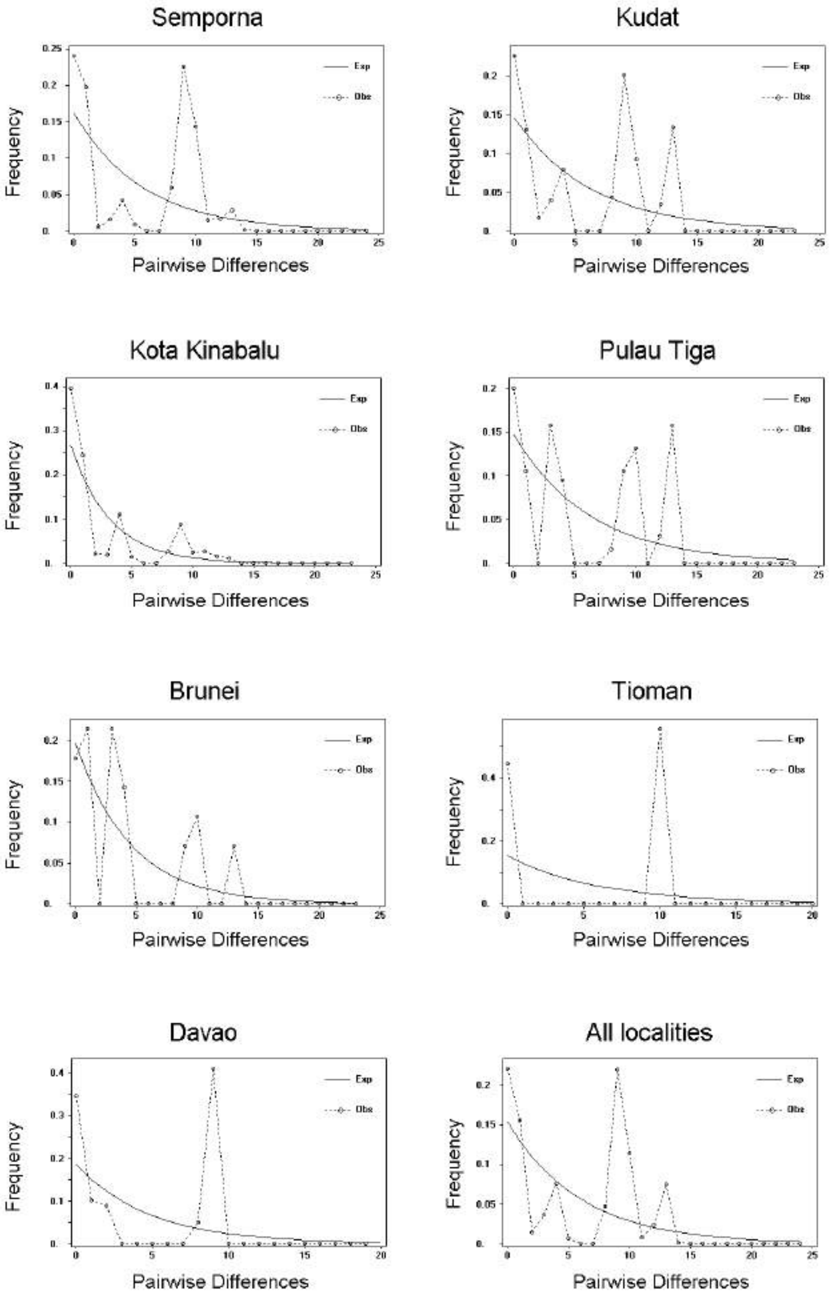


Fig. S2. Mismatch distribution for populations of *Linckia laevigata*

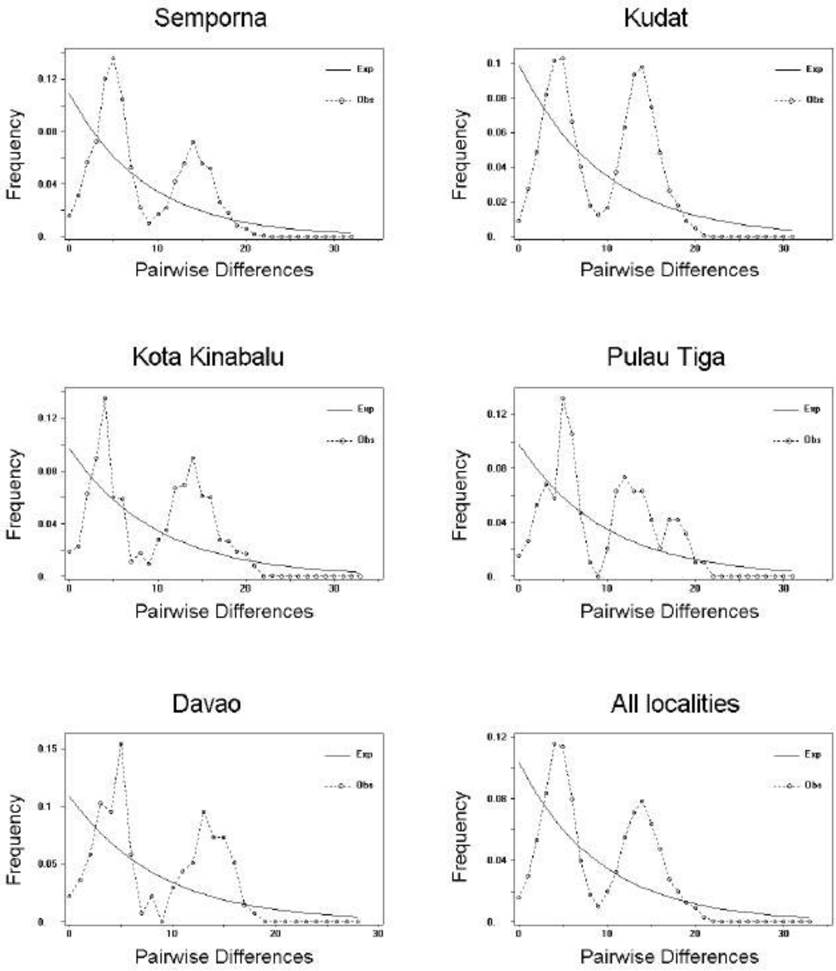


Fig. S3. Mismatch distribution for populations of *Tridacna crocea*

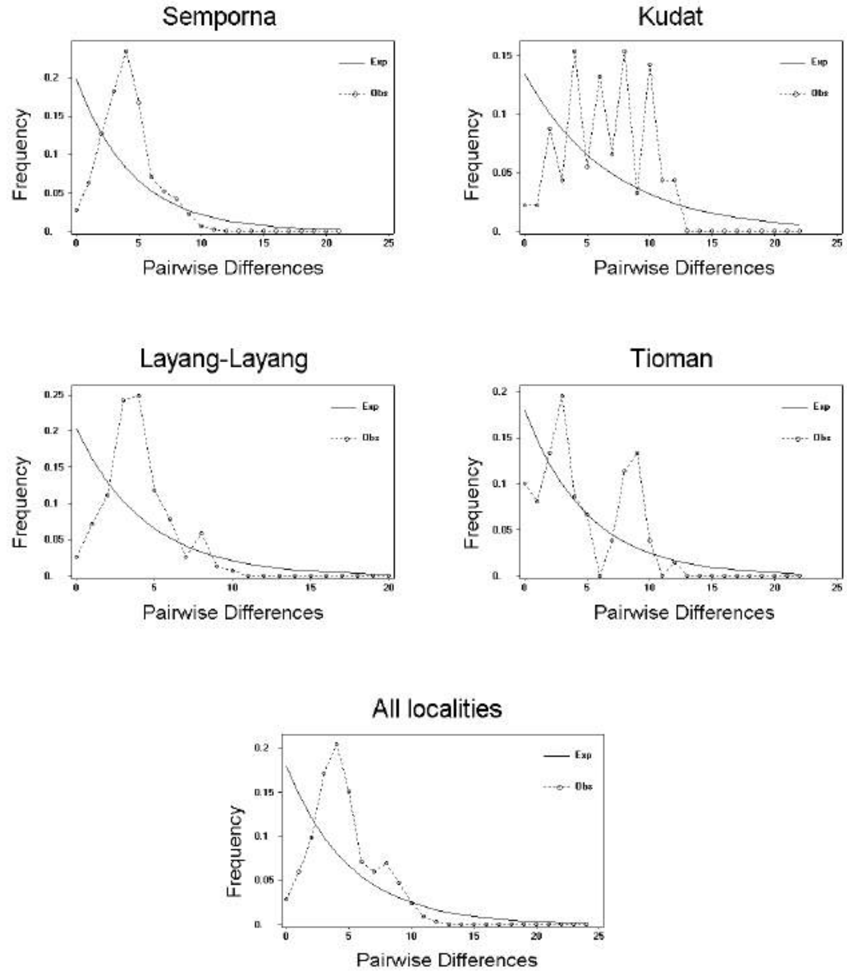


Table S1. Specimens included in the analyses with collection and locality data.

Heliofungia actiniformis							
Haplotype	**Field Col. No.**	**Date**	**Locality**	**Site**	**Latitude**	**Longitude**	**Accession no.**
Haplotype 1	HA01_SEM	29/11/2010	Semporna	SEM 02	04°10′31.5″	118°17′53.5″	Pending
	HA02_SEM	30/11/2010	Semporna	SEM 03	04°08′24.5″	118°10′44.3″	
	HA03_SEM	30/11/2010	Semporna	SEM 03	04°08′24.5″	118°10′44.3″	
	HA05_SEM	01/12/2010	Semporna	SEM 08	04°14′31.9″	118°26′25.0″	
	HA12_SEM	01/12/2010	Semporna	SEM 08	04°14′31.9″	118°26′25.0″	
	HA19_SEM	02/12/2010	Semporna	SEM 12	04°13′49.8″	118°38′12.3″	
	HA22_SEM	02/12/2010	Semporna	SEM 12	04°13′49.8″	118°38′12.3″	
	HA23_SEM	02/12/2010	Semporna	SEM 12	04°13′49.8″	118°38′12.3″	
	HA27_SEM	02/12/2010	Semporna	SEM 12	04°13′49.8″	118°38′12.3″	
	HA29_SEM	03/12/2010	Semporna	SEM 14	04°09′35.8″	118°52′22.2″	
	HA33_SEM	04/12/2010	Semporna	SEM 17	04°18′55.9″	118°51′03.6″	
	HA37_SEM	05/12/2010	Semporna	SEM 20	04°18′58.8″	118°36′17.3″	
	HA44_SEM	08/12/2010	Semporna	SEM 27	04°33′37.7″	118°55′30.4″	
	HA52_SEM	10/12/2010	Semporna	SEM 36	04°37′57.6″	118°45′32.3″	
	HA53_SEM	11/12/2010	Semporna	SEM 37	04°35′00.3″	118°46′39.1″	
	HA58_SEM	12/12/2010	Semporna	SEM 41	04°37′32.2″	118°40′58.0″	
	HA61_SEM	12/12/2010	Semporna	SEM 42	04°34′22.1″	118°43′04.3″	
	HA64_SEM	13/12/2010	Semporna	SEM 47	04°34′27.5″	118°36′15.0″	
	HA65_SEM	15/12/2010	Semporna	SEM 48	04°37′59.6″	118°35′21.6″	
	HA66_SEM	15/12/2010	Semporna	SEM 50	04°43′09.2″	118°28′22.0″	
	HA71_SEM	17/12/2010	Semporna	SEM 55	04°34′29.8″	118°33′59.6″	
	HA72_SEM	17/12/2010	Semporna	SEM 55	04°34′50.9″	118°32′49.4″	
	HA76_SEM	18/12/2010	Semporna	SEM 59	04°07′12.0″	118°37′44.9″	
	HA115_KK	16/07/2011	Kota Kinabalu	KK 30	06°04'26.0"	116°04'47.4"	
	HA125_KK	18/07/2011	Kota Kinabalu	KK 19	06°02'44.6"	116°00'40.5"	
	HA162_KK	26/07/2011	Kota Kinabalu	KK 22	06°01'58.8"	116°02'33.7"	
	HA187_TMP	07/09/2012	Kudat	TMP 01	6°57'08.9"	117°17'01.5"	
	HA188_TMP	07/09/2012	Kudat	TMP 01	6°57'08.9"	117°17'01.5"	
	HA189_TMP	07/09/2012	Kudat	TMP 01	6°57'08.9"	117°17'01.5"	
	HA194_TMP	07/09/2012	Kudat	TMP 03	6°53'45.0"	117°23'15.8"	
	HA204_TMP	09/09/2012	Kudat	TMP 07	6°58'59.3"	117°30'11.2"	
	HA207_TMP	09/09/2012	Kudat	TMP 09	7°02'34.4"	117°27'58.5"	
	HA213_TMP	10/09/2012	Kudat	TMP 11	7°07'06.3"	117°30'42.6"	
	HA214_TMP	10/09/2012	Kudat	TMP 11	7°07'06.3"	117°30'42.6"	
	HA221_TMP	10/09/2012	Kudat	TMP 12	7°03'17.4"	117°22'32.6"	
	HA226_TMP	11/09/2012	Kudat	TMP 14	7°06'50.0"	117°22'36.8"	
	HA228_TMP	11/09/2012	Kudat	TMP 14	7°06'50.0"	117°22'36.8"	

The full list is available upon request.

Table S2. Hierarchical analyses of molecular variance (AMOVA) sequences in *Heliofungia actiniformis*, *Linckia laevigata* and *Tridacna crocea*, with Φ_{CT}, ΦS_{C} and Φ_{ST} values. Generic labels were given to certain groupings: SCS = South China Sea, SS = Sulu Sea, CT = Coral Triangle.

Groupings	Among groups				Among localities within groups				Within localities			
	Var	% Var	Φ_{CT}	P-val	Var	% Var	Φ_{SC}	P-val	Var	% Var	Φ_{ST}	P-val
Heliofungia actiniformis												
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. CT (TMP, SEM, DAV)	**0.54**	**17.47**	**0.17**	**0.029**	0.07	2.30	0.03	0.065	**2.48**	**80.23**	**0.20**	**<0.001**
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. SS (TMP, SEM) vs. DAV	**0.48**	**15.82**	**0.16**	**0.049**	0.07	2.29	0.03	0.055	**2.48**	**81.89**	**0.18**	**<0.001**
SCS (TIO, BRU, PT, KK) vs. CT (TMP, SEM, DAV)	0.45	14.75	0.15	0.055	**0.14**	**4.61**	**0.05**	**0.010**	**2.48**	**80.64**	**0.19**	**<0.001**
West SCS (TIO) vs. East SCS (BRU, PT, KK) vs. North Sabah (TMP) vs. East Sabah. (SEM) vs. DAV	0.32	11.06	0.11	0.231	**0.12**	**3.98**	**0.04**	**0.041**	**2.48**	**84.96**	**0.15**	**<0.001**
Linckia laevigata												
West and north Sabah (PT, KK, TMP) vs. SEM and DAV	0.10	1.81	0.0181	0.102	-0.06	-1.18	-0.01	0.867	5.49	99.37	0.006	0.391
West and north Sabah (PT, KK, TMP) vs. East Sabah (SEM) vs. DAV	0.10	1.78	0.0178	0.106	-0.07	-1.30	-0.01	0.901	5.49	99.51	0.005	0.400
West Sabah (PT, KK) vs. North Sabah (TMP) vs. East Sabah (SEM) vs. DAV	0.10	1.78	0.0178	0.198	-0.09	-1.64	-0.02	0.744	5.49	99.86	0.001	0.396
Tridacna crocea												
TIO vs. (LAC, TMP, SEM)	0.10	4.24	0.04	0.249	0.02	1.02	0.01	0.181	**2.27**	**94.74**	**0.05**	**0.010**
West SCS (TIO) vs. LAC vs. SS (TMP, SEM)	0.06	2.52	0.03	0.336	0.03	1.11	0.01	0.237	**2.27**	**96.38**	**0.04**	**0.011**

Significant at $P < 0.05$ are indicated in bold

References

Abdullah MP (2005) Marine Research Station Layang-Layang Malaysia (MARSAL) 2004 & 2005 highlights. Department of Fisheries Malaysia and Ministry of Agriculture and Agro- based Industry, 52 pp. http://www.fri.gov.my/marsal/publications.html

Abe N (1937) Post larval development of the coral *Fungia actiniformis* var. *palauensis* Doderlein. Palao Tropical Biology Station Studies 1: 73–79.

Ablan MCA, McManus JW, Chen CA, Shao KT, Bell J, Cabanban AS, Tuan VS, Arthana IW (2002) Meso-scale transboundary units for the management of coral reefs in the South China Sea area. NAGA Report 25: 4–9.

Adam A, Mohammad-Noor N, Anton A, Saleh E, Saad S, Muhd Shaleh SR (2011) Temporal and spatial distribution of harmful algal bloom (HAB) species in coastal waters of Kota Kinabalu, Sabah, Malaysia. Harmful Algae 10: 495–502. doi: 10.1016/j.hal.2011.03.006

Affendi YA, Ho N, Kee Alfian AA, Aazani M, Muhammad Ali SH, Nara A, Munirah SS (2012) Reef status. In: Kassem KR, Hoeksema BW, Affendi YA (Eds) Semporna Marine Ecological Expedition. WWF-Malaysia, NCB Naturalis, Universiti Malaysia Sabah. Kota Kinabalu Malaysia, pp. 118–262.

Affendi YA, Rosman FR (2012) Current knowledge on scleractinian coral diversity of Peninsular Malaysia. In: Kamarruddin I, Mohamed CAR, Rozaimi MJ, Kee Alfian AA, Fitra AZ, Lee JN (Eds) Malaysia's Marine Biodiversity: Inventory and Current Status. Department of Marine Park Malaysia, Putrajaya, pp. 21–31.

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19(6): 716–723.

Akhir MFM (2012) Surface circulation and temperature distribution of southern South China Sea from Global Ocean Model (OCCAM). Sains Malaysiana 41(6): 701–714.

Alcazar DSR, Kochzius M (2015) Genetic population structure of the blue sea star *Linckia laevigata* in the Visayas (Philippines). Journal of the Marine Biological Association of the United Kingdom 96(3): 707–713. http://dx.doi.org/10.1017/S0025315415000971

Anton A, Teoh PL, Muhd-Shaleh SR, Mohammad-Noor N (2008) First occurrence of *Cochlodinium* blooms in Sabah, Malaysia. Harmful Algae 7: 331–336. doi: 10.1016/j.hal.2007.12.013

Arrigoni R, Kitano YF, Stolarski J, Hoeksema BW, Fukami H, Stefani F, Galli P, Montano S, Castoldi E, Benzoni F (2014a) A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphological criteria, and its ecological implications. Zoologica Scripta 43: 661–688. doi: 10.1111/zsc.12072

Arrigoni R, Richards ZT, Chen CA, Baird AH, Benzoni F (2014b) Taxonomy and phylogenetic relationships of the coral genera *Australomussa* and *Parascolymia* (Scleractinia, Lobophylliidae). Contributions to Zoology 83(3): 195–215.

Arrigoni R, Terraneo TI, Galli P, Benzoni F (2014c) Lobophylliidae (Cnidaria, Scleractinia) reshuffled: Pervasive non-monophyly at genus level. Molecular Phylogenetics and Evolution 73: 60–64. doi: 10.1016/j.ympev.2014.01.010

Atkinson MA (2011) Biogeochemistry of nutrients. In: Dubinsky Z, Stambler N (Eds) Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht, pp. 199–206.

Avise JC, Arnold J, Ball RM, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC (1987) Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18: 489–522. doi: 10.1146/annurev.es.18.110187.002421

Aw SL (2009) Impact of tourism development and proposed management plan for Mabul Island, Sabah, Malaysia. MSc Thesis, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia.

Aw SL, Muhammad Ali SH (2012) Coral bleaching event in Kota Kinabalu, Sabah, Malaysia. In: International Seminar on Marine Science and Aquaculture, 11–13 March 2012. Universiti Malaysia Sabah, Kota Kinabalu, pp. 80.

Baird AH, Pratchett MS, Hoey AS, Herdiana Y, Campbell SJ (2013) *Acanthaster planci* is a major cause of coral mortality in Indonesia. Coral Reefs 32(3): 803–812. doi: 10.1007/ s00338-013-1025-1

Barber PH (2009) The challenge of understanding the Coral Triangle biodiversity hotspot. Journal of Biogeography 36(10): 1845–1846. doi: 10.1111/j.1365-2699.2009.02198.x

Barber PH, Bellwood DR (2005) Biodiversity hotspots: evolutionary origins of biodiversity in wrasses (*Halichoeres*: Labridae) in the Indo-Pacific and new world tropics. Molecular Phylogenetics and Evolution 35(1): 235–253. doi: 10.1016/j.ympev.2004.10.004

Barber PH, Erdmann MV, Palumbi SR (2006) Comparative phylogeography of three codistributed stomatopods: origins and timing of regional lineage diversification in the Coral Triangle. Evolution 60(9): 1825–1839. doi: 10.1111/j.0014-3820.2006.tb00526.x

Barber PH, Palumbi SR, Erdmann MV, Moosa MK (2002) Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences. Molecular Ecology 11(4): 659–674. doi: 10.1046/j.1365-294X.2002.01468.x

Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (Ed) Coral Reefs. Ecosystems of the World 25. Elsevier Science BV, Amsterdam, pp. 109–131.

Becking LE, Cleary DFR, de Voogd NJ, Renema W, de Beer M, van Soest RWM, Hoeksema BW (2006) Beta diversity of tropical marine assemblages in the Spermonde Archipelago, Indonesia. Marine Ecology 27(1): 76–88. doi: 10.1111/j.1439-0485.2005.00051.x

Beger M, Selkoe KA, Treml E, Barber PH, von der Heyden S, Crandall ED, Toonen RJ, Riginos C (2014) Evolving coral reef conservation with genetic information. Bulletin of Marine Science 90(1): 159–185. doi: 10.5343/bms.2012.1106

Bellwood DR, Hughes TP (2001) Regional-scale assembly rules biodiversity of coral reefs. Science 292(5521): 1532–1535. doi: 10.1126/science.1058635

Bellwood DR, Meyer CP (2009) Searching for heat in a marine biodiversity hotspot. Journal of Biogeography 36(4): 569–576. doi: 10.1111/j.1365-2699.2008.02029.x

Bellwood DR, Renema W, Rosen BR (2012) Biodiversity hotspots, evolution and coral reef biogeography: a review. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST (Eds) Biotic Evolution and Environmental Change in Southeast Asia. Cambridge University Press, New York, pp. 216–245. doi: 10.1017/CBO9780511735882.011

Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (Ed) Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Diego, pp. 5–32.

Ben-Avraham Z, Emery KO (1973) Structural framework of Sunda Shelf. American Association of Petroleum Geologists Bulletin 57(12): 2323–2366.

Benzie JAH (1998) Genetic structure of marine organisms and SE Asian biogeography. In: Hall R, Holloway JD (Eds) Biogeography and Geological Evolution of Southeast Asia. Backhuys Publishers, Leiden, pp. 197–209.

Benzoni F, Stefani F (2012) *Porites fontanesii*, a new species of hard coral (Scleractinia, Poritidae) from the southern Red Sea, the Gulf of Tadjoura, and the Gulf of Aden, and its phylogenetic relationships within the genus. Zootaxa 3447: 56–68. doi: 10.15468/xftkqn

Benzoni F, Arrigoni R, Stefani F, Pichon M (2011) Phylogeny of the coral genus *Plesiastrea* (Cnidaria, Scleractinia). Contributions to Zoology 80(4): 231–249.

Benzoni F, Arrigoni R, Stefani F, Reijnen BT, Montano S, Hoeksema BW (2012a) Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): lost mushroom corals find their way home. Contributions to Zoology 81(3): 125–146.

Benzoni F, Arrigoni R, Stefani F, Stolarski J (2012b) Systematics of the coral genus *Craterastrea* (Cnidaria, Anthozoa, Scleractinia) and description of a new family through combined morphological and molecular analyses. Systematic and Biodiversity 10(4): 417–433. doi: 10.1080/14772000.2012.744369

Benzoni F, Arrigoni R, Waheed Z, Stefani F, Hoeksema BW (2014) Phylogenetic relationships and revision of the genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) with description of a new species. Raffles Bulletin of Zoology 62: 358–378.

Benzoni F, Stefani F, Pichon M, Galli P (2010) The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). Zoological Journal of the Linnean Society 160(3): 421–456. doi: 10.1111/j.1096-3642.2010.00622.x

Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P (2007) Debating phylogenetic relationships of the scleractinian *Psammocora*: molecular and morphological evidences. Contributions to Zoology 76(1): 35–54.

Best MB, Hoeksema BW, Moka W, Moll H, Suharsono, Nyoman Sutarna I (1989) Recent scleractinian coral species collected during the Snellius-II Expedition in Eastern Indonesia. Netherlands Journal of Sea Research 23(2): 107–115. doi: 10.1016/0077-7579(89)90005-7

Bonar SA, Fehmi JS, Mercado-Silva N (2011) An overview of sampling issues in species diversity and abundance surveys. In: Magurran AE, McGill BJ (Eds) Biological Diversity Frontiers in Measurement and Assessment. Oxford University Press, Oxford, pp. 11–24.

Bongaerts P, Frade PR, Ogier JJ, Hay KB, van Bleijswijk J, Englebert N, Vermeij MJA, Bak RPM, Visser PM, Hoegh-Guldberg O (2013) Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2-60 m) on a Caribbean reef. BMC Evolutionary Biology 13: 205. doi: 10.1186/1471-2148-13-205

Bos AR (2012) Fishes (Gobiidae and Labridae) associated with the mushroom coral *Heliofungia actiniformis* (Scleractinia: Fungiidae) in the Philippines. Coral Reefs 31(1): 133. doi: 10.1007/s00338-011-0834-3

Bos A, Hoeksema B (2015) *Cryptobenthic fishes and co-inhabiting shrimps associated with the mushroom coral Heliofungia actiniformis (Fungiidae) in the Davao Gulf, Philippines*. Environmental Biology of Fishes 98(6): 1479–1489. doi: 10.1007/s10641-014-0374-0

Bos AR, Gumanao GS, Mueller B, Saceda-Cardoza MME (2013) Management of crown-of- thorns sea star (*Acanthaster planci* L.) outbreaks: removal success depends on reef topography and timing within the reproduction cycle. Ocean and Coastal Management 71: 116–122. doi: 10.1016/j.ocecoaman.2012.09.011

Boulinier T, Nichols JD, Sauer JR, Hines JE, Pollock KH (1998) Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79(3): 1018–1028. doi: 10.1890/0012-9658(1998)079[1018:ESRTIO]2.0.CO;2

Bowen BW (1999) Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. Molecular Ecology 8(1): S5–S10. doi: 10.1046/j.1365-294X.1999.00798.x

Bowen BW, Rocha LA, Toonen RJ, Karl SA, Craig MT, DiBattista JD, Eble JA, Gaither MR, Skillings D, Bird CE (2013) The origins of tropical marine biodiversity. Trends in Ecology and Evolution 28(6): 359–366. doi: 10.1016/j.tree.2013.01.018

Bowen BW, Shanker K, Yasuda N, Malay MCD, von der Heyden S, Paulay G, Rocha LA, Selkoe KA, Barber PH, Williams ST, Lessios HA, Crandall ED, Bernardi G, Meyer CP, Carpenter KE, Toonen RJ (2014) Phylogeography unplugged: Comparative surveys in the genomic era. Bulletin of Marine Science 90(1): 13–46. doi: 10.5343/bms.2013.1007

Bradbury RH, Young PC (1981) The effects of a major forcing function, wave energy, on a coral reef ecosystem. Marine Ecology Progress Series 5: 229–241.

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monograph 27(4): 325–349. doi: 10.2307/1942268

Briggs JC (1974) Marine Zoogeography. McGraw-Hill, New York, 475 pp.

Briggs JC (1987) Biogeography and Plate Tectonics. Elsevier, Amsterdam, 216 pp.

Briggs JC, BW Bowen (2013) Marine shelf habitat: biogeography and evolution. Journal of Biogeography 40(6): 1023–1035. doi: 10.1111/jbi.12082

Brown BE, Clarke KR, Warwick RM (2002) Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. Marine Biology 141(1): 21–29. doi: 10.1007/s00227-002-0810-0

Brown BE, Holley MC, Sya'rani L, Le Tissier M (1983) Coral assemblages of reef flats around Pulau Pari, Thousand Islands, Indonesia. Atoll Research Bulletin 281: 1–17.

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS ONE 2(8): e711. doi: 10.1371/journal.pone.0000711

Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society 166(3): 465–529. doi: 10.1111/j.1096-3642.2012.00855.x

Burke L, Reytar K, Spalding MD, Perry A (2011) Reefs at Risk Revisited. World Resources Institute, Washington, DC, 114 pp. http://www.wri.org/publication/reefs-risk-revisited

Burke L, Reytar K, Spalding MD, Perry A (2012) Reefs at Risk Revisited in the Coral Triangle. World Resources Institute, Washington, DC, 72 pp. http://www.wri.org/publication/reefs-risk-revisited-coral-triangle

Burke L, Selig E, Spalding M (2002) Reefs at Risk in Southeast Asia. World Resources Institute, Washington DC, 72 pp. http://www.wri.org/publication/reefs-risk-southeast-asia

Burns T (2004) Greenforce Borneo Project for coral reef biodiversity. Fourth annual report (January 2003-April 2004). Greenforce, London, 73 pp.

Burns T, Murphy G, Spence F, Davies L, Colmer M (2005) Greenforce Sabah Project for coral reef biodiversity. Summary of all reports Pantai Kulambu region. Greenforce, London, 23 pp.

Cabanban AS, Nais J (2003) The roles of marine protected areas in Sabah with emphasis on tourism. Sabah Parks Nature Journal 6: 65–77.

Cai S, He Y (2010) Association of the Sulu Sea surface circulation with the South China Sea. Journal of Marine Systems 81(4): 335–340. doi: 10.1016/j.jmarsys.2010.02.010

Cai S, He Y, Wang S, Long X (2009) Seasonal upper circulation in the Sulu Sea from satellite altimetry data and a numerical model. Journal of Geophysical Research 114: C03026. doi: 10.1029/2008JC005109

Cai S, Liu H, Li W, Long X (2005) Application of LICOM to the numerical study of the water exchange between the South China Sea and its adjacent oceans. Acta Oceanologica Sinica 24(4): 10–19.

Cai S, Long X, Wang S (2007) Model study of the upper circulation in the Sulu Sea and its relation to the South China Sea circulation. Acta Oceanologica Sinica 26(5): 1–10.

Camerlengo A, Demmler MI (1997) Wind-driven circulation of Peninsular Malaysia's eastern continental shelf. Scientia Marina 61(2): 203–211.

Carpenter KE, Barber PH, Crandall ED, Ablan-Lagman MCA, Ambariyanto, Mahardika GN, Manjaji-Matsumoto BM, Juinio-Meñez MA, Santos MD, Starger CJ, Toha AHA (2011) Comparative phylogeography of the Coral Triangle and implications for marine management. Journal of Marine Biology 2011, Article ID 396982, 14 pp. doi: 10.1155/2011/396982

Chantrapornsyl S, Kittiwattanawong K, Adulyanukosol K (1996) Distribution and abundance of giant clam around Lee-Pae Island, the Andaman Sea, Thailand. Phuket Marine Biological Center Special Publication 16: 195–200.

Chappell J (1980) Coral morphology, diversity and growth. Nature 286: 249–252. doi: 10.1038/286249a0

Chavanich S, Viyakarn V, Adams P, Klammer J & Cook B (2012) Reef communities after the 2010 mass coral bleaching at Racha Yai Island in the Andaman Sea and Koh Tao in the Gulf of Thailand. Phuket Marine Biological Center Research Bulletin 71: 103–110.

Chen CA (1999) Analysis of scleractinian distribution in Taiwan indicating a pattern congruent with sea surface temperatures and currents: examples from *Acropora* and Faviidae corals. Zoological Studies 38(2): 119–129.

Chen H, Malanotte-Rizzoli P, Koh T-Y, Song G (2014) The relative importance of the wind-driven and tidal circulations in Malacca Strait. Continental Shelf Research 88: 92–102. doi: 10.1016/j.csr.2014.07.012

Chou LM, Wilkinson CR, Licuanan WRY, Alino P, Cheshire AC, Loo MGK, Tangjaitrong S, Sudara S, Ridzwan AR, Soekarno (1994) Status of coral reefs in the ASEAN region. In: Wilkinson C, Sudara S, Chou LM (Eds). Proceedings, Third ASEAN-Australia Symposium on Living Coastal Resources, Volume 1: Status reviews. Chulalongkorn University, Bangkok, pp. 1–10.

Chua TE, Adrian SR, Yu H (1997) Malacca Straits environmental profile. MPP-EAS Technical report, Volume 10, GEF/UNDP/IMO Regional Programme for the Prevention and Management of Marine Pollution in the East Asian Seas, Quezon City, 259 pp.

Chua TE, Charles JJC (1980) Coastal Resources of East Coast Peninsular Malaysia: An Assessment in Relation to Potential Oil Spills. Universiti Sains Malaysia, Penang, 507 pp.

Chua TE, Ross SA (2002) Creating a shared vision for environmental management in the Straits of Malacca. In: Yusoff FM, Shariff M, Ibrahim HM, Tan SG, Tai SY (Eds) Tropical Marine Environment: Charting Strategies for the Millennium. Malacca Straits Research and Development Centre (MASDEC), Universiti Putra Malaysia, Serdang, pp. 19–33.

Claereboudt M, Hoeksema BW (1987) *Fungia* (*Verrillofungia*) *spinifer* spec. nov., a new scleractinian coral (Fungiidae) from the Indo-Malayan region. Zoologische Mededelingen, Leiden 61: 303–309.

Clark AM, Rowe FWE (1971) Monograph of Shallow-Water Indo-West-Pacific Echinoderms. Trustees of the British Museum (Natural History), London, 238 pp. + 31 pls.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18(1): 117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Gorley RN (2006) PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth, 190 pp.

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366(1–2): 56–69. doi: 10.1016/j.jembe.2008.07.009

Clarke KR, Warwick RM (2001) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition. PRIMER-E, Plymouth, 174 pp.

Cleary DFR, Becking LE, de Voogd NJ, Renema W, de Beer M, van Soest RWM, Hoeksema BW (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(3): 557–570. doi: 10.1016/j.ecss.2005.06.025

Cleary DFR, Suharsono, Hoeksema BW (2006) Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. Biodiversity and Conservation 15: 3653–3674. doi: 10.1007/s10531-004-4692-y

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Molecular Ecology 9(10): 1657–1659. doi: 10.1046/j.1365-294x.2000.01020.x

Coelho VR, Manfrino C (2007) Coral community decline at a remote Caribbean island: marine no-take reserves are not enough. Aquatic Conservation 17(7): 666–685. doi: 10.1002/aqc.822

Colgan MW (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. Ecology 68(6): 1592–1605. doi: 10.2307/1939851

Colwell RK (2009) EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application. University of Connecticut, USA. http://viceroy.eeb.uconn.edu/estimates/

Copland JW, Lucas JS (1988) Giant Clams in Asia and the Pacific. Australian Center for International Agricultural Research Monograph No. 9, Canberra, 274 pp.

Cornell HV, Karlson RH (1996) Species richness of reef-building corals determined by local and regional processes. Journal of Animal Ecology 65(2): 233–241. doi: 10.2307/5726

Cornell HV, Karlson RH (2000) Coral species richness: ecological versus biogeographical influences. Coral Reefs 19(1): 37–49. doi: 10.1007/s003380050224

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: an overview. Oceanography 20(3): 14–21. doi: 10.5670/oceanog.2007.26.

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annual Review of Marine Science 1(1): 443–466. doi: 10.1146/annurev.marine.010908.163757

Cowman PF, Bellwood DR (2013) The historical biogeography of coral reef fishes: global patterns of origination and dispersal. Journal of Biogeography 40(2): 209–224. doi: 10.1111/jbi.12003

Crandall ED, Frey MA, Grosberg RK, Barber PH (2008a) Contrasting demographic history and phylogeographical patterns in two Indo-Pacific gastropods. Molecular Ecology 17(2): 611–626. doi: 10.1111/j.1365-294X.2007.03600.x

Crandall ED, Jones ME, Muñoz MM, Akinronbi B, Erdmann MV, Barber PH (2008b) Comparative phylogeography of two seastars and their ectosymbionts within the Coral Triangle. Molecular Ecology 17(24): 5276–5290. doi: 10.1111/j.1365-294X.2008.03995.x

Crandall ED, Sbrocco EJ, Deboer TS, Barber PH, Carpenter KE (2012) Expansion dating: calibrating molecular clocks in marine species from expansions onto the Sunda Shelf following the Last Glacial Maximum. Molecular Biology and Evolution 29(2): 707–719. doi: 10.1093/molbev/msr227

Crandall ED, Treml EA, Liggins L, Gleeson L, Yasuda N, Barber PH, Wörheide G, Riginos C (2014) Return of the ghosts of dispersal past: historical spread and contemporary gene flow in the blue sea star *Linckia laevigata*. Bulletin of Marine Science 90(1): 399–425. doi: 10.5343/bms.2013.1052

Culver M, Fitak R, Herrmann H-W (2011) Genetic methods for biodiversity assessment. In: Magurran AE, McGill BJ (Eds) Biological Diversity Frontiers in Measurement and Assessment. Oxford University Press, Oxford, pp. 208–218.

Curnick DJ, Head CEI, Huang D, Crabbe MJC, Gollock M, Hoeksema BW, Johnson KG, Jones R, Koldewey HJ, Obura DO, Rosen BR, Smith DJ, Taylor ML, Turner JR, Wren S, Redding DW (2015) Setting evolutionary-based conservation priorities for a phylogenetically data-poor taxonomic group (Scleractinia). Animal Conservation 18(4): 303–312. doi: 10.1111/acv.12185.

Dai CF, Lin CH (1992) Scleractinia of Taiwan. Part III. Family Agariciidae. Acta Oceanographica Taiwanica 28: 80–101.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9(8): 772. doi: 10.1038/nmeth.2109

Daw T, Wesson H, Harding S, Lowery C (2002) Pulau Banggi Project for coral reef biodiversity. Second annual report (October 2000-October 2001). Greenforce, London, 68 pp.

Daw T, Wesson H, Harding S, Lowery C, Colmer M (2003) Pulau Banggi Project for coral reef biodiversity. Third annual report (October 2001-December 2002). Greenforce, London, 46 pp.

De’ath G, Moran PJ (1998) Factors affecting the behaviour of crown of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding preferences. Journal of Experimental Marine Biology and Ecology 220(1): 107–126. doi: 10.1016/S0022-0981(97)00100-7

DeBoer TS, Naguit MRA, Erdmann MV, Ablan-lagman MCA, Ambariyanto, Carpenter KE, Toha AHA, Barber PH (2014a) Concordance between phylogeographic and biogeographic boundaries in the Coral Triangle: conservation implications based on comparative analyses of multiple giant clam species. Bulletin of Marine Science 90: 277–300. http://dx.doi.org/10.5343/bms.2013.1003

DeBoer TS, Naguit MRA, Erdmann MV, Ablan-lagman MCA, Ambariyanto, Carpenter KE, Toha AHA, Barber PH (2014b) Concordant phylogenetic patterns inferred from mitochondrial and microsatellite DNA in the giant clam *Tridacna crocea*. Bulletin of Marine Science 90(1): 301–329. http://dx.doi.org/10.5343/bms.2013.1002

DeBoer TS, Subia MD, Ambariyanto, Erdmann MV, Kovitvongsa K, Barber PH (2008) Phylogeography and limited genetic connectivity in the endangered boring giant clam across the Coral Triangle. Conservation Biology 22(5): 1255–1266. doi: 10.1111/j.1523-1739.2008.00983.x

De Silva MWRN, Cabanban AS, Ditlev H, Ridzwan AR (1999) Status of coral reefs of Darvel Bay. In: De Silva MWRN, Ridzwan AR, Saleem M, Cabanban AS (Eds) Ekspedisi Galaxea '98. A Study of Living Marine Resources of Darvel Bay, Sabah, Malaysia. Universiti Malaysia Sabah, Kota Kinabalu, pp. 37–49.

DeVantier LM, De’ath G, Turak E, Done TJ, Fabricius KE (2006) Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. Coral Reefs 25(3): 329–340. doi: 10.1007/s00338-006-0115-8

Dinesen ZD (1980) A revision of the coral genus *Leptoseris* (Scleractinia: Fungiina: Agariciidae). Memoirs of the Queensland Museum 20: 181–235.

Dinesen ZD, Bridge TCL, Luck DG, Kahng SE, Bongaerts P (2012) Importance of the coral genus *Leptoseris* to mesophotic coral communities in the Indo-Pacific. Poster 12th International Coral Reef Symposium, Cairns, 2012, P101. http://www.icrs2012.com/eposters/P101.pdf

Ditlev H (2003) New scleractinian corals (Cnidaria: Anthozoa) from Sabah, North Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology. Zoologische Mededelingen, Leiden 77: 193–219.

Ditlev H, De Silva MWRN, Ridzwan AR, Toerring D, Widt S (1999) Hard Corals of Darvel Bay. In: De Silva MWRN, Ridzwan AR, Saleem M, Cabanban AS (Eds) Ekspedisi Galaxea ’98. A Study of Living Marine Resources of Darvel Bay, Sabah, Malaysia. Universiti Malaysia Sabah, Kota Kinabalu, pp. 51–71.

Dollar SJ (1982) Wave stress and coral community structure in Hawaii. Coral Reefs 1(2): 71–81. doi: 10.1007/BF00301688

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1(2): 95–107. doi: 10.1007/BF00301691

Done TJ (1983) Coral zonation: Its nature and significance. In: Barnes DJ (Ed) Perspectives on Coral Reefs. Manuka, Clouston Publisher, Manuka, pp. 107–147.

Dorman JG, Castruccio FS, Curchitser EN, Kleypas JA, Powell TM (2015) Modeled connectivity of *Acropora millepora* populations from reefs of the Spratly Islands and the greater South China Sea. Coral Reefs 35(1): 169–179. doi: 10.1007/s00338-015-1354-3.

Dubinsky Z, Falkowski P (2011) Light as a source of information and energy in zooxanthellate corals. In: Dubinsky Z, Stambler N (Eds) Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht, pp. 107–118. doi: 10.1007/978-94-007-0114-4_8

Duda Jr TF, Palumbi SR (1999) Population structure of the black tiger prawn *Penaeus monodon*, among western Indian Ocean and western Pacific populations. Marine Biology 134(4): 705–710. doi: 10.1007/s002270050586

Dumaup JNB, Cola RM, Trono RB, Ingles JA, Miclat EFB, Ibuna NP (2003) Conservation Plan for the Sulu-Sulawesi Marine Ecoregion. Stakeholders of the SSME, Technical Working Groups of Indonesia, Malaysia and the Philippines, and the WWF-SSME Conservation Program Team. World Wide Fund for Nature - Sulu-Sulawesi Marine Ecoregion, Quezon City, 88 pp.

Dunn DF (1970) Some observations on marine life at Pulau Aur, Johore. Malayan Nature Journal 23: 158–167.

Ekman S (1934) Indo-Westpazifik und Atlanto-Ostpazifik, eine tiergeographische Studie. Zoogeographica 2(3): 320–374.

Ekman S (1935) Tiergeographie des Meeres. Akademische Verlagsgesellschaft M.B.H., Leipzig, 542 pp.

Ekman S (1953) Zoogeography of the Sea. Sidgwick & Jackson, London, 417 pp.

Emery KO, Uchupi E, Sunderland J, Uktolseja HL, Young EM (1972) Geological structure and some water characteristics of the Java Sea and adjacent continental shelf. United Nations ECAFE, CCOP Technical Bulletin 6: 197–223.

Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA (2012) Environmental impacts of dredging and other sediment disturbances on corals: a review. Marine Pollution Bulletin 64(9): 1737–1765. http://dx.doi.org/10.1016/j.marpolbul.2012.05.008

Excoffier L and Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10(3): 564–567. doi: 10.1111/j.1755-0998.2010.02847.x

Eyal G, Eyal-Shaham L, Cohen I, Tamir R, Ben-Zvi O, Sinniger F, Loya Y (2015) *Euphyllia paradivisa,* a successful mesophotic coral in the northern Gulf of Eilat/Aqaba, Red Sea. Coral Reefs 35(1): 91–102. doi: 10.1007/s00338-015-1372-1

Fairbanks RG (1989) A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep ocean circulation. Nature 342: 637–642. doi: 10.1038/342637a0

Falkowski PG, Jokiel PL, Kinzie III RA (1990) Irradiance and corals. In: Dubinsky Z (Ed) Coral Reefs. Ecosystems of the world 25. Elsevier Science BV, Amsterdam, pp. 89–107.

Fenner D (2001) Reef corals of Banggi area reefs, Sabah, Malaysia. Pulau Banggi Project for Coral Reef Biodiversity. Greenforce, London, 19 pp.

Fenner D (2014) Coral species diversity and abundance. http://chagos-trust.org/2014-biot-expedition

Fisher H (2000) A socio-economic assessment of coastal communities of Pulau Banggi Sabah, East Malaysia. MSc thesis, University of Minnesota, Minneapolis, United States.

Fitch FH (1950) Report of the Geological Survey Department for the Year 1950. British Territories in Borneo. WJ Chater Government Printer, Kuching, 99 pp.

Fleishman E, Noss RF, Noon BR (2006) Utility and limitations of species richness metrics for conservation planning. Ecological Indicators 6(3): 543–553. doi: 10.1016/j.ecolind.2005.07.005

Flot JF (2010) SeqPHASE: a web tool for interconverting PHASE input/output files and FASTA sequence alignments. Molecular Ecology Resources 10(1): 162–166. doi: 10.1111/j.1755-0998.2009.02732.x

Folke C, Carpenter SR, Walker BH, Scheffer M, Elmqvist T, Gunderson LH, Holling CS (2004) Regime shifts, resilience and biodiversity in ecosystem management. Annual Review in Ecology, Evolution and Systematics 35: 557–581. doi: 10.1146/annurev.ecolsys.35.021103.105711

Folmer O, Black M, Hoeh WR, Lutz R, Vrijenhoek RC (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.

Forsman Z, Wellington GM, Fox GE, Toonen RJ (2015) Clues to unravelling the coral species problem: distinguishing species from geographic variation in *Porites* across the Pacific with molecular markers and microskeletal traits. PeerJ 3:e751. doi: 10.7717/peerj.751

Fox HE, Caldwell RL (2006) Recovery from blast fishing on coral reefs: a tale of two scales. Ecological Applications 16(5): 1631–1635. doi:10.1890/1051-0761(2006)016[1631:RFBFOC] 2.0.CO;2

Fox HE, Pet JS, Dahuri R, Caldwell RL (2003) Recovery in rubble fields: long-term impacts of blast fishing. Marine Pollution Bulletin 46(8): 1024–1031. http://dx.doi.org/10.1016/S0025-326X(03)00246-7

Fox J, Weisberg S (2011) An R companion to Applied Regression, 2nd Edition. SAGE Publications, Thousand Oaks, 472 pp.

Fu YX (1997) Statistical tests of neutrality against population growth, hitchhiking and background selection. Genetics 147(2): 915–925.

Fu YX, Li WH (1993) Statistical tests of neutrality of mutations. Genetics 133(3): 693–709.

Fukami H, Chen CA, Budd AF, Collins A, Wallace C, Chuang Y-Y, Chen C, Dai C-F, Iwao K, Sheppard C, Knowlton N (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). PLoS ONE 3(9): e3222. doi: 10.1371/journal.pone.0003222

Gaither MR, Bowen BW, Bordenave T-R, Rocha LA, Newman SJ, Gomez JA, van Herwerden L and Craig MT (2011) Phylogeography of the reef fish *Cephalopholus argus* (Epinephelidae) indicates Pleistocene isolation across the Indo-Pacific Barrier with contemporary overlap in the Coral Triangle. BMC Evolutionary Biology 11: 189. doi: 10.1186/1471-2148-11-189

Gaither MR, Rocha LA (2013) Origins of species richness in the Indo-Malay-Philippine biodiversity hotspot: evidence for the centre of overlap hypothesis. Journal of Biogeography 40(9): 1638–1648. doi: 10.1111/jbi.12126

Gardiner JS (1905) Madreporaria III. Fungida IV. Turbinolidae. In: Fauna and Geography of the Maldives and Laccadives Archipelagoes, Cambridge 2: 933–957, pls. 89–93.

Gaston KJ (2000) Global patterns in biodiversity. Nature 405: 220–227. doi: 10.1038/35012228

Gaston KJ (2010) Biodiversity. In: Sodhi NS, Ehrlich PR (Eds) Conservation Biology for All. Oxford University Press, Oxford, pp. 27–44.

Gaston KJ, Spicer JI (2004) Biodiversity: An Introduction. Second Edition. Blackwell Publishing, Oxford, 208 pp.

George JD, George J (1987) Macroinvertebrates. In: The corals reefs of the Bodgaya Islands (Sabah: Malaysia) and Pulau Sipadan. Malayan Nature Journal 40: 225–260.

Geological Survey Department (1963) Annual Report of the Geological Survey, Borneo Region Malaysia. O.B.E. Government Printer, Kuching, 230 pp.

Gilmour JP (2004) Size-structures of populations of the mushroom coral *Fungia fungites*: the role of disturbance. Coral Reefs 23(4): 493–504. doi: 10.1007/s00338-004-0427-5

Gittenberger A, Hoeksema BW (2006) Phenotypic plasticity revealed by molecular studies on reef corals of *Fungia (Cycloseris)* spp. (Scleractinia: Fungiidae) near river outlets. Contributions to Zoology 75(3–4): 195–201.

Gittenberger A, Reijnen BT, Hoeksema BW (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(2): 107–132.

Glynn PW (1974) The impact of *Acanthaster* on corals and coral reefs in the Eastern Pacific. Environmental Conservation 1(4): 295–303. doi: 10.1017/S037689290000494X

Glynn PW, Wellington GM, Riegl B, Olson DB, Borneman E, Wieters EA (2007) Diversity and biogeography of the scleractinian coral fauna of Easter Island (Rapa Nui). Pacific Science 61(1): 67–90. doi: 10.1353/psc.2007.0005

Google Earth (2013) Version 7.1.2.2014. https://www.google.com/earth/

Google Earth (2015) Version 7.1.5.1557. https://www.google.com/earth/

Gower JC (1966) Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53(3–4): 325–338. doi: 10.1093/biomet/53.3-4.325

Graham EM, Baird AH, Connolly SR (2008) Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27(3): 529–539. doi: 10.1007/s00338-008-0361-z

Green AL, Fernandes L, Almany G, Abesamis R, McLeod E, Aliño PM, White AT, Salm R, Tanzer J, Pressey RL (2014) Designing marine reserves for fisheries management, biodiversity conservation and climate change adaptation. Coastal Management 42(2): 143–159. http://dx.doi.org/10.1080/08920753.2014.877763

Green AL, Mous PJ (2004) Delineating the Coral Triangle, its ecoregions and functional seascapes. Report on an expert workshop, held at the Southeast Asia Center for Marine Protected Areas, Bali, Indonesia (April 30-May 2, 2003). Version 1.1. The Nature Conservancy, Southeast Asia Center for Marine Protected Areas, Bali, Indonesia, 26 pp.

Green AL, Mous PJ (2008) Delineating the Coral Triangle, its ecoregions and functional seascapes. Version 5.0. TNC Coral Triangle Program Report 1/08, 34 pp.

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS One **7**(3): e33353. doi: 10.1371/journal.pone.0033353

Halas D, Winterbottom R (2009) A phylogenetic test of multiple proposals for the origins of the East Indies coral reef biota. Journal of Biogeography 36(10): 1847–1860. doi: 10.1111/j.1365-2699.2009.02103.x

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications 13(1): 117–137. doi: 10.1890/1051-0761(2003)013[0117:TIOMRD] 2.0.CO;2

Hancox D, Prescott V (1995) A geographical description of the Spratly Islands and an account of hydrographic surveys amongst those islands. Maritime Briefing, Volume 1 Number 6. International Boundaries Research Unit, Department of Geography, University of Durham, Durham, UK, 88 pp.

Harborne AD, Fenner D, Barnes A, Beger M, Harding S, Roxburgh T (2000) Status report on the coral reefs of the east coast of peninsula Malaysia. Coral Cay Conservation Ltd., London, 88 pp.

Harding S, Lowery C, Wesson H, Colmer M, Daw T (2001) The Pulau Banggi Project for coral reef biodiversity. First annual report (July 1999-September 2000). Greenforce, London, 65 pp.

Harpending H (1994) Signature of ancient population growth in low-resolution mitochondrial DNA mismatch distribution. Human Biology 66(4): 591–600.

Harpending HC, Batzer MA, Gurven M, Jorde LB, Rogers AR, Sherry ST (1998) Genetic traces of ancient demography. Proceedings of the National Academy of Sciences of the United States of America 95(4): 1961–1967.

Harrison PA, Berry PM, Simpson G, Haslett JR, Blicharska M, Bucur M, Dunford R, Egoh B, Garcia-Llorente M, Geamănă N, Geertsema W, Lommelen E, Meiresonne L, Turkelboom F (2014) Linkages between biodiversity attributes and ecosystem services: a systematic review. Ecosystem Services 9: 191–203. doi: 10.1016/j.ecoser.2014.05.006

Heywood VH, Baste I (1996) Introduction. In: Heywood VH (Ed) Global Biodiversity Assessment. United Nations Environment Programme. Cambridge University Press, Cambridge, pp. 1–19.

Hill J, Wilkinson C (2004) Methods for ecological monitoring of coral reefs: a resource for managers. Australian Institute of Marine Science, Townsville, 117 pp.

Ho N, Kassem KR (2009) Reef status of Semporna Priority Conservation Area. WWF-Malaysia, Kota Kinabalu, 24 pp.

Hodgson G (1999) A global assessment of human effects on coral reefs. Marine Pollution Bulletin 38(5): 345–355. http://dx.doi.org/10.1016/S0025-326X(99)00002-8

Hodgson G, Hill J, Kiene W, Maun L, Mihaly J, Liebeler J, Shuman C, Torres R (2006) Reef Check instruction manual: a guide to Reef Check coral reef monitoring. Reef Check Foundation, Pacific

Hodgson G, Ross MA (1981) Unreported scleractinian corals from the Philippines. Proceedings of the 4th International Coral Reef Symposium, Manila, the Philippines, Volume 2: 171–175.

Hoeksema BW (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zoologische Verhandelingen, Leiden 254: 1–295.

Hoeksema BW (1991) 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. doi: 10.3354/meps075225

Hoeksema BW (1993a) 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): 1–19.

Hoeksema BW (1993b) Phenotypic corallum variability in Recent mobile reef corals. Courier Forschungsinstitut Senckenberg 164: 263–272.

Hoeksema BW (2004) Impact of budding on free-living corals at East Kalimantan, Indonesia. Coral Reefs 23(4): 492. doi: 10.1007/s00338-004-0402-1

Hoeksema BW (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. doi: 10.1007/978-1-4020-6374-9_ 5

Hoeksema BW (2008) Stony corals (Fungiidae). In: Hoeksema BW, van der Meij SET (Eds) Cryptic marine biota of the Raja Ampat Islands group. Progress report Ekspedisi Widya Nusantara (E-Win), pp 8–12.

Hoeksema BW (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 No. 22: 81–90.

Hoeksema BW (2010) Stony corals. In: Hoeksema, BW, van der Meij SET (eds) Crossing marine lines at Ternate: capacity building of junior scientist in Indonesia for marine biodiversity assessments. Progress report Ternate Expedition (2009), pp. 19–25.

Hoeksema BW (2012a) Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. Raffles Bulletin of Zoology 60: 183–212.

Hoeksema BW (2012b) Mushroom corals (Scleractinia: Fungiidae) of Espiritu Santo (Vanuatu, West Pacific) with the description of a new species. Zoosystema 34(2): 429–443. doi: 10.5252/z2012n2a14

Hoeksema BW (2012c) Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). Contributions to Zoology, 81: 199–221.

Hoeksema BW (2012d) Forever in the dark: the cave-dwelling azooxanthellate reef coral *Leptoseris troglodyta* sp. n. (Scleractinia, Agariciidae). ZooKeys 228: 21–37. doi:10.3897/zookeys.228.3798

Hoeksema BW (2013) In search of the Asian-Pacific centre of maximum marine biodiversity: explanations from the past and present. Galaxea, Journal of Coral Reef Studies 15 (Supplement): 1–8.

Hoeksema BW (2014) The "*Fungia patella* group" (Scleractinia, Fungiidae) revisited with a description of the mini mushroom coral *Cycloseris boschmai* sp. n. ZooKeys 371: 57–84. doi: 10.3897/zookeys.371.6677

Hoeksema BW (2015) Latitudinal species diversity gradient of mushroom corals off eastern Australia: a baseline from the 1970s. Estuarine, Coastal and Shelf Science 165: 190–198. doi: 10.1016/j. ecss.2015.05.015

Hoeksema BW, Benzoni F (2013) Multi-species aggregations of mushroom corals in the Gambier Islands, French Polynesia. Coral Reefs 32(4): 1041. doi: 10.1007/s00338-013-1054-9

Hoeksema BW, Bongaerts P, Baldwin CC (2016) High coral cover at lower mesophotic depths: a dense *Agaricia* community at the leeward side of Curaçao, Dutch Caribbean. Marine Biodiversity. doi: 10.1007/s12526-015-0431-8

Hoeksema BW, Dai CF (1991) Scleractinia of Taiwan. II Family Fungiidae (with the description of a new species). Bulletin of the Institute of Zoology, Academia Sinica 30(3): 203–228.

Hoeksema BW, Dautova TN, Savinkin OV, Tuan VS, Ben HX, Hoang PK, Du HT (2010) The westernmost record of the coral *Leptoseris kalayaanensis* in the South China Sea. Zoological Studies 49(3): 325.

Hoeksema BW, Fransen CHJM (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. Coral Reefs 30(2): 519. doi: 10.1007/s00338-011-0736-4

Hoeksema BW, Gittenberger A (2010) High densities of mushroom coral fragments at West Halmahera, Indonesia. Coral Reefs 29(3): 691. doi: 10.1007/s00338-010-0616-3

Hoeksema BW, Koh EGL (2009) Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s–2006) in changing reef conditions. Raffles Bulletin of Zoology Supplement No. 22: 91–101.

Hoeksema BW, Lane DJW (2014) The mushroom coral fauna (Scleractinia: Fungiidae) of Brunei Darussalam (South China Sea) and its relation to the Coral Triangle. Raffles Bulletin of Zoology 62: 566–580.

Hoeksema BW, Matthews JL (2011) Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao, Gulf of Thailand. Coral Reefs 30(1): 95. doi: 10.1007/s00338-010-0675-5

Hoeksema BW, Matthews JL, Yeemin T (2012a) The 2010 coral bleaching event and its impact on the mushroom coral fauna of Koh Tao, western Gulf of Thailand. Phuket Marine Biological Center Research Bulletin 71: 71–81.

Hoeksema BW, Meij SET van der, Fransen CHJM (2012b) The mushroom coral as a habitat. Journal of the Marine Biological Association of the United Kingdom 92(4): 647–663. doi: 10.1017/S0025315411001445

Hoeksema BW, Moka W (1989) Species assemblages and ecomorph variation of mushroom corals (Scleractinia: Fungiidae) related to reef habitats in the Flores Sea. Netherlands Journal of Sea Research 23(2): 149–160. doi: 10.1016/0077-7579(89)90009-4

Hoeksema BW, Scott C, True JD (2013) Dietary shift in corallivorous *Drupella* snails following a major bleaching event at Koh Tao, Gulf of Thailand. Coral Reefs 32(2): 423–428. doi: 10.1007/s00338-012-1005-x

Hoeksema BW, Suharsono, Cleary DFR (2004) Stony corals. In: Hoeksema BW (Ed) Marine biodiversity of the coastal area of the Berau region, East Kalimantan, Indonesia. Progress report East Kalimantan Program - Pilot phase (October 2003), Kalimantan, Indonesia, pp. 7–16.

Hoeksema BW, van der Land J, van der Meij SET, van Ofwegen LP, Reijnen BT, van Soest RWM, de Voogd NJ (2011) Unforeseen importance of historical collections as baselines to determine biotic change of coral reefs: the Saba Bank case. Marine Ecology 32(2): 135–141. doi: 10.1111/j.1439-0485.2011.00434.x

Hoeksema BW, Waheed Z (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. Coral Reefs 30: 1087. doi: 10.1007/s00338-011-0807-6

Hoeksema, BW, Waheed Z (2012) It pays to have a big mouth: mushroom corals ingesting salps at Sabah, Malaysia. Marine Biodiversity 42(2): 297–302. doi: 10.1007/s12526-012-0110-y

Hoeksema BW, Wirtz P (2013) Over 130 years of survival by a small, isolated population of *Favia gravida* corals at Ascension Island (South Atlantic). Coral Reefs 32(2): 551. doi: 10.1007/s00338-012-1002-0

Hoeksema BW, Yeemin T (2011) Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. Coral Reefs 30(4): 975. doi: 10.1007/ s00338-011-0784-9

Huang D (2012) Threatened reef corals of the world. PLoS One, **7**(3): e34459. doi: 10.1371/journal.pone.0034459

Huang D, Benzoni F, Arrigoni R, Baird AH, Berumen ML, Bouwmeester J, Chou LM, Fukami H, Licuanan WY, Lovell ER, Meier R, Todd PA, Budd AF (2014) Towards a phylogenetic classification of reef corals: the Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae). Zoologica Scripta 43(5): 531–548. doi: 10.1111/zsc.12061

Huang D, Hoeksema BW, Affendi YA, Ang PO, Chen CA, Huang H, Lane DJW, Licuanan WY, Vibol O, Vo ST, Yeemin T, Chou LM (2016) Conservation of reef corals in the South China Sea based on species and evolutionary diversity. Biodiversity and Conservation 25(2): 331–344. doi: 10.1007/s10531-016-1052-7

Huang D, Licuanan WY, Hoeksema BW, Chen CA, Ang PO, Huang H, Lane DJW, Vo ST, Waheed Z, Affendi YA, Yeemin T, Chou LM (2015) Extraordinary diversity of reef corals in the South China Sea. Marine Biodiversity 45(2): 157–168. doi: 10.1007/s12526-014-0236-1

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17(8): 754–755. doi: 10.1093/bioinformatics/17.8.754

Huelsken T, Keyse J, Liggins L, Penny S, Treml EA, Riginos C (2013) A novel widespread cryptic species and phylogeographic patterns within several giant clam species (Cardiidae: *Tridacna*) from the Indo-Pacific Ocean. PLoS ONE 8(11): e80858. doi: 10.1371/journal.pone.0080858

Hughes TP, Bellwood DR, Connolly SR (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecology Letters 5(6): 775–784. doi: 10.1046/j.1461-0248. 2002. 00383.x

Hughes TP, Connell JH (2000) Multiple stressors on coral reefs: a long-term perspective. Limnology and Oceanography 44(3): 932–940. doi: 10.4319/lo.1999.44.3_part_2.0932

Hui M, Kraemer WE, Seidel C, Nuryanto A, Joshi A, Kochzius M (2016) Comparative genetic population structure of three endangered giant clams (Cardiidae: *Tridacna* species) throughout the Indo-West Pacific: implications for divergence, connectivity and conservation. Journal of Molluscan Studies. doi: 10.1093/mollus/eyw001

Huntington BE, Karnauskas M, Lirman D (2011) Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation. Coral Reefs 30: 1077–1085. doi: 10.1007/s00338-011-0809-4

Hutchison CS, Vijayan VR (2010) What are the Spratly Islands? Journal of Asian Earth Sciences 39: 371–385. doi: 10.1016/j.jseaes.2010.04.013

International Hydrographic Organization (1953) Limits of Oceans and Seas. Special Publication no. 28. Third edition. http://www.iho-ohi.net/iho_pubs/standard/S-23/S23_1953.pdf

Isley J, Christopher S, Enderby S, Oldfield M, Munns R (2005) Sipadan Mabul Kapalai: Sabah's Underwater Treasure. Natural History Publications (Borneo), Kota Kinabalu, 198 pp.

Ismail G, Shizuri Y, Oakley S, Pilcher N, Miyachi S (1998) Evaluation of marine communities: their potential as bioresources. In: Proceedings of the Tokyo International Forum on Conservation and Sustainable Use of Tropical Bioresources, Tokyo, Japan, 9-10 November 1998. New Energy and Industrial Technology Development Organization (NEDO) and Japan Bioindustry Association (JBA), Japan, pp. 48–83.

Jakobsen F, Hartstein N, Frachisse J, Golingi T (2007) Sabah shoreline management plan (Borneo, Malaysia): ecosystems and pollution. Ocean and Coastal Management 50: 84–102. http://dx.doi.org/10.1016/j.ocecoaman.2006.03.013

Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. Ver. 3.23 BMC Genetics 6: 13. http://ibdws.sdsu.edu/

Jontila JBS, Alarcon R, Bundal M, Parcon J (2010) Benthic communities of Tubbataha Reef Natural Park: status and trends from 1997 to 2010. http://tubbatahareef.org/downloads/research_reports/benthic_report_2010_trnp.pdf

Juinio-Menez MA (2015) Biophysical and genetic connectivity considerations in marine biodiversity conservation and management in the South China Sea. Journal of International Wildlife Law and Policy 18(2): 110–119. doi: 10.1080/13880292.2015.1044803

Juinio-Meñez MA, Magsino RM, Ravago-Gotanco R, Yu ET (2003) Genetic structure of *Linckia laevigata* and *Tridacna crocea* populations in the Palawan shelf and shoal reefs. Marine Biology 142(4): 717–726. doi: 10.1007/s00227-002-0998-z

Jumin R (2009) Occurrence and threats of saltwater crocodile in the proposed Tun Mustapha Park. WWF Malaysia report.

Jumin R, Kassem K (2009) Ecosystem-based management in a proposed marine protected area: Tun Mustapha Park, Sabah. Malaysian Environmental NGOs. http://www.mengo.org/resources/articles/19-ecosystem-based-management-in-a-proposed-marine-protected-area-tun-mustapha-park-sabah

Jumin R, Kassem K, Lim S, Magupin S (2011) Conserving Tun Mustapha Park. Conservation, sustainability and community wellbeing in Malaysia. Decision Point 49: 4. http://community.eldis.org/.59ed3610

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29(2): 255–275. doi: 10.1007/s00338-010-0593-6

Kahng SE, Kelley CD (2007) Vertical zonation of megabenthic taxa on a deep photosynthetic reef (50-140 m) in the Au’au Channel, Hawaii. Coral Reefs 26(3): 679–687. doi: 10.1007/s00338-007-0253-7

Kahng SE, Maragos J E (2006) The deepest, zooxanthellate scleractinian corals in the world? Coral Reefs 25(2): 254. doi: 10.1007/s00338-006-0098-5

Karlson RH (1999) Dynamics of Coral Communities. Springer, Dordrecht, 250 pp.

Karlson RH, Cornell HV (1998) Scale-dependent variation in local vs. regional effects on coral species richness. Ecological Monographs 68(2): 259–274. doi: 10.1890/0012-9615(1998)068[0259:SDVILV]2.0.CO;2

Karlson RH, Cornell HV (1999) Integration of local and regional perspectives on the species richness of coral assemblages. American Zoologist 39(1): 104–112.

Kee Alfian AA, Wong WS, Badrul H, Affendi YA (2005) Macroinvertebrates diversity of Kg. Tekek, Pulau Tioman Marine Park. Proceedings of Second Regional Symposium on Environment and Natural Resources, Volume 2, 22-23 March 2005, Pan Pacific Hotel, Kuala Lumpur, Malaysia, pp. 79–84.

Keith SA, Baird AH, Hughes TP, Madin JS, Connolly SR (2013) Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. Proceedings of the Royal Society B 280: 20130818. http://dx.doi.org/10.1098/rspb.2013.0818

Keshavmurthy S, Yang S-Y, Alamaru A, Chuang Y-Y, Pichon M, Obura D, Fontana S, De Palmas S, Stefani F, Benzoni F, MacDonald A, Noreen AME, Chen C, Wallace CC, Pillay RM, Denis V, Affendi YA, Reimer JD, Mezaki T, Sheppard C, Loya Y, Abelson A, Mohammed MS, Baker AC, Mostafavi PG, Suharsono BA, Chen CA (2013) DNA barcoding reveals the coral “laboratory-rat”, *Stylophora pistillata* encompasses multiple identities. Scientific Reports 3: 1520. doi: 10.1038/srep01520.

Keyse J, Crandall ED, Toonen RJ, Meyer CP, Treml EA, Riginos C (2014) The scope of published population genetic data for Indo-Pacific marine fauna and future research opportunities in the region. Bulletin of Marine Science 90(1): 47–78. doi: 10.5343/bms.2012.1107

Kimura M, Weiss GH (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49(4): 561–576.

Kirk HJC (1962) The geology and mineral resources of the Semporna Peninsula, North Borneo. Geological Survey Department, British Territories in Borneo. Memoir 14: 1–178.

Kitahara MV, Cairns SD, Stolarski J, Blair D, Miller DJ (2010) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. PLoS ONE 5(7): e11490. doi: 10.1371/journal.pone.0011490

Kitahara MV, Stolarski J, Cairns SD, Benzoni F, Stake JL, Miller DJ (2012) The first modern solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural analysis. Invertebrate Systematics 26(3): 303–315. doi: 10.1071/IS11053

Kitano YF, Benzoni F, Arrigoni R, Shirayama Y, Wallace CC, Fukami H (2014) A phylogeny of the family Poritidae (Cnidaria, Scleractinia) based on molecular and morphological analyses. PLoS ONE 9(5): e98406. doi: 10.1371/journal.pone.0098406

Knittweis L, Kraemer WE, Timm J, Kochzius M (2009a) 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. doi: 10.1007/s10592-008-9566-5

Knittweis L, Wolff M (2010) Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: Potential future management approaches. Biological Conservation 143(11): 2722–2729. http://dx.doi.org/10.1016/j.biocon.2010.07.019

Knittweis L, Wolff M, Jompa J, Richter C (2009b) Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia. Coral Reefs 28(3): 793–804. doi: 10.1007/s00338-009-0513-9

Kochzius M, Nuryanto A (2008) Strong genetic population structure in the boring giant clam, *Tridacna crocea*, across the Indo-Malay Archipelago: implications related to evolutionary processes and connectivity. Molecular Ecology 17: 3775–3787. doi: 10.1111/j.1365-294X.2008.03803.x

Kochzius M, Seidel C, Hauschild J, Kirchhoff S, Mester P, Meyer-Wachsmuth I, Nuryanto A, Timm J (2009) Genetic population structure of the blue starfish *Linckia laevigata* and its gastropod ectoparasite *Thyca crystallina*. Marine Ecology Progress Series 396: 211–219. doi: 10.3354/meps08281

Koh LL, Chou LM, Tun KPP (2002) The status of coral reefs of Pulau Banggi and its vicinity, Sabah, based on surveys in June 2002. REST technical report 2/02. National University of Singapore, Singapore, 36 pp.

Kohn AJ (1967) Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. American Naturalist 101(919): 251–259.

Kool JT, Paris CB, Barber PH, Cowen RK (2011) Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. Global Ecology and Biogeography 20(5): 695–706. doi: 10.1111/j.1466-8238.2010.00637.x

Kottelat M (1990) New species and populations of cave nemacheilines in South and Southeast Asia (Osteichthyes: Balitoridae). Mémoires de Biospéléologie 17: 49–55.

Ku Yaacob KK, Ibrahim M (2004) Temperature, salinity and density properties of the south- eastern South China Sea: Pulau Layang Layang area. In: Abdullah MP (Ed) Marine Biodiversity of Pulau Layang-Layang Malaysia, Fisheries Research Institute, Department of Fisheries Malaysia, pp. 89–102. http://www.fri.gov.my/marsal/penerbitan/temperature1.pdf

Lamarck, JBPA de M de (1816) Historie des animaux sans vertebres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie. Déterville & Verdière, Paris, 568 pp.

Lamarck JBPA de M de (1819) Histoire naturelle des animaux sans vertèbres. Tome sixième, 1re partie. Paris: published by the Author, vi + 343 pp.

Lane DJW (2011) Bleaching and predation episodes on Bruneian coral reefs. Scientia Bruneiana 12: 51–58.

Lane DJW (2012) *Acanthaster planci* impact on coral communities at permanent transect sites on Bruneian reefs, with a regional overview and a critique on outbreak causes. Journal of the Marine Biological Association of the United Kingdom 92(4): 803–809. doi: 10.1017/ S0025315411000890

Lane DJW, Hoeksema BW (2016) Mesophotic mushroom coral records at Brunei Darussalam support westward extension of the Coral Triangle to the South China Sea waters of Northwest Borneo. Raffles Bulletin of Zoology 64: 204–212.

Lee JN, Mohamed CAR (2011) Accumulation of settling particles in some coral reef areas of Peninsular Malaysia. Sains Malaysiana 40(6): 549–554.

Lee JN, Mohd S, Ismail MN, Norhayati BA (2012) Carrying capacity of Pulau Redang Marine Park 2011. Department of Marine Parks Malaysia, Putrajaya, 124 pp.

Lee W, Chou LM (2003) The status of coral reefs of Pulau Banggi and its vicinity, Sabah, based on surveys in June 2003. REST technical report 2/03. National University of Singapore, Singapore, 32 pp.

Lee WS (1994) Kajian komuniti karang keras dan ikan chatodontid (Famili Chaetodontidae) di Pulau Mengalum Sabah. BSc Dissertation, Universiti Kebangsaan Malaysia, Malaysia, 193 pp.

Lee YL, Jumin R (2007) Establishing sociological and ecological criteria for zoning in the proposed Tun Mustapha Park. WWF-Malaysia.

Leffler EM, Bullaughey K, Matute DR, Meyer WK, Ségurel L, Venkat A, Andolfatto P, Przeworski M (2012) Revisiting an old riddle: what determines genetic diversity levels within species? PLoS Biology 10(9): e1001388. doi: 10.1371/journal.pbio.1001388

Legendre P, Legendre L (2012) Numerical Ecology. 3rd English Edition. Elsevier, 1006 pp.

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2004) Contribution of rarity and commonness to patterns of species richness. Ecology Letters 7(2): 81–87. doi: 10.1046/j.1461-0248.2004.00548.x

Licuanan WY, Aliño PM (2009) *Leptoseris kalayaanensis* (Scleractinia: Agariciidae), a new coral species from the Philippines. Raffles Bulletin of Zoology 57(1): 1–4.

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae, Laurentii Salvii (Stockholm), 824 pp.

Liu Q, Kaneko A, Jilan S (2008) Recent progress in studies of the South China Sea circulation. Journal of Oceanography 64: 753–762. doi: 10.1007/s10872-008-0063-8.

Lourey MJ, Ryan DAJ, Miller IR (2000) Rates of decline and recovery of coral cover on reefs impacted by, recovering from and unaffected by crown-of-thorns starfish *Acanthaster planci*: a regional perspective of the Great Barrier Reef. Marine Ecology Progress Series 196: 179–186. doi: 10.3354/meps196179

Lucas JS (1988) Giant clams: description, distribution and life history. In: Copland JW, Lucas JS (Eds) Giant Clams in Asia and the Pacific. Australian Centre for International Agricultural Research, Canberra, Australia, pp. 21–32.

Luck DG, Forsman ZH, Toonen RJ, Leicht SJ, Kahng SE (2013) Polyphyly and hidden species among Hawai'i's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae). PeerJ 1: e132. doi: 10.7717/peerj.132

Lulofs RB (1973) A reef survey of Pulau Gaya and associated islands Part I. WWF-Malaysia, 16 pp.

Lulofs RB, Langham NPE, Mathias JA (1974) A reef survey of Pulau Gaya and associated islands Part II. WWF-Malaysia, 7 pp.

Magurran AE (2004) Measuring Biological Diversity. Blackwell, Oxford, 256 pp.

Malaysian Meteorological Department. Monsoon: changing winds. 2013. http://www.met.gov.my/index.php?option=com_content&task=view&id=69&Itemid=160&lang=english

Manly BFJ (1994) Multivariate Statistical Methods: A Primer 2nd edition. Chapman and Hall, New York, 232 pp.

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Research 27(2): 209–220.

Maragos JE, Jokiel PL (1986) Reef corals of Johnston Atoll: one of the world's most isolated reefs. Coral Reefs 4: 141–150. doi: 10.1007/BF00427935

Margules CR and Pressey RL (2000) Systematic conservation planning. Nature 405: 243–253. doi: 10.1038/35012251

Marine Research Unit of Sabah Parks (2005) Hard corals of Tunku Abdul Rahman Park. Unpublished list, 13 pp.

Marsh LM (1974) Shallow-water asterozoans of southeastern Polynesia. I. Asteroidea. Micronesica 10: 65–104.

Marsh LM (1992) Hard corals of the Tunku Abdul Rahman Park, reefs off Semporna and Pulau Sipadan. In: Meagher, TD (Ed) Proposed Semporna Marine Park: Environmental Evaluation for Expanded Tourism Development, Malaysia, 10 pp.

Mathias JA, Langham NPE (1978) Coral reefs. In: Chua TH, Mathias JA (Eds) Coastal resources of West Sabah. Universiti Sains Malaysia, Penang, pp. 117–151.

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones IV SH (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology Progress Series 261: 135–147.

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18(4): 357–367. doi: 10.1007/s003380050213

McIntosh RP (1967) An index of diversity and the relation of certain concepts to diversity. Ecology 48(3): 392–404.

McManus JW (1985) Marine speciation, tectonics and sea-level changes in Southeast Asia. Proceedings of the Fifth International Coral Reef Congress, Tahiti, 4: 133–138.

McManus JW (1994) The Spratly Islands: A marine park. Ambio 23(3): 181–186.

McMonagle LB (2012) A diverse assemblage of corals from the Late Oligocene of eastern Sabah, Borneo: pre-Miocene origins of the Indo-West Pacific marine biodiversity hotspot. MPhil thesis, Durham University, Durham, United Kingdom, 373 pp. http://etheses.dur.ac.uk/5252/

McMonagle LB, Lunt P, Wilson MEJ, Johnson KG, Manning C, Young J (2011) A re-assessment of age dating of fossiliferous limestones in eastern Sabah, Borneo: Implications for understanding the origins of the Indo-Pacific marine biodiversity hotspot. Palaeogeography, Palaeoclimatology, Palaeoecology 305(1–4): 28–42. doi: 10.1016/j.palaeo.2011.02.009

Meagher TD (1992) Proposed Semporna Marine Park. Environmental evaluation for expanded tourism development, 92 pp.

Milne-Edwards H, Haime J (1849) Recherches sur les polypiers. Monographie des Astréides. Annales des Sciences Naturelles, Série 3, Zoologie 11: 233–312.

Mitchell A, Worthington S, Gin O, Bates A, Rushforth J, le Boutillier L (1999) Coral reef survey of TARP. In: Preliminary Report of Oxford University Expedition to Sabah 1999, Oxford, United Kingdom, 60 pp.

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecological Economics 29(2): 215–233. doi: 10.1016/S0921-8009(99)00009-9

Mohamed MIH, Rahman RA, Abdullah MP (1994) Impact of development on Pulau Layang-Layang coral reefs. In: Sudara S, Wilkinson CR, Chou LM (Eds) Proceedings, Third ASEAN-Australia Symposium on Living Coastal Resources, Volume 2 Research Papers, May 1994. Chulalongkorn University, Bangkok, pp. 35–40.

Mohd. Firdaus AN (2013) Preliminary survey of saltwater crocodiles *Crocodylus porosus* and human-crocodile conflicts in Balambangan Island, Kudat Sabah. BSc thesis, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia.

Moll H (1983) Zonation and diversity of Scleractinia on reefs off S.W. Sulawesi, Indonesia. PhD Thesis, Leiden University, Leiden, The Netherlands, 107 pp.

Moll H, Suharsono (1986) Distribution, diversity and abundance of reef corals in Jakarta Bay and Kepulauan Seribu. In: Brown BE (Ed) Human induced damage to coral reefs: results of a regional UNESCO (COMAR) workshop with advanced training. UNESCO Reports in Marine Science 40: 112–125.

Mollusc Specialist Group. 1996. *Tridacna crocea*. The IUCN Red List of Threatened Species 1996: e.T22135A9361892. http://dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T22135A9361892.en

Moolengraaff GAF (1922) Geologie. In: Stok JP van der (Ed) De Zeeën van Nederlandsch Oost-Indië, Brill, Leiden, pp. 272–357, maps I–VII.

Moolengraaff GAF (1929) The coral reefs in the East Indian Archipelago: their distribution and mode of development. Proceedings Fourth Pacific Science Congress, Java, pp. 1–35.

Moolengraaff GAF, Weber M (1921) On the relation between the Pleistocene glacial period and the origin of the Sunda Sea (Java- and South China-Sea), and its influence on the distribution of coral reefs and on the land- and freshwater fauna. Proceedings of the Section of Sciences 23: 395–439. [English translation].

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanography and Marine Biology: an Annual Review 24: 379–480.

Morris PG (1973) Some preliminary notes on Sabah coral reefs. Borneo Research Bulletin 5(2): 57–61.

Morris PG (1977) A note on the occurrence of the Crown of Thorns starfish *Acanthaster planci* (L) on some Sabah coral reefs. Malayan Nature Journal 30(1): 79–85.

Morris PG (1978) Notes on the distribution, geology and invertebrate faunas of some coral reefs in Darvel Bay, Sabah, Malaysia. Sarawak Museum Journal 26: 211–234.

Morton B, Blackmore G (2001) South China Sea. Marine Pollution Bulletin 42: 1236–1263. doi: 10.1016/S0025-326X(01)00240-5

Mouillot D, Parravicini V, Bellwood DR, Leprieur F, Huang D, Cowman PF, Albouy C, Hughes TP, Thuiller W, Guilhaumon F (2016) Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. Nature Communications 7: 10359. doi: 10.1038/ncomms10359

Mumby PJ, Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS ONE 5(1): e8657. doi: 10.1371/journal.pone.0008657

Munro C (2005) Diving systems. In: Eleftheriou A, McIntyre A (Eds) Methods for the Study of Marine Benthos. Blackwell Science, Oxford, pp. 112–159.

Murphy G, Davies L, Spence F (2005) Greenforce Borneo Project for coral reef biodiversity. Fifth annual report. Greenforce, London, 58 pp.

Musa G, Kadir SLSA, Lee L (2006) Layang Layang: an empirical study on SCUBA divers' satisfaction. Tourism in Marine Environments 2(2): 89–102.

Nasrulhakim M, Daud A, Mushidi H (2010) Study of population, distribution and proposed method to control Crown-of-thorns (COT) starfish species outbreak in the waters of Layang- Layang Island, Malaysia. Unpublished report, 15 pp.

Nei M (1987) Molecular Evolutionary Genetics. Columbia University Press, New York, 512 pp.

Nei M, Li W-H (1979) Mathematical model for studying genetic variation in terms of restriction endonucleases. Proceedings of the National Academy of Sciences of the United States of America 76(10): 5269–5273.

Neo ML, Eckman W, Vicentuan K, Teo SL-M, Todd PA (2015) The ecological significance of giant clams in coral reef ecosystems. Biological Conservation 181: 111–123. http://dx.doi.org/10.1016/j.biocon.2014.11.004

Neo ML, Todd PA (2012a) Giant clams (Mollusca: Bivalvia: Tridacninae) in Singapore: history, research and conservation. Raffles Bulletin of Zoology Supplement No. 25: 67–78.

Neo ML, Todd PA (2012b) Population density and genetic structure of the giant clams *Tridacna crocea* and *T. squamosa* on Singapore's reefs. Aquatic Biology 14: 265–275. doi: 10.3354/ab00400

Ng PKL (1988) The freshwater crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore, Shinglee Press, Singapore, 156 pp.

Ng PKL, Yong HS, Sodhi NS (1999) Biodiversity research on Pulau Tioman, Peninsular Malaysia: a historical perspective. Raffles Bulletin of Zoology Supplement No. 6: 5–10.

Nishihira M, Veron JEN (1995) Hermatypic corals of Japan. Kaiyusha Publishers, Tokyo, 440 pp.

Norse EA, Rosenbaum KL, Wilcove DS, Wilcox BA, Romme WH, Johnston DW, Stout ML (1986) Conserving biological diversity in our national forests. Wilderness Society, Washington DC, 116 pp.

Nuryanto A, Kochzius M (2009) Highly restricted gene flow and deep evolutionary lineages in the giant clam *Tridacna maxima*. Coral Reefs. 28(3): 607–619. http://dx.doi.org/10.1007/ s00338-009-0483-y

Nyanti L (1984) Ekologi terumbu karang di Taman Tunku Abdul Rahman. BSc Dissertation, Universiti Kebangsaan Malaysia, Malaysia, 152 pp.

Nyanti L, Johnston NA (1992) The coral reefs of the Tunku Abdul Rahman Park, Sabah. Sabah Society Journal 9(4): 323–348.

Oakley S, Pilcher N (1996) Marine Protected Areas for sustainable fisheries management: Layang Layang reef as a source of larvae in the South China Sea. Proceedings of Workshop on Aquaculture and Sustainable reef fisheries, Kota Kinabalu, Sabah Malaysia, 4-8th December 1996.

Ong C, Yusoff K, Yap C, Tan S (2009) Genetic characterization of *Perna viridis* L. in Peninsular Malaysia using microsatellite markers. Journal of Genetics 88(2): 153–163. doi: 10.1007/s12041-009-0023-0

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2015) vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan

Ormond RFG, Hanscomb NJ, Beach DH (1976) Food selection and learning in the crown- of-thorns starfish *Acanthaster planci* (L). Marine Behaviour and Physiology 4(2): 93–105. doi: 10.1080/10236247609386944

Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). PLoS ONE 6(3): e17516. doi: 10.1371/ journal.pone.0017516

Othman AS, Goh GHS, Todd PA (2010) The distribution and status of giant clams (Family Tridacnidae) – A short review. Raffles Bulletin of Zoology 58(1): 103–111.

Palumbi SR (1997) Molecular biogeography of the Pacific. Coral Reefs 16: S47–S52. doi: 10.1007/s003380050241

Paulay G (1997) Diversity and distribution of reef organisms. In: Birkeland C (Ed) Life and Death of Coral Reefs. Chapman & Hall, New York, pp. 298–353.

Pelé J, Becu JM, Abdi H, Chabbert M (2012) bios2mds: From BIOlogical Sequences to MultiDimensional Scaling. R package version 1.2.2. http://CRAN.R-project.org/package=bios2mds

Penn O, Privman E, Ashkenazy H, Landan G, Graur D, Pupko T (2010a) GUIDANCE: a web server for assessing alignment confidence scores. Nucleic Acids Research 38: W23–W28. doi: 10.1093/nar/gkq443

Penn O, Privman E, Landan G, Graur D, Pupko T (2010b) An alignment confidence score capturing robustness to guide-tree uncertainty. Molecular Biology and Evolution 27(8): 1759–1767. doi: 10.1093/molbev/msq06

Perry CT, Larcombe P (2003) Marginal and non-reef-building coral environments. Coral Reefs 22(4): 427–432. doi: 10.1007/s00338-003-0330-5

Phillips A (1979) Notes on some corals from the west coast of Sabah, Malaysia. Malayan Nature Journal 32(3&4): 327–340.

Pichon M (2007) Scleractinia of New Caledonia: check list of reef dwelling species. In: Payri C, Richer De Forges B (Eds) Compendium of Marine Species of New Caledonia. Documents Scientifiques et Techniques IRD, Nouméa 117(2): 147–157.

Pichon M, Benzoni F (2007) Taxonomic re-appraisal of zooxanthellate scleractinian corals in the Maldive Archipelago. Zootaxa 1441: 21–33. doi: 10.1353/psc.2007.0011

Pilcher NJ, Cabanban AS (2000) The status of coral reefs in eastern Malaysia. Global Coral Reef Monitoring Network (GCRMN) Report. Australia Institute of Marine Science, Townsville, 87 pp.

Pilcher NJ, Oakley SG (1997) Unsustainable fishing practices: crisis in coral reef ecosystems of Southeast Asia. Proceedings of Oceanology International 97 Pacific Rim, Singapore. Spearhead Exhibitions, Surrey, United Kingdom, pp. 77–87.

Pilcher N, Oakley S, Ismail G (1999) Layang Layang a drop in the ocean. Natural History Publications, Kota Kinabalu, 126 pp.

Pillai CSG, Scheer G (1976) Report on the stony corals from the Maldive Archipelago. Zoologica, Stuttgart 126: 1–83, pls. 1–32.

Pope LC, Riginos C, Ovenden J, Keyse J, Blomberg SP (2015) Population genetic diversity in the Australian 'seascape': a bioregion approach. PLoS ONE 10(9): e0136275. doi: 10.1371/journal.pone.0136275

Potts DC (1983) Evolutionary disequilibrium among Indo-Pacific corals. Bulletin of Marine Science 33(3): 619–632.

Potts DC (1984) Generation times and the Quaternary evolution of reef-building corals. Paleobiology 10(1): 48–58.

Potts DC (1985) Sea-level fluctuations and speciation in the Scleractinia. Proceedings of the Fifth International Coral Reef Congress, Tahiti, Volume 4: 127–132.

Pratchett MS (2007) Feeding preferences of *Acanthaster planci* (Echinodermata: Asteroidea) under controlled conditions of food availability. Pacific Science 61(1): 113–120. doi: 10.1353/psc.2007.0011

Pratchett MS (2010) Changes in coral assemblages during an outbreak of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995-1999). Coral Reefs 29(3): 717–725. doi: 10.1007/s00338-010-0602-9

Pratchett MS, Shenk TJ, Baine M, Syms C, Baird AH (2009) Selective coral mortality associ- ated with outbreaks of *Acanthaster planci* L. in Bootless Bay, Papua New Guinea. Marine Environmental Research 67(4–5): 230–236. doi: 10.1016/j.marenvres.2009.03.001

Purchon RD (1956) A list of corals collected in the vicinity of Singapore. Proceedings of the Linnaean Society of New South Wales 81(2): 157–158.

Putchakarn S, Sonchaeng P (2004) Echinoderm fauna of Thailand. History and inventory reviews. Science Asia 30: 417–428.

Qu T (2000) Upper-layer circulation in the South China Sea. Journal of Physical Oceanography 30(6): 1450–1460. doi: 10.1175/1520-0485(2000) 030<1450:ULCITS>2.0.CO;2

Quelch JJ (1886) Report on the reef corals collected by H.M.S. Challenger during the years 1873–76. In: Thomson CW, Murray J (Eds) Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76. Zoology, Volume 16, 203 pp.

Quoy JRC, Gaimard JP (1833). Zoologie IV: Zoophytes. In: Zoologie. Voyage de la corvette l'Astrolabe : exécuté par ordre du roi, pendant les années 1826-1827-1828-1829 / sous le commandement de J. Dumont d'Urville, pp. 1–390.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Ravago-Gotanco RG, Magsino RM, Juinio-Menez MA (2007) Influence of the North Equatorial Current on the population genetic structure of *Tridacna crocea* (Mollusca: Tridacnidae) along the eastern Philippine seaboard. Marine Ecology Progress Series 336: 161–168. http://dx.doi. org/10.3354/meps336161

Raymundo LJ, Maypa AP, Gomez ED, Cadiz P (2007) Can dynamite-blasted reefs recover? A novel, low-tech approach to stimulating natural recovery in fish and coral populations. Marine Pollution Bulletin 54(7): 1009–1019. http://dx.doi.org/10.1016/j.marpolbul.2007.02.006

Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17(1): 230–237. doi: 10.1046/j.1523-1739.2003.01236.x

Reef Check Malaysia (2010). Reef Check Malaysia annual survey report 2010. Reef Check Malaysia, Kuala Lumpur, Malaysia.
http://www.reefcheck.org.my/images/documents/survey_report/RCMSUR_2010.pdf

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43(1): 223–225.

Rizal S, Damm P, Wahid MA, Sundermann J, Ilhamsyah Y, Iskandar T (2012) General circulation in the Malacca strait and Andaman Sea: a numerical model study. American Journal of Environmental Sciences 8(5): 479–488. doi: 10.3844/ajessp.2012.479.488

Rizal S, Setiawan I, Iskandar T, Ilhamsyah Y, Wahid MA, Musman M (2010) Currents simulation in the Malacca Straits by using three-dimensional numerical model. Sains Malaysiana 39(4): 519–524.

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278(5342): 1454–1457. doi: 10.1126/science.278.5342.1454

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1(1): 65–91.

Roe FW (1951) Report of the Geological Survey Department for the Year 1951. British Territory in Borneo. Malaya Publishing House, Singapore, 143 pp.

Rogers AR (1995) Genetic evidence for Pleistocene population expansion. Evolution 49(4): 608–615.

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic differences. Molecular Biology and Evolution 9(3): 552–569.

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62: 185–202.

Romiguier J, Gayral P, Ballenghien M, Bernard A, Cahais V, Chenuil A, Chiari Y, Dernat R, Duret L, Faivre N, Loire E, Lourenco JM, Nabholz B, Roux C, Tsagkogeorga G, Weber AA-T, Weinert LA, Belkhir K, Bierne N, Glémin S, Galtier N (2014) Comparative population genomics in animals uncovers the determinants of genetic diversity. Nature 515: 261–263. doi: 10.1038/nature13685

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12): 1572–1574. doi: 10.1093/bioinformatics/btg180

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. doi: 10.1093/sysbio/sys029

Rooney J, Donham E, Montgomery A, Spalding H, Parrish F, Boland R, Fenner D, Gove J, Vetter O (2010) Mesophotic coral ecosystems in the Hawaiian Archipelago. Coral Reefs 29(2): 361–367. doi: 10.1007/s00338-010-0596-3

Rosen BR (1988) Progress, problems and patterns in the biogeography of reef corals and other tropical marine organisms. Helgoländer Meeresuntersuchungen 42: 269–301. doi: 10.1007/BF02366046

Rosly HAM, Mohd Nor SA, Yahya K, Naim DM (2013) Mitochondrial DNA diversity of mud crab *Scylla olivacea* (Portunidae) in Peninsular Malaysia: a preliminary assessment. Molecular Biology Reports 40(11): 6407–6418. doi: 10.1007/s11033-013-2755-4

Rousseau L (1854) Zoophytes. In: Voyage au pole Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée sous le commandement de MJ Dumont-d'Urville. Zoologie, Paris, pp. 119–124, pls. 27–29.

Roy RN (1977) Red tide and outbreak of paralytic shellfish poisoning in Sabah. The Medical Journal of Malaysia 31(3): 247–251.

Rozihan M, Ismail E (2012) Impact of Malaysian continental drift on the genetic diversity of horseshoe crab inferred through mtDNA sequence analysis. International Journal of Biology 4(1): 104–110. http://dx.doi.org/10.5539/ijb.v4n1p104

Rozihan M, Ismail E, Akbar John B, Jalal KCA, Mohd-Adnan A (2013) Genetic diversity of horseshoe crab (*Tachypleus gigas*) in Malaysia revealed using microsatellite markers. Asian Journal of Animal and Veterinary Advances 8(1): 63–72. doi: 10.3923/ajava.2013.63.72

Russ GR, Alcala AC (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series 132: 1–9. doi: 10.3354/meps132001

Saadon N, Lim PK, Snidvong A, Rojana-Anawat P (1999) Physical characteristics of watermass in the South China Sea, area II: Sarawak, Sabah and Brunei Darussalam waters. In: Proceedings of the second technical seminar on marine fishery resources survey in the South China Sea Area II: Sarawak, Sabah and Brunei Darussalam waters, Kuala Lumpur, Malaysia, 14-15 December 1998. Southeast Asian Fisheries Development Center, Samutprakan, Thailand, pp. 1–22.

Sabah Parks Visitor Statistics (2013) Sabah Parks, Sabah, Malaysia. http://www.sabahparks.org.my/eng/public/visitorfigure.htm

Sabah State Government (1999) Shoreline Management in the ICZM Context. Sabah State Government, Sabah, Malaysia http:// www.townplanning.sabah.gov.my/iczm/Reports/Shoreline%20 Management/mst.pdf

Sahari A, Ilias Z, Sulong N, Ibrahim K (2004) Giant clam species and distribution at Pulau Layang-Layang, Sabah. In: Abdullah MP (Ed.) Marine Biodiversity of Pulau Layang- Layang Malaysia, Fisheries Research Institute, Department of Fisheries Malaysia, pp. 25–28. http://www.fri.gov.my/marsal/penerbitan/giantclam1.pdf

Sanciangco JC, Carpenter KE, Etnoyer PJ, Moretzsohn F (2013) Habitat availability and heterogeneity and the Indo-Pacific warm pool as predictors of marine species richness in the tropical Indo-Pacific. PLoS ONE 8(2): e56245. doi: 10.1371/journal.pone.0056245

Santodomingo N, Renema W, Johnson KG (2016) Understanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia). Coral Reefs 35(3): 765–781. doi: 10.1007/s00338-016-1427-y

Saponari L, Montano S, Seveso D, Galli P (2014) The occurrence of an *Acanthaster planci* outbreak in Ari Atoll, Maldives. Marine Biodiversity 45(4): 599–600. doi: 10.1007/s12526-014-0276-6

Scheer G, Pillai CSG (1983) Report on the stony corals from the Red Sea. Zoologica 45(3): 1–198.

Schmitt EF, Sluka RD, Sullivan-Sealey KM (2002) Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage of southeastern Hispaniola. Coral Reefs 21(2): 216–223. doi: 10.1007/s00338-002-0216-y

Schneider S, Excoffier L (1999) Estimation of past demographic parameters from distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics 152(3): 1079–1089.

Scott CM, Mehrotra R, Urgell P (2014) Spawning observation of *Acanthaster planci* in the Gulf of Thailand. Marine Biodiversity 45(4): 621–622. doi: 10.1007/s12526-014-0300-x

Searle AG (1956) An illustrated key to Malayan hard corals. Malayan Nature Journal 11: 1–26.

Selig ER, Bruno JF (2010) A global analysis of the effectiveness of Marine Protected Areas in preventing coral loss. PLoS ONE 5(2): e9278. doi: 10.1371/journal.pone.0009278

Selig ER, Turner WR, Troëng S, Wallace BP, Halpern BS, Kaschner K, Lascelles BG, Carpenter KE, Mittermeier RA (2014) Global priorities for marine biodiversity conservation. PLoS ONE 9(1): e82898. doi: 10.1371/journal.pone.0082898

Sheppard CRC (1982) Coral populations on reef slopes and their major controls. Marine Ecology Progress Series 7: 83–115.

Shokita S, Kakazu K, Tomori A, Toma T (1991) Aquaculture in Tropical Areas. Midori Shobo, Tokyo, 360 pp.

Slatkin M, Hudson RR (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129(2): 555–562.

Smith TB, Bruford MW, Wayne RK (1993) The preservation of process: the missing element of conservation programs. Biodiversity Letters 1(6): 164–167. doi: 10.2307/2999740

Soegiarto A (2000) Pollution management and mitigation in the Straits of Malacca: priorities, uncertainties and decision making. In: Shariff M, Yusoff FM, Gopinath N, Ibrahim HM, Nik Mustapha RA (Eds) Towards sustainable management of the Straits of Malacca, Malacca Straits Research and Development Center (MASDEC), Faculty of Science and Environmental Studies, Universiti Putra Malaysia, Serdang, pp. 503–518.

Somerfield PJ, Jaap WC, Clarke KR, Callahan M, Hackett K, Porter J, Lybolt M, Tsokos C, Yanev G (2008) Changes in coral reef communities among the Florida Keys, 1996-2003. Coral Reefs 27(4): 951–965. doi: 10.1007/s00338-008-0390-7

Spait M (2001) Marine park management: issues and challenges. 6th Sabah Inter-Agency Tropical Ecosystems (SITE) Research Seminar, 13–14 September 2001. SITE, Kota Kinabalu, Malaysia. 11 pp. http://ww2.sabah.gov.my/jpas/news/SITE/SITEppr16.pdf

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57(7): 573–583. doi: 10.1641/B570707

Spalding MD, Ravilious C, Green EP (2001) World Atlas of Coral Reefs. University of California Press, Berkeley. 416 pp.

Stefani F, Benzoni F, Pichon M, Cancelliere C, Galli P (2008) A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). Zoologica Scripta 37(1): 71–91. doi: 10.1111/j.1463-6409.2007.00309.x

Stefani F, Benzoni F, Yang S-Y, Pichon M, Galli P, Chen CA (2011) Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). Coral Reefs 30(4): 1033–1049. doi: 10.1007/s00338-011-0797-4

Stephens M, Donnelly P (2003) A comparison of Bayesian methods for haplotype reconstruction from population genotype data. *American Journal of Human Genetics* 73(5): 1162–1169. doi: 10.1086/379378

Stephens M, Smith NJ, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics* 68(4): 978–989. doi: 10.1086/319501

Stubbs GC (1961) Some island races of butterflies and their conservation. In: Wyatt-Smith J, Wycherley PR (Ed) Nature Conservation in Western Malaysia. Malayan Nature Journal Special Issue pp. 240–243.

Sturrock K, Rocha J (2000) A multidimensional scaling stress evaluation table. Field Methods 12(1): 49–60. doi: 10.1177/1525822X0001200104

Sukumaran J, Holder MT (2010) DendroPy: A Python library for phylogenetic computing. Bioinformatics 26(12): 1569–1571. doi: 10.1093/bioinformatics/btq228

Sutthacheep M, Yucharoen M, Klinthong W, Pengsakun S, Sangmanee K, Yeemin T (2012) Coral mortality following the 2010 mass bleaching event at Kut Islands, Thailand. Phuket Marine Biological Center Research Bulletin 71: 83–92.

Svrcula K (2008) Layang Layang diving Malaysia’s last frontier. Marshall Cavendish Editions, Malaysia, 168 pp.

Swofford DL (2002) PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), Version 4.0. Sinauer Associates, Sunderland, Massachusetts.

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123(3): 585–595.

Tajima F (1993) Measurement of DNA polymorphism. In: Takahata N, Clark AG (Eds) Mechanisms of Molecular Evolution. Introduction to Molecular Paleopopulation Biology. Scientific Societies Press, Sinauer Associates Inc., Tokyo, Sunderland, MA, pp. 37–59.

Takabayashi M, Carter DA, Loh WKW, Hoegh-Guldberg O (1998a) A coral-specific primer for PCR amplification of the internal transcribed spacer region in ribosomal DNA. Molecular Ecology 7: 928–930.

Takabayashi M, Carter D, Ward S, Hoegh-Guldberg O (1998b) Inter- and intra-specific variability in ribosomal DNA sequence in the internal transcribed spacer region of corals. In: Greenwood JG, Hall NJ (Eds) Proceedings of the Australian Coral Reef Society 75th Anniversary Conference, The University of Queensland, Brisbane, pp. 241–248.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30(12): 2725–2729. doi: 10.1093/molbev/mst197

Tan ASH, Yasin ZB, Salleh IB, Yusof AA (1998) Status of giant clams in Pulau Tioman, Malaysia. Malayan Nature Journal 52(3, 4): 205−216.

Tanggang FT, Xia C, Qiao F, Juneng L, Shan F (2011) Seasonal circulations in the Malay Peninsula Eastern Continental Shelf from a Wave–Tide–Circulation Coupled Model. Ocean Dynamics 61: 1317. doi: 10.1007/s10236-011- 0432-5

Tanzil JTI, Chou LM (2004) The status of coral reefs of Pulau Banggi, Pulau Malawali and the vicinity, Sabah, based on surveys in June 2004. REST technical report no. 6 2004. National University of Singapore, Singapore. 52 pp.

Teh L, Cabanban AS, Sumaila UR (2005) The reef fisheries of Pulau Banggi, Sabah: a preliminary profile and assessment of ecological and socio-economic sustainability. Fisheries Research 76(3): 359–367. http://dx.doi.org/10.1016/j.fishres.2005.07.009

Teh L, Sumaila UR (2007) Malthusian overfishing in Pulau Banggi? Marine Policy 31(4): 451–457. http://dx.doi.org/10.1016/j.marpol.2007.01.001

Teh LSL, Zeller D, Cabanban A, Teh LCL, Sumaila UR (2007) Seasonality and historic trends in the reef fisheries of Pulau Banggi, Sabah, Malaysia. Coral Reefs 26(2): 251–263. doi: 10.1007/s00338-006-0182-x

Templeton AR (1994) Biodiversity at the molecular genetic level: experiences from disparate macroorganisms. Philosophical Transactions: Biological Sciences 345(1311): 59–64.

Templeton AR (1998) The role of molecular genetics in speciation studies. In: DeSalle R, Schierwater B (Eds) Molecular Approaches to Ecology and Evolution. Birkhäuser, Basel, pp. 131–156.

Templeton AR, Crandall KA, Sing CF (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics 132(2): 619−633.

Terraneo TI, Berumen ML, Arrigoni R, Waheed Z, Bouwmeester J, Caragnano A, Stefani F, Benzoni F (2014) *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. ZooKeys 433: 1–30. doi: 10.3897/zookeys.433.8036

Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. Nature 466(7310): 1098–1101. doi: 10.1038/nature09329

Toda T, Okashita T, Maekawa T, Alfian BAAK, Rajuddin MKM, Nakajima R, Chen W, Takahashi KT, Othman BHR, Terazaki M (2007) Community structures of coral reefs around Peninsular Malaysia. Journal of Oceanography 63(1): 113–123. doi: 10.1007/s10872-007-0009-6

Todd PA (2008) Morphological plasticity in scleractinian corals. Biological Reviews 83(3): 315–337. doi: 10.1111/j.1469-185X.2008.00045.x

Tun K, Chou LM, Low J, Yeemin T, Phongsuwan N, Setiasih N, Wilson J, Amri AY, Adzis KAA, Lane D, van Bochove JW, Kluskens B, van Long N, Tuan VS, Gomez E (2010) A regional overview on the 2010 coral bleaching event in Southeast Asia. In: Status of Coral Reefs in East Asian Seas Region 2010. Ministry of the Environment, Japan, pp. 9–27.

Turak E, DeVantier L (2011) Field Guide to the Reef-Building Corals of Brunei Darussalam. Fisheries Department, Ministry of Industry and Primary Resources, Government of Brunei Darussalam, Brunei Darussalam, 256 pp.

Turak E, Sheppard C, Wood E (2008a) *Euphyllia paradivisa*. The IUCN Red List of Threatened Species 2008: e.T133057A3586802. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T133057A3586802.en

Turak E, Sheppard C, Wood E (2008b) *Nemenzophyllia turbida*. The IUCN Red List of Threatened Species 2008: e.T133219A3637817. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T133219A3637817.en

Umbgrove JHF (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 JHF (1940) Madrepora from the Togian Reefs (Gulf of Tomini, North-east Celebes). Zoologische Mededelingen 22: 265–310.

Umbgrove JHF (1947) Coral reefs of the East Indies. Geological Society of America Bulletin 58(8): 729–778. doi: 10.1130/0016-7606(1947)58[729:CROTEI]2.0. CO;2

UNEP/IUCN (1988) Coral reefs of the world. Volume 2: Indian Ocean, Red Sea and Gulf. UNEP Regional Seas Directories and Bibliographies. IUCN Gland, Switzerland and Cambridge, UK/UNEP, Nairobi, Kenya, 389 pp.

UNEP-WCMC (2013) Convention on international trade in endangered species of wild fauna and flora. www.cites.org.

Usup G, Ajmad A & Ismail N (1989) *Pyrodinium bahamense* var. *compressum* red tide studies in Sabah, Malaysia. In: Hallegraeff GM & Maclean JL (eds.) Biology, epidemiology and management of *Pyrodinium* red tides. ICLARM Conference Proceedings 21. Fisheries Department, Ministry of Development, Brunei Darussalam, and International Center for Living Aquatic Resources Management, Manila, Philippines, pp. 97–110.

Van der Meij SET, Hoeksema BW (2013) Distribution of gall crabs inhabiting mushroom corals on Semporna reefs, Malaysia. Marine Biodiversity 43(1): 53–59. doi: 10.1007/s12526-012-0135-2

Van der Meij SET, Suharsono, Hoeksema BW (2010) Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). Marine Pollution Bulletin 60(9): 1442–1454. http://dx.doi.org/10.1016/j.marpolbul.2010.05.011

Van der Meij SET, Visser RR (2011) The *Acropora humilis* Group (Scleractinia) of the Snellius Expedition (1929-30). Raffles Bulletin of Zoology 59: 9–17.

Vaughan TW (1907) Recent Madreporaria of the Hawaiian Islands and Laysan. Bulletin of the United States National Museum 59: 1–427. doi: 10.5479/si.03629236.59.i

Veron JEN (1990) New scleractinia from Japan and other Indo-West Pacific countries. Galaxea 9(2): 95–173.

Veron JEN (1995) Corals in Space and Time: The Biogeography and Evolution of the Scleractinia. Cornell University Press, New York, 336 pp.

Veron JEN (2000) Corals of the World, Volume 2. Australian Institute of Marine Science, Townsville, 429 pp.

Veron JEN, Devantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, Peterson N (2009) Delineating the coral triangle. Galaxea Journal of Coral Reef Studies 11(2): 91–100. doi: 10.3755/galaxea.11.91

Veron JEN, DeVantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, Peterson N (2011) The Coral Triangle. In: Dubinsky Z, Stambler N (Eds) Coral reefs: An Ecosystem in Transition. Springer, Dordrecht, pp. 47–55. doi: 10.1007/978-94-007-0114-4_5

Veron JEN, Pichon M (1980) Scleractinia of Eastern Australia Part III. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae. Australian Institute of Marine Science Monograph Series 4: 1–459. doi: 10.5962/bhl.title.60646

Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Frontiers in Marine Science 1: 81. doi: 10.3389/fmars.2014.00081 von der Heyden S, Beger M, Toonen RJ, van Herwerden L, Juinio-Meñez, MA, Ravago-Gotanco R, Fauvelot C, Bernardi G (2014) The application of genetics to marine management and conservation: examples from the Indo-Pacific. Bulletin of Marine Science 90(1): 123–158. http://dx.doi.org/10.5343/bms.2012.1079

Von Fritsch K (1878) Fossile korallen der Nummulitenschichten von Borneo. Palaeontographica Supplement 3(1): 93–135, pls. 14–19.

Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27(5): 1153–1167. doi: 10.1046/j.1365-2699.2000.00489.x

Wabnitz C, Taylor M, Green E, Razak T (2003) From ocean to aquarium. UNEP-WCMC, Cambridge, United Kingdom, 64 pp. http://www.unep.org/pdf/from_ocean_to_aquarium_report.pdf

Waheed Z, Adnan FAF, Lee CH & Mohd. Hashim SR (2007) Status of coral reefs and sedimentation at Kota Kinabalu: a preliminary study at Gaya Bay and Sepangar Bay. Borneo Science 21: 29–44.

Waheed Z, Ariff AJ, Mustapa I, Brunt H, Yusuf Y, Rahman RA (2009) The status of coral reefs at southeast Malawali, Kudat. Universiti Malaysia Sabah, Kota Kinabalu, 40 pp.

Waheed Z, Rahman RA, Ariff AJ (2012) The status of hard coral diversity in Sabah. In: Kamarruddin I, Mohamed CAR, Rozaimi MJ, Kee Alfian AA, Fitra AZ, Lee JN (Eds) Malaysia's Marine Biodiversity: Inventory and Current Status. Department of Marine Park Malaysia, Putrajaya, pp. 1–19.

Wallace CC (1999) Staghorn Corals of the World: A Revision of the Coral Genus *Acropora* (Scleractinia; Astrocoeniina; Acroporidae) Worldwide, with Emphasis on Morphology, Phylogeny and Biogeography. CSIRO Publishing, Melbourne, 421 pp.

Warta Kerajaan Negeri Sabah (2014). Enakmen Taman-Taman 1984. Jil. LXIX. No. 34. 28 Ogos 2014. ms. 1671–1707. https://www.sabah.gov.my/gazette/docs/002352.pdf

Watts ME, Ball IR, Stewart RS, Klein CJ, Wilson K, Steinback C, Lourival R, Kircher L, Possingham HP (2014) Marxan with zones: Software for optimal conservation based land- and sea-use zoning. Environmental Modelling & Software 24(12): 1513–1521. http://dx.doi.org/10.1016/j.envsoft.2009.06.005

Weeks R, Aliño PM, Atkinson S, Beldia II P, Binson A, Campos WL, Djohani R, Green AL, Hamilton R, Horigue V, Jumin R, Kalim K, Kasasiah A, Kereseka J, Klein C, Laroya L, Magupin S, Masike B, Mohan C, Da Silva Pinto RM, Vave-Karamui A, Villanoy C, Welly M, White AT (2014) Developing marine protected area networks in the Coral Triangle: best practices for expanding the Coral Triangle marine protected area system. Coastal Management 42(2): 183–205. doi: 10.1080/08920753.2014.877768

Weissel JK (1980) Evidence for Eocene oceanic crust in the Celebes Basin. In: Hayes DE (Ed) The Tectonic and Geologic Evolution of Southeast Asian Seas and Islands. American Geophysical Union, Washington DC, pp. 37–47. doi: 10.1029/GM023p0037

Wells DR (1977) The Balambangan report 1977. A survey of the proposed Pulau Balambangan National Park, Sabah. Universiti Malaya, Kuala Lumpur, 68 pp.

Wells JW (1954) Recent corals of the Marshall Islands. Bikini and nearby atolls, Part 2, Oceanography (Biologic). United States Geological Survey Professional Paper 260-I: 385–486.

Wells JW (1969) Aspects of Pacific coral reefs. Micronesica 5: 317–322.

White AT, Aliño PM, Cros A, Ahmad Fatan N, Green AL, Teoh SJ, Laroya L, Peterson N, Tan S, Tighe S, Venegas-Li R, Walton A, Wen Wen (2014) Marine protected areas in the Coral Triangle: progress, issues, and options. Coastal Management 42(2): 87–106. doi: 10.1080/08920753.2014.878177

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR Protocols: A Guide to Methods and Application. Academic Press Inc., San Diego, pp. 315–322. doi: 10.1016/b978-0-12-372180-8.50042-1

Whitaker D, Christman M (2014) clustsig: significant cluster analysis. R package version 1.1. http://CRAN.R-project.org/package=clustsig

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21(2/3): 213–251. doi: 10.2307/1218190

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28(4): 453–470. doi: 10.1046/j.1365-2699.2001.00563.x

Wilkinson CR (1998) The 1997–1998 mass bleaching event around the world. In: Wilkinson CR (Ed) Status of Coral Reefs of the World: 1998. Australian Institute of Marine Science, Cape Ferguson, Western Australia, pp. 15–38.

Wilkinson C (2008) Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia, 296 pp.

Williams ST (2000) Species boundaries in the starfish genus *Linckia*. Marine Biology 136(1): 137–148. doi: 10.1007/s002270050016.

Williams ST, Benzie JAH (1996) Genetic uniformity of widely separated populations of the coral reef starfish *Linckia laevigata* from the East Indian and West Pacific Oceans, revealed by allozyme electrophoresis. Marine Biology 126(1): 99–107. doi: 10.1007/BF00571381

Williams ST, Benzie JAH (1997) Indo-West Pacific patterns of genetic differentiation in the high-dispersal starfish *Linckia laevigata*. Molecular Ecology 6(6): 559–573. doi: 10.1046/j.1365-294X.1997.00221.x

Williams ST, Benzie JAH (1998) Evidence of a biogeographic break between populations of a high dispersal starfish: congruent regions within the Indo-West Pacific defined by colour morphs, mtDNA, and allozyme data. Evolution 52(1): 87–99. doi: 10.2307/2410923

Williams ST, Jara J, Gomez E, Knowlton N (2002) The marine Indo-West Pacific break: contrasting the resolving power of mitochondrial and nuclear genes. Integrative and Computational Biology 42(5): 941–952.

Wilson JR, Harrison PL (1998) Settlement-competency periods of larvae of three species of scleractinian corals. Marine Biology 131(2): 339–345. doi: 10.1007/s002270050327

Wilson MEJ, Rosen BR (1998) Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or centre of origin? In: Hall R, Holloway JD (Eds) Biogeography and Geological Evolution of SE Asia. Backhuys Publisher, Leiden, pp. 165–195.

Winter M, Devictor V, Schweiger O (2013) Phylogenetic diversity and nature conservation: where are we? Trends in Ecology & Evolution 28(4): 199–204. http://dx.doi.org/10.1016/j.tree.2012.10.015

Wong NLWS, Arshad A (2011) A brief review on marine shelled mollusca (Gastropoda and Bivalvia) record in Malaysia. Journal of Fisheries and Aquatic Science 6(7): 669−699. doi: 10.3923/jfas.2011.669.699

Wood CR (1987) Physical features of the islands and coral reefs. In: The corals reefs of the Bodgaya Islands (Sabah: Malaysia) and Pulau Sipadan. Malayan Nature Journal 40: 169–188.

Wood CR (1994) Physical features of the Sipadan reef. In: Pulau Sipadan: Reef life and ecology. Technical report, WWF Project Number MYS 233/92, Petaling Jaya, Malaysia, pp. 11–22.

Wood CR, Wood EM (1987) Fishes. In: The corals reefs of the Bodgaya Islands (Sabah: Malaysia) and Pulau Sipadan. Malayan Nature Journal 40: 285–310.

Wood EM (1977) Coral reefs in Sabah: present damage and potential dangers. Malayan Nature Journal 31(1): 49–57.

Wood EM (1978) Ecological study of coral reefs in Sabah. Technical report, WWF Project Number MYS 15, Petaling Jaya, Malaysia, 163 pp.

Wood EM (Ed) (2001) Management plan for the Semporna Islands Park, Sabah, Malaysia, proposed through the Semporna Islands Project. Marine Conservation Society, Sabah Parks, WWF-Malaysia, Nature Link, 168 pp.

Wood EM (2006a) Report of fish blasting incident in the Tun Sakaran Marine Park, and the need for increased surveillance. Darwin Initiative, Semporna Islands Darwin Project, Marine Conservation Society, 4 pp.

Wood EM (2006b) Sustainable use and conservation of biodiversity in the Tun Sakaran Marine Park. Action plan and proposed regulations. Sabah Parks, Darwin Initiative, Marine Conservation Society, 167 pp.

Wood EM, Dipper F (2008) What is the future for extensive areas of reef impacted by fish blasting and coral bleaching and now dominated by soft corals? A case study from Malaysia. Proceedings of the 11th International Coral Reef Symposium, Fort Lauderdale, Florida, Volume 1, pp. 410–415.

Wood EM, Dipper F, Angkaji A (2004) Patterns of change in reef communities revealed by the monitoring programme for the Semporna Island reefs, Sabah, Malaysia. Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan, pp. 1943–1949.

Wood EM, Irwanshah M, Brunt H (2008) Stop fish blasting campaign: Tun Sakaran Marine Park. Semporna Islands Darwin Project, Sabah Parks, Darwin Initiative, Marine Conservation Society, 7 pp.

Wood EM, Tan BS (1987) Hard Coral. In: The corals reefs of the Bodgaya Islands (Sabah: Malaysia) and Pulau Sipadan. Malayan Nature Journal 40: 189–224.

Wood S, Paris CB, Ridgwell A, Hendy EJ (2014) Modelling dispersal and connectivity of broadcast spawning corals at the global scale. Global Ecology and Biogeography 23(1): 1–11. doi: 10.1111/geb.12101

Woodman G, Wilson S (1994) Changes to coral reef communities in the Tunku Abdul Rahman National Park, Sabah, Malaysia between 1987 and 1994. Final report of Oxford University Expedition to Sabah 1994, Oxford University, Oxford, United Kingdom, 110 pp.

Woodman GH, Wilson SC, Li VYF, Renneberg R (2004) A direction-sensitive underwater blast detector and its application for managing blast fishing. Marine Pollution Bulletin 49(11–12): 964–973. http://dx.doi.org/10.1016/j.marpolbul.2004.06.022

Wooldridge SA (2014) Assessing coral health and resilience in a warming ocean: why looks can be deceptive. Bioessays 36(11): 1041–1049. doi: 10.1002/bies.201400074

Wyrtki K (1961) Physical oceanography of the Southeast Asian waters. NAGA Report Volume 2: Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand, 1959–1961. University of California, La Jolla, USA, 195 pp.

WWF factsheet (2013a) Developing zoning plan for Tun Mustapha Park. November 2013. http://www.coraltriangleinitiative.org/sites/default/files/resources/20_Developing%20Zoning%20Plan%20for%20TMP%20%28factsheet%29.pdf.

WWF factsheet (2013b) Establishment of Tun Mustapha Park (TMP). June 2013. http://www.coraltriangleinitiative.org/sites/default/files/resources/38_Establishment%20of%20TMP%20Factsheet.pdf

Xu D, Malanotte-Rizzoli P (2013) The seasonal variation of the upper layers of the South China Sea (SCS) circulation and the Indonesian through flow (ITF): an ocean model study. Dynamics of Atmospheres and Oceans 63: 103–130. doi: 10.1016/j.dynatmoce.2013.05.002

Yamaguchi M (1973) Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). In: Jones OA, Endean R (Eds) Biology and Geology of Coral Reefs. Academic Press, New York and London, pp. 369–387.

Yamaguchi M (1977) Population structure, spawning and growth of the coral reef asteroid *Linckia laevigata* (Linneaus). Pacific Science 31(1): 13–30. http://hdl.handle.net/10125/1178

Yap CK, Tan SG, Ismail A, Omar H (2002) Genetic variation of green-lipped mussel *Perna viridis* (L.) (Mytilidae: Mytiloida: Mytilicae) from the west coast of Peninsular Malaysia. Zoological Studies 41(1): 376–387.

Yeemin T, Pengsakun S, Yucharoen M, Klinthong W, Sangmanee K, Sutthacheep M (2013) Long-term decline in *Acropora* species at Kut Island, Thailand, in relation to coral bleaching events. Marine Biodiversity 43(1): 23–29. doi: 10.1007/s12526-012-0138-z

Zainal Abidin DH, Mustaffa S, Rahim MA, Nair DM, Naim DM, Mohd Nor SA (2016) Population genetics of the black scar oyster, *Crassostrea iredalei*: repercussion of anthropogenic interference. Mitochondrial DNA Part A 27(1): 647–658. doi: 10.3109/19401736.2014.913137

Zainuddin I, Pauzi MA, Abdul Razak L, Yazid MY (2000) Preliminary study on the diversity and distribution of sponges at Pulau Layang-Layang, Sabah, Malaysia. Malayan Nature Journal 54(2): 77–86.

Zakariah ZM, Ahmad AR, Tan KH, Basiron MN, Yusoff NA (2007) National report on coral reefs in the coastal waters of the South China Sea – Malaysia. In: National reports on coral reefs in the coastal waters of the South China Sea. UNEP/GEF/SCS Technical Publication 11: 37–54. http://www.unepscs.org/components/com_remository_files/downloads/National-Report-Coral-Reefs-Malaysia.pdf

Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD dissertation, The University of Texas, Austin, United States, 115 pp.

Affiliation of co-authors

Francesca Benzoni, Department of Biotechnology and Biosciences, University of Milano-Bicocca, Piazza della Scienza 2, 20126 Milan, Italy.

Bobita Golam Ahad, Scubazoo Images Sdn Bhd., Mile 3-1/2, Jalan Nosoob, 88300 Kota Kinabalu, Sabah, Malaysia.

Bert W. Hoeksema, Department of Taxonomy & Systematics, Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands.

Robecca Jumin, WWF-Malaysia, 6th Floor, CPS Tower, Centre Point Complex, No. 1, Jalan Centre Point, 88000 Kota Kinabalu, Sabah, Malaysia.

Marc Kochzius, Department of Biology, Vrije Universiteit Brussel (VUB), Pleinlaan 2, 1050 Brussels, Belgium.
Department of Biotechnology and Molecular Genetics, FB2-UFT, University of Bremen, Leobener Straße UFT, 28359 Bremen, Germany.

Bastian T. Reijnen, Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands.

Muhammad Ali Syed Hussein, Borneo Marine Research Institute, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia.

Tullia I. Terraneo, Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal 23955, Kingdom of Saudi Arabia.

Sancia E.T. van der Meij, Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, United Kingdom.
Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, the Netherlands.

Harald G.J. van Mil, Institute of Biology Leiden, Leiden University, Sylvius Laboratory, Sylviusweg 72, 2333 BE Leiden, the Netherlands.

Affendi Yang Amri, Institute of Biological Sciences, Faculty of Science, University of Malaya, 50603 Kuala Lumpur, Malaysia.

Summary

Malaysia is composed of two land areas separated by the South China Sea: Peninsular Malaysia (also known as West Malaysia) on the Asian continent, and East Malaysia (the states of Sabah and Sarawak, and the Federal Territory of Labuan) on the island of Borneo. The majority of Malaysia's reefs are located in Sabah. At the onset of this study, only part of Sabah's reefs was considered to be within the Coral Triangle in large part due to a lack of information on the area. Much remains to be discovered about the biodiversity of coral reefs in Malaysia making this area a priority for coral reef research. This thesis aims to provide insights on the patterns of reef coral species richness, and the degree of reef connectivity across Malaysia by examining the genetic population structure of model reef invertebrates. Two main questions were addressed:

1) Is there a reef coral species richness gradient across Malaysia, and if so, does it decrease with increasing distance from the Coral Triangle?
2) Is there connectivity in the coral reefs of Malaysia?

This study was guided by two main hypotheses:

1) Reefs in Peninsular Malaysia and the west coast of Sabah are not as species-rich as reefs in the east coast of Sabah as the marine life were only able to recolonise the southern South China Sea after the Last Glacial Maximum.
2) Reefs on the east coast of Sabah are species-rich as they have been established in the Sulu Sea since the Oligocene Epoch.

In order to address these questions, data on coral species and specimens of reef invertebrates were collected from key coral reef areas in Malaysia. For the coral species richness study, scleractinian coral families Fungiidae, Agariciidae and Euphylliidae were selected as model taxa. Species of these families have a wide geographical distribution in the Indo-Pacific, they can be found in a large range of reef habitat from shallow coastal reefs to deep offshore environments, and they are also easily distinguishable from other coral families. As very little information was available on the reefs of Sabah, East Malaysia, a more detailed investigation of the coral species richness patterns was made at each reef locality. Environmental factors that can influence coral species composition such as reef depth and exposure were also evaluated. To infer the connectivity of reefs, three reef invertebrate species were selected as model species, the mushroom coral *Heliofungia actiniformis*, the blue seastar *Linckia laevigata* and the boring giant clam *Tridacna crocea*. There are existing genetic studies of these three species in the Coral Triangle, but most lacked information from Malaysia. Data collection and sampling occurred throughout five separate fieldtrips at seven localities and from 194 reef sites across Malaysia. The surveys were conducted along a geographical range from east to west, with three localities each in Sabah, East Malaysia (Semporna, Kudat and Kota Kinabalu), and Peninsular Malaysia (Tioman, Redang and Payar), and Layang-Layang Island in the disputed Spratly Islands. An additional 19 sites from the three localities in Sabah were surveyed for mushroom corals only.

The study began by exploring the species richness patterns of reef corals in the Semporna peninsula and part of Darvel Bay on the east coast of Sabah (Chapter 2). This area has the highest concentration of coral reefs in Sabah, and also Malaysia. The reefs consist of five major geomorphological reef types: lagoonal reefs inside a proto-atoll, fringing reefs, continental patch reefs, a barrier reef and a reef capping an oceanic island. All together, they represent various reef environments that can harbour a high diversity of coral species. In total, 89 coral species were observed: 44 Fungiidae, 30 Agariciidae and 15 Euphylliidae, which include 12 new species records for Sabah. Reef exposure was an important factor in influencing the coral fauna compositions. There was an increase in coral diversity from the exposed barrier reef to the relatively sheltered nearshore reefs, where the highest species diversity was found at the latter.

The reef complex at the northernmost tip of Borneo has the second highest concentration of coral reefs in Sabah. It is an area where the Sulu Sea meets the South China Sea and consists of fringing and patch reefs, with banks and shoals situated on a relatively shallow sea floor. In Chapter 3, the main research objectives were twofold, concerning an assessment of 1) species richness patterns of reef corals, and 2) benthic reef assemblages following the Reef Check substrate categories with emphasis on hard coral cover. This resulted in 84 species records of reef corals: 39 Fungiidae, 30 Agariciidae, and 15 Euphylliidae. The number of coral species was highest at reefs with a larger depth gradient i.e. at the peripheral area of the study site and in a deep channel (the South Banggi Channel) separating the mainland (Borneo) from other islands in the north. The average live coral cover across the shallow reef sites (≤ 10m depth) was 49%, with only 7% of the reefs having > 75% coral cover. Reef depth was a significant factor in influencing the coral species composition and benthic reef assemblages in the area.

The next chapter focuses on the fringing and patch reefs of the islands and coast of Kota Kinabalu on the west coast of Sabah (Chapter 4). Here, the total number of scleractinian reef corals was 71 species: 35 Fungiidae, 25 Agariciidae, and 11 Euphylliidae. The coral species compositions were influenced by reef exposure, where the highest species numbers were observed at the exposed and deeper reefs on the windward side of the islands.

It was evident from the study that blast fishing poses a major threat on the reefs of Sabah (Chapters 2–4). Several explosions were heard during dives in Semporna and Kudat. In the latter, a maximum of six denotations was heard in one dive. A number of reefs in the three localities in Sabah had low coral cover and high rubble fragments caused by previous blast fishing activities. Signs of past damage are still evident, even in the reefs within marine park areas in Semporna and Kota Kinabalu.

Research continued on Layang-Layang Island, which is part of an oceanic atoll in the Spratly Islands off Sabah (Chapter 5). Here, 56 species of reef corals were recorded, but the addition of three previously reported corals brings the total to 59 species consisting of 32 Fungiidae, 22 Agariciidae, and five Euphylliidae. Out of this total, 32 species are new records for the atoll and included some rare and unexpected species. The species diversity was noticeably lower as compared to other areas in Sabah, which may be related to its recovery from a crown-of-thorns (COT) seastar outbreak in 2010. During the surveys, a *Pavona* coral with small and extremely thin coralla was collected. Integrative molecular and morphological analyses revealed the coral as *Pavona maldivensis*. Corals from Sabah previously identified as *P. maldivensis* (see Chapters 2 and 4) were found to belong to *P. explanulata*. Based on this finding, *P. maldivensis* is only present in Layang-Layang, and its status in Semporna and Kota Kinabalu remains ambiguous until further data is available.

In the next chapter, coral data from reefs around Peninsular Malaysia, specifically, the Tioman, Redang and Payar group of islands were obtained (Chapter 6). Collectively, data from this fieldwork and the findings from the previous chapters provided the means to address the first question in this thesis. Indeed, there was a gradient of decreasing coral species richness from east to west Malaysia, directing away from the Coral Triangle. Longitude appeared to be a significant factor in structuring species richness composition. The coral species richness patterns of Malaysia were consistent with the marine ecoregion classifications of Spalding et al. (2007). In the course of this study, nine species have been added to the number of reef corals in Malaysia (excluding coral records from Layang-Layang). Coral species composition varied with reef type, depth, exposure, and distance offshore. Some coral species exhibited explicit habitat preference. However, high species richness was usually found in areas with high habitat heterogeneity, such as in Semporna, East Malaysia. Most species had widespread distributions and could be found across Malaysia, whereas several species showed limited geographical ranges. These patterns of species richness and geographical distribution are most likely influenced by the geological history of the area on a larger scale and environmental heterogeneity and current circulation patterns on a local scale. The present results support that the northwestern boundary of the Coral Triangle should be extended westward to include Kota Kinabalu and the west coast of north Borneo.

The final chapter focused on investigating the connectivity patterns of coral reefs in Malaysia by examining the genetic population structure of three model invertebrate species (Chapter 7). Samples were collected from five out of the seven localities in this study, excluding the islands of Payar and Redang, where none of the model species were encountered. Based on the genetic population structure, there was support for three main groupings in the mushroom coral *Heliofungia actiniformis*: 1) west South China Sea 2) east South China Sea, and 3) Sulu-Sulawesi Seas, suggesting restricted gene flow among these three groups. The lack of population structure in the blue seastar *Linckia laevigata* implies connectivity among the reef localities. Subtle genetic structuring was observed in populations of the boring giant clam *Tridacna crocea*, and distinctions could be made between populations of Tioman and Semporna, and Tioman and Layang-Layang. To address the second question of this thesis, the data supports connectivity in populations of some reef invertebrate species across reefs in Malaysia, as observed by the differing genetic population structure and scale in connectivity in the model species. Connectivity is influenced by the life histories of the model species, such as the pelagic larval duration. It can also be attributed to factors such as current patterns in the South China Sea and the Sulu Sea, and the geological history of the area, both of which are similar factors influencing the coral species richness patterns in this area as well.

Taken together, the findings in this thesis showed the patterns of coral species richness and reef invertebrate connectivity in Malaysia based on our model taxa. These findings may be relevant for the conservation and management of coral reef areas in Malaysia. Nevertheless, some information gaps remain to be considered in future studies. For example, very little data is available on the reefs of Sarawak (e.g. reefs off Kuching and Miri). Additional localities around Peninsular Malaysia would give a better representation of the reefs there. Also, the reefs of Layang-Layang should be revisited after allowing for more recovery time from the COT seastar destruction. Such information from these localities would give further credence to the current findings of the coral species richness patterns and reef connectivity across Malaysia.

Nederlandse samenvatting

Koraalriffen behoren tot de meest productieve mariene ecosystemen ter wereld. Koralen vormen de ruggengraat van riffen en herbergen een enorme diversiteit aan leven. De grootste biodiversiteit in het mariene milieu bevindt zich in de Koraaldriehoek, een regio bestaande uit zes landen: Indonesië, Maleisië, Filipijnen, Oost-Timor, Papoea-Nieuw-Guinea en de Salomonseilanden. Dit centrum van maximale mariene biodiversiteit bevat meer dan 600 soorten steenkoraal. Het is een bekend gegeven dat de diversiteit aan soorten afneemt met toenemende afstand van dit centrum, maar de processen die dit patroon sturen en onderhouden zijn onzeker.

Het begrijpen van de patronen van biodiversiteit is essentieel voor ecologische studies. Het is belangrijk om de huidige staat van de biodiversiteit te kennen, om zo de toekomstige respons op milieuveranderingen te kunnen voorspellen. Componenten van biodiversiteit, zoals soortenrijkdom, worden algemeen gebruikt voor beschermingsmaatregelen. Daarnaast wordt informatie over de genetische diversiteit en de genetische populatiestructuur meer en meer gezien als een belangrijk gegeven voor het bepalen van beschermende maatregelen. Deze gegevens kunnen biodiversiteitspatronen onthullen en inzicht geven in de connectiviteit tussen populaties en mogelijke barrières voor verspreiding.

Maleisië bestaat uit twee landmassa's die worden gescheiden door de Zuid-Chinese Zee: West-Maleisië (Maleisisch Schiereiland) op het Aziatisch continent en Oost-Maleisië (Sabah, Sarawak en Labuan) op het eiland Borneo. De meeste koraalriffen bevinden zich in Sabah, Oost-Maleisië. Alleen een deel van de riffen in Sabah werd beschouwd als onderdeel van de Koraaldriehoek, grotendeels vanwege een gebrek aan informatie over de rest van het gebied. Er valt nog veel te ontdekken over de biodiversiteit van koraalriffen in Maleisië, waardoor dit gebied prioriteit heeft voor dergelijk onderzoek. Dit proefschrift streeft ernaar inzicht te geven in de patronen van soortenrijkdom van steenkoralen en de mate van connectiviteit tussen de riffen in Maleisië door de genetische populatiestructuur van enkele modelorganismen te bestuderen. Twee hoofdvragen komen daarbij aan bod:

1) Is er een gradiënt in de soortenrijkdom van koralen in Maleisië en, zo ja, neemt die af met toenemende afstand van de Koraaldriehoek?
2) Is er connectiviteit tussen de koraalriffen in Maleisië?

Het onderzoek werd gestuurd door twee hypotheses:

1) Riffen in West-Maleisië en aan de westkust van Sabah zijn niet zo soortenrijk als riffen aan de oostkust van Sabah, omdat het zeeleven het zuidelijke deel van de Zuid-Chinese zee pas weer kon koloniseren na het Laatste Glaciale Maximum,
2) Riffen aan de oostkust van Sabah zijn soortenrijker, omdat ze zich al in de Sulu Zee hebben gevestigd in het geologisch tijdperk Oligoceen.

Om deze vragen te beantwoorden, zijn gegevens over koraalsoorten en mariene ongewervelden verzameld van de voornaamste riffen in Maleisië. Voor het onderzoek naar soortenrijkdom werden de koraalfamilies Fungiidae, Agariciidae en Euphylliidae geselecteerd als modeltaxa. Soorten behorende tot deze families hebben een wijde geografische verspreiding in het Indo-Pacifisch gebied, ze komen voor in veel verschillende rifhabitats, van ondiepe kustriffen tot diepere *offshore* milieus, en ze zijn makkelijk te onderscheiden van de soorten uit andere koraalfamilies. Omdat er zeer weinig informatie beschikbaar was over de riffen van Sabah (Oost-Maleisië) werd daar een meer gedetailleerde studie van de patronen van soortenrijkdom per locatie gemaakt. Milieufactoren die de samenstelling van soorten kunnen beïnvloeden, zoals diepte en *exposure* werden ook geëvalueerd. Om de connectiviteit tussen riffen te kunnen bepalen, werden drie soorten ongewervelden geselecteerd als modelorganismen: het paddenstoelkoraal *Heliofungia actiniformis*, de blauwe zeester *Linckia laevigata* en de doopvontschelp *Tridacna crocea.* Er was al genetisch onderzoek naar deze soorten gedaan in de Koraaldriehoek, maar van Maleisië was maar weinig informatie beschikbaar. Gegevens werden verzameld tijdens vijf verschillende veldwerkperiodes op zeven locaties, van in totaal 194 koraalriffen in Maleisië. Het veldwerk werd uitgevoerd langs een geografische lijn van oost naar west, met drie locaties in Sabah, Oost-Maleisië (Semporna, Kudat en Kota Kinabalu), drie locaties in West-Maleisië (Tioman, Redang en Payar) en verder Layang-Layang in de betwiste Spratly-eilandengroep. Daarnaast werden van 19 extra locaties in Sabah gegevens van paddenstoelkoralen verzameld.

Dit onderzoek begon met het onderzoeken van de patronen van soortenrijkdom van rifkoralen in Semporna en Darvel Bay aan de oostkust van Sabah (Hoofdstuk 2). Dit gebied heeft de hoogste concentratie van koraalriffen in Sabah (en Maleisië). De riffen bestaan uit vijf geomorfologische types: riffen in lagunes binnen een proto-atol, kustriffen, *continental patch reefs*, barrièreriffen en riffen die een oceanisch eiland omzomen. Samen vormen ze een veelvoud aan rifhabitats die een hoge diversiteit aan koraalsoorten kunnen herbergen. In totaal werden 89 soorten geobserveerd: 44 Fungiidae, 30 Agariciidae en 15 Euphylliidae, waarvan 12 nieuwe waarnemingen voor Sabah. Rif *exposure* was een belangrijke factor in de soortensamenstelling. Er werd een toename gevonden in koraaldiversiteit van de geëxponeerde barrièreriffen naar de beschutte riffen dicht bij de kust, waar de hoogste diversiteit werd gevonden.

De meest noordelijke punt van Borneo heeft de op één na hoogste concentratie riffen in Sabah. Dit gebied, waar de Sulu Zee grenst aan de Zuid-Chinese Zee, bestaat uit kustriffen en *patch* riffen, met ondiepe riffen en banken op een vrij ondiepe zeebodem. In Hoofdstuk 3 zijn de belangrijkste onderzoeksdoelen tweevoudig: 1) het bepalen van de patronen van soortenrijkdom van rifkoralen en 2) de bentische samenstelling volgens de Reef Check substraatcategorieën, met nadruk op steenkoraal. Dit resulteerde in 84 geobserveerde koraalsoorten: 39 Fungiidae, 30 Agariciidae en 15 Euphylliidae. Het aantal soorten was het hoogste op riffen met grotere dieptegradiënten, zoals aan de periferie van de onderzoekslocatie en in een diep kanaal (South Banggi Channel) die het vasteland (Borneo) scheidt van de noordelijke eilanden. De gemiddelde koraalbedekking op de ondiepe locaties (≤ 10 m diep) was 49%; slechts 7% van de riffen had een bedekking van >75%. Rifdiepte was een belangrijke factor in de samenstelling van de koraalsoorten en bentische soorten in het gebied.

Hoofdstuk 4 richt zich op de kust- en *patch*-riffen van de eilanden en de kust van Kota Kinabalu aan de westkust van Sabah. Het totaal aantal koraalsoorten was 71: 35 Fungiidae, 25 Agariciidae en 11 Euphylliidae. De koraalsamenstelling werd beïnvloed door rif *exposure*; de hoogste soortenaantallen werden geobserveerd op de geëxponeerde en diepere riffen aan de loefzijde van de eilanden.

Het onderzoek toont duidelijk aan dat dynamietvissen een grote bedreiging vormt voor de riffen van Sabah (Hoofdstukken 2–4). Verschillende explosies werden gehoord tijdens duiken in Semporna en Kudat. In Kudat werden tijdens een duik zes ontploffingen gehoord. Een aantal bezochte riffen op de drie locaties in Sabah had een lage koraalbedekking en veel koraalfragmenten, wat was veroorzaakt door dynamietvisserij. De tekenen van eerdere schade waren ook nog duidelijke zichtbaar op riffen in de mariene parken van Semporna en Kota Kinabalu.

Het onderzoek werd vervolgd op Layang-Layang, een oceanisch atol in de Spratly-eilandengroep voor de kust van Sabah (Hoofdstuk 5). Hier werden 56 soorten koraal geobserveerd. Met de toevoeging van drie soorten die eerder geobserveerd waren kwam het totaal op 59, bestaande uit 32 Fungiidae, 22 Agariciidae en vijf Euphylliidae. In totaal waren er 32 nieuwe waarnemingen voor het atol, waaronder een aantal zeldzame soorten. De soortendiversiteit was beduidend lager dan in de andere gebieden in Sabah, wat mogelijk een gevolg is van het herstel van een uitbraak van doornenkroonzeesterren (COT) in 2010. Tijdens het veldwerk werd een *Pavona* koraal met kleine, extreem dunne poliepen verzameld. Integratieve moleculaire en morfologische analyses toonden aan dat het koraal behoorde tot de soort *Pavona maldivensis.* Koralen in Sabah die eerder als *Pavona maldivensis* (zie Hoofdstukken 2 en 4) waren geïdentificeerd, behoorden tot de soort *P. explanulata.* Volgens deze nieuwe gegevens komt *P. maldivensis* alleen voor rondom Layang-Layang; het voorkomen van *P. maldivensis* in Semporna en Kota Kinabalu blijft onduidelijk totdat meer gegevens beschikbaar komen.

In Hoofdstuk 6 zijn koraalgegevens verkregen van de riffen in West-Maleisië, meer specifiek Tioman, Redang en Payar. De gegevens van dit veldwerk, samen met de resultaten van de eerdere hoofdstukken, worden gebruikt om de eerste vraag van dit proefschrift te beantwoorden. Er is inderdaad een gradiënt van afnemende soortenrijkdom van oost naar west in Maleisië, met toenemende afstand van de Koraaldriehoek. Geografische lengtegraden bleken een belangrijke factor te zijn voor de soortensamenstelling. De patronen van soortenrijkdom in Maleisië komen overeen met de indeling van mariene ecoregio's [ecologische regio's] door Spalding et al. (2007). Gedurende het onderzoek voor dit proefschrift zijn negen soorten toegevoegd aan de lijst van koralen in Maleisië (de datapunten van Layang-Layang niet meegerekend). De samenstelling van koraalsoorten varieerde met riftype, diepte, *exposure*, en de afstand naar de kust. Sommige koraalsoorten vertoonden een specifieke voorkeur voor een bepaald habitat. Een hoge soortenrijkdom werd voornamelijk gevonden in gebieden met een grote heterogeniteit aan habitats, zoals Semporna (Oost-Maleisië). Sommige soorten hadden een wijde verspreiding en werden in heel Maleisië gevonden, terwijl verschillende andere soorten een kleine geografische spreiding hadden. Deze patronen van soortenrijkdom en geografische verspreiding worden waarschijnlijk beïnvloed door de geologische geschiedenis van het gebied, en op kleinere schaal door de heterogeniteit van het milieu en de huidige circulatiepatronen. De resultaten ondersteunen een verschuiving van de grenzen van de Koraaldriehoek naar het westen, waardoor deze ook Kota Kinabalu en de westkust van noordelijk Borneo omvat.

Hoofdstuk 7 richt zich op de patronen van connectiviteit op koraalriffen in Maleisië door de genetische populatiestructuren van drie ongewervelde modelorganismen te bestuderen. Materiaal werd verzameld op vijf van de zeven onderzochte locaties. De modelorganismen werden niet aangetroffen op de eilanden Payar en Redang. De genetische populatiestructuur laat drie groepen zien in het paddenstoelkoraal *Heliofungia actiniformis*: 1) de westelijke Zuid-Chinese Zee, 2) de oostelijk Zuid-Chinese Zee, en 3) de Sulu-Sulawesi Zee, wat wijst op een beperkte genenstroom [*gene flow*] tussen deze drie groepen. Het gebrek aan populatiestructuur in de blauwe zeester *Linckia laevigata* duidt op een bij die soort grotere connectiviteit tussen de verschillende locaties. Een geringe genetische diversiteit werd gevonden in populaties van de doopvontschelp *Tridacna crocea*; er kon onderscheid worden gemaakt tussen populaties van Tioman en Semporna en tussen Tioman en Layang-Layang. De tweede vraag van dit proefschrift kan hiermee worden beantwoord. De gegevens laten zien dat er gradaties in connectiviteit bestaan tussen de Maleisische populaties van uiteenlopende ongewervelde soorten modelorganismen. Connectiviteit wordt beïnvloed door de *life histories* van de organismen, zoals bijv. de duur van het pelagisch larvestadium. Het kan ook worden toegeschreven aan factoren zoals de huidige circulatiepatronen in de Zuid-Chinese Zee en de Sulu Zee, en de geologische geschiedenis van het gebied. Beide factoren beïnvloeden eveneens de patronen van soortenrijkdom in dit gebied.

Samenvattend laten de resultaten van dit proefschrift de patronen van soortenrijkdom van koralen en de connectiviteit van ongewervelden in Maleisië zien, gebaseerd op onze modeltaxa. Deze bevindingen kunnen relevant zijn voor de bescherming en het management van de koraalriffen in Maleisië. Sommige lacunes in de beschikbare gegevens verdienen nader onderzoek in toekomstige studies. Zo is er bijvoorbeeld zeer weinig bekend over de riffen van Sarawak (Kuching en Miri). Extra locaties in West-Maleisië zouden een betere weergave van de diversiteit in de riffen ter plaatse kunnen geven. Daarnaast zouden de riffen van Layang-Layang nogmaals bezocht moeten worden, nadat ze tijd hebben gekregen om te herstellen van de COT uitbraak. Informatie met betrekking tot de soortensamenstelling op deze locaties zal een nog betere onderbouwing kunnen geven aan de hier gepresenteerde bevindingen aangaande de patronen van soortenrijkdom van steenkoralen en rifconnectiviteit in Maleisië.

Ringkasan Bahasa Malaysia

Terumbu karang merupakan salah satu ekosistem marin yang paling produktif di dunia. Karang merupakan teras kepada terumbu karang yang mempunyai biodiversiti tinggi. Biodiversiti marin tertinggi di dunia terletak di Segitiga Terumbu Karang, iaitu kawasan yang dirangkumi enam negara: Indonesia, Malaysia, Filipina, Timor-Leste, Papua New Guinea dan Kepulauan Solomon. Kawasan ini mempunyai lebih 600 spesies karang skleraktinia. Telah diketahui kepelbagaian spesies semakin berkurangan apabila menjauhi kawasan kepelbagaian maksima ini, namun proses yang memacu dan mengekalkan corak tersebut masih belum jelas.

Memahami corak biodiversiti adalah penting dalam kajian ekologi. Pengetahuan mengenai status semasa penting bagi meramal tindakbalas biodiversiti terhadap perubahan persekitaran di masa hadapan. Komponen biodiversiti seperti kekayaan spesies seringkali digunakan dalam langkah-langkah pemuliharaan. Maklumat kepelbagaian genetik dan struktur genetik populasi dianjurkan sebagai komponen penting dalam pengutamaan pemuliharaan. Kedua-dua aspek mampu mendedahkan corak biodiversiti, memberi gambaran tentang kesalinghubungan populasi dan penghalang penyebaran berpotensi.

Malaysia terbentuk dari dua kawasan daratan yang terpisah oleh Laut Cina Selatan: Semenanjung Malaysia (juga dikenali sebagai Malaysia Barat) yang bersambung dengan tanah besar Asia dan Malaysia Timur (terdiri oleh negeri Sabah, Sarawak dan Wilayah Persekutuan Labuan) di pulau Borneo. Sebahagian besar terumbu karang Malaysia terletak di Sabah. Pada permulaan kajian ini, hanya sebahagian terumbu karang di Sabah dianggap termasuk dalam Segitiga Terumbu Karang, sebahagian besarnya kerana kekurangan maklumat mengenai terumbu karang di kawasan ini. Masih banyak belum diketahui mengenai biodiversiti terumbu karang di Malaysia menjadikan kawasan ini keutamaan bagi penyelidikan terumbu karang. Matlamat tesis ini bertujuan memberikan satu gambaran mengenai corak kekayaan spesies karang dan kadar kesalinghubungan terumbu seluruh Malaysia dengan mengkaji struktur populasi genetik invertebrata terumbu karang. Dua persoalan utama telah disentuh:

1) Adakah terdapat kecerunan spesies karang merentasi Malaysia, dan sekiranya ada, adakah ia berkurangan dengan peningkatan jarak menjauhi Segitiga Terumbu Karang?
2) Adakah terdapat sebarang salinghubung antara terumbu karang di Malaysia?

Kajian ini telah dipandu oleh dua hipotesis utama:

1) Terumbu karang di Semenanjung Malaysia dan pantai barat Sabah tidak mempunyai bilangan spesies sebanyak terumbu di pantai timur Sabah memandangkan hidupan marin hanya dapat mengkolonisasi semula kawasan selatan Laut China Selatan selepas Glasial Maksimum Terakhir.
2) Terumbu karang di pantai timur Sabah adalah kaya spesies kerana ia telah wujud di Laut Sulu sejak Epok Oligosen.

Dalam usaha menangani persoalan ini, data berkaitan spesies karang dan spesimen invertebrata marin telah dikutip dari kawasan terumbu karang utama di Malaysia. Bagi kajian kekayaan spesies karang, karang skleraktinia dari famili Fungiidae, Agariciidae dan Euphylliidae telah dipilih sebagai taksa model. Spesies dari famili tersebut mempunyai taburan geografi yang luas di Indo-Pasifik, ia boleh ditemui di pelbagai habitat terumbu karang dari terumbu cetek pesisiran pantai hingga ke persekitaran luar pesisir yang dalam, dan mereka juga senang dikenalpasti dari famili karang yang lain. Berikutan kekurangan maklumat mengenai terumbu karang di Sabah, Malaysia Timur, kajian yang lebih terperinci berkenaan corak kekayaan spesies karang telah dibuat pada setiap lokaliti terumbu karang. Faktor persekitaran yang mampu mempengaruhi komposisi spesies karang seperti kedalaman dan dedahan terumbu turut dinilai. Untuk merumuskan salinghubungan terumbu karang, tiga spesies invertebrata terumbu telah dipilih sebagai spesies model, karang cendawan *Heliofungia actiniformis*, tapak sulaiman biru *Linckia laevigata* dan kima pengorek *Tridacna crocea*. Terdapat kajian genetik sedia ada ke atas tiga spesies ini di kawasan Segitiga Terumbu Karang, namun kekurangan maklumat dari Malaysia. Penyampelan dan pengumpulan data telah dilakukan melalui lima kerja lapangan yang berbeza di tujuh lokaliti dan 194 kawasan terumbu seluruh Malaysia. Tinjauan telah dilakukan sepanjang julat geografi dari timur ke barat, yang mana tiga lokaliti masing-masing di Sabah, Malaysia Timur (Semporna, Kudat dan Kota Kinabalu) dan Semenanjung Malaysia (Tioman, Redang dan Payar), dan Pulau Layang-Layang di Kepulauan Spratly yang dipertikai milik. Sebanyak 19 kawasan tambahan di tiga lokaliti di Sabah telah ditinjau untuk karang cendawan sahaja.

Kajian ini telah dimulakan dengan meneroka corak kekayaan spesies terumbu karang di semenanjung Semporna dan sebahagian Teluk Darvel di pantai timur Sabah (Bab 2). Kawasan ini mempunyai penumpuan terumbu karang yang tertinggi di Sabah dan juga Malaysia. Terumbu karangnya terdiri dari lima jenis geomorfologi terumbu utama: terumbu lagun di dalam proto-atol, terumbu pinggir, terumbu tompok benua, terumbu sawar dan terumbu meliputi pulau lautan. Kesemuanya mewakili pelbagai jenis persekitaran terumbu karang yang mampu menampung kepelbagian spesies karang yang tinggi. Secara keseluruhannya, 89 spesies karang telah dicerap: 44 Fungiidae, 30 Agariciidae dan 15 Euphylliidae, termasuk 12 rekod spesies baru untuk Sabah. Pendedahan terumbu karang adalah salah satu faktor penting dalam mempengaruhi komposisi fauna karang. Terdapat peningkatan kepelbagaian karang dari terumbu tebing yang terdedah hingga ke terumbu persisir yang agak terlindung, yang mana kepelbagaian spesies tertinggi ditemui di kawasan yang kedua.

Kompleks terumbu karang di penghujung utara Borneo mempunyai konsentrasi terumbu karang kedua tertinggi di Sabah. Ianya merupakan kawasan di mana Laut Sulu bertemu dengan Laut China Selatan dan terdiri dari terumbu pinggir dan tompok, dengan tebing dan beting terletak di dasar laut yang agak cetek. Dalam Bab 3, objektif penyelidikan utama adalah dua iaitu, berkenaan penilaian 1) corak kekayaan spesies terumbu karang, dan 2) himpunan bentik terumbu berdasarkan kategori substrat Reef Check dengan penekanan terhadap taburan batu karang keras. Hasilnya, 84 spesies karang telah direkod: 39 Fungiidae, 30 Agariciidae, dan 15 Euphylliidae. Spesies karang tertinggi ditemui di terumbu yang mempunyai cerun kedalaman yang besar dengan kata lain di kawasan pinggir kawasan kajian dan di selat yang dalam (Selat Banggi Selatan) yang memisahkan tanah besar (Borneo) dengan kepulauan lain di utara. Purata taburan karang hidup di kawasan terumbu cetek (kedalaman ≤ 10 m) adalah 49% dengan hanya 7% terumbu karang mempunyai > 75% taburan kerang hidup. Kedalaman terumbu karang merupakan faktor yang penting dalam mempengaruhi komposisi spesies karang dan himpunan dasar terumbu karang di kawasan tersebut.

Bab berikutnya tertumpu kepada terumbu pinggir dan tompok di pulau-pulau dan pesisiran Kota Kinabalu di pantai barat Sabah (Bab 4). Di sini, jumlah terumbu karang skleraktinia adalah 71 spesies: 35 Fungiidae, 25 Agariciidae, dan 11 Euphylliidae. Komposisi spesies karang dipengaruhi oleh pendedahan terumbu, yang mana jumlah spesies tertinggi telah diperhatikan di kawasan yang terumbu yang terdedah dan lebih dalam yang terletak di kawasan pulau yang menghadap angin.

Dari kajian yang dilakukan, jelas bahawa pengeboman ikan merupakan ancaman terbesar terumbu karang Sabah (Bab 2–4). Beberapa letupan didengari ketika selaman di Semporna dan Kudat. Di Kudat, sebanyak enam letupan telah didengari dalam satu sesi selaman. Sebilangan terumbu karang di ketiga-tiga lokaliti di Sabah mempunyai litupan karang yang rendah dan jumlah serpihan karang yang tinggi disebabkan aktiviti pengeboman ikan yang lalu. Tanda-tanda kerosakan lampau masih wujud, termasuk di terumbu karang yang terletak dalam kawasan taman laut di Semporna dan Kota Kinabalu.

Kajian diteruskan di Pulau Layang-Layang, yang merupakan sebahagian daripada atol lautan di Kepulauan Spratly luar Sabah (Bab 5). Di sini, 56 spesies karang telah direkod, tetapi dengan tambahan dari tiga karang yang telah dilaporkan sebelum ini menjadikan jumlah keseluruhan karang 59 spesies yang terdiri daripada 32 Fungiidae, 22 Agariciidae dan lima Euphylliidae. Dari jumlah ini, 32 spesies adalah rekod baru bagi atol tersebut dan ini termasuk yang spesies nadir dan tidak dijangka. Kepelbagaian spesies di kawasan ini adalah jelas lebih rendah berbanding kawasan lain di Sabah, di mana ia mungkin berkait dengan pemulihan dari penularan tapak sulaiman Mahkota Berduri pada 2010. Ketika tinjauan, karang *Pavona* yang mempunyai coralla yang kecil dan sangat nipis telah dikutip. Analisis molekular dan morfologi bersepadu mendapati karang tersebut adalah *Pavona maldivensis*. Karang dari Sabah yang sebelum ini dikenal pasti sebagai *P. maldivensis* (lihat Bab 2 dan 4) telah ditemui tergolong dalam *P. explanulata*. Berdasarkan penemuan ini, *P. maldivensis* hanya terdapat di Layang-Layang, dan statusnya di Semporna dan Kota Kinabalu adalah kabur hingga terdapat data lebih lanjut.

Dalam bab berikutnya, data karang sekitar Semenanjung Malaysia, khususnya, kepulauan Tioman, Redang dan Payar telah diperolehi (Bab 6). Secara kolektif, data dari kerja lapangan ini dan penemuan dari bab-bab sebelumnya membolehkan menangani soalan pertama dalam tesis ini. Sesungguhnya, terdapat kecerunan yang menunjukkan kekayaan spesies karang berukurangan dari Malaysia Timur ke Malaysia Barat, menjauhi Segitiga Terumbu Karang. Longitud kelihatan seperti faktor penting dalam penstrukturan komposisi kekayaan spesies. Corak kekayaan spesies karang Malaysia adalah sejajar dengan klasifikasi *ecoregion* marin Spalding *et al.* (2007). Sepanjang kajian ini, sembilan spesies telah ditambah dalam jumlah karang di Malaysia (tidak termasuk rekod karang dari Layang-Layang). Komposisi spesies karang berbeza mengikut jenis terumbu karang, kedalaman, keterdedahan, dan jarak dari pesisir pantai. Sesetengah spesies karang menonjolkan pemilihan habitat yang jelas. Bagaimanapun, kekayaan spesies yang tinggi seringkali ditemui di kawasan dengan kepelbagaian habitat yang tinggi, seperti di Semporna, Malaysia Timur. Kebanyakan spesies mempunyai taburan yang meluas dan dapat ditemui di seluruh Malaysia, manakala sebahagian spesies menunjukkan julat geografi yang terhad. Corak kekayaan spesies dan taburan geografi besar kemungkinan dipengaruhi oleh sejarah geografi kawasan tersebut pada skala yang lebih besar dan kepelbagaian persekitaran dan corak peredaran arus pada skala tempatan. Dapatan terkini menyokong sempadan barat laut Segitiga Terumbu Karang harus diperluaskan ke barat untuk merangkumi Kota Kinabalu dan pantai barat Borneo utara.

Bab terakhir menyiasat corak kesalinghubungan terumbu karang di Malaysia melalui pemeriksaan struktur populasi genetik tiga model spesies invertebrata (Bab 7). Sampel-sampel telah diperolehi di lima daripada tujuh lokaliti dalam kajian ini, tidak termasuk Pulau Payar dan Redang, di mana spesies model tersebut tidak ditemui. Berdasarkan struktur populasi genetik, terdapat sokongan bagi tiga kumpulan utama karang cendawan *Heliofungia actiniformis*: 1) Laut China Selatan barat 2) Laut China Selatan timur, dan 3) Laut Sulu-Sulawesi, yang mencadangkan terdapat aliran gen terhad antara tiga kumpulan ini. Ketiadaan struktur populasi bagi tapak sulaiman biru *Linckia laevigata* mencadangkan salinghubungan antara lokaliti terumbu karang. Penstrukturan genetik yang tidak ketara diperhatikan pada populasi kima pengorek *Tridacna crocea,* dan perbezaan dapat dibuat antara populasi Tioman dan Semporna, dan Tioman dan Layang-Layang. Bagi menjawab soalan kedua tesis ini, data yang diperoleh menyokong salinghubungan populasi sesetengah spesies invertebrata terumbu karang bagi terumbu karang merentasi Malaysia, seperti yang diperhatikan dalam struktur populasi genetik dan skala salinghubungan dalam spesies model. Kesalinghubungan dipengaruhi oleh sejarah kehidupan spesies model, seperti tempoh larva pelagik. Ianya mungkin juga berpunca dari faktor-faktor seperti corak arus di Laut China Selatan dan Laut Sulu, serta sejarah geologi kawasan tersebut, yang mana kedua-duanya juga merupakan faktor yang mempengaruhi corak kekayaan spesies karang dalam kawasan ini.

Secara keseluruhan, penemuan dalam tesis ini menunjukkan corak kekayaan spesies karang dan salinghubungan invertebrata terumbu karang di Malaysia berdasarkan taksa model kami. Penemuan ini mungkin relevan bagi pemuliharaan dan pengurusan kawasan-kawasan terumbu karang di Malaysia. Namun demikian, masih terdapat jurang maklumat yang wajar dipertimbangkan bagi kajian masa akan datang. Contohnya, amat sedikit data terdapat bagi terumbu karang di Sarawak (seperti di terumbu karang luar pesisir Kuching dan Miri). Penambahan lokaliti sekitar Semenanjung Malaysia boleh memberikan gambaran terumbu karang yang lebih baik di sana. Tambahan lagi, terumbu karang di Layang-Layang harus dilawat semula setelah memberi lebih masa untuk pemulihan dari kemusnahan tapak sulaiman Mahkota Berduri. Maklumat dari lokaliti-lokaliti tersebut dapat memberikan lebih sokongan terhadap penemuan semasa mengenai corak kekayaan spesies karang dan salinghubungan terumbu karang seluruh Malaysia.

Acknowledgements

This thesis marks the end of my PhD journey. It was a journey that I did not make alone, and I have many people to thank, be it to those who traversed with me for the whole stretch, or to those who joined me during parts of the twists and turns along the way. First and foremost, I would like to express my gratitude to my Promoter, Edmund Gittenberger for his guidance on various aspects of the thesis and the Leiden University PhD procedures. I am grateful to my Co-promoter, Bert W. Hoeksema for his steadfast support towards my research efforts, for reading countless drafts of my chapters and providing the necessary tools that enabled me to complete this thesis.

I am indebted to the former Directors of the Borneo Marine Research Institute (BMRI), Prof. Ridzwan Abdul Rahman and Prof. Saleem Mustafa, and the current Director, Prof. Rossita Shapawi for allowing me the freedom to pursue this PhD degree. A huge thank you to my colleagues and support staff of BMRI for their kind words and help in way of academic, administrative and fieldwork logistic matters. In particular, I thank Pushpa Palaniappan, Annita Yong Seok Kian, Faihanna Ching Fui Fui and Muhammad Ali Syed Hussein for aid when I needed it. Additional thanks to Ali and Mohd Firdaus Akmal Nooramli for translating the summary of this thesis into Bahasa Malaysia.

I would like to reiterate my thanks to the various funding bodies and institutions that have made this research possible (as listed at the end of each chapter): the Ministry of Higher Education Malaysia and Universiti Malaysia Sabah for a scholarship; AM Buitendijkfonds and TREUB-maatschappij (Society for the Advancement of Research in the Tropics) for travel grants; the Economic Planning Unit, Chief Minister's Department, Sabah Parks, Sabah Fisheries Department, Sabah Biodiversity Council and Department of Marine Park, Malaysia for research permits. I also thank WWF-Malaysia for funding and co-organising the Semporna Marine Ecological Expedition (SMEE) 2010, and the Tun Mustapha Parks Expedition (TMPE) 2012. The National Oceanographic Directorate through the Ministry of Science, Technology and Innovation (MOSTI), Malaysia and USAID Coral Triangle Support Partnership (CTSP) are also acknowledged for funding TMPE 2012.

A big thank you to Affendi Yang Amri, Kee Alfian Abdul Adziz and Yusri Yusuf for providing helpful comments on my initial research proposal in 2009 and giving advice on fieldwork matters in Peninsular Malaysia. I also acknowledge the various dive operators, dive masters and boat crew for diving logistics throughout this research.

My sincere thanks to members of the DNAmarkerpoint laboratory in the Sylvius Building: Klass Vrieling for kindly accepting me in the Molecular Biological Techniques course and setting me up in the lab; Bastian T. Reijnen for teaching and guiding me through crucial aspects of lab work and helping me navigate the world of molecular biology; Laura Bertola for guidance on working with microsatellites; Marcel C.M. Eurlings, Kevin Beentjes, Dick S.J. Groenenberg, Frank Stokvis, and former members, Rene Glas, Natasha S. Schidlo, Peter Steenbergen for general advice on lab and molecular work.

My appreciation goes to the Naturalis Biodiversity Center for creating a highly conducive working atmosphere. Everyone that I had the pleasure of interacting with has been

supportive and accommodating. An extended thank you to the Research Coordination Office: Johan Mols and Cynthia Crul for their role in administrative matters and in initiating the Naturalis PhD monthly meetings. The Zeeteam had warmly accepted me as part of their fold. I will fondly reminisce the conversations and light-hearted moments over morning coffee, lunches and monthly ABC sessions. Most of all, I will miss the strong sense of camaraderie after being part of the team for so long. A special mention goes to Charles H.J.M. Fransen for sharing his workspace with me. His calm, collected demeanour and occasional pep talks added to the pleasure of going to work. And I must acknowledge Leen van Ofwegen, whose emails with messages of "what is taking you so long? Just get on with it!" not only brightened my days, but also provided the impetus for me to "get on with it".

I would like to thank the scientists and curators of the natural history museums: Stephen D. Cairns, Cheryl Bright and Paul Greenhall of the Smithsonian Institution in Washington, D.C. for coral type specimens loan; Miranda Lowe, Natalina Bonassera, Andrew Cabrinovic, Jill Darrell and Nadia Santodomingo of the Natural History Museum in London for facilitating my visit to the hard coral collection in Wandsworth, South London.

I have had the privilege of meeting and collaborating with Francesca Benzoni, whose dedication in coral research is truly an inspiration. Our earlier communications on some odd looking *Leptoseris* led to many stimulating discussions and a few joint-projects together with Tullia I. Terraneo. Tullia and Roberto Arrigoni have been very kind to answer all of my questions on molecular work and GenBank. Harald G.J. van Mil spared time and effort to help me make sense of my data using statistical analyses. Erik-Jan Bosch and Sikula Magupin created most of the maps in this thesis.

Heartfelt thanks to my paranymps and dear friends Bastian Reijnen and Sancia E.T. van der Meij, both who have in their own ways encouraged, assured and motivated me. They were with me throughout the whole stretch, from being my sounding wall at work, to hand delivering sustenance to my home. The value of their friendship and how it has enriched my living abroad experience is immeasurable. Sancia also translated the summary of this thesis into Dutch, to which I am appreciative.

Very special thanks to those who have made my life that much better in Leiden: Silvy Puntowati for her kindness and generosity; Nadia Santodomingo for her words of wisdom, positive take on life, and for being lovely all around; Lisa Becking for her strength, resilience and our discussions on phylogeography and art; Yee Wah Lau for her constant "you got this" encouragements and for designing the awesome cover; Liew Thor Seng for reminding me that a thesis is the end result of an exploration to acquire the skills to do better research.

And finally, words cannot express my love and gratitude for my parents and their unconditional love and support in every aspect of my life. My sister Moniza, whose persistence and endless drive to excel inspires me. A warm thank you to other family members and friends for their support and best wishes. Viv, whose unwavering faith in me is humbling. And last but not least, Faz, my better half, who gave me the courage to follow my heart and intuition.

Curriculum Vitae

Zarinah Waheed was born on 27 October 1978 in Kota Kinabalu, on the west coast of Sabah and grew up near the (back then idyllic and quaint) Tanjung Aru beach. She received her early education in St. Francis Convent, Kota Kinabalu. Her formative years in a coastal town sparked a fascination and deepening curiosity for all things marine-related. She started diving on the reefs of the Tunku Abdul Rahman Park, Kota Kinabalu in 1998. She obtained a BSc. (Hons.) in Marine Science from the National University of Malaysia (UKM) in Bangi, Selangor in 2000. While pursuing her undergraduate degree, she was keen on physical oceanography and her dissertation compared temperature and salinity data of water masses from different locations between the Pacific Ocean and South China Sea. She moved back to Kota Kinabalu and was offered an MSc. scholarship from Universiti Malaysia Sabah (UMS), funded by the Danish Government (DANCED). Research took her to Lahad Datu in Darvel Bay, on the east coast of Sabah, where she examined the seasonal diversity and abundance of fish larvae on the reefs within the bay. She sacrificed over 26,000 baby fishes in the name of science. The casualties lead to a thesis, which resulted in an MSc. in Marine Biology in 2003. In the same year, she accepted a lecturer position in the Borneo Marine Research Institute (BMRI), UMS. Through a series of fortunate events, she was introduced to Dr. Bert W. Hoeksema (who became her PhD supervisor) by Dr. Annadel S. Cabanban (her former MSc. supervisor) in 2005. At the end of 2008, she spent three months in Naturalis under the Martin Fellowship, where she had her first exposure to coral taxonomy. She also developed a proposal for a PhD research towards the end of her fellowship. In 2010, she moved to Leiden to pursue her PhD degree supported by the Ministry of Higher Education, Malaysia. The results obtained over the course of five fieldtrips and almost 200 dives during her candidature are presented in this thesis. At present, she has resumed her duties in BMRI, UMS.

Publications

Publications resulting from this thesis:

Waheed Z**,** Hoeksema BW (2013) A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia. Marine Biodiversity 43(1): 37–51.

Waheed Z, Hoeksema BW (2014) Diversity patterns of scleractinian corals at Kota Kinabalu, Malaysia, in relation to exposure and depth. Raffles Bulletin of Zoology 62: 66–82.

Waheed Z, Benzoni F, van der Meij, SET, Terraneo TI, Hoeksema BW (2015) Scleractinian corals (Fungiidae, Agariciidae and Euphylliidae) of Pulau Layang-Layang, Spratly Islands, with a note on *Pavona maldivensis* (Gardiner, 1905). ZooKeys 517: 1–37.

Waheed Z, van Mil HG, Muhammad Al SH, Jumin R, Bobita GA, Hoeksema BW (2015) Coral reefs at the northernmost tip of Borneo: An assessment of scleractinian species richness patters and benthic reef assemblages. PloS ONE 10(12): e0146006.

Other publications during the PhD candidature:

Hoeksema BW, Waheed Z (2011) Size-dependent dispersal by *Goniopora stokesi* corals at Semporna, eastern Sabah, Malaysia. Galaxea, Journal of Coral Reef Studies 13(1): 9–10.

Hoeksema BW, Waheed Z (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. Coral Reefs 30(4): 1087.

Hoeksema BW, Waheed Z (2012) Onset of autotomy in an attached *Cycloseris* coral. Galaxea, Journal of Coral Reef Studies 14: 25–26.

Hoeksema BW, Waheed Z (2012) It pays to have a big mouth: mushroom corals ingesting salps at Sabah, Malaysia. Marine Biodiversity 42(2): 297–302.

Waheed Z, Hoeksema BW (2012) Coral-mimicking corallimorpharians on the reefs of Kota Kinabalu, Malaysia. Coral Reefs 31(2): 519.

Hoeksema BW, Waheed Z, Alamaru A (2013) Out of sight: aggregations of epizoic comb jellies underneath mushroom corals. Coral Reefs 32(4): 1065.

Benzoni F, Arrigoni R, Waheed Z, Stefani F, Hoeksema BW (2014) Phylogenetic relationships and revision of the genus *Blastomussa* (Cnidaria: Anthozoa: Scleractinia) with description of a new species. Raffles Bulletin of Zoology 62: 358–378.

Terraneo TI, Berumen ML, Arrigoni R, Waheed Z, Bouwmeester J, Caragnano A, Stefani F, Benzoni F (2014) *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. ZooKeys 433: 1–30.

Hoeksema BW, Waheed Z, Voogd NJ de (2014) Partial mortality in corals overgrown by the sponge *Terpios hoshinota* at Tioman Island, Peninsular Malaysia (South China Sea). Bulletin of Marine Science 90(4): 989–990.

Huang D, Licuanan WY, Hoeksema BW, Chen CA, Ang PO, Huang H, Lane DJW, Vo ST, Waheed Z, Amri AY, Yeemin T, Chou LM (2015) Extraordinary diversity of reef corals in the South China Sea. Marine Biodiversity 45(2): 157–168.

Propositions

accompanying the thesis

Patterns of coral species richness and reef connectivity in Malaysia

1. There is decreasing reef coral species richness from an east to west geographical range across Malaysia.
   This thesis.

2. Reef coral species richness patterns in Malaysia follow the general ecoregion classifications of Spalding et al. (2007) instead of the coral-related definitions of Veron et al. (2009, 2015).
   This thesis.
   Pro: Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57: 573–583.
   Contra: Veron JEN, Devantier LM, Turak E, Green AL, Kininmonth S, et al. (2009) Delineating the Coral Triangle. Galaxea, Journal of Coral Reef Studies 11: 91–100.
   Contra: Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Frontiers in Marine Science 1: 81.

3. Patterns of connectivity among the coral reefs across Malaysia can be attributed to the geological history and the water circulation patterns, which are driven by seasonal monsoon winds in the area.
   This thesis.

4. Even allegedly well-defined species can be misinterpreted.
   This thesis.

5. Priorities for coral reef research should not exclusively be dictated by usefulness.

6. Regarding marine biodiversity, Malaysia is species-rich, but poorly investigated.
   Pro: Yasin Z, Tan ASH, Shirayama Y (2014) Research on the biodiversity of the seas surrounding Malaysia. In: Nakano S, Yahara T, Nakashizuka T (Eds.) Integrative observations and assessments. Springer, Tokyo. pp 167–206.

7. The use of model taxa in diversity studies should not be underestimated.

8. To judge the health status of coral reefs, the deeper reef zones should also be taken into account.

9. Riding a bicycle is like writing a thesis; there is joy in the journey.

10. Two digits (0, 1) and four letters (A, G, C, T) are the basis of this thesis.