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The reef coral fauna of Bali in the centre of marine diversity

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ABSTRACT

Despite Bali's diving industry, little is known about its underwater fauna and marine species richness. Four areas at Bali have been monitored with regard to their scleractinian reef coral fauna: (1) West: Bali Barat; (2) East: Tulamben and Amed; (3) Southeast: Sanur, Nusa Dua, and Padangbai; (4) Lombok Strait: Nusa Lembongan and Nusa Penida. Mushroom corals (Fungiidae) and scleractinian genera have been selected as model taxa for diversity studies. Bali Barat, mainly consisting of uplifted limestone, appears to be the least rich, an effect of bleaching. The Tulamben-Amed area, predominantly consisting of volcanic sand with limestone outcrops, is the richest. The islands Nusa Lembongan and Nusa Penida, also characterised by uplifted limestone, have special fauna elements due to cold up-welling and strong currents. At Sanur and Nusa Dua, species occur that previously were only known from the Pacific. Compared to nearby areas, the coral fauna of Bali, on the boundary between west and east Indonesia, resembles most the fauna of species-rich eastern areas. With regard to reef corals Bali appears to be the south-westernmost area in the centre of maximum marine diversity.

Keywords Bali, Indonesia, Biogeography, Centre of diversity, Corals

Introduction

The centre of maximum benthic diversity

The centre of marine benthic biodiversity is situated somewhere within the Indo-Malayan region, SE Asia (Ekman 1953). This region is hypothesised to be species-rich because it acts as a centre of evolutionary radiation (Briggs 1974, 1987, 1992, 1995, 1999a, 1999b), which is not necessarily consistent with the geological history of coral reef distributions and with ecological requirements of species (Pandolfi 1992, Paulay 1997, Wallace 1997, 1999a, Wilson and Rosen 1998).

The origin of the centre may be understood better when its exact boundaries are known. These boundaries are not clearly defined. Brigg's (1999a: Fig. 1) East Indies Triangle of marine diversity is probably based on the borders of countries involved and the position of islands in the Indo-Malayan region. Veron's (1995: Fig. 50) maximum coral species diversity contour (n = 450) is more relevant but of unclear origin, since it is a hypothetical addition to lower-value boundaries that are projections of generic diversity contours.

Since reef coral diversity patterns are usually expressed in genus richness (Best et al. 1989, Veron 1995), more information is needed on the variation in species composition and diversity in and around the Indo-Malayan region. The analysis of individual species ranges and their overlaps within large taxa may help us to get more insight in how diversity patterns are built up (Hoeksema 1992, Wallace 1999b).

To know these ranges, various areas in and around the diversity centre have to be studied in detail. By setting up sampling programmes using selected model taxa (Kohn 1997) as target groups, such as the mushroom coral family Fungiidae (Hoeksema and Moka 1989, Hoeksema 1989, 1992, 1997) and the staghorn coral genus *Acropora* (Wallace 1999b), reliable data sets can be obtained on species presence or absence. Per area, data gathering should cover the complete habitat range of each model taxon to prevent too much sampling bias.

The coral fauna of Bali

The marine fauna of Bali is not well known. Ship-based expeditions in the past (e.g. Siboga, Snellius, Snellius-II) focused mainly on eastern Indonesia. There are only few examples of publications that specifically or predominantly deal with the fauna and management of coral reefs at Bali (Polunin et al. 1984, Woesik 1996, Wallace and Wolstenholme 1998, Putra and Widyastuti 1999). This is surprising since Balinese reefs are of much importance to the tourist industry (Pickell and Sagian 2000). Anyway, the position of Bali with regard to the centre of marine diversity is not clear.

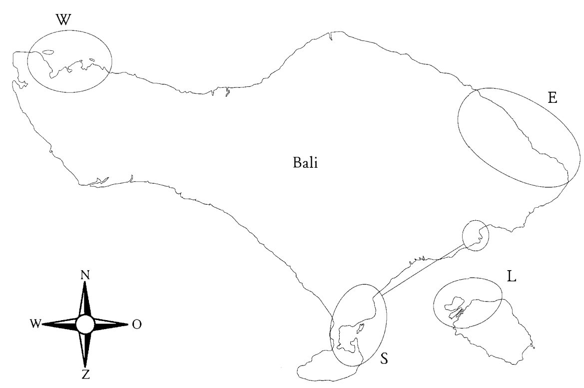

Fig. 1 Map of Bali indicating the four areas investigated: W = West Bali (Bali Barat), E = Eastern Bali; S = Southern Bali; L:= Lombok Strait: Nusa Penida and Nusa Lembongan.

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In the present paper, data on mushroom coral species (Fungiidae) and scleractinian genera of Bali are presented. This will be used for comparison with areas previously investigated (Hoeksema 1989, 1992, 1997). The generic richness of Bali is presented here to supplement previous data on generic diversity contours (e.g. Best et al. 1989, Veron 1995). We hypothesise that Bali, especially eastern Bali and the Lombok Strait, is located within the centre of diversity for three reasons: (1) The Lombok Strait, bordering the Indian Ocean, is a passage for currents from the Pacific Ocean and the Java Sea to the Indian Ocean (Gordon and Fine 1996). This may result in fauna elements from both oceans. (2) Around Bali corals probably did not disappear during Quaternary sea level drops, whereas the Sunda shelf seas (e.g. Java Sea) became completely drained. (3) There is a high variation in reef environments at Bali with regard to water temperature, substrates, salinity, reef relief, wave exposure, and current velocity.

Methods

Four areas around Bali were selected for scleractinian coral diversity surveys with emphasis on scleractinian coral genera and mushroom corals (Fungiidae) as model taxa (Fig.1). The aim was to monitor as many different coral habitats as possible. Each area was visited during a period of 7-10 days with approximately 15-25 dives:

1. West Bali (W): Bali Barat, mainly consisting of fringing reefs around uplifted limestone (including Menjangan Island) and some patch reefs off the northern coastline.
2. East Bali (E): Tulamben and Amed, predominantly consisting of volcanic sand with limestone outcrops. In addition, Gili Selang, a small rocky islet off the easternmost point of Bali.
3. South Bali (S): Sanur, Nusa Dua, and Padangbai, southeast Bali, with well-developed reef flats, slopes and reef bases.
4. Lombok Strait islands (L): Nusa Lembongan and N. Penida with cold up-welled water and strong currents.

In order to compare the mushroom coral fauna of Bali with neighbouring faunas, a UPGMA cluster analysis was performed.

Results

Four Balinese reef areas

Of the four areas monitored, Bali Barat (W) appears the poorest in mushroom coral species (Table 1) and poor in scleractinian reef coral genera (Table 2), together with the Lombok Strait islands Nusa Penida and Nusa Lembongan (L). The latter two islands are also not particularly rich in species. Eastern Bali (E), Tulamben in particular, is the richest in both categories. Some fungiids occurring here, have not been found elsewhere at Bali: *Fungia (Cycloseris) somervillei*, *F. (Verrillofungia) scabra*, *Lithophyllon mokai*, *L. undulatum*, *Podabacia motuporensis*, and an unidentified *Podabacia* species. Southern Bali (S) is also rich in coral genera, and moderately rich in Fungiidae.

The reef coral fauna of Bali

The occurrence of *F. (Pleuractis) taiwanensis* at Bali is remarkable since this species was previously only recorded from Taiwan and Ambon (Table 3). Specimens were found in complete shape and in fragmented-regenerated condition. Fragmented corals of *Sandalolitha dentata* are also common at South Bali, which is exposed to oceanic waves. This form, becoming circular during regeneration, was recently recorded from Sanur as *Halomitra meierae*, a *nomen nudum* (Veron 2000). Like *F. taiwanensis*, fragmented specimens of *S. dentata* are common at southern Taiwan (Hoeksema and Dai 1991).

Table 1 Fungiidae recorded at West Bali (W), East Bali (E), South Bali (S), and Nusa Lembongan and N. Penida, Lombok Strait (L), - = no record.

Cantharellus doederleini (Von Marenzeller, 1907)	-	-	-	-
C. noumeae Hoeksema & Best, 1984	-	-	-	-
C. jebbi Hoeksema, 1993	-	-	-	-
Ctenactis albitentaculata Hoeksema, 1989	W	E	-	L
C. crassa (Dana, 1846)	W	E	-	L
C. echinata (Pallas, 1766)	W	E	S	L
Fungia (Cycloseris) costulata Ortmann, 1889	W	E	S	L
F. (C.) curvata Hoeksema, 1989	-	-	-	-
F. (C.) cyclolites Lamarck, 1816	-	E	S	L
F. (C.) distorta Michelin, 1842	-	-	-	L
F. (C.) fragilis (Alcock, 1893)	-	E	S	L
F. (C.) hexagonalis M. Edwards & Haime, 1848	-	-	-	-
F. (C.) cf marginata Boschma, 1924	-	E	S	L
F. (C.) somervillei Gardiner, 1909	-	E	-	-
F. (C.) sinensis (M. Edwards & Haime, 1851)	-	E	S	-
F. (C.) tenuis Dana, 1846	W	E	S	L
F. (C.) vaughani Boschma, 1923	-	-	S	L
F. (C.) spec.	-	-	-	-
F. (Danafungia.) fralinae Nemenzo, 1955	-	-	-	-
F. (D.) horrida Dana, 1846	W	E	S	L
F. (D.) scruposa Klunzinger, 1879	W	E	S	L
F. (Fungia) fungites (Linnaeus, 1758)	W	E	S	L
F. (Lobactis) scutaria Lamarck, 1801	W	E	S	L
F. (Pleuractis) gravis Nemenzo, 1955	W	E	S	L
F. (P.) moluccensis Van der Horst, 1919	W	E	S	L
F. (P.) paumotensis Stutchbury, 1833	W	E	S	L
F. (P.) seychellensis Hoeksema, 1992	-	-	-	-
F. (P.) taiwanesis Hoeksema & Dai, 1991	-	-	S	-
F. (Verrillofungia) concinna Verrill, 1864	W	E	S	L
F. (V.) repanda Dana, 1846	W	E	S	L
F. (V.) scabra Döderlein, 1901	-	E	-	-
F. (V.) spinifer Claereboudt & Hoeksema, 1987	-	E	S	-
F. (Wellsofungia) granulosa Klunzinger, 1879	W	E	S	L
Halomitra clavator Hoeksema, 1989	-	-	-	-
H. pileus (Linnaeus, 1758)	W	E	S	L
Heliofungia actiniformis (Quoy & Gaimard, 1833)	W	E	S	L
Herpolitha limax (Esper, 1797)	W	E	S	L
Lithophyllon mokai Hoeksema, 1989	-	E	-	-
L. undulatum Rehberg, 1892	-	E	-	-
Podabacia crustacea (Pallas, 1766)	W	E	S	L
P. motuporensis Veron, 1990	-	E	-	-
P. spec.	-	E	-	-
Polyphyllia novaehiberniae (Lesson, 1831)	-	-	-	-
P. talpina (Lamarck, 1801)	W	E	S	L
Sandalolitha dentata Quelch, 1884	W	E	S	L
S. robusta (Quelch, 1886)	W	E	S	L

Zoopilus echinatus Dana, 1846	-	-	-	-
Total Bali: 36	22	33	27	27

Table 2 Scleractinian genera recorded at Bali Barat (West Bali = W), Tulamben, Amed, Gili Selang (East Bali = E), Padang Bai, Sanur, E Nusa Dua, Sarangan Island (SE Bali = S), Nusa Lembongan, Nusa Penida (Lombok Strait = L), - = no record.

Acroporidae				
Acropora Oken, 1815	W	E	S	L
Anacropora Ridley, 1884	W	E	-	L
Astreopora Blainville, 1830	W	E	S	L
Montipora Blainville, 1830	W	E	S	L
Agariciidae				
Coeloseris Vaughan, 1918	W	E	S	L
Gardineroseris Scheer & Pillai, 1974	W	E	S	L
Leptoseris M. Edwards & Haime, 1849	W	E	S	L
Pachyseris M. Edwards & Haime, 1849	W	E	S	L
Pavona Lamarck, 1801	W	E	S	L
Astrocoeniidae				
Stylocoeniella Yabe & Sugiyama, 1935	W	E	S	L
Caryophylliidae				
Catalaphyllia Wells, 1971	-	-	-	-
Euphyllia Dana, 1846	W	E	S	L
Gyrosmilia M. Edwards & Haime, 1851	-	-	-	-
Heterocyathus M. Edwards & Haime, 1848	-	-	S	-
Physogyra Quelch, 1884	W	E	S	L
Plerogyra M. Edwards & Haime, 1848	-	E	S	-
Montigyra Matthai, 1928	-	-	-	-
Dendrophylliidae				
Dendrophyllia Blainville, 1830	W	E	S	L
Duncanopsammia Wells, 1936	-	-	-	-
Heteropsammia M. Edwards & Haime, 1848	-	-	S	-
Tubastraea Lesson, 1829	W	E	S	L
Turbinaria Oken, 1815	W	E	S	L
Faviidae				
Astreosmilia Ortmann, 1892	-	-	-	-
Australogyra Veron & Pichon, 1982	-	-	-	-
Barabattoia Yabe & Sugiyama, 1941	-	-	S	-
Caulastrea Dana, 1846	-	E	S	-
Cyphastrea M. Edwards & Haime, 1848	W	E	S	L
Diploastrea Matthai, 1914	W	E	S	L
Echinopora Lamarck, 1816	W	E	S	L
Erythrastrea Scheer & Pillai, 1983	-	-	-	-
Favia Oken, 1815	W	E	S	L
Favites Link, 1807	W	E	S	L
Goniastrea M. Edwards & Haime, 1848	W	E	S	L
Leptastrea M. Edwards & Haime, 1848	W	E	S	L
Leptoria M. Edwards & Haime, 1848	W	E	S	L
Montastrea Blainville, 1830	W	E	S	N
Moseleya Quelch, 1884	-	-	-	-
Oulastrea M. Edwards & Haime, 1848	-	E	S	-
Oulophyllia M. Edwards & Haime, 1848	-	E	S	L
Parasimplastrea Sheppard, 1985	-	-	-	-
Platygyra Ehrenberg, 1834	W	E	S	L
Plesiastrea M. Edwards & Haime, 1848	-	E	S	L
Fungiidae				
Cantharellus Hoeksema & Best, 1984	-	-	-	-
Ctenactis Verrill, 1864	W	E	S	L
Fungia Lamarck, 1801	W	E	S	L
Halomitra Dana, 1846	W	E	S	L
Heliofungia Wells, 1966	W	E	S	L
Herpolitha Eschscholtz, 1825	W	E	S	L
Lithophyllon Rehberg, 1892	-	E	-	-
Podabacia M. Edwards & Haime, 1849	W	E	-	L
Polyphyllia Blainville, 1830	W	E	S	L
Sandalolitha Quelch, 1884	W	E	S	L
Zoopilus Dana, 1846	-	-	-	-
Meandrinidae				
Ctenella Matthai, 1928	-	-	-	-
Merulinidae				
Boninastrea Yabe & Sugiyama, 1935	-	-	-	-
Hydnophora Fischer de Waldheim, 1807	W	E	S	L
Merulina Ehrenberg, 1834	W	E	S	L
Paraclavarina Veron, 1985	-	-	-	-
Scapophyllia M. Edwards & Haime, 1848	-	-	-	-
Mussidae				
Acanthastrea M. Edwards & Haime, 1848	W	E	S	L
Australomussa Veron, 1985	W	E	S	-
Blastomussa Wells, 1961	-	-	-	-
Cynarina Brüggemann, 1877	W	E	-	-
Indophyllia Gerth, 1921	-	-	-	-
Lobophyllia Blainville, 1830	W	E	S	L
Scolymia Haime, 1952	-	E	S	L
Symphyllia M. Edwards & Haime, 1848	W	E	S	L
Oculinidae				
Acrhelia M. Edwards & Haime, 1849	W	-	-	-
Galaxea Oken, 1815	W	E	S	L
Pectiniidae				
Echinophyllia Klunzinger, 1879	W	E	S	L
Mycedium Oken, 1815	W	E	S	L
Oxypora Saville-Kent, 1871	W	E	-	L
Pectinia Oken, 1815	W	E	S	L
Physophyllia Duncan, 1884	-	-	-	-
Pocilloporidae				
Madracis M. Edwards & Haime, 1849	-	-	-	-
Palauastrea Yabe & Sugiyama, 1941	-	E	-	-
Pocillopora Lamarck, 1816	W	E	S	L
Seriatopora Lamarck, 1816	W	E	S	L
Stylophora Schweigger, 1819	W	E	S	L
Poritidae				
Alveopora Blainville, 1830	W	E	S	-
Goniopora Blainville, 1830	W	E	S	L
Porites Link, 1807	W	E	S	L
Stylaraea M. Edwards & Haime, 1851	-	-	S	-
Siderastreidae				
Anomastrea Marenzeller, 1901	-	-	-	-
Coscinarea M. Edwards & Haime, 1848	-	E	S	L
Horastrea Pichon, 1971	-	-	-	-
Psammocora Dana, 1846	W	E	S	L
Pseudosiderastrea Yabe & Sugiyama, 1935	-	E	-	-
Siderastrea Blainville, 1830	-	-	-	-
Trachyphylliidae				
Trachyphyllia M. Edwards & Haime	-	-	S	-
Total Bali: 66	53	61	58	52

At Nusa Penida and Nusa Lembongan large populations of the hydrocoral *Distichopora vervoorti* Cairns and Hoeksema, 1998, occur. This colourful species has not yet been recorded from elsewhere (Cairns and Hoeksema 1998; Goud and Hoeksema 2001).

In comparison with nine neighbouring areas (Table 4), Bali ranks fifth, with Ambon, in fungiid species richness (n =36). It is also fifth in the number of scleractinian genera (n =66).

The UPGMA dendrogram (Fig. 2) shows that with regard to its fungiid fauna, Bali is less related to westward areas (W Sumatra and NW Java) than eastward ones, and that it is most similar to Ambon. For some coral species Bali is the south-westernmost position of their distribution range;

examples are *Fungia (Pleuractis) gravis*, *F. (Verrillofungia) spinifer*, and *Podabacia motuporensis.* It has these species in common with other species-rich areas in the Indo-Malayan region (Table 3).

Table 3 Fungiidae occurrence (1) and absence (0) at Bali and nine surrounding areas (data collected by first author since 1983). This data set is the basis for the cluster analysis resulting in the dendrogram (Fig. 2). For genus names see Table 1.

Area	W Sumatra	NW Java	Bali	SW Sulawesi	Togian Is	Komodo/ Sumbawa	North Sulawesi	Ambon	North P.N.G.	Central Philipp.
Fungiidae										
C. doederleini	0	0	0	0	0	0	0	0	0	0
C. jebbi	0	0	0	0	0	0	0	0	1	0
C. noumeae	0	0	0	0	0	0	0	0	0	0
C. albitentaculata	1	1	1	1	1	1	1	1	1	1
C. crassa	1	1	1	1	1	1	1	1	1	1
C. echinata	1	1	1	1	1	1	1	1	1	1
F. (C.) costulata	1	1	1	1	1	1	1	1	1	1
F. (C.) curvata	0	0	0	0	0	0	0	0	1	1
F. (C.) cyclolites	0	1	1	1	0	1	1	1	1	1
F. (C.) distorta	0	0	1	1	0	1	1	1	1	1
F. (C.) fragilis	0	1	1	1	1	1	1	1	1	1
F. (C.) hexagonalis	0	0	0	0	0	1	1	1	1	1
F. (C.) cf.	0	0	1	1	1	1	1	1	1	1
F. (C.) sinensis	0	0	1	1	1	1	1	1	1	1
F. (C.) somervillei	0	0	1	1	0	1	0	1	1	1
F. (C.) tenuis	1	0	1	1	1	1	1	1	1	1
F. (C.) vaughani	0	0	1	1	0	1	0	1	1	1
F. (C.) spec.	0	1	0	1	0	1	0	0	0	0
F. (D.) fralinae	0	0	0	1	0	1	1	0	1	1
F. (D.) horrida	1	1	1	1	1	1	1	1	1	1
F. (D.) scruposa	0	1	1	1	1	1	1	1	1	1
F. (F.) fungites	1	1	1	1	1	1	1	1	1	1
F. (L.) scutaria	1	1	1	1	1	1	1	1	1	1
F. (P.) gravis	0	0	1	1	1	1	1	1	1	1
F. (P.) moluccensis	1	1	1	1	1	1	1	1	1	1
F. (P.)	1	1	1	1	1	1	1	1	1	1
F. (P.)	0	0	0	0	0	0	0	0	0	0
F. (P.) taiwanesis	0	0	1	0	0	0	0	1	0	0
F. (V.) concinna	1	1	1	1	1	1	1	1	1	1
F. (V.) repanda	1	1	1	1	1	1	1	1	1	1
F. (V.) scabra	0	1	1	1	0	1	0	0	0	1
F. (V.) spinifer	0	0	1	1	0	1	0	1	1	1
F. (W.) granulosa	1	1	1	1	1	1	1	1	1	1
H. pileus	0	1	1	1	1	1	1	1	1	1
H. clavator	0	0	0	1	0	1	0	0	1	1
H. actiniformis	0	1	1	1	1	1	1	1	1	1
H. limax	1	1	1	1	1	1	1	1	1	1
L. undulatum	0	1	1	1	0	1	1	1	1	1
L. mokai	1	1	1	1	0	1	1	1	1	1
P. crustacea	0	1	1	1	1	1	1	1	1	1
P. motuporensis	0	0	1	1	1	1	1	1	1	1
P. spec.	1	1	1	0	1	0	0	0	0	1
P. novaehiberniae	0	0	0	0	0	0	0	0	1	0
P. talpina	1	1	1	1	1	1	1	1	1	1
S. dentata	1	1	1	1	1	1	1	1	1	1
S. robusta	0	1	1	1	1	1	1	1	1	1
Z. echinatus	0	0	0	1	1	1	1	1	1	1
Total per area	18	27	36	38	28	39	33	36	40	40

Table 4 Bali and nine neighboring Indo-Malayan areas (Fig. 3), monitored for Fungiidae and scleractinian genera.

Area	**Number of Fungiidae (n =47)**	**Number of Scleractinian Genera (n=78)**
West Sumatra	18	48
Northwest Java	27	60
Togian Is (East Sulawesi)	28	57
North Sulawesi	33	62
Bali	**36**	**66**
Ambon	36	68
South Sulawesi	38	76
Komodo + W Sumbawa	39	72
North Papua New Guinea	40	74
Central Philippines	40	76

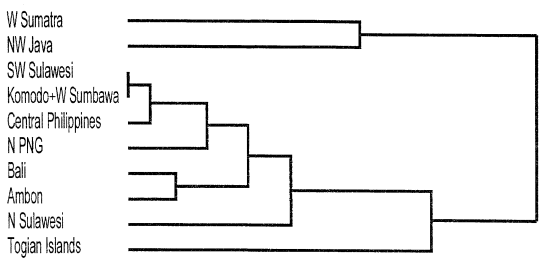

Fig. 2 UPGMA dendrogram (Q mode) of Bali and nine neighbouring areas (Fig. 3) with regard to their fungiid faunas.

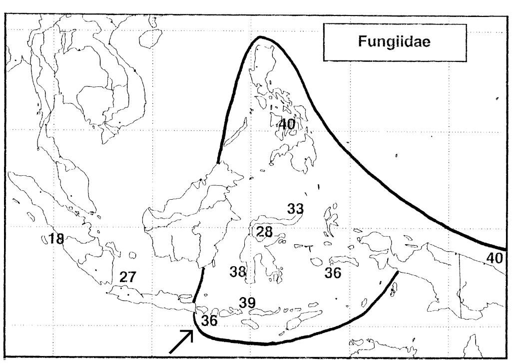

Fig. 3 The Indo-Malayan region with the probable centre of diversity for Fungiidae. The position of Bali is indicated (→).

Conclusions

West Bali appears to be poorer than the other areas investigated, a probable effect of bleaching in 1997 (pers. obs.). This is one of the few locations where the rare *Acropora suharsonoi* Wallace, 1994, has been observed (Wallace and Wolstenholme 1998, Wallace 1999b).

The Tulamben - Amed area, East Bali, is the richest. At Sanur and Nusa Dua, South Bali, fungiid species have been recorded that previously were recorded from the Pacific. The habitat of fragmented-regenerated fungiid corals, lower reef slopes exposed to waves, is also known from southern Taiwan (Hoeksema and Dai 1992). The deep-living *Fungia taiwanensis* has not been found at intermediate localities, such as North and South Sulawesi, which may be due to a lack of deep-penetrating wave action.

At Nusa Lembongan and Nusa Penida some rare species have been found, like the hydrocoral *Distichopora vervoorti* (Cairns and Hoeksema 1998) with its gastropod symbiont (Goud and Hoeksema 2001), and also *Acropora* species not well-known from other Indonesian areas (Wallace and Wolstenholme 1998, Wallace 1999b), such as *A. glauca* (Brook, 1893), *A. palmerae* Wells, 1954, and *A. sukarnoi* Wallace, 1997. The two Lombok Strait islands are characterised by uplifted limestone, cold upwelling and strong currents. The last two factors may be most important for the habitat of the unique species, which perhaps also dwell at greater depths.

For several species, Bali is the south-westernmost distribution locality, which is also the most remote from the Pacific. Possible explanations are:

1. During the Pliocene-Quaternary glaciations, the Balinese coastline and its coral communities shifted downward with the sea level, like more east- and northward areas. The coral reefs of the Java Sea and the shelf off west Sumatra emerged above sea level (Potts 1984). Marine species only could re-establish here after new transgressions (Edinger et al. 2000).
2. The Lombok Strait at Bali is in direct contact with the Indonesian throughflow from the west Pacific to the eastern Indian Ocean (Gordon and Fine 1996). During the Pliocene-Quaternary sea level regressions it was not isolated from such inter-oceanic currents, in contrast to north-west Java and west Sumatra, both with less diversity. Consequently, the marine fauna of Bali has elements that are only known from West-Pacific areas and elements that are more typical for the Indian Ocean.

Although the boundaries of the marine diversity centre are not exactly known, it is clear that Bali should be included with regard to corals. Among the species-rich areas, Bali is the south-westernmost, excluding westward areas. That Bali has not been included before in hypothetical centres of diversity (e.g. Veron 1995) was due to a lack of research at Bali.

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