RAFFLES BULLETIN OF ZOOLOGY Supplement No. **22**: 91–101
Date of Publication: 30 Dec.2009

DEPAUPERATION OF THE MUSHROOM CORAL FAUNA (FUNGIIDAE) OF SINGAPORE (1860s–2006) IN CHANGING REEF CONDITIONS

Bert W. Hoeksema
National Museum of Natural History Naturalis,
P.O. Box 9517, 2300 RA Leiden, The Netherlands
E-mail: hoeksema@naturalis.nnm.nl

Esther G. L. Koh
Singapore Immunology Network (SigN), 8A Biomedical Grove,
IMMUNOS Building #3-4, BIOPOLIS, Singapore 138648, Republic of Singapore
Email: esther_koh@immunol.a-star.edu.sg

***ABSTRACT*. –** A study of museum collections (since the 1860s) in comparison with observations during fieldwork (1970, 1987 and 2006) suggests a reduction of the mushroom coral fauna (Scleractinia: Fungiidae) of Singapore. After a revision of 19 Singaporean fungiid species either collected or recorded and photographed in the field, the presence of only 15 species could be confirmed during the latest survey (2006). This number includes a species that was discovered as new to science. Species richness estimators indicate that additional species are not to be expected. This local depauperation of the mushroom coral fauna may be a result of deforestation in the hinterland and land reclamation works in the harbour area, both of which have caused increasing siltation and lower visibility in the coastal waters of Singapore. Coral bleaching on Singapore's reefs (1998) may have played a less prominent role.

***KEY WORDS*. –** Mushroom coral fauna, Singapore, collections, field observations, depauperation, long-term, deforestation, land reclamation.

INTRODUCTION

Information on biodiversity loss in Singapore predominantly concerns terrestrial and freshwater taxa (Brook et al., 2006). Little is known about the extinction of Singapore's marine species, because they are comparatively less well-known (Tan et al., 2004). Studies on local marine biota started with the establishment of the Department of Zoology at the National University of Singapore in 1950 (Khoo, 1991). Scientific museum collections, including those of the university, are ideal tools for detecting long-term changes in biodiversity, especially if the specimens are well maintained and accompanied by reliable collection data. Old natural history museums and herbariums may harbour samples that have been kept for over 100 years. At present such specimens can be important as reference material for studies on the history of biota. In Singapore, natural history collections have been stored in the Raffles Museum, which was founded in 1849 and later became known as the Raffles Museum of Biodiversity Research (RMBR), which contains the present Zoological Reference Collection (ZRC).

Scientific reference collections may indicate local species loss of reef-dwelling species (Meij et al., 2009), but on the other hand can also be used to proof that species have greater distribution ranges, and therefore are less vulnerable than previously assumed. For example, after the 1982–1983 El Niño warming event, the hydrocoral *Millepora boschmai* De Weerdt & Glynn, 1991, was considered extinct when only dead specimens were observed at its type locality, the East Pacific coast of Panama (Glynn & Weerdt, 1991; Weerdt & Glynn, 1991). Only one year later, five living corals were discovered at the same locality (Glynn & Feingold, 1992). Moreover, specimens of the same species appeared to have been collected alive in 1984 at South Sulawesi, Indonesia. These corals remained unnoticed until a revision of Indonesian *Millepora* corals was conducted (Razak & Hoeksema, 2003). Therefore natural history collections are a valuable tool for detecting changes in biodiversity over time.

Animals with hard skeletons are relatively easy to study, because they can be collected, stored and examined in dried condition without the help of preservatives or special preparations. Sea shells, stony corals (scleractinians and hydrocorals), sea urchins, and reef-dwelling foraminifera are therefore well represented in natural history collections and ideal for establishing historical baselines for studies on species occurrences. Due to their sensitivity to elevated seawater temperatures, zooxanthellate stony corals form a rational choice as indicator taxa for the detection of global change signals (Brown, 1997). Since it is time consuming to deal with all species of stony coral, it may help to select a recently revised family or genus as indicator group, such as the mushroom coral family Fungiidae (Hoeksema, 1989) or the staghorn coral genus *Acropora* (Wallace, 1999). Both taxa are abundantly represented in museum collections.

Due to limitations in identifying benthic organisms to species level, it has been difficult to make assessments of changes in the fauna of Singapore's coastal waters and therefore there is a need for indicator taxa (Khoo, 1991). In the present study, mushroom corals were selected as a model group. They can easily be collected in the field, especially corals belonging to the free-living species (Hoeksema, 1989; Koh & Chou, 1989). Because they can be counted as individuals in density studies, they are also suitable for quantitative ecological analyses (Koh, 1987; Hoeksema, 1990, 1991, 2004). However, in comparisons of fungiid species compositions over long time periods, which are partly based on museum collections, only species presence and absence records can be taken into account.

THE RESEARCH AREA

The coastline of Singapore is continuously changing due to land reclamation activities and dredging (Yong et al., 1991; Lim et al., 1994; Hilton & Manning, 1995; Chou, 1996; Hilton & Chou, 1999). The map used to indicate study sites in 1987 and 2006 (Fig. 1) does not show the present situation anymore, (Anonymous, 2002; Chou, 2006; Loh et al., 2006) but indicates the earliest field situation presented in this study (Koh, 1987). Singapore is one of the busiest ports of the world and land area is very limited. Therefore, space needed for industrial activities depending on maritime resources was created at the coast or in sea (Wong, 2000; Chou, 2006). During our 2006 survey, sediment was dumped at Pulau Ular to build land area for the oil industry. This notably caused suspended matter to decrease light penetration at the neighbouring Pulau Hantu, which appeared to be one of the Singapore's most species-rich coral reefs. Besides the creation of landfills and dredging activities for port extensions, the seawater may also become sediment-enriched by logging and subsequent terrigenous run-off along the nearby coastline of the adjacent Malacca Strait. Finally, it was also noticed in 2006 that the heavy ship traffic passing through the channels along the Southern Islands generates waves that may cause recurring sediment re-suspension on the reefs. All these activities may cause damage to coral growth and survival (Dodge et al. 1974; Dodge & Vaisnys, 1977; Rogers, 1991; McClanahan & Obura, 1997).

In fact, the reef conditions at Singapore have already been characterized by poor visibility for decades, which always had a negative impact here (Wong, 1985; Chua & Chou, 1991; Goh & Chou, 1992; Low & Chou, 1994; Hilton & Manning, 1995), especially since some coral species are more resistant to overcome sedimentation than others (Stafford-Smith, 1993). Turbidity has a lot of impact on the reef community zonation, because poor light penetration has a limiting effect on reef coral cover, especially on lower reef slopes (Chuang, 1977; Chou, 1988; Lane, 1991; Chou et al, 1994; Goh et al., 1994; Tun et al., 1994). However, besides the present study, there is no clear baseline regarding the coral composition of Singapore reefs before human activities affected the reefs.

MATERIAL AND METHODS

Old museum specimens from Singapore dating back since the 1850s were studied in the Museum of Comparative Zoology (MCZ), Harvard University, at Cambridge (Mass.) and in the Yale Peabody Museum of Natural History (YPM), Yale University, New Haven (Hoeksema, 1989). Such old coral collections were not found in the Zoological Reference Collection (ZRC) in Singapore, although the Raffles Museum was founded in 1849. Most MCZ mushroom corals were collected by Capt. W. H. A. Putnam before June 1862, when these specimens were registered in the MCZ Stony Coral Catalogue (Mrs Ardis Baker Johnston, pers. comm.). A few corals were collected between 1861 and 1868 by J. M. Barnard and by Capt. Parker. Some corals collected by Capt. Putnam (donated to the MCZ in October 1858) came from the Essex Institute (est. 1799), now the Peabody Essex Museum in Salem (Mass.). All mushroom corals from Singapore at YPM were received from the same institute as well, in the period 1865–1868 (Mr. Eric A. Lazo-Wasem, pers. comm.). They were collected in Singapore mainly by Capt. Putnam, but also by Mr. Charles G. Brewster and Mr N. Dwight Williams, who might have been ship captains as well. Due to the various collection dates, these corals are presently categorized as being collected in the 1860s. The locality data are not more specific than "Singapore". There is no reason to assume that they were traded to Singapore from far away, since coral reefs were present very close to the harbour and mushroom corals have always been easy to collect. Since the old (1860s) mushroom coral collections are quite large, differences in numbers of species may indicate that sampling was not really restricted. The collectors probably took as many specimens as possible and differences in species representation may indicate that some species were more abundant and available than others or because some species could be collected more easily due to their shallow depth ranges. Since the reefs at Singapore are shallow, depth may have been a limiting factor for only the deepest species.

In the 1890s, corals from Singapore were brought to Europe, especially to the British Museum of Natural History (BMNH), presently The Natural History Museum, in London (Hoeksema, 1989).

In the period 1986–1991, many mushroom corals were

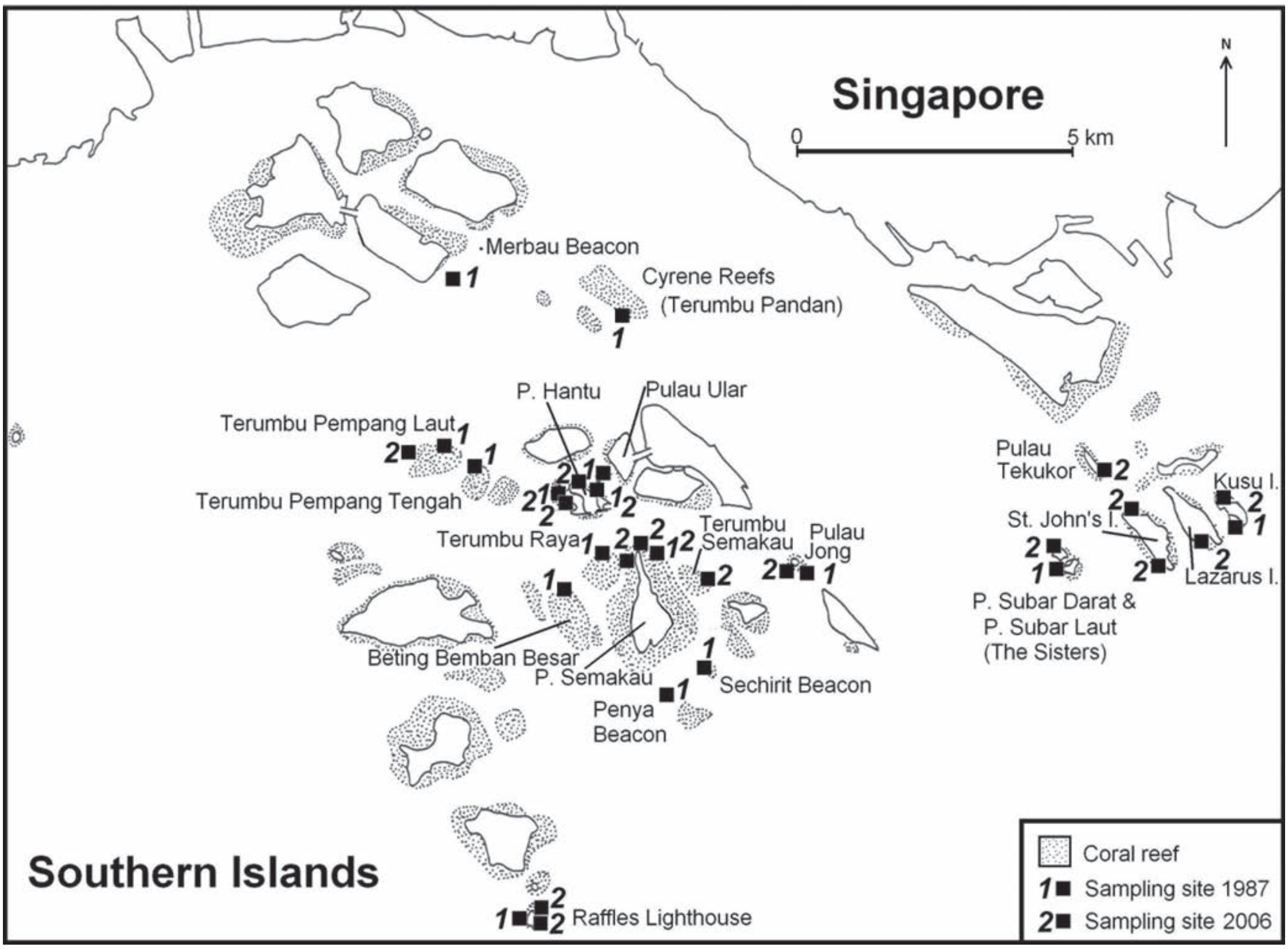

Fig. 1. Map of Singapore's Southern Islands (1987 situation) indicating reef sites studied in 1987 and in 2006.

collected from the reefs of the Southern Islands off Singapore, mostly with accurate collection data. These specimens have been deposited in the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research (RMBR), National University of Singapore. Many of these were collected and identified in 1987 by the second author (EGLK), whereas corals already present in the collection were re-examined (Koh, 1987; Koh & Chou, 1989). Specimens reported from Singapore in an earlier study (Tan, 1970) were not present in the museum collection, but coral photographs in the report are consistent with the identifications. All mushroom corals present in the ZRC and photographed specimens were examined and re-identified by the first author (BWH) in 2006 according to species concepts presented in the last taxonomic revision of the Fungiidae (Hoeksema, 1989).

The earlier study by Koh (1987) was connected to an ecological survey on the bathymetrical distribution of mushroom corals at 16 reef sites varying from near-shore to offshore (Fig. 1, Table 1). Species abundances and incidences were measured in four 10 × 1 m transects, each in a different reef zone (reef flat, crest, slope, and bottom, respectively) at each study site. Since densities of most species were low, especially on the muddy reef bottoms, the 1987 data has been pooled per site for species richness analyses. Species richness estimators were calculated with the programme EstimateS (Colwell, 2006). These estimators represent species accumulation curves in which the sample order has been randomised and the values have been averaged. The mean and standard deviation of species richness at each specific sample number can be calculated (Ugland et al., 2003; Magurran, 2004). They can be extrapolated to indicate the total species richness in an area. When the curves of the estimators flatten out and become asymptotic with a minimal standard deviation (i.e. 0), a very reliable measure for species richness is obtained (Fig. 2). Indicators based on abundance data are Chao 1, ACE, S Obs, and Singleton values; those based on incidence (presence/absence) data are Chao 2, ICE, S Obs and Unique values (Colwell, 2006). The estimators indicate whether the number of Singaporean mushroom coral species observed in 1987 was similar to the expected number of species. However, the 1987 survey only involved free-living mushroom corals and excluded species that remain attached during their life history (Koh, 1987).

Research on the Singapore mushroom coral fauna was continued on a total of 18 reef sites in 2006, also varying from near-shore to offshore and some of which were similar to the sites investigated in 1987 (Fig. 1, Table 1). The main purpose of this field study was to record all fungiid species for biogeographic comparisons with other areas located in or outside the Coral Triangle (Hoeksema, 2007). Therefore, only occurrence or incidence data (presence/absence) of species

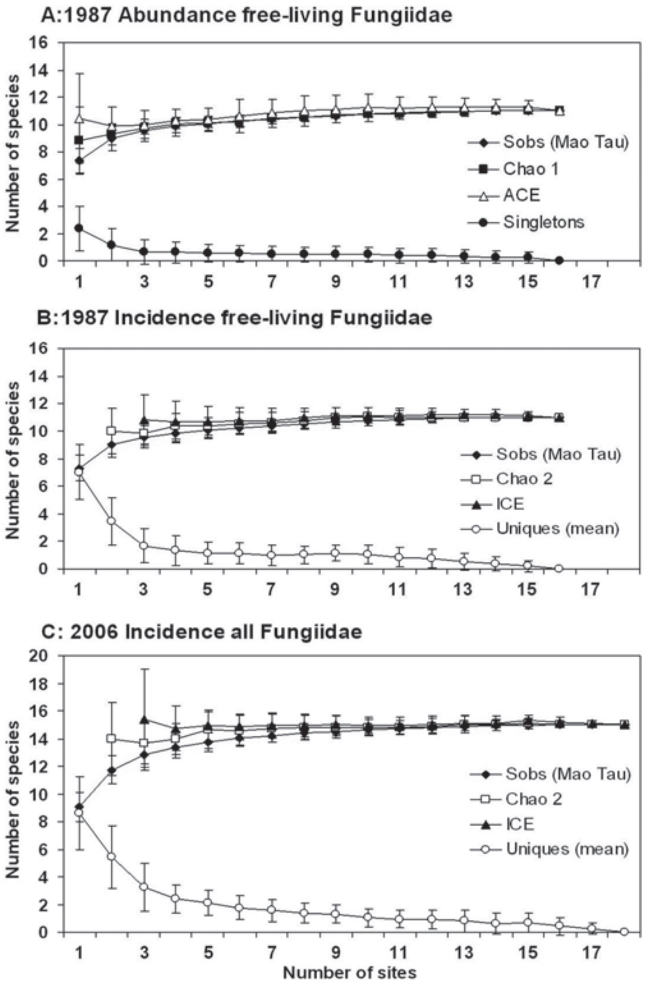

Fig. 2. Species richness estimators (Colwell, 2006). Abundance data (A) and Incidence records (B) from 16 transects sites in 1987 indicate presence of 11 free-living mushroom corals species. S Obs (Observed species number or Mao Tau estimator based on 11 species actually discovered); Chao 1 and Chao 2 (mean among runs with standard deviations), ACE and ICE (Abundance- / Incidence -based Coverage Estimator of species richness; mean among runs with standard deviations) indicate that not more than 11 species are expected, whereas Singletons (species with only one individual) in pooled samples (mean among runs) and Uniques (species that occur in a only one sample; mean among runs) indicate that no extra species are expected. C: Likewise, incidence records from 18 sites surveyed in 2006 by roving diving technique from reef base to reef flat indicate that not more than 15 mushroom coral species (free-living and attached) are expected.

was recorded at each site over the complete depth range in which mushroom corals occurred by the so-called roving diving survey method or roving diving technique (Schmitt et al., 2002; Munro, 2005). This data was used to verify the observed species richness, also with the help of EstimateS (Colwell, 2006). Since, only incidence data were used, these estimators involved Chao 2, ICE, Sobs and Unique values. Although only presence/absence records were made per site, many more coral specimens could be observed and checked than during transect surveys, because no time was spent on collecting. Furthermore, once a species has been identified and recorded in the field, the search can concentrate on species not yet observed at the same site, and therefore this method is the most efficient in obtaining species records. The species richness indicators show that the observations are sufficiently reliable, although no quantitative records have been made.

RESULTS

All records of mushroom corals from Singapore together (1860s, 1890s, 1970, 1986–1991, and 2006) show a total number of 19 species (Table 2). Four species represented in collections made before 2006, were not observed during the 2006 survey: *Ctenactis albitentaculata*, *C. crassa*, *Fungia horrida*, and *F. granulosa*. These four species have never been abundantly collected at Singapore, though. The period 1986–1991 showed the highest number of species (n = 18), while it lacks an attached species that was not described yet. This fungiid species was most likely overlooked because it resembles juveniles of other fungiid species due to its small size (Hoeksema, 2009). Because it was unobserved, the total number of species was most probably 19 in the period 1986–1991. In 2006, only a total of 15 mushroom coral species was encountered at Singapore.

It is remarkable that species most commonly collected in the mid 19th Century, are also among the most abundantly represented in the last collection (1986–1991): e.g. *Fungia repanda*, *Herpolitha limax*, *F. concinna*, *F. fungites*, and *F. scruposa*. *F. moluccensis* is also common but it may not be well represented in older collections because it occurs too deep for easy sampling. The abundance records of common species show the same patterns of relative frequencies (Table 3), indicating *F. repanda*, *F. fungites* and *F. concinna* as the three most densely distributed species. Species most commonly represented among sites in 1987 (Table 3) were also the most widespread at sites in 2006 (Table 4), in particular *F. fungites*. Two species, *Heliofungia actiniformis* and *Polyphyllia talpina*, were present at only a few sites in both 1987 (Table 3) and 2006 (Table 4).

The number of free-living species per site varied from four to ten in 1987 and from six to 14 in 2006. Two sites at Pulau Hantu showed the highest numbers of species in 2006. In order to test the reliability of the species numbers of 1987 and in 2006, species richness estimators were applied to compare the observed species richness with the expected species richness based on abundance (if available) and incidence (presence/absence) records.

The abundance data of 1987 (Table 3) result in asymptotes at an average value of 11 species in Chao 1, ACE, and S Obs analyses (with the eventual standard deviation reaching 0), whereas the number of singletons reaches 0 at 16 samples (Fig. 2), which indicates that no additional species were to be expected. The presence/absence (incidence) records of species (Table 3) show similar asymptotic functions for respectively Chao 2, ICE, and Unique values, respectively (Fig. 2). These analyses indicate that the sampling in 1987 was sufficient to show a reliable species composition and richness, and that it is unlikely that any species of free-living mushroom corals was overlooked.

Table 1. Sites investigated in 1987 (free-living mushroom coral species only) and in 2006 (all Fungiidae).

Site #	Reef site 1987	Site #	Reef site 2006
A01	Beting Bemban Besar, NE	B01	Pulau Hantu Kecil, NE
A02	Pulau Hantu West, NE	B02	Pulau Hantu Kecil, E
A03	Kusu I. (Pulau Tembakul), SW	B03	Pulau Hantu Besar, NW
A04	Merbau Beacon, SW	B04	Pulau Semakau, N
A05	Penya Beacon, N	B05	Pulau Semakau, NW
A06	Pulau Hantu Besar, E	B06	P. Satumu (Raffles Lighthouse), SE
A07	Pulau Jong, SW	B07	P. Satumu (Raffles Lighthouse), NE
A08	Pulau Semakau, NW side	B08	P. Sakijang Bendera (St John's I.), N
A09	P. Subar Laut (The Sisters), SW	B09	P. Sakijang Pelepah (Lazarus I.), SW
A10	Sechirit Beacon, NW	B10	P. Sakijang Bendera (St John's I.), SW
A11	P. Satumu (Raffles Lighthouse), NE	B11	Kusu I. (Pulau Tembakul), N
A12	Terumbu Pandan, SW	B12	Pulau Tekukor (Monkey I.), SE
A13	Terumbu Pempang Laut, NE	B13	Pulau Semakau, NE
A14	Terumbu Pempang Tengah, NW	B14	Terumbu Semakau, E
A15	Terumbu Raya, NW	B15	Pulau Subar Darat (The Sisters), NW
A16	Pulau Ular, SW	B16	Pulau Jong, SW side
		B17	Terumbu Pempang Laut, W side
		B18	Pulau Hantu Besar, W side

Table 2. Mushroom coral species (Fungiidae) numbers recorded from Singapore (n=19) based on studies of museum specimens (MCZ and YPM collected in the 1860s, BMNH collected in the 1890s, ZRC collected in 1986-1991), a BSc study (Tan 1970), and field observations (presence / absence in 2006). Numbers only indicate how well species are represented in museum collections. The high numbers of specimens of some species (1860s, 1986-1991) suggest that collecting was not restricted if a sufficient number of specimens was obtained. Therefore, high numbers suggest that species were easy to collect due to their abundance or due to their shallow depth. Names in bold print indicate species represented in museum collections but not observed in 2006.

	1860s	1890s	1970	1986–91	2006
***Ctenactis albitentaculata* Hoeksema, 1989**	**3**	0	0	**1**	-
***C. crassa* (Dana, 1846)**	0	0	0	**2**	-
C. echinata (Pallas, 1766)	1	0	5	26	+
***Fungia (Danafungia) horrida* (Dana, 1846)**	0	0	0	**2**	-
F. (Danafungia) scruposa Klunzinger, 1879	45	2	9	62	+
F. (Fungia) fungites (Linnaeus, 1758)	55	0	10	148	+
F. (Pleuractis) moluccensis Van der Horst, 1919	1	0	7	80	+
F. (Pleuractis) paumotensis Stutchbury, 1833	10	1	4	28	+
F. (Verrillofungia) concinna Verrill, 1864	62	2	11	82	+
F. (Verrillofungia) repanda (Dana, 1846)	129	2	11	191	+
F. (Verrillofungia) scabra Döderlein, 1901	1	1	0	19	+
***F. (Wellsofungia) granulosa* Klunzinger, 1879**	0	0	0	**2**	-
Heliofungia actiniformis (Quoy & Gaimard, 1833)	0	1	8	11	+
Herpolitha limax (Esper, 1766)	65	2	4	62	+
Lithophyllon undulatum Rehberg, 1892	0	0	0	14	+
Podabacia crustacea (Pallas, 1766)	12	0	0	2	+
P. motuporensis Veron, 1990	0	0	0	10	+
P. kunzmanni Hoeksema, 2009	0	0	0	0	+
Polyphyllia talpina (Lamarck, 1801)	9	1	6	5	+
Number of species observed	12	8	10	17	15

The analyses of the 2006 incidence data (Table 4) of 15 mushroom coral species recorded give a slightly different result. The asymptotic functions for respectively Chao 2, ICE, S Obs and Unique values, indicate that 15 species can be expected. Because all standard deviations reach 0 and because the value of Uniques reaches 0 (Fig. 2), no additional species are to be expected.

DISCUSSION AND CONCLUSIONS

The results of the present study suggest that the mushroom coral fauna of Singapore was richer in the past than it is at present. The period 1986–1991 shows the highest species record (Table 1). Four species were lacking in 2006. One of them was already found in the 1860s. The missing species used to be rare and are likely also the most vulnerable and the first to disappear in the event of habitat degradation. The lost species, with the exception of *Fungia horrida*, are usually absent on reefs close to river outlets and most abundant on offshore reefs (Hoeksema & Moka, 1989; Hoeksema, 1990, 1993). This suggests that they are less capable to withstand sedimentation. Therefore, the suspended increase in sediment load at Singapore is a likely cause for their disappearance.

Different sampling methods have been used for the various periods compared. In the 1860s, corals were collected abundantly. Relative frequencies of specimens per species may be related to relative abundances and how well specimens could be sampled according to their depth distributions. *Fungia moluccensis* may have been under-represented in the 1860s collections due to its deeper depth range, but at that time it was also not yet recognized as a separate species since it was known since 1919 (Hoeksema, 1989). Nevertheless, despite this under-representation in the collections, one specimen is enough to show that the species was present (Table 1). The quantitative records for the period 1986–1991 are partly reflected by the numbers counted in transects by Koh (1987) as indicated in Table 3. However, the 1986–1991 collection data (Table 1) appears to contain more species than only those encountered in the 1987 transects and therefore they give a higher species number. Finally, species presence/absence records based on the roving diving technique applied in 2006 do not offer quantitative data per species for comparisons with abundance data for other time periods, but the observed species composition is very reliable. Once a species is recorded at a site, the remainder of the observation time can be dedicated to a search for the species not yet recorded. No time needs to be invested in duplicate records. The reliability of the data is also demonstrated by the asymptotic curves of the species richness indicators in Fig. 2 (Ugland et al., 2003; Magurran, 2004). Therefore, species collected before 1991 but not observed in 2006, can be considered as having disappeared from Singapore's reefs for the time being. Since, three of the four lost species (*Ctenactis albitentaculata*, *C. crassa* and *Fungia granulosa*) usually do not occur near river outlets (Hoeksema & Moka, 1989; Hoeksema 1990, 1993), the high sediment content of the water is a likely cause for their present absence.

A well-known threat to marine biodiversity is the mortality and possible local extinction of coral reef species as an effect of the El Niño-Southern Oscillation (ENSO) events. This is most striking in the case of coral bleaching events, which became obvious during the sea water warming of the 1982/83 and 1997/98 ENSO events at various coral reef localities, such as in the Java Sea Indonesia (Brown & Suharsono, 1990; Hoeksema, 1991; Brown, 1997) and in the East Pacific (Glynn 1988, 1993, Feingold, 2001; Glynn et al., 2001). Despite reports on coral recovery, ENSO events may have long-lasting damaging effects on coral reefs, especially when they occur in combination with harmful human activities, such as in West Sumatra (Kunzmann, 1997, 2002; Hoeksema & Cleary, 2004). Species that depend very strongly on corals for their survival (food, shelter, symbiosis) may also become affected. A bleaching event at Okinawa in 1998, for instance, may have wiped out a local population of a corallivorous filefish species when their feeding territories were depleted of *Acropora* corals (Kokita & Nakazono, 2001). Although, Singapore's reefs suffered severe coral bleaching in 1998, some species (among which *Fungia* spp.) were also known to have recovered quite soon (Chou, 2001). Likewise, coral populations in the offshore Thousand Islands off Jakarta showed recovery after the 1983 bleaching event (Brown & Suharsono, 1990; Hoeksema, 1991). During a coral reef survey in 2005 (Meij et al., in prep.) species richness of mushroom corals in the same area showed no visible decrease in species numbers although one species (*Fungia scutaria*) was only represented by a few juvenile specimens (Hoeksema, personal observation). Therefore, coral bleaching is not a likely cause for a decrease in fungiid species richness in Singapore.

Studies aiming at detecting any biodiversity changes should include recurring surveys at selected areas over long time periods. The Thousand Islands, off Jakarta, is a good example, since changes in the fauna have been noticed after several 10-year intervals (1985, 1995, 2005). From the Bay of Jakarta to the outer islands offshore, various environmental gradients can be discerned that influence the biota over time (Moll & Suharsono, 1986; Cleary et al., 2006). Various species of corals represented in old zoological collections from Bay of Jakarta (1920–1930), apparently have disappeared from near-shore reefs when the last reef survey in this area was carried out in 2005 (Meij et al., 2009). *Millepora* species, for example, were abundantly present on the reefs close to Jakarta (Razak & Hoeksema, 2003), but have disappeared in the course of time, which is most likely caused by siltation. A study on mollusc shell collections from Jakarta Bay also indicates changes in species composition linked to human-induced degradation of coral reefs (Meij et al., 2009). The visibility of the seawater on the reefs in the Bay of Jakarta is very poor, comparable to many of the reefs studied off Singapore, while reports on old studies suggest that the water quality was much better (Umbgrove & Verwey, 1929). The observed loss in mushroom coral species in Singapore is therefore most likely linked to an increased sediment load of the water and the reefs as a result of land reclamation projects in the harbour of Singapore (Hilton & Chou, 1999) and deforestation of Singapore's hinterland (Brook et al., 2006).

Some species occurring abundantly in neighbouring regions appear to have been absent from Singapore for much longer time. Such well-known species can easily be recognized in the field, but mostly on reefs that are not too close near river outlets, like *Fungia scutaria*, *F. tenuis*, and *Sandalolitha robusta*. (Hoeksema, 1990, 1991, 1993). Although Singapore is within their distribution ranges, their long-term absence at Singapore suggests that the reefs here have already been subjected to sediment stress for a long period of time. Therefore, the richness of the mushroom coral fauna of Singapore is clearly limited by sediment stress and not by biogeographic range boundaries.

ACKNOWLEDGEMENTS

The 14th International Marine Biology Workshop held in Singapore was organized by Dr Tan Koh Siang (Tropical Marine Science Institute, National University of Singapore), Dr Lena Chan (National Biodiversity Centre, National Parks Board, Singapore), Prof. Chou Loke Ming (Department of Biological Sciences, National University of Singapore) and Prof. Peter Ng (Raffles Museum of Biodiversity Research, National University of Singapore). Publication of the workshop proceedings was made possible with funds provided by the National University of Singapore and National Parks Board. We are grateful to the staff of TMSI who helped in the field and in the laboratory: Mr Jeff Chouw, Mr Justin Sih, Ms Michelle Lee, Dr Sin Tsai Min, Mr Abdol Razak bin Bujang (skipper of TMSI vessel "Whitetip"). Assistance was also given by the skipper and crew of the Department of Biological Sciences research vessel "Mudskipper": Mr Salam bin Semy, Mr Rahmat bin Wahab and Mr Ishak bin Nis. Prof. Peter K.L. Ng, director of the Raffles Museum of Biodiversity Research granted access to the ZRC. We appreciate the support given by Prof. Chou Loke Ming. Mrs Ardis Baker Johnston (MCZ) and Mr Eric A. Lazo-Wasem (YPM) kindly provided us with additional information on the old coral specimens that were collected in Singapore in the 1860s. The research by the first author (BWH) was partly funded by the Schure-Beijerinck-Popping Fund (grant SBP-2006-49). This paper is linked to the project "Climate change and Indonesian coral reef biotas" within the research theme "Biodiversity in relation to Global Change" of the Council for Earth and Life Sciences of the Netherlands Organisation for Scientific Research (ALW-NWO grant 852.000.50). The helpful remarks on the manuscript by Ms. Sancia van der Meij and two anonymous reviewers are very much appreciated.

LITERATURE CITED

Anonymous, 2002. *Tuas View to Pulau Sakijang Bendara (St. John's Island)*. Chart 4040. Hydrographic Department, Maritime and Port Authority of Singapore, and the United Kingdom National Hydrographer, Taunton.

Brook, B. W., N. S. Sodhi & P. K. L. Ng, 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**: 420–423.

Brown, B. E., 1997. Coral bleaching: causes and consequences. *Coral Reefs*, **16** (suppl.): S129–S138.

Brown, B. E. & Suharsono, 1990. Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand islands, Indonesia. *Coral Reefs*, **8**: 163–170.

Chou, L. M., 1988. Community structure of sediment-stressed reefs in Singapore. *Galaxea*, **7**: 101–111.

Chou, L. M., 1996. Response of Singapore reefs to land reclamation. *Galaxea*, **13**: 85–92.

Chou, L. M., 2001. Country report: Singapore. Report of the International Coral Reef Initiative (ICRI).

Chou, L. M., 2006. Marine habitats in one of the world's busiest harbours. In: Wolanski, E. (ed.), *The Environment in Asia Pacific Harbours*. Springer, Dordrecht. Pp. 377–391.

Chou, L. M., J. K. Y. Low & M. G. K. Loo, 1994. The state of coral reefs and coral reef research in Singapore. In: Wilkinson, C. R., S. Sudara & L. M. Chou (eds.), *Proceedings Third ASEAN-Australia Symposium on Living Coastal Resources, Vol. 1: Status Reviews.* Chulalongkorn University, Bangkok. Pp. 77–88.

Chua, C. Y. Y. & L. M. Chou, 1991. The scleractinian coral community of Southern Islands's reefs, Singapore. In: Alcala, A. C. (ed.), *Proceedings of the Regional Symposium on Living Resources in Coastal Areas*. Marine Science Institute, University of the Philippines, Quezon City. Pp. 41–46.

Chuang, S. H., 1977. Ecology of Singapore and Malayan coral reefs – preliminary classification. *Proceedings Third International Coral Reef Symposium, Miami*, **1**: 55–61.

Cleary, D. F. R., Suharsono & B. W. Hoeksema, 2006. Coral diversity across a disturbance gradient in the Pulau Seribu reef complex off Jakarta, Indonesia. *Biodiversity and Conservation*, **15**: 3653–3674.

Colwell, R. K., 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. User's Guide and application published at: http://purl.oclc.org/estimates.

Dodge, R. E., R. C. Aller & J. Thomson, 1974. Coral growth related to resuspension of bottom sediments. *Nature*, **247**: 574–577.

Dodge, R. E. & J. R. Vaisnys, 1977. Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research*, **35**: 715–730.

Feingold, J. S., 2001. Responses of three coral communities to the 1997–98 El Niño-Southern Oscillation: Galápagos Islands, Ecuador. *Bulletin of Marine Science*, **69**: 61–77.

Glynn, P. W., 1988. El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea*, **7**: 129–160.

Glynn, P. W., 1993, Coral reef bleaching: ecological perspectives. *Coral Reefs*, **12**: 1–17.

Glynn, P. W. & J. S. Feingold, 1992. Hydrocoral species not extinct. *Science*, **257**: 1845.

Glynn. P. W., J. L. Maté & A. C. Baker, 2001. Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons withy the 1982–1983 event. *Bulletin of Marine Science*, **69**: 79–109.

Glynn, P. W. & W. H. de Weerdt, 1991. Elimination of two reef-building hydrocorals following the 1982–83 El Niño warming event. *Science*, **235**: 69–71.

Goh, N. K. C. & L. M. Chou, 1992. A comparison of benthic life-form characteristics of a reef (Cyrene) nearest to and a reef (Raffles Lighthouse) furthest from mainland Singapore. In: Chou, L. M. & C. R. Wilkinson (eds.), *Third ASEAN Science and Technology Week Conference Proceedings, Vol. 6, Marine Science: Living Coastal Resources.* National University of Singapore and National Science and Technology Board, Singapore. Pp. 55–62.

Goh, N. K. C., C. Y. Y. Chua & L. M. Chou, 1994. Depth-related morphology of scleractinian corals on Singapore reefs. *In:* Sudara, S., C. R. Wilkinson & L. M. Chou (eds.), *Proceedings Third ASEAN-Australia Symposium on Living Coastal Resources, Vol. 2: Research Papers.* Chulalongkorn University, Bangkok. Pp. 61–67.

Hilton, M. J. & L. M. Chou, 1999. Sediment facies of a low-energy, meso-tidal fringing reef, Singapore. *Singapore Journal of Tropical Geography*, **20**: 111–130.

Hilton, M. J. & S. S. Manning, 1995. Conversion of coastal habitats in Singapore: indications of unsustainable development. *Environmental Conservation*, **22**: 307–322.

Hoeksema, B. W., 1988. Mobility of free-living fungiid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. *Proceedings 6th International Coral Reef Symposium, Townsville*, **2**: 715–720.

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

Hoeksema, B. W., 1990. *Systematics and ecology of mushroom corals (Scleractinia: Fungiidae).* PhD Thesis, University of Leiden. 471 pp.

Hoeksema, B. W., 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.

Hoeksema, B. W., 1993. Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an anonotated check-list with the description of *Cantherellus jebbi* spec. nov., *Zoologische Mededelingen*, Leiden, **67**: 1–19.

Hoeksema, B. W., 2004. Impact of budding on free-living corals at East Kalimantan, Indonesia. *Coral Reefs*, **23**: 492.

Hoeksema, B. W., 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema, W. (ed.), *Biogeography, Time and Place: Distributions, Barriers and Islands*. Springer, Dordrecht. Pp. 117–178.

Hoeksema, B. W., 2009. Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singapore, including a new species and a new record. *Raffles Bulletin of Zoology*, Supplement No. **22**: 81–90.

Hoeksema, B. W. & D. F. R. Cleary, 2004. The sudden death of a coral reef. *Science*, **303**: 1293.

Hoeksema, B. W. & W. Moka, 1989. Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. *Netherlands Journal of Sea Research*, **23**: 149–160.

Khoo, H. W., 1991. Benthic communities of the rivers and coastal waters of Singapore. In: Chia, L. S. & L. M. Chou (eds.), *Urban coastal area management: the experience of Singapore. ICLARM Conference Proceedings*, **25**: 31–46.

Koh, E. G. L., 1987. *Systematics and ecology of mushroom corals (Scleractinia: Fungiidae) in Singapore reefs.* BSc thesis, Department of Zoology, National University of Singapore, Singapore. 113 pp.

Koh, E. G. L. & L. M. Chou, 1989. *The Mushroom Corals of Singapore*. Department of Zoology, National University of Singapore, Singapore. 45 pp.

Kokita, T. & A. Nakazono, 2001. Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. *Coral Reefs*, **20**: 155–158.

Kunzmann, A., 1997. The coral reefs of West Sumatra. In: Tomascik, T., A. J. Mah, A. Nontji & M. K. Moosa (eds.), *The ecology of the Indonesian Seas. Part Two.* Periplus Editions, Singapore. Pp. 1249–1262.

Kunzmann, A., 2002. On the way to management of West Sumatra's coastal ecosystems, *NAGA The ICLARM Quarterly*, **25**: 4–10.

Lane, D. J. W., 1991. Growth of scleractinian corals on sediment-stressed reefs at Singapore. In: Alcala, A.C. (ed.), *Proceedings of the Regional Symposium on Living Resourves in Coastal Areas*. Marine Science Institute, University of the Philippines, Quezon City. Pp. 97–106.

Lim, T. M., M. G. K. Loo & L. M. Chou, 1994. Natural habitat status of some Singapore Southern Islands before major landuse changes. In: Sudara, S., C. R. Wilkinson & L. M. Chou (eds.), *Proceedings Third ASEAN-Australia Symposium on Living Coastal Resources, Vol. 2: Research Papers.* Chulalongkorn University, Bangkok. Pp. 669–673.

Loh, T. L., J. T. I. Tanzil & L. M. Chou, 2006. Preliminary study of community development and scleractinian recruitment on fibreglass artificial reef units in the sedimented waters of Singapore. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**: 61–76.

Low, J. K. Y. & L. M. Chou, 1994. Sedimentation rates in Singapore waters. In: Sudara, S., C. R. Wilkinson & L. M. Chou (eds.), *Proceedings Third ASEAN-Australia Symposium on Living Coastal Resources, Vol. 2: Research Papers.* Chulalongkorn University, Bangkok. Pp. 697–701.

Magurran, A. E., 2004. Measuring biological diversity. Blackwell, Oxford.

McClanahan, T. R. & D. Obura, 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology*, **209**: 103–122.

Meij, S. E. T., van der, R. Moolenbeek & B. W. Hoeksema, 2009. Decline of the Jakarta Bay molluscan fauna linked to human impact. *Marine Pollution Bulletin.* doi:10.1016/j.marpolbul.2009.02.021.

Meij, S. E. T. van der, Suharsono & B.W. Hoeksema (in prep). Effects of long-term stress on coral assemblages in Jakarta Bay (1920–2005).

Moll, H. & Suharsono, 1986. Distribution, diversity and abundance of reef corals in Jakarta Bay and Kepulauan Seribu, *UNESCO Reports in Marine Science*, **40**: 112–125.

Munro, C., 2005. Diving systems. In: Eleftheriou, A. & A. McIntyre (eds.), *Methods for the study of marine benthos, third edition*. Blackwell Science, Oxford. Pp. 112–159.

Razak, T. B. & B. W. Hoeksema, 2003. The hydrocoral genus *Millepora* (Hydrozoa: Capitata: Milleporidae) in Indonesia. *Zoologische Verhandelingen*, Leiden, **345**: 313–336.

Rogers, C. S., 1990. Reponses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, **62**: 185–202.

Schmitt, E. F., R. D. Sluka & K. M. Sullivan-Sealey, 2002. Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. *Coral Reefs*, **21**: 216–223.

Stafford-Smith, M. G., 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology*, **115**: 229–243.

Tan, B. C., B. Goh & C. Chia, 2004. Preliminary report on biodiversity researches in Singapore. *ASEAN Biodiversity*, **4**: 32–34.

Tan, I. C., 1970 *Some studies on the biology of the Fungiidae of Singapore.* B. Sc. thesis, Department of Zoology, National University of Singapore, Singapore (Unpublished). 85 pp.

Tun, K., A. C. Cheshire & L. M. Chou, 1994. Photosyntyhetic production of four scleractinian corals from Singapore. In: Sudara, S., C. R. Wilkinson & L. M. Chou (eds.), *Proceedings Third ASEAN-Australia Symposium on Living Coastal Resources, Vol. 2: Research Papers.* Chulalongkorn University, Bangkok. Pp. 69–77.

Ugland, K. I., J. S. Gray, K. E. Ellingsen, 2003. The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, **72**: 888–897.

Umbgrove, J. H. F. & J. Verwey, 1929. The coral reefs in the Bay of Batavia. *Fourth Pacific Science Congress Java, Excursion*, **A2**: 1–30.

Wallace, C. C., 1999. *Staghorn corals of the world. A revision of the coral genus* Acropora *(Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography.* SCIRO Publishing, Collingwood, Australia. 421 pp.

Weerdt, W. H. de & P. W. Glynn, 1991. A new and presumably now extinct species of *Millepora* (Hydrozoa) in the eastern Pacific. *Zoologische Mededelingen*, Leiden, **65**: 267–276.

Wong, P. P., 1985. Artificial coastlines: the example of Singapore. *Zeitschrift für Geomorphologie*, **57**: 175–192.

Wong, P. P., 2000. Malacca Strait including Singapore and Johore Straits. *In:* Sheppard, C. (ed.), *Seas at the Millenium: An Environmental Evaluation. Volume II, Regional Chapters: The Indian Ocean to the Pacific.* Elsevier, Amsterdam. Pp. 331–344.

Yong, K. Y., S. L. Lee & G. P. Karunaratne, 1991. Coastal reclamation in Singapore: a review. In: Chia, L. S. & L. M. Chou (eds.), *Urban coastal area management: the experience of Singapore. ICLARM Conference Proceedings*, **25**: 59–67.

Table 3. Abundance records with depth ranges of free-living mushroom coral species (1987, n = 11) recorded in four 10 x 1 m transects per reef site at Singapore (A01–A16; see Table 2) and for 16 sites together, along with total number of sites with presence records. Belt transects were situated at the flat, crest, slope and bottom of each site.

Reef site	A01	A02	A03	A04	A05	A06	A07	A08	A09	A10	A11	A12	A13	A14	A15	A16	Total Corals	Total Sites	Depth (m)
Species																			
Ctenactis echinata	1	0	0	0	2	0	3	0	1	5	0	2	0	4	3	1	22	9	1–6
Fungia (D.) scruposa	2	1	0	2	1	0	3	4	4	2	1	3	10	6	3	1	43	14	2–9
Fungia (F.) fungites	5	1	1	2	0	1	5	6	6	9	1	7	6	12	17	12	91	15	1–9
Fungia (P.) moluccensis	9	14	6	0	0	0	1	1	3	1	1	3	6	1	3	3	52	13	2–11
Fungia (P.) paumotensis	4	0	0	0	1	0	5	1	0	0	1	6	3	0	3	2	26	9	2–8
Fungia (V.) concinna	6	0	1	1	4	1	5	8	3	2	1	8	10	6	3	1	60	15	1–12
Fungia (V.) repanda	10	0	0	0	1	1	5	9	9	17	2	11	18	9	10	8	110	13	1–10
Fungia (V.) scabra	2	1	0	0	1	1	1	3	1	1	1	7	5	5	6	0	35	13	1–6
Heliofungia actiniformis	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	2	3–5
Herpolitha limax	11	0	2	1	0	0	1	2	0	1	2	10	4	3	1	3	41	12	1–6
Polyphyllia talpina	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	3	2	2–3
Total number of corals	53	17	11	6	10	4	29	35	27	38	10	59	62	46	49	31			
Total number of species	10	4	5	4	6	4	9	9	7	8	8	10	8	9	9	8			

Table 4. Occurrence records (presence/absence) of free-living and attached mushroom coral species together (2006, n = 15) recorded off Singapore in 2006 at 18 sites (B01–B18; see Table 2) by roving diver survey.

Reef site	B01	B02	B03	B04	B05	B06	B07	B08	B09	B10	B11	B12	B13	B14	B15	B16	B17	B18	Total records
Species																			
Ctenactis echinata	1	0	1	0	0	1	1	1	1	1	1	0	1	0	1	1	1	1	13
Fungia (D.) scruposa	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	0	1	14
Fungia (F.) fungites	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	18
Fungia (P.) moluccensis	0	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	1	1	9
Fungia (P.) paumotensis	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0	1	1	1	9
Fungia (V.) concinna	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	13
Fungia (V.) repanda	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	15
Fungia (V.) scabra	1	1	1	0	0	1	0	0	1	1	1	0	1	0	1	1	1	1	12
Heliofungia actiniformis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Herpolitha limax	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	15
Lithophyllon undulatum	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	14
Podabacia crustacea	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	15
Podabacia kunzmanni	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	1	7
Podabacia motuporensis	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	5
Polyphyllia talpina	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2
Total number of species	9	8	13	9	6	6	6	7	6	9	9	6	12	11	8	11	13	14	