

Dynamics and pattern of coral recolonization following the 1998 bleaching event in the reefs of the Maldives

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Abstract The 1998 bleaching event caused widespread coral mortality in the reefs of the Maldives. As early as 1999, recolonization had started and many newly settled colonies were recorded. A dramatic decrease in numbers of juveniles was observed between 1999 and 2000, followed by a stabilization in 2001 and 2002. The taxonomic composition of recruits shifted from a dominance of Agariciidae in the early stages of recolonization toward a dominance of Acroporidae and Pocilloporidae. An inventory of scleractinian species carried out in 2002 showed that the diversity of Maldivian corals has not decreased. However, some previously abundant species are now rare. Conversely, substratum cover is still very low, and the three-dimensional structure of the reef is largely lost due to the destruction of dead colonies, which were reduced to rubble. Contrary to early expectations, Maldivian reefs do not seem to be undergoing a phase shift toward a dominance of fleshy algae, sponges, or corals different from *Acropora* and *Pocillopora*. Rather, reef recovery seems to follow a predictable ecological succession toward the pre-existing situation. The present situation in the Maldives allows for a cautious optimism about the recovery potential of the reefs. However, the expected increased frequency of thermal anomalies that may lead to bleaching introduces a major risk. Long term monitoring of Maldivian coral communities remains the only means to understand their future evolution.

Keywords Maldives, coral bleaching, mortality, recruitment, recovery, long-term monitoring

Introduction

The consequences of high sea surface temperature in 1998, the warmest year in the 20th century and the strongest El Niño event ever recorded (Wilkinson 2000), led to the largest bleaching event on a world scale followed by a massive coral mortality, especially in the Indian Ocean (Wilkinson et al. 1999; Spencer et al. 2000). The Maldives have been among the most affected

areas in the world, with 60 to 100 % coral mortality reported (Ciarapica and Passeri 1999; Longo et al. 2000; Zahir 2000).

Since 1989 we have been studying geological and ecological aspects of coral reefs in the Maldives (Bianchi and Morri 1994; Aliani et al. 1995; Morri et al. 1995; Bianchi et al. 1997). Since 1997, our studies have been taking place annually during scientific cruises (Bianchi et al. 1998), hence we collected data on the state of coral reefs in the Maldives before, during and after the bleaching event of 1998 (Bianchi et al. in press). In this paper we integrate our data on coral mortality and recolonization with information from other authors (McClanahan, 2000; Edwards et al. 2001; Loch et al. 2002), aiming at evaluating the recovery potential of the reefs of the Maldives following the 1998 bleaching event.

Material and methods

Study area

The Maldives Archipelago forms the central part of the Chagos-Maldives-Laccadive ridge in the central Indian Ocean, extending from 7° 07' N to 0° 42' S and from 72° 33' to 73° 45' E. The Maldives are comprised of around 1120 islands forming a single atoll chain in the north and in the south, and a double atoll chain in the central part (Fig. 1). Recent descriptions of the Maldivian coral reefs can be found in Ciarapica and Passeri (1993, 1995), Price and Clark (2000) and Risk and Sluka (1999).

The Albatros Top Boat scientific cruises take place annually in April in the central atolls of the Maldives Archipelago Malé North, Malé South, Felidhoo, Wattaru, Ari, Rasdhoo (Table 1).

Methods

All data were collected during SCUBA dives at coral reefs either on the ocean or the lagoon side of the atolls. Every year, 12 sites, chosen haphazardly, were surveyed in the visited atolls.

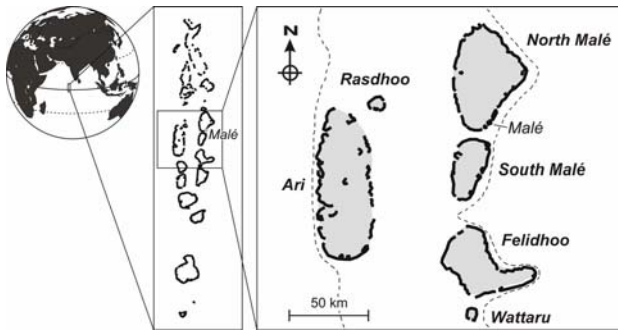


Fig. 1. Map of the study area and position of the studied atolls.

Table 1. Maldivian Atolls visited by the Albatros Scientific Cruises between 1997 and 2003 (analysis of data for 2003 is still in progress and the cruise is only mentioned here in the sake of completeness).

Year	Atolls
1997	Rasdho, Ari
1998	Malé South, Felidhoo, Wattaru
1999	Malé North, Malé South
2000	Malé North, Malé South, Rasdho, Ari
2001	Malé North, Malé South, Rasdho, Ari
2002	Malé South, Felidhoo, Wattaru
2003	Malé South, Ari

Coral cover was estimated along transects parallel to the reef crest (English et al. 1997) between 3 and 30 m depth. In 1999, coral mortality data were collected at different depths using the following mortality index (MI %):

$$MI \% = M / (V + M) \times 100$$

where M is recently dead coral cover and V living coral cover (Gomez et al. 1994).

Since 2000 small coral colonies have been counted within 1 m² quadrats randomly placed at 5, 10 and 20 m depth (three replicates per depth). We defined recruits as coral colonies smaller than 5 cm in diameter, and juveniles as those between 5 and 20 cm. Both recruits and juveniles were categorized as *Acropora*, *Pocillopora* or other hard coral (Baird and Hughes 1997).

To understand the impacts of the massive 1998 mortality on coral species richness in the Maldives, an inventory of coral species (recruits, juveniles and surviving adults) was compiled in 2002, using a plotless time-based visual census: species were inventoried during a 40 min dive between 3 and 20 m depth approximately. All coral species were photographed in situ using a digital camera in a housing with red filter. Colonies which could not be readily identified underwater were collected for subsequent examination. Specimens were bleached in a solution of sodium hypochlorite for 24 hours, rinsed with freshwater and air-dried.

Results

Pre-bleaching Situation

In April 1997 the coral cover in the studied sites in

the Maldives was generally between 30 and 60 %, often reaching 100 % in shallow water. The reef 3D structure was well developed (Fig. 2), and branching and tabular *Acropora* colonies were abundant at almost every site. *Millepora* colonies were common and soft corals locally important. Reef structure and coral community composition was consistent with previously published descriptions (Spencer Davies et al. 1971; Scheer 1971, 1972, 1974; Allison 1995; Morri et al. 1995; Bianchi et al. 1997, Allison 2002).



Fig. 2. A Maldivian reef in shallow waters in 1997: note the three-dimensional structure and the large *Acropora* tables.

The 1998 Bleaching Event

In early April 1998 the water temperature was 32-34 °C down to 30 m depth, compared to normal values of 27-29 °C. Most *Acropora* colonies had bleached but were still alive, as the white polyps could easily be seen expanded at night. No mass mortality was recorded at the studied reefs. Local divers reported that mortality began at the end of April 1998 and continued through August 1998.

Post-bleaching Mortality

In April 1999 most corals were dead and had been colonized by cyanobacterial turfs, encrusting or filamentous algae and other sessile organisms, with sponges and the colonial ascidian *Atrium robustum* most visible. Branching coral colonies, primarily *Acropora* and *Pocillopora*, had undergone total mortality (Fig. 3a), while most of the massive coral colonies (e.g., *Porites*, *Diploastrea*) exhibited partial mortality (Fig. 3b). *Millepora* had completely disappeared, as well as zooxanthellate soft corals that were previously common (e.g., *Heteractis*, *Sinularia*). As also noted by Loch et al. (2002), *Heliopora coerulea* was not particularly affected by bleaching. In general, the mortality of individual species reflected the differential bleaching susceptibility as described by Marshall and Baird (2000) for the Great Barrier Reef.

Live coral cover was reduced to 2-8 %, thus confirming the data from other surveys (McClanahan 2000; Zahir 2000; Edwards et al. 2001; Loch et al. 2002). Branching coral mortality was on average 90 % within 20 m depth (Fig. 4), but was about 50 % between 20 and

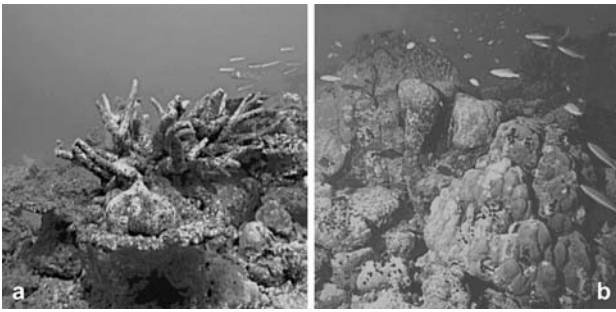


Fig. 3. Examples of total mortality of branching coral colonies (a) and of partial mortality of the massive colonies (b) in April 1999.

30 m. Massive coral mortality was up to 30 % within the first 20 m, but was negligible between 20 and 30 m (Fig. 4).

Notwithstanding the severe loss in living coral cover, 3D reef structure in 1999 was still preserved, primarily due to the largest dead colonies still being in place. By 2000 we observed the destruction of dead coral colonies and the loss of 3D structure of the Maldivian reefs.

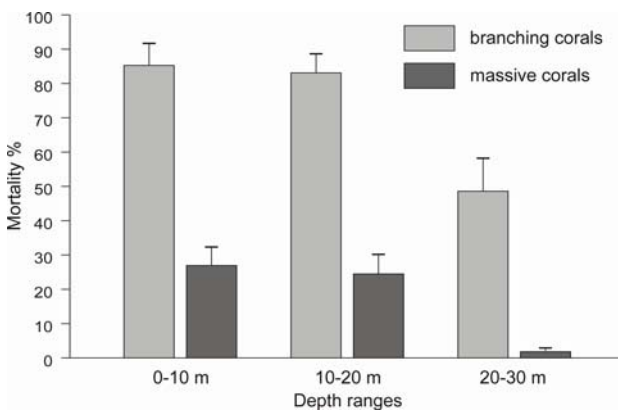


Fig. 4. Coral mortality observed in April 1999 per coral type at different depths (mean + SE).

Post-bleaching Recolonization and Recovery

In 1999, small coral colonies were found on dead coral colonies, especially in shallow depths. The most abundant among these small colonies were encrusting Agariciidae, followed by massive Faviidae and Poritidae. *Tubastraea micranthus* and *Heliopora coerulea* were also abundant. *Acropora* was comparatively scarce, but largest colonies reached 14 cm in height. This size is compatible with the yearly growth rate reported for several species in the genus (Sorokin 1993), and we can infer that the first recruitment waves for some of the observed species arrived soon after the mortality event in 1998. By April 1999, many of those young colonies had died. No *Pocillopora* or *Millepora* recruits were recorded in 1999.

In April 2000, *Acropora* showed an average density of 2 recruits m^{-2} between 5 and 20 m depth, twice the rates recorded in 2001 and 2002. *Pocillopora* was less abundant, reaching a mean density of 1 recruit m^{-2} at 5 m depth in 2000 and 2001. The other corals showed a

higher (up to 9 recruits m^{-2}) but variable recruitment rates (Fig. 5).

Juveniles showed higher densities in 2000, but their abundance dropped in the following years, indicating an elevated mortality of young colonies (Fig. 6). *Acropora*

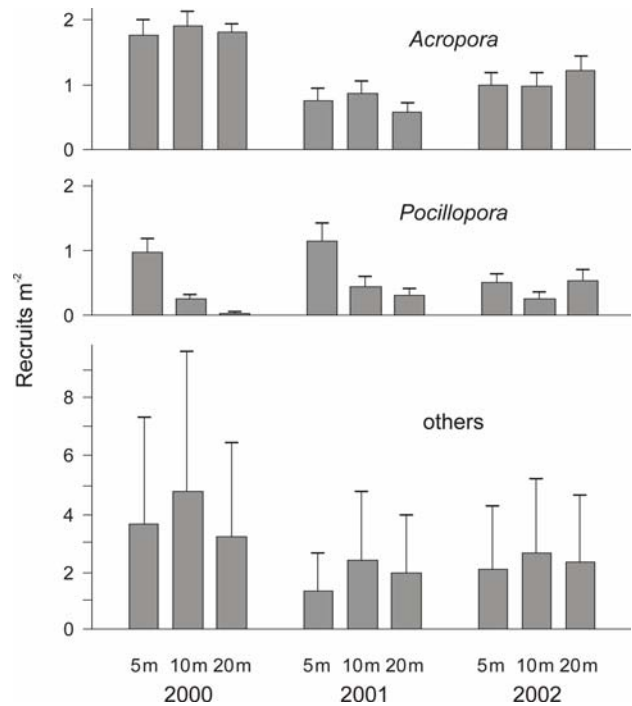


Fig. 5. Coral recruit density at three depths from 2000 to 2002 (mean + SE). Note that the scale for “other corals” is different from the one in *Acropora* and *Pocillopora*.

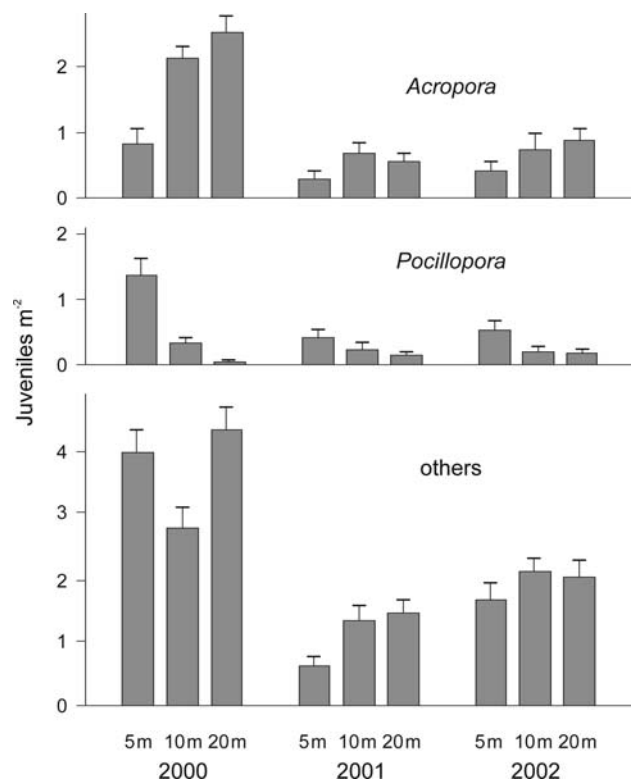


Fig. 6. Coral juvenile density at three depths from 2000 to 2002 (mean + SE).

juveniles were more abundant at 10 and 20 m, *Pocillopora* juveniles were more abundant at 5 m depth. Other corals showed no significant differences with depth. No difference in the mean size of juveniles was recorded from 2000 to 2002 but for *Pocillopora*, which showed an average increase of approximately 2.5 cm year⁻¹. This value is comparable to the potential yearly growth rate for this genus (Sorokin 1993).

In 2002, a total of 146 coral species (see Appendix) was recorded in 12 dives (Fig. 7). Taking into account the low sampling effort of our survey (12 dives), this number can be considered similar to the 187 species reported from the Maldives by Sheppard (1987) based on data of Pillai and Scheer (1976).

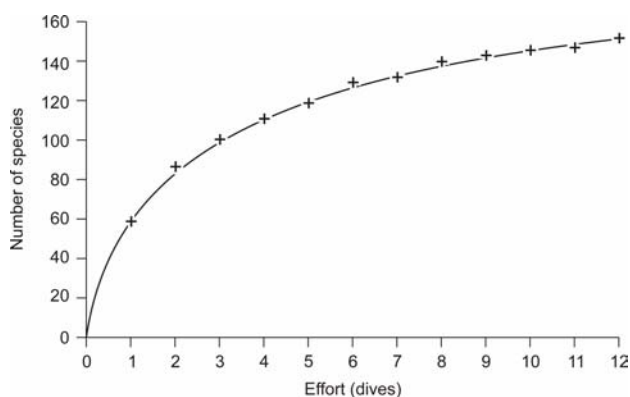


Fig. 7. Species-effort curve (Species = 59.94 Effort^{0.362}, R² = 0.972) for the scleractinians in 2002. Effort is measured in number of dives.

Discussion and Conclusions

Our data confirm that coral mortality in the Maldives in 1998 was amongst the highest in the Indian Ocean, and hence in the world (Wilkinson et al. 1999; Goreau et al. 2000; Rajasuriya et al. 2000). The coral mortality pattern in the Maldives appeared similar to that described in the south Ryukyus (Japan) by Kayanne et al. (2002), who estimated that recovery will require “at least” 2 years. There is not much information on the time of recovery after mass-mortality following bleaching compared to other causes of coral mass-mortality, but there is no reason to think that recovery processes are different. According to Connell (1997), coral reefs exposed to major perturbations (including bleaching) in the Indo-Pacific would recover between 1 and 11 years. In the Caribbean, Stoddart (1974) estimated the recovery of reefs destroyed by a hurricane to require approximately 30 years. In a review of the effects of cyclones on coral reefs, Harmelin-Vivien (1994) stated that recovery time after large mortalities can vary from 5-6 years to more than 100 years. Such different estimates could, at least in part, depend on what is actually measured to evaluate recovery. Pearson (1981) underlined the lack of studies that simultaneously measured multiple parameters of coral recovery: percent coral cover, mean colony size, reef structure complexity, specific diversity, and similarity with the pre-mortality condition.

Four years after the 1998 mass mortality, coral cover in the Maldives was still very low. Living coral cover was still significantly lower than the dead coral cover. Such low cover was not due to a small number of living coral colonies but rather to their size, most of them being recruits. Apparently, many coral species recruited intensively soon after the mortality event. A comparison of our data with those collected by McClanahan (2000) with similar methods (although he used smaller quadrats: 30 × 30 cm) at 5 and 10 m showed that the recruit density had decreased dramatically from 1999 to 2000, and to a lesser extent from 2000 to 2001, and apparently stabilized between 2001 and 2002 (Fig. 8). Changes were recorded not only in the abundance of recruits, but also in their taxonomic composition. According to McClanahan (2000), only 11 of the 16 coral families known from the Maldives had recruited in 1999, and almost the half of the recruits were Agariciidae, with Acroporidae and Pocilloporidae being rare. In 2002, 13 families had recruited, the most frequent being Acroporidae and Pocilloporidae, while the Agariciidae had declined to the fifth rank. Moreover, the proportional abundance among all families was more even in 2002 compared to 1999 (Fig. 9).

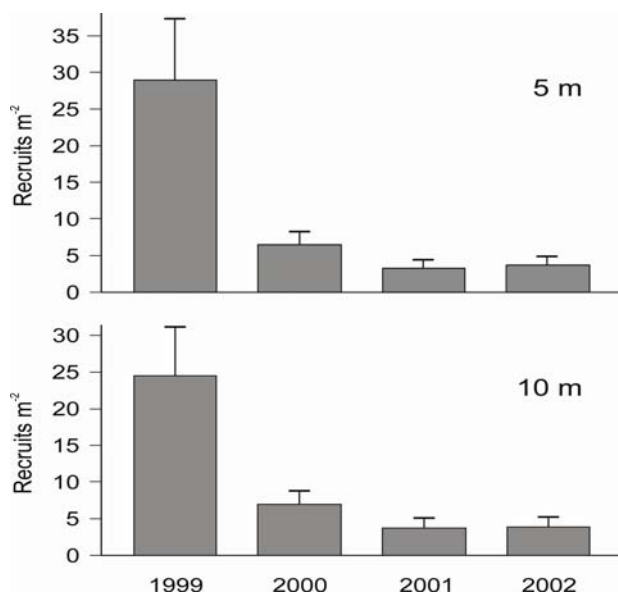


Fig. 8. Total coral recruit density at two depths from 1999 to 2002 (mean + SE). Data for 1999 are taken from McClanahan (2000).

To 2003, the reef complexity was still very limited. Dead coral colonies broken down by bioerosion and wave action have led to the formation of large areas of coral rubble similar to reports from Chagos (Sheppard et al. 2002).

The situation looks better with respect to the number of coral species. In 2002, four years after the mortality event, the species richness of corals in the Maldives was encouragingly high, 146 species in 12 dives compared to the pre-existing total of 187 (Sheppard 1987). Results of a more complete species inventory in 2003 listed 191 species (Pichon and Benzoni in prep). Whether there has

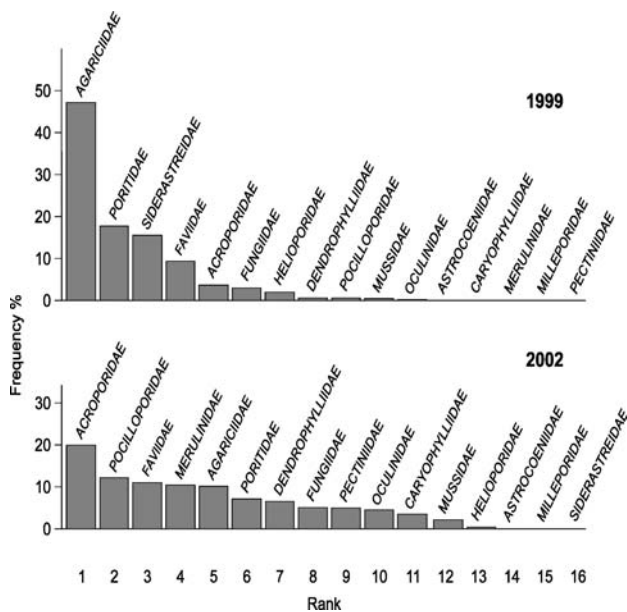


Fig. 9. Frequency of coral recruits by family (16 reported families from the Maldives) in 1999 and in 2002. Data for 1999 are taken from McClanahan (2000).

been any local extinction of coral species in the Maldives remains an open question. To April 2003, no colonies of *Stylophora* or *Seriatopora*, two genera previously reported in the Maldives prior to 1998, were observed at any site. *Millepora*, a common genus before the bleaching, was not found before 2003, suggesting a local or regional extinction. However, small encrusting *Millepora* colonies were observed in 2003. In the eastern Pacific, *Millepora* had apparently disappeared after the 1982-83 bleaching (Glynn and de Weert 1991) but was recorded again a few years later (Glynn and Feingold 1992): the genus, however, is still considered “at risk” (Fenner 2001). In the Maldives, as in the eastern Pacific, *Millepora* seems to recruit more slowly than in the Caribbean (Kojis and Quinn 2001).

The high loss of hard corals suggested a possible phase shift in the coral reefs of the Maldives. According to the phase shift hypothesis (Done 1992; Hughes 1994), a reef dominated by hard corals (hence capable of bioconstruction), may shift, following a major disturbance, to a reef dominated by algae and sponges, therefore more exposed to erosion, and hence to destruction. Such a perspective would be tragic for an atoll nation as the Maldives (Risk et al. 1994). In French Polynesia, Adjeroud et al. (2002) did not observe a phase shift following the 1998 bleaching event. In the Maldives, the dominance by algae, sponges and ascidians was transitory, and coral dominance is on the way of returning due to recruitment and rapid growth of the newly settled (especially *Acropora* and *Pocillopora*) or surviving colonies (Loch et al. 2002; Schuhmacher et al. 2002). However, the first coral recruits belonged to families different from those that were dominant before the bleaching, leading McClanahan (2000) to hypothesize a phase shift within the hard coral community itself. A coral community dominated by

Agariciidae would have a smaller bioconstruction potential than one dominated by Acroporidae and Pocilloporidae, and therefore could imply reduced survivorship of coral reefs in the Maldives. The possibility of such a change has also been underlined by Edwards et al. (2001) and Loch et al. (2002). In 2000, however, the taxonomic composition of recruits and juveniles was similar to that of the adults before the bleaching, with an increased abundance of *Acropora* and *Pocillopora*.

Our data showed a variable recruit density at different sites, as other authors had already reported for other regions (Connell et al. 1997; Hughes et al. 1999). Juvenile density was less variable. Four years after the mortality event, the pre-existing vertical reef zonation could be recognized again, with *Pocillopora* returning as dominant at shallow depths. The recolonization of coral reefs in the Maldives seems to be going more through a predictable recovery process, reminiscent of a classical ecological succession in the marine environment (Bianchi et al. 1998).

The present situation in the Maldives following the mass coral mortality of 1998 encourages a cautious optimism with respect to reef recovery. Coral communities are recovering at a slow pace, especially whit respect to coral cover. The changes that occurred between 1999 and 2002 in the coral reefs of the Maldives remind us clearly that we cannot predict the future status of an ecosystem from short term observations (Bianchi 1997). In addition, the risk of increased magnitude and frequency of temperature anomalies leading to bleaching has been evoked (Wilkinson et al. 1999; Goreau et al. 2000; Wilkinson 2000). Not many studies on the effect of recurring bleaching events exist (e.g., Glynn et al. 2001). Historic series of data are available for very few reefs (e.g., Connell 1997), and the long-term monitoring of the coral community status remains the only way to track future trends.

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Appendix

Alphabetic list of the scleractinian species inventoried in 2002.

Acanthastrea echinata (Dana 1846)
Acropora abrotanoides (Lamarck 1816)
Acropora clathrata (Brook 1891)
Acropora cytherea (Dana 1846)
Acropora digitifera (Dana 1846)
Acropora divaricata (Dana 1846)
Acropora elseyi (Brook 1892)
Acropora gemmifera (Brook 1892)
Acropora granulosa (Milne Edwards and Haime 1860)
Acropora hemprichii (Ehrenberg 1834)
Acropora humilis (Dana 1846)
Acropora hyacinthus (Dana 1846)
Acropora intermedia (Brook 1891)
Acropora latistella (Brook 1891)
Acropora longicyathus (Milne Edwards and Haime 1860)
Acropora lutkeni Crossland 1952
Acropora muricata Linnaeus 1758
Acropora nasuta (Dana 1846)
Acropora palifera (Lamarck 1816)
Acropora robusta (Dana 1846)
Acropora valida (Dana 1846)
Alveopora allingi Hoffmeister 1925
Astreopora listeri Bernard 1896
Astreopora myriophthalma (Lamarck 1816)
Astreopora sp
Blastomussa merleti Wells 1961
Coscinaraea columnata (Dana 1846)
Coscinaraea monile (Forskål 1775)
Cynarina lacrymalis (Milne Edwards and Haime 1848)
Cyphastrea chalcidicum (Forskål 1775)
Cyphastrea microphthalma (Lamarck 1816)
Cyphastrea serailia (Forskål 1775)
Diploastrea heliopora (Lamarck 1816)
Echinophyllia aspera (Ellis and Solander 1788)
Echinopora hirsutissima Milne Edwards and Haime 1849
Echinopora lamellosa (Esper 1795)
Euphyllia ancora Veron and Pichon 1980
Favia fava (Forskål 1775)

Favia matthaii Vaughan 1918
Favia pallida (Dana 1846)
Favia rotumana (Gardiner 1899)
Favia speciosa Dana 1846
Favia stelligera (Dana 1846)
Favites abdita (Ellis and Solander 1786)
Favites chinensis (Verrill 1866)
Favites complanata (Ehrenberg 1834)
Favites flexuosa (Dana 1846)
Favites halicora (Ehrenberg 1834)
Favites pentagona (Esper 1794)
Favites russelli (Wells 1954)
Fungia (Cycloseris) costulata Ortmann 1889
Fungia (Fungia) fungites (Linnaeus 1758)
Fungia (Lobactis) scutaria Lamarck 1801
Fungia (Pleuractis) paumotensis Stutchbury 1833
Fungia (Verrillofungia) repanda Dana 1846
Fungia (Wellsofungia) granulosa Klunzinger 1879
Galaxea astreata (Lamarck 1816)
Galaxea fascicularis (Linnaeus 1767)
Gardineroseris planulata (Dana 1846)
Goniastrea edwardsi Chevalier 1971
Goniastrea favulus (Dana 1846)
Goniastrea palauensis (Yabe and Sugiyama 1936)
Goniastrea pectinata (Ehrenberg 1834)
Goniastrea retiformis (Lamarck 1816)
Goniopora columna Dana 1846
Goniopora djiboutiensis Vaughan 1907
Goniopora minor Crossland 1952
Halomitra pileus (Linnaeus 1758)
Herpolitha limax (Houttuyn 1772)
Herpolitha weberi Horst 1921
Hydnophora exesa (Pallas 1766)
Hydnophora microconos (Lamarck 1816)
Leptastrea inaequalis Klunzinger 1879
Leptastrea purpurea (Dana 1846)
Leptastrea transversa Klunzinger 1879
Leptoria phrygia (Ellis and Solander 1786)
Leptoseris hawaiiensis Vaughan 1907
Leptoseris incrustans (Quelch 1886)
Leptoseris mycetoseroides Wells 1954
Leptoseris scabra Vaughan 1907
Lobophyllia corymbosa (Forskål 1775)
Lobophyllia hemprichii (Ehrenberg 1834)
Merulina ampliata (Ellis and Solander 1786)
Merulina vauhani Horst 1921
Montastrea annuligera (Milne Edwards and Haime 1849)
Montastrea curta (Dana 1846)
Montastrea magnistellata Chevalier 1971
Montastrea valenciennesi (Milne Edwards and Haime 1848)
Montipora aequituberculata Bernard 1897
Montipora danae (Milne Edwards and Haime 1851)
Montipora floweri Wells 1954
Montipora informis Bernard 1897
Montipora maldivensis Pillai and Scheer 1976
Montipora monasteriata (Forskål 1775)
Montipora sinuosa Pillai and Scheer 1976
Montipora undata Bernard 1897
Montipora venosa (Ehrenberg 1834)
Montipora verrucosa (Lamarck 1816)
Mycedium elephantotus (Pallas 1776)
Oulophyllia crista (Lamarck 1816)
Oxypora lacera (Verrill 1864)
Pachyseris rugosa (Lamarck 1801)
Pachyseris speciosa (Dana 1846)
Pavona clavus (Dana 1846)
Pavona explanulata (Lamarck 1816)
Pavona maldivensis (Gardiner 1905)
Pavona minuta Wells 1954
Pavona varians Verrill 1864
Pavona venosa (Ehrenberg 1834)
Pectinia alvicornis (Saville-Kent 1871)
Pectinia lactuca (Pallas 1776)
Physogyra lichtensteini (Milne Edwards and Haime 1851)
Platygyra daedalea (Ellis and Solander 1786)
Platygyra lamellina (Ehrenberg 1834)
Platygyra pini Chevalier 1975
Plerogyra sinuosa (Dana 1846)
Plesiastrea versipora (Lamarck 1816)
Pocillopora damicornis (Linnaeus 1758)
Pocillopora meandrina Dana 1846
Pocillopora verrucosa (Ellis and Solander 1786)
Podabacia crustacea (Pallas 1776)
Porites (Synarea) rus (Forskål 1775)
Porites cylindrica Dana 1846
Porites lichen Dana 1846
Porites lobata Dana 1846
Porites lutea Milne Edwards and Haime 1851
Porites solida (Forskål 1775)
Porites vauhani Crossland 1952
Psammocora contigua (Esper 1797)
Psammocora digitata Milne Edwards and Haime 1851
Psammocora explanulata Horst 1922
Psammocora haimeana Milne Edwards and Haime 1851
Psammocora nierstraszi Horst 1921
Psammocora profundacella Gardiner 1898
Psammocora superficialis Gardiner 1898
Sandalolitha robusta Quelch 1886
Scolymia cf. vitiensis Brüggemann 1877
Stylocoeniella armata (Ehrenberg 1834)
Stylocoeniella guentheri Bassett-Smith 1890
Symphyllia radians Milne Edwards and Haime 1849
Symphyllia valenciennesi Milne Edwards and Haime 1849
Tubastraea micranthus (Ehrenberg 1834)
Turbinaria mesenterina (Lamarck 1816)
Turbinaria peltata (Esper 1794)
Turbinaria reniformis Bernard 1896
Turbinaria stellulata (Lamarck 1816)