

# Bleaching susceptibility and mortality among corals with differing growth forms

Dominique M. McCowan<sup>1</sup>, Morgan S. Pratchett<sup>1</sup>, Andrew H. Baird<sup>1</sup>

<sup>1</sup>ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville QLD 4811 Australia

Corresponding author: [dmmccowa@gmail.com](mailto:dmmccowa@gmail.com)

**Abstract.** Differences in bleaching susceptibility and mortality are apparent among coral species, and have been variously ascribed to differences in physiology and morphology, in particular overall growth form (e.g., branching versus massive corals). However, coral morphology is highly confounded with taxonomy, and no studies have tested for differences in bleaching susceptibility among corals with varying morphology within (rather than between) coral families. For this study, data were compiled for bleaching susceptibility and mortality from 65 published studies that monitored coral health throughout the bleaching event. Overall patterns of bleaching susceptibility were significantly different among coral growth forms, whereby a much higher proportion of branching, tabular, and submassive corals bleached compared to encrusting, massive, and free-living corals. However, differences in bleaching susceptibility and mortality were not consistent among growth forms within families. Branching faviid species (e.g., *Echinopora*) had much lower incidence of bleaching compared to massive species, but the reverse was true for Acroporidae and Poritidae. Moreover, mortality was markedly different amongst growth forms within families, such that massive Acroporidae (e.g. Montipora) suffered highest mortality when compared to Faviidae and Poritidae, but branching Acroporidae suffered lowest mortality compared to branching Faviidae and Poritidae. Our data suggest that generalities about the susceptibility of branching versus massive corals (and among other major growth forms) arise at least in part because certain growth forms are over-represented by highly susceptible coral taxa (e.g., *Acropora*) or perhaps because branching corals generally maintain higher dominance than massive corals.

**Key words:** Coral reef, Morphology, Mass bleaching, Scleractinia

## Introduction

Climate change affects coral reef ecosystems in a multitude of ways (Knowlton 2001, Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Pratchett et al. 2011). However, the direct effects of increased ocean temperatures have had the greatest impacts (Hoegh-Guldberg 1999), and generate the most concern among coral reef scientists and managers (Knowlton 2001, McWilliams et al. 2005). Increased ocean temperatures have been linked to large-scale and multi-specific bleaching of scleractinian corals (Williams & Bunkley-Williams 1990, Glynn 1991, McWilliams et al. 2005), as well as increased occurrence and virulence of coral disease (Willis et al. 2004). Mass bleaching events have caused widespread mortality of scleractinian corals (Hoegh-Guldberg 1999, Wilkinson 1998) and extensive degradation of coral reef habitats (Hughes et al. 2003).

Mass bleaching events are highly selective (e.g., Marshall and Baird 2000) and cause changes to the community structure of coral assemblages (Hughes et al. 2003). In general, families of corals that are mostly characterised by branching growth forms (e.g., Acroporidae and Pocilloporidae) are considered to be

most susceptible to bleaching and experience highest rates of mortality once bleached (Baird and Marshall 2002, Jones 2008). In contrast, families of corals that typically have massive morphologies (e.g., Faviidae, Mussidae, and Poritidae) appear fairly resistant to increasing temperature, being among the last to bleach and more frequently experience partial, rather than whole colony mortality (Brown and Suharsono 1990, McClanahan 2000, Baird and Marshall 2002, Riegl 2002). These patterns of differential bleaching susceptibility and mortality have led authors to group corals into either branching or massive growth forms without consideration for taxonomy (Arthur 2000, Iluz et al. 2008, Spencer et al. 2000); however, coral morphology is highly confounded with taxonomic affinity (Veron 2000) and the role of differential morphology within (rather than between) coral families in explaining bleaching susceptibility has not been tested. Therefore, the purpose of this study was to utilise an extensive database of bleaching observations to test whether bleaching susceptibility and mortality is related to coral morphology, independent of taxonomic (family-level) affinities among coral species.

## Materials and Methods

A database of field observations of bleaching susceptibility and mortality among scleractinian corals was compiled based on 95 scientific papers published from 1982 to 2011 (1520 entries). All bleaching observations were arranged by species, and then categorized according to the specific location, climatic conditions, habitat, and the timing of observations relative to occurrence of bleaching (months since onset of bleaching or if observations were continuous (e.g. permanent transects)). Bleaching susceptibility ( $(\#bleached/\#observed)*100$ ) was recorded as the percent of colonies within a given species (or alternative taxonomic grouping) that exhibited any sign of bleaching, inclusive of slight or partial paling through to recent whole colony mortality. Explicit information on the fate of bleached corals (e.g. long-term survival or mortality) was also recorded; mortality =  $(\#died/\#observed)*100$  or partial mortality =  $(\text{mean \% of colony mortality}/\# \text{ of colonies with mortality})/\#observed*100$ ; however, there were few studies where mortality could confidently be attributed to bleaching (e.g. Baird and Marshall 2002, Obura 2001).

For this study, the database was restricted to studies where morphology was categorized ( $n=65$ ); 820 entries for bleaching susceptibility (29% of which had repeated observations throughout the bleaching event) and 706 entries for bleaching mortality (31% monitored throughout). The database was used to test whether colony morphology influences susceptibility to mass coral bleaching. Where possible, the morphology of corals was entered directly from the source. Although when not specified, species were categorized to growth forms using descriptions provided in Veron (2000). Major categories of growth morphologies used were (1) branching, (2) tabular, (3) columnar, (4) submassive, (5) massive, (6) encrusting, and (7) free-living.

Variation in bleaching susceptibility and mortality was analysed using ANOVA. All data were arcsine-square root transformed and only growth forms for which there were  $>20$  records were included. Pairwise Tukey's tests were conducted. 1-way ANOVAs were used to compare proportional bleaching and mortality among major growth forms (Fig. 1) regardless of taxonomy. The three most commonly studied families (Acroporidae, Faviidae and Poritidae), which also exhibit a range of different growth forms, were analysed to establish the proportion of variation explained by family, versus growth form within family. As such, growth form was nested within family and 1-way ANOVAs were run to test for differences in both the mean proportion of colonies that bleached and the mean proportion of colonies that subsequently died. Data met model assumptions when

arcsine square root transformed. Tukey's post hoc tests were used to explore significant results.

## Results

A total of 816 bleaching records, mostly for branching (293 records) and massive corals (334 records), were used to test for differences in bleaching susceptibility and mortality. Taxonomy aside, bleaching susceptibility varied significantly among growth forms (ANOVA,  $F_{(6, 815)} = 717.7$ ,  $p < 0.001$ ), but Tukey's post-hoc tests revealed just two distinct groups. Branching and tabular corals bleached significantly more than massive and free-living corals, but not columnar, encrusting, or submassive corals. Variation in subsequent rates of mortality were also significant (ANOVA,  $F_{(6,699)} = 114.9$ ,  $p < 0.001$ ) and much more apparent (Fig. 1). Tukey's post hoc tests showed that branching, columnar, and tabular corals had significantly higher mortality compared to massive, encrusting, submassive, and free-living corals.

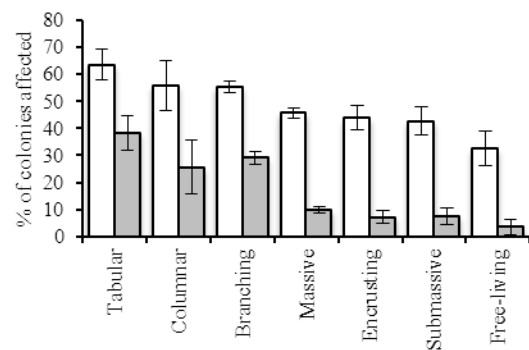


Figure 1: Mean ( $\pm$ SE) bleaching susceptibility (white) and mortality (grey) for different growth forms, irrespective of taxonomy. Data are averaged across studies with complete observations of the event.

When considering both growth form and taxonomy, growth form accounted for a greater proportion of variation in bleaching susceptibility (44%) than family (34%), but differences among growth forms were not consistent across families (Fig. 2). Moreover, the rank order of growth form susceptibility without taxa (Fig. 1) was not consistent for Acroporidae, Faviidae, or Poritidae. Some massive acroporid species (e.g., *Montipora venosa*) had higher bleaching susceptibility than branching species, while some branching faviids (e.g. *Cladocora arbuscula*) had lower bleaching susceptibility than massive species. Significant differences in bleaching susceptibility among growth forms nested within families (Table 1) swamped any differences among families.

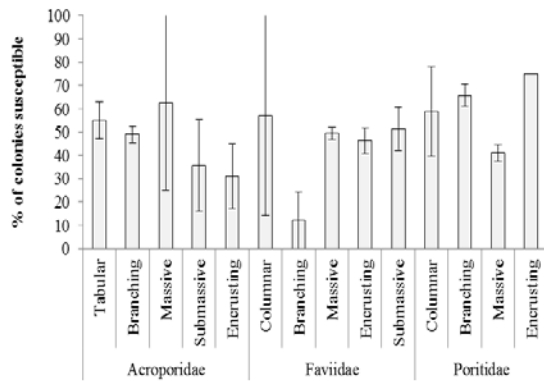


Figure 2: Mean ( $\pm$ SE) bleaching susceptibility for different growth forms, within three families of scleractinian corals (Acroporidae, Poritidae, and Faviidae) that exhibit a range of growth forms.

The proportion of colonies that died following bleaching differed significantly among growth forms within families (Fig. 3), but also among the three key families (Table 2). More than half (51%) of the variation in proportional mortality was explained by growth form, but a further 41% was explained by family. Post-hoc tests show that Faviidae had lower mortality than either Acroporidae or Poritidae, even though susceptibility was similar for all three families (Table 2). However, the overall differences between mortality of growth forms within these three families are such that Acroporidae had the highest mean mortality of massive colonies, but the lowest mean mortality of branching colonies. Moreover, encrusting and submassive corals showed minimal mortality due to bleaching. Mortality patterns among Acroporidae growth forms were consistent with bleaching susceptibility (e.g., high susceptibility led to high mortality), but this was not the case among Faviidae growth forms (Fig. 3).

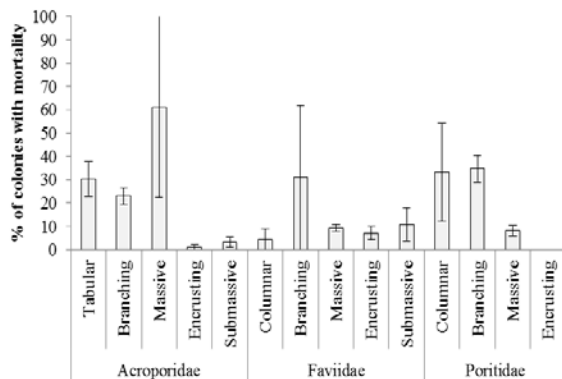


Figure 3: Mean ( $\pm$ SE) bleaching mortality for different growth forms (in order of bleaching susceptibility, Fig. 2), within three families of scleractinian corals (Acroporidae, Poritidae and Faviidae) that exhibit a range of growth forms.

| Factor      | Bleaching |    |      | Mortality |    |      |
|-------------|-----------|----|------|-----------|----|------|
|             | F         | df | p    | F         | df | p    |
| Family      | 1.5       | 2  | 0.23 | 5.4       | 2  | 0.03 |
| Growth form | 2.0       | 11 | 0.03 | 7.1       | 11 | 0.00 |

Table 1: ANOVA on proportional bleaching (A) and proportional mortality (B), comparing corals with different morphologies nested within three key families (Acroporidae, Poritidae and Faviidae).

### Discussion

It is generally assumed that branching corals are more susceptible to bleaching than massive colonies (e.g., Loya et al. 2001). Our analyses of published literature support this claim among major growth forms, whereby branching, columnar and tabular corals have greater susceptibility and mortality than massive, submassive, encrusting and free-living corals (Fig. 1). At least some of the observed differences in bleaching susceptibility among growth forms are attributable to variations in taxonomic susceptibility (Fig. 2). For example, Acroporidae, Pocilloporidae, and Poritidae dominate branching corals, which are generally more abundant and sensitive when compared to Faviidae. The trends for mortality (Fig. 3) show that branching Acroporidae generally have less mortality than branching species in either Faviidae or Poritidae, while the opposite is true for massive growth forms.

The rank order of bleaching susceptibility recorded in this study is not entirely consistent with patterns reported elsewhere. Columnar corals, for example, are often grouped with massive species and thought to have relatively low susceptibility to bleaching (e.g., Obura 2001). However, the observed order is consistent with differences in mass-transfer capacity, whereby flatter and smaller corals have a greater capacity to remove potentially deleterious superoxides and other oxygen radicals, compared to more erect and branching forms (Nakamura and van Woessik 2001). This may further explain why branching corals generally experienced higher rates of mortality compared to massive corals (Fig. 3), especially after very severe bleaching.

Variability in the timing of observations of bleaching susceptibility and mortality relative to the onset of the stress event may also partially explain these differences. For instance, branching and tabular *Acropora* colonies are most susceptible during the first two months of stress (Baird and Marshall 2002, Obura 2001); whereas massive colonies have been observed bleached from 3- 14 months after the onset of the event (Lang et al. 1992, Moothien-Pillay et al. 2006). Furthermore, when temperatures remain above the average into the following summer, massive growth forms become more susceptible than branching species (Brandt 2009, Goorah et al. 1998, Guest et al. 2012, Guzman and Cortes 2001, Mohammed and Mohamed 2005, Moothien-Pillay et al. 2006, Obura 2001) which suggests that branching

colonies are showing an acclimatory response to the continuous exposure of increased temperatures and/or massive growth forms accumulate thermal stress over time.

Morphological variations in bleaching susceptibility may also be attributable to inherent differences in growth rates (reflective of life-history strategies) (Baird and Marshall 2002), thermal tolerances of photoendosymbionts (Berkelmans and van Oppen 2006), tissue thickness, and/ or marked differences in colony size and age (Loya et al. 2001). Perhaps the best explanation of consistent difference in bleaching susceptibility is the level of physiological integration (Baird and Marshall 2002), which is highly linked with morphology, particularly within taxa. We hypothesize that in species with polyps that are physiologically independent, (e.g. massive colonies) only polyps directly affected by both heat and light respond, as predicted by the photoinhibition model of coral bleaching of Jones et al. (1998). The result is that bleaching within the colony is patchy and rates of whole colony mortality are low, which is the typical response of most massive species. Moreover, taxa that are highly integrated cannot contain the damage and rates of whole colony mortality are therefore high (e.g. *Acropora*).

Generalities in bleaching susceptibility and mortality are important to understand potential mechanisms by which corals could adapt, but the role of morphology must be considered in light of marked differences in the taxonomic composition of corals that exhibit these different growth forms.

## References

- Aronson A, Precht F, Toscano M, Koltes K (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Mar Biol* 141: 435-447
- Arthur R (2000) Coral bleaching and mortality in three Indian reef regions during an El Nino southern oscillation event. *Cur Sci* 79:1723-1729
- Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. *Trends Ecol Evol* 24:16-20
- Baird A, Marshall P (1998) Mass Bleaching of corals on the Great Barrier Reef. *Coral Reefs* 17:376
- Baird A, Marshall P (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar Ecol Progr Ser* 237:133-141
- Berkelmans R, van Oppen MJH (2006) The role of zooxanthella in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society, B* 273:2305-2312
- Brandt M (2009) The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. *Coral Reefs* 28:911-924
- Brown B, Phongsuwan N (1998) Extensive coral mortality as a result of bleaching in the Andaman Sea in 1995. *Coral Reefs* 17:70
- Brown B, Suharsono (1990) Damage and recovery of coral reefs affected by El Nino related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163-170
- Bruno J, Siddon C, Witman J, Colin P, Toscano M (2001) El Nino related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* 20:127-136
- CARICOMP (1997) Studies on Caribbean coral bleaching, 1995-1996. *Proc 8<sup>th</sup> Int Coral Reef Sym* 1: 673-678
- Carriquiry J, Cupul-Magana A, Rodriguez-Zaragoza F, Medina-Rosas P (2001) Coral bleaching and mortality in the Mexican Pacific during the 1997-98 El Nino and prediction from a remote sensing approach. *Bul Mar Sci* 69:237-249
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310
- Cowan C (2006) Coral Bleaching and Disease: Recovery and Mortality on Martinique Reefs following the 2005 Caribbean Bleaching events. MSc Thesis, Uni of Newcastle upon Tyne
- Davies J, Dunne R, Brown B (1997) Coral Bleaching and elevated sea-water temperature in Milne Bay Province, Papua New Guinea, 1996 *Mar Freshwater Res* 48:513-6
- Drollet F, Faucon M, Maritorea S, Martin P (1994) A survey of environmental physico-chemical parameters during a minor mass bleaching event in Tahiti in 1993. *Aust J Mar Freshwater Res* 45:1149-56
- Drollet F, Faucon M, Martin P (1995) Elevated seawater temperature and solar UV-B flux associated with two successive coral mass bleaching events in Tahiti. *Mar Freshwater Res* 46:1153-7
- Feingold J (2001) Responses of three coral communities to the 1997-98 El Nino Southern Oscillation: Galapagos Islands, Ecuador. *Bull Mar Sci* 1:123-124
- Floros (2004) Taxonomic patterns of bleaching within a South African coral assemblage. *Bio Cons* 13:1175-1194
- Fong P, Glynn P (2001) Population abundance and size-structure of an eastern tropical Pacific reef coral after the 1997-1998 ENSO: a simulation model predicts field measures *Bull Mar Sci* 69:187-202
- Gladfelter EH (1983) Circulation of fluids in the gastrovascular system of the reef coral *Acropora cervicornis*. *Biol Bull* 165: 619-636
- Glynn P (1983) Extensive bleaching and death of reef corals on the Pacific coast of Panama. *Env Cons* 10:149-154
- Glynn P, Colgan M (1992) Sporadic disturbances in fluctuating coral reef environments: El Nino and coral reef development in the Eastern Pacific. *Am Zool* 32:707-718
- Glynn P, de Weerd W (1991) Elimination of two reef-building hydrocorals following the 1982-83 El Nino warming event. *Science* 253:69-71
- Glynn P, Cortes J, Guzman H, Richmond R (1988) El Nino (1982-83) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific. *Proc 6<sup>th</sup> Int Coral Reef Sym* 3:237-243
- Goenaga C, Vicente V, Armstrong R (1989) Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: a precursor of change in the community structure of coral reefs? *Carib J Sci* 25:59-65
- Goorah B, Rathacharen B, Kulputee D (1998) Occurrence of coral bleaching in the marine parks of Mauritius. AMAS 98. Food and Agricultural Research Council, Réduit, Mauritius 135-41
- Goreau T (1992) Bleaching and reef community change in Jamaica: 1951-1991. *Am Zool* 32: 683-695
- Goreau T (2000) Conservation of coral reefs after the 1998 global bleaching event. *Cons Biol* 14:5-15
- Guest JR, Baird AH, Maynard JM, et al (2012) Changing patterns of coral bleaching susceptibility suggests an adaptive response to thermal stress. *Plos One*: Accepted 16 Feb
- Guzman H, Cortes J (2001) Changes in reef community structure after fifteen years of natural disturbances in the Eastern Pacific (Costa Rica). *Bul Mar Sci* 69:133-149
- Hardman E, Meunier M, Turner J, Lynch T, Taylor M, Klaus R (2004) The extent of coral bleaching in Rodrigues, 2002. *J Nat Hist* 38:3077-3089

- Hardman E, Stampell N, Hunt L, Perrine S, Perry A, Raffin J (2007) The impacts of coral bleaching in Rodrigues, Western Indian Ocean. *Atoll Res Bull* 555:1-10
- Harriott V (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar Ecol Prog Ser* 21:81-88
- Hoegh-Guldberg O, Salvat B (1995) Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Mar Ecol Prog Ser* 121:181-190
- Hoegh-Guldberg O (1999) Climate change, coral bleaching, and the future of the world's coral reefs. *Mar Fresh Res* 50:839-866
- Hoeksema B (1991) Control of bleaching in mushroom coral populations in the Java Sea: stress tolerance and interference by life history strategy. *Mar Ecol Prog Ser* 74:225-237
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke CS, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas JA, Lough JM, Marshall PA, Nystrom M, Palumbi SR, Pandolfi JM, Rosen BR, Roughgarden J (2003) Climate Change, Human Impacts, and the resilience of coral reefs. *Science* 301:929-933
- Iluz D, Vago R, Chadwick N, Hoffman R, Dubinsky Z (2008) Seychelles lagoon provides corals with a refuge from bleaching. *Res Lett Ecol* 2008:1-4
- Jeffrey C, Clark R, Woody K, Menza C, Kendall M, Monaco M (2006) Coral bleaching and recovery observed at Buck Island, St. Croix, US Virgin Islands, October and December 2005. NOAA Biogeography Branch, SSMC-4 N/SCI-1
- Jimenez C (2002) Effects of recent warming events on coral reef communities of Costa Rica (Central America). PhD Thesis, University of Bremen
- Jimenez C, Cortes J, Leon A, Ruiz E (2001) Coral bleaching and mortality associated with the 1997-98 El Nino in an upwelling environment in the Eastern Pacific (Gulf of Papagayo, Costa Rica). *Bul Mar Sci* 69:151-169
- Jones R (2008) Coral bleaching, bleaching-induced mortality and the adaptive significance of the bleaching response. *Mar Biol* 154:65-80
- Jones RJ, Hoegh-Guldberg O, Larkum AWL, Schreiber U (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell Environ* 21: 1219-30
- Kayanne H, Harii S, Ide Y, Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. *Mar Ecol Prog Ser* 239:93-103
- Knowlton N (2001) The future of coral reefs. *PNAS* 98:5419-5425
- Kramer P, Kramer P (2000) Transient and lethal effects of the 1998 coral bleaching event on the Meso-American reef system. *Proc 9th Int Coral Reef Sym* 2:1175-1180
- Lang C, Lasker H, Gladfelter E, Hallock P, Jaap W, Losada F, Muller R (1992) Spatial and temporal variability during periods of recovery after mass bleaching on Western Atlantic coral reefs. *Am Zool* 32: 696-706
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122-131
- Marshall P, Baird A (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155-163
- Maynard J, Anthony K, Marshall P, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. *Mar Biol* 155:173-182
- McClanahan T (2004) The relationship between bleaching and mortality of common corals. *Mar Biol* 144:1239-1245
- McClanahan T, Muthiga N, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380-391
- McClanahan T, Baird A, Marshall P, Toscano M (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Mar Poll Bull* 48: 327-335
- McField M (1999) Coral response during and after mass bleaching in Belize. *Bul Mar Sci* 64:155-172
- McWilliams JP, Côté IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* 86:2055-2060
- Miller M, Piniak G, Williams D (2011) Coral mass bleaching and reef temperatures at Navassa Island, 2006. *Est Cstl Shlf Sci* 91:42-50
- Mohammed T, Mohamed M (2005) Some ecological factors affecting coral reef assemblages off Hurghada, Red Sea, Egypt. *Egypt J Aq Res* 31:133-142
- Moothien-Pillay K, Terashima H, Kawasaki H, Chineah V (2006) Recovery of massive poritid corals from bleaching at Albion, Mauritius. *Proc 10<sup>th</sup> Int Coral Reef Sym* 1:617-623
- Mumby P (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Mar Ecol Prog Ser* 190:27-35
- Mumby P, Chisolm J, Edwards A, Clark C, Roark E, Andrefouet S, Jaubert J (2001) Unprecedented bleaching-induced mortality in *Porites* spp. At Rangiroa Atoll, French Polynesia. *Mar Biol* 139:183-189
- Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol Prog Ser* 212:301-304
- O'Farrell S, Day O (2005) Tobago Bleaching Report
- Obura D (2001) Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress? *Bul Mar Sci* 69:421-442
- Oxenford H, Roach R, Brathwaite A, Nurse L, Goodridge R, Hinds F, Baldwin K, Finney C (2008) Quantitative observations of a major coral bleaching event in Barbados, Southeastern Caribbean. *Clim Chg* 87:435-449
- Porter J Fitt W, Spero H, Rogers C, White M (1989) Bleaching in reef corals: physiological and stable isotopic responses. *PNAS* 86:9342-9346
- Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity* 3:424-452
- Quinn N, Kojis B (2008) The recent collapse of a rapid phase-shift reversal on a Jamaican north coast coral reef after the 2005 bleaching event. *Rev Biol Trop* 56:149-159
- Reyes-Bonilla H (1993) 1987 coral reef bleaching at Cabo Pulmo Reef, Gulf of California, Mexico. *Bull Mar Sci* 52:827-837
- Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). *Mar Biol* 140:29-40
- Sebastian C, Sink K, McClanahan T, Cowan D (2009) Bleaching response of corals and their *Symbiodinium* communities in southern Africa. *Mar Biol* 156:2049-2062
- Soong K, Lang JC (1992) Reproductive integration in reef corals. *Biol Bull Mar Biol Lab Woods Hole* 183: 418-431
- Spencer T, Teleki K, Bradshaw C, Spalding M (2000) Coral bleaching in the Seychelles during the 1997-1998 Indian Ocean warm event. *Mar Poll Bull* 40:569-586
- Steiner S, Kerr J (2008) Stony corals in Dominica during the 2005 bleaching episode and one year later. *Rev Biol Trop* 56:139-148
- Stimson J, Sakai K, Sembali H (2002) Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. *Coral Reefs* 21:409-421
- Veron JEN (1986) Corals of Australia and the Indo-Pacific. Angus & Robertson, Sydney, p. 321
- Veron J (2000) Corals of the World. Australian Institute of Marine Science and CRR Qld Pty Ltd
- Whelan K, Miller J, Sanchez O, Patterson M (2007) Impact of the 2005 coral bleaching event on *Porites porites* and *Colpophyllia natans* at Tektite Reef, US Virgin Islands. *Coral Reefs* 26: 689-693
- Wilkinson CR (1998) Status of coral reefs of the world. 1998 Australian Institute of Marine Science, Townsville

- Wilkinson C (2002) Status of Coral Reefs of the World 2000. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre, Townsville, 376 p.
- Williams E, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Res Bul* 335:1-73
- Willis BL, Page CA, Dinsdale EA (2004) Coral Disease on the Great Barrier Reef. In: Rosenberg E, Loya Y (eds) *Coral Health and Disease*, pp 37
- Winter A, Appeldoorn R, Bruckner A, Williams Jr. E, Goenaga C (1998) Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* 17:377-382