ATOLL RESEARCH BULLETIN

NO. 507

CORAL SPECIES DIVERSITY AND ENVIRONMENTAL FACTORS IN THE ARABIAN GULF AND THE GULF OF OMAN: A COMPARISON TO THE INDO-PACIFIC REGION

BY

S.L. COLES

ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C., U.S.A.
AUGUST 2003

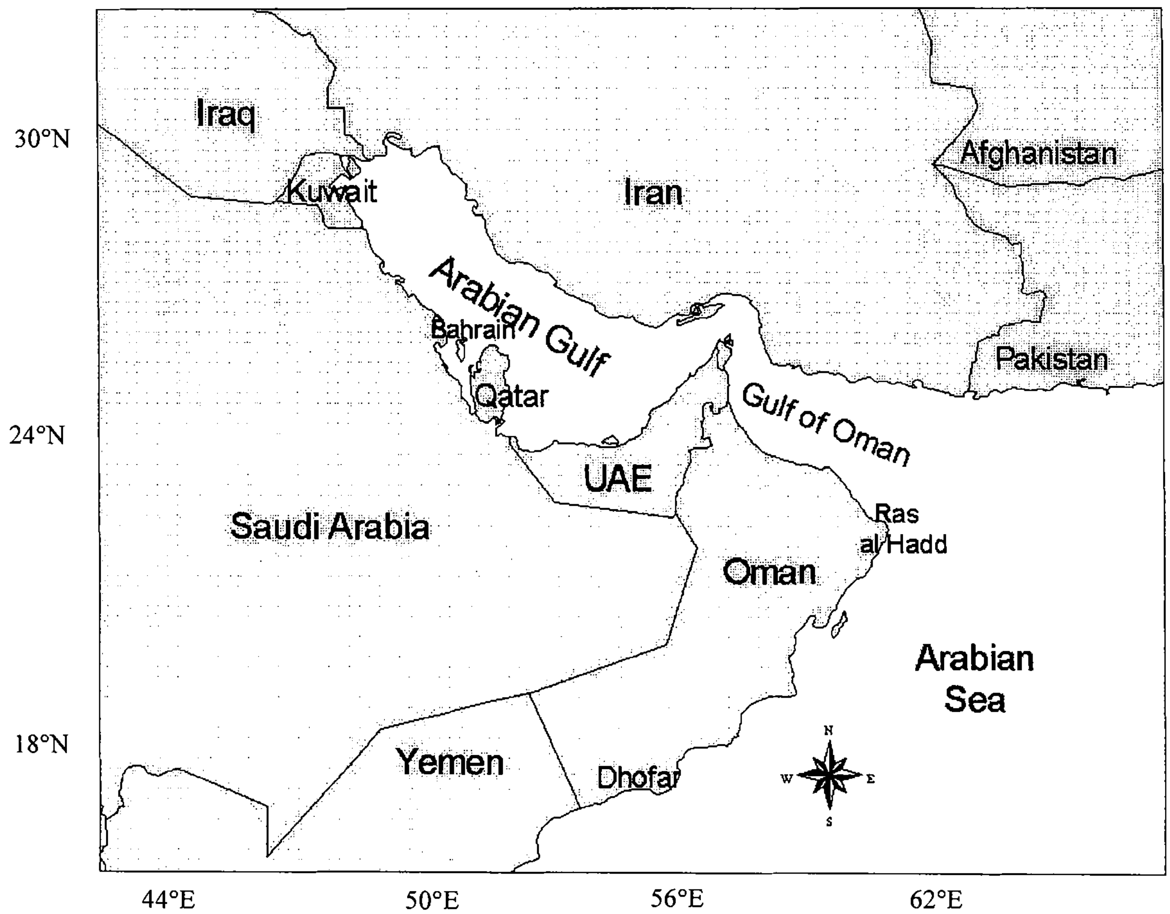

Figure 1. Map of the Arabian Gulf and Gulf of Oman

CORAL SPECIES DIVERSITY AND ENVIRONMENTAL FACTORS IN THE ARABIAN GULF AND THE GULF OF OMAN: A COMPARISON TO THE INDO-PACIFIC REGION

BY

S. L COLES[1]

ABSTRACT

The reef corals of the Arabian Gulf and the Gulf of Oman comprise a substantially reduced subset of the Indo-Pacific coral fauna. Only about 10% of the species that occur in the Indo-Pacific are found in the Gulf region and community species compositions are substantially altered from assemblages that normally dominate Indo-Pacific reefs. For example, the highly diverse family Acroporidae is under-represented in the Gulf region while the families Dendrophylliidae, Faviidae and Siderastreidae are over-represented. Some of this regional uniqueness may be due to geographic isolation but it probably is primarily a result of physical and environmental conditions that are among the most extreme and stressful in the world and act to limit the diversity of corals that occur in the region. Seawater temperatures in the Arabian Gulf have historically ranged up to 25°C at coral study sites, approximately 6°C above and below the temperatures traditionally considered limiting to coral survival. Short-term temperature fluctuations in the Gulf of Oman due to upwelling can range up to 8°C in a day without visible effect on resident corals. Salinities survived by Gulf corals range up to 50 parts per thousand (ppt), about 15 ppt higher than normal ocean salinity in the Indo-Pacific. Other factors, such as relatively high turbidity and competition with macroalgae favored by low winter water temperatures, may combine with temperature and salinity to limit the development of diverse coral populations in the Gulf. The implications of the potential contribution of this region's reservoir of hardy coral phenotypes to the Indo-Pacific coral fauna during an era of general worldwide environmental stress are discussed.

INTRODUCTION

"*...reef corals flourish best in the range 25°-29°C...within a salinity range of 34-36 parts per thousand....However, in the Abu Dhabi area coral reefs are growing under conditions of elevated temperature and salinity. The only indication of extreme conditions is the reduction in the number of genera.*" Kinsman (1964).

This landmark paper by D.J.J. Kinsman represented a major paradigm shift for coral biologists in their thinking about the tolerances of corals to physical stresses. Corals had been traditionally considered to be highly stenotopic organisms with very limited endurance of changes in temperature, salinity, turbidity and nutrient

[1] Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA

Manuscript received 9 January 2002; revised 11 April 2002

concentrations typical of clear, oligotrophic open ocean water (Dana, 1843, 1872; Mayer, 1914, 1915; Vaughan, 1916, 1918; Edmondson, 1928; Wells, 1957). Water temperature was considered to be especially limiting and corals were believed to live close to fixed upper temperature limits usually considered to be around 30°C and lower limits of around 16°C, with little chance of survival outside of this limited temperature range (Mayer, 1914, 1918; Edmondson, 1928).

Kinsman's observations along the Abu Dhabi coastline in the 1960s indicated that tolerances of Arabian Gulf corals well exceeded such limits. He found 11 species surviving temperatures up to 36°C and in salinities up to 48°/oo, substantially expanding the temperature and salinity environments previously considered to limit coral survival. With the increased opportunities for making reef surveys and conducting research in the Arabian Gulf that have occurred in the past 40 years, our knowledge of the environmental conditions of this unique area and the number of species that occur there has greatly increased. The following report summarizes information for the coral communities that occur in the Arabian Gulf region and discusses the principal factors that define and limit these communities. These findings are compared to conditions that generally apply to corals and reefs in the Indo-Pacific region, and the implications of the generally more hardy Arabian Gulf corals in the context of Pacific-wide coral bleaching events will be discussed

COMPARISON OF GULF CORAL DIVERSITY TO THE INDO-PACIFIC

The coral community of the Gulf is a subset of the great Indo-Pacific tropical faunas, which stretch across the Pacific and Indian Oceans from the west coast of Central and South America to the east coast of Africa. The pattern of distribution of numbers of coral genera indicated for this vast region (Veron, 1993) shows maximum numbers of genera and species in the triangle enclosed by the Philippines, Indonesia and New Guinea with numbers of genera decreasing in all directions to lows of less than 10 east of Hawaii, along Japan, south Australia and South Africa. Numbers of genera in the Gulf region are shown in Figure 2 in Veron (1993) to be >20 in both the Arabian Gulf and the Gulf of Oman with latest figures of 28 and 33 genera, respectively (Table 1). By comparison, estimates of numbers of coral genera in the Red Sea range >75 including 57 reef forming genera (Sheppard and Sheppard, 1991), substantially more than the number for the Gulf region.

Greater detail on the composition and diversity of zooxanthellate coral genera and species in the Gulf region (Figure 1) are provided in Table 1 and these data are compared with similar information for the entire Indo-Pacific region from Cairns (1999). The Cairns (1999) values unite numerous synonymies from previous estimates of taxonomic listings and therefore represent a conservative estimate of coral diversity for the Indo-Pacific region. The estimates for the Arabian Gulf and the Gulf of Oman are synthesized from many sources throughout the Gulf region. Of the 656 species among 109 genera of zooxanthellate corals for the Indo-Pacific listed by Cairns (1999), only about 10%, or 68 species among 28 genera, occur in the Arabian Gulf and 68 species among 33 genera in

Table 1. Numbers of genera, species and numbers of species in a family as a percent of all species found (% Total) in the Indo-Pacific Region, Arabian Gulf and Gulf of Oman.

	Indo-Pacific[1]			Arabian Gulf[2,3,4,5,6,7]			Gulf of Oman[3,7,8,9,10]		
Taxa	Genera	Species	% Total	Genera	Species	% Total	Genera	Species	% Total
All Families	109	656		28	68		33	68	
Acroporidae	4	199	30%	2	11	16%	3	10	15%
Fungiidae	11	44	7%	1	1	1%	1	1	1%
Siderastreidae	6	27	4%	5	8	12%	5	7	10%
Faviidae	24	103	16%	8	21	31%	4	20	29%
Dendrophylliidae	3	15	2%	2	4	6%	3	4	6%

[1] Cairns (1999)
[2] Burchard (1979)
[3] Sheppard and Sheppard (1991)
[4] Hodgson and Carpenter (1995)
[5] Carpenter et al (1996)
[6] Riegl (1999)
[7] Sheppard (1987)
[8] Sheppard and Salm (1988)
[9] Glynn 1993
[10] Coles (1996)

the Gulf of Oman. Within the Gulf region the distribution of species among families is quite anomalous compared to the Indo-Pacific as a whole. The family Acroporidae, which is the most diverse in the Indo-Pacific with nearly 200 species or 30% of all species reported, has only 10-11 species in the Gulf region or about 15% of the total species reported. A similar reduction in species is shown for Fungiidae in the Gulf with only one species reported (1% of total) compared to 44 species (7% of total) for the Indo-Pacific. By contrast, the families Siderastreidae, Faviidae and Dendrophylliidae have percentages of total species two to three times greater in the Gulf region than in the Indo-Pacific (Table 1).

Within the Arabian Gulf (Table 2), there are moderate geographic variations in numbers of species and species types found in various areas. Maximum numbers of species reported thus far have been in the central Gulf along the coasts of Saudi Arabia and Bahrain (Burchard, 1979; Sheppard, 1988) where about 40 species have been reported. Reported numbers of species decrease going north and south with about 35 species reported for both Kuwait (Hodgson and Carpenter, 1995) and the UAE (Reigl, 1999). By comparison, in the Gulf of Oman (Table 2), 68 species have been reported for the Capital Area of Muscat and Daymaniat Islands alone (Sheppard and Salm, 1988; Coles, 1996) equal to the total number for the entire Gulf inside of the Strait of Hormuz. The differences in species occurrence within the Gulf probably correspond to different environmental factors affecting corals in various areas and they may also relate to greater habitat diversity available for coral settlement and growth on the reefs around the island areas offshore of Saudi Arabia and Bahrain.

Table 2. Gulf region variations and contrasts in coral species numbers.

Area	Species	Source
Kuwait	35	Hodgson & Carpenter (1995)
Saudi Arabia	41	Burchard (1979)
Bahrain	40	Sheppard (1988)
Dubai, UAE	34	Reigl (1999)
Gulf of Oman	68	Sheppard & Salm (1988)Coles (1996)

Disjunct distributions of many genera and species contribute to the differences in species numbers within the Gulf indicated above. Species of the acroporid genus *Montipora* and the poritid genus *Goniopora* are quite common in the waters of the northern Gulf from Saudi Arabia to Kuwait but are not reported from along the coast of the UAE. Nor has any fungiid genus or species been reported along the UAE coast although fungiids rarely have been found further north (Burchard, 1979; Hodgson and Carpenter, 1995). By contrast, Reigl (1999) found two new *Acropora*, three *Porites* and three faviid species not previously reported in the Gulf off Dubai in the UAE. Surprisingly for an area so isolated, only three endemic coral species have been listed for the Arabian Gulf, *Acropora arabensis* Hodgson and Carpenter, 1995, *Acropora* *downingi* Wallace, 1999 and *Porites harrisoni* Veron, 2000, which is the finger *Porites* common in the Arabian region that was formerly called *Porites compressa*. Two endemic species have been listed for the Gulf of Oman. *Acanthastrea maxima* Sheppard and Salm, 1988 was first collected from the Gulf of Oman and has since been found in the northern Gulf off Kuwait (Hodgson and Carpenter, 1995; Carpenter et al., 1997). *Parasimplastrea simplicitexta,* previously considered to be a newly discovered "living fossil" (Sheppard and Salm, 1988; Coles, 1996), has also recently been renamed *Parasimplastrea sheppardi* Veron, 2000.

POTENTIAL CAUSES OF LIMITED GULF CORAL DIVERSITY

With only about 10% of Indo-Pacific coral species occurring in the Arabian Gulf, some combination of factors has limited the recruitment, settlement, survival and growth of reef corals in the region, eliminating many species and perhaps favoring a few that are adapted to the uniquely harsh conditions of the Gulf. Potential limiting factors include:

- temperature extremes above and/or below usual coral tolerance limits
- high salinities
- macroalgal competition
- past and present isolation of the Arabian Gulf from the Indo-Pacific
- oil production and pollution

Dealing with these in reverse order, there is little indication that oil production and pollution have substantially impacted corals resident in the Gulf region despite the vast production and transport of petroleum that has been underway for over 50 years. During the last two decades two extensive oil spills have occurred in the northern Arabian Gulf without apparent effect on reef corals in the area. The bombing of the Nowruz oil platforms in 1983 during the Iran-Iraq war caused the release of an estimated 500,000 barrels into the northern Gulf (Linden et al., 1990), one of the largest spills that had been recorded up to that time. No impact or change that could be related to this spill was detected by monitoring of reef corals at Jana, Juryad, Karan and Kurayn Islands, Manifa, or Tarut Bay during studies conducted from 1985 to 1987 (Coles et al., 1988). The Nowruz spill was relatively minor compared to the release of over 10 million barrels of oil from three oil terminals and a number of tankers near Mina al-Ahmadi, Kuwait in January 1991 at the end of the Gulf War (Sadiq and McCain, 1993). No indication of oil pollution or impact on corals from this series of oil spills was detected on reef surveys around three islands off the coast of Kuwait in July 1991 (Downing, 1991, 1992), off Saudi Arabia in December 1991-January 1992 (Jones and Richmond, 1992; McCain et al., 1992), or on reefs from Bahrain to Kuwait in May 1992 (Fadlallah et al., 1993). Raw petroleum's most toxic low molecular weight compounds rapidly evaporate to the atmosphere and impacts of oil slicks act primarily at the water surface, where the major impact on corals would be on coral planulae before settlement. It is likely that oil spills are less toxic to adult corals in the Gulf than usually assumed, unless the oil contamination is continuous (Guzman et al., 1991; Loya, 1975) or is brought into direct contact with coral surfaces (Johannes et al., 1972).

The entrance to the Gulf at the Strait of Hormuz is only about 50 km wide, restricting circulation of water to the Gulf from the Arabian Sea. During the last glacial period at about 17,000 years ago sea level lowering reduced water in the Gulf to a minimum and it was largely a dry basin with only a small area of sea water extending in from the Gulf of Oman (Sheppard et al., 1992). All coral settlement and growth in the Gulf therefore has occurred since the beginning of the present interglacial period about 15,000 years ago. However, it is unlikely that isolation has been a primary determinant of the limited species diversity in the Arabian Gulf since the same or even greater isolation has occurred in the Red Sea. Sheppard and Sheppard (1991) report over 180 species of corals to occur in the Red Sea where coral species diversity is the highest of any area in the western Indian Ocean (Veron, 1993). Since the Red Sea has a sill at its entrance, it is likely that it was cut off from the Indian Ocean during the last glacial period and became hypersaline, prohibiting coral survival until sea level rose high enough to allow free exchange of seawater (Sheppard et al., 1992). Although seasonal northward blowing winds drive surface water into the Red Sea more than is the case for the Gulf, surface circulation in both water bodies is primarily driven by excess net evaporation over precipitation which results in net inflow of surface water for both. The resulting turnover time is approximately 3 to 5.5 years in the Gulf compared to about 200 years for the Red Sea (Sheppard et al., 1992), probably due to the much lower total volume of the Gulf. This indicates that the Arabian Gulf has ample exchange with the Indian Ocean via the Gulf of Oman, and that the much more limited diversity of corals within the Gulf is probably due to factors other than isolation.

Competition with macroalgae has been proposed to be a primary limiting factor to reef corals on high latitude reefs (Johannes et al., 1983) that may exceed in importance the restrictive influences of low temperatures. Seasonal blooms of macroalgae which dominate reef surfaces do occur during the winter in the Arabian Gulf (McCain et al., 1984; Coles, 1988; Coles and Fadlallah, 1991) and along the coast of Oman from Dhofar to Ras al Hadd during summer upwelling when water temperatures reach 18°C or lower (Sheppard et al., 1992). In the northern Arabian Gulf winter extensive growths of macroalgae such as *Sargassum* and *Colpomenia* may proliferate and overgrow corals to the point that the coral surfaces are invisible from above (McCain et al., 1984; Coles, 1988; Sheppard et al, 1992). After return of summer temperatures starting in April, the algae rapidly disintegrate and disappear, leaving reef corals, primarily *Porites harrisoni,* with no apparent tissue damage as the dominant benthic form. Live coral coverage was not negatively affected by seasonal algal overgrowth during monitoring from 1985 to 1987 when total coral coverage ranged up to 75% and algal coverage up to 74% in different seasons (Coles, 1988). A similar phenomenon occurs in coral areas along the southeast Oman coast during summer northeast monsoons, except that the dominant algae are species of *Sargosiopsis zanadini* and the kelp, *Eklonia radiata* which begin appearing in about May during the seasonal low temperatures and high nutrients caused by upwelling. The algae then disappear by October with the after the end of the monsoon (Barratt et al., 1988; Sheppard et al., 1992). Thus seasonal low temperature is likely a primary factor limiting corals through both direct influences on coral life processes, and indirectly through competition by macroalgae, the other dominant potential occupant of the benthic habitat.

The Arabian Gulf, along with the Red Sea and certain areas off Western Australia, is one of the few areas in the world where corals occur in a region of elevated salinity (Coles and Jokiel, 1992). Restriction by the narrow opening of the Strait of Hormuz, high surface evaporation and minimal freshwater inflow other than from the Tigris-Euphrates River result in the salinity of the Arabian Gulf averaging around 42 ppt in open water (John et al., 1990). Salinity further increases going southward along the Saudi Arabian coastline to an average greater than 50 ppt in open water and increases to 70 ppt in bays in the Gulf of Salwah, (Coles and McCain, 1990; John, et al., 1990). The maximum salinity reported to be survived by reef corals along the Saudi Arabian coast is 46 ppt (Coles, 1988), but Kinsman (1964) reported massive *Porites* in Abu Dhabi waters with salinity up to 48 ppt. Sheppard (1988) listed three species of corals surviving salinities of 48-50 ppt off the coast of Bahrain and found a decrease of approximately one species of corals with each ppt increase in salinity from 41-50 ppt.

Table 3. Comparison of coral salinity limits (from Coles 1993).

Location	Ambient Range (°/oo)	Tolerance Range(°/oo)	
		Upper	Lower
Atlantic-Pacific	35-37	40-45	15-20
Arabian Gulf	40-42	47-49	20-23

Corals dominant in the Gulf's high salinity environment have been tested for their upper and lower salinity tolerances and compared with corals from more typically oceanic conditions (Coles, 1988). Twenty-day exposures to salinities above and below ambient levels for *Porites* species in the Arabian Gulf, Hawaii and Florida (Table 3) indicated that the upper salinity tolerance limits of Gulf *Porites* is about 5 °/oo higher than the Porites from Hawaii or Florida. This suggests an upward shift in upper salinity tolerance limits by Gulf corals that corresponds closely to the increased salinity of ambient Gulf water above usual oceanic conditions. These comparisons included one species, previously identified as *Porites compressa* in both Hawaii and the Arabian Gulf (Coles and Fadlallah, 1991; Hodgson and Carpenter, 1995; Coles, 1988, Carpenter et al., 1997), now renamed *Porites harrisoni* in the Gulf and Red Sea regions (Veron, 2000). An attempt to acclimate *P. harrisoni* from the Gulf to higher salinities over a 25-day period did not result in increasing the coral's tolerance above 49 °/oo. However, the lower salinity tolerance limit of this species was experimentally reduced to about the lower tolerance limit of Hawaiian *Porites compressa* by gradually reducing the salinity environment of Arabian *P. harrisoni* over a period of 35 days (Coles, 1988).

These results and observations suggest that the elevated salinity of the Arabian Gulf is an important limiting factor in determining the composition of the resident coral community and that the upper limit for coral survival is about 50 ppt. The decreasing numbers of coral species that occur with increasing salinity and the relatively few species that occur overall suggest that salinity tolerance has been a major factor in limiting the coral species diversity of reef corals within the Gulf.

Table 4. Seawater temperature ranges reported for high latitude coral reefs (from Coles and Fadlallah 1991).

			Temperature (°C)		
Location	Lat.	Long.	Min.	Max.	Range
Saudi Arabia	27° N	50°E	11.4	36.2	24.8
Qatar	25° N	51°E	14.1	36.0	21.9
Abu Dhabi	24° N	54°E	16.0	36.0	20.0
Florida	25° N	80°W	13.3	32.8	19.5
Heron Island	23° S	152°E	16.0	35.0	19.0
Kuwait	29° N	48°E	13.2	31.5	18.3
Japan	35° N	140°E	18.0	29.5	16.5
Abrolhos Is.	29° S	113°E	17.0	28.0	11.0
Midway Is.	28° N	177°W	18.2	28.3	10.6
Gulf of Aqaba	29° N	35°E	20.0	28.0	6.0

In addition to elevated salinity, the temperature environment of the Gulf region presents one of harshest challenges in the world to resident corals. Table 4 indicates regions of high seawater temperature ranges where corals and reefs occur. Locations in the Gulf have the highest ranges with reported values for the Saudi Arabian coastline ranging about 11 to 36°C, or nearly 25°C, and Qatar and Abu Dhabi ranging 20°C or more. By contrast, temperature environments more typical of tropical and subtropical areas are shown in Figure 2. In the tropics, as shown for Enewetak in the Marshall Islands, annual temperature extremes range only about 26-30°C, while in Hawaii, the range is about 21-27°C. Even a difference as small as this between ambient temperature ranges has been shown to result in differences in coral temperature tolerance (Coles et al., 1976) that are closely linked with ambient conditions. Corals at Enewetak survived upper stress temperatures about 2°C higher than congeners in Hawaii, a difference closely corresponding to the 2°C difference in summer ambient sea temperatures between the two areas. In both areas, continuous increments of 1-2°C above ambient annual maximum temperature induced loss of zooxanthellae and pigmentation (bleaching), and 3-4°C above annual ambient maximum was lethal after exposure of a few days.

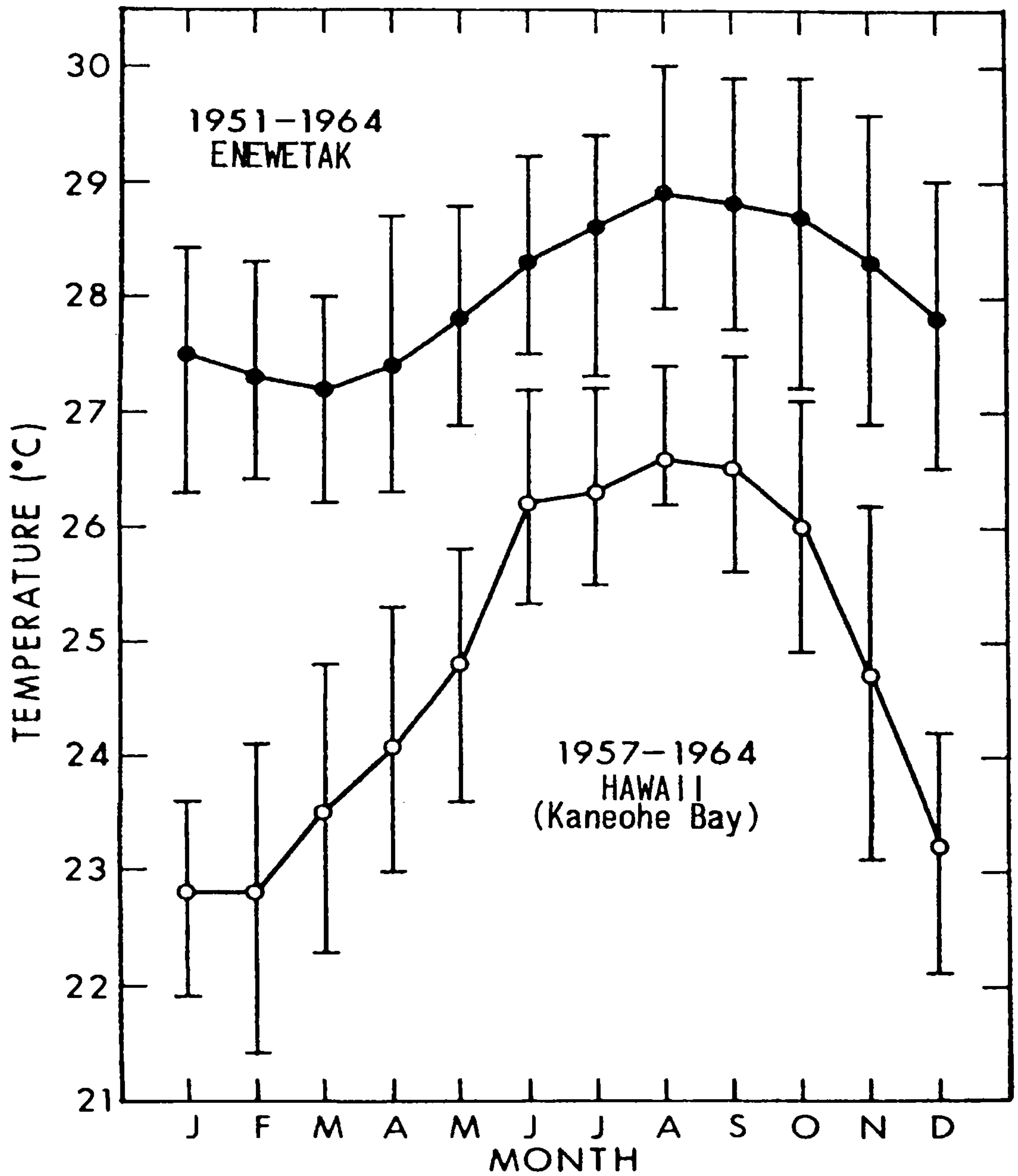

Figure 2. Annual seawater temperatures for Kaneohe Bay, Oahu, Hawaii and Enewetak Atoll, Marshall Islands. Bars indicate upper and lower monthly mean maxima and minima (from Coles et al., 1976).

In contrast to upper temperature limits of 29 to 31°C that apply to corals in most tropical and subtropical regions, reef corals in the Arabian Gulf routinely live in summer temperatures of 32-33°C and may survive up to 35°C for limited periods of time. Kinsman (1964) reported annual water temperatures of up to 40°C at Abu Dhabi where corals occurred and where dominated by *Acropora*, normally considered a temperature sensitive genus. Coles (1988) reported temperatures in Tarut Bay, Saudi Arabia of up to 35-36°C without visible effects on corals, and Sheppard (1988) reported August temperatures over 35°C where *Porites harrisoni (*listed as *P. nodifera)* thrives and forms reefs off Bahrain. Subsequent observers in the Gulf have extended these observations to continuous measurements which indicate that the maximum temperature that can be tolerated by corals in the Gulf for any substantial period of time is around 35°C. Temperatures exceeding 35°C along Saudi Arabia (Fadlallah and Lindo, in Wilkinson, 1998), Bahrain (Uwate in Wilkinson, 1998; Wilkinson, 2000), and the UAE (George and John, 1999; Riegl, 1999) for weeks in 1996 and 1998 resulted in extensive bleaching of all coral species, followed by death of table *Acropora* and recovery of *Porites* species.

Remarkably, temperature tolerance has been extended at the lower end of the tolerance range for corals in the Arabian Gulf as well, probably through adaptation to periodic cold exposures. Annual temperatures do not normally drop below 26°C in the tropics and 21°C in the subtropics (Figure 2) and coral reefs have been traditionally considered to be restricted from areas where temperatures decrease below 18°C. A lower temperature limit of 18°C for coral feeding has long been considered to restrict long term coral survival (Mayer, 1915; Edmondson, 1928), and more recent studies have indicated that corals in Hawaii survive only two weeks below 18°C (Jokiel and Coles, 1977) and that metabolic activity for Australian corals ceases below this temperature (Crossland, 1984).

Corals in the Arabian Gulf withstand temperatures well below these traditionally accepted lower limits for extended periods. Shinn (1976) observed substantial recovery of *Acropora* off Qatar two-and-a-half years after temperatures estimated at 13°C killed all corals in the area. Downing (1985) stated temperatures below 15°C as likely to be encountered in coral areas off Kuwait over several days or weeks, and temperatures at Kubbar (Island) to be as low as 13.2°C (Downing, 1992). Figure 3 shows the

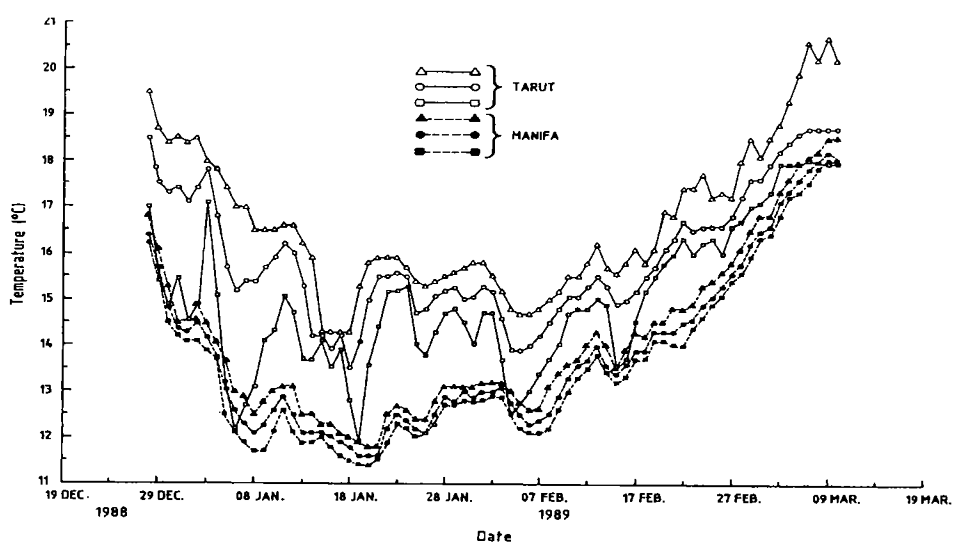

Figure 3. Daily mean, maximum and minimum temperatures based on hourly averages at Manifa (2 m) and Tarut Bay (1 m), Saudi Arabia December 1988 – March 1989 (from Coles and Fadlallah, 1991).

seawater temperatures that occurred on reefs of Saudi Arabia during a cold event in December 1988 to March 1989 when mean daily temperatures were as low as 13-14°C (Coles and Fadlallah, 1991). Minimum daily temperatures at fell below 11.5°C at 2.5 m depth on four consecutive days the northern site (Manifa) and below 12.5°C at 1.5 m depth at the southern site (Tarut Bay). Temperatures did not rise above 16°C for 62 days at the Manifa site or for 35 days at the Tarut Bay site. Only nominal stress symptoms and no mortality were observed for corals at the Tarut Bay reef. In contrast, extensive mortality occurred at the Manifa reef, where all *Acropora* and most *Platygyra* corals were killed and *Porites* species showed pronounced stress symptoms with loss of zooxanthellar pigment and sloughing of surface tissue. However, recovery of this species was evident by April and *Porites* corals appeared normal by September. *Platygyra* and faviid corals that had apparently lost all their coral tissue were found to have areas of regrowth along their bases, but no recovery of *Acropora* was indicated.

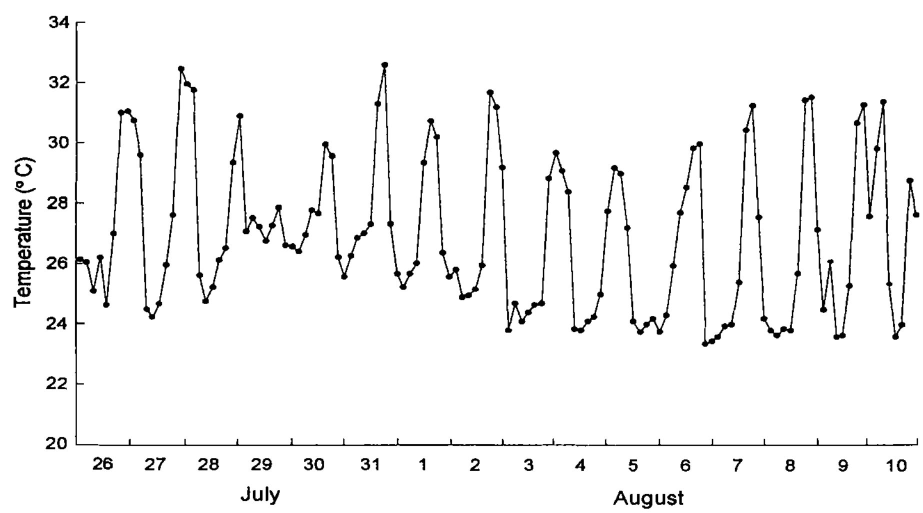

Figure 4. Bottom temperatures at three-hour intervals at 10 m depth off Fahal Island, Oman, July - August 1992 (from Coles, 1997).

Another unique and interesting temperature environment occurs in the Gulf of Oman, which is influenced by upwelling from the Arabian Sea south of Ras al Hadd. Along the southeastern Oman coast directly exposed to upwelling, temperatures decrease between May and September to 18°C or lower and macroalgae growth competes with reef corals for bottom cover as previously described. Gyres of this cold water sweep into the Gulf of Oman where the cold water becomes covered with sun-heated surface water of 30°C or more and a steep shallow thermocline is formed at around 5 to 10 m depth. Under tidal and current influences, both water masses can reach corals in this depth range within a few hours, exposing them to rapid temperature fluctuations of up to 6 to 8°C in 24 hours (Quinn and Johnson, 1996; Coles, 1997) off Fahal Island in the Muscat Capital Area. Overall, bottom temperatures ranged 7°C or more on 14 of 163 days sampled June through August in 1992 and 1994 (Figure 4). No stress symptoms were observed for the abundant and diverse coral community that lives in this area (Coles, 1997), and quantitative measurements along transects showed no significant changes in coral abundances or species composition from this highly fluctuating temperature environment (Coles, unpublished data).

These findings indicate that exposure to temperature and salinity extremes characteristic of the Gulf region is selective for varieties and species of corals that are adapted to the conditions that are unique for this area. The most unusual aspect of this adaptation is that coral temperature tolerances have apparently been extended at both the upper and lower limits of the normal temperature tolerance range.

GULF CORALS AND INDO-PACIFIC CORAL BLEACHING

During the last 20 years, there have been repeated instances of coral bleaching and mortality over extensive areas of coral reefs throughout the world. First noted on a large scale in 1982 in the eastern Pacific (Glynn, 1983, 1984) and the Great Barrier Reef (Oliver, 1985), coral bleaching reports have increased, correlating with occurrences of the El Ni o Southern Oscillation (ENSO) (Glynn, 1993b; Hoegh-Guldberg, 1999; Wilkinson et al., 1999; Wilkinson, 2000) and associated increases in water temperatures above normal ambient maxima (Jokiel and Coles, 1990; Brown, 1997a). A major concern is that El Ni o events may be increasing in both strength and frequency above a increasing temperature baseline, causing frequent coral bleaching and damage and resulting in permanent alteration or elimination of coral dominated reefs throughout much of the Indo-Pacific (Hoegh-Guldberg, 1999).

The 1998 El Ni o bleaching event was the most extensive and severe that has been recorded, with large areas of bleaching and subsequent death of corals occurring on the Great Barrier Reef, Palau, Tahiti, Samoa and throughout the East Pacific, Southeast Asia, the Indian Ocean and the Arabian Gulf (Wilkinson, 1998, 2000; Carriquiry et al., 2001; Glynn et al., 2001; Jimenez et al., 2001). Along with El Ni o events is a long-term trend of increasing ambient water temperatures, and some computer model projections have suggested that the temperature stresses thus far associated with El Ni o years will become ambient maxima within 30 years, exceeding presently recognized temperature tolerance limits annually (Hoegh-Guldberg, 1999). Coral bleaching and mortality during this event was especially severe within the Indian Ocean in areas outside of the Arabian Peninsula where temperature elevations above long term mean maxima reached as high as 2.5°C and were >1°C for up to 7 months (Spencer et al, 2000). This produced coral bleaching up to 100% and mortality up to 95% in the Maldives, Seychelles, Chagos Archipelago and Kenyan Coast. In the year after the 1998 bleaching event in the Indian Ocean McClanahan, *et al.* (2001) found a 75-85% decrease in hard and soft corals on Kenyan reefs and 88-220% increases in turf and fleshy algae. Sheppard et al. (2002) reported near total mortality to 15 depth in the northern atolls and to >35m depth in the southern atolls of the Chagos Archipelago, followed by substantial bioerosion of the dead colonies. Interestingly, both Spencer et al. (2000) and Sheppard et al. (2002) reported that corals in lagoon sites and areas of restricted circulation showed less bleaching and survived better than those on seaward slopes, suggesting local adaptation by corals more routinely exposed to warmer temperatures in shallow areas.

In contrast to the extensive mortality that occurred in the open Indian Ocean, little to no coral bleaching and mortality resulted during the 1998 El Ni o along the Arabian Sea coast of Oman or in the Gulf Oman. In southern Oman up to 95% of the more sensitive coral species showed some bleaching near Mirbat, but no mortality followed (Wilson and Claereboudt, in press). No bleaching occurred further north on the Arabian Sea coast, nor in the Gulf of Oman, where Wilson and Claereboudt, (in press) reported that surface temperatures of 30-32°C occurred from mid-April to December 1998. The onset of upwelling from the summer monsoon probably helped prevent higher seawater temperatures from inducing coral bleaching, but previous short-term exposures to temperatures such as was reported for 1990 to be as high as 39°C (Salm, 1993) may have induced acclimatization or selective adaptation for thermal tolerant corals.

If the upper temperature tolerances of corals are fixed limits and the projected trends in water temperatures do occur, we may be facing a potential demise of coral as a major biotope and constructor of reefs in the lower latitudes of the tropics. Coral bleaching has consistently occurred where normal summer sea temperatures have exceeded ambient by 1-2°C for more than a few days (Hoegh-Guldberg, 1999) and coral mortality has followed where these elevated temperatures have persisted for weeks. This has meant a bleaching and mortality threshold of around 30°C for most of the tropics. However, both experimental studies and temperature information for the Arabian region suggest that upper temperature limits are not fixed, but rather related to the thermal history of the area where they occur. Thus Gulf region corals, while tolerating long-term normal summer temperatures up to 33°C that would be lethal to corals elsewhere in the Pacific, but still show bleaching and mortality when temperatures reach 35°C or above for days to weeks (Salm, 1993; George and John, 1999; Riegl, 1999).

Given the low diversity of corals in the Gulf relative to the Indo-Pacific, it appears that comparatively few species have adapted to the harshness of the conditions there, and that not all corals will have the capacity to adapt to the increasing water temperatures projected for the next half century. Whether such adaptation can happen at all will depend on the rapidity with which temperature increases occur compared to the corals' genetic and physiological capabilities to adjust to this environmental challenge. One viewpoint is skeptical: "...Present evidence...suggests that corals and their zooxanthellae are unable to acclimate or adapt fast enough to keep pace with the rapid rate of warming of tropical oceans" (Hoegh-Guldberg, 1999). Direct experimental evidence of coral capability for short-term acclimation is limited to results from a single study (Coles and Jokiel, 1978; Brown, 1997b) and more research is needed on this important issue. However, evidence for the existence of adaptive processes in corals and zooxanthellae is ample, as reviewed by Brown (1997b) who concluded: "It is also possible that bleaching may be a damage-limitation process which permits corals to withstand stressful periods while harbouring a reduced zooxanthellae population....On a geological time scale, corals have shown themselves capable of colonizing extreme environments such as the Arabian Gulf where rigorous physical conditions have...demanded the evolution of particular genetic strains of both the coral hosts and their zooxanthellae."

As we enter a new era of environmental challenges for the survival of corals and coral reefs, the survival of this biotope through millennia of stressful conditions in the Arabian Gulf perhaps provides some hope that sufficient adaptation can occur to moderate the worst impacts of projected temperature elevations.

ACKNOWLEDGMENTS

This review is based upon a presentation by the author at the Second Arab International Conference and Exhibition on Environmental Biotechnology in Abu Dhabi, April 8-12, 2000. Appreciation is extended to the Emirates Heritage Club of Abu Dhabi for the invitation and support to attend the conference. Special thanks to Drs. Peter Glynn, Charles Sheppard and Lu Eldredge for review and comments on the manuscript.

REFERENCES

Barratt, L., R. F. G. Ormond and T. J. Wrathall
1988. *Ecology and productivity of the sublittoral algae Ecklonia radiata and Sargassiopsis zanadini. Ecological Studies of Southern Oman Kelp Communities.* Summary report, ROPME/GC-6/001, Regional Organization for the Protection of the Marine Environment, Kuwait.

Brown, B. E.
1997a. Coral bleaching: causes and consequences. *Coral Reefs* 16: S129-S138.

Brown, B .E.
1997b. Adaptations of reef corals to physical environmental stress. *Advances in Marine Biology* 31: 222-299.

Brown, B. E., R. P. Dunne, M. S. Goodson and A. E. Douglas
2000. Bleaching patterns in reef corals. *Nature* 404: 142-143.

Burchard, J. E.
1979. *Coral fauna of the Arabian Gulf.* Unpublished report., ARAMCO Environmental Affairs Division, Dhahran, Saudi Arabia.

Cairns, S. D.
1999. Species richness of recent Scleractinia. *Atoll Research Bulletin* No. 459: 1-46.
Carriquiry, J. D., A. L. Cupul-Magana, F. Rodriguez-Zaragoza and P. Medina-Rosas
2001. Coral bleaching and mortality in the Mexican pacific during the 1997-98 El Ni o and prediction from a remote sensing approach. *Bull. Mar. Sci.* 69: 237-249.
Carpenter, K. E., P. L. Harrison, G. Hodgson, A. H. Alsaffar and S. H. Alhazeem
1997. *The Corals and Coral Reef Fishes of Kuwait.* Kuwait Institute of Scientific Research, Kuwait City, 166 pp.
Coles, S. L.
1988. Limitations on reef coral development in the Arabian Gulf: temperature or algal competition. *Proceedings of the 6th International Coral Reef Symposium, Australia* 3: 211-216.
Coles, S. L.
1993. Experimental comparison of salinity tolerances of reef corals from the Arabian Gulf and Hawaii. Evidence for hyperhaline adaptation. *Proc. of the 7th Intern. Coral Reef Symp., Guam,* 1: 227-234.
Coles, S. L.
1996. *Corals of Oman.* R. Keech, Thornes, Hawes, North Yorkshire, 106 pp.
Coles, S. L.
1997. Reef corals occurring in a highly fluctuating temperature environment at Fahal Island, Gulf of Oman (Indian Ocean). *Coral Reefs* 16: 269-272.
Coles, S. L. and Y.H. Fadlallah
1991. Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9: 231-237.
Coles, S. L. and P. L. Jokiel
1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa. Marine Biology* 49: 187-195.
Coles, S. L. and P. L. Jokiel
1992. Effects of salinity on coral reefs. In: D.W. Connell and D. H. Hawker (Editors), Pollution in Tropical Aquatic Systems. CRC Press, Cleveland, pp. 2-25.
Coles, S. L., P. L. Jokiel and C .R. Lewis
1976. Thermal tolerance in tropical versus subtropical Pacific reef corals. *Pacific Science* 30: 159-166.
Coles, S. L. and J. C. McCain
1990. Environmental factors affecting benthic infaunal communities of the Western Arabian Gulf. *Mar. Environ. Res.* 29: 289-315.
Coles, S. L. and A. B. Tarr
1991. Reef fish assemblages in the western Arabian Gulf: a geographically isolated population in an extreme environment. *Bull. Mar. Sci.* 47: 696-720.
Coles, S. L., A. B. Tarr and Y. Fadlallah
1988. *Final Report, Marine Monitoring and Baseline Survey, Vol. 3. Coral Reef Studies*, Prepared for the Saudi Arabian Meteorological and Environmental Protection Agency (MEPA), Jeddah, and the Regional Organization for the Protection of the Marine Environment (ROPME), Kuwait.

Crossland, C .J.
1984. S easonal v ariations i n t he r ates o f c alcification a nd p roductivity i n t he c oral *Acropora formosa* on a high-latitude reef. *Marine ecology-progress series* 15: 135-140.

Dana, J. D.
1843. On the temperature limiting the distribution of corals. *Amer. J. Sci.* 45: 130-131.

Dana, J. D.
1872. *Corals and Coral Islands.* Dodd and Mead Co., New York, New York, New York, 398 pp.

Downing, N.
1985. Coral reef communities in an extreme environment: the Northwestern Arabian Gulf. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 6: 343-348.

Downing, N.
1991. A survey of the islands of Kubbar, Qaru and Umm at Maradem, Kuwait, 13-19 July 1991. IUCN and WWF, Gland.

Downing, N.
1993. Kuwait's coral reefs: what future after the Gulf War? *Proc. 7th Intern. Coral Reef Symp., Guam* 2: 959-968.

Edmondson, C. H.
1928. *The ecology of an Hawaiian coral reef.* Bernice Bishop Mus. Bull., 45, Honolulu, Hawaii, 64 pp.

Fadlallah, Y. H, C. M Eakin, K. W. Allen, R. A. Rahim, M. Reaka-Kudla and S. A. Earle
1992. Reef coral distribution and reproduction, community structure, and reef health (Qatar, Bahrain, Saudi Arabia, Kuwait):results of the R/V Mt. Mitchell Cruise, May 1992, Proc. Sci. Workshop on the results of the Mt. Mitchell cruise in the ROPME Sea Area, Kuwait, January 1993, Kuwait City, pp. 2-25.

George, D. and D. John
1998. High sea temperatures along the coast of Abu Dhabi (UAE), Arabian Gulf - their impact upon corals and macroalgae. *Reef Encounter* 25: 21-23.

Glynn, P. W.
1983. Extensive 'bleaching' and death of reef corals on the Pacific coast of Panama. *Environmental Conservation* 10: 149-153.

Glynn, P. W.
1984. Widespread coral mortality and the 1982-83 El Ni o warming event. *Environmental Conservation* 11: 133-146.

Glynn, P. W.
1993a. Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Research Bulletin* 379, 66.

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

Glynn, P. W., J. L. Mate, A. C. Baker and M. O. Calderon
2001. Coral bleaching and mortality in Panama and Equador during the 1997-98 El Ni o Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. *Bull. Mar. Sci.* 69: 79-109.

Guzman, H. M., J. B. C. Jackson and E. Weil
1991. Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* 10: 1-12.

Hodgson, G. and K. Carpenter
1995. Scleractinian corals of Kuwait. *Pacific Science* 49: 227-246.

Hoegh-Guldberg, O.
1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshwater Res.* 50: 839-66.

Jimenez, C., J. Cortes, A. Leon and E. Ruiz
2001. Coral bleaching and mortality associated with the 1997-98 El Ni o in an upwelling environment in the eastern Pacific (Gulf of Papagyo, Costa Rica). *Bull. Mar. Sci.* 69: 151-169.

Johannes, R. E., J. E. Maragos and S. L. Coles
1972. Oil damages corals exposed to air. *Mar. Poll. Bull.* 3: 29-30.

Johannes, R. E., W. J. Wiebe, C. J. Crossland, D. W. Rimmer and S. V. Smith
1983. Latitudinal limits of coral reef growth. *Marine Ecology-Progress Series* 11: 105-111.

John, V. C., S. L. Coles and A. I. Abozed
1990. Seasonal cycles oif temperature, salinity and water masses of the Western Arabian Gulf. *Oceanologica Acta* 13: 273-281.

Jokiel, P. L. and S. L. Coles
1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* 43: 201-208.

Jokiel, P. L. and S. L. Coles
1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8: 155-162.

Kinsman, D. J. J.
1964. Reef coral tolerance of high temperatures and salinities. *Nature* 202: 1280-1282.

LeGore, R. S. and J. E. Hoffman
1983. A field experiment to assess impact of chemically dispersed oil on Arabian Gulf corals. *Proc. Middle East Tech. Conf. Soc. Petroleum Engineers, Mar 14-17,* SPE 11444: 51-57.

Linden, O.
1990. *State of the marine environment in the ROPME Sea area.* UNEP Regional Seas Reports and Studies 112, Nairobi.

Loya, Y.
1975. Possible effects of water pollution on the community structure of Red Sea corals. *Marine Biology* 29: 177-185.

Mayer, A. G.

1914. The effects of temperature on tropical marine animals. *Carnegie Inst. Washington Publ.* 183: 3-24.

Mayer, A. G.

1915. The lower temperature at which reef corals lose their ability to to capture food. *Carnegie Inst. Wash. Year Book* 14: 212.

McCain, J. C., K. E. Carpenter, B. Tarr and S. L. Coles

1984. A survey of the coral reefs and reef fishes in the Northern Area, Arabian Gulf, Saudi Arabia. *Marine Fauna of Saudi Arabia* 6: 102-136.

McCain, J. C., M. Sadiq, A. Al Rabeh, N. Fayad and Y. H. Fadlallah

1992. The impact of the 1991 Gulf oil spill on the coastline of Saudi Arabia. *Proc. Third World Acad. Sciences Fourth General Conference, Kuwait 23-26 November 1992.*

McClanahan, T. R., N. A. Muthiga and S. Mangi

2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19: 380-391.

Oliver, J.

1985. Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 4: 201-206.

Quinn, N. J. and D. W. Johnson

1996. Cold water upwellings cover Gulf of Oman coral reefs. *Coral Reefs* 15: 214.

Riegl, B.

1999. Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. *Coral Reefs* 18: 63-73.

Sadiq, M. and J. C. McCain

1993. *The Gulf War Aftermath. An Environmental Tragedy.* Kluwer Academic Publishers, Dordecht, Netherlands, 296 pp.

Salih, A., A. Larkum, G. Cox, M. Kuhl and O. Hoegh-Guldberg

2000. Fluorescent pigments in corals are photoprotective. *Nature* 408: 850-853.

Salm, R.

1993. Coral reefs of the Sultanate of Oman, *Atoll Res. Bull.*, pp. 1-84.

Sheppard, C. R. C.

1987. Coral species of the Indian Ocean and adjacent seas: a synonymized compilation and some regional distributional patterns. *Atoll Res. Bull.* 307: 1-31.

Sheppard, C. R. C.

1988. Similar trends, different causes: responses of corals to stressed environments in Arabian Seas. *Proceedings of the 6th International Coral Reef Symposium, Australia, 1988* 3: 297-302.

Sheppard, C. R. C., A. Price and C. Roberts

1992. *Marine Ecology of the Arabian Region. Patterns and processes in extreme tropical environments.* Academic Press, London, 347 pp.

Sheppard, C. R. C., M. Spalding, C. Bradshaw and S. Wilson
2002. Erosion vs. recovery of coral reefs after 1998. El Ni o: Chagos Reefs, Indian Ocean. *Ambio* 30:40-48
Shinn, E. A.
1976. Coral reef recovery in Florida and the Persian Gulf. *Environmental Geology* 1: 241-254.
Spencer, T., K. Teleki, C. Bradshaw and M. Spalding
1998. Coral bleaching in the southern Seychelles during the 1997-199 Indian Ocean warm event. *Mar Poll. Bull.* 40: 569-586
Vaughan, T. W.
1916. The results of investigation of the ecology of the Floridian and Bahaman shoal-water corals. *Proc. Nat. Acad. Sci.* 2: 95-100.
Vaughan, T. W.
1918. The temperature of the Florida coral-reef tract. *Carnegie Inst. Wash. (Papers Tortugas Lab. vol. ix)* 31: 321-339.
Veron, J. E.
1993. A biogeographic database of hermatypic corals. *Aust. Inst. Mar. Sci. Ser.* 10: 39.
Wallace, C. C.
1999. *Staghorn Corals of the World.* CSIRO Publications, Melbourne.
Wells, J. W.
1957. Coral reefs. In: J. Hedgepeth (Editor), Treatise on Marine Ecology and Paleontology. *Geolog. Soc. Am. Mem.* 67, pp. 609-632.
Wilkinson, C.,
1998. *Status of coral reefs of the world: 1998.*
Wilkinson, C.
2000. *Status of coral reefs of the world: 2000.* A.I.M.S., Townsville, 363 pp.
Wilkinson, C., O. Linden, H. Cesar, G. Hodgson, J. Rubens and A. E. Strong.
1998. Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: an ENSO impact and a warning of future change? *Ambio*: 188-196.
Wilson, S. C. and M. Claereboudt
In press. Seawater temperatures and bleaching events in Oman. *Proceedings of the International workshop on the extent and impact of coral bleaching in the Arabian region*, Riyadh, Feb. 5-9 2000.