11. Responses of Coral Reefs to El Niño–Southern Oscillation Sea-Warming Events

Gerard M. Wellington and Peter W. Glynn

11.1 Introduction

Prior to Chesher's (1969) stunning prediction that the corallivorous sea star, *Acanthaster planci*, could spell the initial phases of extinction of reef-building corals in the Pacific Ocean, coral reefs were regarded as highly stable and resilient ecosystems in near equilibrium with their physical and biotic environmental controls (e.g., Odum and Odum 1955; Wells 1957; Margalef 1968). Widespread outbreaks of *A. planci* and resulting coral mortality over the Indo-Pacific region have caused considerable alarm, and although the causes of these outbreaks are still unknown, some workers link them to favorable conditions in the water column promoting larval survival followed by heavy settlement and high recruitment (Birkeland and Lucas 1990). The effects of this predator are still a significant management problem in many areas (Wilkinson 1990; Wilkinson and Macintyre 1992; DeVantier and Done, Chapter 4), but concerns about *A. planci* disturbances have been increasingly supplanted by concerns about other global-scale disturbances that are linked to significant coral reef decline, including the deterioration of water quality from runoff (Ginsburg 1994), overfishing (Jackson 1997; Pandolfi et al. 2003), coral diseases (Harvell et al. 1999), and coral bleaching (Glynn 1993; Brown 1997; Wilkinson 2000; Hughes et al. 2003). This essay focuses on coral reef degradation due to coral bleaching, which is considered by many to be the largest threat to coral reef ecosystems (Hoegh-Guldberg 1999; Wilkinson 2002).

Beginning with the very strong 1982 to 1983 El Niño event, and continuing at high frequency through the 1980s, workers became aware of unprecedented coral reef bleaching: the sudden loss of endosymbiotic dinoflagellates that often leads to widespread coral mortality (Glynn 1984, 1990a; Brown 1987; Guzmán et al. 1987; Carriquiry et al. 1988; Williams and Bunkley-Williams 1988, 1990). Similar to the alarm precipitated by *Acanthaster* disturbances of the previous decade, the global coral bleaching and mortality events stimulated widespread concern in the coral reef research community, resulting in workshops, symposium addresses, and special journal publications focusing on this issue (e.g., Ogden and Wicklund 1988; Brown 1990; D'Elia et al. 1991; Buddemeier 1992). Several field and laboratory studies have demonstrated that the majority of these recent coral bleaching and mortality events are caused by elevated seawater temperatures that exceed the stress-response thresholds of temperature- and light-sensitive coral–algal symbioses (Glynn and D'Croz 1990; Jokiel and Coles 1990; Glynn et al. 1992, 2001; Gleason and Wellington 1993; Goreau and Hayes 1994; Rowan et al. 1997; Hoegh-Guldberg 1999; Lough 2000; Berkelmans 2002). A multitude of stressors often associated with sea warming disturbances, either during the event or with some time lag, often exacerbate the already weakened state of corals. These may include increased rainfall, flooding and runoff, reduced cloud cover and wind speed (favoring increased light penetration), sedimentation, pollution, violent storms, intensified upwelling, and sea level lowering during La Niña events. Additionally, several recent studies have demonstrated increasing incidences of epizootics that are often correlated with elevated thermal conditions (Kushmaro et al. 1996; Harvell et al. 1999; Porter 2001). Finally, taking into account predicted sea-level rise and changes in the carbonate mineral saturation state, effects that could interact to reduce calcification rates and reef building (Smith and Buddemeier 1992; Kleypas et al. 1999, 2001; Pittock 1999), it will become necessary to deal with a suite of disturbances affecting coral reefs during global warming.

New and stronger evidence indicates that most of the global warming observed over the last 50 years is attributable to anthropogenic forcings, namely, greenhouse gas and aerosol emissions (compare IPCC 1992, 1996, and 2001). The observed mean sea-surface temperature (estimated subsurface bulk temperature; i.e., the upper few meters depth) has increased from 0.4 to 0.8 °C since the late 19th century. The sea-surface temperature data obtained from 1961 to 1990 show a 0.23 to 0.27 °C warming during this 30-year period. The two warmest years globally were 1998 and 2005, which were the highest observed over an instrumental record beginning in 1880 (Shein 2006). Positive anomalies above the 1961 to 1990 mean were +0.50 °C (1998) and +0.53 °C (2005), the latter in the absence of a strong El Niño signal. The globally averaged surface temperature is projected to increase by 1.4 to 5.8 °C over the period 1990 to 2100 (full range of 35 IPCC emission scenarios based on several climate models). The projected rate of warming is greater than the observed changes during the 20th century and, based on paleoclimate data, is very likely to be without precedent during at least the last 10,000 years (IPCC 2001).

In this chapter we address sea-warming disturbances associated with El Niño–Southern Oscillation (ENSO) events, with a focus on the eastern tropical Pacific and the effects of ENSO disturbances on coral bleaching, mortality, and recovery. While no generally accepted definition of El Niño exists (see Trenberth 1997), historically it refers to local sea warming off coastal Peru. The ENSO phenomenon is more wide-ranging, involving the migration of the south Pacific warm pool across the International Dateline, and causing atmospheric and oceanic perturbations along the entire eastern Pacific as well as the western Atlantic and Indian Oceans. Here we use El Niño and ENSO for local (eastern tropical Pacific) and global effects, respectively. The eastern Pacific region is particularly suited for an assessment of ENSO effects on coral reefs because it experiences a strong warming signal and because a long-term database of the condition of pre- and post-disturbance coral communities is available. Other coral reef areas are also discussed where they provide insight into how the varied effects of sea warming disturbances influence coral reef ecosystems.

11.2 The Nature of ENSO Events

In the marine realm, one of the first and most notable effects of ENSO is a sudden warming of the central to eastern tropical Pacific Ocean. In the eastern Pacific, elevated sea level, thermocline depression, local flooding or drought conditions, and increased storm activity often accompany sea warming. The frequency of ENSO events over the past century is once about every four years, but their onset is erratic, and their intensity, duration, and spatial extent are highly variable (Philander 1990; Enfield 1992; Allan et al. 1996). The atmospheric manifestation of ENSO, the Southern Oscillation, is synchronous with the marine phase and involves linkages between remote climatic perturbations—so-called teleconnections—that can influence all of the world's oceans and continental regions (Riegl, Chapter 10). For example, El Niño warming in the eastern Pacific is usually correlated with: (1) high SSTs in the western equatorial and southwest Pacific (Great Barrier Reef region) about one year before and following an event (Rasmusson and Carpenter 1982; Lough 1994); (2) high SSTs contemporaneously and basin-wide in the Indian Ocean (Baquero-Bernal et al. 2002); and (3) high SSTs in the northwestern tropical Atlantic and Caribbean Sea 4 to 5 months following the eastern Pacific mature phase (Enfield and Mayer 1997).

In terms of ENSO activity, the 1980s and 1990s were unusual in several respects. The two strongest ENSO events in recorded history—1982 to 1983 and 1997 to 1998—occurred only 15 years apart, and during this same time one of the most protracted El Niño warming periods, lasting from 1990 to 1995, was recorded (Trenberth and Hoar 1996). Some workers, however, have concluded that this was not an extended El Niño event, but rather a prolonged warm phase of a Pacific decadal mode of variability (Lau and Weng 1999). The 1982 to 1983 event was touted as the "event of the century" (Cane 1983, 1986; Hansen 1990) and the 1997 to 1998 event was considered comparable or even stronger than the earlier event (McPhaden 1999; Enfield 2001). The warming intervals were comparable during the two events, with each about 14 months in duration. A comparison of SST metrics in the eastern Pacific, in Niño 1 + 2 and Niño 3 zones, shows both SSTs and SSTAs (SST anomalies) rose faster in mid-1997 than in mid-1982 (Fig. 11.1). These data are from an optimally interpolated (OI) analysis of ship, drifter, and satellite measurements produced by the NOAA National Centers for Environmental Prediction (NCEP; Reynolds and Smith 1994). Niño 3 SSTAs also were ~0.5 °C higher in 1997 to 1998 than in 1982 to 1983.

Several regional- to local-scale differences between the 1982 to 1983 and 1997 to 1998 events have been recognized, including diverse physical and biotic characteristics and responses. For example, coral bleaching and mortality associated

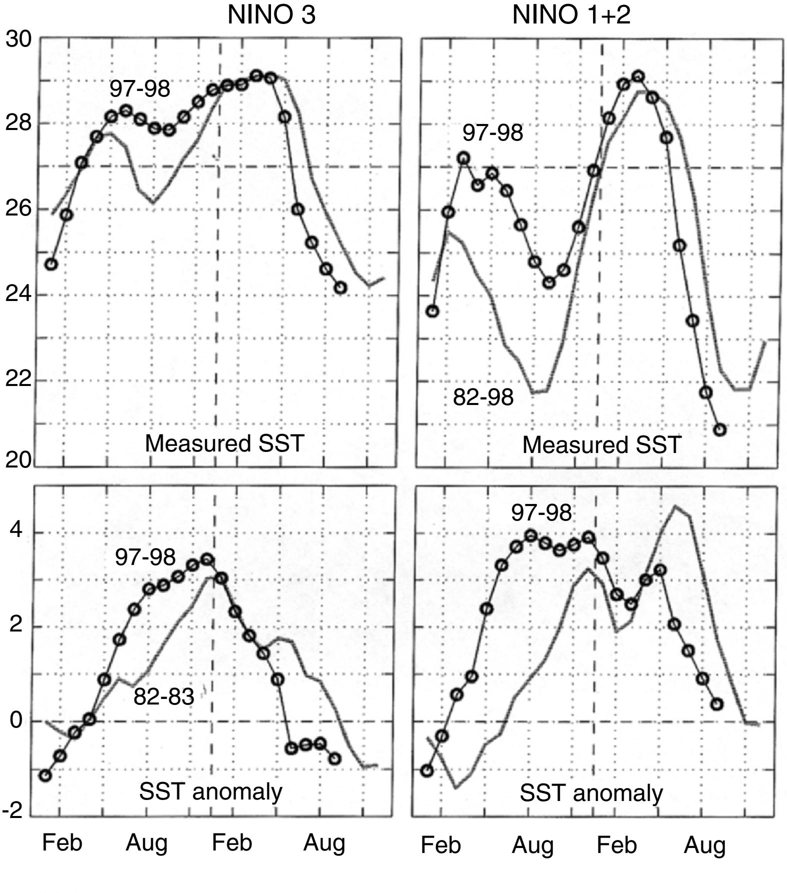

Figure 11.1. Comparisons of SSTs and SSTAs in Niño zones 3 (90°–150°W, 5°N–5°S) and 1+2 (80°–90°W, 0°–10°S) during the 1982 to 1983 and 1997 to 1998 ENSO events. These Niño regions were selected to coincide with historical ship tracks where reliable data were available (Rasmusson and Carpenter 1982). Niño 3 is centered offshore and far to the west along the equator, and Niño 1+2 refers to the region near the South American coast. Horizontal dashed lines are plotted at 27 °C (upper) and 0 °C (lower) for reference. After Enfield (2001).

with ENSO-elevated SSTs in 1982 to 1983 were largely confined to the eastern Pacific, the central and northern sectors of the Great Barrier Reef, the Java Sea, southern Japan, the western Indian Ocean, and the Caribbean Sea and adjacent waters (Glynn 1984; Brown 1987; Coffroth et al. 1990), and included 68 reported bleaching events. In contrast, during the 1997 to 1998 ENSO, frequent and widespread coral bleaching and mortality were reported in all major coral reef regions, totaling 2,070 events (Figs. 11.2A,B, 11.3). Notable newly impacted areas were Belize, Brazil, northeastern Australia, the Philippines, Southeast Asia, south India,

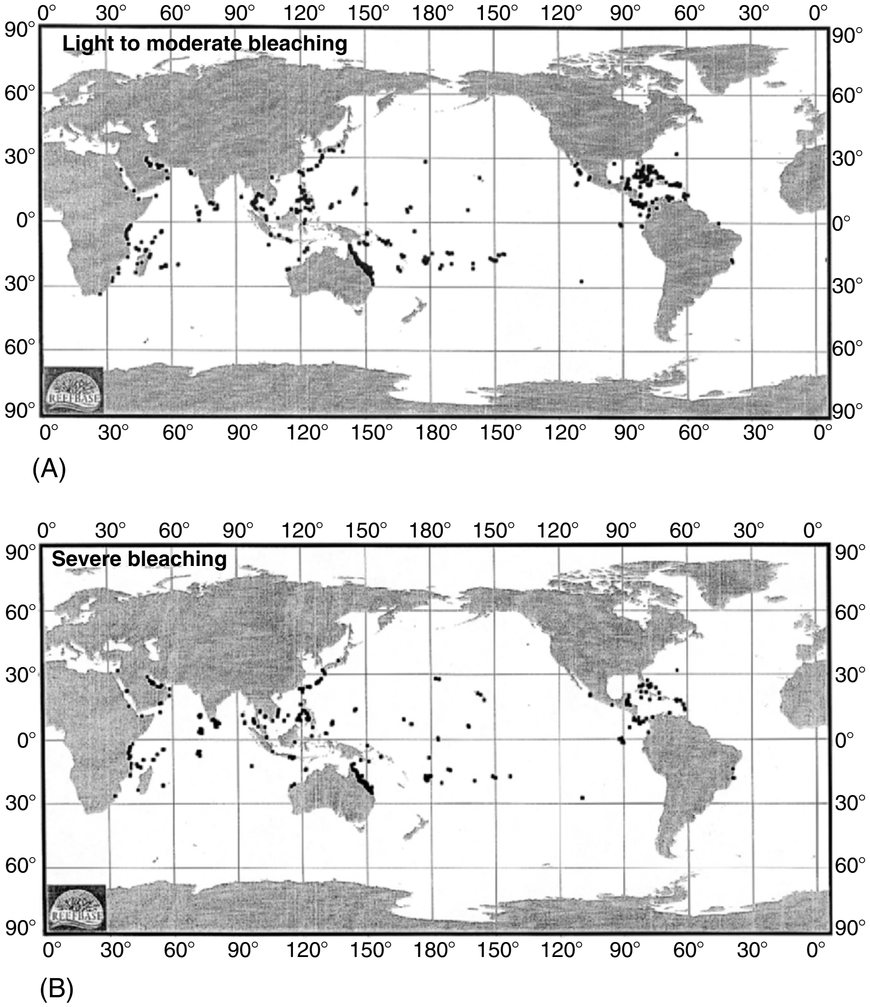

Figure 11.2. Global distribution of all known coral bleaching events (1963–2002). (**A**) Light (<10%) to moderate (10–50%) coral bleaching (n = 1629 events). (**B**) Severe (>50%) coral bleaching (n = 955 events). Map produced on 15 November 2002 from ReefBase (2002).

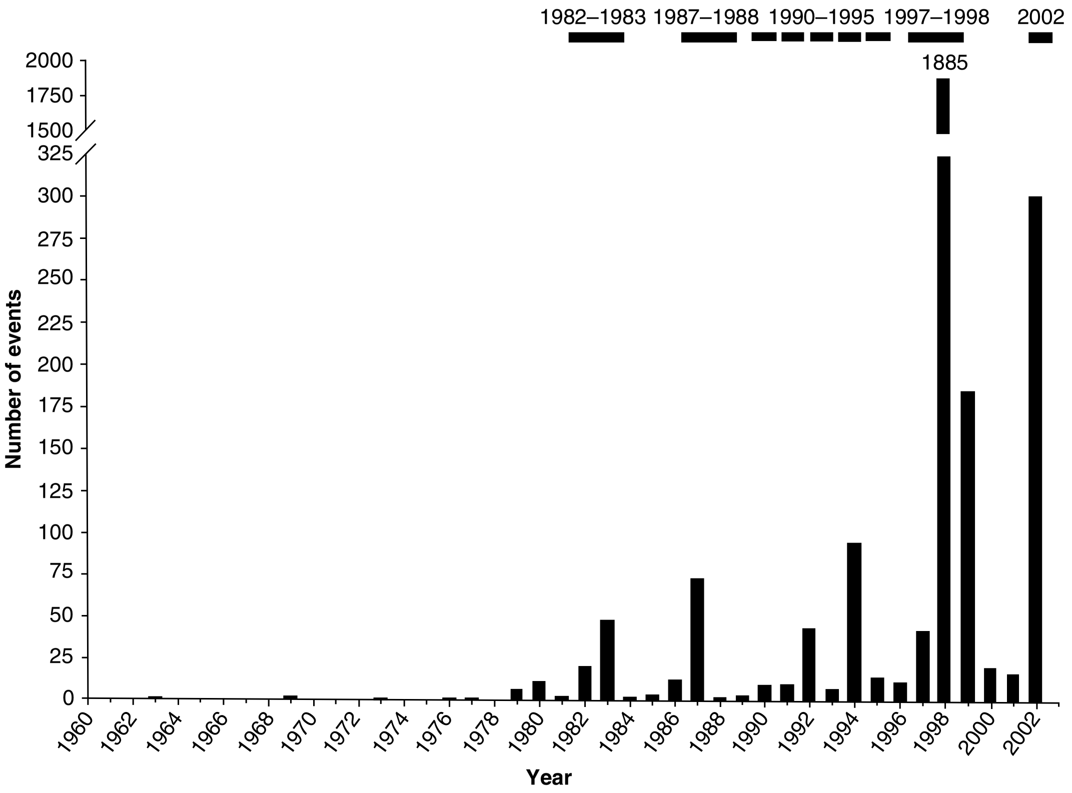

Figure 11.3. The total number of coral reef bleaching observations for each year globally, 1963 to 2002. The 1998 bleaching records (*n* = 1885) are severely truncated. From ReefBase (2002) data set, 10 August 2002. The duration of ENSO events during the 1980s and 1990s is noted above.

the Laccadive and Maldive Islands, continental East Africa, and the Red Sea. The only region where no bleaching was reported is off western tropical Africa, perhaps due to the absence of observers. The latest data available for 2002 indicate the occurrence of 452 coral bleaching events (ReefBase 2002). This was the greatest bleaching year ever reported for the Great Barrier Reef region, and was related to a large thermal anomaly observed by NOAA. The other reports in 2002 may be due to local thermal events more than to any major regional-scale pattern. Some proportion of the large increase in extent and number of reports between the earlier and latter events is certainly due to a greater awareness and documentation in recent years and the use of the Internet to aid transmission and collection of reports.

Given the general similarity of the 1982 to 1983 and 1997 to 1998 El Niño events in the eastern Pacific, we still note some marked local-scale differences between the two disturbances in both occurrence and timing of temperature stressors, and the severity and distribution of coral mortality. An example of one area where corals experienced severe bleaching and mortality in 1982 to 1983 (with overall mean mortality ~90%), and no adverse effects in 1997 to 1998 is the Pearl Islands in the Gulf of Panamá (Table 11.1). Seasonal upwelling typically occurs in the Gulf from late December to about the end of April. Upwelling was largely suppressed in 1983, and coral bleaching/mortality coincided with high maximum SSTs (>30 °C) and high stressful temperature duration (degree days, DD > 400; a "degree-days" index is the combined effect of SST anomalies and their duration; Podestá and Glynn 1997). Upwelling occurred immediately preceding and during the height of El Niño warming in 1998 (Glynn et al. 2001), with maximum SSTs <30 °C and degree days duration <400. Another difference was noted in the Galápagos Islands, which experienced similarly stressful high sea temperatures during 1982 to 1983 and 1997 to 1998. Critically high temperatures persisted in the Galápagos Islands in 1997 to 1998, resulting in coral bleaching and mortality (~24% overall), but of significantly lower magnitude than in 1982 to 1983 (~97%) (Feingold 2001; Podestá and Glynn 2001). The more recent, relatively low coral mortality could be attributed in part to marked semidiurnal temperature fluctuations, ranging from 2 to 4 °C, which occurred at sites where bleaching and mortality were not severe. A third difference probably was related to a respite from elevated sea temperatures in 1997 to 1998. In 1982 to 1983, coral bleaching and mortality occurred more or less continuously over the El Niño period, from 4 to 10 months depending on locality. In 1997 to 1998, two distinct bleaching bouts were detected at three equatorial eastern Pacific sites, each corresponding to local sea-warming pulses. The initial period of elevated temperatures and bleaching occurred over varying time intervals from August to November 1997 in Colombia (Vargas-Ángel et al. 2001), Panamá (Glynn et al. 2001), and Costa Rica (Jiménez et al. 2001). These were followed by 4- to 6-month intervals of lower temperatures, then a return of stressful temperatures from March to August 1998, depending upon locality. These high-temperature pulses were recorded in situ in coral communities, and also were visible as transitory filaments online in NOAA near-real-time weekly animated satellite imagery. In summary, several

Table 11.1. Mean (± SE) coral mortality at various eastern Pacific sites during the 1982 to 1983 and 1997 to 1998 El Niño warming events

Locality	Latitude	Percent mortality		Authority
		1982-83	1997-98	
Ecuadorean Coast	1.0–2.0°S	~ 80[2]	8.1 ±0.6	Glynn et al. (2001)
Galápagos Islands	1.5°S–1.5°N	97.0 ±1.4	24.3 ±1.0	Glynn et al. (2001)
Gorgona Island	3N	>50[3]	<1	Vargas-Ángel et al. (2001)
Malpelo Island	4N	?	<1	Vargas-Ángel et al. (2001)
Cocos Island	5N	96.8	20.4 ± 22.0	Guzmán and Cortés (1992), and unpublished data
Utría-Tebada	6.0–6.5°N	?	<1	Vargas-Ángel et al. (2001)
Gulf of Chiriquí	7.0–8.0°N	76.3 ±6.5	13.2 ±0.5	Glynn et al. (2001)
Gulf of Panamá	7.5–9.0°N	89.9[4] ±4.6	0	Glynn et al. (2001)
Caño Island	9°N	63.4[4] ±7.3	2.7	Guzmán and Cortés (1992)
Costa Rican coast[1]	10.5– 11.0°N	?	5.7	Jiménez et al. (2001)
Huatulco	16°N	?	98.9[6]	Reyes-Bonilla et al. (2002)
Banderas Bay	20°N	?	62.1 ±7.8[7]	Carriquiry et al. (2001)
Baja California	23–25°N	10.2[5] ±4.0	18.2 ±1.8	Reyes-Bonilla (2001)

[1] Three localities were surveyed: Murciélagos Islands, Culebra Bay, and Golfo Dulce.

[2] Based on surveys conducted in 1986, which revealed wholly dead pocilloporid reefs similar to those in the Galápagos Islands that experienced 100% mortality in 1983 (Glynn et al. 2001). Numerous massive corals, contributing relatively little to live coral cover, survived the warming event with varying amounts of partial colony mortality.

[3] According to Prahl (1983, 1985), about 85% of the corals on a Gorgona Island reef were bleached and a few months later most of these were dead and covered with macroalgae.

[4] The percent coral mortalities at two localities in Figure 2 in Glynn et al. (1988) are incorrect and should be emended to 89.9% (from 85%) for the Gulf of Panamá and to 63.4% (from 51%) for Caño Island.

[5] This figure was reported for the 1987 El Niño bleaching event; apparently corals in the southern sector of Baja California were not affected in 1982-83, however, no data are available for this period (Reyes-Bonilla 1993).

[6] This figure is from two reefs surveyed, namely, Tijera and Mazunte reefs.

[7] The 96.0% mean mortality reported in Carriquiry et al. (2001) is for sampling sites at the north end of Banderas Bay. The 62.1% mean mortality is for all 9 sites sampled across the bay (A. L. Cupul-Magaña, personal communication).

factors may have contributed to the reduced coral mortality in 1997 to 1998 in the equatorial eastern Pacific: (1) timing of the largest SST anomalies, which occurred in the Galápagos Islands during the cool season; (2) unabated upwelling in the Gulf of Panamá; (3) temperature fluctuations in the Galápagos Islands; (4) a 4- to 6-month respite from stressful temperatures at several sites; and (5) the presence of host/symbiont combinations more resistant to high temperatures in corals that survived the 1982 to 1983 bleaching event. Evidence for the latter effect is presented by Glynn et al. (2001), who proposed a bleaching model to explain the variable coral bleaching responses observed during El Niño events in Panamá and the Galápagos Islands.

Perhaps the greatest intraregional difference between events was the relatively low coral mortality rates in 1997 to 1998 compared to 1982 to 1983 (Glynn and Colley 2001; Glynn 2002). In general, every surveyed site in the equatorial eastern Pacific, over a latitudinal spread of 11° (2°S to 9°N), experienced notably lower coral mortalities in 1997 to 1998 compared with 1982 to 1983 (Table 11.1). At higher eastern Pacific latitudes, off the west coast of Mexico (16 to 20°N), coral mortalities were high at Banderas Bay during the 1997 to 1998 El Niño event and along the Huatulco reef tract in 1998. At Banderas Bay, overall mean coral mortality ranged from 62% to 96%, and the high coral cover in 1991 indicated no prior ENSO-induced changes, at least in the short term (Carriquiry and Reyes-Bonilla 1997). The high mean coral mortality of 98.9% reported at Huatulco occurred during a La Niña cool phase, but the lowest available temperatures, monthly mean values of 25 and 26 °C in February and May, respectively, did not appear to reach critically low levels (Reyes-Bonilla et al. 2002). (La Niña refers to large-scale changes in atmospheric and oceanographic conditions opposite to El Niño, e.g., the westerly location of the equatorial warm pool, and in the eastern tropical Pacific shoaling of the thermocline, anomalously cool sea surface temperatures, nutrient-rich surface waters, and high primary and secondary productivity.) Coral cover was also high on the Huatulco reef tract in 1996, but relatively large sections of dead and eroded pocilloporid reef frames at some sites and massive corals that recruited in 1989 suggest that a thermal disturbance might have occurred during the 1987 El Niño event (Glynn and Leyte Morales 1997). Coral mortality off southern Baja California was unknown in 1982 to 1983, but it was relatively low after the 1987 (10.2%) and 1997 to 1998 (18.2%) ENSO events (Table 11.1). The relatively low-level coral bleaching and mortality at Baja California is attributed to the lower and less prolonged stressful temperatures there, and the seasonal timing of positive temperature anomalies, which tend to occur during the low-temperature periods of winter and spring (Reyes-Bonilla et al. 2002).

Violent storms affecting reef areas in the eastern tropical Pacific were markedly different during 1997 to 1998 compared to 1982 to 1983. Four cyclones traversed the west coast of Mexico in 1997 and 1998. While the greatest damage on shallow pocilloporid reefs amounted to ~50% to 60% mortality, with some dislodgment of reef frame blocks, most reefs were not seriously affected (Lirman et al. 2001; S. S. González and H. Reyes-Bonilla personal communication).

No storm damage to corals was reported off Mexico or any Pacific Central American region in 1982 to 1983, but large swells and contrary seas caused considerable damage to coral reefs in the Galápagos Islands. Storm-generated seas uprooted branching and massive corals at Floreana and Pinta Islands in the Galápagos, depositing large amounts of coral and reef-associated animals on the shoreline (Robinson 1985). In 1982 to 1983, storm activity was greater in the South Pacific. Between December 1982 and April 1983, six hurricanes passed through French Polynesia, causing 50 to 100% destruction of corals on some deep (40 to >100 m) atoll reef slopes (Laboute 1985; Harmelin-Vivien and Laboute 1986).

11.3 ENSO-Related Disturbances to Coral Reefs

ENSO disturbances to coral reefs may be classified into short-term and longer-term temporal scales. Elevated sea water temperatures, often in combination with high irradiance levels (including UV radiation), are short-term disturbances that can cause coral responses of bleaching, tissue loss, and partial or whole colony mortality. Longer-term or delayed ENSO-related disturbances are: (1) violent storms; (2) high rainfall and flooding with increased coastal runoff and sedimentation; (3) periods of sudden and marked sea-temperature decline, resulting from thermocline shoaling and upwelling; (4) elevated nutrient concentrations; (5) dinoflagellate blooms; (6) disease epizootics; and (7) subaerial exposure of corals due to sea-level fluctuations. Detailed information on these sorts of disturbances is available in the reviews of Williams and Bunkley-Williams (1990), Glynn (1993, 2000), Brown (1997), and Hoegh-Guldberg (1999). Conditions (3), (4), (5), and (7), often associated with post-ENSO activities (La Niña events), can affect corals several months to more than a year following a period of elevated temperature.

The loss of zooxanthellae and/or decline in chlorophyll concentration in surviving tissues retards calcification and skeletal growth (Goreau and Macfarlane 1990; Glynn 1993; Hoegh-Guldberg 1999), interferes with reproduction (Szmant and Gassman 1990; Glynn et al. 2000; Hirose and Hidaka 2000; Omori et al. 2001), and lowers a coral's capacity to repair tissue damage and resist epizootics (Meesters and Bak 1993; Mascarelli and Bunkley-Williams 1999; Harvell et al. 2001). Lipid production also declines rapidly in bleached corals, negatively impacting the obligate crustacean symbionts of branching corals that are dependent on their hosts for trophic sustenance (Glynn et al. 1985). In some areas and for some coral taxa, e.g., *Oculina* in the eastern Mediterranean, bacteria have been shown to cause coral bleaching and may therefore precede a bleaching response induced solely by high-temperature stress (Kushmaro et al. 1996). However, it is likely that an increase in temperature may weaken a coral's resistance and increase the virulence of pathogenic bacteria (Kushmaro et al. 1996; Harvell et al. 2001). Finally, long-term consequences of bleaching that may continue for many years include: (8) changing patterns of predation on corals; (9) lowered rates of coral recruitment; (10) bioerosion and loss of stable coral frameworks; and (11) local to regional-scale coral extinctions.

11.4 History of ENSO Events

> After the annual cycle, the Pacific El Niño-Southern Oscillation (ENSO) and its climatic impacts around the world constitute the strongest, most spatially coherent climate signal that exists in both the ocean and the atmosphere.
>
> —Enfield and Mestas-Nuñez (1999).

Prior to the early 1970s little was known about the phenomenon now referred to as ENSO. The earliest accounts of these events, described by Murphy (1926) and others, came from the coastal shores of Ecuador and northern Perú during the mid- to late 1800s and were characterized by prolonged periods of high SSTs, accompanied by heavy precipitation and the cessation of coastal winds. During the 1920s Walker and Bliss (1930) described the occurrence of periodic "seesaw" shifts in atmospheric pressure systems resulting in the reversal of ocean currents and atmospheric pressures across the Pacific and Indian Oceans. However, it was not until Bjerknes (1969, 1972) that it became clear that the El Niño phenomenon was related to the Southern Oscillation through teleconnections linking the interaction of both atmospheric and ocean processes. Finally, Wyrtki (1973) demonstrated that the El Niño phenomenon could be explained by Pacific-wide changes in sea level responding to shifts in the trade winds. Even though much is now known about the dynamics of ENSO events, our ability to predict the occurrence and intensity of this phenomenon remains elusive.

In this review we describe several recent studies that have shed light on the history of ENSO events ranging from recent to millennial time scales. How long have ENSOs and ENSO-like phenomena existed? And, how might their frequency and strength change under a future global warming scenario? Several recent studies provide compelling evidence linking anthropogenic factors as contributing significantly to the severity of both the 1982 to 1983 and 1997 to 1998 ENSO events.

One of the first multicentury, coral-based climate reconstructions was conducted by Dunbar et al. (1994) in the Galápagos Islands, located at the epicenter of ENSO activity. A 10-m-wide, 5-m-high coral colony was sampled at a site located on the equator, at the "center of action" for recording thermal anomalies in the eastern Pacific. In this landmark study, a 367-year growth chronology and 347-year annual $\delta^{18}O$ analysis produced a climate record extending from 1586 to 1953 AD. In addition to the coral proxy records, written historical archives extend the record from 1586 to recent times (Quinn et al. 1987; Quinn and Neal 1995). This isotopic record made it possible to examine eastern Pacific SST variability over a time span not previously available and, more importantly, at such a pivotal site for recording ENSO events. An evolutionary spectral plot of the isotopic data reveals distinct step-like shifts in the frequency of ENSOs (Fig. 11.4). From 1750 to 1750 AD an ENSO event occurred every 6 to 4.6 years. By 1850 it shifted to 3.4 years. The comprehensive approach by Quinn and Neal (1995) involved the reconstruction of past El Niño events through an investigation of historical records. Their definition of an El Niño event is as follows: "the appearance of anomalously warm water along the coast of Ecuador and Perú as far south as

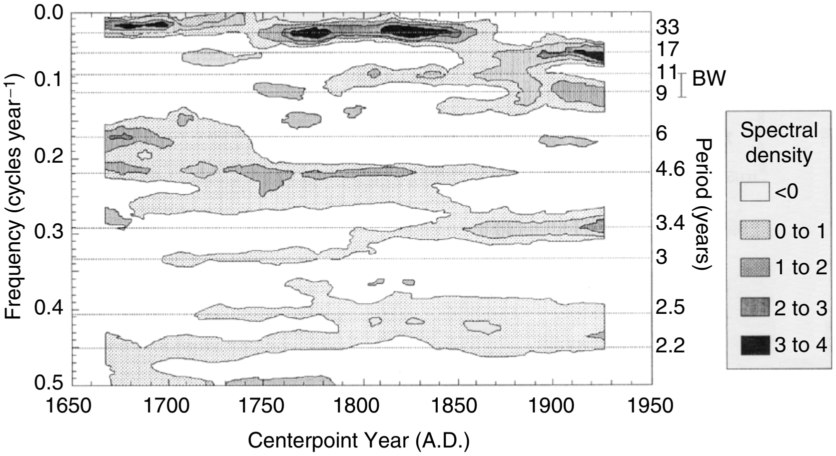

Figure 11.4. Evolutionary spectral density plot based on $\delta^{18}O$ coral showing progression of dominant oscillatory modes in the Urvina Bay (Galápagos Islands) annual record. The shaded areas indicate relative concentrations of variance. Results are consistent with historical records showing a progressive increase in frequency of ENSO from 6 to 2.3 years between events. Reproduced from Dunbar et al. (1994) with permission from the American Geophysical Union.

Lima (12° South) during which a normalized sea surface temperature (SST) anomaly exceeded one standard deviation for at least four consecutive months at three or more coastal stations.” Under this criterion, Quinn and Neal were able to identify the El Niño events of 1957, 1965, 1972 to 1973, and 1976, based on 1956 to 1981 data. They classified the powerful 1982 to 1983 event as very strong, based on SST anomalies that were three times higher than their minimal criteria. In their essay they outlined 12 characteristics that could be used to identify very strong events, including SST anomalies 6 to 12 °C above normal in peak months, a rise in sea level resulting in coastal flooding, mass mortality of sea birds, and a drastic reduction in fisheries production. The level of confidence in these records is clearly higher after 1800. A simple analysis of Quinn and Neal’s records from 1525 to 1987 AD, categorized by the number of strong, severe, and very severe El Niño events (Fig. 11.5), matches extremely well with shifts in the recurrence interval of El Niños reported in Dunbar et al. (1994). The fact that these two independent records are highly correlated provides confidence that this historical record may be largely correct. However, the accuracy of the historically based El Niño records (Quinn et al. 1987) has been called into question. Ortlieb and Machare (1993) argued that the observations of Dunbar et al. (1994) and Quinn and Neal (1995) did not necessarily match those from coastal Ecuador and northern Perú in terms of intensity and timing. This, however, could be related to errors in the historical record and/or the fact that the very strong Galápagos record reflected a more oceanic signal (Quinn and Neal 1995). Quinn and Neal’s (1995) reconstruction suggests that the very strong 1982 to 1983 and 1997 to 1998

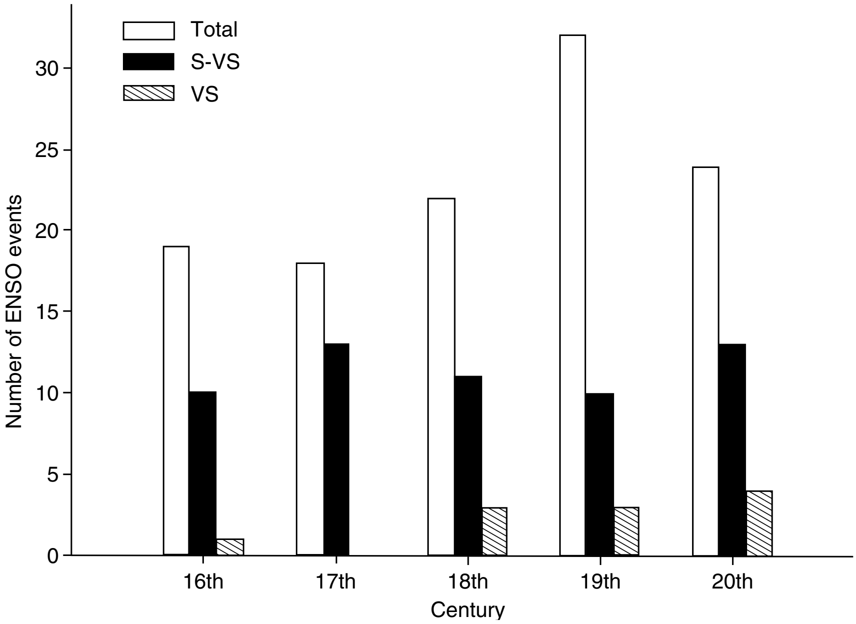

Figure 11.5. Historical occurrences of severe and very severe ENSO events from the 16th through the 20th century, indicating an increased frequency in total ENSO events during the 19th and 20th centuries. Data from Quinn and Neal (1995).

El Niño events may have been unique over the past four centuries in terms of their strength and overwhelming deleterious effects on coral growth and survivorship. These combined events led to the destruction of many of the modest coral reef formations present in the eastern Pacific. Corals living in warm-water areas without seasonal upwelling (e.g., the Gulf of Chiriquí, western Panamá) generally fared better than those experiencing upwelling in the Gulf of Panamá. Surprisingly, however, in 1998 SSTs in the Gulf of Panamá did not surpass levels sufficient for severe bleaching to occur, due in part to the timing and early fluctuations in SST anomalies in 1998 (Glynn et al. 2001).

A recent study in the Galápagos Islands conducted by Riedinger et al. (2002) produced an ~6100-year-long ^{14}C sediment record from a hypersaline lake, providing evidence of the frequency and intensity of El Niño events since the mid-Holocene. Data from their study indicate that El Niño activity was quite high from the present to ~3100 ybp. However, between about 4600 and 7130 ybp El Niño activity, particularly strong to very strong El Niño events, was much reduced in frequency. Their data indicate that from the present to ~3100 ybp, there were 80 strong to very strong events, while from 4000 to 6100 ybp only 23 events of comparable magnitude occurred. Support for these findings includes studies by Sandweiss et al. (1996) who also provide evidence for a prolonged warming period along the Peruvian coast as far as 10°S during the mid-Holocene period from 5000 to 800 ybp (see Fig. 11.6). Their conclusions were based on the presence of shallow, warm-water fossil bivalve assemblages dated to this interval.

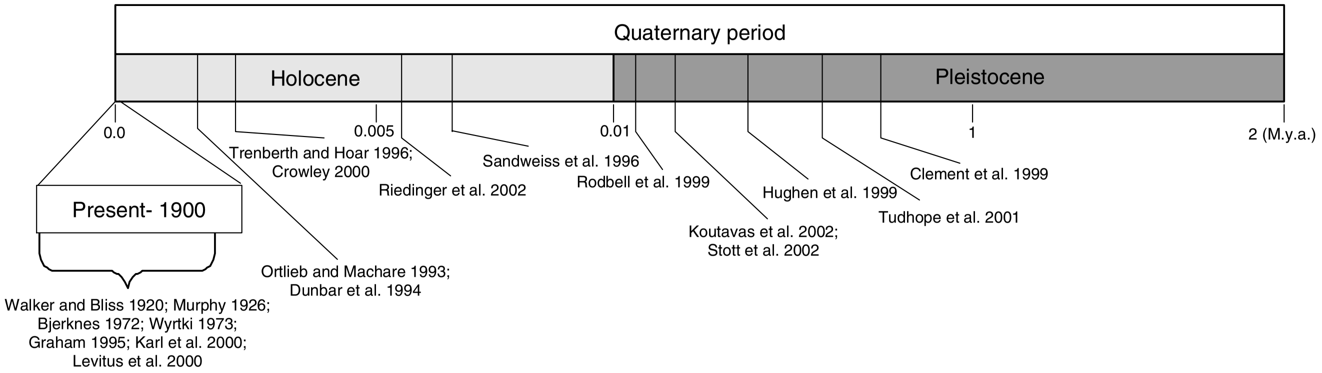

Figure 11.6. The age (or oldest age) of samples in studies of ENSO events from the recent to the middle Pleistocene. Present–1900 AD: developed understanding of ENSO frequency and dynamics. 1600 AD: isotopic record and historical El Niño reconstructions in good agreement, showing low temperatures during the early 1600s and early 1800s, and relatively warmer conditions during the 1700s; a slight cooling observed between 1880 and 1940. 1000 AD: late 20th century warming that closely agrees with the response predicted from greenhouse gas forcing; prolonged 1990–1995 ENSO unusual with expected occurrence once in 1100 years ~6100 ^{14}C ybp: laminated sediments from a hypersaline crater lake in the Galápagos Islands indicate that at least 435 moderate to very strong El Niño events have occurred since ~6100 ^{14}C ybp; the frequency and intensity of events increased at about 3000 ^{14}C ybp. 5000–8000 ybp: stable, warm tropical waters in northern Peru, based on geoarchaeological evidence, suggest that El Niño events did not occur for some millennia preceding 5000 ybp. 7000–15,000 ybp: ^{14}C-dated debris flows suggest that El Niño periodicity ≥15 years to 7000 ybp then increased to 2–8.5 years by 5000 ybp, which is modern El Niño periodicity. 20–70 ka: based on δ^{18}O and Mg/Ca composition of planktonic foraminifera, the last glacial maximum cooling between 21 and 23 ka implies a persistent El Niño-like pattern in the tropical Pacific; more frequent and perhaps more severe El Niño events are linked to stadial (glacial) conditions during the last 70 kyr. 124 ka: δ^{18}O and Sr/Ca records from a fossil Indonesian coral indicate robust ENSO activity during the last interglacial period when global climate was slightly warmer than present. 130 ka: using the δ^{18}O composition of fossil corals from Papua New Guinea, it was shown that ENSO has existed through a glacial–interglacial cycle for the past 130,000 years. 150 ka: a model study shows that the mean global climate response of precessional (Milankovitch) forcing is due to an interaction between an altered seasonal cycle and the ENSO.

In support of the Galápagos coral-based study by Dunbar and co-workers (1994), Rodbell et al. (1999) examined dated inorganic laminae derived from storm deposits in an alluvial alpine lake in Ecuador. These data from a 9.2-m core yielded climate information spanning from less than 200 ybp to as far back as 15 ka. They found that El Niño events were longer in periodicity and lower in amplitude. Rodbell et al. (1999) were able to show a strong match between the timing of clastic laminae and historical records of moderate to severe El Niño events occurring from 1800 to 1976. Overall they identified the occurrence of 26 moderate El Niño events between 1800 and 1976 AD. From about 15 to 7 ka, the periodicity of the clastic sediments was ≥15 years followed by a progressive increase toward lower frequencies that became established around 5000 ybp. This result was consistent with the studies of Sandweiss et al. (1996) and Riedinger et al. (2002). Using a simple numerical ocean–atmospheric model, Clement et al. (1999) found that during the mid-Holocene the occurrence of ENSO events was likely to have been less intense in both amplitude and frequency compared to the present.

Focusing on past ENSO behavior during the Last Glacial Maximum (LGM), Koutavas et al. (2002) reconstructed a ^{14}C-dated Mg/Ca SST record based on δ^{18}O values of foraminifera preserved in the marine sediments at the Galápagos Islands. Their results showed that over the past 30 kyr the intensity of the Cold Tongue varied in step with precession-induced seasonal changes. During the LGM, temperatures cooled by 1.2 °C and Koutavas et al. (2002) suggested that such a shift would have resulted in the relaxation of temperature gradients, which in turn would have reduced gradients in both the Hadley and Walker circulation systems. This would have led to a southerly shift in the position of the Intertropical Convergence Zone (ITCZ)—in essence chronic, quasi-continuous ENSO conditions. In support of this putative climate shift, Koutavas et al. (2002) cited evidence of wetter climate conditions in the Bolivian Altiplano and drier conditions in northern South America. Additional studies by Rodbell et al. (1999), Tudhope et al. (2001), and others provide evidence in support of their results.

Stott et al. (2002) recently offered evidence for a "super" ENSO during the Late Pleistocene. Using δ^{18}O and Mg/Ca ratios from planktonic foraminifera as a proxy for temperature and salinity these workers differentiated the calcium δ^{18}O record, revealing a dominant salinity signal that varied with Dansgaard/Oeschger cycles over Greenland. Salinities were found to be higher during periods of latitudinal cooling and lower during interstadials. These variations in salinity shifts are analogous to Pacific ocean–atmospheric cycles. ENSO events correlated with stadials at high latitudes while La Niña conditions correlated with interstadials. According to Stott et al. (2002), at times of cooling at high latitudes, the tropical Pacific experienced either more frequent or more persistent ENSO events.

Millennial-scale shifts in atmospheric convection away from the western tropical Pacific may explain many paleo-observations, including atmospheric CO_2, N_2O, and CH_4 during stadials and patterns of extratropical ocean variability that have tropical source functions positively correlated with ENSO.

The fossil coral records reported by Tudhope et al. (2001) extend back to 130,000 years, through the last glacial–interglacial cycle. These investigators used $\delta^{18}O$ and $\delta^{13}C$ proxies to examine paleo-SST and to establish the time series of the records. The fossil corals analyzed grew when sea level was 70 to 100 m lower than present, ca. 40 and 130 ka, respectively, during the penultimate interglacial period. Interannual variations were interpreted as reflective of a paleo-ENSO system. Spectral analysis further provided data on ENSO periodicity during these periods. One of the conclusions of Tudhope et al. (2001) was that the variance in the ENSO band is greater in the modern coral record compared with fossil corals. However, they did find some periods in the last interglacial and late Holocene that matched current ENSO frequencies. The key point is that ENSO events have been a prominent climatic feature during interglacial periods, extending perhaps from the last interglacial up through the Holocene. Tudhope et al. (2001) suggested that SSTs were similar to present conditions and 2 to 3 °C cooler during four low sea-level stands between 130 ka and the last glacial period.

Tudhope and co-workers found that ENSO was weak and suggested that at 6.5 ka the $\delta^{18}O$ values indicated similar or slightly cooler SSTs. Overall, however, the evidence from several proxy records in the eastern Pacific, including Sandweiss et al. (1996), Rodbell et al. (1999), Riedinger et al. (2002) as well as others, support their arguments. Lastly, Tudhope and co-workers suggested that orbital precession-glacial dampening (Crowley and North 1991) may have controlled the frequency and strength of ENSO events, and that the pacing and strength of ENSOs are higher now than at any time over the past 150,000 years. However, Hughen et al. (1999) reconstructed a fossil record from a 124,000-year-old coral in Indonesia that suggests that during the last interglacial period temperatures were slightly warmer than present but distinct from the recent records since the mid-1970s, when global SSTs shifted to an average warmer state.

From the recent paleoclimate studies presented above, it is clear that ENSO events have been one of the dominant features shaping global climate change at least as far back as the late Pleistocene, and perhaps earlier (Fig. 11.6). The major question at present is how much warmer will it become in the near future and how fast will this change occur?

11.5 What Factors Are Causing Recent Warming?

Certainly the well-documented shift to warmer subsurface sea temperatures associated with El Niño (Guilderson and Schrag 1998) appears to have had a major impact on the heat budget across the Pacific and is thought to be responsible for the increase in frequency and intensity of ENSO events since 1976. Evidence supporting this abrupt shift is based on bomb ^{14}C that showed enrichment in surface water via shoaling of the undercurrent in the equatorial eastern Pacific. In 1960 ^{14}C values ranged seasonally from 20 to 30%. By the mid-1970s, the isotopic values increased from 50 to 100% indicating a significant shoaling of the Equatorial Undercurrent and hence warmer surface waters. Although the phenomenon was described from eastern Pacific surface waters, heat levels have increased in all the major oceans (Fig. 11.7; Levitus et al. 2000).

One of the first studies to assess global temperature trends was conducted by Graham (1995). Using the most recent portion of the observed ocean SST data set (1970–1992), he was able to reproduce the results of the atmospheric models using ocean surface temperatures alone. The conclusion from the modeling effort

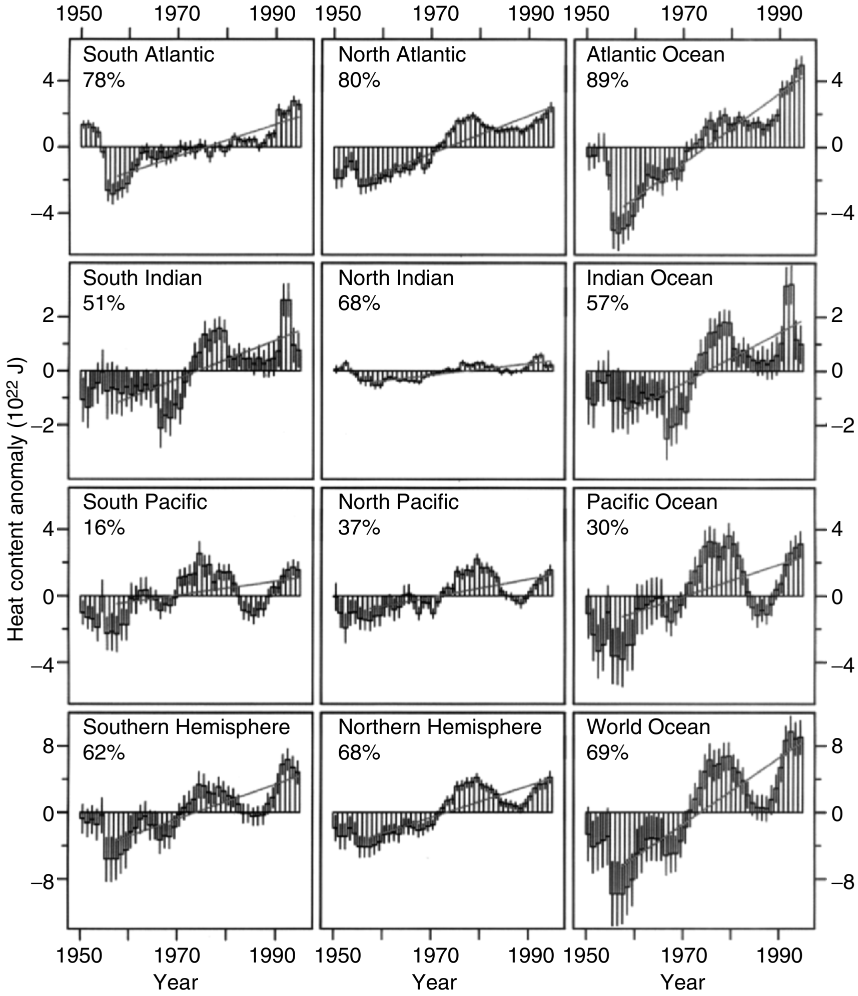

Figure 11.7. Time series of 5-year running composites of heat content (10^{22} J) in the upper 3000 m for each major ocean basin. Vertical lines represent ±1 SE of the 5-year mean estimate of heat content. The linear trend is estimated for each time series for the period 1955 to 1996, which corresponds to the period of best data coverage. The trend is plotted as a black line. The percent variance accounted for by this trend is given in the upper left corner of each panel. Reproduced from Levitus et al. (2000) with permission from the American Association for the Advancement of Science.

indicated that simulated temperatures are caused by enhancement of the tropical hydrologic cycle resulting from increasing SST, in essence suggesting that model results could be due to natural climate variability, but are most likely attributable to increasing levels of atmospheric CO_2.

Further evidence of forced warming was reported in Trenberth and Hoar (1996), who noted that ENSO-level warming occurred continuously in the Niño 4 region from 1990 to 1995, marking the longest ENSO event over the past 113 years. This manifestation was mainly driven by the static position of the Southern Oscillation, which remained negative from early 1990 to June 1995. Statistical analyses based on modern ENSO frequencies predict that this prolonged negative SOI would only be expected to occur every 1100 years and an ENSO as prolonged as the 1990 to 1995 one would occur only once every 1500 to 3000 years.

By identifying and quantifying all potential sources giving rise to recent warming over the past 1000 years, Crowley (2000) presented results from an energy balance model showing that 41 to 64% of pre-anthropogenic (pre-1850) variation could be explained by natural variation in solar radiation and volcanic activity. In addition, the contribution of solar forcing was evaluated and compared with greenhouse gases from the middle of the last century. Those results indicated that the climate effects due to greenhouse gases were four times larger than the effect due to solar variability and that temperature changes since 1850 could not be explained by natural variability alone. Using a linear upwelling/diffusion energy balance model (EBM) to calculate mean annual changes in forcing, the results indicated that during pre-1850 there was a 0.05 °C decrease in the 17th and 18th centuries reflecting a CO_2 decrease of ~6 parts per million in an ice-core record. Combining solar and volcanic variability, model responses indicated only a 0.15 to 0.20 °C increase in temperature between 1905 and 1955, representing one quarter of the total observed 20th-century warming.

Crowley (2000) provided two independent lines of evidence indicating that Northern Hemisphere temperatures were unusually high over the past 1000 years. First, the warming over the past century is unprecedented in the past 1000 years. Second, the same climate model explaining much of the variability in temperature over the interval 1000 to 1850 can only account for about 25% of the 20th-century temperature increase attributable to natural variability. Crowley (2000) concluded by suggesting that recent increases are due to an already present warming trend from greenhouse gas forcing that is likely to accelerate in the near future.

Recent empirical observations provide strong evidence that global temperatures have risen from +0.3 °C to a value closer to +0.6 °C, based on a series of unprecedented warming events that broke consecutive temperature records in the 1990s. To assess the significance of these results, Karl et al. (2000) employed an autoregressive moving-average (ARMA) model to separate the timing of change points in temperatures over the past 500 to 1000 years. The difference in the rates of change over the two periods, 1912 to 1941 and 1976 to 1998, was highly significant. Statistical methods employed ARMA to calculate the probability of 16 consecutive months of record-breaking mean monthly temperatures. The resulting probabilities varied from 0.009 to 0.04, using a rate of warming between 2.5 and 3.0 °C per century.

In attempts to predict future climate change based on the results of rigorous model/observation analyses, incorporating a coupled ocean–atmospheric model, Stott et al. (2000) were able to show that model analyses could successfully simulate global mean land temperature variations over large scales, indicating that external forces (i.e., increased greenhouse gas effects) have had a strong influence on observed temperature change. Their models were also able to explain more than 80% of the observed variation in decadal temperature changes during the 20th century and indicated that temperatures would continue to rise to 2100 at a rate comparable to current levels (~0.2 K per decade).

To assess the effects of natural forcing attributable to changes in stratospheric aerosols, specifically those due to volcanic eruptions and fluctuations in solar irradiance, Stott et al. (2000) evaluated three climate ensembles based on the DADCM3 dynamical climate model. The ensemble comprised four simulations that varied only in their initial conditions, ALL, ANTHRO, and NATURAL forcing. The ALL ensembles revealed temperature changes since 1860, which were consistent with observations of changes over the past 30 years. The NATURAL model showed no warming over the past 30 years, while the ANTHRO model showed a 0.2 °C warming relative to the period 1881 to 1920. By comparing both anthropogenic and natural forcing, their model successfully predicted significant large-scale responses to observed temperatures. The global mean model (ALL) trends were consistent with observations. The NATURAL ensemble was conclusively rejected, indicating that anthropogenic forcing is, in fact, the most likely cause of recent warming.

Perhaps one of the most important and telling pieces of evidence in support of significant climate change, with respect to global warming, is the recent data compiled by Levitus et al. (2000). These workers documented dramatic increases in oceanic heat content over a 40-year period (the mid-1950s to the mid-1990s), corresponding to a warming rate of 0.3 °C between 300 and 1000 m depth in each of the major ocean basins (Fig. 11.7). From 0 to 300 m depth, the measured increase was 0.31 °C. This warming began in the 1950s in the Pacific and Atlantic Oceans, with the Indian Ocean showing a warming trend since the mid-1960s. Maximum heat content was observed during the 1997 to 1998 ENSO event. These data suggest the possibility that enhancement of the Pacific Decadal Oscillation (PDO) contributed significantly to the warming signal.

11.6 ENSO Markers on Coral Reefs

11.6.1 Geomorphological and Ecological Markers

Several lines of geomorphological and ecological evidence have been proposed to help identify ENSO effects on coral reefs, on decadal to centennial time scales. None of these features alone can serve as unique signals of ephemeral ENSO warming events (DeVries 1987), but in combination, and with additional markers from geochemical analyses (see below), they can offer reasonably convincing evidence of past ENSO disturbances.

Geomorphological evidence. The death of entire coral reef frameworks in the Galápagos Islands (Glynn 1994), at Cocos Island (Guzmán and Cortés 1992), and along coastal Ecuador (Glynn 2003) can be attributed to the sudden and prolonged sea warming associated with the 1982 to 1983 El Niño event. Many of these frameworks have suffered from significant erosion and collapse since 1982 to 1983. Several reef structures in the Galápagos Islands have disappeared entirely, whereas some at Cocos Island and along coastal Ecuador are still standing but in varying stages of disintegration. Those frameworks that are still intact could serve as indicators of El Niño for two or possibly more decades. Colgan (1990) offered evidence from a tectonically uplifted and well-preserved coral assemblage that the 1941 El Niño event caused widespread mortality of pocilloporid frameworks at Urvina Bay, Galápagos Islands. The destabilization and disintegration of in situ reef structures may also result in off-reef submarine and/or strand-line clastic deposits that could be dated and possibly related to El Niño activity (Scott et al. 1988; Glynn 2000). For example, an approximately 1-m-high berm of coral debris on the south end of Pinta Island (Galápagos Islands) most likely represents the remnants of an incipient pocilloporid patch reef that was present just offshore before the 1982 to 1983 El Niño event (Fig. 11.8). Coral tempestites were formed in the Galápagos in 1983 due to storms, swell reversals, and high sea-level stands, which caused coral breakage, dislodgment, and transport onto the shoreline (Robinson 1985).

Figure 11.8. Coral rubble berm at the south end of Pinta Island, Galápagos Islands (17 May 2002). This feature, about 1 m high and 5 to 8 m wide, is composed of coral debris originating from a pocilloporid patch reef killed during the 1982 to 1983 El Niño disturbance. Courtesy of T. Smith.

From preliminary analyses of carbonate sediment production rates, and reef and offshore sediment stratigraphy, Scott et al. (1988) argued that intense bioerosion following massive El Niño-induced coral death would accelerate the deposition of coral sediments. These workers reported increases in coral sediment grain sizes after the 1982 to 1983 El Niño, indicative of intense lithophagine bioerosion. Since the size and texture of bioeroded sediments are often uniquely produced by different taxa, it is possible that the composition of postdisturbance sediments can be related to the relative abundances of bioeroder taxa (Glynn 2000). Rapid rates of bioerosion have been quantified on several reefs impacted by El Niño warming disturbances (Glynn 1988; Eakin 1996, 2001; Reaka-Kudla et al. 1996). In an analysis of erosion on an entire 2.5-ha Panamanian reef, Eakin (1996) reported overall net losses of 4800 kg $CaCO_3$/year after the 1982 to 1983 El Niño event, compared with predisturbance net depositional rates of 8600 kg $CaCO_3$/year. The reef continues in a highly variable, habitat-specific erosional mode, with net losses of 3000 to 18,000 kg $CaCO_3$/year in the aftermath of the 1997 to 1998 El Niño event. Much of this variability is due to changes in (a) the community composition of calcifying organisms, (b) topographic complexity, and (c) echinoid population densities. Coral mortalities due to La Niña-forced low tidal exposures (1989 and 1993) actually had a larger effect on these erosional rates than coral mortalities due to elevated SSTs during the 1997 to 1998 El Niño event (Eakin 2001).

The sudden death of long-lived massive corals that have grown continuously for several centuries can also indicate El Niño activity. For example, numerous old colonies of *Porites lobata* and *Pavona clavus* in the Galápagos Islands, with maximum estimated ages ranging from 347 to 423 years, died during the 1982 to 1983 El Niño event (Glynn 1990b). Also, *P. clavus* demonstrated continuous skeletal growth at Urvina Bay (Galápagos Islands) for 367 years before the colony was uplifted and killed in 1954 (Dunbar et al. 1994). These growth records suggest that coral mortality resulting from the 1982 to 1983 ENSO warming event in the Galápagos Islands was a unique event over the prior four centuries.

Ecological evidence. Colgan (1990) observed several markers within branching and massive coral skeletons that he attributed to the 1941 El Niño disturbance. These features were present on corals at the Urvina Bay uplift, which, as of 2002, were still in a high state of preservation. After death, branching coral (*Pocillopora* spp.) frameworks formed towers through the interaction of damselfish that defended and reduced bioersion on the coral summits, and echinoids (*Eucidaris*) that grazed and caused undercutting of the tower bases. This differential erosion eventually led to the collapse and disintegration of the towers. In massive coral colonies (*Porites lobata* and *Pavona* spp.), algae and epifauna colonized the dead upper surfaces until surviving coral tissues on the sides of the colonies eventually spread laterally by regrowth and began to cover the scars on the summits. Relating species-specific growth rates to the amount of regrowth that occurred on these massive corals, Colgan (1990) calculated that this could have occurred between the strong 1941 El Niño event and the tectonic uplift and death of these corals in 1954.

Similar scarring and coral regrowth have produced lobes on the massive coral *Gardineroseris planulata* in Panamá (Fig. 11.9) and on *Porites lobata* (Fig. 11.10)

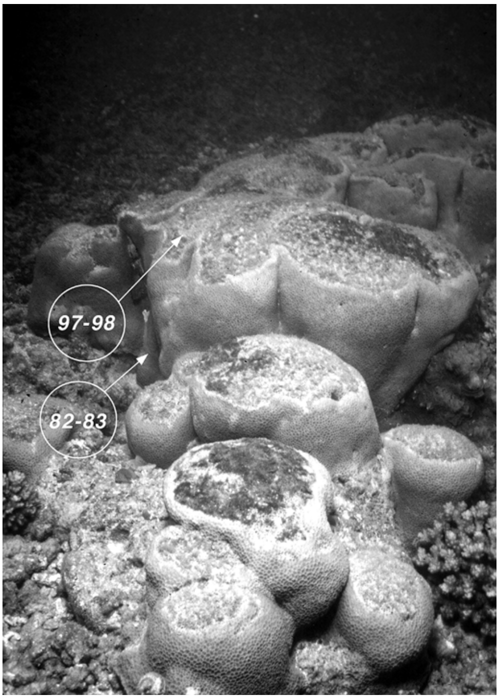

Figure 11.9. Skeletal regeneration lobes on *Gardineroseris planulata* that formed following partial colony mortality during the 1982 to 1983 ENSO event at Uva Island, Gulf of Chiriquí, Panamá (6 m depth, 15 May 1999). The summits of the lobes, covered with turf algae, bleached and suffered partial mortality again during the 1997 to 1998 ENSO event. The heights of the lobes, excluding losses due to erosion, ranged from 10 to 20 cm.

at Clipperton Atoll. In Panamá, the bottoms and tops of these lobes respectively mark the 1982 to 1983 and 1997 to 1998 El Niño disturbances at the Uva Island reef in the Gulf of Chiriquí (Glynn 2000). At Clipperton, the regenerated lobes on *P. lobata* have been correlated with the 1987 ENSO event, which at that location was more severe than the ENSO event of 1982 to 1983 (based on the magnitude and intensity of SST anomalies; Glynn et al. 1996). Regenerating lobes also form on massive *Porites* spp. colonies that have been partially consumed by the corallivorous sea star *Acanthaster planci* (Done 1987; DeVantier and Done, Chapter 4). Stable oxygen isotope ($^{18}O/^{16}O$) thermometry of skeletal growth immediately preceding and following the partial mortality event should help to distinguish between thermally induced bleaching and death from predation, uplift, or other factors.

Another example of ecological processes that may offer evidence of past El Niño activity relates to predator–prey interactions (Glynn 1985). Before the 1982–83 El Niño, several ~100- to 200-year-old colonies of *G. planulata* on the Uva Island reef were protected from *A. planci* attack by a barrier of pocilloporid corals and their obligate crustacean guards. Almost all of the *G. planulata*

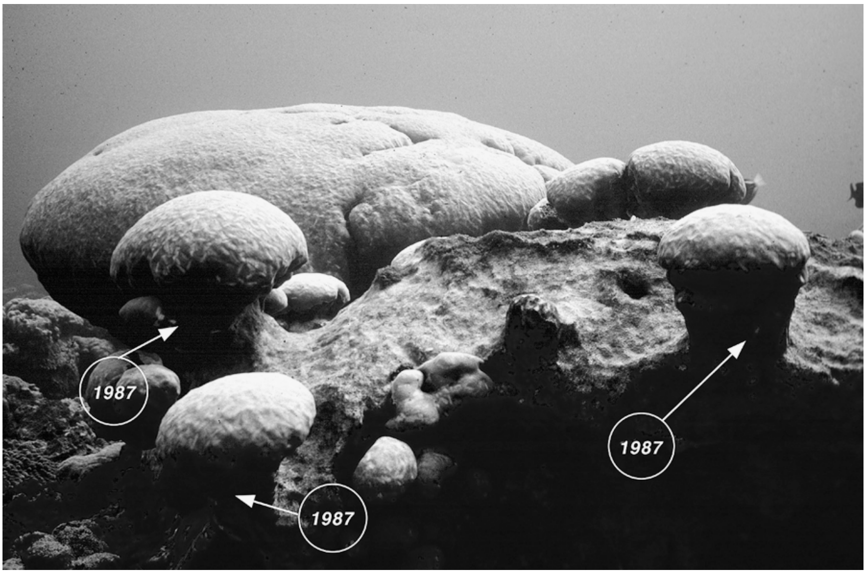

Figure 11.10. Skeletal regeneration lobes on *Porites lobata* that formed following partial colony mortality during the 1987 ENSO event at Clipperton Atoll (10 m depth, 23 April 1994). The live summits bear numerous pufferfish bite marks. The heights of the dated lobes since 1987, excluding losses from bioerosion, ranged from 12 to 15 cm.

colonies survived the elevated temperatures of 1982 to 1983, but the branching pocilloporid corals did not. This resulted in the death of the crustaceans, which allowed *A. planci* access to the more temperature-resistant massive corals within the refuge. Sclerochronologic analysis of cores from the largest *Gardineroseris* colony showed no signs of prior growth discontinuities, which suggested that the biotic barrier had protected this massive coral for up to 200 years. This approach is no longer relevant due to the recent severe reduction in the abundance of *A. planci*. Although a pocilloporid barrier has not re-formed (as of March 2005), *A. planci* predation is no longer an important factor on the Uva Island reef (Fong and Glynn 1998).

11.6.2 Geochemical Markers

The carbonate skeletons of corals are capable of providing accurate, high-resolution climatic data sets stored over a vast range of temporal scales from diurnal to millennial. They are recorders of natural events such as solar activity, volcanic eruptions, human-induced forcing of greenhouse gases, and other environmental changes. In addition, tree rings, varved sediments, ice cores, and other such markers are capable of storing past information on climate change.

Studies of growth patterns in massive corals indicate that two skeletal bands are typically formed annually: one wide, low-density band that usually forms in the cool season, and a narrow, denser band that forms during warmer periods (Fig. 11.11). It should be noted that this pattern varies geographically. Periodic

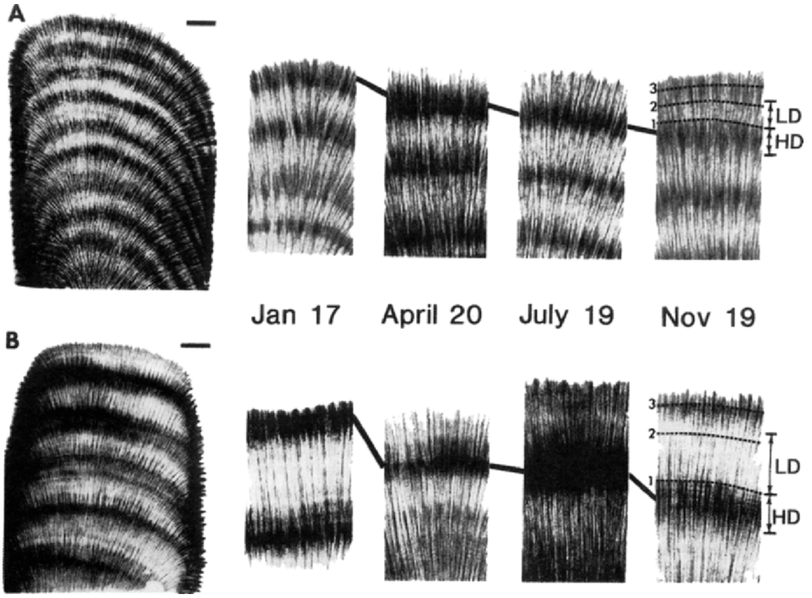

Figure 11.11. X-radiographic positives showing the changes in skeletal density from 17 January to 19 November 1979 for the corals (**A**) *Pavona gigantea* and (**B**) *Pavona clavus* at Contadora Island, Pearl Islands, Gulf of Panamá. The time series in samples to the right were collected from the same colonies over the time periods indicated. Solid lines connect the high-density bands formed in the preceding wet, nonupwelling season (June–December). Scale bars are 1 cm. Linear dimensions of low-density (LD) and high-density (HD) bands are shown on the far right. Dotted lines (1, 2, 3) on the November 19 samples indicate position of Alizarin Red stain lines. Corals were stained on 25 January, 24 May, and 25 September 1979. From Wellington and Glynn (1983).

extremes in either warm or cool temperatures can result in the formation of narrow stress bands. In the case of corals, moderate to severe ENSOs can result in interrupted skeletal growth that can provide a history of ENSO disturbances or extreme cooling events that periodically occur on reefs at higher latitudes during severe winters (Hudson et al. 1976; Hudson 1981; Halley and Hudson, Chapter 6).

One of the first studies to observe and suggest the annual nature of high- and low-density banding in coral was conducted by Ma (1933). Following this initial observation, Knutson et al. (1972) demonstrated that coral bands were formed on an annual basis. This important study paved the way to investigate not only the factors controlling rates of growth but also their capacity to capture a history of climate change based on reasonably well-understood biochemical proxies such as $\delta^{18}O$ and Sr/Ca ratios. Traditionally, $\delta^{18}O$ has been the primary method used to reconstruct proxy sea surface temperatures. This proxy signal, however, is constrained by potential variation in sea surface salinities that can alter the relationship between $\delta^{18}O$ and sea surface temperatures. This problem is largely circumvented where variations in $\delta^{18}O_{seawater}$ are minimal.

In attempts to reconstruct a paleo-SST relationship using Sr/Ca ratios, de Villiers et al. (1995) called into question the validity of a 4 to 6 °C cooling in the tropics, which was reported to have occurred during the LGM. Based on observed variations in the Sr/Ca content of sea surface waters, latitudinal transects across both the Pacific and Atlantic Oceans revealed uncertainties of 2 to 3 °C with regard to the Sr/Ca thermometer. One of the major problems observed, however, was that differences in coral growth rates appear to have an effect on the slope of the Sr/Ca relationship, with slower-growing corals showing higher Sr/Ca levels. de Villiers et al. (1995) concluded that biological factors, such as variations in metabolic rate, could play a significant role in influencing the actual Sr/Ca signal.

In contrast to de Villiers' study, an instrumental calibration study conducted in the laboratory by Schrag (1999) has shown that Sr/Ca ratios in corals have a high potential for providing very accurate information on SSTs, to within ± 0.2 °C. In comparing these results with the field observations of de Villiers et al. (1995) and a recent laboratory study by Meibom et al. (2003), it is obvious that the accuracy of the Sr/Ca tracer technique is inconsistent. The latter workers found that the temperature signal could vary by as much as 10%, resulting from metabolic changes synchronized with the lunar cycle.

Cohen et al. (2001, 2002) evaluated the relationship between SST and skeletal Sr/Ca in a temperate coral living over a broad temperature range. *Astrangia poculata* occurs naturally with or without algal symbionts. In comparing the relationship between SST and Sr/Ca values, it was found that 65% of the Sr/Ca variability in the symbiotic state was related to metabolic activity independent of SST, as earlier shown by de Villiers et al. (1995). Based on the derived Sr/Ca–SST relationship they found that the slopes of the temperature curves were virtually identical between symbiotic and nonsymbiotic colonies. Moreover, Cohen and co-workers showed that variations in Sr/Ca in the asymbiotic form are primarily controlled by variation in SST, whereas the Sr/Ca ratio in the symbiotic coral is under strong biological control. More work on this problem requires robust protocols that can provide accurate proxy SSTs under a variety of biotic and abiotic conditions. Despite the recent recognition of these potential pitfalls in achieving accurate SST proxies, several studies have produced remarkably high correlations between SST and Sr/Ca ratios (Linsley et al. 2000; Fig. 11.12).

11.7 Spatial and Temporal Scales of ENSO-Related Coral Bleaching

Given the high variability of stressful levels of temperature and irradiance distributions on coral reefs and the varying sensitivities of zooxanthellate corals to these conditions, it is not surprising that numerous microscale spatial patterns of bleaching and mortality have been described. Severe coral bleaching often coincides with elevated temperatures in shallow reef habitats, direct exposure to downwelling solar irradiance, and reduced water circulation or mixing. Back-reef corals that are often exposed to greater extremes in temperature than fore-reef corals may not bleach while bleaching is pronounced in other reef habitats.

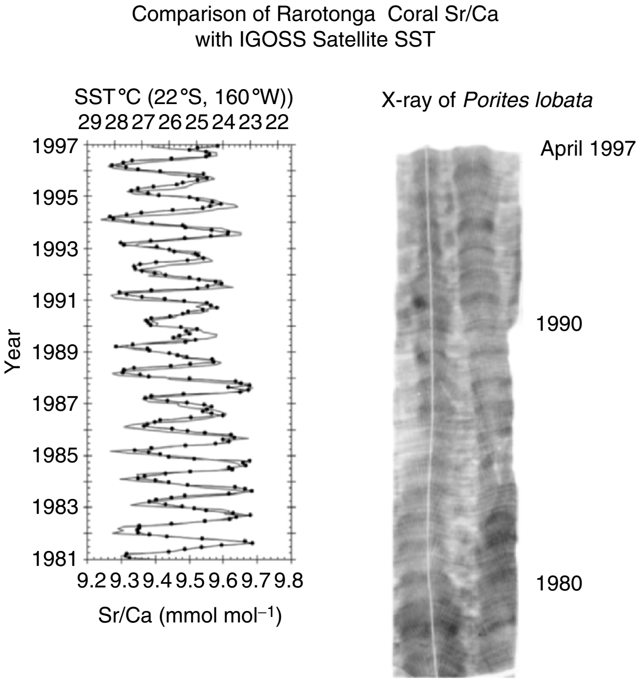

Figure 11.12. Comparison of Rarotonga coral Sr/Ca with IGOSS satellite SST showing a high correlation between SSTs and Sr/Ca (mmol/mol) proxy values. Reproduced from Schrag and Linsley (2002) with permission from the American Association for the Advancement of Science.

Corals in deeper reef zones, exposed to vigorous circulation, subdued irradiance, and mixing with deeper, cooler waters, often are less severely impacted during mass bleaching events. Recent studies have demonstrated that patterns of bleaching in some reef-coral species, both across colonies at different depths and within a single colony, are controlled by diverse communities of symbiotic zooxanthellae with varying tolerance limits for elevated temperature and irradiance stressors (Rowan et al. 1997; Baker 2001; Rowan 2004). These sorts of environmental influences affecting bleaching susceptibility/resistance are addressed extensively in the literature (e.g., Goreau and Macfarlane 1990; Jokiel and Coles 1990; Williams and Bunkley-Williams 1990; Glynn 1993; Brown 1997; Hoegh-Guldberg 1999; Goreau et al. 2000; Feingold 2001; Glynn et al. 2001; Baker et al. 2004; Riegl, Chapter 10).

In terms of meso- (reefs) to macro-scale (reef regions) patterns of bleaching, whole-reef ecosystems and entire biogeographic regions underwent unprecedented mass bleaching in the 1980s and 1990s. Except for the equatorial west African region, some level of coral reef bleaching has now been observed in all of the world's coral reef provinces, from 27°S (Easter Island) to ~34°N (Japan; H. Yamano personal communication; Fig. 11.2A,B). It should be recognized, however, that intraregional variability in coral bleaching has been observed. For example, Reyes-Bonilla and co-workers (2002) have suggested that Mexican Pacific coral reefs have been relatively little affected by ENSO events because temperature anomalies are less pronounced in that area and coral recruitment has been normal to high, at least since 1997. Compared with the first global compilations of

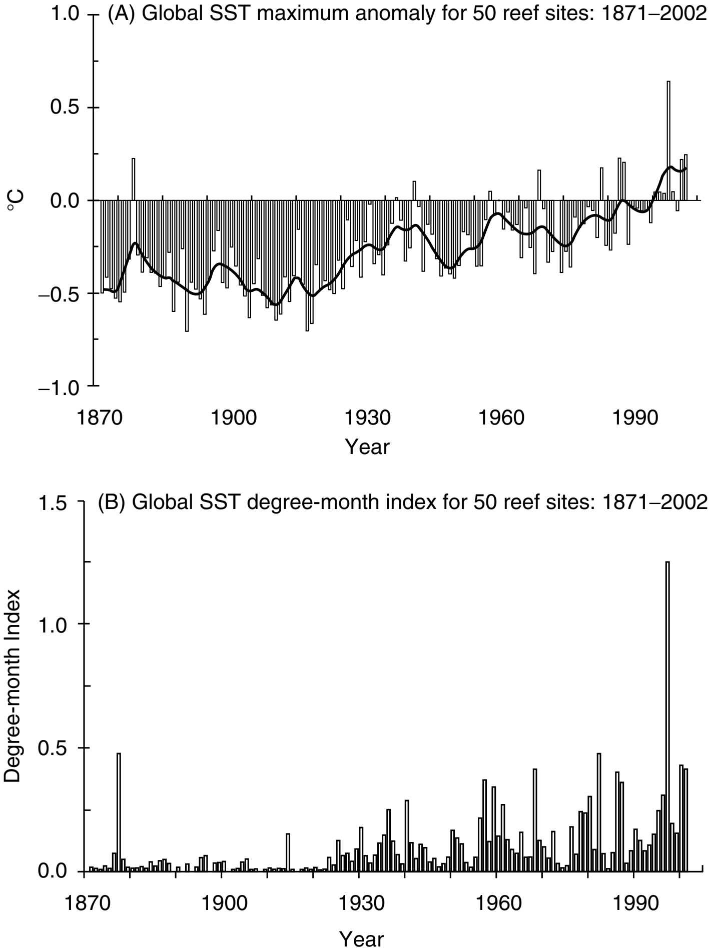

Figure 11.13. (**A**) Mean SST maximum anomaly and (**B**) mean degree-month index at 50 coral reef sites that bleached in 1997 to 1998 (source data 1871–2002, Had1SST, 2000–2002, IGOSS-NMC product). Black curve in (**A**) is a 10-year Gaussian filter. Base period for calculating the anomalies is 1982–1999. The degree-month index combines both the magnitude and duration of warm season SST anomalies by summing positive anomalies for the months the mean maximum monthly SST was exceeded for each year. Courtesy J. M. Lough; see Lough (2000) for additional information on analyses.

bleaching events in the 1980s (Glynn 1984; Brown 1987; Coffroth et al. 1990; Williams and Bunkley-Williams 1990), it is clear that through the 1990s this class of disturbance spread to include nearly every coral reef assemblage worldwide.

It is cautioned, however, that the more recent bleaching events reported by ReefBase include numerous discrete coral reefs whereas the earlier records were often for larger reef regions. To illustrate the high correlation between thermal stress and coral bleaching worldwide during 1997 to 1998, Lough (2000, personal communication) analyzed the occurrence of bleaching at 50 reef sites in the Indian Ocean/ Middle East, Southeast Asia, Pacific Ocean, and the Caribbean/Atlantic. She found that the level of thermal stress at the vast majority of these sites was unmatched during the period 1871 to 1999 (Fig. 11.13A,B).

During the temporal development of a bleaching episode, Hoegh-Guldberg (1999) suggested that coral reefs are generally affected first in the southwestern Pacific and Indian Ocean, then around Southeast Asia, and finally in the Caribbean basin. He further proposed that coral reef bleaching begins in the Southern Hemisphere and spreads into the Northern Hemisphere with the evolution of ENSO events. Coral reef bleaching in the eastern Pacific typically occurs during the warm season about one year following bleaching in the southwestern Pacific (Podestá and Glynn 2001). The timing may vary, however, as bleaching occurred in the eastern Pacific (Panamá) in August to September 1997, preceded by five months of bleaching on the Great Barrier Reef. A second bout of bleaching occurred in Panamá from March to June 1998. In addition, severe bleaching events at Easter Island and Fiji in the Southern Hemisphere occurred during February and March 2000, about two years following the 1997 to 1998 ENSO (Wellington et al. 2001). Clearly, local conditions such as the duration of temperature anomalies, water-column transparency, and cloud cover influence the timing of these events.

11.8 Recovery

Even though hundreds of severe coral bleaching events have been documented during the 1980s and 1990s, relatively few studies are available on the extent of coral community recovery. From quantitative long-term studies, Connell (1997) listed eight examples of changes in coral cover following bleaching events, which were likely caused in large part by elevated seawater temperature or by a combination of elevated temperature and irradiance. This represents only about 10% of the 77 cases available with data spanning at least 4 years. The majority of the changes in coral cover were tentatively assigned to predation, storm damage, sedimentation, reduction in herbivore abundances, and disease epizootics. Sufficient observations were available to judge whether recovery had occurred or not in only five of the eight ENSO-related examples. All western Pacific reefs but one demonstrated significant recovery (>50% increase as percent of loss) over periods of 7 to 13 years. These included coral reefs in the Thousand Islands region of Indonesia (Brown and Suharsono 1990) and at Phuket Island, Thailand (Brown et al. 1993). Some sites at Phuket Island showed no significant declines in coral cover over an 11-year period of study (Chansang and Phongsuwan 1993). The only site showing no recovery was the Uva Island reef (Panamá) in the eastern Pacific (Glynn 1990a).

Here we augment and update the record of changes in coral cover for several equatorial eastern Pacific coral reefs subjected to multiple El Niño/La Niña disturbances over the past two decades. Recovery of coral reefs from the Galápagos Islands to the Gulf of California, Mexico, monitored over the longest periods (15–31 years), is evaluated in terms of live coral cover. Statistical testing of pre- and post-disturbance mean differences in coral cover is noted where possible.

Shallow (1–5 m depth) Galápagos coral reefs that experienced high coral mortality (97% overall, Glynn et al. 1988) in 1982 to 1983 have not demonstrated significant recovery over a period of nearly 20 years, from just after the El Niño disturbance to the most recent sampling (1983–2002; Table 11.2). Indeed, nearly all of the coral reef buildups described in Glynn and Wellington (1983) have been reduced to sediment piles due to intense bioerosion (Glynn 1994; Reaka-Kudla et al. 1996). Although the relatively deep (14–20 m) coral community east of Onslow Island experienced severe to moderate bleaching in 1982 to 1983 and 1997 to 1998, mortality was negligible, with dense aggregations of corals persisting for 25+ years. Declines in coral cover of 16.1% to 56.1% reported by Feingold (2001) over a 2-year period were probably due to the redistribution of the mobile fungiid (*Diaseris*) and siderastreid (*Psammocora*) corals comprising this assemblage. The small areas of pocilloporid buildups at Española and Santa Fe Islands, now consisting of fragmented and dispersed rubble, also did not show signs of recovery when sampled in 2002.

Off the Pacific coast of Colombia, coral reefs at Gorgona Island experienced high mortality (>50%) in 1983 (Table 11.1). By 1998, coral cover was significantly higher on La Azufrada reef than in 1979, demonstrating recovery since the 1982 to 1983 El Niño event (Table 11.2). Panamanian reefs experienced marked declines in coral cover—76% to 90% overall—following the 1982 to 1983 El Niño event (Glynn et al. 1988). Two of the three Panamanian reefs examined here have recovered to pre-El Niño live cover levels. The Saboga Island reef, in the upwelling Gulf of Panamá, recovered fully over only an eight-year period (1984–1992). Coral cover on this reef has remained relatively constant and high during the past 10 years (1992–2002). In the nonupwelling Gulf of Chiriquí, coral cover in the shallow and deep reef zones at the Uva Island reef has fluctuated since 1983, generally showing a downward trend. Reef-flat corals in particular experienced high mortalities in 1989 and 1993, a result of extreme midday low-water exposures. At Caño Island, off the southwestern coast of Costa Rica, coral cover in all shallow to deep reef zones combined (0–14 m) declined significantly in 1985, by nearly 70%, and has remained at a low level over a 15-year period (1985–1999). Dinoflagellate blooms in 1985 caused high mortalities of pocilloporid corals, especially in shallow reef zones (Guzmán and Cortés 2001). The northernmost site examined, the Cabo Pulmo pocilloporid coral reef in the lower part of the Gulf of California, Mexico, suffered nearly a 53% decline in live cover between 1986 and 2002. Over this period, the majority of the corals died from the

Table 11.2. Long-term changes in coral cover in the equatorial eastern Pacific following coral bleaching/mortality caused by elevated sea water temperature associated with El Niño events of the 1980s and 1990s. NA, not applicable

Locality and coral reef site	Depth m	% live coral cover year	% live coral cover mean ± SD	% change	Recovery	No. years observed	t-test	Source
Galápagos Islands								
Onslow Is. reef	0.5–5	1975	37.1 ±20.8	−99.2	no	27	$p<0.001$	Glynn, unpublished data
		2002	0.3 ±0.5					
Onslow Is. east	14–20	1975	80-100[1]	negligible	yes	25	NA	Glynn and Wellington (1983)
		2000	80-100					Robinson (1985)
								Feingold (2001)
Española Is.								
Xarifa coral community	1–3	1975	37.0 ±12.1	−99.7	no	27	$p<0.001$	Glynn, unpublished data
		2002	0.1 ±0.2					
Santa Fe Is.,								
NE anchorage	2–3	1976	48.0 ±23.2	−100	no	26	NA	Glynn, unpublished data
		2002	0					
Colombia								
Gorgona Is.								
La Azufrada reef	0.3–15	1979	36.5 ±29.6	+44.9	yes	19	0.001	Glynn et al. (1982)
		1998	66.2 ±20.6				$<p<0.01$	Vargas-Ángel et al. (2001)
Panamá								
Gulf of Panamá								
Saboga Is. reef	2–3	1971	45–55[2]	−100	no	13	NA	Glynn, unpublished data
		1984	0					Richmond, unpublished data
		1992–2002	47-52	+100	yes	10	NA	
Gulf of Chiriquí								
Uva Is. reef	3–5[3]	1974	34.7 ±21.4	−65.1	no	28	$p<0.01$	Glynn, unpublished data
		2002	12.1 ±9.2					

(*Continued*)

Table 11.2. Long-term changes in coral cover in the equatorial eastern Pacific following coral bleaching/mortality caused by elevated sea water temperature associated with El Niño events of the 1980s and 1990s. NA, not applicable (*Continued*)

Locality and coral reef site	Depth m	% live coral cover		% change	Recovery	No. years observed	t-test	Source
		year	mean ± SD					
Uva Is. reef	1 [4]	1974	39.2 ±34.0	−93.6	no	26	$p<0.001$	Glynn (1976)
		2000	2.5 ±5.1					Eakin (2001)
Secas Is. reef	3–7	1974–75	10.6 ±7.6	−28.3	yes	27–28	$p>0.6$	Glynn, unpublished data
		2002	7.6 ±12.1					
Costa Rica								
Caño Is. [5]	0.5–6	1980	17.8 ±7.2	−51.7	NA	4	$0.10>p$	Guzmán et al. (1987)
		1984	8.6 ±5.1				>0.05	
	0–14	1984	32	−68.8	no	15	–	Guzmán and Cortés (2001)
		1999	10					
Mexico								
Gulf of California								
Cabo Pulmo	0–12	1986	45.1 ±14.2	−52.6	no	16	$p<0.001$	Reyes-Bonilla and Calderón
		2002	21.4 ±15.3					Aguilera, unpublished data

[1] Estimates of range of percent coral cover within densest population aggregations of *Diaseris distorta* and *Psammocora stellata*.

[2] Range of percent cover, no replicate sampling conducted; Richmond (personal communication) recorded 100% mortality following the 1982-83 El Niño event; full recovery observed in 1992, then live cover fluctuated between 47 and 52% to 2002.

[3] Windward reef slope and reef base zones.

[4] Reef flat zone.

[5] Sampling conducted on reefs located on the north and east sides of island.

elevated temperature stress that accompanied the 1997 to 1998 ENSO, but coral mortality continued to 2002 from various causes.

In summary, about one-third of the eastern Pacific areas examined have demonstrated varying levels of recovery over periods of from 10 to 20 years. Following El Niño perturbations, coral community decline often continues due to strong upwelling, algal blooms, extreme low tidal exposures, and bioerosion. Considering present limited data, it appears that the potential for reef recovery is higher in the western Pacific than in the eastern Pacific. Possibly this is related to interregional differences in: (1) coral species diversity; (2) connectivity among reefs vis-à-vis source populations, larval dispersal, and recruitment; (3) ENSO intensity and return intervals; and (4) bioerosion.

Finally, although live coral cover is useful as an index of coral reef community recovery, one must be cognizant of the importance of other community attributes such as species composition, relative abundances, contributors to framework construction, integrity of coral frameworks, and the abundances and activities of other community members such as noncoral epibenthos (algae, sponges, zoanthids, *inter alia*), herbivores, corallivores, symbionts, and bioeroders. With the hundreds of coral reefs that have suffered high coral mortalities during recent ENSO disturbances, additional information should soon become available on the recovery process, including the mechanisms and time scales required.

11.9 The Future of Coral Reefs

Bleaching is a complex phenomenon that is generally defined as a breakdown of the symbioses between animal host and algal symbionts, and the resultant loss of algal cells or their pigments, in response to a variety of stressors. These have been characterized as "physiological bleaching," "algal-stress bleaching," and "animal-stress bleaching" by Fitt et al. (2001). While many factors have been implicated in coral bleaching responses (see for example Brown 1997), high and/or prolonged thermal and irradiance anomalies such as those associated with increasing SST and ENSO events are undoubtedly foremost in terms of their role in bleaching.

Since the unusually strong 1982 to 1983 ENSO there has been a progressive increase in sea-surface warming in both the Northern and Southern Hemispheres (Levitus et al. 2000). As a consequence of this warming, virtually every shallow (≤10–15 m) coral reef area worldwide has incurred negative effects in terms of reduced coral cover, with losses ranging from moderate to severe (especially in the eastern Pacific). Only the western African region remains unknown in this regard. As of 2002, nearly every coral reef area in the tropics and extratropics has been affected, including Easter Island (Chile), Baja California (Mexico), the Line Islands in the central Pacific, and the Houtman-Abrolhos Islands (western Australia). In the Line Islands, one of the last to have incurred bleaching for the first time, water temperatures had not previously exceeded coral bleaching thresholds (see Goreau and Hayes 1994; Strong et al. 1997).

Although good physiological models now exist describing the proximate mechanisms responsible for temperature-related coral bleaching (Warner et al. 1996, 1999; Jones et al. 1998, 2000; Gates and Edmunds 1999; Fitt et al. 2001), additional studies are needed to distinguish between the mechanisms accounting for differential responses to elevated SST and UVR. Such studies should include phenotypic responses leading to acclimation, assessment of the efficacy of natural selection, and the interactions of these processes with respect to both the coral host and its algal symbiont composition.

What is the future of coral reefs? Here we address several factors that may have a significant negative impact on reef corals. These major effects include significant increases in downwelling of potentially detrimental levels of UVR (ultraviolet radiation), including both UV-A and UV-B wavelengths. The penetration of potentially harmful UV-B wavelengths, particularly in the upper 10 m, can occur during a reduction in the vertical mixing of the water column. The second factor is sea-surface warming, which can result in coral bleaching. These two physical factors may act synergistically to damage 2 coral symbionts' photosynthetic systems PS1 and PS2 (Jones et al. 1998, 2000).

Factors that might be expected to mitigate the damaging effects of elevated temperature and light include genetic strains of corals/symbiotic algae that are able to tolerate local conditions or rapidly adapt to increased exposure to elevated temperatures and UVB radiation. We know that some coral taxa (e.g., *Porites*) are able to withstand a broad range of conditions while others are physiologically limited to a very narrow range of conditions (Hoegh-Guldberg and Salvat 1995; Marshall and Baird 2000) and are usually the first to manifest signs of bleaching (e.g., *Acropora*). Even closely related species may show marked differences in their tolerances to environmental disturbances. The high mortality and low recovery potential of *Agaricia tenuifolia* compared with *Agaricia agaricites* during and following the 1997 to 1998 ENSO event in Belize suggest that the former species has a lesser ability to produce heat shock proteins for protection against stressful elevated temperatures (Robbart et al. 2004).

What are some of the factors that correlate with an ability to resist bleaching? In general, any physical or environmental variables that serve to reduce stresses to the symbiosis between coral and zooxanthellae will tend to mitigate bleaching. In particular, the reduction of temperature and irradiance stress, increased bleaching tolerance or thresholds, or limits to the cellular damage that can occur in the bleaching response help ensure the resistance of corals and the resilience of the community (reviewed in West and Salm 2003). One common observation often made during bleaching events is that coral colonies exposed to high water flow—currents, wave action, or vertical mixing in the water column—are generally less affected by high temperatures (Jokiel and Coles 1990).

Nakamura and van Woesik (2001) described the physical mechanisms relating to the causes of bleaching in regard to water motion. Using the relationship between diffusion, shear stress, and water velocity passing over a colony, they were able to explain the mechanism responsible for observed differences in bleaching between and among individual colonies. In general, smaller colonies in high water motion environments would be expected to experience lower levels of bleaching than large colonies under the same conditions. Through empirical studies these workers determined that corals subjected to a “high-flow treatment” at 50–70 cm/s showed no bleaching compared to corals in a “low-flow treatment” at <3 cm/s, which suffered high levels of bleaching at the same temperature.

Another important factor comes from the general observation that during bleaching events corals living at deeper depths (> 15 m) generally exhibit reduced levels of bleaching compared to colonies at shallow and intermediate depths. The likely explanation is that UVR attenuates rapidly with depth, particularly the shorter and more potent UV wavelengths between 300 and 320 nm (Gleason and Wellington 1993, 1995; Wellington and Fitt 2003). Hence, depth could provide an important refuge for shade-loving, deep-water corals.

The history of previous exposure to stresses may also play a role in predicting future ability to acclimate to increasing temperatures. For example, Coles and Jokiel (1978) demonstrated that corals exposed to 32.5 °C, after being previously held at 20, 24, 26, and 28 °C, exhibited variable survival rates of 47, 30, 61, and 74%, respectively. It is not clear, however, whether these “adaptive” changes represented differential survivorship based on genetic differences or physiological adaptation.

Arising from this initial work, Buddemeier and Fautin (1993) proposed that corals could adapt to environmental extremes by changing their algal partners involved in the symbiosis. The “adaptive bleaching hypothesis” (ABH) posits the formation of new symbiotic consortiums with different zooxanthellae more suited to current conditions experienced by the host coral. The fundamental tenets of the ABH assume that different types of zooxanthellae respond differently to environmental conditions, particularly temperature, and that bleached corals can acquire zooxanthellae from the environment. Recently, Kinzie et al. (2001) conducted simple tests of the ABH assumptions. They found that (1) bleached adult hosts could acquire algae secondarily from the environment in a dose-dependent manner and (2) genetically different strains of zooxanthellae exhibited variations in growth rate at different temperatures.

Is coral bleaching really adaptive? To address this question, Baker (2001) performed an experiment with several common reef-building species that contained different “high light” and “low light” symbionts at different depths. Corals were reciprocally transplanted between shallow (2–4 m) and deep (20–23 m) sites on a Caribbean reef in Panamá. Baker observed that corals transplanted upward were significantly more bleached than those transplanted downward. However, corals transplanted downward showed significantly higher rates of mortality after one year when compared to upward transplants, despite the fact that they did not initially bleach.

These findings have stimulated interest and continuing investigations. Most work on the systematics of zooxanthellae and their potentially flexible symbioses has, until recently, involved Caribbean species. During the past few years, symbiotic associations in the Indo-Pacific have been assessed in greater detail (LaJeunesse et al. 2003; Fabricius et al. 2004), and the identification of the thermally stress-tolerant clade D zooxanthellae has allowed for further investigations of the ABH. It is now recognized that considerable flexibility of symbioses can and does occur in many, but not all, coral species. Additionally, coral species may tend to harbor en hospite symbionts adapted to ambient environmental conditions, and differential bleaching susceptibilities do exist among zooxanthellae clades, types, and species. Across numerous Indo-Pacific locations, bleaching events resulted in mortality of coral species harboring intolerant zooxanthellae, while species harboring stress-tolerant types not only survived bleaching events, but also increased their populations on reefs formerly dominated by less tolerant symbiosomes (Baker et al. 2004; Fabricius et al. 2004; Rowan 2004). Some workers share a cautiously optimistic view of the future of coral reefs and their ability to adapt to global temperature change (Baker et al. 2004; Rowan 2004) whereas others (Jokiel and Coles 1990; Hoegh-Guldberg 1999; Hughes et al. 2003; McWilliams et al. 2005) are less confident considering the present high rate of environmental change.

11.10 Summary

Despite many seemingly discordant studies indicating variability in the specifics of ENSO-related effects to coral reefs, we can offer several assertions based on a preponderance of data presented here. First, sea surface temperatures are increasing, and these increases are likely to be a signal of global warming. Second, this warming trend is contributing to increasing frequencies and intensities of ENSO events. Third, both warming sea temperatures and ENSO-related climate change have a pronounced deleterious effect on corals and coral reefs, primarily through temperature and ENSO-related coral bleaching events that directly affect the structure and function of reef communities. When added to the numerous other biotic and abiotic stressors currently affecting coral reefs globally, there is considerable uncertainty over the short-term and even long-term persistence of these diverse and critically important biological and geological structures.

Acknowledgments. Thanks are due J. K. Oliver for providing data on bleaching events and permission to reproduce Figures 2A and 2B, and C. M. Eakin, A. Hazra, J.A. Kleypas, J. Luo, J.L. Maté, H. Reyes-Bonilla, and B. Riegl for data and critiques that helped to improve this review. Special thanks are due R.B. Aronson for his various editorial skills. The US National Science Foundation ESH Program (GMW), the Paleoclimate Program of NOAA (GMW), the National Geographic Society (GMW), the National Center for Caribbean Coral Reef Research (PWG), and the Biological Oceanography Program of the U.S. National Science Foundation (PWG) supported much of this work. We acknowledge the generous assistance of the administrative staff of the Charles Darwin Research Station, the Galápagos National Park Service, and the Smithsonian Tropical Research Institute, Panamá. Assistance from E. Borneman and D. Holstein in the final manuscript preparation is also gratefully acknowledged.

References

Allan, R., J. Lindesay, and D. Parker. 1996. El Niño Southern Oscillation and climatic variability. Australia, CSIRO.

Baker, A.C. 2001. Reef corals bleach to survive change. *Nature* 411:765–766.

Baker, A.C., C.J. Starger, T.R. McClanahan, and P.W. Glynn. 2004. Corals' adaptive response to climate change. *Nature* 430:741.

Baquero-Bernal, A., M. Latif, and S. Legutke. 2002. On the dipolelike variability of sea surface temperature in the tropical Indian Ocean. *J. Climate* 15:1358–1368.

Berkelmans, R. 2002. Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 229:73–82.

Birkeland, C., and J.S. Lucas. 1990. *Acanthaster planci*: *Major Management Problem of Coral Reefs*. Boca Raton: CRC Press.

Bjerknes, J. 1969. Atmospheric teleconnections from the equatorial Pacific. *Mon. Weather Rev.* 97:163–172.

Bjerknes, J. 1972. Large-scale atmospheric response to the 1964–65 Pacific equatorial warming. *J. Phys. Oceanogr.* 2:212–217.

Brown, B.E. 1987. Worldwide death of corals—Natural cyclical events or man-made pollution? *Mar. Pollut. Bull.* 18:9–13.

Brown, B.E. (ed.). 1990. Coral bleaching. *Coral Reefs* (special issue) 8:153–232.

Brown, B.E. 1997. Coral bleaching: Causes and consequences. *Proc. Eighth Int. Coral Reef Symp., Panamá* 1:65–74.

Brown, B.E., M.D. Le Tissier, R.P. Dunne, and T.P. Scoffin. 1993. Natural and anthropogenic disturbances on intertidal reefs of S.E. Phuket, Thailand 1979–1992. In *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History,* compiler R.N. Ginsburg, 278–285. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida.

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

Buddemeier, R.W. 1992. Corals, climate and conservation. *Proc. Seventh Int. Coral Reef Symp., Guam* 1:3–10.

Buddemeier, R.W., and D.G. Fautin. 1993. Coral bleaching as an adaptive mechanism. *BioScience* 43:320–326.

Cane, M.A. 1983. Oceanographic events during El Niño. *Science* 222:1189–1195.

Cane, M.A. 1986. El Niño. *Ann. Rev. Planet. Sci.* 4:43–70.

Carriquiry, J.D., A.L. Cupul-Magaña, F. Rodríguez-Zaragoza, and P. Medina-Rosas. 2001. Coral bleaching and mortality in the Mexican Pacific during the 1997-98 El Niño and prediction from a remote sensing approach. *Bull. Mar. Sci.* 69:237–249.

Carriquiry, J.D., and H. Reyes-Bonilla. 1997. Community structure and geographic distribution of the coral reefs of Nayarit, Mexican Pacific. *Cienc. Mar*. 23:227–248.

Carriquiry, J.D., M.J. Risk, and H.P. Schwarcz. 1988. Timing and temperature record from stable isotopes of the 1982-1983 El Niño warming event in eastern Pacific corals. *Palaios* 3:359–364.

Chansang, H., and N. Phongsuwan. 1993. Health of fringing reefs of Asia through a decade of change: A case history from Phuket Island, Thailand. In *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History,* compiler R.N. Ginsburg, 286–292. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida.

Chesher, R.H. 1969. Destruction of Pacific corals by the sea star *Acanthaster planci. Science* 165:280–283.

Clement, A., C.R. Seager, and M.A. Cane. 1999. Orbital controls on the El Niño/Southern Oscillation and the tropical climate. *Paleoceanography* 14:441–456.

Coffroth, M.A., H.R. Lasker, and J.K. Oliver. 1990. Coral mortality outside of the eastern Pacific during 1982–1983: Relationship to El Niño. In *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation,* ed. P.W. Glynn, 141–182. Amsterdam: Elsevier Oceanography Series 52.

Cohen, A.L., G.D. Layne, S.R. Hart, and P.S. Lobel. 2001. Kinetic control of skeletal Sr/Ca in a symbiotic coral: Implications for the paleotemperature proxy. *Paleoceanography* 16:20–26.

Cohen, A.L., K.E. Owens, G.D. Layne, and N. Shimizu. 2002. The effect of algal symbionts on the accuracy of Sr/Ca paleotemperatures from coral. *Science* 296: 331–333.

Coles, S.L., and P.L. Jokiel. 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Mar. Biol.* 49:187–195.

Colgan, M.W. 1990. El Niño and the history of eastern Pacific reef building. In *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation,* ed. P.W. Glynn, 183–232. Amsterdam: Elsevier Oceanography Series 52.

Connell, J.H. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16:S101–S113.

Crowley, T.J., 2000. Causes of climate change over the past 1000 years. *Science* 289:270–277.

Crowley, T.J., and G.R. North. 1991. Time series analysis of paleoclimate records. In *Paleoclimatology*, 132–151. New York: Oxford Monographs on Geology and Geophysics, No. 16.

D'Elia, C.F., R.W. Buddemeier, and S.V. Smith. 1991. Workshop on coral bleaching, coral reef ecosystems, and global change: Report of proceedings. Maryland Sea Grant Coll. Publ. No. UM-SG-TS-91-03. College Park: University of Maryland.

de Villiers, S., B.K. Nelson, and A.R. Chivas. 1995. Biological controls on coral Sr/Ca and $\delta^{18}O$ reconstructions of sea surface temperatures. *Science* 269:1247–1249.

DeVries, T.J. 1987. A review of geological evidence for ancient El Niño activity in Peru. *J. Geophys. Res.* 92:14,471–14,479.

Done, T.J. 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: Evidence of population resilience? *Coral Reefs* 6:75–90.

Dunbar, R.B., G.M. Wellington, M.W. Colgan, and P.W. Glynn. 1994. Eastern Pacific sea surface temperature since 1600 A.D.: The $\delta^{18}O$ record of climate variability in Galápagos corals. *Paleoceanography* 9:291–315.

Eakin, C.M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15:109–119.

Eakin, C.M. 2001. A tale of two ENSO events: Carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panamá. *Bull. Mar. Sci.* 69:171–186.

Enfield, D.B. 1992. Historical and prehistorical overview of El Niño/Southern Oscillation. In *El Niño: Historical and Paleoclimatic Aspects of the Southern Oscillation*, eds. H.F. Diaz and V. Markgraf, 95–117. Cambridge: Cambridge University Press.

Enfield, D.B. 2001. Evolution and historical perspective of the 1997-1998 El Niño-Southern Oscillation event. *Bull. Mar. Sci.* 69:7–25.

Enfield, D.B., and M.A. Mestas-Nuñez. 1999. Multiscale variabilities in global sea surface temperatures and their relationships with tropospheric climate patterns. *J. Climate* 12:2719–2733.

Enfield, D.B., and D.A. Mayer. 1997. Tropical Atlantic sea surface temperature variability and its relation to El Niño-Southern Oscillation. *J. Geophys. Res.* 102:929–945.

Fabricius, K.E., J.C. Mieog, P.L. Colin, D. Idip, and M.J.H. van Oppen. 2004. Identity and diversity of coral endosymbionts (zooxanthellae) from three Palauan reefs with contrasting bleaching, temperature and shading histories. *Mol. Ecol.* 13:2445–2458.

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

Fitt, W.K., B.E. Brown, M.E. Warner, and R.P. Dunne. 2001. Coral bleaching: Interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51–65.

Fong, P., and P.W. Glynn. 1998. A dynamic size-structured population model: Does disturbance control size structure of a population of the massive coral *Gardineroseris planulata* in the eastern Pacific. *Mar. Biol.* 130:663–674.

Gates, R.D., and P.J. Edmunds. 1999. The physiological mechanisms of acclimation in tropical corals. *Am. Zool.* 39:30–43.

Ginsburg, R.N., (compiler). 1993. *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History*. Rosenstiel School of Marine and Atmospheric Science, University of Miami.

Gleason, D.F., and G.M. Wellington. 1993. Ultraviolet radiation and coral bleaching. *Nature* 365:836–838.

Gleason, D.F., and G.M. Wellington. 1995. Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Mar. Biol.* 123:693–703.

Glynn, P.W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecol. Monogr.* 46:431–456.

Glynn, P.W. 1984. Widespread coral mortality and the 1982/83 El Niño warming event. *Environ. Conserv.* 11:133–146.

Glynn, P.W. 1985. El Niño-associated disturbance to coral reefs and post disturbance mortality by *Acanthaster planci*. *Mar. Ecol. Prog. Ser.* 26:295–300.

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

Glynn, P.W. (ed.). 1990a. *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation*. Amsterdam: Elsevier Oceanography Series 52.

Glynn, P.W. 1990b. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In *Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation*, ed. P.W. Glynn, 55–126. Amsterdam: Elsevier Oceanography Series 52.

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

Glynn, P.W. 1994. State of coral reefs in the Galápagos Islands: Natural vs anthropogenic impacts. *Mar. Pollut. Bull.* 29:131–140.

Glynn, P.W. 2000. El Niño-Southern Oscillation mass mortalities of reef corals: A model of high temperature marine extinctions? In *Carbonate Platform Systems: Components and Interactions*, eds. E. Insalaco, P.W. Skelton, and T.J. Palmer, 117–133. Geological Society, London, Special Publications.

Glynn, P.W. 2002. Effects of the 1997–98 El Niño-Southern Oscillation on eastern Pacific corals and coral reefs: An overview. *Proc. Ninth Int. Coral Reef Symp., Bali* 2:1169–1174.

Glynn, P.W. 2003. Coral communities and coral reefs of Ecuador. In *Latin American Coral Reefs*, ed. J. Cortés, 449–472. Amsterdam: Elsevier.

Glynn, P.W., and S.B. Colley. 2001. A collection of studies on the effects of the 1997–98 El Niño-Southern Oscillation event on corals and coral reefs in the eastern tropical Pacific. *Bull. Mar. Sci.* 69:1–288.

Glynn, P.W., S.B. Colley, J.H. Ting, J.L. Maté, and H.M. Guzmán. 2000. Reef coral reproduction in the eastern Pacific: Costa Rica, Panamá and Galápagos Islands (Ecuador). IV. Agariciidae, recruitment and recovery of *Pavona varians* and *Pavona* sp. a. *Mar. Biol.* 136:785–805.

Glynn, P.W., J. Cortés, H.M. Guzmán, and R.H. Richmond. 1988. El Niño (1982-83) associated coral mortality and relationship to sea surface temperature deviations in the tropical eastern Pacific. *Proc. Sixth Int. Coral Reef Symp., Australia* 3:237–243.

Glynn, P.W., and L. D'Croz. 1990. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8:181–191.

Glynn, P.W., R. Imai, K. Sakai, Y. Nakano, and K. Yamazato. 1992. Experimental responses of Okinawan (Ryukyu Islands, Japan) reef corals to high sea temperature and UV radiation. *Proc. Seventh Int. Coral Reef Symp., Guam* 1:27–37.

Glynn, P.W., and G.E. Leyte Morales. 1997. Coral reefs of Huatulco, west México: Reef development in upwelling Gulf of Tehuantepec. *Rev. Biol. Trop.* 45:1033–1047.

Glynn, P.W., J.L. Maté, A.C. Baker, and M.O. Calderón. 2001. Coral bleaching and mortality in Panamá and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull. Mar. Sci.* 69:79–109.

Glynn, P.W., M. Perez, and S.L. Gilchrist. 1985. Lipid decline in stressed corals and their crustacean symbionts. *Biol. Bull.* 168:276–284.

Glynn, P.W., H.V. Prahl, and F. Guhl. 1982. Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on coral community structure and development. *An. Inst. Invest. Mar. Punta Betín* 12:185–214.

Glynn, P.W., J.E.N. Veron, and G.M. Wellington. 1996. Clipperton Atoll (eastern Pacific): Oceanography, geomorphology, reef-building coral ecology and biogeography. *Coral Reefs* 15:71–99.

Glynn, P.W., and G.M. Wellington. 1983. *Corals and Coral Reefs of the Galápagos Islands*. Berkeley: University of California Press.

Goreau, T.J., and R.L. Hayes. 1994. Coral bleaching and ocean "hot spots". *Ambio* 23:176–180.

Goreau, T.J., and A.H. Macfarlane. 1990. Reduced growth rate of *Montastraea annularis* following the 1987–1988 coral-bleaching event. *Coral Reefs* 8:211–215.

Goreau, T., T. McClanahan, R. Hayes, and A. Strong. 2000. Conservation of coral reefs after the 1998 global bleaching event. *Conserv. Biol.* 14:5–15.

Graham, N.E. 1995. Simulation of recent global temperature trends. *Science* 267:666–671.

Guilderson, T., and D.P. Schrag. 1998. Abrupt shift in subsurface temperatures in the tropical Pacific associated with changes in El Niño. *Science* 281:240–243.

Guzmán, H.M., and J. Cortés. 1992. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982–83 El Niño disturbance. *Rev. Biol. Trop.* 40:309–324.

Guzmán, H.M., and J. Cortés. 2001. Changes in reef community structure after fifteen years of natural disturbance in the eastern Pacific (Costa Rica). *Bull. Mar. Sci.* 69:133–149.

Guzmán, H.M., J. Cortés, R.H. Richmond, and P.W. Glynn. 1987. Efectos del fenómeno de "El Niño Oscilación Sureña" 1982/83 en los arrecifes coralinos de la Isla del Caño, Costa Rica. *Rev. Biol. Trop.* 35:325–333.

Hansen, D.V. 1990. Physical aspects of the El Niño event of 1982–1983. In *Global Ecological Consequences of the 1982–1983 El Niño-Southern Oscillation*, ed. P.W. Glynn, 1–20. Amsterdam: Elsevier Oceanography Series 52.

Harmelin-Vivien, M.L., and P. Laboute. 1986. Catastrophic impact of hurricanes on atoll outer reef slopes in the Tuamotu (French Polynesia). *Coral Reefs* 5:55–62.

Harvell, C.D., K. Kim, J.M. Burkholder, R.R. Colwell, P.R. Epstein, J. Grimes, E.E. Hofmann, E.K. Lipp, A.D.M.E. Osterhaus, R. Overstreet, J.W. Porter, G.W. Smith, and G.R. Vasta. 1999. Emerging marine diseases—Climate links and anthropogenic factors. *Science* 285:1505–1510.

Harvell, C.D., K. Kim, C. Quirolo, J. Weir, and G. Smith. 2001. Coral bleaching and disease contributors to 1998 mass mortality in *Briareum asbestinum* (Octocorallia, Gorgonacea). *Hydrobiologia* 460:97–104.

Hirose, M., and M. Hidaka. 2000. Reduced reproductive success in scleractinian corals that survived the 1998 bleaching in Okinawa. *Galaxea* 2:17–21.

Hoegh-Guldberg, O. 1999. Coral bleaching, climate change and the future of the world's coral reefs. *Mar. Freshwater Res.* 50:839–866.

Hoegh-Guldberg, O., and B. Salvat. 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.

Hudson, J.H. 1981. Growth rates in *Montastraea annularis*: A record of environmental change in Key Largo Marine Sanctuary, Florida. *Bull. Mar. Sci.* 31:444–459.

Hudson, J.H., E.A. Shinn, R.B. Halley, and B. Lidz. 1976. Sclerochronology—A tool for interpreting past environments. *Geology* 4:361–364.

Hughen, K.A., D.P. Schrag, S.B. Jacobsen, and W. Hantoro. 1999. El Niño during the last interglacial period recorded to a fossil coral from Indonesia. *Geophys. Res. Lett.* 26:3129–3132.

Hughes, T.P., A.H. Baird, D.R. Bellwood, M. Card, S.R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J.B.C. Jackson, J. Kleypas, J.M. Lough, P. Marshall, M. Nyström, S.R. Palumbi, J.M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933.

IPCC. 1992. Climate change 1992: The supplementary report to the IPCC scientific assessment. Intergovernmental Panel on Climate Change, eds. J.T. Houghton, B.A. Callander, and S.K. Varney. Cambridge: Cambridge University Press.

IPCC. 1996. Climate change 1995: The science of climate change. Contribution of working group I to the second assessment report of the Intergovernmental Panel on Climate Change, eds. J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg, and K. Maskell. Cambridge: Cambridge University Press.

IPCC. 2001. Climate change 2001: The scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change, eds. J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson. Cambridge: Cambridge University Press.

Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs* 16:S23–S32.

Jiménez, C., J. Cortés, A. León, and E. Ruíz. 2001. Coral bleaching and mortality associated with the 1997-98 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). *Bull. Mar. Sci.* 69:151–169.

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.

Jones, R.J., O. Hoegh-Guldberg, W.D. Larkum, and U. Schreiber. 1998. Temperature-inducing bleaching of corals begins with impairment of the carbon dioxide fixation mechanism in zooxanthellae. *Plant Cell Environ.* 21:1219–1230.

Jones, R.J., S. Ward, A.Y. Amri, and O. Hoegh-Guldberg. 2000. Changes in quantum efficiency of Photosystem II of symbiotic dinoflagellatateses after heat stress, and of bleached corals sampled after the 1998 Great Barrier Reef mass bleaching event. *Mar. Freshwater Res.* 51:63–71.

Karl, T.R., W. Knight, and B. Baker. 2000. The record breaking global temperatures of 1997–1998: Evidence for an increase in the rate of global warming? *J. Geophys. Res.* 27:719–722.

Kinzie, R.A., III, M. Takayama, S.R. Santos, and M.A. Coffroth. 2001. The adaptive bleaching hypothesis: Experimental tests of critical assumptions. *Biol. Bull.* 200:51–58.

Kleypas, J.A., R.W. Buddemeier, D. Archer, J.-P. Gattuso, C. Langdon, and B. Opdyke. 1999. Geochemical consequences of increased atmospheric CO_2 on coral reefs. *Science* 284:118–120.

Kleypas, J.A., R.W. Buddemeier, and J.-P. Gattuso. 2001. The future of coral reefs in an age of global change. *Int. J. Earth Sci. (Geol. Rundsch.)* 90:426–437.

Knutson, D.W., R. Buddemeier, and S.V. Smith. 1972. Coral chronometers: Seasonal growth bands in reef corals. *Science* 177:270–272.

Koutavas, A., J. Lynch–Stieglitz, T.M. Marchitto, Jr., and J.P. Sachs. 2002. El Niño-like pattern in ice age tropical Pacific sea surface temperature. *Science* 297:226–229.

Kushmaro, A., Y. Loya, M. Fine, and E. Rosenberg. 1996. Bacterial infection and coral bleaching. *Nature* 380:396.

Laboute, P. 1985. Evaluation of damage done by the cyclones of 1982–1983 to the outer slopes of the Tikehau and Takapoto Atolls (Tuamotu Archipelago). *Proc. Fifth Int. Coral Reef Congr.*, *Tahiti* 3:323–329.

LaJeunesse, T.C., W.K.H. Loh, R. van Woesik, O. Hoegh-Guldberg, G.W. Schmidt, and W.K. Fitt. 2003. Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. *Limnol. Oceanogr.* 48:2046–2054.

Lau, K.-M., and H. Weng. 1999. Interannual, decadal-interdecadal, and global warming signals in sea surface temperature during 1955–1997. *J. Climate* 12:1257–1267.

Levitus, L., J.I. Antonov, P.B. Boyer, and C. Stephens. 2000. Warming of the world ocean. *Science* 287:2225–2229.

Linsley, B.K., G.M. Wellington, and D.P. Schrag. 2000. Decadal sea surface temperature variability in the subtropical South Pacific from 1726 to 1997 A. D. *Science* 290:1145–1148.

Lirman, D., P.W. Glynn, A.C. Baker, and G.E. Leyte Morales. 2001. Combined effects of three sequential storms on the Huatulco coral reef tract, Mexico. *Bull. Mar. Sci.* 69:267–278.

Lough, J.M. 1994. Climate variation and El Niño-Southern Oscillation events on the Great Barrier Reef: 1958 to 1987. *Coral Reefs* 13:181–195.

Lough, J.M. 2000. 1997–98: Unprecedented thermal stress to coral reefs? *Geophys. Res. Lett.* 27:3901–3904.

Ma, T.Y.H. 1933. On the seasonal change of growth in some Palaeozoic corals. *Proc. R. Acad. Tokyo* 9:407–409.

Margalef, R. 1968. *Perspectives in Ecological Theory*. Chicago: University of Chicago Press.

Marshall, P.A., and A.H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs* 19:155–163.

Mascarelli, P., and L. Bunkley-Williams. 1999. An experimental field evaluation of healing in damaged, unbleached and artificially bleached star coral, *Montastrea annularis. Bull. Mar. Sci.* 65:577–586.

McPhaden, M.J. 1999. Genesis and evolution of the 1997–98 El Niño. *Science* 283:950–954.

McWilliams, J.P., I.M. Côté, J.A. Gill, W.J. Sutherland, and A.R. Watkinson. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* 86:2055–2060.

Meesters, E.H., and R.P.M. Bak. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar. Ecol. Prog. Ser.* 96:189–198.

Meibom, A., M. Stage, J. Wooden, B.R. Constantz, R.B. Dunbar, A. Owen, N. Grumet, C.R. Bacon, and C.P. Chamberlain. 2003. Monthly strontium/calcium oscillations in symbiotic coral aragonite: biological effects limiting the precision of the paleotemperature proxy. *Geophys. Res. Lett.* 30(7, 1418), doi:10.1029/2002GLO16864. 71-1–71-4.

Murphy, R.C. 1926. Oceanic and climatic phenomena along the west coast of South America during 1925. *Geogr. Rev.* 16:26–54.

Nakamura, T., and R. van Woesik. 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.

Odum, H.T., and E.P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25:291–320.

Ogden, J., and R. Wicklund. (eds.). 1988. Mass bleaching of coral reefs in the Caribbean: A research strategy. *NOAA's Undersea Research Program, Res. Rep.* 88–2.

Omori, M., H. Fukami, H. Kobinata, and M. Hatta. 2001. Significant drop of fertilization of *Acropora* corals in 1999: An after-effect of heavy coral bleaching? *Limnol. Oceanogr*. 46:704–706.

Ortlieb, L., and J. Machare. 1993. Former El Niño events: Records from western South America. *Global Planet. Change* 7:181–202.

Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R.R. Warner, and J.B.C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958.

Philander, S.G.H. 1990. *El Niño, La Niña, and the Southern Oscillation*. New York: Academic Press.

Pittock, A.B. 1999. Coral reefs and environmental change: Adaptation to what? *Am. Zool.* 39:10–29.

Podestá, G.P., and P.W. Glynn. 1997. Sea surface temperature variability in Panamá and Galápagos: Extreme temperatures causing coral bleaching. *J. Geophys. Res.* 102:15,749–15,759.

Podestá, G.P., and P.W. Glynn. 2001. The 1997-98 El Niño event in Panamá and Galápagos: An update of thermal stress indices relative to coral bleaching. *Bull. Mar. Sci*. 69:43–59.

Porter, J.W. (ed.). 2001. *The Ecology and Etiology of Newly Emerging Marine Diseases*. Dordrecht: Kluwer Academic Publishers.

Prahl, H. von. 1983. Blanqueo masivo y muerte de corales en la Isla de Gorgona, Pacífico Colombiano. *Cespedesia* 12:125–129.

Prahl, H. von. 1985. Blanqueo y muerte de corales hermatípicos en el Pacífico Colombiano atribuidos al fenómeno de El Niño 1982–83. *Bol. ERFEN* 12:22–24.

Quinn, W.H., and V.T. Neal. 1995. The historical record of El Niño events. In *Climate Since A.D. 1500*, eds. R.S. Bradley and P.D. Jones, 623–648. New York: Routledge.

Quinn, W.H., V.T. Neal, and S.E. Antunez de Mayolo. 1987. El Niño occurrences over the past four and a half centuries. *J. Geophys. Res.* 92:14449–14461.

Rasmusson, E.M., and T.H. Carpenter. 1982. Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. *Mon. Weather Rev.* 110:354–384.

Reaka-Kudla, M.L., J.S. Feingold, and P.W. Glynn. 1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. *Coral Reefs* 15:101–107.

ReefBase. 2002. Online map. In *ReefBase: A global information system on coral reefs*, eds. J. Oliver and M. Noordeloos. World Wide Web electronic publication. 6 August 2002.

Reyes-Bonilla, H. 1993. The 1987 coral bleaching at Cabo Pulmo reef, Gulf of California. *Bull. Mar. Sci.* 52:832–837.

Reyes-Bonilla, H. 2001. Effects of the 1997–1998 El Niño-Southern Oscillation on coral communities of the Gulf of California, Mexico. *Bull. Mar. Sci.* 69:251–266.

Reyes-Bonilla, H., J.D. Carriquiry, G.E. Leyte-Morales, and A.L. Cupul-Magaña. 2002. Effects of the El Niño-Southern Oscillation and the anti-El Niño event (1997–1999) on coral reefs of the western coast of México. *Coral Reefs* 21:368–372.

Reynolds, R.W., and T.M. Smith. 1994. Improved sea surface temperature analysis using optimal interpolation. *J. Climate* 7:929–948.

Riedinger, M.A., M. Steinitz-Kannan, W.M. Last, and M. Brenner. 2002. A ~ 6100 ^{14}C yr record of El Niño activity from the Galápagos Islands. *J. Paleolimnol.* 27:1–7.

Robbart, M.L., P. Peckol, S.P. Scordilis, H.A. Curran, and J. Brown-Saracino. 2004. Population recovery and differential heat shock protein expression for the corals *Agaricia agaricites* and *A. tenuifolia* in Belize. *Mar. Ecol. Prog. Ser.* 283:151–160.

Robinson, G. 1985. Influence of the 1982–83 El Niño on Galápagos marine life. In *El Niño in the Galápagos Islands: The 1982-1983 event*, eds. G. Robinson and E.M. del Pino, 153–190. Charles Darwin Foundation for the Galápagos Islands, Quito, Ecuador.

Rodbell, D.T., G.S. Seltz, D.M. Anderson, M.B. Abbott, D.B. Enfield, and J.H. Newman. 1999. An ~15,000-year record of Niño-driven alluviation in southwest Ecuador. *Science* 283:516–520.

Rowan, R. 2004. Thermal adaptation in reef coral symbionts. *Nature* 430:742.

Rowan, R., N. Knowlton, A. Baker, and J. Jara. 1997. Landscape ecology of algae symbionts creates variation in episodes of coral bleaching. *Nature* 388:265–269.

Sandweiss, D.H., J.B. Richardson, III, E.J. Reitz, H.B. Rollins, and K.A. Maasch. 1996. Geoarchaeological evidence from Perú for a 5000 years B.P. onset of El Niño. *Science* 273:1531–1533.

Schrag, D.P. 1999. Rapid analysis of high-precision Sr/Ca ratios in scleractinian corals and other marine carbonates. *Paleoceanography* 14:97–102.

Schrag, D.P., and B.K. Linsley. 2002. Corals, chemistry and climate. *Science* 296:277–278.

Scott, P.J.B., M.J. Risk, and J.D. Carriquiry. 1988. El Niño, bioerosion and the survival of east Pacific reefs. *Proc. Sixth Int. Coral Reef Symp.*, *Australia* 2:517–520.

Shein, K.A. (ed.). 2006. State of the climate in 2005. *Bull. Amer. Meteorol. Soc. (Spec. Suppl.)* 87:S1–S102.

Smith, S.V., and R.W. Buddemeier. 1992. Global change and coral reef ecosystems. *Ann. Rev. Ecol. Syst.* 23:89–118.

Stott, L., C. Poulsen, S. Lund, and R. Thunell. 2002. Super ENSO and global climate oscillations at millennial time scales. *Science* 297:222–226.

Stott, P.A., S.F.B. Tett, G.S. Jones, M.A. Allen, J.F.B. Mitchell, and G.J. Jenkins. 2000. External control of 20th century temperature by natural and anthropogenic forcings. *Science* 290:2133–2137.

Strong, A., C.B. Barrientos, C. Duda, and J. Sapper. 1997. Improved satellite techniques for monitoring coral reef bleaching. *Proc. Eighth Int. Coral Reef Symp.*, *Panamá* 2:1495–1498.

Szmant, A.M., and N.J. Gassman. 1990. The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastraea annularis. Coral Reefs* 8:217–224.

Trenberth, K.E. 1997. The definition of El Niño. *Bull. Am. Meteorol. Soc.* 78:2771–2777.

Trenberth, K.E., and T.J. Hoar. 1996. The 1990-1995 El Niño-Southern Oscillation event: Longest on record. *Geophys. Res. Lett.* 23:57–60.

Tudhope, A.W., C.P. Chilcott, M.T. McCulloch, E.R. Cook, J. Chappell, R.M. Ellam, D.W. Lea, J.M. Lough, and G.B. Shimmield. 2001. Variability in the El Niño-Southern Oscillation through a glacial-interglacial cycle. *Science* 291:1511–1517.

Vargas-Ángel, B., F.A. Zapata, H. Hernández, and J.M. Jiménez. 2001. Coral and coral reef responses to the 1997-98 El Niño event on the Pacific coast of Colombia. *Bull. Mar. Sci.* 69:111–132.

Walker, G.T., and E.W. Bliss. 1930. World weather IV: Some applications to seasonal foreshadowing. *Mem. R. Meteorol. Soc.* 3:82–95.

Warner, M.E., W.K. Fitt, and G.W. Schmidt. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae *in hospite* from four species of reef coral: A novel approach. *Plant Cell Environ.* 19:291–299.

Warner, M.E., W.K. Fitt, and G.W. Schmidt. 1999. Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. *Proc. Natl. Acad. Sci. USA* 96: 8007–8012.

Wellington, G.M., and W.K. Fitt. 2003. Influence of UV radiation on the survival of larvae from broadcast-reef corals. *Mar. Biol.* 143:1185–1192.

Wellington, G.M., and P.W. Glynn. 1983. Environmental influences on skeletal banding in eastern Pacific (Panamá) corals. *Coral Reefs* 1:215–222.

Wellington, G.M., P.W. Glynn, A.E. Strong, S.A. Navarrete, E. Wieters, and D. Hubbard. 2001. Crisis on coral reefs linked to climate change. *EOS* 82:1,5.

Wells, J.W. 1957. Coral reefs. In *Treatise on Marine Ecology and Paleoecology*, ed. J.W. Hedgpeth. Geol. Soc. Amer. Mem. 67:609–631.

West, J.M., and R.V. Salm. 2003. Resistance and resilience to coral bleaching, implications for coral reef conservation and management. *Conserv. Biol.* 17:956–967.

Wilkinson, C.R. (ed.). 1990. *Acanthaster planci. Coral Reefs* (special issue) 9:93–172.

Wilkinson, C.R. (ed.). 2000. *Status of Coral Reefs of the World: 2000*. Cape Ferguson, Queensland: Australian Institute of Marine Science.

Wilkinson, C.R. (ed.). 2002. *Status of Coral Reefs of the World: 2002*. Cape Ferguson, Queensland: Australian Institute of Marine Science.

Wilkinson, C.R., and I.G. Macintyre. (eds.). 1992. The *Acanthaster* debate. *Coral Reefs* (special issue)11:51–122.

Williams, E.H., Jr., and L. Bunkley-Williams. 1988. Bleaching of Caribbean coral reef symbionts in 1987–1988. *Proc. Sixth Int. Coral Reef Symp.*, *Australia* 3:313–318.

Williams, E.H., Jr., and L. Bunkley-Williams. 1990. The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Res. Bull.* 335:1–71.

Wyrtki, K. 1973. Teleconnections in the equatorial Pacific Ocean. *Science* 180:66–68.