Climate flickers and range shifts of reef corals

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Staghorn coral (*Acropora cervicornis*) and elkhorn coral (*Acropora palmata*), are important reef builders in the Caribbean. In the early to middle Holocene (10 000–6000 years ago), when sea temperatures were warmer than today, *Acropora*-dominated reefs were common along the east coast of Florida as far north as Palm Beach County. The fossil record shows that the northern limits of these two cold-sensitive species subsequently contracted to Biscayne Bay, south of Miami, apparently as a result of climatic cooling. This response of the *Acropora* species to climate provides a context for interpreting recent shifts in their geographic distribution. Despite recent disease-induced mass mortalities throughout the Caribbean and western Atlantic, the two species are now re-expanding their ranges northward along the Florida Peninsula and into the northern Gulf of Mexico, coincident with increasing sea temperatures. In the face of continued global warming, the northernmost limit of this range expansion will ultimately be determined by a combination of temperature and other physical constraints.

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Natural populations face impending changes in the global climate to which they will have to acclimate or adapt, or else perish. Their responses to climate change will have widespread species-level and community-level consequences, and a number of ecologists have predicted changes in the composition and distribution of future ecosystems (Fields *et al.* 1993). The fingerprint of global climate change can be mapped via the response of species to changes in their physiographic environmental settings. Hundreds of species have responded to recent warming trends by expanding their ranges to higher latitudes, as well as by changing the timing and duration of their flowering, breeding, migration, and other climate-related behaviors (Parmesan and Yohe 2003; Root *et al.* 2003).

In a nutshell:

- The ranges of staghorn and elkhorn corals were more expansive during the early to middle Holocene, when sea temperatures in the western Atlantic were warmer than they are at present
- These two coral species are currently expanding their geographic ranges northward along the Florida Peninsula and into the northern Gulf of Mexico
- The range expansion appears to be related to warming sea temperatures
- The continued northward expansion of the geographic ranges of coral species should not be accompanied by temperature-induced extinction at lower latitudes
- On the other hand, geographic shifts will not mitigate expected ecological and economic losses resulting from the reduced functions of tropical reef systems

Most predictions about the effects of global climate change on coral reefs have been confined to temperature-induced coral bleaching (Hoegh-Guldberg 1999; Walther *et al.* 2002), rising sea levels (Graus and Macintyre 1998), and changing ocean chemistry (Kleypas *et al.* 2001). Recent reports establish the first example of range expansion of a Caribbean coral genus towards the Poles, in response to climatic warming. First, spatially extensive thickets of the staghorn coral, *Acropora cervicornis* (Figure 1), were discovered off Fort Lauderdale in Broward County, Florida in 1998 (Vargas-Ángel *et al.* 2004), where they had not been observed during the 1970s and 1980s. More recently, colonies of the elkhorn coral, *Acropora palmata*, have been observed as far north as Pompano Beach in northern Broward County (Precht pers obs; Figure 2). Also, elkhorn coral was seen for the first time in 2002 on reefs of the Flower Garden Banks in the northern Gulf of Mexico (S Bernhardt pers comm). The sudden appearance of Caribbean acroporid corals well north of their previously known extant range is associated with decadal-scale increases in annual sea-surface temperature (SST) in the western Atlantic (Hoegh-Guldberg 1999; Levitus *et al.* 2000; Barnett *et al.* 2001).

Although one cannot prove directly that the recent expansion of acroporid corals is related to the impacts of climate change, fossil reefs in Florida provide an opportunity to examine the response of coral reefs to past global change, especially rapid changes in SST. Well-developed fossil Holocene reefs situated at the latitudinal extremes of reef development are juxtaposed with depauperate (low-diversity) living coral assemblages. The fossil reefs provide a baseline for understanding the response of reef systems to fluctuating climates, as well as for predicting the future response of coral reefs to global change.

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***Figure 1.** Underwater photograph showing luxuriant thickets of staghorn coral (*Acropora cervicornis*) recently found off Ft Lauderdale, FL. This is approximately 50 km north of the previous known extant range of Caribbean acroporids.*

One of the most startling aspects of the recent discovery of flourishing northern populations of *Acropora* is related to the overall poor condition of Caribbean reefs. Gardner *et al.* (2003) used meta-analysis to assess the extent of coral decline across the Caribbean since the 1970s. Their study revealed that reefs from all sectors of the region were badly affected. Disturbances of various kinds have been invoked to explain the changing face of Caribbean reefs over the past 25 years, and coral mortality, especially the mortality of *Acropora* spp, has been a major driving force in the transition (Aronson and Precht 2001). Many factors have been responsible for *Acropora* mortality, but white-band disease, temperature stress, predation, and hurricanes have all played key roles in reducing populations both locally and regionally. The acroporids are among the most important reef builders in the Caribbean, so their loss has been a major reason that Caribbean reefs have declined. In the face of this massive mortality, the recent range expansion of *Acropora* was unexpected.

Effects of temperature

Reef-building hard corals (order Scleractinia) are distributed along a latitudinal diversity gradient, with the highest species richness in the tropics. The origin and maintenance of this pattern, and especially its persistence through time, are not completely understood, but temperature has long been considered the main controlling factor on the distribution of these species. The optimum temperature for coral growth is about 26° to 28°C. Low-temperature tolerances are not well defined for corals, but early experiments documented 16°C as stressful to most species and showed that exposure to temperatures below 15°C can result in mortality (see Shinn 1989). The present-day global distribution of coral reefs generally coincides with the 18°C monthly minimum seawater isotherm (Buddemeier *et al.* 2004).

***Figure 2.** Underwater photograph of the northernmost known colony of elkhorn coral (*Acropora palmata*) in the western Atlantic, located off Pompano Beach, FL.*

Coral reefs in the Florida Keys are at the northern limit of reef growth in the Americas. Caribbean acroporids are especially sensitive to cold water, and sustained low temperatures associated with the passage of winter cold fronts have caused episodic mass mortalities of staghorn and elkhorn corals in Florida and the Bahamas (Precht and Miller in press). Rapid diminution of generic diversity northwards along the east coast of Florida is due primarily to cold-temperature limitations (Porter and Tougas 2001). Although the 18°C isotherm is the approximate boundary for reef building in the western Atlantic, the ranges of a number of reef-building species extend further northwards along the east coast due to the poleward transport of warm water, via the Florida Current (a southern segment of the Gulf Stream), and to the Flower Garden Banks in the northern Gulf of Mexico, due to the influence of the warm Loop Current. During the recent past, Fowey Rocks, located southeast of Miami, was the northern extent of reef growth dominated by acroporids (Shinn *et al.* 1989; Figures 3 and 4). Assemblages of scleractinians and gorgonians (soft corals) were found north of Fowey Rocks, off

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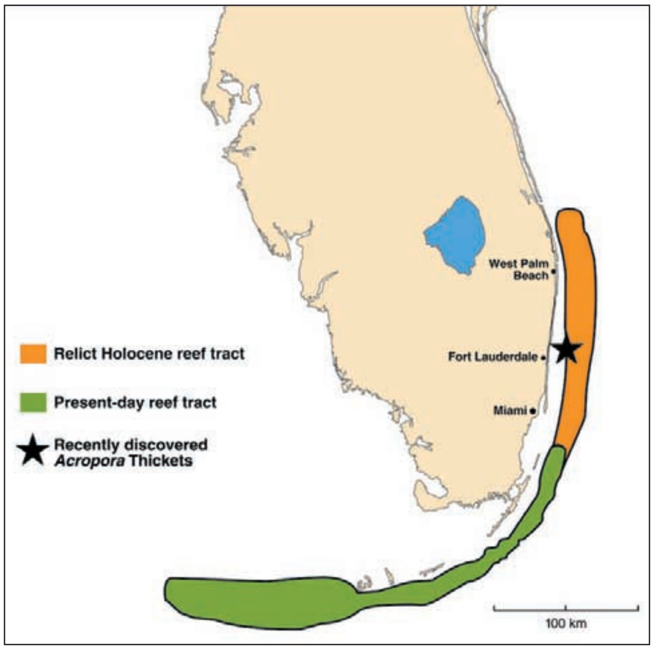

Figure 3. *Map of Florida showing the present-day distribution of the reef tract and the northern limit of acroporid corals (green), the relict Holocene reef tract dominated by acroporid corals (orange), and the location of recently discovered thickets of acroporid corals (star).*

Broward and Palm Beach Counties, with acroporid corals generally being rare (staghorn coral) or absent (elkhorn coral) (Goldberg 1973).

Corals are typically exposed during local summertime to temperatures near the upper limits of their thermal tolerances (Hoegh-Guldberg 1999). Although elevated water temperatures are clearly detrimental to corals, the response of reef ecosystems to high temperature is less clear. Unlike cold stress, there is little evidence to suggest that maximum temperature currently limits the latitudinal distribution of coral reefs (Kleypas in press). Nevertheless, coral reefs are considered to be the ecosystems most threatened by global warming (Hoegh-Guldberg 1999; Kleypas *et al.* 2001; Walther *et al.* 2002).

Field and laboratory studies have shown unequivocally that sustained, anomalously high summertime water temperatures are associated with bleaching (the expulsion of zooxanthellae by corals and other symbiotic reef organisms; Figure 5). If temperatures rise above the average maximum for a prolonged period, bleaching leads to death in many species (Hoegh-Guldberg 1999). Bleaching is not always fatal, however, and some episodes have been followed by recovery of most of the affected coral colonies (Fitt *et al.* 1993).

Coral bleaching in response to anomalously high summer-season temperatures has become more frequent since the early 1980s (Hoegh-Guldberg 1999). The widespread nature of these bleaching events over the past two decades is correlated with increases in maximum SST (Kleypas *et al.* 2001). On a global scale, temperature-induced bleaching is usually correlated with inter-annual climatic fluctuations, of which the El Niño–Southern Oscillation (ENSO) is the most important. During the ENSO-induced global coral bleaching of 1998, an estimated 16% of the world's reef-building corals died (Walther *et al.* 2002). These bleaching episodes are dramatic, but they have not been tied to the extinction of any reef-building species in the Caribbean or elsewhere. The projected continuing increase in bleaching episodes on coral reefs, related to ENSO events and augmented by global warming, is likely to decrease coral abundance in the future (Hoegh-Guldberg 1999; Wellington *et al.* 2001; Aronson *et al.* 2002; Hughes *et al.* 2003; Sheppard 2003).

The catastrophic loss of coral cover on Florida's reefs over the past 25 years (Shinn 1989; Precht and Miller in press) could persist for decades or longer. It is unclear how future global climate change will interact with disease (Figure 6) and other stresses (Harvell *et al.* 1999; Aronson and Precht 2001; Kleypas *et al.* 2001; Knowlton 2001; Hughes *et al.* 2003), but it is known that the virulence of some coral diseases increases with rising temperature (Rosenberg and Ben-Haim 2002). We are faced with two essential questions related to global temperatures: (1) will the latitudinal ranges of coral species and coral reefs expand toward the Poles?; and (2) will corals and coral reefs be eliminated from low-latitude tropical regions?

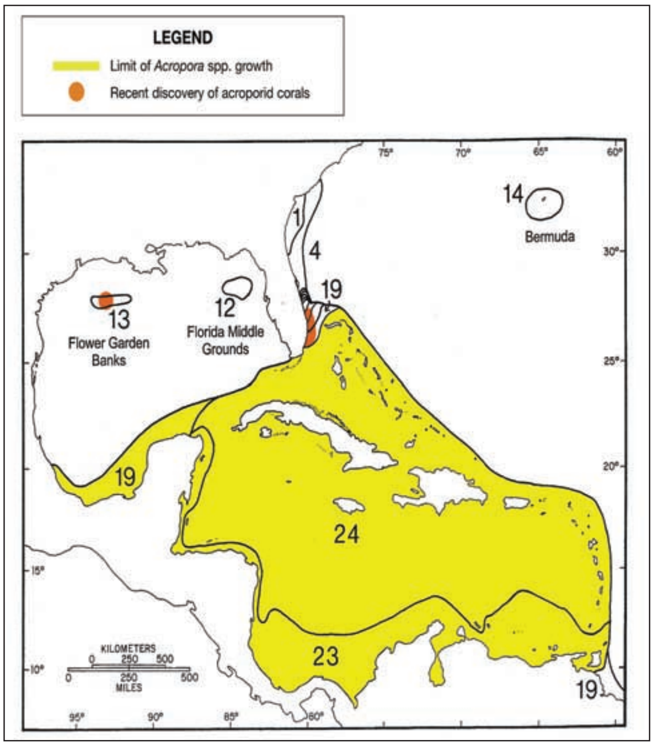

Figure 4. *Patterns of generic diversity of scleractinian corals in the Caribbean. Rapid faunal diminution along the east coast of Florida is due to cold temperature limitations. The area in yellow represents the known distribution of Caribbean acroporids. Modified from Porter and Tougas (2001).*

Figure 5*. Colony of completely bleached elkhorn coral during a severe coral bleaching event in 1998. Global coral bleaching episodes have been linked to elevated sea surface temperatures. Photo taken at Looe Key, FL, in August 1998.*

The present

Recent studies of marine and coastal systems at middle and high latitudes have suggested biogeographical shifts, with increased numbers of warm-water species and decreased numbers of cold-water species (Weinberg *et al.* 2002). Few studies have documented such changes in the tropics, and we know very little about the response of the extant biota at lower latitudes in the marine realm. Predicted increases in tropical temperatures (Buddemeier *et al.* 2004) will probably have dramatic effects on the structure and function of these ecosystems and their services (Walther *et al.* 2002), including the introduction, spread, and dominance of exotic species, and the possible extinction of native species (McLaughlin *et al.* 2002; Stachowicz *et al.* 2002).

There is mounting evidence that coral species are responding to recent patterns of increased SSTs by expanding their latitudinal ranges. One example is the recent range expansion in the Caribbean and Gulf of Mexico of *Tubastrea coccinea*, the first Indo–Pacific coral species known to have been introduced to the western Atlantic (Fenner 2001). In Florida, numerous thickets of staghorn coral, some up to 700 m^2 in area, are now established north of their previously known range. Detailed studies documenting the composition, structure, and reproductive viability of these populations have been conducted in seven of these thickets (Vargas-Ángel *et al.* 2004). Elkhorn coral has also been observed colonizing shallow reef areas north of extant populations. The two *Acropora* species have expanded more than 50 km northward in just the last few decades.

Many factors could be causing the recent change in distribution of acroporid corals, including competition with macroalgae, changes in habitat quality, short-term population variability, indirect interspecific interactions, and variations in reproductive and recruitment success. Abiotic parameters influencing their distribution could include changes in turbidity and water quality, the magnitude and frequency of ENSO events, variations in local and regional hydro-meteorological forcing patterns, changes in the direction and intensity of the northward-flowing Florida Current, and changing patterns in the frequency and duration of upwelling. Although it is likely that many of these processes are occurring and interacting with one another, the most obvious explanation for the recent range expansion of acroporids is climatic warming. We draw this inference based on the following observations:

(1) The geographic distribution of reef-building corals along the east coast of Florida is, in general, strongly correlated with temperature
(2) *Acropora* spp are temperature-sensitive, and episodes of mass mortality in Florida have been linked to cold-water outbreaks
(3) The recent range expansion of the acroporids coincides with a known period of climatic warming and measured increases in SSTs
(4) The range expansion coincides with a period of thermal stress (bleaching) of reef-building corals worldwide
(5) The range expansion in Florida coincides with the discovery of elkhorn coral at the Flower Garden Banks in the northern Gulf of Mexico
(6) The range expansion coincides with similar range shifts in Indo-Pacific coral species
(7) The present-day range expansion of western Atlantic acroporids resembles a change in the geographic distribution of acroporid-dominated reef systems during a millennial-scale climate flicker thousands of years ago.

The past

Florida's biogeographic precedent for today's range expansion correlates with a period of global warming earlier in the Holocene epoch. This historical example (Lighty *et al.* 1978) can be used as an analogue to model the future response of the Florida reef tract to high-amplitude climate flickers and global warming, even though

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the climatic mechanisms producing the earlier warm period were different from those operating at present. SSTs in the subtropical western Atlantic increased from 14 000 years before present (ybp) to the beginning of the Holocene, about 10 000 ybp; these were higher than today's SSTs during the early to middle Holocene, 10 000 to 6000 ybp; and declined to modern values in the late Holocene, 6000 ybp to present (Balsam 1981; Ruddiman and Mix 1991). This millennial-scale temperature pattern was probably caused by a reorganization of North Atlantic circulation similar to Dansgaard-Oeschger cycles (Kerr 1996). Through the Quaternary, Dansgaard-Oeschger cycles have occurred every few thousand years and have been characterized by abrupt jumps in temperature.

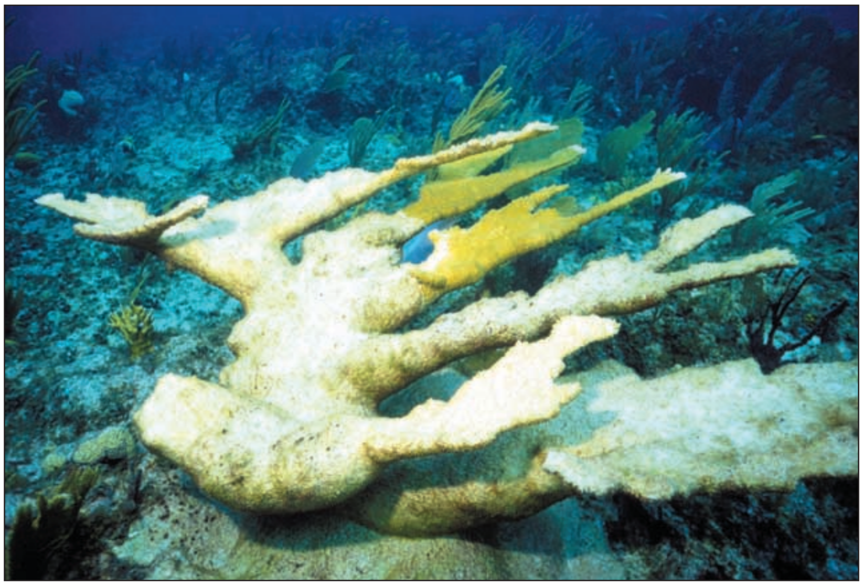

Figure 6. *White-band disease and resultant "branch-to-tip" mortality pattern observed on a colony of elkhorn coral at Carysfort Reef, FL. Photo taken in 1999.*

Relict, submerged, early to middle Holocene reefs are found throughout southeast Florida (Toscano and Macintyre 2003; Figure 7). Warmer conditions during this period apparently permitted a more northerly distribution of acroporid-dominated reefs (Figure 3). As temperatures cooled after the middle Holocene, the northern limit of the Florida reef tract moved south to its current position.

In the early to middle Holocene, *Acropora*-dominated reefs up to 10 m thick were well developed as far north as Palm Beach County (Lighty *et al.* 1978), indicating that conditions along the platform margin were more conducive than today to the growth of acroporid corals and the deposition of acroporid-dominated reef framework (Figure 8). We interpret the more northerly distribution of *Acropora* as a reflection of northward excursions of warm water related to a unique conjunction of factors. First, lower sea levels during this time placed the active shelf-margin reef system in closer proximity to the warmer waters of the Florida Current. Second, the period from about 9000–5000 ybp corresponds to the warmest interval of the Holocene, the Mid-Holocene Warm (Kerwin *et al.* 1999) or Altithermal (Buddemeier *et al.* 2004).

Although tropical temperatures remained relatively stable through the middle Holocene, within 1.0–1.5°C of present values (Arz *et al.* 2001), paleotemperatures reconstructed from the extratropical North Atlantic indicate SSTs 2–3°C warmer than at present (Balsam 1981; Ruddiman and Mix 1991). Climate simulations suggest that North Atlantic SSTs at 6000 ybp were as much as 4°C warmer than today (Kerwin *et al.* 1999). Evidence from both terrestrial and coastal habitats shows that warming during this millennial-scale, high-amplitude climate flicker caused many species from a variety of ecosystems to expand their ranges northwards (COHMAP 1988; Delcourt and Delcourt 1991; Dahlgren *et al.* 2000).

The climate flicker during the middle Holocene also correlates with maximal coral diversity at the northernmost position of coral reefs in the Pacific. The world's highest latitude Pacific coral reef is currently in Tateyama, Japan (33.5°N). Veron's (1992) study of a mid-Holocene

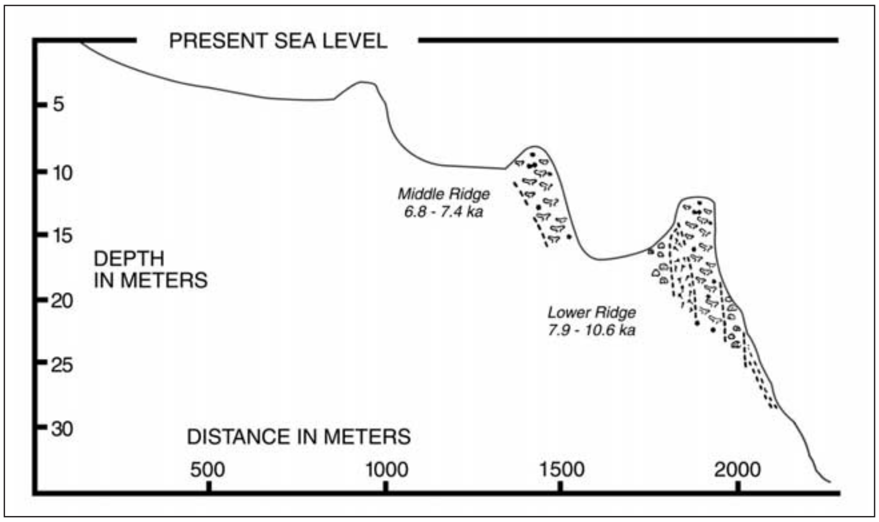

Figure 7. *Idealized cross-section showing three shore-parallel relict reef ridges off Broward County, FL. The lower ridge was described by Lighty* et al. *(1978) at Hillsborough Inlet and the middle ridge by Precht* et al. *(2000) at Dania Beach. Radiocarbon dates of recovered elkhorn coral revealed substantial early- to middle-Holocene reef development off the east coast of Florida, extending north to Palm Beach County. Figure modified from originals in Lighty* et al. *(1978) and Toscano and Macintyre (2003).*

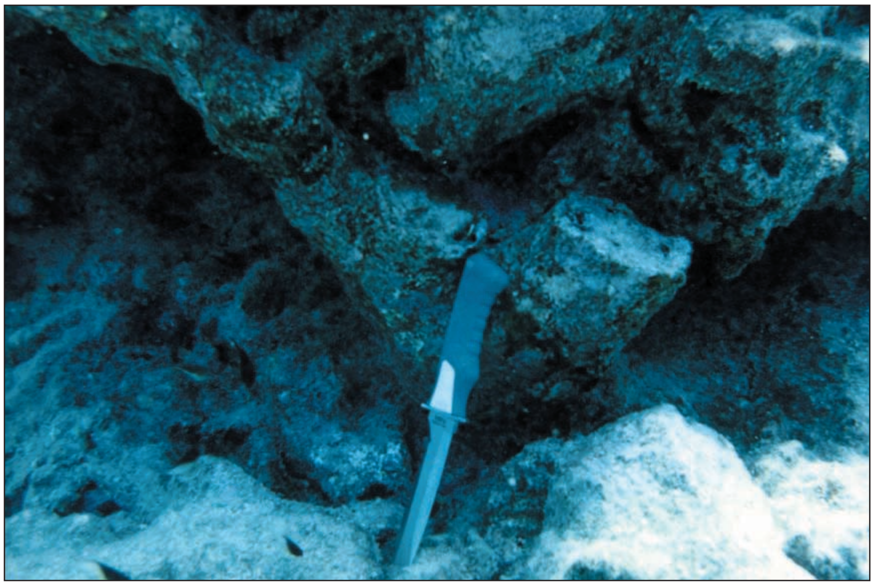

Figure 8. *Underwater photograph of excavated in situ colony of elkhorn coral from a Holocene-age relict reef off Ft Lauderdale, FL. Colony in photo was radiocarbon-dated to 6980 calendar years before present.*

fossil reef at Tateyama showed that even a brief period of warming of only 2°C doubled species richness from 35 to 72 species at the latitudinal extreme of extant corals. At the southernmost living reef in the Pacific Ocean, Lord Howe Island in Australia (31.3°S), evidence indicates that reefs were better developed in the early to middle Holocene than today, suggesting similar responses of corals to fluctuating SSTs.

Another paleoecological example is found in the Pleistocene reef community at Rottnest Island off Western Australia (32°S). The living reef at this locality has some 25 species of zooxanthellate corals. Most are at the southern limit of their range, with *Acropora* spp being rare (Marsh 1992); however, during the last major interglacial (about 125 000 ybp), when the water was a few degrees warmer, major reefs were formed by both staghorn and tabular *Acropora* spp (Szabo 1979). These paleoecological examples of species replacements and range expansions, especially those concerning acroporids, emphasize the varied responses of coral species and their ability to reconstitute reef communities in the face of rapid environmental change not related to human modification of the seascape. Understanding the response of reef organisms to warm climates of the past, regardless of the underlying causes, will help us predict the future of coral reefs in a warming world.

■ The future

The modeled range of global temperature increase is 1.4–5.8°C for the period 1990–2100 (Buddemeier *et al.* 2004). However, these models predict an SST warming of only 1–3°C in the tropics during the same period. Relative conservatism of tropical temperatures and greater warming of extratropical areas are likely to result from feedbacks in the ocean–atmosphere system, which prevents SSTs from exceeding 32°C (Kleypas in press). General circulation models indicate that tropical heating, especially near the equator, increases latent heat flux away from the tropics. The predicted difference in temperature rise between the tropics and extratropical areas is remarkably similar to those recorded through the glacial–interglacial cycles of the Quaternary Period (the last 1.8 million years; CLIMAP 1984).

The National Research Council (1988) recommended that studies documenting population, community, and ecosystem responses to rapid environmental changes of the Quaternary be used to provide insight into the rates and directions of future biotic change. Specifically, such paleoecologic studies allow us to evaluate biotic response to environmental changes of magnitudes that are beyond recent values but within the range of projected global change. Although fossil assemblages from a number of ecosystems have no analogues in modern communities (Roy *et al.* 1996), modern reef communities closely resemble fossil reef assemblages (Pandolfi and Jackson 1997).

It has been argued that tropical coral assemblages exhibit stability and persistence through Quaternary time and therefore constitute the most important database for studying abrupt change in modern reefs (Pandolfi and Jackson 1997). A key aspect of this argument is that warmer temperatures during the last major interglacial period were not associated with contraction of the southern range of the acroporids or the demise of reef systems in the tropics. Based on these results, and because SSTs in global climate models generally do not exceed 32°C in the Caribbean, it is unlikely that future global warming will lead to the catastrophic collapse of reef systems, the extirpation of acroporid corals, or the contraction of their southern range in the tropical Caribbean, as some have predicted (eg Hoegh-Guldberg 1999; Reaser *et al.* 2000). Reefs living under non-optimal conditions in more thermally reactive areas, including those in Florida, the Gulf of Mexico, and Bermuda, are more likely to show changes in species richness and diversity with climatic warming (Precht and Miller in press).

At the latitudinal extremes of Caribbean reef systems, an increase in SST of only 1–2°C should encourage temperature-sensitive corals such as the acroporids to expand their ranges. Reyes Bonilla and Cruz Piñón (2002) made a similar prediction for warming seas along the Pacific coast of Mexico, suggesting that coral species richness will increase the most at subtropical latitudes. Along the eastern Pacific, as many as eight coral species have recently

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been identified north of their previously known ranges (H Reyes Bonilla pers comm), while at Lord Howe Island in Australia the arrival of six species has been observed within the past decade (JEN Veron pers comm). In addition to temperature, however, other factors including light, carbonate saturation state, pollution, and disease influence reef development (Buddemeier *et al.* 2004). Increases in extreme weather and climate events will also probably occur in the future, especially at middle to high latitudes (Easterling *et al.* 2000). Associated habitat loss due to these multiple stressors will further complicate our ability to project geographic distributions of species and communities under future climates (Pyke 2004). We cannot predict how these controls will interact, meaning that further climate change could cause the latitudinal ranges of coral reefs to expand, remain stable, or even contract (Kleypas in press). Furthermore, the northward expansion of Caribbean reefs will be limited by the shift from a carbonate-dominated to a siliciclastic-dominated sedimentary regime, as well as by increasing nutrient concentrations, as one moves north along the east coast of the Florida Peninsula, further confounding future predictions.

The staghorn coral thickets off Fort Lauderdale present an interesting case. Are these remnant populations, or are they the recent product of a chance recruitment event? Do they represent a temporary range expansion that is likely to be obliterated by the passage of the next subfreezing cold front, disease outbreak, or hurricane? Are they an indicator of global climate change? These possibilities are not mutually exclusive, but only through genetic analysis of populations and long-term monitoring will we be able to answer such questions definitively.

The fossil record of coral reefs is helping us predict the impacts of future climatic warming. Although it is likely that reef-building corals will expand their ranges to higher latitudes in response to global warming, geographic shifts of marginal reefs will not mitigate the expected ecological and economic losses due to localized coral mortality and reduced function in tropical reef systems. Understanding the causal links between climate change and the dynamics of reefs and other ecosystems will continue to be a challenge in the face of natural variability, uncertainties inherent in predictive models, and the complex impacts of human activity all over the planet.

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