PARTICLE FLUX

See **TEMPORAL VARIABILITY OF PARTICLE FLUX**

PAST CLIMATE FROM CORALS

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doi:10.1006/rwos.2001.0270

Introduction

The influence of the tropics on global climate is well recognized. Our ability to understand, model and predict the interannual, decadal and long-term variability in tropical climate depends on our knowledge of past climate. However, our understanding of the natural variability in tropical climate is limited because long-term instrumental records prior to 1950 are sparse or nonexistent in many tropical regions. Continuous satellite monitoring did not begin until the 1970s and *in situ* equatorial Pacific Ocean monitoring has only existed since the 1980s. Therefore, we depend on proxy records to provide information about past climate. Proxy records are indirect measurements of the physical and chemical structure of past environmental conditions chronicled in natural archives such as ice cores, sediment cores, coral cores and tree rings.

In the tropical oceans, the isotopic, trace and minor elemental signatures of coral skeletons can vary as a result of environmental conditions such as temperature, salinity, cloud cover and upwelling. As such, coral cores offer a suite of proxy records with potential for reconstructing tropical paleoclimate on intraannual-to-centennial timescales. Massive, symbiotic stony corals are good tropical climate proxy recorders because: (1) they are widely distributed throughout the tropics; (2) their unperturbed annual skeletal banding pattern offers excellent chronological control; (3) they incorporate a variety of climate tracers from which paleo sea surface temperature (SST), sea surface salinity (SSS), cloud cover, upwelling, ocean circulation, ocean mixing patterns, and other climatic and oceanic features can be reconstructed; (4) their proxy records can be almost as good as instrumental records; (5) their records can span several centuries; and (6) their high skeletal growth rate (usually in the range of 5–25 mm y^{-1}) permits subseasonal sampling resolution. Thus proxy records in corals provide the best means of obtaining long seasonal-to-centennial timescale paleoclimate information in the tropics.

Coral-based paleoclimate research has grown tremendously in the last few decades. Most of the published records come from living corals and report the reconstructed SST, SSS, rainfall, water circulation pattern, or some combination of these variables. Records from fossil and deep-sea corals are also increasing. The goal of this chapter is to provide an overview of the current state of coral-based paleoclimate research and a list of further readings for those i]nterested in more detailed information.

Coral Biology

General

Corals are animals in the cnidarian family, order Scleractinia (class Anthozoa). Their basic body plan consists of a polyp containing unicellular endosymbiotic algae known as zooxanthellae overlaying a calcium carbonate exoskeleton (**Figure 1**). Most coral species are colonial and include many polyps interconnected by a lateral layer of tissue. The polyp, consisting of tentacles (used to capture prey), an oral opening and a gastrovascular cavity, has three tissue layers: the epidermis, mesoglea, and gastrodermis. The symbiotic zooxanthellae are located in the gastrodermis. Corals deposit a calcium carbonate ($CaCO_3$) aragonite skeleton below the basal epidermis. Corals reproduce sexually during mass-spawning events by releasing egg and/or sperm, or egg–sperm bundles into the water column. Mass spawning events typically occur a few times a year for each species, and are triggered by the lunar cycle. Corals can also reproduce asexually by fragmentation.

Animal–Zooxanthellae Symbiosis

Corals acquire the greater part of their food energy by two mechanisms: photosynthesis and heterotrophy (direct ingestion of zooplankton and other organic particles in the water column by the coral animal). Photosynthesis is carried out by the endo-

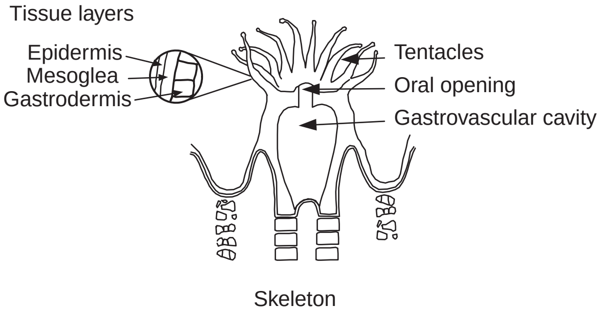

Figure 1 Cross-section of coral polyp and skeleton.

symbiotic zooxanthellae. The bulk of photosynthetically fixed carbon is translocated directly to the coral host. In some cases, the coral animal can obtain all of its daily energy requirements via photosynthesis alone. In general, as light intensity increases, photosynthesis increases.

Skeleton

Corals deposit skeleton below the basal epidermis. Typically, corals deposit one high-density and one low-density band of skeleton each year. The high-density band has thicker skeletal elements than the low-density band. Each band is often composed of several finer bands called dissepiments, deposited directly at the base of the coral tissue. At discrete intervals, the polyp presumably detaches from the dissepiment, and begins to lay down a new skeletal dissepiment. Some evidence suggests that dissepiments may form on a lunar cycle.

High- and low-density bands are deposited seasonally. Overall, high-density bands form during suboptimal temperature conditions and low-density bands form during optimal temperature conditions. At higher latitudes (i.e., Hawaii, Florida) optimal growth temperature occurs in summer. At lower latitudes (i.e., Galápagos, equatorial Pacific regions, Australian Great Barrier Reef), optimal growth temperatures occur in the cooler months. The width and density of growth bands also vary with environmental variables such as light, sedimentation, season length, and salinity. In general, as light levels decrease due to increased cloud cover, increased sedimentation or due to increasing depth, maximum linear skeletal extension decreases, calcification decreases, and skeletal density increases.

The Interpretation of Isotopes, Trace Elements, and Minor Elements in Corals

Several environmental variables can be reconstructed by measuring changes in the skeletal isotope ratios, trace and minor elemental composition, and growth rate records in coral cores (**Table 1**). The width, density, and chemical composition of each band are generally thought to reflect the average environmental conditions that prevailed during the time over which that portion of the skeleton was calcified. Reconstructions of seawater temperature, salinity, light levels (cloud cover), upwelling, nutrient composition and other environmental parameters have been obtained from coral records (**Table 1**).

Method

Continuous records of past tropical climate conditions can be obtained by extracting a core from an individual massive coral head along its major axis of growth. Typically, this involves placing a coring device on the top and center of the coral head (**Figure 2A**). The extracted core is cut longitudinally into slabs ranging in thickness from 0.7 to 1 cm that are then X-rayed. X-ray-positive prints reveal the banding pattern of the slab and are used: (1) as a guide for sample drilling and (2) to establish a chronology for the entire coral record when the banding pattern is clear (**Figure 2B**). Samples are drilled out along the major axis of growth by grinding the skeletal material with a diamond-tipped dental drill. For high-resolution climate reconstructions, samples are extracted every millimeter or less down

Table 1 Environmental variable(s) that can be reconstructed from coral skeletal isotopes, trace and minor elements, and growth records

Proxy	*Environmental variable*
Isotopes	
$\delta^{13}C$	Light (seasonal cloud cover), nutrients/zooplankton levels
$\delta^{18}O$	Sea surface temperature, sea surface salinity
$\Delta^{14}C$	Ocean ventilation, water mass circulation
Trace and minor elements	
Sr/Ca	Sea surface temperature
Mg/Ca	Sea surface temperature
U/Ca	Sea surface temperature
Mn/Ca	Wind anomalies, upwelling
Cd/Ca	Upwelling
$\delta^{11}B$	pH
F	Sea surface temperature
Ba/Ca	Upwelling, river outflow, sea surface temperature
Skeleton	
Skeletal growth bands	Light (seasonal changes), stress, water motion, sedimentation, sea surface temperature
Fluorescence	River outflow

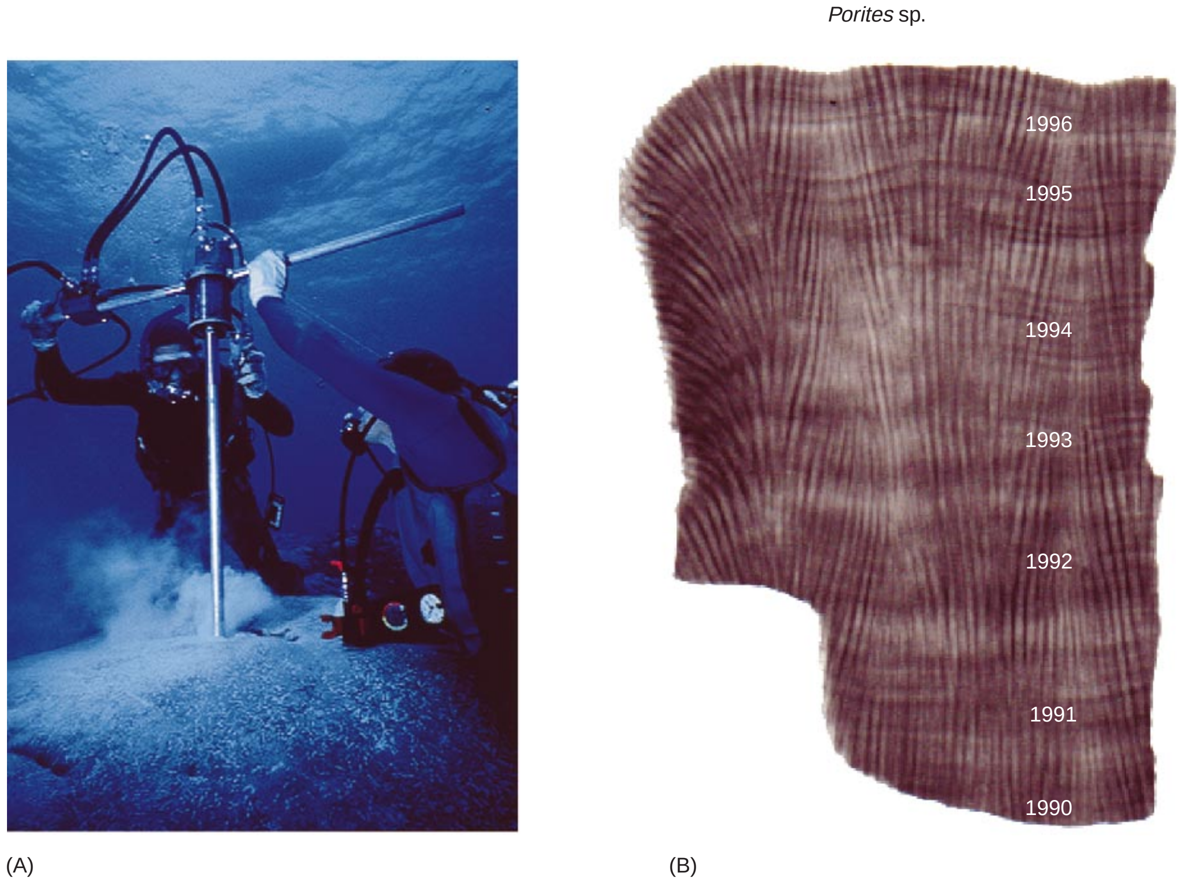

Figure 2 Collecting coral cores. (A) Coral core being extracted from top and center of an individual massive coral head using a pneumatic coring device. (Photo courtesy of M. Kazmers/Shark Song Tax ID #374-50-5314.) (B) X-ray positive print reveals the banding pattern of the slab and is used to help establish a chronology for the entire coral record.

the entire length of the core. Since corals grow about 5–15 mm per year, this sampling method can yield approximately bimonthly-to-monthly resolution. Much higher resolution sampling is possible, yielding approximately weekly samples, but this is not commonly performed. In most cases, the $\delta^{13}C$ (the per mil deviation of the ratio of $^{13}C/^{12}C$ relative to the Peedee Belemnite (PDB) Limestone Standard) and $\delta^{18}O$ (ratio of $^{18}O/^{16}O$ relative to PDB) values of each sample are measured. Since the $\delta^{13}C$ and/or $\delta^{18}O$ compositions of corals usually have a strong seasonal component, they are often used to establish an accurate chronology and/or to confirm the chronology established from the X-rays.

Temperature and Salinity Reconstructions

Coral skeletal $\delta^{18}O$ reflects a combination of the local SST and SSS. In the many regions of the tropical ocean where the natural variation in salinity is small, changes in coral skeletal $\delta^{18}O$ primarily reflect changes in SST. The $\delta^{18}O$ of coral skeleton responds to changes in temperature usually according to the standard paleotemperature relationship for carbonates. Based on empirical studies, a 1°C increase in water temperature corresponds to a decrease of about 0.22‰ (parts per thousand) in $\delta^{18}O$. Precipitation has a low $\delta^{18}O$ value relative to that of sea water. Therefore, in regions with pronounced variability in rainfall and/or river runoff, coral $\delta^{18}O$ values reflect changes in SSS. Thus, depending on the nature of the coral collection site, the $\delta^{18}O$ record is used to reconstruct the SST and/or SSS. Additional studies show that other proxy indicators of temperature include the ratios of strontium/calcium (Sr/Ca), magnesium/calcium (Mg/Ca), and uranium/calcium (U/Ca), fluorine levels (F) and skeletal band thickness (**Table 1**). The ratios of Sr/Ca, Mg/Ca, and U/Ca incorporated into the skeleton is largely determined by the temperature-dependent distribution coefficient of Sr/Ca, Mg/Ca, and U/Ca between aragonite and sea water. As temperatures increase, the Sr/Ca and U/Ca ratios decrease and the Mg/Ca ratio increases.

Cloud Cover and Upwelling

δ^{13}C seems to indicate seasonal changes in cloud cover and upwelling. Thus far, only a small number of studies have used δ^{13}C records to confirm seasonal rainfall patterns established using the δ^{18}O signature. Only one study has directly linked a δ^{13}C record with seasonal upwelling. δ^{13}C in coral skeletons has been difficult to use as a paleoclimate tracer because it is heavily influenced by metabolic processes, namely photosynthesis and heterotrophy. Firstly, as light levels decrease due to cloud cover, the rate of photosynthesis by the coral's symbiotic zooxanthellae decreases, and skeletal δ^{13}C decreases. The reverse occurs when light levels increase. Secondly, zooplankton have a low δ^{13}C value relative to coral. During upwelling events in the Red Sea, nutrient and zooplankton level increases have been linked to decreases in coral skeletal δ^{13}C values. Other upwelling tracers include cadmium (Cd) and barium (Ba) concentrations, and Δ^{14}C. Cadmium and barium are trace elements whose concentrations are greater in deep water than in surface water. During upwelling events, deep water is driven to the surface and cadmium/calcium (Cd/Ca) and barium/calcium (Ba/Ca) ratios in the surface water, and consequently in the coral skeleton, increase (**Table 1**). Although SST also influences Ba/Ca ratios, most of the variation in Ba/Ca ratios in corals is due to nutrient fluxes and upwelling. Δ^{14}C is also an excellent tracer for detecting upwelling and changes in seawater circulation (Δ^{14}C is the per mil deviation of the ratio of ^{14}C/^{12}C relative to a nineteenth century wood standard). For example, in the eastern equatorial Pacific Ocean, the Δ^{14}C value of deep water tends to be very low relative to the Δ^{14}C of surface water. Here, increased upwelling or increases in the proportion of deep water contributing to surface water results in a decrease in the Δ^{14}C of the coral skeleton. Manganese (Mn) is a trace element whose concentration is highest in surface waters and decreases with depth. Therefore, during upwelling events, Mn/Ca ratios decrease. The ratio of Mn/Ca can also record prolonged and sustained changes in winds. In at least one case, Mn/Ca ratios from a Tarawa Atoll coral increased during El Niño events as a result of strong and prolonged wind reversals that had remobilized manganese from the lagoon sediments.

Other Proxy Indicators

Other environmental parameters that can be inferred from coral skeleton structure and composition are river outflow (fluorescence bands) and pH (boron isotope levels) (**Table 1**). Large pulses in river outflow can result in an ultraviolet-sensitive fluorescent band in the coral record. New evidence strongly suggests that the fluorescent patterns in coral skeletal records are due to changes in skeletal density, not terrestrially derived humics as previously thought. Variations in salinity associated with fresh water discharge pulses from rivers appear to cause changes in coral skeletal growth density which can be observed in the skeletal fluorescence pattern. In the case of boron, δ^{11}B levels in sea water increase as pH increases. Changes in the pH at the site of coral calcification seem to reflect changes in productivity of the symbiotic zooxanthellae. As photosynthesis increases, pH increases, and δ^{11}B levels in the coral skeleton increase.

Coral Records: What Has Been Learned About Climate From Corals?

To date, there are over 100 sites where coral cores have been recovered and analyzed (**Figure 3**). Of these, at least 22 have records that exceed 120 years in length. In most cases, δ^{13}C and δ^{18}O have been measured at annual-to-subannual resolution. δ^{18}O as a SST and/or SSS proxy is the best understood and most widely reported of all the coral proxy measurements. In a few cores, other isotopic, trace, and minor elements, or skeletal density and growth measurements have also been made.

Typically, coral-derived paleoclimate records are studied on three timescales: seasonal, interannual-to-decadal, and long-term trends. The seasonal variation refers to one warm and one cool phase each year. An abrupt shift in the proxy's long-term mean often indicates a decadal modulation in the data. Long-term trends are usually associated with a gradual increase or decrease in the measured proxy over the course of several decades or centuries. The following sections explore some of the seasonal, decadal and long-term trends in coral-derived paleoclimate records and some of the limitations associated with interpreting coral proxy records.

Seasonal Variation in Coral Climate Records

Seasonal variation accounts for the single largest percentage of the variance in most coral isotope, trace, and minor element records. In regions such as Japan and the Galápagos with distinct SST seasonality, the annual periodicity in δ^{18}O, Sr/Ca, Mg/Ca, and U/Ca is pronounced. In regions heavily affected by monsoonal rains such as Tarawa Atoll, the seasonal variation in δ^{13}C is regular and pronounced. Δ^{14}C also has an annual periodicity in coral from regions with a strong seasonal upwelling regime such as is seen in the Galápagos (see next section). The strength and duration of the upwelling season is

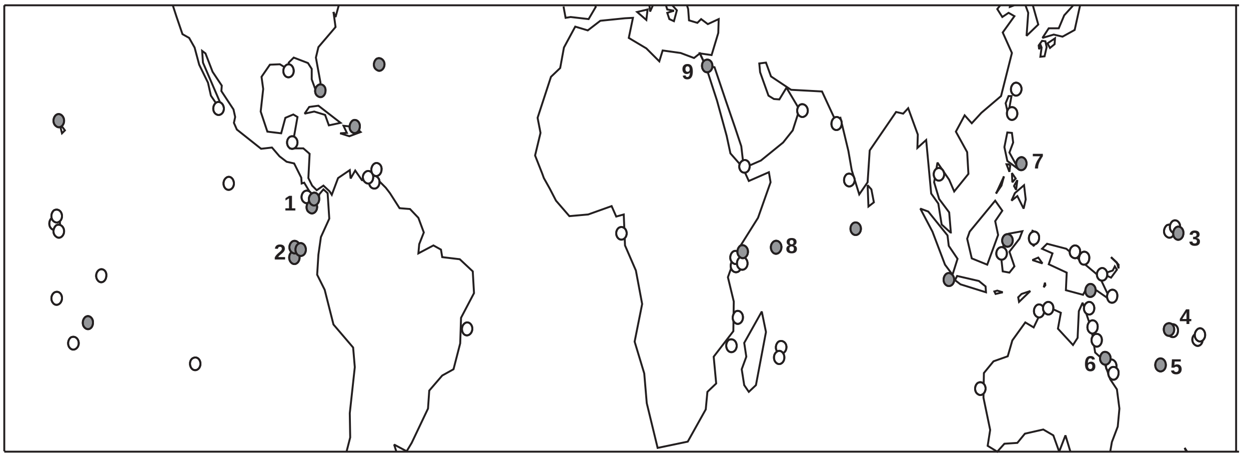

Figure 3 Map indicating the approximate locations of current paleoclimate research. The coral sites involve the work of many investigators and may be incomplete. The δ^{18}O records from the numbered sites are shown in **Figure 5** and are discussed in the text. ●, sites with records longer than 120 years (most are published); ○, sites where cores have been recovered and data collection is underway. (Reproduced from Gagan *et al.* (2000), with permission from Elsevier Science.)

reflected in the length and degree of Δ^{14}C decrease in the coral record.

Interannual-to-decadal Variation in Climate and El Niño Southern Oscillation (ENSO)

The second largest component of the variance in Pacific coral isotope records is associated with the interannual-to-decadal variation in the El Niño Southern Oscillation (ENSO)[1]. Several of the longer Pacific δ^{18}O coral records reveal that the frequency of ENSO has changed on decadal timescales over the past few centuries. Over the last 300 years, the dominant mode of ENSO recorded by a Galápagos coral has been at 4.6 years. However, during that time period there have been shifts in that mode from 4.6 to 7 years during the 1600s, 3–4.6 years from 1700–1750, and 3.5 years from 1800–1850. These major shifts in ENSO frequency may indicate major reorganizations in Pacific climate at various intervals over time. A 101-year long δ^{18}O record from Clipperton Atoll reveals a pronounced period of reduced ENSO frequency from ~1925 to 1940 suggesting a reduced coupling between the eastern and western Pacific. At Clipperton, decadal timescale variability represents the largest percentage of the variance in δ^{18}O and appears to be related to the processes influencing the Pacific Decadal Oscillation phenomenon (PDO)[2].

Another component of ENSO variability recovered from coral δ^{18}O records is the shift in rainfall patterns during El Niños associated with: (1) the migration of the Indonesian Low pressure cell to the region of the date line and the equator in the western Pacific, and (2) the northern migration of the intertropical convergence zone (ITCZ) in the eastern Pacific. Eastward migration of the Indonesian Low

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[1] ENSO refers to the full range of variability observed in the Southern Oscillation, including both El Niño and La Niña events in the Pacific. The Southern Oscillation Index (SOI) is a measure of the normalized difference in the surface air pressure between Tahiti, French Polynesia and Darwin, Australia. Most of the year, under normal seasonal Southern Oscillation cool phase conditions, easterly trade winds induce upwelling in the eastern equatorial Pacific and westward near-equatorial surface flow. The westward flowing water warms and piles up in the western Pacific creating a warm pool and elevating sea level. The wind-driven-transport of this water from the eastern Pacific leads to an upward tilt of the thermocline and increases the efficiency of the local trade-wind-driven equatorial upwelling to cool the surface resulting in an SST cold tongue that extends from the coast of South America to near the international date line. Normal seasonal Southern Oscillation warm-phase conditions are marked by a relaxation of the zonal component of trade winds, reduced upwelling, and a weakening or reversal of the westward flowing current coupled with a deepening of the thermocline in the eastern equatorial Pacific Ocean, and increased SST in the central and eastern equatorial Pacific. This oscillation between cool and warm phases normally occurs annually. Exaggerated and/or prolonged warm-phase conditions are called El Niño events. They usually last 6–18 months, occur irregularly at intervals of 2–7 years, and average about once every 3–4 years. The SOI is low during El Niño events. Exaggerated and/or prolonged ENSO cool phase conditions are called La Niña events. They often follow El Niño events (but not necessarily). La Niña events are marked by unusually low surface temperatures in the eastern and central equatorial Pacific and a high SOI. For a detailed description of ENSO, *see* **El Niño Southern Oscillation (ENSO)**.

[2] The PDO appears to be a robust, recurring two-to-three decade pattern of ocean–atmosphere climate variability in the North Pacific. A positive PDO index is characterized by cooler than average SST in the central North Pacific and warmer than average SST in the Gulf of Alaska and along the Pacific Coast of North America and corresponds to warm phases of ENSO. The reverse is true with a negative PDO.

results in decreased precipitation in the Indian Ocean and increased precipitation in the western and central Pacific. These phenomena are reflected in the $\delta^{18}O$ record of Seychelles and Tarawa Atoll corals, respectively. Decadal variability in the Seychelles record suggests that regional rainfall variability may originate from the ocean. Decadal variability in a 280-year $\delta^{18}O$ record from a Panamanian coral indicates decadal periods in the strength and position of the ITCZ.

Changes in the decadal variability of coral skeletal $\Delta^{14}C$ reveals information about the natural variability in ocean circulation, water mass movement and ventilation rates in surface water. Biennial-to-decadal shifts in $\Delta^{14}C$ between 1880 and 1955 in a Bermuda coral indicates that rapid pulses of increased mixing between surface and subsurface waters occurred in the North Atlantic Ocean during the past century and that these pulses appeared to correlate with fluctuations in the North Atlantic Oscillation. In a post-bomb Galápagos coral record, abrupt increases in monthly $\Delta^{14}C$ values during the upwelling season after 1976 suggest a decadal timescale shift in the vertical thermal structure of the eastern tropical Pacific (**Figure 4**). The decadal variability in $\Delta^{14}C$ in the Bermuda and Galápagos records are testimony to the power of coral proxy records to provide information about ocean circulation patterns. Additional $\Delta^{14}C$ records from Nauru, Fanning Island, Great Barrier Reef, Florida, Belize, Guam, Brazil, Cape Verde, French Frigate Shoals, Tahiti, Fiji, Hawaii and a few other locations are either published or in progress. As the number of coral $\Delta^{14}C$ records increases, our understanding of the relationship between climate and ocean circulation patterns will also increase.

Some decadal-to-centennial trends in climate are consistent among many of the longer $\delta^{18}O$ coral records. For example in **Figure 5**, all six records longer than 200 years show a cooler/dryer period from AD 1800 to 1840. Cooling may be related to enhanced volcanism during this period. Following this cooler/dryer interval, four of the six records show shifts towards warmer/wetter conditions around 1840–1860 and five of the six show another warming around 1925–1940. These abrupt shifts towards warmer/wetter conditions detected in corals from a variety of tropical locations suggest that corals may be responding to global climate forcing.

Long-term Trends in Climate

There are three major long-term trends observed in several coral records: (1) a prolonged cool phase prior to 1900 generally consistent with the Little Ice Age; (2) a gradual warming/freshening trend over the past century; and (3) evidence of increased burning of fossil fuels. First, in three of the four longest $\delta^{18}O$ coral records the cool/dry period of the Little

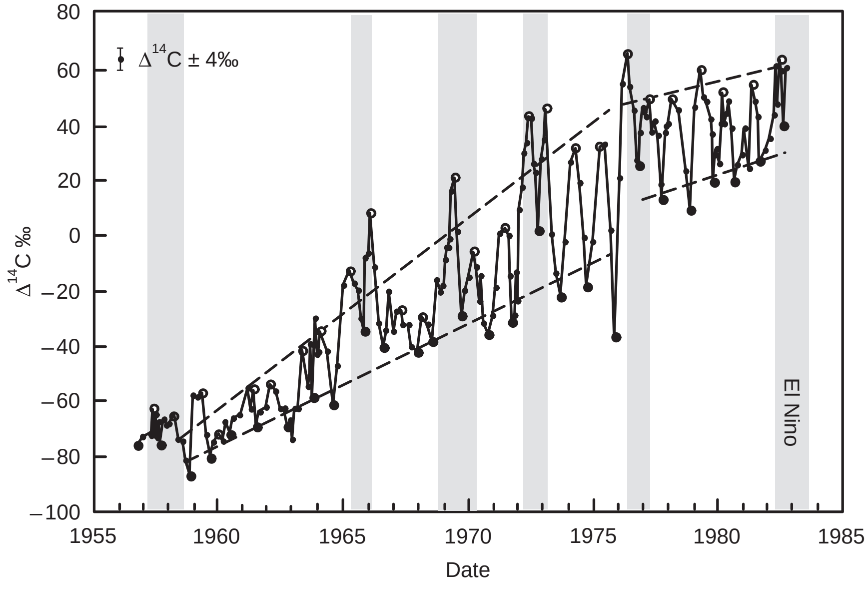

Figure 4 Galápagos coral $\Delta^{14}C$‰ record from 1957 to 1983. El Niños are indicated by the shaded bars. ●, upwelling maxima; ○, nonupwelling season. Dashed lines indicated linear trend in the upwelling and nonupwelling seasons. The seasonal variation in $\Delta^{14}C$ is pronounced with high $\Delta^{14}C$ during the nonupwelling season and low $\Delta^{14}C$ values during the upwelling season. A shift in $\Delta^{14}C$ baselines began in 1976. (Reproduced from Guilderson TP and Schrag DP (1998) Abrupt shift in subsurface temperatures in the tropical Pacific associated with changes in El Niño. *Science* 281: 240–243; with permission from the American Association for the Advancement of Science.)

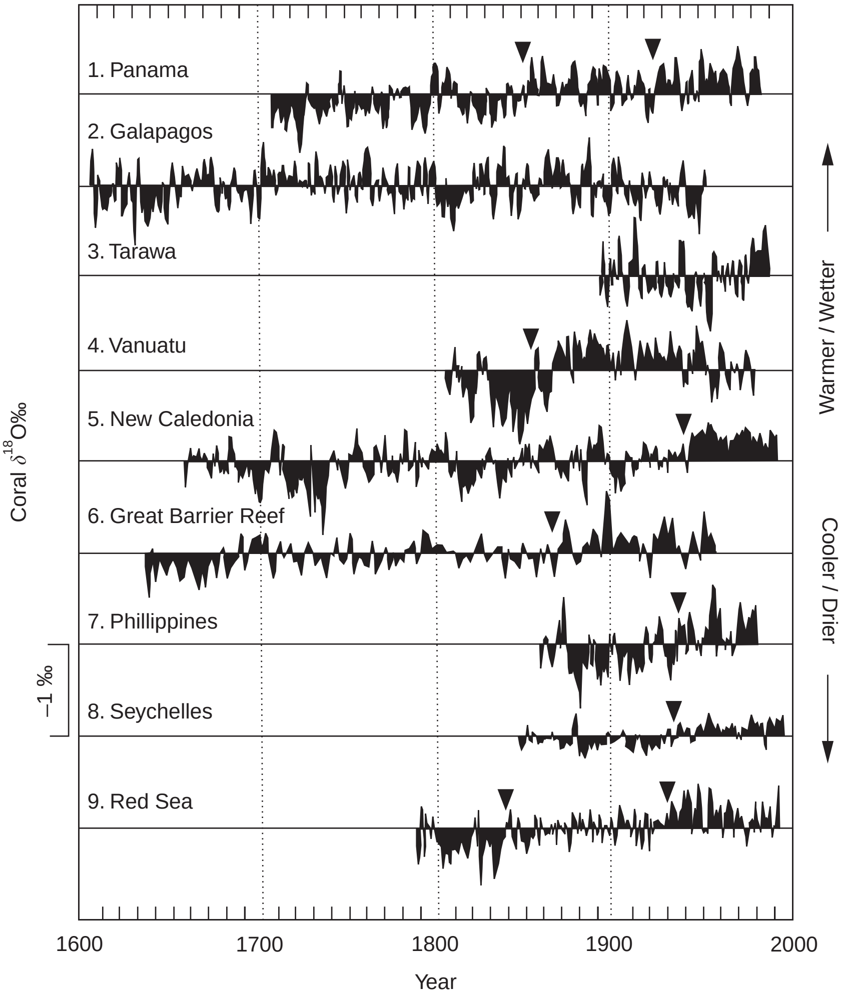

Figure 5 Annual mean coral δ^{18}O records in the Pacific and Indian Ocean region extending back at least for 100 years (locations of cores are indicated in **Figure 3**). Mean δ^{18}O values for each site indicated with a horizontal line. Abrupt shifts in δ^{18}O towards warmer/wetter conditions indicated by black triangles. Data are from the World Data Center-A for Paleoclimatology, NOAA/NGDC Paleoclimatology Program, Boulder, Colorado, USA (http://www.ngdc.noaa.gov/paleo/corals.html) and the original references. Core details list locality, species name, record length, and original reference: 1, Gulf of Chiriqui, Panama, *Porites lobata* 1708–1984 Linsley BK, Dunbar RB, Wellington GM, Mucciarone DA (1994) A coral-based reconstruction of intertropical convergence zone variability over Central America since 1707. *Journal of Geophysical Research* 99: 9977–9994); 2, Urvina Bay, Galápagos, *Pavona clavus* and *Pavona gigantea*, 1607–1981 Dunbar RG, Wellington GM, Colgan MW, Glynn PW (1994) Eastern Pacific sea surface temperature since 1600 A.D.: the δ^{18}O record of climate variability in Galápagos corals. *Paleoceanography* 9: 291–315; 3, Tarawa Atoll, Republic of Kiribati, *Porites* spp., 1893–1989 Cole JE, Fairbanks RG, Shen GT (1993) Recent variability in the Southern Oscillation: isotopic results from Tarawa Atoll coral. *Science* 260: 1790–1793; 4, Espiritu Santo, Vanuatu, *Platygyra lamellina*, 1806–1979 Quinn TM, Taylor FW, Crowley TJ (1993) A 173 year stable isotope record from a tropical south Pacific coral. *Quaternary Science Review* 12: 407–418; 5, Amedee Lighthouse, New Caledonia, *Porites lutea*, 1657–1992 Quinn TM, Crowley TJ, Taylor FW, Henin C, Joannot P, Join Y (1998) A multicentury stable isotope record from a New Caledonia coral: Interannual and decadal sea surface temperature variability in the southwest Pacific since 1657 A.D. *Paleoceanography* 13: 412–426; 6, Abraham Reef, Great Barrier Reef, Australia, *Porites australiensis*, 1635–1957 Druffel ERM, Griffin S (1993) Large variations of surface ocean radiocarbon: evidence of circulation changes in the southwestern Pacific. *Journal of Geophysical Research* 98: 20 249–22 259; 7, Cebu, Philippines, *Porites lobata*, 1859–1980 Pätzold J (1986) Temperature and CO_2 changes in the tropical surface waters of the Philippines during the past 120 years: record in the stable isotopes of hermatypic corals. Berichte Reports, Gol.-Paläont, Inst. Univ. Kiel, 12; 8, Mahe Island, Seychelles, *Porites lutea*, 1846–1995 Charles CD, Hunter ED, Fairbanks RG (1997) Interaction between the ENSO and the Asian monsoon in a coral record of tropical climate. *Science* 277: 925–928; 9, Aqaba, Red Sea, *Porites* sp., 1788–1992 Heiss GA (1996) Annual band width variation in *Porites* sp. from Aquaba, Gulf of Aquaba, Red Sea. *Bulletin of Marine Science* 59: 393–403; (Reproduced from Gagan (2000), with permission from Elsevier Science.)

Ice Age is observed from the beginning of their respective records, up to the mid to late 1800s (**Figure 5**). However, the lack of this cool/dry period in the Galápagos coral indicates that the Little Ice Age effects may not have been uniform throughout the tropical oceans.

Second, this cool phase was followed by a general warming/freshening of the global tropical ocean beginning during the nineteenth century (**Figure 5**). This overall warming/freshening trend is observed in seven of the nine records. The timing of the onset of this warming/freshening is consistent with the onset of industrialization and the consequent increases in greenhouse gases due to increased emissions from fossil fuel consumption. If the shift in δ^{18}O were solely due to increases in SST, it would be equivalent to an increase of 0.3–2.0°C since 1800. Instrumental data indicate that the tropics only warmed by ~0.5°C since 1850. The influence of SSS on δ^{18}O is probably responsible for the difference and needs to be taken into account when interpreting δ^{18}O records. Although Sr/Ca ratios are thought to be unaffected by SSS, only a few shorter coral records are currently published. Until recently, Sr/Ca measurements were very time-consuming. With recently developed technology, the use of Sr/Ca as a paleothermometer proxy should increase. Two main limitations exist with the correct interpretation of decadal and long-term δ^{18}O trends: (1) an interdecadal cycle of unknown origin is commonly identified in long coral δ^{18}O records; and (2) long-term trends of increasing δ^{18}O are observed in some coral while other coral δ^{18}O records show a decreasing trend. Whether these trends are due to biological processes or are the result of gradual environmental changes (i.e., global warming) is unclear.

Finally, evidence of increased fossil fuel emission into the atmosphere can be seen in the general decrease in Δ^{14}C from 1850 to 1955 in shallow corals from the Atlantic and Pacific Oceans. This phenomenon, referred to as the Suess Effect, is mainly the result of ^{14}C-free CO_2 produced from combusted fossil fuel entering the atmosphere, the oceans and eventually, the coral skeleton (post-1950, coral Δ^{14}C values skyrocketed as a result of ^{14}C produced by thermonuclear bombs effectively swamping out the Suess effect).

Fossil Corals

Fossil corals provide windows into past climate. Records covering several decades to centuries offer the opportunity to compare the same three components (seasonal, interannual-to-decadal, and long term) in climate in the distant past to the present. A 3.0 million-year-old south-western Florida coral reveals a seasonal δ^{18}O derived temperature pattern similar to today but ~3.5°C cooler. A North Sulawesi, Indonesian coral indicates that 124 000 years BP the variability in ENSO was similar to modern ENSO frequency from 1856 to 1976. However, the shift in ENSO frequency observed in modern records after 1976 is not found in the fossil coral record nor in pre-1976 instrumental records. This suggests that the current state of ENSO frequency is outside of the natural range of ENSO variability. Perhaps anthropogenic effects are having an effect on ENSO frequency. Finally, long-term changes in climate can also be reconstructed from fossil coral records. A series of coral records from Vanuatu indicate that ~10 300 years BP the south-western tropical Pacific was 6.5°C cooler than today followed by a rapid rise in temperature over the subsequent 15 000 years. This rapid rise in temperature lags the post-Younger Dryas warming of the Atlantic by ~3000 years suggesting that the mechanism for deglacial climate change may not have been globally uniform. How seasonal, decadal (ENSO) and long-term climate changes varied in the distant past throughout the tropics can be addressed using fossil coral records and can offer us a better idea of the natural variability in tropical climate over geologic time.

Deep-sea Corals

Deep sea corals do deposit calcium carbonate exoskeleton but do not contain endosymbiotic zooxanthellae and are not colonial. Their isotopic and trace mineral composition reflects variation in ambient conditions on the seafloor. Although this does not directly reflect changes in climate on the surface, ocean circulation patterns are tightly coupled with atmospheric climatic conditions. Understanding the history of deep and intermediate water circulation lends itself to a better understanding of climate. For example, the origin of the Younger Dryas cooling event (13 000 to 11 700 years BP) has recently been attributed to a cessation or slowing of North Atlantic deep water formation and subsequent reduction in heat flux. Isotopic evidence from deep-sea corals suggests that profound changes in intermediate-water circulation also occurred during the Younger Dryas. Other studies of deep-sea corals show rapid changes in deep ocean circulation on decadal-to-centennial timescales at other intervals during the last deglaciation. Reconstructing intermediate and deep ocean circulation patterns and their relationship to climate using isotopic, trace element and minor element records in deep sea coral promises to be an expanding line of paleoclimate research.

Discussion

The geochemical composition of coral skeletons currently offers the only means of recovering multicentury records of seasonal-to-centennial timescale variation in tropical climate. δ^{18}O-derived SST and SSS records are the workhorse of coral-based paleoclimate reconstructions to date. Improved methodologies are now making high resolution, multicentury Sr/Ca records feasible. Since Sr/Ca is potentially a less ambiguous SST recorder, coupling Sr/Ca with δ^{18}O records could yield more reliable SST and SSS reconstructions. δ^{13}C as a paleorecorder of seasonal variation in cloud cover and upwelling is also gaining credibility. However, more experimental research needs to be done before δ^{13}C records can be used more widely for paleoclimate reconstructions. Coral Δ^{14}C records are highly valued as an ocean circulation/ventilation proxy. Increasing numbers of high-resolution Δ^{14}C coral records are being published shedding invaluable new light on links between climate and ocean circulation processes. Coral trace and minor element records are also becoming more common and can add critical information about past upwelling regimes, wind patterns, pH, river discharge patterns, and SST.

The growing number of multicentury coral oxygen isotope records is yielding new information on the natural variability in tropical climate. Eastern equatorial Pacific corals track ENSO-related changes in SST and upwelling. Further west, coral records track ENSO-related changes in SST and SSS related to the displacement of rainfall associated with the Indonesian Low. Decadal timescale changes in ENSO frequency and in ocean circulation and water mass movement detected in δ^{18}O and Δ^{14}C records, respectively, indicate a major reorganization in Pacific climate at various intervals over time. Long-term trends in coral oxygen isotope records point to a gradual warming/freshening of the oceans over the past century suggesting that the tropics are responding to global forcings.

Although the coral-based paleoclimate records reconstructed to date are impressive, much work remains to be done. It is necessary to develop multiple tracer records from each coral record in order to establish a more comprehensive reconstruction of several concurrent climatic features. In addition, replication of long isotopic and elemental records from multiple sites is invaluable for establishing better signal precision and reproducibility. Coupled with fossil and deep-sea coral records, coral proxy records offer a comprehensive and effective means of reconstructing tropical paleoclimates.

Acknowledgments

I thank B Linsley, E Druffel, T Guilderson, J Adkins and an anonymous reviewer for their comments on the manuscript. I thank the Henry and Camille Dreyfus Foundation for financial support.

See also

Coral Reefs. El Niño Southern Oscillation (ENSO). Pacific Ocean Equatorial Currents.

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PATCH DYNAMICS

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doi:10.1006/rwos.2001.0290

Introduction

Once out of sight of land, the vastness and apparently unchanging nature of the open ocean might lead one to think that the plankton would be distributed evenly in space. In fact, this is rarely the case. Rather, planktonic organisms are generally distributed unevenly, in clumps of all shapes and sizes usually referred to as patches. As oceanographic platforms and various sensors for observing plankton have improved, we have discovered that plankton patches exist on scales of less than a meter (microscales) right up to scales of hundreds of kilometers (called the mesoscale) that are characteristic of the oceanic equivalent of storms.

We have also learned that the two main groups of plankton – phytoplankton (the microscopic plants in the ocean) and zooplankton (the small animals that usually feed on phytoplankton) – are not patchy in the same way. Rather, zooplankton seem to be organized into many more patches at smaller scales, such that their distributions sometimes approach being random. This characteristically smaller patch size of zooplankton is believed to reflect their greater ability for swimming, swarming, or other directed motions, perhaps in response to patchiness in their food sources or other environmental cues. Similarly, the spatial distribution of larval fish, which have an even greater capability for directed motion and are capable of swimming and orienting themselves in groups in response to cues in their environment, is usually even more patchy.

What does all this mean? What causes plankton patchiness? Are the causes physical, biological, or both? Are there ecological advantages or disadvantages to plankton patchiness? Does such patchiness promote or interfere with the transfer of energy and biomass from phytoplankton to zooplankton and larval fish and on to higher trophic levels?

The related issue of how small-scale physical processes influence the biology of planktonic organisms is addressed elsewhere (*see* **Small-scale Physical Processes and Plankton Biology**). There the focus is on how individual predators interact with individual prey within their physical environment. Observations of interactions between individual planktonic organisms are possible primarily in the laboratory. Here we consider patches as being comprised of groups of individual planktonic organisms: how they are actually observed by oceanographers in the ocean, how we then analyze such observations and assess their potential significance to food web dynamics.

The two approaches (patch-based versus individual-based observations) are connected as follows. Better understanding and prediction of patch dynamics and their importance to food web dynamics requires understanding of the processes by which individual organisms interact with each other and with the fluid flow. Generally, we are not yet able to make detailed observations of interactions between individual organisms in the ocean, and so we must rely on laboratory observations of individual organisms. To put these individual-based observations into an appropriate ecological context, however, it is also necessary to formulate or generalize how such individual interactions contribute to the behavior and responses at the level of a patch, which may contain millions of individuals. The other point of contact between the two approaches is to consider the case of an individual predator interacting with a patch of prey. One might reasonably ask whether there is some threshold difference in size between predator and prey at which an individual predator begins to interact with a patch of prey organisms (e.g., a gray whale feeding on a swarm of mysids) rather than with individual prey.

Because the observational technologies and analytic techniques used to study plankton patchiness