This explanation requires a correction of the model processes that transport trace constituents into the upper troposphere from lower altitudes where they are abundant. Such a correction will have a strong impact on the prediction of the photochemical O_3 production in the upper troposphere (*1*).

In contrast, the ground-based measurement of OH in remote or rural areas shows better agreement with the model-predicted values. There is, however, a consistent overprediction by the models of about 30% (*2*, 6). Because the difference is much smaller and the chemical system much more complex than those in the upper troposphere, there are many possible explanations for the difference, few of which can be excluded at present. On the other hand, the approximate agreement that holds for a broad range of environments, including NO_x levels of a few parts per billion, indicates that our basic understanding of the processes controlling OH is correct. Still, there is much to do. Only a few of the atmospheric chemical regimes have been tested by OH measurements. In particular, the more polluted environments have hardly been investigated. The few older measurements that exist indicate larger discrepancies and poor correlation between measured and modeled OH concentrations (*2*). Only recently have accurate and fast measurements of OH and HO_2 in the troposphere been possible, and only by a few groups worldwide. Moreover, proper interpretation requires a large number of support measurements to determine the various parameters that control OH, which in turn demands large field campaigns. Such work is in progress, hopefully at an accelerated pace as more groups join the field.

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CLIMATE

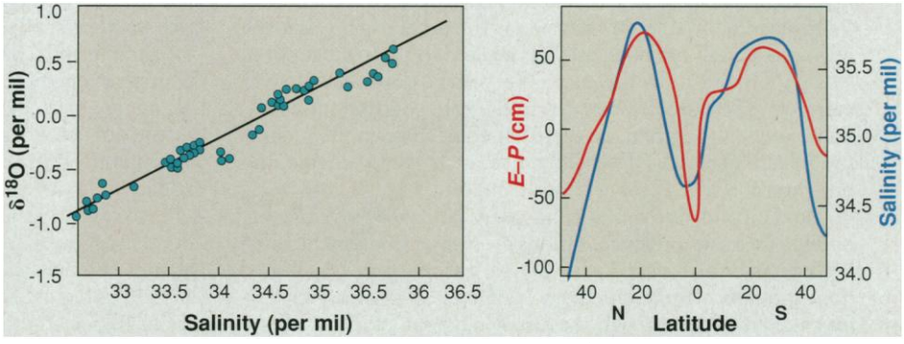
Warmer and Wetter 6000 Years Ago?

Warren Beck

Since the first quantitative measurements of ice-age temperatures (*1*) in the early 1950s, there has been controversy over the use of oxygen isotopes of marine carbonates in reconstructing past climate. Originally viewed as the Rosetta Stone for unlocking the mysterious causes of climate change, measurements of past temperatures based on oxygen isotope data have never quite lived up to expectations. The main defect of this technique has been that there are too many variables and not enough equations. More particularly, the $^{18}O/^{16}O$ ratio of marine carbonates varies as a function of temperature and the $^{18}O/^{16}O$ ratio of seawater. The latter ratio is not constant, however, changing substantially on glacial to interglacial time scales because of fluctuations in the volume of the polar ice caps. This variability results from fractional distillation of ^{18}O from ^{16}O during the formation of vapor and precipitation as water is transferred between the oceans and ice caps (*2*). Various clever strategies (*3*) have been employed as means of placing bounds on this ocean water $^{18}O/^{16}O$ variability, but these methods have not been entirely successful, particularly for sea-surface temperature (SST) reconstructions. High spatial and temporal variability in ocean surface water $^{18}O/^{16}O$ has hampered such efforts. This variability is linked to changes in the salinity of the sea surface, which is caused by fluctuations in the patterns of rainfall, evaporation, and water mass transport fields (*4*). Altogether, these salinity-related effects can have an impact on the $^{18}O/^{16}O$ ratio of marine carbonates formed at the ocean surface that is as large or larger than the impact of temperature variations.

As reported on page 1014 of this issue, Gagan *et al.* turn this defect in the oxygen isotope thermometer into a strength through use of coupled $^{18}O/^{16}O$ and Sr/Ca concentration measurements in corals (*5*). Because coral Sr/Ca ratios also vary as a function of SST (*6*), the use of both tracers in parallel apparently allows for simultaneous solution of SST and ocean surface $^{18}O/^{16}O$ ratios. The latter can tell us a great deal about the patterns of evaporation, precipitation, and ocean surface salinity over the ocean basins (see figure). Gagan and colleagues have used this technique on a ~6000-year-old coral (*5*) from the Great Barrier Reef, Australia, to show that mean SST was then 1.2°C warmer than present, and that the sea surface in this region was enriched in ^{18}O by a substantial 0.5 per mil (1 per mil = 0.1%) relative to modern seawater. These authors suggest that these two observations may be coupled, that is, increased tropical SST may have enhanced evaporation from the tropical Pacific, causing ^{18}O enrichment of the residual sea surface.

To sustain this ^{18}O enrichment, the additional water vapor distilled from the tropical oceans, they argue, must also have been exported to higher latitudes. If Gagan and colleagues are correct, then the extratropics should have experienced wetter conditions at this time as a result of intensified Hadley circulation. This is, in fact, a result predicted by some general circulation models as a consequence of increased tropical temperatures (*7*). Secondary effects of this moisture redistribution may have included changes in the high-latitude surface ocean salinity field, which might have triggered



How rainy was it? The salinity of ocean surface waters (*9*) covaries with $^{18}O/^{16}O$ (as $\delta^{18}O$) (**left**). This covariance is linked to the difference between precipitation to evaporation (*9*) occurring over the ocean surface (**right**). These linkages allow us to recover information about the variations in past rainfall and atmospheric moisture transport from paleorecords of ocean surface $^{18}O/^{16}O$.

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changes in the strength or structure of the oceanic thermohaline circulation. Although there may be other interpretations of Gagan and colleagues' primary findings, the implications of their findings are quite wide reaching.

But does the coral Sr/Ca thermometer really work? The long ocean residence times of Sr and Ca would suggest that its Sr/Ca ratio should be relatively constant on 100,000-year time scales. If so, this proxy thermometer should not suffer from the same defect as the oxygen-isotope thermometer, namely ocean water variability. Some work (8) suggests, however, that this variability may be larger than supposed. There is also the issue of differing calibrations for the Sr/Ca thermometer among the various researchers in this fledgling field (8): these differences lead to discrepancies of up to 3°C. Some researchers have suggested that these discrepancies are associated with differences in the calcification rate (or growth rate) of the corals used in the different calibration studies. Alternatively, the calibration differences may be artifacts of local temperature variations, resulting from temperature differences between the site at which the coral used for calibration grew and the site at which the temperature records were taken from for calibration. Gagan *et al.* attempt to address these issues by deriving calibrations for *Porites lutea* corals from three widely separated sites where the corals grew in suboptimal environmental conditions. These corals were exposed to wide seasonal extremes in SST, salinity, coastal upwelling, and water column turbidity, but all yielded essentially the same calibration. In one of these studies, corals from the same locality but with a factor of 2 difference in annual growth rate were compared. Virtually no difference was found between these two corals for either the Sr/Ca or the $^{18}O/^{16}O$ thermometer calibrations.

Studies of this type certainly help to reassure us that these proxy thermometers (and salinometers) are working, although more careful studies of this type are necessary before the calibration issues can truly be put to rest. If thoroughly validated, this double-tracer technique promises to elucidate many important new clues about the dynamics of the coupled ocean-atmosphere-climate system for climate modelers to digest.

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UPDATE: MUSCLE CONTRACTION

Heartthrobs

Dottie Hanck

Each beat of the heart is triggered by an electrical stimulus that launches a cascade of events involving tens of proteins and free ions and ending in contraction of the heart muscle. We've come to understand most of the elements of this elegant cascade. In the heart, depolarization of the sarcolemma (the muscle cell membrane) opens voltage-dependent calcium channels; calcium ions enter the cytoplasm through these channels and bind to sites on release channels located close by in the membrane of the sarcoplasmic reticulum, a complex intracellular network of membranes. The calcium stored in the sarcoplasmic reticulum exits through the activated release channels into the cytoplasm, where it interacts with the actin-myosin machinery and initiates contraction.

In skeletal muscle, the cascade is the same except that the release channels are physically connected to the voltage-gated calcium channels. In this case, the voltage-dependent movement of the sarcolemmal calcium voltage-gated channels themselves, rather than the ions that enter through them, open the release channels. Two different muscles: same theme, minor variation. Puzzle solved—well, almost.

Santana *et al.* discuss a puzzling result noticed by several laboratories. In heart, under conditions of stress or excitement when β-adrenergic inputs are highly active, calcium can be released from the sarcoplasmic reticulum even after all known pathways for calcium to get through the sarcolemma are blocked. Maybe Mother Nature didn't really vary the theme after all; perhaps sometimes in heart voltage-gated calcium channels can directly couple to sarcoplasmic reticulum channels to release calcium. On page 1027 of this issue Santana and colleagues dash our hopes that this reasonable explanation is correct.

These authors used one of the cleanest pharmacological tools known—tetrodotoxin, a puffer fish toxin that blocks sodium channels with high specificity. Surprisingly, in the presence of tetrodotoxin the residual calcium release disappears; this result is not what's expected if voltage-gated calcium channels are directly coupled to release channels. None of the pathways by which calcium may be crossing the sarcolemma seem suitable to explain these data. So which protein is acting uncharacteristically?

Santana and colleagues accuse the voltage-gated sodium channel, even though there are no previous data to indicate that appreciable calcium can permeate these channels. This is not the only provocative proposal they make; they also suggest a new connection between sodium channels and drugs such as ouabain and digoxin, which inhibit the sodium/potassium ATPase and so indirectly augment cardiac contractility. The authors suggest that these two drugs can also augment flux of calcium through the sodium channel. This action may help these drugs regulate contraction under pathophysiological conditions like heart failure.

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