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Supporting Online Material

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Dynamical Response of the Tropical Pacific Ocean to Solar Forcing During the Early Holocene

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We present a high-resolution magnesium/calcium proxy record of Holocene sea surface temperature (SST) from off the west coast of Baja California Sur, Mexico, a region where interannual SST variability is dominated today by the influence of the El Niño–Southern Oscillation (ENSO). Temperatures were lowest during the early to middle Holocene, consistent with documented eastern equatorial Pacific cooling and numerical model simulations of orbital forcing into a La Niña–like state at that time. The early Holocene SSTs were also characterized by millennial-scale fluctuations that correlate with cosmogenic nuclide proxies of solar variability, with inferred solar minima corresponding to El Niño–like (warm) conditions, in apparent agreement with the theoretical “ocean dynamical thermostat” response of ENSO to exogenous radiative forcing.

The influence of solar variability on Earth’s climate over centennial to millennial time scales is the subject of considerable debate. The change in total solar irradiance over recent 11-year sunspot cycles amounts to <0.1%, but greater changes at ultraviolet wavelengths (*I*) may have substantial impacts on stratospheric ozone concentrations, thereby altering both stratospheric and tropospheric circulation patterns (2). Estimates of the secular increase in total irradiance since the late 17th century Maunder sunspot minimum range from ~0.05 to 0.5% (*I*). Values in the middle of this range are sufficient to force the intermediate-complexity Zebiak-Cane model of El Niño–Southern Oscillation (ENSO) dynamics into a more El Niño–like state during the Little Ice Age (A.D. ~1400 to 1850) (3), a response dubbed the “ocean dynamical thermostat” because negative (or positive) radiative forcing results in dynamical ocean warming (or cooling, respectively) of the eastern tropical Pacific (ETP) (4). This model prediction is supported by paleoclimatic proxy reconstructions over the past millennium (3, 5, 6). In contrast, fully coupled general circulation models (GCMs) lack a robust thermostat response because of an oppo-

sing tendency for the atmospheric circulation itself to strengthen under reduced radiative forcing (7).

ENSO is a leading source of interannual climate variability over large regions of the globe, so it is crucial to gain an improved understanding of its past responses to external forcing at various time scales. Tropical fossil corals provide the most reliable means for reconstructing ENSO conditions from the past (5), but the record is currently too

fragmented to test for any relation to persistent solar forcing before the past millennium. Few sea surface temperature (SST) reconstructions from well-placed tropical Pacific sediment cores have sufficient temporal resolution to address this question.

Sediment core composite MV99-GC41/PC14 was raised from a water depth of 540 m on the floor of Soledad Basin, which is located off the west coast of Baja California Sur, Mexico (25.2°N, 112.7°W), and has an effective sill depth of 290 m (8). Although this site is just outside of the tropical band, modern conditions here are strongly teleconnected to ENSO. The modern annual cycle of SST has an amplitude of ~8°C on average, with minimum temperatures during spring, the season of strongest coastal upwelling (9, 10). Yet interannual variability in SST is much more strongly dependent on ENSO than on local upwelling winds. Over the 30-year period covered by satellite observations, the Niño 3 index explains 37% of the monthly SST anomaly near Soledad Basin (correlation coefficient $r = 0.61$ maximum correlation with a 2-month lag), whereas the local upwelling index explains only 2% ($r = -0.16$ with zero lag) (Fig. 1). ENSO is crucial for SST because the regional thermocline deepens during El Niño years, so that even with vigorous local upwelling the ascending waters are warmer than during La Niña or neutral years (11). Recent spring SST minima have ranged from 17°C during strong La Niñas to 20°C during

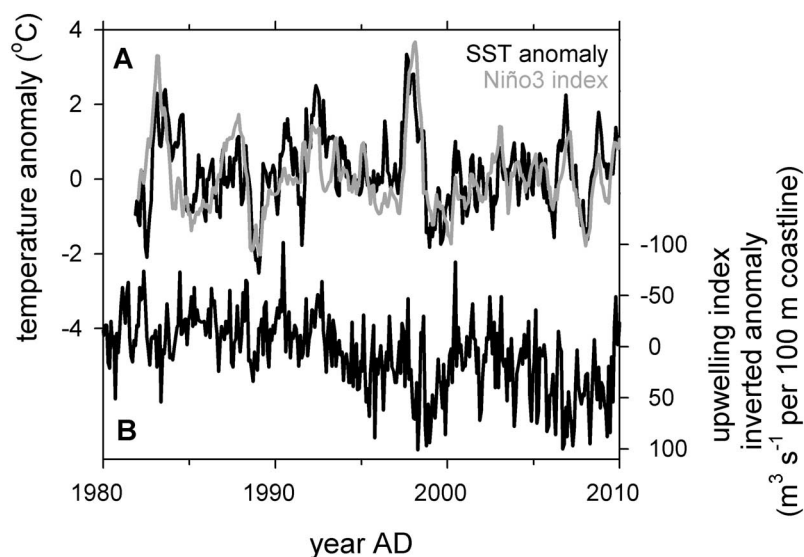


Fig. 1. (A) Monthly SST anomaly for the 1° grid cell situated over Soledad Basin (black) (9), compared to the monthly Niño 3 SST index on the same vertical scale but lagged by 2 months (gray) (9) and (B) the local (24°N, 113°W) monthly upwelling index (offshore Ekman transport computed from wind stress) anomaly (10), shown inverted.

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El Niños. Surface warming off the coast of Baja California Sur can be further enhanced under El Niño conditions by the northeastward expansion of subtropical surface waters that effectively block the admixture of southward-flowing subarctic (California Current) waters (12).

An age model based on 22 calibrated accelerator mass spectrometry radiocarbon dates (fig. S1) reveals that the composite core spans the past 13.9 thousand years (ky) with an average sedimentation rate of $>1 \text{ m ky}^{-1}$. During the Holocene, the sediments are laminated, indicating negligible bioturbation under low- O_2 conditions on the sea floor (8). Preservation of planktonic foraminifera is excellent throughout the core, with glassy tests and spines commonly present. We measured the SST proxy Mg/Ca in the planktonic foraminifer *Globigerina bulloides* (13), which lives at the sea surface primarily during the spring peak upwelling season along this margin (14). Samples were nominally spaced at 5-cm intervals and contained 30 to 60 foraminifera each, so each measurement theoretically averages 30 to 60 month-long (foraminiferal lifespan) upwelling-season snapshots spread over roughly a decade (1-cm sample width), with ~ 50 -year spacing between samples. Although not capable of resolving the typical ENSO periodicities of 2 to 7 years, this sampling is sufficient to detect any multicentennial/millennial-scale changes in spring SSTs.

Our Mg/Ca-based SST reconstruction indicates that early to middle Holocene [~ 4 to 10 thousand years ago (ka)] spring temperatures were $\sim 1^\circ\text{C}$ cooler, on average, than during the rest of the past 14 ky (Fig. 2). By analogy with modern ETP dynamics, we suggest that the cooling is best explained by a shallower thermocline and a reduced influence of subtropical surface waters. This scenario is consistent with previous suggestions of a more La Niña-like state during the early to middle Holocene. Mg/Ca reconstructions from the equatorial Pacific indicate an enhanced zonal SST gradient at this time, with a colder eastern cold tongue and warmer western warm pool (Fig. 2) (15, 16). At Baja California Sur, the cooling may have been amplified by a strengthened California Current (17). In contrast, alkenone-based SST reconstructions from both Baja California Sur (18) and the cold tongue (19) do not exhibit a mid-Holocene cooling. This disparity might be due to a summer/fall habitat for coccolithophores, resulting in an overprinting of La Niña-like cooling by orbitally forced seasonal radiative heating (20).

Numerical models of varying complexity have simulated a La Niña-like cooling of the ETP during the early to middle Holocene in response to enhanced boreal summer/fall insolation. Easterly winds strengthen because of zonally asymmetric heating of the tropical ocean and atmosphere

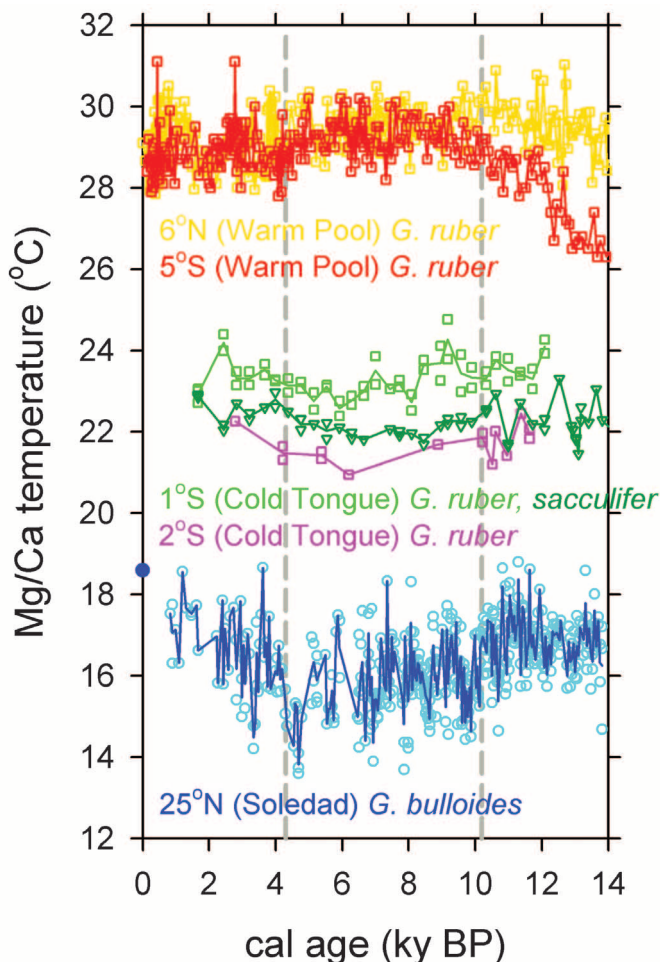
(21, 22), increased atmospheric baroclinicity (23), and/or intensification of the Asian summer monsoon (24). Although local Baja California Sur upwelling-favorable winds may also respond positively to orbital forcing, the maximum in spring insolation occurred much earlier (~ 15 ka) than our observed cooling. In support of more distant teleconnections, the shift toward warmer upwelling conditions just before 4 ka is close to the timing of widespread evidence for an abrupt and permanent weakening of the Asian summer monsoons (25), which may have helped the Pacific relax into a more El Niño-like state (24).

In addition to orbital-scale changes, the Soledad Basin Mg/Ca record displays strong variance at millennial time scales, as seen in the five-depth (nominally 200 to 300 years) running mean of the Mg/Ca data (Fig. 3). Before the data gap at ~ 5.9 to 6.5 ka, sample density is high enough (48 measurements per thousand years), and the relative noise low enough, to give us confidence that the smoothed record captures a meaningful millennial-scale climate history. We observe five cold intervals between ~ 7 and 11 ka, with roughly 1-ky spacing. In light of model- and proxy-based results supporting a solar influence on ENSO over the past millennium (3, 6), we compare the smoothed record to cosmogenic nuclide proxies for solar activity.

For the period before the beginning of sunspot observations in A.D. 1610, reconstructions of solar variability are based on the cosmogenic nuclides ^{14}C (recorded in tree rings) (26) and ^{10}Be (preserved in polar ice cores) (27, 28). An active Sun generates a higher total irradiance and a stronger interplanetary magnetic field that helps to shield Earth from the galactic cosmic rays that produce ^{14}C and ^{10}Be in the atmosphere. However, the relation between solar irradiance and cosmic-ray shielding is not well understood over long time scales. In addition, atmospheric levels of ^{14}C may be affected by changes in Earth's carbon cycle, ^{10}Be fluxes to ice sheets may be influenced by local climate, and the production rates of both nuclides are modulated by long-term variations in Earth's magnetic field. Nevertheless, the shared variance of high-pass-filtered (to correct for presumed slow variations in the geomagnetic field) ^{14}C and ^{10}Be records can be taken as an indication of fluctuations in solar activity over the Holocene.

Each of the early Holocene millennial-scale coolings at Soledad Basin corresponds to an inferred millennial-scale increase in solar activity (decreased cosmogenic nuclides) (Fig. 3). Cross-wavelet analysis of the unsmoothed data indicates significant common power (in phase) between Mg/Ca and the nuclides in the ~ 800 - to 1000-year band (fig. S2). After performing a ~ 250 -year smoothing and $\frac{1}{1800} \text{ year}^{-1}$ high-pass filtering of each record, Mg/Ca (before the ~ 5.9 -6.5 ka data gap) correlates significantly with ^{14}C production ($r = 0.49$, $p = 0.02$, with 50-year lag on Mg/Ca) and reasonably well with ^{10}Be flux ($r = 0.41$, $p = 0.07$, with 100-year lag on Mg/Ca) (Fig. 4) (13). These correlations are based on completely independent age models. Given the strong link between this region and ENSO variability today, we suggest that this correspondence

Fig. 2. SST reconstructions based on Mg/Ca in surface-dwelling planktonic foraminifera from the western equatorial Pacific warm pool (15) (gold and red), eastern equatorial Pacific cold tongue (16) (green and pink), and Soledad Basin (this study) (blue). Symbols denote individual measurements, and lines trace the mean at each depth. Along the equator, *G. ruber* and *G. sacculifer* are believed to represent mean annual conditions, whereas at Soledad Basin, *G. bulloides* reflects spring upwelling. The solid blue circle on the y axis denotes the modern average SST during the coldest month of the year (spring peak upwelling) at Soledad Basin (9). Vertical gray dashed lines bracket the early to middle Holocene interval of increased zonal SST gradient. BP, before the present.



provides support for the idea that the ocean dynamical thermostat (4) acts effectively at centennial-millennial time scales (3). Indeed, these early Holocene oscillations between warm El Niño-like and cool La Niña-like conditions were recently predicted by solar-forcing experiments using the Zebiak-Cane model (29). Although it is possible that local upwelling-favorable winds responded directly to positive solar forcing and amplified the cool SST signal, we argue, on the basis of modern observations (Fig. 1), that the impact would have been minor without a concomitant La Niña-like shoaling of the regional thermocline. Between ~2.2 and 5.9 ka, the poor

correlation between Mg/Ca and the solar proxies may be due to the lower sample density (less than half that of the earlier interval) and/or the reduced amplitude of inferred solar variability, in line with the model prediction (29).

The observed sensitivity of the tropical Pacific to modest radiative forcing may have been achieved through positive feedback with other regions that also responded to solar variability. La Niña has historically been associated with stronger summer monsoons over Asia, as both are linked to strong easterlies over the tropical Pacific (30). Oxygen isotopes from speleothems in southern China (31) and Oman (32) indicate monsoon

strengthening during early Holocene solar maxima, suggesting that an Asian teleconnection may have helped push the Pacific into a La Niña-like state during these intervals, or vice versa. Although the period of overlap is relatively short, the smoothed speleothem records bear strong resemblance to the Soledad Basin SST history (China: $r = 0.74$, $p = 0.01$; Oman: $r = 0.76$, $p = 0.003$) (Fig. 4). It is interesting to note that during the interval of greatest mismatch between Soledad Basin and the solar proxies, the cave records agree with our SST history: At 8.2 ka, the ETP was in an El Niño-like state and the monsoons were weak, despite the inferred secular increase in solar activity. This apparent anomaly may be attributed to the well-known “8.2-ka event,” during which a large Laurentide meltwater discharge is believed to have cooled the North Atlantic and Eurasia, thereby weakening the Asian summer monsoons (33), which possibly fostered El Niño-like conditions in the ETP.

Additionally, Bond *et al.* (34) showed that there was increased ice-rafted debris (IRD) delivery from the Labrador and Nordic Seas into the North Atlantic during inferred Holocene solar minima. Their stacked IRD record correlates with Soledad Basin SSTs even more strongly than do the solar proxies ($r = 0.70$, $p < 0.001$, with 100-year lag on Mg/Ca) (Fig. 4). A cold North Atlantic during solar minima may have reinforced ETP warming through either the Asian monsoon linkage (24) or a southward shift of the intertropical convergence zone (16). Closure of this hypothetical positive feedback loop has been suggested to occur through an El Niño-forced shift in the prevailing winds that deliver drift ice from the Nordic Seas into the North Atlantic (29).

Persistent, decadal-scale droughts over the western United States have been linked to La Niña-like SST patterns in the ETP during the instrumental period (35). Tree-ring reconstructions extend this relationship back to the Medieval Warm Period (MWP, A.D. ~900 to 1300), which was seemingly characterized by positive solar forcing, inactive tropical volcanism, La Niña-like conditions, and multidecadal “megadroughts” (3, 5, 6, 35). The first high-resolution, continuous Holocene speleothem proxy precipitation record from the southwestern United States documents a robust connection between inferred solar-activity maxima and dry conditions, which may be explained by solar forcing of La Niña-like states (36). Taken together with our SST record, these observations are consistent with solar-induced dynamical cooling of the ETP and provide predictions for millennial-scale fluctuations in the hydrologic balance over the western United States during the early Holocene.

GCMs fail to reproduce the La Niña-like nature of the MWP because the ocean thermostat mechanism is either absent or dampened by atmospheric effects in such models (6, 7). If our observations are supported by future SST reconstructions from the equatorial Pacific, then it is possible that the sensitivity of the climate system to solar forcing is underestimated by current GCMs. The nature of the climate response appears to be one of

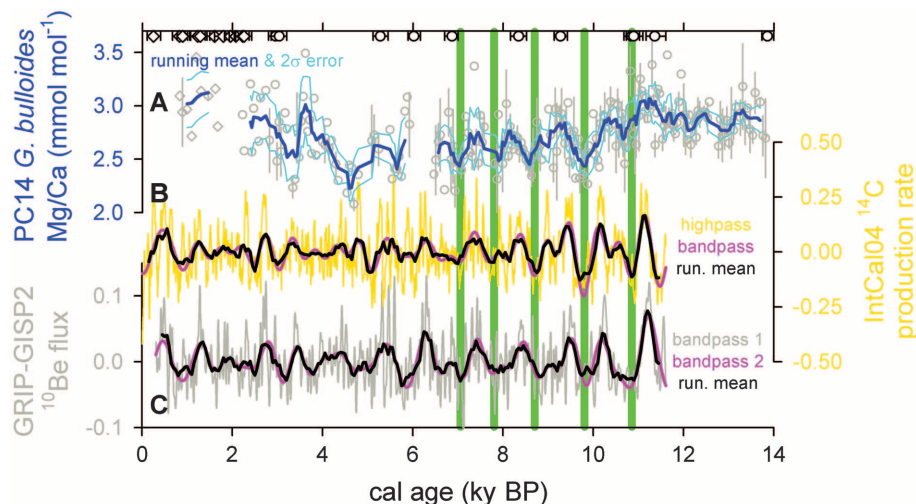


Fig. 3. Soledad Basin Mg/Ca record compared to solar proxies ^{14}C and ^{10}Be (13). (A) *G. bulloides* Mg/Ca mean and standard deviation at each depth (gray) with five-depth running mean (blue) and associated 2σ uncertainty estimate (light blue). Open black symbols at the top of the figure denote calibrated ^{14}C ages with 1σ errors. Diamonds are from GC41, and circles are from PC14. (B) Holocene tree-ring-derived $\Delta^{14}\text{C}$ (26) converted to ^{14}C production rate, with high values corresponding to low inferred solar activity. Data were high-pass filtered at $\frac{1}{1800}$ year $^{-1}$ to remove secular changes that are probably related to Earth’s magnetic field (gold), band-pass filtered at $\frac{1}{1800}$ to $\frac{1}{500}$ year $^{-1}$ as in (34) (pink), and smoothed with a 250-year running mean before $\frac{1}{1800}$ year $^{-1}$ high-pass filtering (black). (C) Holocene ice core ^{10}Be flux (27, 28) filtered as in (B), except that the gray curve is a $\frac{1}{1800}$ to $\frac{1}{50}$ year $^{-1}$ band pass that additionally eliminates subdecadal-scale noise. Green vertical lines indicate Soledad Basin cold intervals that correspond to times of increased solar activity.

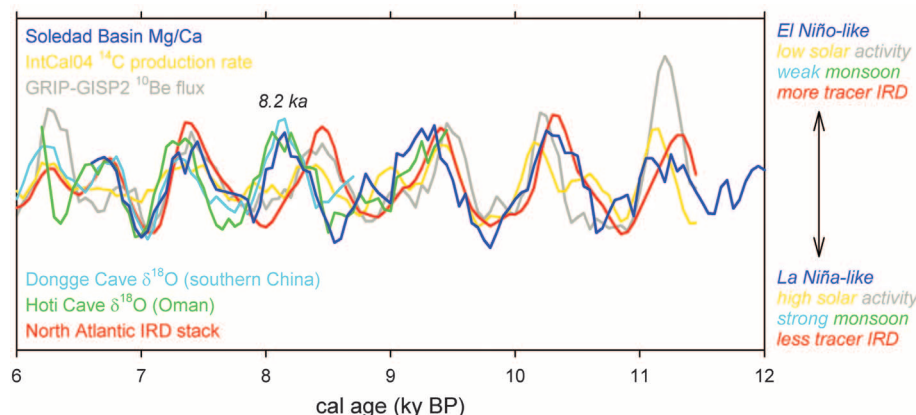


Fig. 4. Likely teleconnected climatic and solar proxy records spanning the early Holocene, each smoothed at ~250 years and high-pass filtered at $\frac{1}{1800}$ year $^{-1}$ (13). Records are Soledad Basin *G. bulloides* Mg/Ca (this study) (blue), tree-ring-derived (26) ^{14}C production rate (gold), ice core ^{10}Be flux (27, 28) (gray), Dongge Cave (southern China) stalagmite $\delta^{18}\text{O}$ (31) (light blue), Hoti Cave (Oman) stalagmite $\delta^{18}\text{O}$ (32) (green), and North Atlantic stack of IRD petrologic tracers (34) (red). All records are on their independent and untuned age models.

shifting atmosphere-ocean circulation patterns, with the tendency for global radiative surface warming being countered by the ocean dynamical thermostat.

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Supporting Online Material

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Plasticity of Animal Genome Architecture Unmasked by Rapid Evolution of a Pelagic Tunicate

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Genomes of animals as different as sponges and humans show conservation of global architecture. Here we show that multiple genomic features including transposon diversity, developmental gene repertoire, physical gene order, and intron-exon organization are shattered in the tunicate *Oikopleura*, belonging to the sister group of vertebrates and retaining chordate morphology. Ancestral architecture of animal genomes can be deeply modified and may therefore be largely nonadaptive. This rapidly evolving animal lineage thus offers unique perspectives on the level of genome plasticity. It also illuminates issues as fundamental as the mechanisms of intron gain.

Tunicates, viewed as the closest living relatives of vertebrates, were probably simplified from more complex chordate ancestors (*I*). Larvacean tunicates represent the second most abundant component of marine zooplankton and filter small particles by their gelatinous house. *Oikopleura dioica* is the most cosmopolitan larvacean, has a very short life cycle (4 days at 20°C), and can be reared in the laboratory for hundreds of

generations (2). Unique among tunicates, it has separate sexes. We sequenced its genome with high-coverage shotgun reads (14X) using males resulting from 11 successive full-sib matings (figs. S1 and S2 and tables S1 to S3) (3). Two distinct haplotypes were retained, despite inbreeding. Their comparison yielded a high estimate of population mutation rate ($\theta = 4N_e\mu = 0.0220$) that is consistent with a large effective population size (N_e) and/or a

high mutation rate per generation (μ) (3). Sequence comparisons among populations from the eastern Pacific and eastern Atlantic and within the latter revealed low dN/dS values (dN , rate of substitutions at nonsilent sites; dS , rate of substitutions at silent sites) consistent with strong purifying selection, as expected for large populations (3). In 17 of 18

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