REPORT

FOSSIL RECORD

Global record of "ghost" nannofossils reveals plankton resilience to high CO_2 and warming

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Predictions of how marine calcifying organisms will respond to climate change rely heavily on the fossil record of nannoplankton. Declines in calcium carbonate ($CaCO_3$) and nannofossil abundance through several past global warming events have been interpreted as biocalcification crises caused by ocean acidification and related factors. We present a global record of imprint—or "ghost"—nannofossils that contradicts this view, revealing exquisitely preserved nannoplankton throughout an inferred Jurassic biocalcification crisis. Imprints from two further Cretaceous warming events confirm that the fossil records of these intervals have been strongly distorted by $CaCO_3$ dissolution. Although the rapidity of present-day climate change exceeds the temporal resolution of most fossil records, complicating direct comparison with past warming events, our findings demonstrate that nannoplankton were more resilient to past events than traditional fossil evidence suggests.

As CO_2 levels in the atmosphere rise, resultant ocean acidification (OA) and declining seawater carbonate ion concentrations will likely make it more difficult for marine organisms to form their calcium carbonate ($CaCO_3$) skeletons or shells (*1*, *2*). Coccolithophores, a group of unicellular phytoplanktonic algae (also known as nannoplankton), are the most productive marine calcifiers (*3*), but predicting their response to future environmental change has proven challenging. Experiments testing the effects of high CO_2 and temperatures on living coccolithophores and their calcitic exoskeletons have shown apparently contradictory results within and between species (*4*–*8*). However, interpretations of geological and fossil-based evidence have evoked globally catastrophic responses in nannoplankton during past intervals of high temperature and CO_2. Specifically, prominent studies have observed substantial declines in $CaCO_3$ and nannoplankton abundance through past global warming events—especially throughout the Mesozoic oceanic anoxic events (OAEs)—and have interpreted these signals as biocalcification crises, whereby OA, and related environmental change, directly compromised biogenic $CaCO_3$ production (reviewed in data S1 to S3). Conversely, others have argued that these declines in $CaCO_3$ are caused by dissolution of carbonate at the seafloor during these warming events and that independent evidence for nannoplankton responses to OA must be better understood and demonstrated before biocalcification crises are invoked (*9*, *10*). Given that the biocalcification crisis paradigm continues to be widely applied to past warming episodes (data S1 to S3) and that this model predicts potentially disastrous changes to future marine biodiversity and carbon cycle function, we tested this hypothesis using a novel methodology.

We examined the biocalcification crisis associated with the Toarcian OAE [T-OAE; ~183 million years ago (Ma)] in the Early Jurassic—considered as one of the most severe such events of the past 200 million years. The T-OAE was a geologically rapid global warming event caused by volcanism in the Southern Hemisphere (*11*) and is characterized by a range of environmental, geological, and ecological changes, including high CO_2, OA, oceanic anoxia, the deposition of organic-rich sediments, a major negative carbon isotope excursion, and widespread extinction [(*12*) and references therein]. Previous interpretations of the biocalcification crisis are primarily based on declining $CaCO_3$ in the sedimentary rock record and decreased nannoplankton species abundances and sizes (data S1), but this evidence is dependent on conventional nannofossil analyses, whereby data are derived from calcite "body" fossils. Here we report on an overlooked form of preservation—namely, imprint (or "ghost") nannofossils—which provides critical information that may be lost from the more routinely studied body fossil record.

Toarcian rock samples from the UK, Germany, Japan, and New Zealand (fig. S1) were processed for organic matter analysis. Scanning electron microscopy (SEM) of organic particles revealed nannoplankton imprints preserved on the surfaces of marine organic-walled plankton (dinoflagellate cysts, prasinophytes, and acritarchs), amorphous organic matter (AOM), and spores and pollen from land plants (Fig. 1). Imprints are also visible with the use of transmitted light, fluorescence, and confocal microscopy (fig. S2), but fine details are evident when SEM is used, with specimens displaying diagnostic coccolith rims, radial and imbricating sutures, and fragile axial and radiating central structures (figs. S3 to S12). Preservation is often pristine, and digital inversion of imprint images provides "virtual casts" that assist in visualization and identification of the original nannofossils (Fig. 1). Imprints were found as single or multiple specimens of the same or different species and cover a range of forms, including small coccoliths (<3 μm; fig. S3I), larger nannoplankton (figs. S3, J to O, and S8, A to D), and collapsed coccolithophore exoskeletons (coccospheres) (figs. S5, A and B, and S8F). Nannoplankton imprints on organic matter have only occasionally been reported from the fossil record (*13*–*15*), presumably because of their cryptic mode of preservation and minute size. Some studies have interpreted imprints as the negative molds of coccoliths that were dissolved during acid digestion of rock samples in the laboratory (*14*). However, we recorded imprints on unprocessed rock surfaces (fig. S6) and in samples devoid of $CaCO_3$, indicating that these fossils occur naturally.

Reduced nannoplankton abundances during the T-OAE have been reported from multiple locations (data S1), but this signal is most extreme in the Cleveland Basin, Yorkshire (UK), where a nannoplankton disappearance event has been observed (*16*). Samples from Yorkshire, which we studied using traditional nannoplankton body fossil methods, were either barren or yielded rare or very rare nannofossils (figs. S13 and S14). These observations essentially replicate previous findings of reduced species abundances or absences throughout the T-OAE (*16*) and seemingly support the biocalcification crisis paradigm. However, imprints from the same samples challenge this view, revealing abundant and rich nannoplankton communities throughout the T-OAE interval, refuting the disappearance event hypothesis. Imprints are not just confined to the Cleveland Basin but have been discovered in a wide range of depositional settings in globally distributed lower Toarcian strata (e.g., Germany, Japan, and New Zealand; Figs. 1 and 2). These results indicate that observed decreases in $CaCO_3$ and nannofossil abundance through the T-OAE are due to $CaCO_3$ dissolution after burial rather than representing a primary crisis of the living nannoplankton. The imprint fossils from Japan and New Zealand (Fig. 1) are the oldest coccoliths recorded from these countries, demonstrating that this approach is widely applicable and can expand nannofossil records, even in rocks where body fossils are absent and

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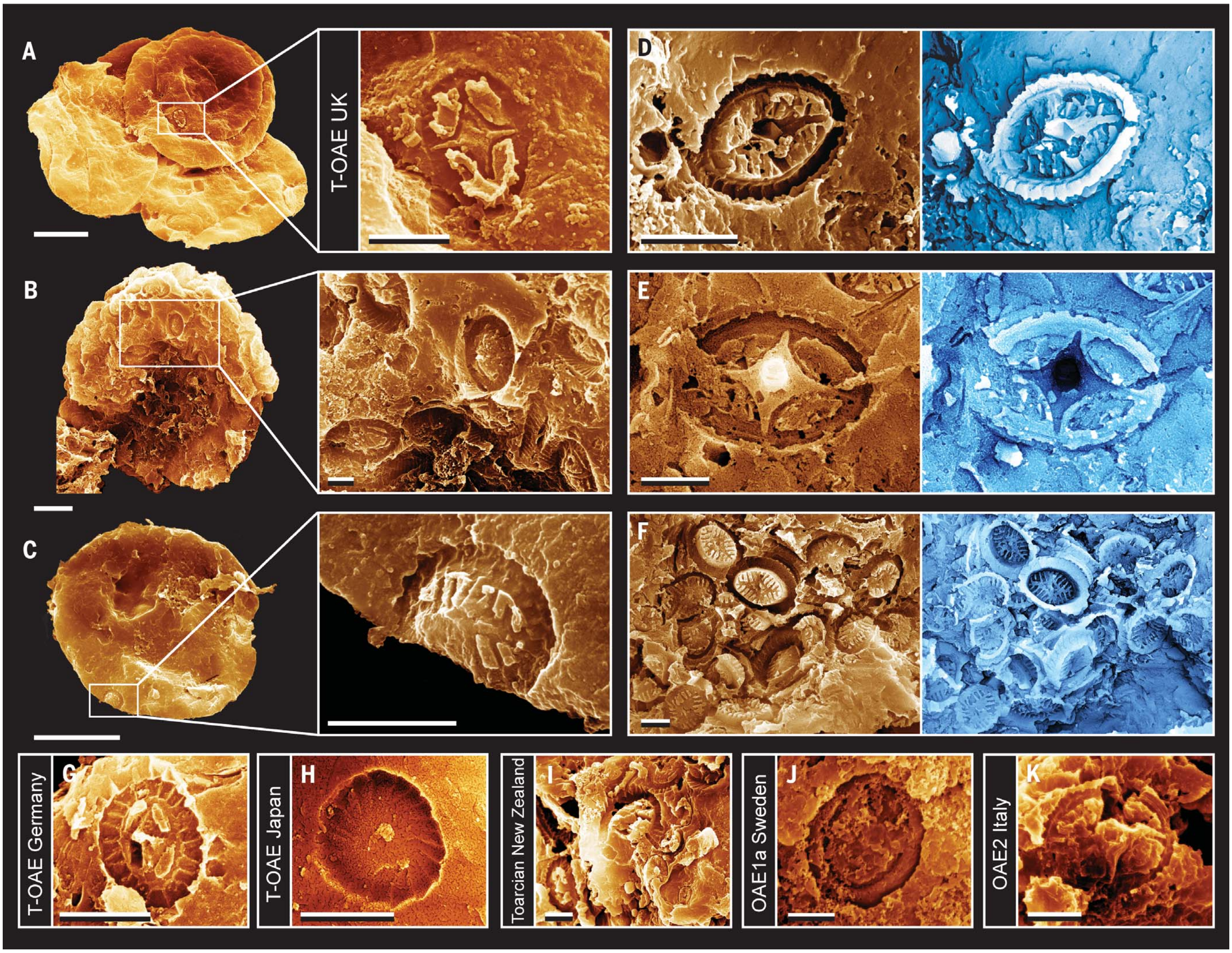

Fig. 1. Ghost nannofossils imprinted on organic matter. (**A**) *Staurolithites* sp. imprint on *Classopollis* sp. (pollen) [NHMUK PM FM 2355 (2)]. (**B**) *Crepidolithus impontus* imprints on *Cerebropollenites macroverrucosus* (pollen) [NHMUK PM FM 2355 (2)]. (**C**) *Bussonius prinsii* imprint on prasinophyte alga [NHMUK PM FM 2355 (2)]. (**D** to **K**) Imprints on AOM. (D) *B. prinsii* [NHMUK PM FM 2355 (2)]. (E) *Axopodorhabdus atavus* [NHMUK PM FM 2377 (1)]. (F) *Calyculus serrai* coccosphere [NHMUK PM FM 2377 (1)]. (G) *Axopodorhabdus* sp. [S043981]. (H) *Lotharingius hauffii* [S043957]. (I) *Calyculus* sp., *Staurolithites* sp., and others [S043993]. (J) *Manivitella pemmatoidea* [S043946]. (K) *Stoverius achylosus* [S043941]. Blue images are inverted virtual casts. Scale bars in overview images in (A) to (C) are 10 μm; all other scale bars are 2 μm.

have been subjected to thermal alteration [e.g., Japanese material studied here; see also (*17*)].

We further extended our study to test for imprints through two Cretaceous OAEs—the early Aptian OAE1a (~120 Ma) and the Cenomanian-Turonian OAE2 (~94 Ma)—for which there are also claims of biocalcification crises (reviewed in data S2 and S3). The Cretaceous OAEs are also associated with distinct episodes of volcanism and are characterized by comparable suites of environmental, geological, and ecological changes [(*12*) and references therein]. We found imprint fossils through both Cretaceous OAEs (Figs. 1 and 2 and figs. S11 and S12), demonstrating that ghost nannofossil preservation is not limited to the T-OAE and that observed decreases in $CaCO_3$ and nannoplankton abundances during OAE1a and OAE2 (data S2 and S3) are probably linked to the secondary removal of $CaCO_3$ from the rock record. Imprints from the OAE2 Contessa section, Italy, are particularly important because these were recorded during an inferred nannoplankton biocalcification "blackout," corresponding to the Bonarelli Level (a ~1-m-thick black shale virtually devoid of $CaCO_3$), which abruptly interrupts a limestone succession rich in body fossils (fig. S14 and data S3). Our results overturn the blackout hypothesis and indicate that the original $CaCO_3$ has been lost through post-burial dissolution, leaving a misleading signal of declining carbonate production during OAE2.

The recurrence of imprints in OAE-related sediments demonstrates that these organic-rich intervals are especially prone to this type of nannofossil preservation—indeed, the OAE intervals record the richest imprint assemblages (Fig. 2). Abundances of imprints and AOM are generally positively correlated (fig. S15), which suggests that plentiful organic matter was an important requirement, providing the necessary "plastic" substrate for imprinting. This also explains the subsequent dissolution of $CaCO_3$, because high amounts of organic matter can lead to acidic pore waters during diagenesis (*18*). The formation of imprints also required overburden pressure before the loss of body fossils, indicating that dissolution took place after burial, and the absence of compressed imprints reveals that this occurred after lithification.

Nannofossil abundances in sedimentary rocks are the product of a range of factors,

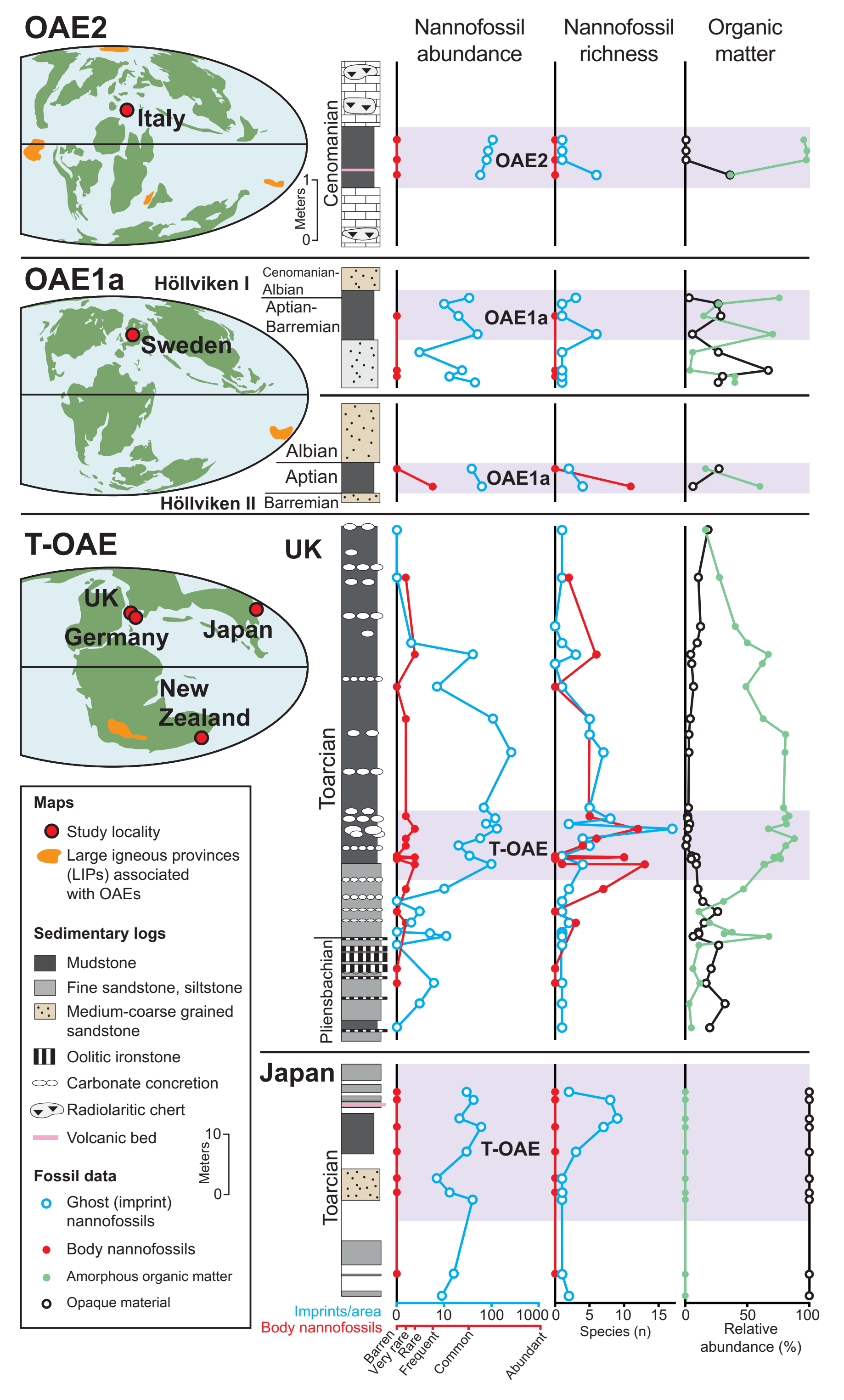

Fig. 2. Ghost nannofossil, body nannofossil, and organic matter records through the T-OAE (Japan and UK), OAE1a (Sweden), and OAE2 (Italy). Imprints/area denotes the number of imprints recorded across a standard area of organic matter. Body nannofossil abundance categories: Abundant, >10% of particles; Common, >1 to 10%; Frequent, 0.1 to 1%; Rare, <0.1%; Very Rare, <20 specimens in total; Barren, no body nannofossils. See materials and methods for further details, including richness and organic matter data collection methods. Note the different vertical scale for OAE2. Figure S14 is an extended version of this figure that includes data from Germany and New Zealand. For raw data, see data S4.

including those that affect original populations (temperature, nutrients, water chemistry), export pathways (grazing, ballasting), secondary abundances (exported plankton versus siliciclastic dilution), and preservation (diagenesis). None of these factors necessarily disrupts calcification in the living nannoplankton, and therefore preserved abundance changes alone do not provide evidence of biocalcification crises. On the contrary, our observations show that $CaCO_3$ and nannoplankton body fossil abundances can be severely modified or eradicated after deposition, indicating that these records are unreliable proxies for OA or pelagic carbonate production. Independent geochemical proxy evidence for OA at the T-OAE remains contentious (*19*, *20*). Given the uncertainty about rates of carbon injection that drove this and other OAEs, these rates may well have been too slow to have induced prolonged or high-magnitude surface water OA (*10*, *21*). However, regardless of the severity or duration of OA during the T-OAE—or other proposed causes of a nannoplankton crisis, such as changes in temperature, salinity, nutrients, or anoxia (data S1)—our records challenge the concept of a crisis. More generally, these findings call for the reexamination of other inferred biocalcification crises, and ghost nannofossils represent a tool with which to test such claims.

Our imprint record shows that nannoplankton communities were more resilient to environmental changes during the T-OAE—including high CO_2 and warming, evident from independent proxies [(*12*) and references therein]—than traditional nannofossil and $CaCO_3$ records suggest. However, several previously observed species-specific changes, such as declines in *Schizosphaerella punctulata* and nannoconids during the T-OAE and OAE1a, respectively, may still represent primary responses of nannoplankton to environmental change (data S1 and S2). At the community level, however, the imprint record shows that nannoplankton flourished during the T-OAE, and their resilience is supported by observations of increased speciation rates and an absence of elevated extinctions across the T-OAE and OAE1a (data S1 and S2).

The abundance of prasinophyte algae in many T-OAE intervals has been interpreted as a rise to dominance at the expense of nannoplankton (*16*), but the close association of imprints and prasinophyte fossils observed here demonstrates that both groups coexisted or occurred in close succession (Fig. 1C). Near-monospecific assemblages of prasinophytes during the T-OAE likely represent persistent algal blooms (*22*); similarly, the monospecific concentrations of nannofossil imprints (Fig. 1F and figs. S3B and S7A) are pellets or aggregates that provide snapshots of high-dominance communities. Rather than being considered casualties of the T-OAE, our findings indicate

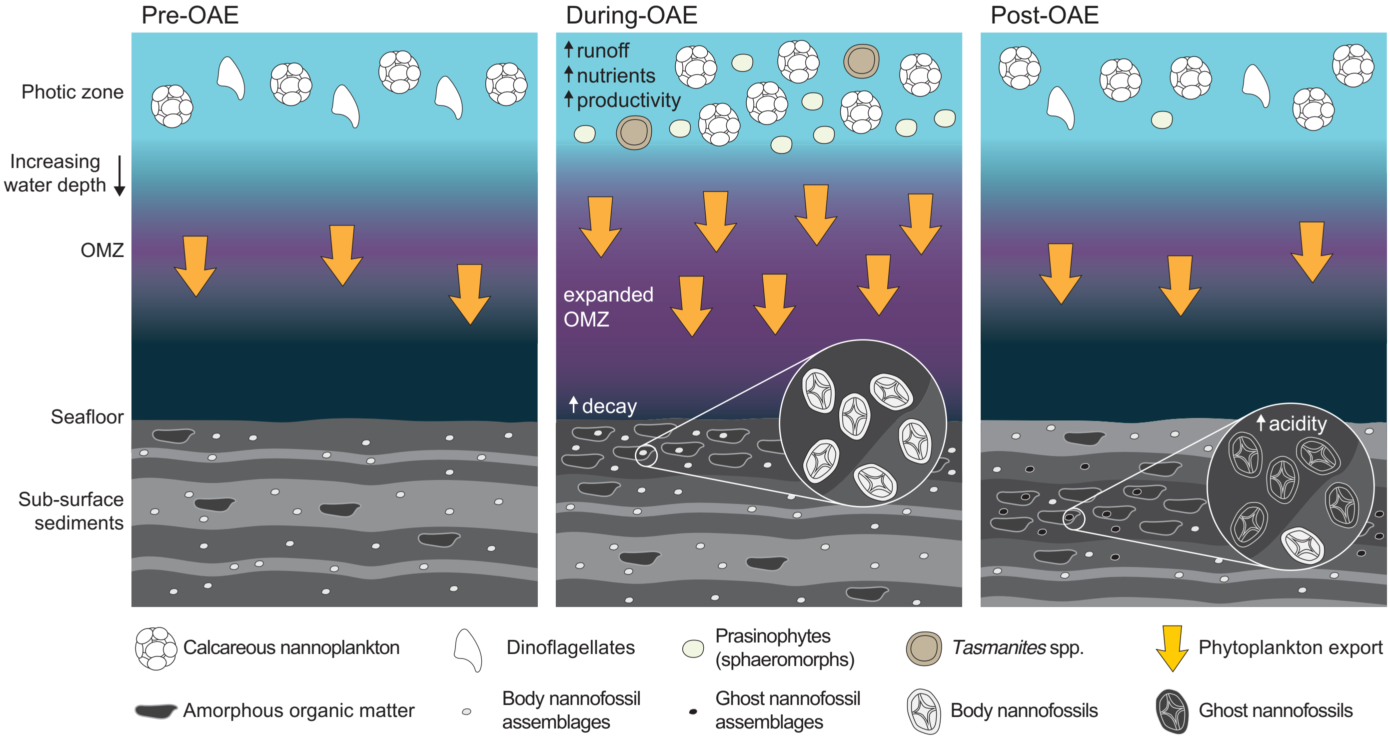

Fig. 3. Schematic summary of the major changes in phytoplankton groups through the T-OAE, showing changes in phytoplankton export and the formation of nannofossil imprints. Note that the oxygen minimum zone (OMZ) expands during the OAE and that, after the OAE, the acidic pore waters within subsurface sediments lead to the dissolution of nannoplankton body fossils and the formation of imprints.

that nannoplankton continued to draw down CO_2 and sequester carbon in seafloor sediments, which in the long-term likely expedited the termination of the event. However, high production, blooms, and potential toxicity (*23*) suggest that in the short term nannoplankton, like prasinophytes, fueled anoxia through eutrophication and increased accumulation of organic matter at the seafloor, enhanced by coccolith ballasting (*24*) (Fig. 3).

Our records of ghost nannofossils, discovered through unconventional methods, indicate no evidence of biocalcification crises during the studied Mesozoic OAEs, at least for plankton that form calcite, the more stable $CaCO_3$ polymorph compared to aragonite. Instead, these findings show how diagenesis can completely reshape the geological archive and highlight that a literal reading of the fossil record can mislead interpretations. Given that atmospheric CO_2 concentrations are currently rising at previously unseen rates, the use of individual OAEs as past analogs of current change may be premature because carbon-input rates—and therefore the duration and intensity of surface water OA—remain uncertain for these events (*10*, *21*). Nevertheless, our imprint record demonstrates the resilience of nannoplankton communities during multiple past global warming events and shows that plankton proliferation can accelerate the development of OAEs. Our findings also indicate that the conditions that prevailed during OAEs may become more prevalent (*25*, *26*), with plankton blooms and hypoxic dead zones becoming widespread across globally warming oceans.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S15
References (*27–74*)
Data S1 to S5

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Science

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Ghosts of the past

The marine geological records of some past global warming events contain relatively few nannoplankton fossils, the lack which some interpret as being evidence of the impact of ocean acidification and/or related environmental factors on biocalcification. Slater *et al*. present a global record of imprint, or “ghost,” nannofossils throughout several of those intervals during the Jurassic and Cretaceous periods (see the Perspective by Henderiks). This finding implies that a literal interpretation of the fossil record can be misleading, and demonstrates that nannoplankton were more resilient to past warming events than traditional fossil evidence would suggest. —HJS