Science AAAS

Giant Larvacean Houses: Rapid Carbon Transport to the Deep Sea Floor

Bruce H. Robison, *et al.*

Science **308**, 1609 (2005);
DOI: 10.1126/science.1109104

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by clicking here.

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines here.

The following resources related to this article are available online at www.sciencemag.org (this information is current as of February 13, 2010):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:
http://www.sciencemag.org/cgi/content/full/308/5728/1609

Supporting Online Material can be found at:
http://www.sciencemag.org/cgi/content/full/308/5728/1609/DC1

This article **cites 24 articles**, 8 of which can be accessed for free:
http://www.sciencemag.org/cgi/content/full/308/5728/1609#otherarticles

This article has been **cited by** 11 article(s) on the ISI Web of Science.

This article has been **cited by** 7 articles hosted by HighWire Press; see:
http://www.sciencemag.org/cgi/content/full/308/5728/1609#otherarticles

This article appears in the following **subject collections**:
Oceanography
http://www.sciencemag.org/cgi/collection/oceans

Downloaded from www.sciencemag.org on February 13, 2010

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2005 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.

20. P. J. Schuck, D. P. Fromm, A. Sundaramurthy, G. S. Kino, W. E. Moerner, *Phys. Rev. Lett.* **94**, 017402 (2005).
21. K. Li, M. I. Stockman, D. J. Bergman, *Phys. Rev. Lett.* **91**, 227402 (2003).
22. J. B. Pendry, L. Martin-Moreno, F. J. Garcia-Vidal, *Science* **305**, 847 (2004).
23. R. R. Alfano, S. L. Shapiro, *Phys. Rev. Lett.* **24**, 584 (1970).
24. Y.-D. Qin, D.-L. Wang, S.-F. Wang, Q.-H. Gong, *Chin. Phys. Lett.* **18**, 390 (2001).
25. P.-A. Champert *et al.*, *Opt. Express* **12**, 4366 (2004).
26. G. T. Boyd, Z. H. Yu, Y. R. Shen, *Phys. Rev. B* **33**, 7923 (1986).
27. M. R. Beversluis, A. Bouhelier, L. Novotny, *Phys. Rev. B* **68**, 115433 (2003).
28. M. Paulus, O. J. F. Martin, *J. Opt. Soc. Am. A* **18**, 854 (2001).
29. W. Rechberger *et al.*, *Opt. Commun.* **220**, 137 (2003).
30. P. B. Johnson, R. W. Christy, *Phys. Rev. B* **6**, 4370 (1972).
31. We gratefully acknowledge continuous support by H.-J. Güntherodt. We thank J. Boudaden, I. Mack, and P. Oelhafen for the preparation of ITO substrates, Ch. Schönenberger for providing access to his microfabrication facilities, and Ph. Gasser Eidgenössische Materialprüfungsanstalt (EMPA) for FIB support. We further acknowledge stimulating discussions with J. Y. P. Butter, J. N. Farahani, W. Grange, S. Karotke, A. Lieb, Y. Lill, and J. Toquant. Financial support came from the Swiss National Science Foundation through the National Center of Competence in Research (NCCR) in Nanoscale Science and a research professorship for B.H. O.J.F.M. acknowledges support from NCCR Quantum Photonics.

Supporting Online Material
www.sciencemag.org/cgi/content/full/308/5728/1607/DC1
Figs. S1 to S5

7 March 2005; accepted 20 April 2005
10.1126/science.1111886

Giant Larvacean Houses: Rapid Carbon Transport to the Deep Sea Floor

Bruce H. Robison,* Kim R. Reisenbichler, Rob E. Sherlock

An unresolved issue in ocean science is the discrepancy between the food requirements of the animals living on the deep sea floor and their food supply, as measured by sediment traps. A 10-year time-series study of the water column off Monterey Bay, California, revealed that the discarded mucus feeding structures of giant larvaceans carry a substantial portion of the upper ocean's productivity to the deep seabed. These abundant, rapidly sinking, carbon-rich vectors are not detected by conventional sampling methods and thus have not been included in calculations of vertical nutrient flux or in oceanic carbon budgets.

Most deep benthic communities are supplied with food by a process described more than a century ago as a "rain of detritus" (*1*). The vertical flux of organic carbon in small particles, fecal pellets, and aggregates of marine snow is typically measured by sediment traps (*2*). Most of the particles that reach the deep sea floor are less than 5 mm in size, sink slowly, and have organic carbon levels that are reduced by microbial mineralization during their descent, which may last for months (*3*, *4*). Pulses of small particle flux are coupled to surface productivity (*5–7*). In studies of the relationship between organic carbon flux and the nutritional requirements of the deep benthic fauna, there is a discrepancy between the amount of food used by these animals and what can be accounted for by sediment traps on the supply side (*8–10*). This gap may be linked to declines in productivity that have accompanied the recent warming of the upper ocean (*9*, *11–13*). A number of secondary sources have been suggested that might make up the difference between supply and demand, including carrion falls, pulses of phytodetritus, and lateral transport from continental shelves (*9*, *14–16*). All of these probably contribute to the deep benthic food supply, but none have been shown to occur in sufficient quantity or with the consistency necessary to compensate for the disparity.

Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA.

*To whom correspondence should be addressed. E-mail: robr@mbari.org

Here we discuss a class of particles consisting of the large, discarded feeding structures of giant mesopelagic larvaceans (appendicularians). These planktonic tunicates feed on suspended particles by secreting intricate filtration structures made of mucopolysaccharides (Fig. 1A), through which they pump water by beating their tails (*17*). An active filter structure is called a "house" because the animal lives inside it. Typically, each house has two nested filters: a coarse outer mesh and a fine-mesh inner structure. Giant larvaceans attain lengths up to 60 mm, and their houses are frequently greater than a meter in diameter (*17*, *18*).

The first giant larvacean identified, *Bathochordaeus charon*, was discovered in 1898, but their feeding structures were unknown until the 1960s, when they were observed during submersible dives (*18*). Subsequently, giant larvacean houses have been reported by observers using undersea vehicles in the eastern and western Pacific and in the Atlantic (*17*, *19*, *20*). These large houses are very fragile and do not survive capture by plankton nets. As a consequence, their potential contribution to vertical carbon flux was not recognized until they were observed in situ (*21*).

Larvacean houses are disposable, and when one becomes clogged with particles, the animal simply discards it and makes another. The structures collapse when water is no longer pumped through them (Fig. 1B). Once abandoned, they sink rapidly to the sea floor at a rate of ~800 m day^{-1} (*17*). At this rate, there is little time for mineralization by microbes. Discarded houses have not been accounted for by conventional methods for sampling sinking detritus (*22*), and thus their contribution to nutrient flux has not been factored into oceanic carbon budgets (*23*).

We used remotely operated vehicles (ROVs) to measure the abundance of both occupied and discarded giant larvacean houses (called "sinkers") and to collect them for chemical analyses. Abundance was measured by quantitative video transects at 100-m depth intervals, down to 1000 m, on about a monthly basis from 1994 through 2003. By calibrating a camera to record a measured area and then measuring the distance traveled during each transect, we were able to examine a known volume of water at each depth (*24*).

Samples for chemical analysis were collected with specialized samplers by skilled pilots, who carefully positioned the open containers around the delicate sinkers, then gently sealed them inside. Because the sinkers are so very easily fragmented and dispersed, only about 1 in 4 of our collection attempts was successful, and it is easy to see how sediment traps have missed them (*25*). As the sinkers descend, hydrodynamic forces shape them into increasingly compact forms (Fig. 1C); nevertheless, they remain easily disrupted by mechanical contact.

We surveyed the water column at three sites along the axis of the Monterey Canyon, off the California coast. These direct observations revealed a distinct class of large sinking aggregates, clearly derived from giant larvacean houses. The midwater fauna off Monterey Bay contains at least three giant larvacean species, each with a characteristic depth range and a large (>30 cm in diameter), distinctive house (*26–28*). The abundance of occupied houses and sinkers varied seasonally and interannually, but both were present year-round (Fig. 2). Estimates of the house-production rate of *Bathochordaeus* range from one per day (*16*) to one per month (*17*). On the basis of our counts of occupied houses, sinkers, and their sinking rate, we calculate that *Bathochordaeus* produces a new house every day (*24*) (Fig. 3). Sinkers are commonly observed during dives along the floor of the Canyon, with densities as

Downloaded from www.sciencemag.org on February 13, 2010

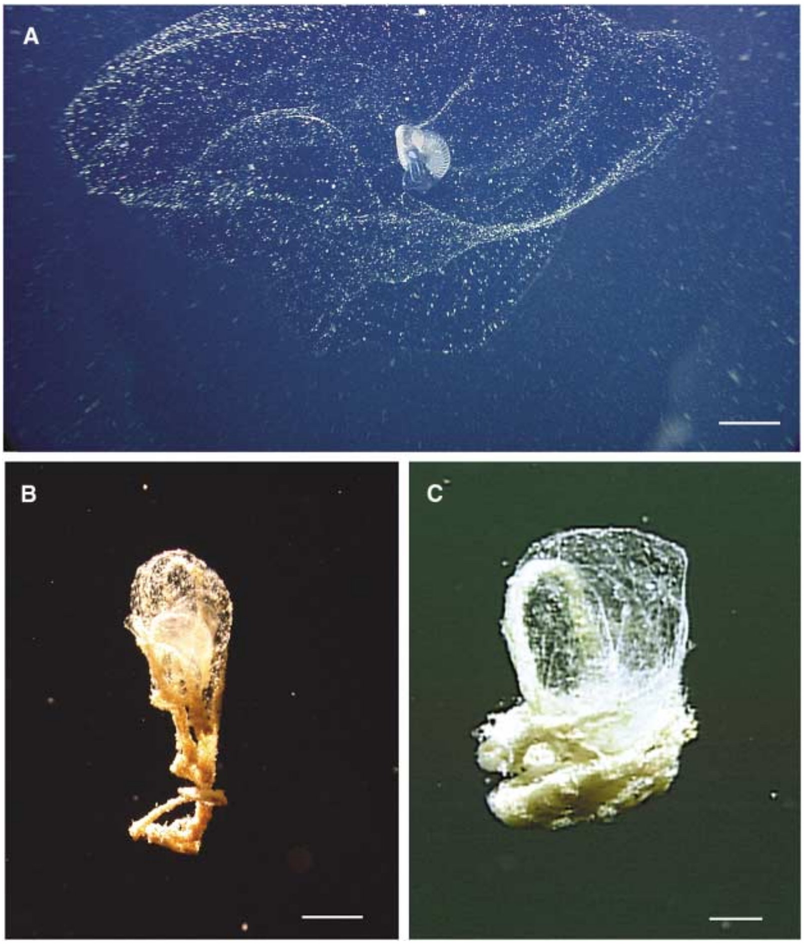

Fig. 1. In situ video frame grabs of steps in the progression from an actively filtering giant larvacean house to a descending sinker. (**A**) An active house occupied by *Bathochordaeus*; the coarse mesh outer filter surrounds a fine mesh inner filter, to which the tadpole-shaped animal is attached. (**B**) An abandoned and collapsed house, with most of the outer filter condensed into ropy strands and a small portion domed over the inner filter. (**C**) As the sinker rapidly descends, the mass becomes more compacted, and the inner filter is usually the last part to collapse. Scale bars: (A) and (B), 10 cm; (C), 1 cm.

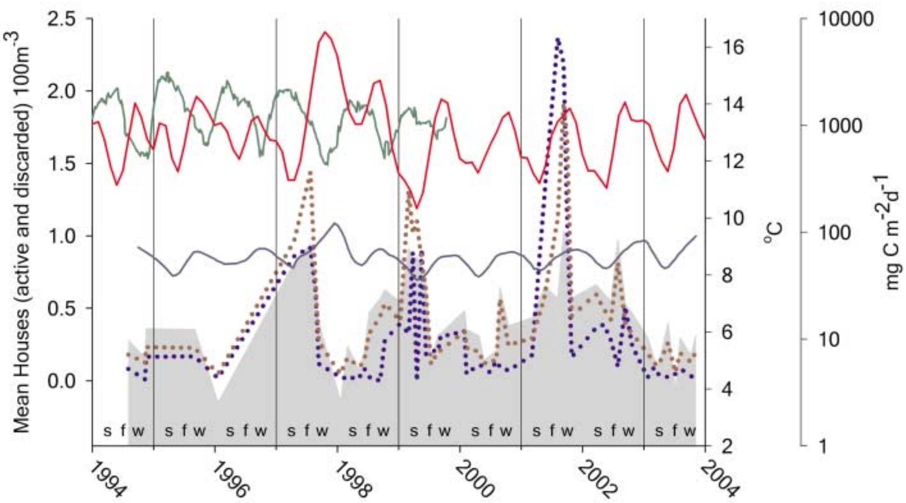

Fig. 2. Carbon flux (gray area) to the deep sea floor and the abundance of active (dotted blue line) and discarded (dotted red line) giant larvacean houses. Data collected in a 10-year ROV-based time series in Monterey Bay, California, show a consistent supply of carbon over summer (s), fall (f), and winter (w) seasons. Integrated primary productivity values (green line) and temperatures (at the surface, solid red line; at 200-m depth, solid blue line) were taken at a permanent mooring adjacent to the transect site (*32*). A negative exponential (second-degree polynomial function) was used to smooth the temperature and integrated carbon data.

high as 1 sinker per m^2 (*17*). Over the 10-year span of this study, the average flux of sinkers to the sea floor was 3.9 m^{-2} day^{-1}. We measured the particulate organic carbon (POC) and dissolved organic carbon content of 105 sinker samples, collected over a 2-year period at depths from 200 m to 2979 m (*24*). The average of total organic carbon was 5.4 mg, and the average C:N ratio was 6.09.

When we calculate nutrient flux by multiplying the average organic carbon content of a sinker by the number reaching the bottom each year, we get a rate of 7.6 g of C m^{-2} year^{-1} (Fig. 2). Data from sediment traps deployed in the same region as our dive sites have shown annual carbon flux rates from 14.4 to 24.0 g of C m^{-2} year^{-1} at depths around 500 m and from 7.2 to 14.4 g of C m^{-2} year^{-1} at sea-floor depths (*16*, *29*–*31*). Our calculations of sinker carbon flux are conservative because (i) we undercounted the number of deep sinkers, which are more compact, sink faster, and thus are less likely to be seen; (ii) our sampling was biased toward smaller specimens, because large sinkers did not fit into our samplers; and (iii) we did not count sinkers that had fragmented naturally. Although the measured flux of sinker carbon was variable, the changes did not appear to be closely linked to gross primary production, temperature, or season (*32*) (Fig. 2).

The discarded houses of giant larvaceans thus compose a distinct class of sinking particles that provide a substantial portion of the vertical carbon flux in the deep water column. This is the case off Monterey Bay and probably elsewhere as well. The balance of POC supply and demand measured by Smith and Kaufmann (*9*) at a deep benthic station off central California ranged from occasional surpluses to extended discrepancies of 8 mg of C m^{-2} day^{-1} or more over 7 years. In Monterey Canyon, the daily average of carbon transport by sinking larvacean houses was more than enough to close this gap. Present-day models of carbon flux through the deep water column predict that only ~10% of the POC that sinks below 100 m reaches depths beyond 1000 m (*33*). Our results reveal a pathway through this region that carries substantially more carbon than has been measured by conventional methods. Carbon that reaches the deep sea floor is effectively removed from the atmosphere for geological time scales (*33*).

References and Notes

1. A. Agassiz, *Three Cruises of the U.S. Coast and Geodetic Survey Steamer Blake* (Houghton Mifflin, Cambridge, MA, 1888), vol. 1.
2. R. Francois, S. Honjo, M. P. Bacon, *Oceanography* **14**, 65 (2001).
3. J. K. Volkman, E. Tanque, *J. Oceanogr.* **58**, 265 (2002).
4. A. L. Alldredge, M. W. Silver, *Prog. Oceanogr.* **20**, 41 (1988).
5. W. M. Berelson, *Oceanography* **14**, 59 (2001).

Downloaded from www.sciencemag.org on February 13, 2010

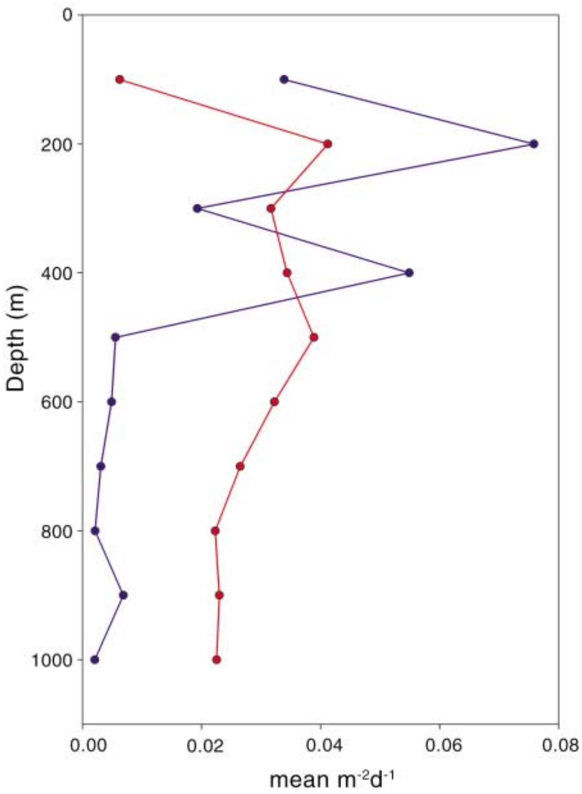

Fig. 3. Comparative plot of active houses of giant larvaceans (blue line) and discarded sinkers (red line) versus depth, in square meters of area swept. The data are derived from a 10-year time series of quantitative video transects at depth intervals between 100 and 1000 m (n = 679 transects). With an average sinking rate of 800 m day^{-1}, the difference between the integrated areas beneath the curves indicates that these animals produce a new house each day (*24*).

6. K. L. Smith Jr., R. S. Kaufmann, R. J. Baldwin, *Limnol. Oceanogr.* **39**, 1101 (1994).
7. R. J. Baldwin, R. C. Glatts, K. L. Smith Jr., *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **45**, 643 (1998).
8. K. L. Smith Jr., *Limnol. Oceanogr.* **32**, 201 (1987).
9. K. L. Smith Jr., R. S. Kaufmann, *Science* **284**, 1174 (1999).
10. K. L. Smith Jr., R. J. Baldwin, D. M. Karl, A. Boetius, *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **49**, 971 (2002).
11. D. Roemmich, J. A. McGowan, *Science* **267**, 1324 (1995).
12. D. Roemmich, J. A. McGowan, *Science* **268**, 352 (1995).
13. J. A. McGowan, D. R. Cayan, L. M. Dorman, *Science* **281**, 210 (1998).
14. C. E. Reimers, R. A. Jahnke, D. C. McCorkle, *Global Biogeochem. Cycles* **6**, 199 (1992).
15. E. M. Druffel, B. H. Robison, *Science* **284**, 1139 (1999).
16. M. W. Silver, S. L. Coale, C. H. Pilskaln, D. R. Steinberg, *Limnol. Oceanogr.* **43**, 498 (1998).
17. W. M. Hamner, B. H. Robison, *Deep-Sea Res.* **39**, 1299 (1992).
18. E. G. Barham, *Science* **205**, 1129 (1979).
19. P. J. Davoll, M. J. Youngbluth, *Deep-Sea Res.* **37**, 285 (1990).
20. J. C. Hunt, D. J. Lindsay, *Plankt. Biol. Ecol.* **46**, 75 (1999).
21. C. P. Galt, *Fish. Bull.* **77**, 514 (1979).
22. S. E. Beaulieu, K. L. Smith Jr., *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **45**, 781 (1998).
23. Small larvacean species are often very abundant in near-surface waters. Most have bodies less than 10 mm long, with house diameters commonly twice as large. Their houses may be produced at a rate of six or more each day, depending on the density of food particles. Discarded small houses are important components of organic aggregate flux in the ocean's upper layers, but they rarely reach the deep sea floor (*34–36*).
24. Materials and methods are available as supporting material on *Science* Online.
25. Sediment traps catch what they were designed to catch, namely, small, slowly sinking particles. Although sediment traps may occasionally collect sinker fragments, physical contact, particularly with traps that have interior baffles, is certain to exclude, disrupt, or disperse this material (*16*). The easily recognized rectangular mesh structures of larvacean filters have not been reported in analyses of sediment trap contents.
26. R. Fenaux, Q. Bone, D. Deibel, in *The Biology of Pelagic Tunicates*, Q. Bone, Ed. (Oxford Univ. Press, New York, 1998), chap. 15.
27. *Bathochordaeus* sp. is found chiefly at depths from 100 to 300 m; *Mesochordaeus erythrocephalus* occurs principally between 300 and 500 m (*17*, *28*).
28. R. R. Hopcroft, B. H. Robison, *J. Plankton Res.* **21**, 1923 (1999).
29. J. H. Martin, G. A. Knauer, D. M. Karl, W. W. Broenkow, *Deep-Sea Res.* **34**, 267 (1987).
30. C. H. Pilskaln, J. B. Paduan, F. P. Chavez, R. Y. Anderson, W. M. Berelson, *J. Mar. Res.* **54**, 1149 (1996).
31. This value considerably exceeds the amount of flux estimated by Silver, Coale, Pilskaln, and Steinberg (*16*), for *Bathochordaeus* in the same region. Although our measurements of the abundance and turnover of houses and sinkers agree, our measurements of the carbon content of sinkers are substantially greater, principally because of incomplete sampling in the earlier study.
32. F. P. Chavez *et al.*, *Prog. Oceanogr.* **54**, 205 (2002).
33. A. B. Burd, G. A. Jackson, R. S. Lampitt, M. Follows, *Eos* **83**, 573 (2002).
34. A. L. Alldredge, *Science* **177**, 885 (1972).
35. A. L. Alldredge, *Limnol. Oceanogr.* **21**, 14 (1976).
36. D. Deibel, *Mar. Biol.* **93**, 429 (1986).
37. We thank the pilots of the ROVs *Ventana* and *Tiburon*, for their skills and patience in the difficult task of collecting these specimens, and the officers and crews of the research vessels *Point Lobos* and *Western Flyer*. Supported by the David and Lucile Packard Foundation.

Supporting Online Material
www.sciencemag.org/cgi/content/full/308/5728/1609/DC1
Materials and Methods
SOM Text
Figs. S1 to S4
References and Notes

23 December 2004; accepted 15 April 2005
10.1126/science.1109104

Downloaded from www.sciencemag.org on February 13, 2010

Rapid Acidification of the Ocean During the Paleocene-Eocene Thermal Maximum

James C. Zachos,[1]* Ursula Röhl,[2] Stephen A. Schellenberg,[3] Appy Sluijs,[4] David A. Hodell,[6] Daniel C. Kelly,[7] Ellen Thomas,[8,9] Micah Nicolo,[10] Isabella Raffi,[11] Lucas J. Lourens,[5] Heather McCarren,[1] Dick Kroon[12]

The Paleocene-Eocene thermal maximum (PETM) has been attributed to the rapid release of $\sim$2000 $\times$ 10^9 metric tons of carbon in the form of methane. In theory, oxidation and ocean absorption of this carbon should have lowered deep-sea pH, thereby triggering a rapid (<10,000-year) shoaling of the calcite compensation depth (CCD), followed by gradual recovery. Here we present geochemical data from five new South Atlantic deep-sea sections that constrain the timing and extent of massive sea-floor carbonate dissolution coincident with the PETM. The sections, from between 2.7 and 4.8 kilometers water depth, are marked by a prominent clay layer, the character of which indicates that the CCD shoaled rapidly (<10,000 years) by more than 2 kilometers and recovered gradually (>100,000 years). These findings indicate that a large mass of carbon ($\gg$2000 $\times$ 10^9 metric tons of carbon) dissolved in the ocean at the Paleocene-Eocene boundary and that permanent sequestration of this carbon occurred through silicate weathering feedback.

During the Paleocene-Eocene thermal maximum (PETM), sea surface temperature (SST) rose by 5°C in the tropics and as much as 9°C at high latitudes (*1–3*), whereas bottom-water temperatures increased by 4° to 5°C (*4*). The initial SST rise was rapid, on the order of $\sim$$10^3$ years, although the full extent of warming was not reached until some $\sim$30,000 years (30 ky)