Seawater oxygenation during the Paleocene-Eocene Thermal Maximum

Alexander J. Dickson*, Anthony S. Cohen, and Angela L. Coe

Department of Environment, Earth and Ecosystems, Centre for Earth, Planetary, Space and Astronomical Research, The Open University, Walton Hall, Milton Keynes, Buckinghamshire MK7 6AA, UK

ABSTRACT

Uncertainty over the trajectory of seawater oxygenation in the coming decades is of particular concern in the light of geological episodes of abrupt global warming that were frequently accompanied by lowered seawater oxygen concentrations. Here we present an assessment of global seawater oxygenation from an interval of one of these warming episodes, the Paleocene-Eocene Thermal Maximum (PETM, 55.9 m.y. ago). Our results, obtained from Integrated Ocean Drilling Program Expedition 302 Site M0004 in the Arctic Ocean, are based on molybdenum isotope determinations and molybdenum, rhenium, and uranium abundances. These data indicate a small global expansion of low-oxygen marine environments in the upper part of the PETM interval compared with the present day. More extensive seawater deoxygenation may have occurred for as long as ~100 k.y., associated with a high rate of global warming and carbon oxidation at the start of the PETM. Our data also reveal molybdenum isotope compositions in Arctic Ocean deposits that are outside the range currently documented in marine environments. These exceptional compositions could reflect either the influence of **hydrothermal inputs or equilibrium isotope fractionations associ**ated with molybdenum sulfide speciation.

INTRODUCTION

Observations of declining oxygen concentrations and expansion of several of the world's oxygen minimum zones have highlighted the potential for continued global warming to lead to enhanced seawater hypoxia, where dissolved oxygen concentrations are too low to support many forms of marine life (Matear and Hirst, 2003; Stramma et al., 2008; Keeling et al., 2010). One way to better understand the possible course of future seawater oxygenation is to examine the response of the oceans to past intervals of rapid global warming (Cohen et al., 2007; Pearce et al., 2008). One such interval is the Paleocene-Eocene Thermal Maximum (PETM), ~55.9 m.y. ago (Kennett and Stott, 1991). The PETM is represented in the geological record by a negative isotope excursion in the exogenic carbon reservoir, reflecting the addition of \sim 3000–6800 Pg C into the ocean-atmosphere system over a period of no more than a few tens of thousands of years (Panchuk et al., 2008; Zeebe et al., 2009). This rapid addition of carbon contributed to global warming of 5–8 °C superimposed on a background climate that was already warmer than the present day. The PETM was accompanied by ocean acidification, extinction of benthic foraminifera, changes in surface ocean productivity, migration and adaptation in land mammals, and an enhanced hydrological cycle that promoted terrestrial weathering and the enhanced delivery of nutrients to ocean margins (Ravizza et al., 2001; McInerney and Wing, 2011). Some data pertaining to local seawater oxygenation are available for the PETM, based on changes in benthic foraminifera assemblages, redox-sensitive trace element and organic carbon enrichments, organic biomarkers, and sedimentary structures such as laminations (see Table DR1 in the GSA Data Repository¹). However, our knowledge of changes in the areal extent of different redox environments during the PETM remains fragmented because of the limited spatial coverage afforded by existing work. In this study we have obtained a global perspective on seawater redox conditions during the PETM by determining the molybdenum (Mo) isotope compositions of samples from Integrated Ocean Drilling Program (IODP) Expedition 302, Site M0004 (Site 302–4; 87°51.995′N, 136°10.641′E, 1288 m water depth) in the Arctic Ocean. Site 302–4 is located on the Lomonosov Ridge, which rifted from the Gakkel Ridge in latest Paleocene time. This is the only sedimentary section yet analyzed that contains PETM-age material suitable for the successful application of this global seawater redox proxy.

MO ISOTOPES AS A GLOBAL SEAWATER REDOX PROXY

The isotope composition of Mo (expressed as $\delta^{98/95}$ Mo) dissolved in seawater reflects changes in the proportion of Mo extracted into areas of the ocean with different redox characteristics. Under well-oxygenated conditions, adsorption of dissolved molybdate $(MoO₄^{2–})$ to manganese oxides occurs with a $\delta^{98/95}$ Mo of \sim -0.7‰ (Siebert et al., 2003; Barling and Anbar, 2004), leaving seawater enriched in the heavier Mo isotopes. The $\delta^{98/95}$ Mo of dissolved Mo in present-day seawater (2.3‰; Siebert et al., 2003) is also controlled by the flux of Mo into suboxic and anoxic depositional environments (δ^{98/95}Mo ranging from 0‰ to 1.8‰; Siebert et al., 2006; Poulson et al., 2006; Poulson-Brucker et al., 2009) and into euxinic depositional environments (anoxic with the presence of free hydrogen sulfide, H_2S). Assuming that Mo enters the oceans with an average $\delta^{98/95}Mo$ between 0‰ and 0.7‰ (Siebert et al., 2003; Archer and Vance, 2008) and that inputs and outputs of Mo are roughly equal, isotope mass balancing indicates that the Mo flux into euxinic sediments accounts for $\langle 5\%$ of oceanic Mo removal at the present day, with oxic and anoxic regions accounting for ~40%–70% and 25%–55%, respectively (Poulson-Brucker et al., 2009). Changes in the proportion of Mo removed from seawater into these distinctive redox environments will have a direct effect on the coeval seawater δ98/95Mo, which decreases if the amount of Mo removed into reducing environments expands at the expense of its removal in oxygenated regions. The $\delta^{98/95}$ Mo of seawater in the past can be inferred from euxinic sediments enriched in hydrogenous Mo that preserve the seawater δ ^{98/95}Mo with no fractionation due to the high efficiency of Mo removal as MoS4 (Erikson and Helz, 2000; Neubert et al., 2008).

RESULTS

In this study, Mo isotope compositions and abundances and associated rhenium (Re) and uranium (U) trace element abundances have been determined for a set of samples from Site 302–4 (for methodological details, see the Data Repository). Site 302–4 contains deposits spanning the PETM, but the onset of the event as defined by the negative carbon isotope excursion (CIE) is absent due to incomplete core recovery. All measured samples are marked by enrichment of Mo above average crustal abundances of ~1 ppm. Below and above the negative CIE (~381–386 meters composite depth, mcd), Mo concentrations range from 2 to 15 ppm, characteristic of suboxic to anoxic continental margin sites in the present-day ocean (Poulson-Brucker et al., 2009). During the CIE, Mo concentrations reach >40 ppm, consistent with highly reducing depositional conditions.

δ98/95Mo are on average −0.4‰ from the base of magnetochron C24r, and decrease to between −2‰ and −3‰ in core 32X, below the CIE

^{*}E-mail: a.dickson@open.ac.uk.

¹ GSA Data Repository item 2012173, supplemental information, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@ geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

Figure 1. Geochemical data from Integrated Ocean Drilling Program Site 302–4 against composite core depth, and magnetic (Chron 25n-24r boundary) and biostratigraphic (first and last occurrences of *Apectodinium augustum*) age datums (Backman et al., 2008). A: Compilation of new and published δ¹³C_{org} data (large open diamonds from this study; small open squares from Sluijs et al., 2006; closed circles from
Stein et al., 2006). B: δ^{98/95}Mo data (closed squares; this study). Open squar **for** δ**98/95Mo are smaller than symbols. Error bar denotes 2 standard deviation external reproducibility calculated from repeat digestions of in-house mudrock standard. Horizontal black bars denote typical ranges of** δ**98/95Mo compositions observed in oxic, suboxic and anoxic, and** euxinic sedimentary environments. C: Mo and Re concentrations (this study). D: Mo/U and Re/Mo ratios (this study). E: TEX₈₆' temperature **data from Site 302–4 (Sluijs et al., 2006). Recovered core intervals and coring gaps are indicated by shaded gray boxes and dashed lines, respectively. Horizontal shaded band indicates period of stable** δ**98/95Mo during Paleocene-Eocene Thermal Maximum. Black rectangle marks stratigraphic interval characterized by presence of isorenieratene (Sluijs et al., 2006; Weller and Stein, 2008).**

(Fig. 1). During the CIE in cores $30X$ and $31X$, $\delta^{98/95}$ Mo are the highest observed in our data set and remain approximately constant at ~2.08‰. Above the CIE, δ98/95Mo decreases to <1.8‰, typical of suboxic to anoxic locations in the modern ocean (Siebert et al., 2006; Poulson et al., 2006; Poulson-Brucker et al., 2009).

Many of the δ^{98/95}Mo that we have determined for samples from Site 302–4 are associated with comparatively low Mo concentrations and are likely to be governed by local redox variations (Gordon et al., 2009). There is, however, an interval of persistently high $\delta^{98/95}$ Mo (2.08% ± 0.11% σ ; n = 13, 1 standard deviation) associated with elevated Mo concentrations in the upper part of the CIE in cores 31X and part of 30X (~386–383 mcd). The low variability of δ^{98/95}Mo in this interval is consistent with the presence of a stable redox boundary, which suggests that the primary sedimentary Mo isotope signal has been preserved. We argue that this interval records the contemporaneous seawater $\delta^{98/95}$ Mo and document here the several lines of evidence that support this inference.

GLOBAL SEAWATER REDOX DURING THE PETM

For the $\delta^{98/95}$ Mo of Mo in seawater to be preserved in sediments, the presence of local euxinia needs to be verified (Gordon et al., 2009). Four independent lines of evidence suggest that these conditions were present during the CIE interval at Site 302–4 (Fig. 1). First, concentrations of redox sensitive elements (including Mo) are greatly elevated throughout this interval. Second, Re/Mo and Mo/U ratios of the samples remain close to their respective modern seawater values of 0.4 and 7.7, suggesting that these elements were removed from seawater at $\sim 100\%$ efficiency such that their relative abundances were preserved. Third, the interval in cores 31–30X, within which $\delta^{98/95}$ Mo remains at ~2.08‰, is characterized by the presence of isorenieratene, a compound synthesized by sulfur-reducing bacteria that inhabit the photic zone of the water column and indicate localized euxinia (Sluijs et al., 2006; Weller and Stein, 2008) (Fig. 1). Fourth, the inference of euxinia extending through the local water column is also supported by organic carbon/sulfur ratios <1 within the PETM interval and by the presence of pyrite framboids in the same section (Stein et al., 2006).

Exchange of seawater between the Arctic and surrounding oceans is also necessary for the average $\delta^{98/95}$ Mo measured within the CIE of Site 302–4 to be interpreted as a global signal. Seawater exchange has previously been inferred from dinocyst biostratigraphy (Sluijs et al., 2008a), which demonstrated that migration pathways into the Arctic Ocean existed during the PETM, most likely through shallow seaways into the North Atlantic and Tethys Oceans. This inference is supported by ε_{Nd} values of fish debris recovered from Site 302–4 that are similar to ε_{Nd} values from the adjacent North Atlantic and Tethys Oceans, indicating an exchange of seawater between those regions during Early Eocene time (Gleason et al., 2009). In Figure 2 we add to this body of evidence with Mo and U abundances obtained from the period of stable $\delta^{98/95}$ Mo in the CIE interval of Site 302–4. The gradient defined by the abundances of these two redox sensitive elements is very similar to that defined by dissolved Mo and U in the present-day oceans, indicating that the supply of dissolved Mo from surrounding ocean basins was not limited, and thus that seawater exchange took place (Algeo and Tribovillard, 2009). The Mo/U relationship during the PETM contrasts markedly with the relationship for the later *Azolla* interval of Site 302–4 (Brinkhuis et al., 2006; März et al., 2010), when the Arctic Ocean became severely restricted due to the closure of the Turgay Straits (Akhmet'ev et al., 2010; Brinkhuis et al., 2006). The Mo/U gradient for the *Azolla* interval is significantly lower than that of modern seawater (Fig. 2), and instead is similar to seawater values found for restricted basins in the present day (Algeo and Tribovillard, 2009).

The observations of (1) localized Arctic Ocean euxinia and (2) seawater exchange with surrounding ocean basins are strong evidence that the average $\delta^{98/95}$ Mo of 2.08% in Site 302–4 records the global seawater δ98/95Mo during the latter part of the PETM. The seawater δ98/95Mo for the latter part of the PETM was ~0.2‰ lower than its present-day value and is consistent with a small expansion of low-oxygen seawater environments compared to present. The magnitude of this expansion can be quantified using mass balance considerations. These calculations suggest that relative to the size of reducing marine environments in the present-day ocean, the seawater $\delta^{98/95}$ Mo of ~2.08‰ could be achieved with a ~0.5% increase in the magnitude of Mo precipitation in anoxic environments at

Figure 2. Abundances of Mo and U in samples from Integrated Ocean Drilling Program (IODP) Site 302–4 analyzed in this study. Squares are Mo and U abundances from Paleocene-Eocene Thermal Maximum (PETM) carbon isotope excursion interval in IODP 302–4 (this study). Circles are Mo and U abundances from top of Chron 25n to base of PETM carbon isotope excursion interval in IODP 302–4. Diamonds are Mo and U abundances from Azolla interval (298.81–302.63 m composite depth) in IODP 302–4 (data from März et al., 2010). Dashed reference lines show present-day seawater ratio and 0.1 × seawater ratio. Solid black lines show linear regressions for data from PETM and pre-PETM intervals (this study) and from Azolla interval data.

the expense of precipitation in well-oxygenated environments, or alternatively by an ~2%–3% expansion of Mo precipitation in euxinic environments at the expense of precipitation in anoxic environments. Our data are consistent with published studies that have documented slightly dysoxic conditions in regions outside the Arctic Ocean toward the end of the CIE, which is the interval of the PETM that correlates with our data from Site 302–4 (Table DR1).

It is noteworthy that the $\delta^{98/95}$ Mo values of -2% to -3% between 391 and 389 mcd in Site 302–4 are some of the lowest ever published. These values are unlikely to be the product of diagenesis, given that studies of diagenesis observe the oxic end member (−0.7‰) to set a lowermost limit on the influence of these processes on $\delta^{98/95}$ Mo (Reitz et al., 2007). One possibility is that the exchange of Arctic Ocean seawater with the surrounding oceans was restricted for a short period immediately prior to the PETM, a suggestion supported by geochemical indices such as Mo/U ratios (Fig. 2). Restriction may have triggered hydrological conditions that contributed to unusual Mo sulfide speciation effects (Neubert et al., 2008; Helz et al., 2011; Nägler et al., 2011), which did not occur during the CIE as rising sea levels enhanced the exchange of seawater with surrounding ocean basins (Sluijs et al., 2008b; Harding et al., 2011). A second possibility is that the Mo budget of seawater in the Arctic Basin at that time was dominated by a hydrothermal flux with low $\delta^{98/95}$ Mo from the North Atlantic Igneous Province (e.g., Svensen et al., 2004), a suggestion supported by a recent measurement of hydrothermally influenced Icelandic river water with a $\delta^{98/95}$ Mo of -3.4% (Pearce et al., 2010). At present, however, our data do not allow us to resolve these two hypotheses.

CONCLUSION

Our seawater $\delta^{98/95}$ Mo data for the latter part of the PETM, a time when temperatures were elevated by several degrees centigrade above Late Paleocene background levels (e.g., Sluijs et al., 2006) (Fig. 1), imply a small but significantly higher level of low-oxygen marine environments compared with the present day. Furthermore, we document extremely low δ98/95Mo (−2‰ to −3‰) below the CIE interval at Site 302–4. These values are outside the current range of observations from marine sedimentary environments. These low $\delta^{98/95}$ Mo may reflect the influence of local hydrothermal sources on the seawater $\delta^{98/95}$ Mo, or alternatively the influence of equilibrium fractionations linked to Mo-sulfide speciation.

Several studies have hinted at more extreme deoxygenation at specific locations accompanying rapid global warming at the onset of the PETM (Table DR1), an interval missing from IODP 302–4. Testing and quantifying the extent of any trend toward greater seawater deoxygenation in the early stages of the PETM and during other hyperthermal events remain important goals for future studies.

ACKNOWLEDGMENTS

We thank Manuela Fehr, Marc Davies, Samantha Hammond, and Mabs Gilmour for laboratory support. The Integrated Ocean Drilling Program provided sample material. This research was supported by the Natural Environment Research Council (NE/F021313/1 to Cohen and Coe) and the Open University.

REFERENCES CITED

- Akhmet'ev, M.A., Zaporozhets, N.I., Iakovleva, A.I., Aleksandrova, G.N., Beniamovsky, V.N., Oreshkina, T.V., Gnibidenko, Z.N., and Dolya, Z.A., 2010, Comparative analysis of marine Paleogene sections and biota from west Siberia and the Arctic region: Stratigraphy and Geological Correlation, v. 18, p. 635–659, doi:10.1134/S0869593810060043.
- Algeo, T.J., and Tribovillard, N., 2009, Environmental analysis of paleoceanographic systems based on molybdenum-uranium covariation: Chemical Geology, v. 268, p. 211–225, doi:10.1016/j.chemgeo.2009.09.001.
- Archer, C., and Vance, D., 2008, The isotopic signature of the global riverine molybdenum flux and anoxia in the ancient oceans: Nature Geoscience, v. 1, p. 597–600, doi:10.1038/ngeo282.
- Backman, J., and 13 others, 2008, Age model and core-seismic integration for the Cenozoic Arctic Coring Expedition sediments from the Lomonosov Ridge: Paleoceanography, v. 23, PA1S03, doi:10.1029/2007PA001476.
- Barling, J., and Anbar, A.D., 2004, Molybdenum isotope fractionation during adsorption by manganese oxides: Earth and Planetary Science Letters, v. 217, p. 315–329, doi:10.1016/S0012-821X(03)00608-3.
- Brinkhuis, H., and 22 others, 2006, Episodic fresh surface waters in the Eocene Arctic Ocean: Nature, v. 441, p. 606–609, doi:10.1038/nature04692.
- Cohen, A.S., Coe, A.L., and Kemp, D.B., 2007, The Late Palaeocene–Early Eocene and Toarcian (Early Jurassic) carbon isotope excursions: A comparison of their timescales, associated environmental changes, causes and consequences: Geological Society of London Journal, v. 164, p. 1093–1108, doi:10.1144 /0016-76492006-123.
- Erickson, B.E., and Helz, G.R., 2000, Molybdenum (IV) speciation in sulphidic waters: Stability and lability of thiomolybdates: Geochimica et Cosmochimica Acta, v. 64, p. 1149–1158, doi:10.1016/S0016-7037(99)00423-8.
- Gleason, J.D., Thomas, D.J., Moore, T.C., Jr., Blum, J.D., Owen, R.M., and Haley, B.A., 2009, Early to middle Eocene history of the Arctic Ocean from Nd-Sr isotopes in fossil fish debris, Lomonosov Ridge: Paleoceanography, v. 24, PA2215, doi:10.1029/2008PA001685.
- Gordon, G.W., Lyons, T.W., Arnold, G.L., Roe, J., Sageman, B.B., and Anbar, A.D., 2009, When do black shales tell molybdenum isotope tales?: Geology, v. 37, p. 535–538, doi:10.1130/G25186A.1.
- Harding, I.C., Charles, A.J., Marshall, J.E.A., Palike, H., Roberts, A.P., Wilson, P.A., Jarvis, E., Thorne, E., Morris, E., Moremon, E., Pearce, R.B., and Akbari, S., 2011, Sea-level and salinity fluctuations during the Paleocene-Eocene thermal maximum in Arctic Spitsbergen: Earth and Planetary Science Letters, v. 303, p. 97–107, doi:10.1016/j.epsl.2010.12.043.
- Helz, G.R., Bura-Nakić, E., Mikac, N., and Ciglenečki, I., 2011, New model for molybdenum behaviour in euxinic waters: Chemical Geology, v. 284, p. 323–332, doi:10.1016/j.chemgeo.2011.03.012.
- Keeling, R.F., Körtzinger, A., and Gruber, N., 2010, Ocean deoxygenation in a warming world: Annual Review of Marine Science, v. 2, p. 199–229, doi:10.1146/annurev.marine.010908.163855.
- Kennett, J.P., and Stott, L.D., 1991, Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene: Nature, v. 353, p. 225–229, doi:10.1038/353225a0.
- März, C., Schnetger, B., and Brumsack, H.-J., 2010, Paleoenvironmental implications of Cenozoic sediments from the Central Arctic Ocean (IODP Expedition 302) using inorganic geochemistry: Paleoceanography, v. 25, PA3206, doi:10.1029/2009PA001860.
- Matear, R.J., and Hirst, A.C., 2003, Long-term changes in dissolved oxygen concentrations in the ocean caused by protracted global warming: Global Biogeochemical Cycles, v. 17, 1125, doi:10.1029/2002GB001997.
- McInerney, F.A., and Wing, S.L., 2011, The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate and biosphere with implications for the future: Annual Review of Earth and Planetary Sciences, v. 39, p. 489–516, doi:10.1146/annurev-earth-040610-133431.
- Nägler, T.F., Neubert, N., Böttcher, M.E., Dellwig, O., and Schnetger, B., 2011, Molybdenum isotope fractionation in pelagic euxinia: Evidence from the modern Black and Baltic Seas: Chemical Geology, v. 289, p. 1–11, doi:10.1016/j.chemgeo.2011.07.001.
- Neubert, N., Nägler, T.F., and Böttcher, M.E., 2008, Sulphidity controls molybdenum isotope fractionation into euxinic sediments: Evidence from the modern Black Sea: Geology, v. 36, p. 775–778, doi:10.1130/G24959A.1.
- Panchuk, K., Ridgwell, A., and Kump, L.R., 2008, Sedimentary response to Paleocene-Eocene Thermal Maximum carbon release: A model-data comparison: Geology, v. 36, p. 315–318, doi:10.1130/G24474A.1.
- Pearce, C.R., Cohen, A.S., Coe, A.L., and Burton, K.W., 2008, Molybdenum isotope evidence for global ocean anoxia coupled with perturbations to the carbon cycle during the Early Jurassic: Geology, v. 36, p. 231–234, doi:10.1130/G24446A.1.
- Pearce, C.R., Burton, K.W., Pogge van Strandmann, P.A.E., James, R.H., and Gíslason, S.R., 2010, Molybdenum isotope behaviour accompanying weathering and riverine transport in a basaltic terrain: Earth and Planetary Science Letters, v. 295, p. 104–114, doi:10.1016/j.epsl.2010.03.032.
- Poulson, R.L., Siebert, C., McManus, J., and Berelson, W.M., 2006, Authigenic molybdenum isotope signatures in marine sediments: Geology, v. 34, p. 617– 620, doi:10.1130/G22485.1.
- Poulson-Brucker, R.L., McManus, J., Severmann, S., and Berelson, W.M., 2009, Molybdenum behaviour during early diagenesis: Insights from Mo isotopes: Geochemistry Geophysics Geosystems, v. 10, Q06010, doi:10.1029 /2008GC002180.
- Ravizza, G., Norris, R.N., Blusztajn, J., and Aubry, M.-P., 2001, An osmium isotope excursion associated with the Late Paleocene thermal maximum: Evidence of intensified chemical weathering: Paleoceanography, v. 16, p. 155–163, doi:10.1029/2000PA000541.
- Reitz, A., Wille, M., Nägler, T.F., and de Lange, G.J., 2007, Atypical Mo isotope signatures in eastern Mediterranean sediments: Chemical Geology, v. 245, p. 1–8, doi:10.1016/j.chemgeo.2007.06.018.
- Siebert, C., Nägler, T.F., von Blanckenburg, F., and Kramers, J.D., 2003, Molybdenum isotope records as a potential new proxy for paleoceanography: Earth and Planetary Science Letters, v. 211, p. 159–171, doi:10.1016/S0012 -821X(03)00189-4.
- Siebert, C., McManus, J., Bice, A., Poulson, R., and Berelson, W.M., 2006, Molybdenum isotope signatures in continental marine margin sediments: Earth and Planetary Science Letters, v. 241, p. 723–733, doi:10.1016/j.epsl.2005.11.010.
- Sluijs, A., and 15 others, 2006, Subtropical Arctic Ocean temperatures during the Paleocene/Eocene Thermal Maximum: Nature, v. 441, p. 610–613, doi:10.1038/nature04668.
- Sluijs, A., Röhl, U., Schouten, S., Brumsack, H.-J., Sangiorgi, F., Sinninghe Damste, J.S., and Brinkhuis, H., 2008a, Arctic late Paleocene–early Eocene paleoenvironments with special emphasis on the Paleocene-Eocene thermal maximum (Lomonosov Ridge, Integrated Ocean Drilling Program Expedition 302): Paleoceanography, v. 23, PA1S11, doi:10.1029/2007PA001495.
- Sluijs, A., and 14 others, 2008b, Eustatic variations in the Paleocene-Eocene greenhouse world: Paleoceanography, v. 23, PA4216, doi:10.1029/2008PA001615.
- Stein, R., Boucsein, B., and Meyer, H., 2006, Anoxia and high primary production in the Paleogene central Arctic Ocean: First detailed records from Lomonosov Ridge: Geophysical Research Letters, v. 33, L18606, doi:10.1029 /2006GL026776.
- Stramma, L., Johnson, G.C., Sprintall, J., and Mohrholz, V., 2008, Expanding oxygen minimum zones in the tropical oceans: Science, v. 320, p. 655–658, doi:10.1126/science.1153847.
- Svensen, H., Planke, S., Malthe-Sørenssen, A., Jamtveit, B., Myklebust, R., Rasmussen Eidem, T., and Rey, S.S., 2004, Release of methane from a volcanic basin as a mechanism for initial Eocene global warming: Nature, v. 429, p. 542–545, doi:10.1038/nature02566.
- Weller, P., and Stein, R., 2008, Paleogene biomarker records from the central Arctic Ocean (Integrated Ocean Drilling Program Expedition 302): Organic carbon sources, anoxia, and sea surface temperature: Paleoceanography, v. 23, PA1S17, doi:10.1029/2007PA001472.
- Zeebe, R.E., Zachos, J.C., and Dickens, G.R., 2009, Carbon dioxide forcing alone insufficient to explain Paleocene-Eocene Thermal Maximum warming: Nature Geoscience, v. 2, p. 576–580, doi:10.1038/ngeo578.

Manuscript received 28 October 2011 Revised manuscript received 2 February 2012

Manuscript accepted 9 February 2012

Printed in USA