# THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY CCANOGRAPHY SOCIETY

#### **CITATION**

Fornari, D.J., K.L. Von Damm, J.G. Bryce, J.P. Cowen, V. Ferrini, A. Fundis, M.D. Lilley, G.W. Luther III, L.S. Mullineaux, M.R. Perfit, M.F. Meana-Prado, K.H. Rubin, W.E. Seyfried Jr., T.M. Shank, S.A. Soule, M. Tolstoy, and S.M. White. 2012. The East Pacific Rise between 9°N and 10°N: Twenty-five years of integrated, multidisciplinary oceanic spreading center studies. *Oceanography* 25(1):18–43, http://dx.doi.org/10.5670/oceanog.2012.02.

#### DOI

http://dx.doi.org/10.5670/oceanog.2012.02

#### **COPYRIGHT**

This article has been published in *Oceanography*, Volume 25, Number 1, a quarterly journal of The Oceanography Society. Copyright 2012 by The Oceanography Society. All rights reserved.

#### **USAGE**

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: info@tos.org or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.

#### Ridge 2000 PROGRAM RESEARCH







## The East Pacific Rise Between 9°N and 10°N

TWENTY-FIVE YEARS OF INTEGRATED, MULTIDISCIPLINARY OCEANIC SPREADING CENTER STUDIES

BY DANIEL J. FORNARI, KAREN L. VON DAMM, JULIA G. BRYCE, JAMES P. COWEN, VICKI FERRINI, ALLISON FUNDIS, MARVIN D. LILLEY, GEORGE W. LUTHER III, LAUREN S. MULLINEAUX, MICHAEL R. PERFIT, M. FLORENCIA MEANA-PRADO, KENNETH H. RUBIN, WILLIAM E. SEYFRIED JR., TIMOTHY M. SHANK, S. ADAM SOULE, MAYA TOLSTOY, AND SCOTT M. WHITE



ABSTRACT. The East Pacific Rise from ~ 9–10°N is an archetype for a fast-spreading mid-ocean ridge. In particular, the segment near 9°50′N has been the focus of multidisciplinary research for over two decades, making it one of the best-studied areas of the global ridge system. It is also one of only two sites along the global ridge where two historical volcanic eruptions have been observed. This volcanically active segment has thus offered unparalleled opportunities to investigate a range of complex interactions among magmatic, volcanic, hydrothermal, and biological processes associated with crustal accretion over a full magmatic cycle. At this 9°50′N site, comprehensive physical oceanographic measurements and modeling have also shed light on linkages between hydrodynamic transport of larvae and other materials and biological dynamics influenced by magmatic processes. Integrated results of high-resolution mapping, and both in situ and laboratory-based geophysical, oceanographic, geochemical, and biological observations and sampling, reveal how magmatic events perturb the hydrothermal system and the biological communities it hosts.

#### INTRODUCTION

The East Pacific Rise between the Siqueiros and Clipperton Transform Faults is the archetype of a fast-spreading mid-ocean ridge (Figure 1). It was the focus of numerous disciplinary and interdisciplinary studies even before 2002, when the region from 8°N to 11°N became one of the three Integrated Study Sites (ISSs) of the Ridge 2000 Program, transforming it into one of the most intensively studied ridges in the world. In the heyday of mid-twentieth century global oceanographic exploration, yearly expeditions would venture into the relatively uncharted waters of the eastern Pacific. With each new bathymetric, geophysical, and oceanographic data set came new insights into the shape, structure, and geological implications of the broad, shallow rise that extended in long segments nearly the entire length of South and Central America—what we now recognize as the East Pacific Rise (EPR; Menard, 1960, 1964). The southern EPR was first recognized by early soundings carried out on the HMS Challenger expedition in the 1870s and then followed by the

Albatross expedition in the late 1890s. The Albatross Plateau became the accepted name for the southern EPR in tribute to those early explorations (Murray and Renard, 1891). Menard (1960, 1964) identified the EPR north of the equator as a broad, shallow rise with long segments interrupted by several major fracture zones between the equator and the spreading center's transition into the Gulf of California (Figure 1). The recognition of mid-ocean ridges (MORs) as a central element of plate tectonics (Hess, 1960) where Earth's oceanic volcanic crust is formed (Dietz, 1961) focused much attention on comparisons between Pacific and Atlantic mid-ocean ridges. At the time, a debate began, focused on the position of each ridge within its ocean basin and their markedly different morphologies, and the consequent implications for their origin and context within the developing plate tectonic theory (e.g., Heezen et al., 1959; Menard, 1960). Part of the motivation for studying the EPR in the late twentieth and early twenty-first century sprang from those early observations of the dramatic differences between

slow- and fast-spreading MORs, and the idea that the best place to adequately resolve volcanic processes at mid-ocean ridges was to look at magmatically robust spreading centers, where the ridge was behaving like an elongate volcano (e.g., Lonsdale, 1977, 1985).

Much of the EPR is likely volcanically active, but one area near 9°50'N stands out because it has experienced two documented volcanic eruptions since 1990 (e.g., Rubin et al., 2012, in this issue). Indeed, the area between 9°N and 10°N is currently one of the most magmatically robust segments of the global mid-ocean ridge system. In this article, we focus on a subset of field and laboratory research conducted at the EPR ISS as an example of the power of integrated studies that have furthered our knowledge of oceanic spreading center processes from "mantle to microbe" during the past decade (Figure 2). In particular, we discuss how integrated field and laboratory studies following volcanic eruptions at 9°50'N have provided important opportunities for better understanding how oceanic crust at a fast-spreading MOR responds to magmatic cycles. We further emphasize how tightly integrated experiments yielded significant benefits both to guiding post-eruption studies and to revealing how magmatic events perturb the hydrothermal system, thereby affecting vent fluid compositions and biological/microbial processes. Similar long-term experiments, ocean-observatory monitoring, and multidisciplinary data sets, including those acquired at the Endeavour ISS, will permit robust comparisons between that intermediate-rate spreading center and the fast-spreading EPR (see Kelley et al., 2012, in this issue).

## DEVELOPING A MULTIDISCIPLINARY APPROACH TO STUDYING MID-OCEAN RIDGES

With the discovery of high-temperature black smoker hydrothermal vents at 21°N on the EPR in 1979 (Spiess et al., 1980), and a series of primarily US and French cruises throughout the 1980s and early 1990s along the northern EPR and in several of its major transform faults, the EPR between ~ 8°N and 21°N (Figure 1) became a focal point for geological, geophysical, biological, and hydrothermal research (e.g., Orcutt et al., 1976; Francheteau et al., 1979; RISE Project Group, 1980; Francheteau and Ballard, 1983; Hekinian et al., 1983a,b; Lonsdale, 1983; Macdonald and Fox, 1983; Fustec et al., 1987; Fox and Gallo, 1989; Pockalny et al., 1997). One of the seminal findings from the early use of academic multibeam sonars was that the elongate fast-spreading ridge axis was actually divided into discontinuous segments (Macdonald and Fox, 1983, 1988; Lonsdale, 1983). This segmentation has profound implications for

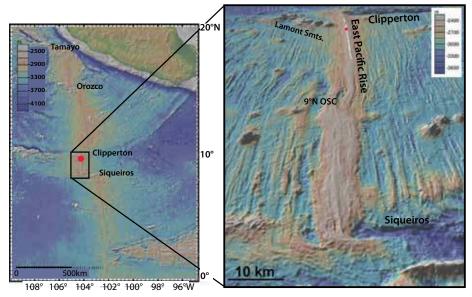


Figure 1. (left) Bathymetry of the East Pacific Rise (EPR) based on data compilation and archiving enabled by the Ridge 2000 Data Portal at the Marine Geoscience Data System (http://www.marine-geo.org; Carbotte et al., 2004; Ryan et al., 2009). (right) Perspective image of multibeam bathymetry for the EPR second-order segment between Clipperton and Siqueiros Transform Faults. The EPR Integrated Study Site (ISS) focused study area near 9°50'N is marked by the red dot. The white line traces the axial summit trough (Soule et al., 2009) where most of the hydrothermal vents and biological communities are located.

understanding nearly all aspects of magmatic, volcanic, tectonic, hydrothermal, and vent-related biological processes. Questions regarding the underlying causes of ridge segmentation and axial discontinuities—whether they arose in the upper mantle or were

crustal features, how they evolved with spreading center accretionary history—led to numerous geophysical experiments that explored linkages between the morphology and tectonic fabric of the EPR and mantle dynamics in the eastern Pacific.

Daniel J. Fornari (dfornari@whoi.edu) is Senior Scientist, Geology and Geophysics Department, Woods Hole Oceanographic Institution (WHOI), Woods Hole, MA, USA. Karen L. Von Damm (deceased) was Professor, Department of Earth Sciences, University of New Hampshire, Durham, NH, USA. Julia G. Bryce is Associate Professor, Department of Earth Sciences, University of New Hampshire, Durham, NH, USA. James P. Cowen is Research Professor, Department of Oceanography, University of Hawaii, Honolulu, HI, USA. Vicki Ferrini is Associate Research Scientist, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, USA. Allison Fundis is Research Scientist, School of Oceanography, University of Washington, Seattle, WA, USA. Marvin D. Lilley is Professor, School of Oceanography, University of Washington, Seattle, WA, USA. George W. Luther III is the Maxwell P. and Mildred H. Harrington Professor, School of Marine Science and Policy, College of Earth, Ocean and Environment, University of Delaware, Lewes, DE, USA. Lauren S. Mullineaux is Senior Scientist, Biology Department, WHOI, Woods Hole, MA, USA. Michael R. Perfit is Professor, Department of Geological Sciences, University of Florida, Gainesville, FL, USA. M. Florencia Meana-Prado is Research Technician, Department of Earth Sciences, University of New Hampshire, Durham, NH, USA. Kenneth H. Rubin is Professor, Department of Geology and Geophysics, University of Hawaii at Manoa, Honolulu, HI, USA. William E. Seyfried Jr. is Professor, Department of Earth Sciences, University of Minnesota, Minneapolis, MN, USA. Timothy M. Shank is Associate Scientist, Biology Department, WHOI, Woods Hole, MA, USA. S. Adam Soule is Associate Scientist, Geology and Geophysics Department, WHOI, Woods Hole, MA, USA. Maya Tolstoy is Associate Professor, Department of Earth and Environmental Sciences, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, USA. Scott M. White is Associate Professor, Department of Earth and Ocean Sciences, University of South Carolina, Columbia, SC, USA.

Our understanding of the basic geophysical framework of the EPR between 8° and 11°N has benefitted enormously from early seismological studies that yielded tomographic images of the upper mantle and the crust, and from multichannel seismic studies that revealed the presence of melt bodies and their distribution in the mid-crust beneath the spreading axis (Figure 2; e.g., Detrick et al., 1987; Vera et al., 1990; Kent et al., 1993; Harding et al., 1993; Toomey et al., 1994; Wilcock et al., 1995; Barth and Mutter, 1996; Dunn and

Toomey, 1997, 2001; Dunn et al., 2000). These studies defined how melt was distributed beneath the EPR crest and allowed investigators to better understand relationships between melt storage and delivery processes, the morphology and structure of the ridge crest, and relationships to sites of hydrothermal venting (e.g., Langmuir et al., 1986; Haymon et al., 1991; Reynolds et al., 1992; Baker et al., 1994; Perfit et al., 1994; Kelemen et al., 1995; Von Damm, 1995; Lundstrom et al., 1999; Schouten et al., 1999). It was this holistic,

process-oriented approach to studying mid-ocean ridges that typified the Ridge Interdisciplinary Global Experiments (RIDGE) Program during the decade of the 1990s (http://www.ridge2000.org/science/info/meetings.php). RIDGE researchers and scientists participating in the program's international counterpart InterRidge greatly expanded their understanding of relationships between MOR morphology and structure, ranging from spreading rates to mantle driving forces and their impacts on geological, geochemical, and, ultimately,

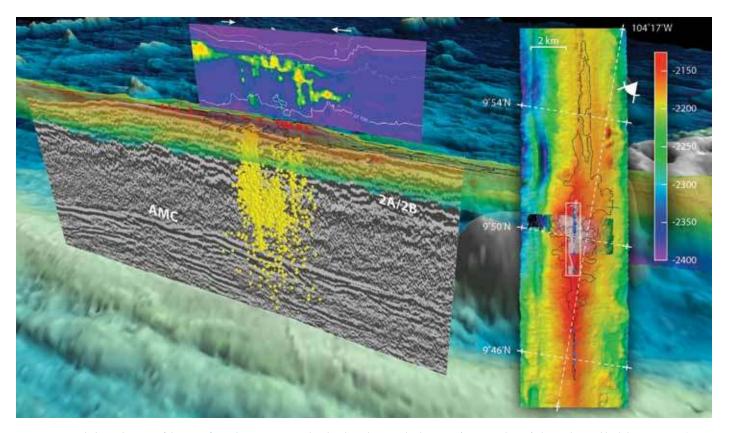


Figure 2. Compiled visualization of data sets from the EPR ISS. At right, ship-based EM300 bathymetry (25 m resolution) shows the axial high between 9°46'N and 9°56'N (White et al., 2006). A higher-resolution bathymetry data set (5 m resolution) collected in 2001 by the autonomous underwater vehicle (AUV) ABE is overlain and shows greater details of the volcanic terrain (Fornari et al., 2004; Escartín et al., 2007). A black line shows the extent of the lava flows produced during the 2005–2006 eruption (Soule et al., 2007), and high-temperature vents are indicated by blue diamonds. A perspective view from the northeast is at left. The EM300 bathymetry is elevated above a regional bathymetric map (Macdonald et al., 1992). Multichannel seismic reflection data collected in 2008 (Carbotte et al., 2012, in this issue) are shown relative to the EM300 seafloor. White labels mark the seismic crustal Layer 2A/B reflector and the top of the axial magma lens. Hypocenters of microearthquakes recorded during 2003–2004 from Tolstoy et al. (2008) are shown by yellow dots, hydrothermal vents by red diamonds. A profile of turbidity recorded in late May 2006 appears above the EM300 seafloor (Cowen et al., 2007). The EPR ISS "bull's-eye" is indicated by white arrows above the turbidity profile and by a white box in the plan view map. The "eyeball" icon shows the direction of the perspective view shown in the main figure. All data depicted are available at the Ridge 2000 Data Portal (http://www.marine-geo.org/portals/ridge2000).

biological and water-column processes near the ridge crest. Those studies and the well-coordinated programmatic approach to studying MORs around the globe strongly influenced the development and conduct of US academic community Ridge 2000 Program efforts, which were designed to further investigate a range of interconnected multidisciplinary processes associated with oceanic spreading centers (e.g., Rubin and Fornari, 2011).

In the late 1980s and through the 1990s era of RIDGE Program research, detailed seafloor mapping at the EPR from ~ 9° to 10°N based on in situ observations and sampling of hydrothermal, volcanic, and biological features provided some of the first examples of truly "integrated" multidisciplinary results from an oceanic spreading center (e.g., Haymon et al., 1991, 1993; Wright et al., 1995; Shank et al., 1998; Fornari et al., 1998a,b; Perfit and Chadwick, 1998; White et al., 2002, 2006). These studies began to develop the case for causal relationships among volcano-magmatic, hydrothermal, and biological phenomena.

A transformative event in MOR science occurred at the EPR in April 1991, when the ongoing or immediate aftermath of a volcanic eruption was discovered during a DSV *Alvin* cruise investigating results of the 1989 ARGO-I deep-towed camera survey in the 9°50'N region of the EPR (Figure 3; Haymon et al., 1991, 1993). Radiometric dating of samples taken then and later showed that the eruption began just weeks before the April 1 discovery and was likely followed by additional eruptions extending into early 1992 (Rubin et al., 1994; see also Rubin et al., 2012, in this issue).

Observers diving in *Alvin* in early

April 1991 noted that well-developed faunal communities seen in 1989 ARGO-I images were buried by new lava flows at several sites along the floor of the axial summit trough (AST; Fornari et al., 1998a) and replaced by extensive areas of vigorous diffuse flow and an abundance of thick, white "bacterial" mats with no characteristic vent megafauna (Nelson et al., 1991; Lutz et al., 1994, 2001; Shank et al., 1998). A linear array of 210 number-bearing panels dubbed "biomarkers" was deployed between 9°49.61'N and 9°50.36'N in March 1992 to facilitate assessment of temporal and spatial changes in biological and geological features over time. The resulting "Biotransect" (Shank et al., 1998) was documented using Alvin on 12 cruises between 1992 and 2005 using 35 mm, high-resolution video, and digital still camera systems (http://www. ridge2000.org/science/iss/epr/projects. php). Data from Biotransect imaging surveys and the presence of biomarkers throughout the area provided unequivocal spatial referencing that was used by the full suite of studies, including those aimed at correlating changes in biological community structure with chemical, earthquake, volcanic, and hydrodynamic activity in the region (e.g., Von Damm, 2004; Von Damm and Lilley, 2004; Lutz et al., 2008; Luther et al., 2008).

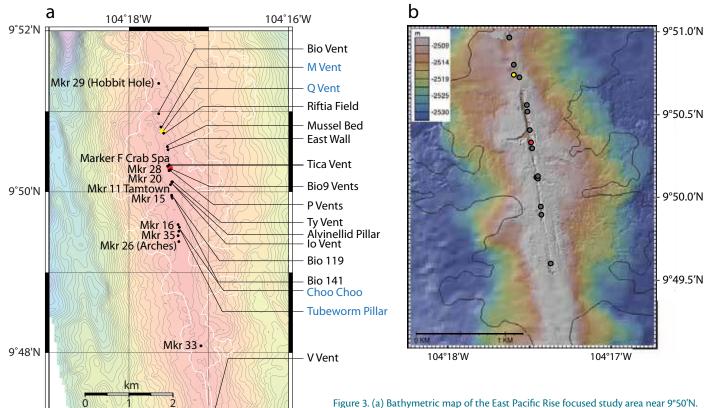
Soon thereafter, other MOR eruptions were detected (for instance, at the CoAxial segment of the Juan de Fuca Ridge in 1993 and at Axial Seamount in 1998; see summaries and references in Baker et al., 2012, and Rubin et al., 2012, both in this issue). Insights gleaned from 1991–1992 EPR eruption studies helped guide research there and elsewhere on the MOR where researchers

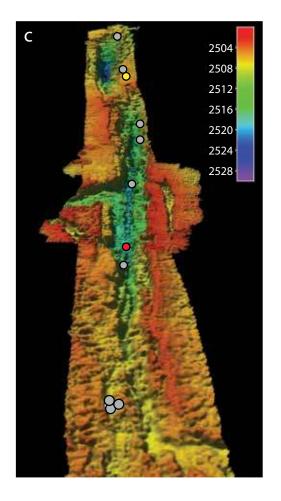
sought to unravel causal relationships between sub-ridge magma storage and delivery, volcanism, and hydrothermal circulation patterns and fluid chemistry that influenced biological and oceanographic processes.

The profound effects of a volcanic eruption on hydrothermal and biological processes led many to speculate about whether the EPR 9°50'N site would continue to be active hydrothermally and how and if the vent fluid chemistry would change, as well as what effects those changes would have on the evolving vent macro- and micro-fauna. These questions helped to form the justification for selecting the 9°50'N area as a focused study site for Ridge 2000. Also subject to speculation was whether the magmatic/volcanic cycle would approximate a relationship governed by plate separation over time (5.5 cm yr<sup>-1</sup>; Carbotte and Macdonald, 1992) and a mean dike width of  $\sim 1-2$  m for each crustal accretion event (e.g., Hooft et al., 1996; Schouten et al., 1999). Using those basic constraints, it was inferred that the fast-spreading EPR could erupt every 10-20 years, but when and where the next magmatic event would occur, and whether it would only be intrusive or actually erupt at the seafloor, was anyone's guess.

## UNDERSTANDING INTERRELATED MOR ACCRETIONARY PROCESSES FROM TWO ERUPTIONS 13 YEARS APART

Near-bottom side-scan sonar mapping of the EPR crest suggested that frequent volcanic repaying occurred along the 9°20′–55′N region by relatively small-volume extrusions, and that the eruptive





Mkr 19:

-2600

-2550

-2500

-2750

-2700

-2650

Black dots indicate the location of high- and low-temperature vents, and are labeled at right. Vents that remained active through the 2005–2006 eruption are labeled in black; those that became extinct post-eruption are labeled in blue. New, post-eruption vent sites are labeled at left (e.g., Mkr #s). Bio 9 vent and Q vent are labeled with red and yellow dots, respectively, and reproduced in Figure 3b,c for reference. The estimated extent of 2005–2006 lava flows between 9°47.5' and 9°55.7'N is shown as a white line, based on images acquired by TowCam and *Alvin* during several cruises to the area (Cowen et al., 2007; Soule et al., 2007; Fundis et al., 2010). Maps shown in each panel (a–c) were compiled using bathymetric data available at the Ridge 2000 Data Portal (Carbotte et al., 2004; Ryan et al., 2009; http://www.marine-geo.org/portals/ridge2000).

- (b) Bathymetric map of the EPR crest near 9°50'N made using 675 kHz scanning altimetric sonar on the autonomous underwater vehicle ABE (Autonomous Benthic Explorer) during cruise AT7-4 on R/V Atlantis in 2001 (Fornari et al., 2004). ABE data were gridded at 5 m intervals, while the background EM300 multibeam data (White et al., 2006) were gridded at 30 m intervals (note pixilated texture of lower resolution bathymetric data). The estimated extent of 2005–2006 lava flows is shown as a black line and is based on images acquired by TowCam and Alvin during several cruises to the area (Cowen et al., 2007; Soule et al., 2007; Fundis et al., 2010). Pre-eruption vent sites shown correspond to labels in Figure 3a. The yellow dot is Q vent and the red dot is Bio 9 vent.
- (c) Perspective view (constructed in QPS Fledermaus<sup>\*\*</sup>) of near-bottom multibeam data acquired in the axial summit trough (AST) using the remotely operated vehicle *Jason* at the EPR near 9°50'N in mid-2007, the year following the most recent volcanic eruptions. The view is to the north-northwest. Data were gridded at ~ 2 m pixels and cover the area between 9°50.0'N and 9°51.1'N. Note the AST offset (to the west) near 9°50.5'N, just south of M and Q vent locations. Those vents are located on the east wall of the AST and align with the extension of the eruptive fissures that comprise the AST south of that location. Most of the other vents are located along primary eruptive fissures within the AST floor (Fornari et al., 2004). The AST floor in the southern portion of the image is shallower and more complex compared to the deeper and more prominent fissured terrain to the north and especially around the Bio 9 and P vent area. Interestingly, the plan view morphology of the AST width in the breakout area along the west wall north of those vents remained unchanged by the most recent volcanic outpourings. Grey dots show vent locations also shown in (b), with a yellow dot for Q vent and a red dot for Bio 9 vent. Width across the bottom of the data swath is ~ 150 m.

vents were nearly all located in or proximal to the axial trough (Fornari et al., 2004; Escartín et al., 2007; Soule et al., 2009). It would not take long to learn how frequent these eruptions were.

In April 2006, another seminal event in MOR studies occurred. Unsuccessful attempts to recover ocean-bottom seismometers (OBSs) that formed the geophysical array at the EPR ISS centered on 9°50'N, and subsequent water column surveys and one dredge conducted on an R/V Knorr cruise, indicated a recent volcanic eruption along the ridge crest between 9°48'N and 9°51'N (Tolstoy et al., 2006). Had this eruption entrapped the seismometers? Within a few weeks of those findings, a rapid event response expedition onboard R/V New Horizon was mobilized. Conductivity, temperature, depth (CTD) surveys, hydrocasts, one dredge, and TowCam towed digital imaging (Fornari and the WHOI TowCam Group, 2003) surveys along the EPR axis between ~ 9°46'N and 9°57'N confirmed the occurrence of recent and extensive seafloor volcanic eruptions (Cowen et al., 2007). Radiometric dating of young lavas collected from throughout the subsequently identified flow field indicated that it was the site of a series of eruptions starting in the summer of 2005 with a large outpouring of lava, and culminating in January 2006 with a much smaller lava effusion (Rubin et al., 2008, and 2012, in this issue). The nonresponsive seismometers were covered by or trapped in fresh lava. Geophysical data show the primary seismic crisis occurred on January 22, 2006 (Tolstoy et al., 2006; Dziak et al., 2009), perhaps indicating the culmination of eruptive activity. The dating work used a large number of short-lived <sup>210</sup>Po analyses of

lava to define, for the first time with any confidence, the duration of a submarine eruption sequence.

These two seafloor eruptions at the same location separated by ~ 13 years presented a unique and extraordinary opportunity to study cause-and-effect links among magmatic, hydrothermal, and ecological systems. Because Ridge 2000 studies conducted between 2002 and 2006 had already generated a wealth of collocated and synchronous data that spanned geological, geophysical, geochemical, and biological characteristics of the eruption site, there was ample opportunity to make robust observations and correlations between pre- and post-eruption features and processes. For instance, in 2001–2004, soon after being identified as a Ridge 2000 ISS, additional near-bottom mapping and geological, geochemical, and biological sampling studies were carried out at EPR 9-10°N. These studies allowed scientists to relate along-strike width, depth, and continuity of the AST to volcanic features and processes along the EPR crest and to establish relationships between its character and the locations of vent sites and biological colonization (Kurras et al., 2000; Fornari et al., 2004; Soule et al., 2005, 2009; Bowles et al., 2006; Escartín et al., 2007; Ferrini et al., 2007; Williams et al., 2008). This fieldwork also served to accurately locate microearthquake experiment arrays and in situ biological experiments within the context of volcanic and structural features present on the EPR axis. The resulting data were crucial for assessing the topographic and structural impacts of the eruption that occurred in 2005-2006 (see Soule et al., 2007, and Rubin et al., 2012, in this issue for

details), and they provided a baseline for quantitatively constraining eruption volume (Soule et al., 2007) and changes in the hydrothermal system (Figure 3). In the discussion that follows, we explore key facts known about these two eruptions, how the pre- and post-eruption studies in both cases provided important insights for how a fast-spreading midocean ridge "works" in all the disciplinary facets of its behavior, and, where possible, we develop ideas related to the interconnected nature of the processes.

#### EVOLUTION OF THE HYDROTHERMAL SYSTEM AT EPR 9°50'N

The hydrothermal system at oceanic spreading centers serves as the connective pathway between the crustal rock column and the seafloor and overlying ocean; it has been particularly well studied at the EPR ISS. Von Damm (2000, 2004) and Von Damm et al. (2003) played a key role in recognizing the importance of phase separation in the NaCl-H2O system at the EPR (and elsewhere) on subseafloor hydrothermal alteration processes and the flux of heat and chemicals between seawater and the oceanic crust. Phase separation substantially changes the Cl content of vent fluids (values from < 6% to ~ 200% of the seawater concentration have now been observed), as well as concentrations of other chemical species. The serendipitous 1991-1992 discoveries of very young lava, coupled with unusual and vigorous hydrothermal flow at the EPR 9°50'N area less than one month after the eruptions (Haymon et al., 1993; Rubin et al., 1994), provided clear and compelling evidence of the fundamental linkage between the formation of

oceanic crust at MORs and conditions and processes of phase separation in hydrothermal fluids and hydrothermal alteration of oceanic crust (Von Damm, 1995, 2000; Lilley et al., 2003). Timeseries observations from hydrothermal vent fluid chemistry at EPR 9-10°N have provided unparalleled information on the chemical and physical responses of hydrothermal systems to subseafloor magmatic and tectonic processes. In addition, complementary studies of volatile concentrations in erupted lavas indicate that they have excesses of Cl, suggesting contamination of erupted magmas through seawater dynamic interactions during eruption and by brines stored within shallow crustal hydrothermal pathways and reservoirs (Perfit et al., 2003; le Roux et al., 2006; Soule et al., 2006).

Time-series changes in chloride dissolved in vent fluids are very illustrative (Figures 4–6), showing that the first fluid to be expelled in the immediate aftermath of magmatic activity is the "vapor" phase, likely due to its lower density, confirming models developed earlier at other vent systems (Butterfield et al., 1997). What is most certainly the case at the EPR, however, is that following initial vapor-phase expulsion, some vents progressed much faster to venting fluids with chlorinity greater than seawater ( $\leq$  3 years; e.g., F vent at 9°17'N; Oosting and Von Damm, 1996) than others (~ 10 years; e.g., P vent), while others have never made the transition (e.g., Bio 9 vent; Von Damm, 2000; Figures 3 and 4). Analyses of fluids sampled in 2004, and after the eruption in 2006-2008 (Foustoukos and Seyfried, 2007a, b; and recent work of author Seyfried), from the same vents

first sampled in 1991 show a noteworthy decrease in dissolved chloride content for hydrothermal fluids issuing from most vents, followed by nonmonotonic increases in chloride contents leading up to the most recent eruptions. Immediately after the eruptions, all vents sampled (starting in June 2006), including those that previously expelled brines, were venting low-salinity vaporphase-separated fluids (Figures 4-5). By late 2006, some of the vents began to return to their pre-eruption chemistries. Interestingly, the hydrothermal response to magmatic activity and seafloor volcanism can manifest itself distinctly at each vent, even for vents located within tens of meters of each other, providing clear evidence of distinct and complex plumbing systems feeding the seafloor vent structures (e.g., Fornari et al., 2004).

A more quantitative approach for investigating hydrothermal vent chemical time series involves the use of silica and chloride relationships. Experimental studies of Fournier (1983) and Von Damm et al. (1991) linked silica saturation in high-temperature fluids with the pressure of equilibration inferred for basalt-hosted hydrothermal alteration. More recent experimental data and theoretical models (Foustoukos and Seyfried, 2007b; Fontaine et al., 2009) have extended this approach, especially for vapor-phase fluids, and temperatures and pressures particularly relevant to the EPR 9-10°N hydrothermal system (Figure 5). The silica contents of Bio 9 vent fluids (Figures 3 and 6) clearly change with time, and in a manner consistent with a deepening equilibration pressure, hence deepening

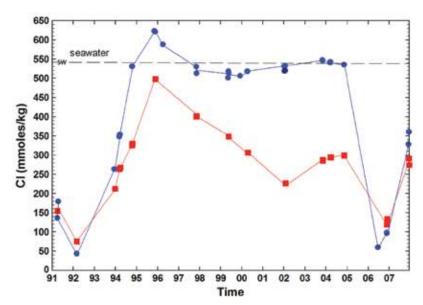


Figure 4. Time-series changes in dissolved chloride for P (blue) and Bio 9 (red) vents at EPR 9°50'N (see Figure 3 for locations). The data used are from Von Damm (2000, 2004, and unpublished data). These data indicate that these vents responded differently to the magmatic events in 1991–1992 and 2005–2006, although in both cases a relatively rapid return to pre-event conditions is suggested. Moreover, data indicate that vents closely spaced at the seafloor have distinct and complex plumbing systems that tap different source fluids at depth (e.g., Fornari et al., 2004).

heat source, for the five to seven years following the 1991–1992 eruptions. The temporal evolution of dissolved Cl and the modeled equilibrated pressures in the 1997–2004 timeframe suggest subsequent shoaling of the heat source (Figures 4 and 5). These observations led Von Damm (2004) to predict an imminent eruption in the 9°50'N EPR area.

Thermobarometric modeling of fluids with chloride concentrations in excess of seawater is less certain because of a dearth in thermodynamic data for such fluids, but similar trends are nevertheless

evident. In the case of Q vent (Figures 3 and 6), modest changes in chloride were apparent leading up to the 2005–2006 eruptions. Post-eruptive sampling in June 2006 revealed vapor-phase fluids. However, by November 2006, Q vent had ceased activity, attesting to the disruption of the hydrothermal system by the volcanic eruptions. Notably, Q vent was located on the east AST wall within ~ 300 m of M vent (which had ceased activity in February 2006 based on in situ HOBO temperature logger data; observations of authors Von Damm, Fornari,

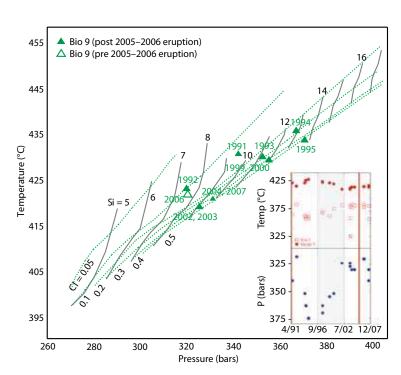


Figure 5. Thermobarometric implications of silica-chloride contents of the Bio 9 hydrothermal vent across two eruptive cycles (see Figure 3 for location). Measured silica (mmolal) and chloride (molal) data are superposed onto the Fontaine et al. (2009) model to predict temperatures and pressures of equilibration. After each eruption, the vapors are noticeably chloride-poor. The top figure in the inset shows measured exit temperatures (open squares) compared to modeled reaction temperatures (filled squares), derived from temperatures predicted by the silica-chloride model (at left) across the eruptive cycle. Note that the extremely low exit temperatures are from fluids with high end-member Mg contents, suggesting dilution with seawater prior to sampling. The modeled pressures (bottom figure in the inset) correspond to the depth of equilibration for the fluid and oceanic crust as derived from application of the Fontaine et al. (2009) model. In the inset, the red vertical lines indicate the 1991–1992 and 2005–2006 eruptions.

Meana-Prado, and Bryce; Figure 3), and one idea is that the primary fissure during one of the eruptive phases may have intersected the hydrothermal plumbing in this area and plugged it. To date, no clear evidence of redirected high-temperature or low-temperature flow has been found proximal to the O or M vent sites.

For most of these hydrothermal fluids, temperatures and pressures generally exceed 410°C and 300 bars at depth (Von Damm, 2004; Foustoukos and Seyfried, 2007b; Fontaine et al., 2009; Figure 5). The relatively high temperature and low-to-moderate pressures suggest mass-transfer reactions focused above the axial magma chamber, likely at the base of the sheeted dike complex (Figure 2). The unusually low dissolved chloride concentrations and anomalous Br/Cl ratio of vent fluids in the aftermath of the 1991 eruption (Oosting and Von Damm, 1996), reinterpreted with new experimental data by Berndt and Seyfried (1997), indicate halite-vapor-equilibria is important in the evolution of post-eruption vent fluids. Subsequent changes in temperature and pressure following the diking/ eruption event would cause halite to dissolve, decreasing the Br/Cl ratio of the vent fluids, as observed. It is not clear from the data that are presently available whether or not halite stability was achieved during the 2005–2006 eruptions. However, there can be no question from the magnitude of the observed chloride decrease in vent fluids following those eruptions (Figure 4) that halite stability might have been possible in the short term. In the longer term, it is now clear that hydrothermal systems perturbed by subseafloor magmatism

recover relatively quickly owing to the rate and effectiveness of phase equilibria involving minerals and fluids at elevated temperatures and pressures (Von Damm, 2000, Lilley et al., 2003; Foustoukos and Seyfried, 2007a; Rouxel et al., 2008).

#### LINKING THE VENT ENVIRONMENT TO BIOLOGICAL COMMUNITIES

An exotic assemblage of macrofauna and microorganisms flourishes at hydrothermal vents in the EPR ISS. Much has been learned at 9°50'N about biological community structure and evolution since the 1991-1992 eruptions, including temporal links to hydrothermal and volcanic changes (e.g., Shank et al., 1998; Fornari et al., 2004; Dreyer et al., 2005; and Ferrini et al., 2007; see Highlight by Govenar et al. on page 28). During this time, the abundance and species composition of planktonic vent larvae also varied (Kim and Mullineaux, 1998; Mullineaux et al., 2005; Adams et al., 2011), likely in response to a combination of benthic (spawning) and hydrodynamic (retention or export in flows) processes. Temperature and time-series fluid chemistry data, including maximum levels of total  $H_2S$  (FeS +  $H_2S/HS^-$ ) were reported from April 1991 to May 2000 by Shank et al. (1998) and Von Damm and Lilley (2004). At most sites, the succession of the biological community from microbial mats to tubeworm-dominance to musseldominance and increasing species richness followed a trend of decreasing temperatures, total sulfide concentrations, and hydrothermal flux over time. In addition, comprehensive experiments revealed the physiology and metabolic functions of deep-sea vent fauna

(Childress and Fisher, 1992), and they were combined with studies of biological community structure at EPR hydrothermal vents, including initial studies of larval dispersal (e.g., Mullineaux et al., 2005) and colonization (e.g., Mullineaux et al., 1998; Shank et al., 1998) as well as vent fauna distributions along various segments of the northern EPR (e.g., Van Dover, 2003). Snapshot characterizations of larval, faunal, and microbial distribution in the early 1990s

gave way to both time-series observing systems (e.g., in situ chemical sensing technologies; Luther et al., 2001; Le Bris et al., 2006) and experimental manipulations (e.g., Van Dover and Lutz, 2004; Lutz et al., 2008).

Following the 1991–1992 eruptions, this combination of time-series observations and experiments led to clear correlations among habitat conditions (e.g., temperature, chemistry, substrate), ...continued on page 30

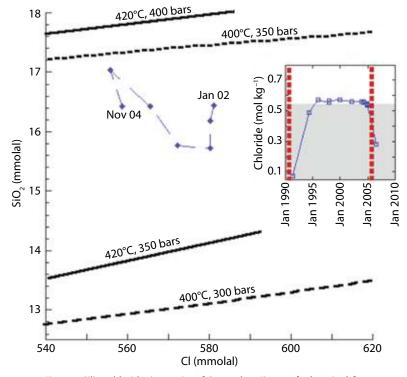


Figure 6. Silica-chloride time series of Q vent (see Figure 3 for location) from January 2002 to November 2004. Superimposed on the fluid chemical data are fields of temperature and pressure relevant for high-chloride fluids, based on experiments of Fournier (1983) and Von Damm et al. (1991), as described in Foustoukos and Seyfried (2007a, b). For comparison, post-eruptive silica and chloride contents of a Q vent sampled in June 2006 suggest, based on the thermodynamic model of Fontaine et al. (2009), pressure and temperature relationships of  $\sim$  390 bars and 445°C, suggesting that after the eruption, the peak pressure recorded in the hydrothermal fluid chemistry is at depths just above the axial magma lens. The inset shows the variation in chloride chemistry across the eruptive cycle. After both the 1991–1992 and the 2005–2006 eruptions, Q vented vapors. For a long period of time in between the eruptions, Q vented chloride-rich fluids. The two eruptions are denoted as dashed red lines in the inset. The gray field on the inset denotes fluids with chloride contents less than seawater.

### HIGHLIGHT | REBUILDING A VENT COMMUNITY: LESSONS FROM THE EAST PACIFIC RISE INTEGRATED STUDY SITE

BY BREEA GOVENAR, SHAWN M. ARELLANO, AND DIANE K. ADAMS

The discovery of a seafloor eruption at the East Pacific Rise (EPR) in 1991 presented an opportunity to examine the colonization and assembly of macrofaunal communities at newly formed diffuse-flow vents as well as to document the changes in community composition (Shank et al., 1998) in the context of temperature variation (Scheirer et al., 2006) and fluid chemistry (Von Damm and Lilley, 2004). The eruption site became a focus of the Ridge 2000 EPR Integrated Study Site (ISS) established to facilitate studies of the interaction of biological, geochemical, and/or physical processes associated with seafloor spreading. A second seafloor eruption in 2005–2006 provided opportunities to not only observe changes in community composition and environmental conditions, but also to deploy colonization substrata and other specialized equipment from "time zero." Here we focus on how larval dispersal and recruitment contribute to the establishment of hydrothermal vent communities.

Following the 1991 eruption, the pattern of ecological succession at diffuse-flow vents was generally correlated with decreasing temperatures and concentrations of hydrothermal fluids over time (Shank et al., 1998). At new diffuse-flow hydrothermal vents, the tubeworms Tevnia jerichonana were the initial megafaunal settlers, followed by the colonization of the larger tubeworm Riftia pachyptila, which dominated most of the diffuse-flow habitats within 2.5 years (Shank et al., 1998). Although differences in the habitat preferences of T. jerichonana and R. pachyptila (Luther et al., 2012, in this issue) may determine the sequence of colonization, R. pachyptila only colonized basalt block deployments (see figure) that were also colonized by T. jerichonana (Mullineaux et al., 2000) but not the uninhabited tubes of T. jerichonana (Hunt et al., 2004). Together, these studies suggest that a biogenic cue produced by T. jerichonana may facilitate recruitment of R. pachyptila in the early stages of community development after a seafloor eruption. Once R. pachyptila was established as the dominant foundation species, recruitment of additional R. pachyptila appeared to occur in pulses throughout the vent field (Thiébaut et al., 2002). Larvae of the mussel Bathymodiolus thermophilus settled within and outside of R. pachyptila aggregations and became the dominant foundation species more than five years after the eruption.

Although mussels were associated with cooler temperatures and lower concentrations of hydrothermal fluids (Luther et al., 2012, in this issue), biotic factors seem to have also contributed to the change from tubeworm to mussels, including changes in larval supply and recruitment. In addition, the shift in community composition may have been due to post-settlement factors, including the redirection of hydrothermal fluids (Johnson et al., 1994, Lutz et al., 2008) and the ingestion of *R. pachyptila* and other invertebrate larvae by adult mussels (Lenihan et al., 2008).

Because larval supply and colonization were being monitored at the EPR ISS prior to the 2005-2006 eruptions, the most recent eruptions provided a natural experiment to investigate the role of larval supply in recolonization of the site. Prior to the 2005–2006 eruptions, gastropods (mostly *Lepetodrilus* species) were the numerically dominant epifauna in aggregations of R. pachyptila (Govenar et al., 2005) and B. thermophilus (Dreyer et al., 2005) and exhibited gregarious settlement but discontinuous recruitment due to high juvenile mortality resulting from predation by fish (e.g., Sancho et al., 2005). Following the 2005–2006 eruptions, however, two other species—L. tevnianus and Ctenopelta porifera—became the numerically dominant epifaunal gastropods. The reproductive traits of L. tevnianus and C. porifera were similar to the previously dominant gastropod species and did not explain the settlement or recruitment of these pioneers (Bayer et al., 2011). Instead, it appears that the supply of larvae had drastically changed. The eruption seems to have removed the local sources of the previously dominant gastropods, enabling colonization by pioneer larvae such as C. porifera and L. tevnianus from distant sources (Mullineaux et al., 2010). With respect to the megafauna, the patterns of ecological succession following the 2005–2006 eruptions initially appeared to be similar to what was observed after the 1991 eruption, but more than two years later, the tubeworm T. jerichonana remained the dominant megafaunal species over R. pachyptila at most diffuse-flow vents (Mullineaux et al., 2010). Further monitoring of larval supply concurrent with multidisciplinary investigations of dispersal and colonization at the Ridge 2000 ISS will reveal the specific mechanisms of abiotic factors and biological interactions in the ecological succession of vent communities following seafloor eruptions.

Recovery of basalt block used for succession studies, after deployment for five months (Hunt et al., 2004). Photo by R.L. Williams, WHOI Alvin group

Breea Govenar (bgovenar@ric.edu) is Assistant Professor, Rhode Island College, Providence, RI, USA. Shawn M. Arellano is Postdoctoral Scholar, Biology Department, Woods Hole Oceanographic Institution (WHOI), Woods Hole, MA, USA.

Diane K. Adams is Guest Investigator, Biology Department, WHOI, Woods Hole, MA, USA.

#### **REFERENCES**

- Bayer, S.R., L.S. Mullineaux, R.G. Waller, and A.R. Solow. 2011. Reproductive traits of pioneer gastropod species colonizing deep-sea hydrothermal vents after an eruption. *Marine Biology* 158:181–192, http://dx.doi.org/10.1007/s00227-010-1550-1.
- Dreyer, J.C., K.E. Knick, W.B. Flickinger, and C.L. Van Dover. 2005. Development of macrofaunal community structure in mussel beds on the northern East Pacific Rise. *Marine Ecology Progress Series* 302:121–134, http://dx.doi.org/10.3354/meps302121.
- Govenar, B., N. Le Bris, S. Gollner, J. Glanville, A.B. Aperghis, S. Hourdez, and C.R. Fisher. 2005. Epifaunal community structure associated with *Riftia pachyptila* in chemically different hydrothermal vent habitats. *Marine Ecology Progress Series* 305:67–77, http://dx.doi.org/10.3354/meps305067.
- Hunt, H.L., A. Metaxas, R.M. Jennings, K.M. Halanych, and L.S. Mullineaux. 2004. Testing biological control of colonization by vestimentiferan tubeworms at deep-sea hydrothermal vents (East Pacific Rise, 9°50'N). Deep-Sea Research Part I 51:225–234, http://dx.doi.org/10.1016/j.dsr.2003.10.008.
- Johnson, K.S., J.J. Childress, C.L. Beehler, and C.M. Sakamoto. 1994.
   Biogeochemistry of hydrothermal vent mussel communities:
   The deep-sea analogue to the intertidal zone. Deep-Sea Research
   Part I 41:993-1,011, http://dx.doi.org/10.1016/0967-0637(94)90015-9.
- Lenihan, H.S., S.W. Mills, L.S. Mullineaux, C.H. Peterson, C.R. Fisher, and F. Micheli. 2008. Biotic interactions at hydrothermal vents: Recruitment inhibition by the mussel *Bathymodiolus thermophilus*. *Deep-Sea Research Part I* 55:1,707–1,717, http://dx.doi.org/10.1016/j.dsr.2008.07.007.
- Luther, G.W. III, A. Gartman, M. Yücel, A.S. Madison, T.S. Moore, H.A. Nees, D.B. Nuzzio, A. Sen, R.A. Lutz, T.M. Shank, and C.R. Fisher. 2012. Chemistry, temperature, and faunal distributions at diffuse-flow hydrothermal vents: Comparison of two geologically distinct ridge systems. *Oceanography* 25(1):234–245, http://dx.doi.org/10.5670/oceanog.2012.22.
- Lutz, R.A., T.M. Shank, G.W. Luther III, C. Vetriani, M. Tolstoy, D.B. Nuzzio, T.S. Moore, F. Waldhauser, M. Crespo-Medina, A. Chatziefthimiou, and others. 2008. Interrelationships between vent fluid chemistry, temperature, seismic activity, and biological community structure at a mussel-dominated deep-sea hydrothermal vent along the East Pacific Rise. Journal of Shellfish Research 27:177–190, http://dx.doi.org/10.2983/0730-8000(2008)27[177:IBVFCT]2.0.CO;2.



- Mullineaux, L.S., D.K. Adams, S.W. Mills, and S.E. Beaulieu. 2010. Larvae from afar colonize deep-sea hydrothermal vents after a catastrophic eruption. *Proceedings of the National Academy of Sciences of the United States of America* 107:7,829–7,834, http://dx.doi.org/10.1073/pnas.0913187107.
- Mullineaux, L.S., C.R. Fisher, C.H. Peterson, and S.W. Schaeffer. 2000. Tubeworm succession at hydrothermal vents: Use of biogenic cues to reduce habitat selection error? *Oecologia* 123:275–284, http:// dx.doi.org/10.1007/s004420051014.
- Sancho, G., C.R. Fisher, S. Mills, F. Micheli, G.A. Johnson, H.S. Lenihan, C.H. Peterson, and L.S. Mullineaux. 2005. Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents. *Deep-Sea Research Part* I 52:837–844, http://dx.doi.org/10.1016/j.dsr.2004.12.002.
- Scheirer, D.S., T.M. Shank, and D.J. Fornari. 2006. Temperature variations at diffuse and focused flow hydrothermal vent sites along the northern East Pacific Rise. *Geochemistry Geophysics Geosystems* 7, Q03002, http:// dx.doi.org/10.1029/2005GC001094.
- Shank, T.M., D.J. Fornari, K.L. Von Damm, M.D. Lilley, R.M. Haymon, and R.A. Lutz. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research II* 45:465–515, http://dx.doi.org/10.1016/ S0967-0645(97)00089-1.
- Thiébaut, E., X. Huther, B. Shillito, D. Jollivet, and F. Gaill. 2002. Spatial and temporal variations of recruitment in the tube worm *Riftia pachyptila* on the East Pacific Rise (9°50'N and 13°N). *Marine Ecology Progress Series* 234:147–157, http://dx.doi.org/10.3354/meps234147.
- Von Damm, K.L., and M.D. Lilley. 2004. Diffuse flow hydrothermal fluids from 9°50'N East Pacific Rise: Origin, evolution and biogeochemical controls. Pp. 245–268 in *The Subseafloor Biosphere at Mid-Ocean Ridges*. W.S.D. Wilcock, E.F. DeLong, D.S. Kelley, J.A. Baross, and S.C. Cary, eds, Geophysical Monograph Series, vol. 144, American Geophysical Union, Washington, DC, http://dx.doi.org/10.1029/GM144.

the spatial and temporal variability of these systems (e.g., from tidal periodicities evident in vent exit temperatures; Scheirer et al., 2006), earthquake occurrence (Tolstoy et al., 2008), rates of colonization and growth (Lutz et al., 1994), and observed temporal changes in biological community structure (species composition and colonization order). Manipulative experiments also revealed that interactions between species, such as facilitation and settlement cues (Mullineaux et al., 2000; Govenar et al., 2004; Govenar and Fisher, 2007), competition (Mullineaux et al., 2003; Lenihan et al., 2008), and predation (Micheli et al., 2002; Sancho et al., 2005), strongly influenced community composition and development (see Govenar, 2012, in this issue).

Microbial investigations at the EPR after the 1991-1992 eruptions expanded on early studies of chemoautotrophy (e.g., Wirsen et al., 1986), making the site a hotbed of discovery of new microbes with novel physiological and biochemical capabilities. Over the past decade, more than two dozen new microbial species have been detected or isolated, including ones that oxidize hydrogen (Alain et al., 2002), reduce nitrate to ammonia (Vetriani et al., 2004a), reduce sulfur (Alain et al., 2009), and are adapted to mercury exposure (Vetriani et al., 2004b). Microbes function in many ecological roles as producers, prey, remineralizers, and possibly as settlement cues for invertebrate larvae. Although symbiotic interactions between microbes and vent animals are well characterized, other interactions are not; these gaps stimulate many questions for future investigation. EPR studies have also revealed that microbial production is

not necessarily constrained to vent sites, and may continue in the hydrothermal vent plume. Theory suggests that the latter may represent an important source of organic carbon to the deep ocean (McCollom, 2000), and field studies support this idea (Toner et al., 2009).

The initial recolonization of vents after eruptive disturbance depends on the availability of planktonic larvae of vent species (see Highlight by Govenar et al. on page 28). When an eruption eliminates local communities, transport of larvae to the site is controlled by deep currents that carry them from spawning populations elsewhere. Over the course of RIDGE and Ridge 2000 studies, we have gained important insights on the dynamics of ocean currents and mixing near the ridge and their influence on exchange of larvae between vents as a result of the LADDER project (LArval Dispersal on the Deep East Pacific Rise) and other interdisciplinary studies. For instance, a prominent feature of flows near the EPR at 9°50'N is a pair of jet-like currents aligned with the ridge axis that lies at  $\sim 2,500$  m depth (Lavelle et al., 2010, and 2012, in this issue). These jets, and other hydrodynamic processes at the EPR (e.g., Jackson et al., 2010; Thurnherr et al., 2011; Liang and Thurnherr, 2011; Thurnherr and St. Laurent, 2012, in this issue) influence larval transport in ways that can be counterintuitive. Larvae that disperse very near the seafloor may stay near their natal vent (Adams and Mullineaux, 2008), those entrained in the jets may be transported to vents hundreds of meters away, but those that rise a few hundred meters off the seafloor appear not to go far (McGillicuddy et al., 2010). Long-distance transport, sufficient to move larvae of a pioneer species over

300 km to an eruption site, may result from larger-scale oceanic features, such as wind-generated mesoscale eddies (Adams et al., 2011). These coupled biophysical studies have helped explain the faunal response to the 2005–2006 eruptions and also inform more general questions about larval exchange and community resilience at vents.

Dispersal and retention of larvae influence the diversity of vent communities and genetic exchange between them. A metapopulation study (Neubert et al., 2006) found that dispersal resulted in elevated diversity in transient vent systems as long as suitable vent habitat remained plentiful. This theoretical result is consistent with studies along the EPR (where vents are numerous) showing that diversity is remarkably similar among geographically separated communities in both mussel beds (Turnipseed et al., 2003) and tubeworm thickets (Govenar et al., 2005). Furthermore, while dispersal appears to facilitate high levels of genetic exchange between EPR segments (Craddock et al., 1997; Won et al., 2003; Hurtado et al., 2004; Plouviez et al., 2010), there is genetic structure suggestive of larval retention in the tubeworm Riftia pachyptila along the EPR (Shank and Halanych, 2007), and there are physical barriers such as the equator, the Rivera Fracture Zone, and the Easter Microplate that impede genetic exchange in some species (reviewed in Vrijenhoek, 2010).

#### BIOLOGICAL AND HYDRO-THERMAL CHANGES BIASED BY THE 2005–2006 ERUPTIONS

To document the impacts of the 2005–2006 eruptions, TowCam photographic surveys were run along the EPR crest

where there was a high concentration of hydrothermal activity, between 9°49.7'N and 9°51.5'N, and in other relatively active vent areas near 9°47.5'N and 9°53'N. Murky diffuse flow was found in deep fissures, collapsed pits, and small cracks in sheet flows and lava remnant in the AST floor, and white microbial mats were evident in extensive areas of vigorous diffuse flow, surrounded by olive-brown mats. There was an absence of sessile megafauna in newly venting areas, or any intact community in pre-eruptive zones, but abundant and small brachyuran crabs were observed throughout the area surveyed.

Approximately two weeks following the May 2006 R/V New Horizon response effort, a rapid-response Alvin expedition collected vent fluids from sulfide chimneys and areas of new diffuse flow using traditional and in situ chemical techniques, and sampled recent faunal colonists and fresh lavas colonized by microbes (Shank et al., 2006). The diving studies confirmed that previously deployed seafloor markers and biomarkers, extant biological communities, and ongoing faunal colonization experiments had been completely buried by new lava. During late 2006 to 2007, additional TowCam surveys were conducted throughout the eruption area on every available Alvin diving cruise to constrain the areal extent of the flows and determine the distribution and type of lava flows (Soule et al., 2007; Fundis et al., 2010). It was determined that fresh lavas covered > 18 km along the ridge axis and up to 3 km off axis (Soule et al., 2007; Figure 3).

As in April 1991, the eruption, drainback, and collapse of lava in the AST floor produced broad (1–3 m wide)

fissures, sheet flows, and remnant basalt pillars that often formed dramatic "archways" (Figure 7a). Extensive white microbial mats and staining surrounded the openings of diffuse-flow vents, where shimmering water and flocculent "microbial" material were also abundant > 6 months after the eruptions. Visible colonists were dominated by small

(< 1–40 mm length), sparsely distributed individuals of the gutless tubeworm *Tevnia jerichonana* (hereafter referred to as *Tevnia*) within areas of white microbial mats. These early colonists were observed on exposed surfaces of the basalt in vigorous diffuse flow and found attached to the sides and bottom surfaces of collected basalt rocks. Limpets were

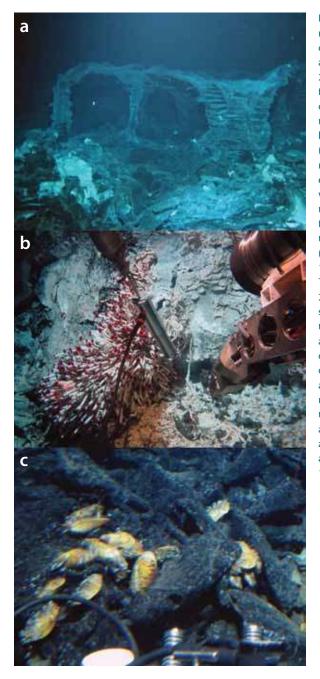


Figure 7. (See Figure 3a for location maps). (a) The Arches area south of the Tubeworm Pillar location about one year after the 2005-2006 eruption(s), with diffuse vent flow, white staining, brachyuran crabs, and Tevnia jerichonana tubeworm colonization at the base of eruptive lava remnants (2,503 m depth). (b) Tevnia colonization following the 2005-2006 eruption(s) in the TICA vent area with outstretched Alvin manipulators imaging and collecting in situ fluid chemical data associated with this assemblage (2,517 m depth). (c) Living mussels rafted more than 150 m south from the Choo Choo Train vent site by a lobe of 2005-2006 lava (2,507 m depth). No vent site was known in this area prior to the 2005-2006 eruption. Byssus attachment sites (white threads on the mussel shells) indicate not only the frequency of previously attached mussels but also the relative age of these mussels as these remnants of attachments accumulate over time. Distances across the bottoms of the images are approximately 2.2 m (a), 1.3 m (b), and 0.5 m (c).

also among the early pioneers, including one species, Ctenopelta porifera, that appeared to have arrived from a population over 300 km away (Mullineaux et al., 2010). The highest densities of Tevnia collected were about four individuals per centimeter (in the 9°47.5'N area). Among recently settled Tevnia at 9°49.8'N (former Biomarker #141 site, Figures 3 and 8), H<sub>2</sub>S concentrations were as high as 1.1 mmol kg<sup>-1</sup> in 30°C fluids, two orders of magnitude higher than measured one year earlier at this location when mussels were dominant (Nees et al., 2009; Moore et al., 2009; Luther et al., 2012, and Govenar, 2012, both in this issue). During subsequent visits to the eruption area (e.g., November 2006 and January 2007), detailed high-definition imaging surveys with collocated in situ fluid

chemical sensing (both autonomous and via submersible), microbial and faunal sampling of over 30 nascent habitats (including both natural and artificial substrates), time-lapse camera deployments, and recoveries of OBS data were conducted. These post-eruption studies began a new phase of EPR ISS research directed toward understanding eruption impacts on biological and chemical processes (Shank et al., 2006; Nees et al., 2009; Moore et al., 2009; Luther et al., 2012, in this issue).

The most recent EPR eruptions both exposed the links among geological, biological, and chemical processes (e.g., the partitioned recruitment of fauna and microbes to open habitats hosting elevated sulfide, temperature, and anoxic conditions) and provided a unique opportunity to compare the

May 2005

November 2006

Figure 8. Pre- and posteruption Biomarker 141 animal communities at the East Pacific Rise (see Figure 3a for location). (top) A well-developed **Bathymodiolus** thermophilus assemblage with galatheid crabs along the central eruptive fissure on the axial summit trough floor in May 2005 (pre-eruption). (bottom) The same location hosting an actively colonizing Tevnia jerichonana tubeworm community in November 2006, after the 2005-2006 eruptions. Field of view across the bottom of each photo is ~ 2 m.

biological, chemical, and geological links between pre-and post-eruptive dynamics from "time zero" using the more modern in situ instrumentation developed during the Ridge 2000 Program (e.g., see Luther et al., 2012; Sievert and Vetriani, 2012; Rubin et al., 2012; and Baker et al., 2012, all in this issue).

Eighteen months following the 2005–2006 eruptions, hydrothermal activity was most vigorous and extensive between 9°47'N and 9°52'N, a prior locus of hydrothermal activity that formed the "bull's-eye" of the EPR ISS (Figures 1–3). With the exception of M and Q vents in the northern region (chimney structures present, but inactive) and Tubeworm Pillar in the southern region (this previous 11 m tall structure was absent) at 9°49.6'N (Figure 3), the preeruption high-temperature venting chimneys between 9°49'N and 9°52'N (e.g., Biovent, Bio 9, and P vent chimneys) survived the eruption and were highly active (Figure 3). Pre-eruptive areas of vigorous diffuse flow were also post-eruptive sites of the most vigorous activity. A year after the eruption, Biovent (Figure 3) consisted of two smokers hosting alvinellid polychaetes surrounded by fresh pillow lava, with white bacterial mats in cracks. Diffuse flow in the vicinity hosted bacterial mats and lepetodrilid gastropod limpets.

The well-known site Mussel Bed (Figure 3), which had been active since ~ 1996 first as a diffuse-flow and then as a high-temperature vent site, had no visible diffuse flow, only fresh basalt following the 2005–2006 eruptions. The East Wall site had little diffuse flow, large accumulations of mussel shells, and empty tubes of the gutless tubeworm *Riftia pachyptila* (hereafter referred to

as Riftia; Nees et al., 2009). Live (adult) mussels and attached tubes of Riftia appeared to be in their pre-eruptive location and were not covered with new lava. The Bio 9 vent area (Figure 3) (Von Damm and Lilley 2004; Ferrini et al., 2007) consisted of three pre-eruption chimneys, two of which were recognizable from pre-eruption morphology, but post-2005-2006 consisted of a large black smoker complex of more than 20 spires, many hosting alvinellid polychaetes. The three spires that made up the P vent complex (Figure 3) prior to the most recent eruptions were still active and recognizable with sparse alvinellid polychaetes covering the upper mid-section of the active sulfide walls, above patches of Tevnia, and a single large (1 m long) individual of Riftia that may have survived the eruption. As noted above, dissolved chloride for P and Bio 9 vents (Figures 5 and 6) reveal vapor-rich fluids subsequent to the 2005-2006 eruptions, although the specific concentration levels generally suggest a return to pre-event temperature and pressure conditions.

South of Bio 9 and P vents, the next active high-temperature vent area prior to the 2005–2006 eruptions was ~ 300 m distant and consisted of a series of several small (1-3 m tall) black smokers with extensive assemblages of the heat-tolerant polychaete Alvinella pompejana (Ty and Io vents, Figure 3b,c; Ferrini et al., 2007). The newly created active post-eruption chimneys were within 10 m of the pre-existing Alvinella Pillar, Ty, and Io black smoker vents. Diffuse flow was vigorous throughout this area with patches of white bacterial mats, zoarcid fish, gastropod limpets, and both bythograeid and galatheid

crabs. Clumps of Tevnia up to at least 30 cm in length were observed, most in deep cracks and pits not present prior to the eruption. The hydrothermal activity extended further south along the steep, eastern wall of AST in this area on which several extensive Tevnia clumps had formed. The Choo Choo Train diffuse-flow site, located just meters north of the Tubeworm Pillar (Figure 3) was a massive mussel field prior to the 2005-2006 eruptions. As of January 2007, one year post-eruption, that area was paved with fresh basalt broken up with white staining and small patches of diffuse flow. These most recent eruptions presumably engulfed the Tubeworm Pillar, which prior to the eruption hosted more than a dozen vent species, including Riftia, mussels, polychaetes, gastropods, and brachyuran and galatheid crabs. The Choo Choo Train marker (the site named after this marker) was later found 170 m south its original location with more than two dozen live (adult) mussels (Figure 7c) attached to its rope. These mussels and plastic marker (with plastic anchor rope still intact) apparently were transported on the chilled skin of lava down the center of the AST to this location. (Shank et al., 2006). While the approximate locations of high-temperature venting largely stayed the same between the 1991-1992 and 2005-2006 eruptions, some vents became inactive and some disappeared (Figure 3). Based on data collected to date (the most recent cruise to the EPR ISS occurred in November 2011), no new hightemperature areas have developed, and diffuse-flow venting has largely been concentrated in the same locations as pre-eruptive venting, primarily

along zones of eruptive fissuring in the AST floor and along the bounding walls of the AST.

## IN SITU GEOPHYSICAL STUDIES OF ERUPTION AND HYDROTHERMAL PROCESSES

A dense ~ 4 x 4 km OBS array centered at 9°50'N was deployed from October 2003 to January 2007 to characterize EPR microearthquake activity (Tolstoy et al., 2008) and to elucidate crustal processes critical to understanding variability in hydrothermal vent chemistry, temperature, and biology. The array of OBSs was serviced on an approximately yearly basis, and one of the first significant results of this multiyear effort was identification of a steady increase in the rate of earthquake activity in the roughly seven-month deployment between 2003 and 2004. Rapid analysis of the 2004 to 2005 event rate in late 2005 showed that this trend was continuing, suggesting that the EPR at this site was primed for an eruption. The microearthquake data were buttressed by changes in the fluid chemistry and increasing temperatures for some of the high-temperature vents that also suggested the site might erupt soon (Von Damm, 2004). On this basis, the array was approved for redeployment for an additional year (2006-2007) while the 2005-2006 array was still on site. In April 2006, the eruption forecast was validated when eight of 12 OBSs in the deployed array failed to return following an eruption that buried many of them in newly erupted lava (Tolstoy et al., 2006; http://media.marine-geo.org/video/ obs-recovery-epr-with-jason-2-2007). Analysis of the complete data set confirms that the event rate steadily increased and remained high through

January 22, 2006, when a seismic crisis, interpreted as a final diking and eruption event, led to a dramatic decrease in activity (Tolstoy et al., 2006), which remained low through the end of the microseismicity monitoring in January 2007 (recent work of author Tolstoy and colleagues). The years-long build up in seismicity is likely due to a combination of increasing extensional stresses caused by plate spreading, excess pressure from inflation of the axial magma chamber (AMC) melt lens, and higher levels of

heat driving water-rock reactions in the hydrothermal system as new magma is injected into the crust. Because Ridge 2000 seismic monitoring at the EPR began only in 2003, the period between the 1991–1992 eruptions and the onset of the 2005–2006 eruptive phase is not well constrained. However, it appears that a microearthquake swarm below the Bio 9 and P vent area (Figure 3) in 1995 (Sohn et al., 1998, 1999; Fornari et al., 1998b) could be related to increased heat due either to

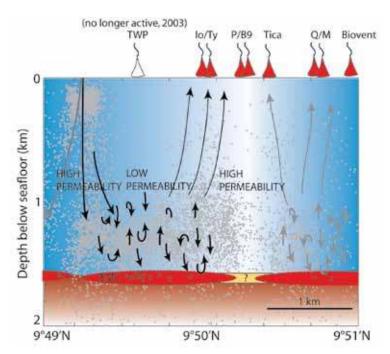


Figure 9. Cross section of the East Pacific Rise axis between 9°49'N and 9°51'N showing relocated microearthquake locations (grey dots) from 2003-2004 (Waldhauser and Tolstoy, 2011) and inferred associated structure of hydrothermal circulation (figure after Tolstoy et al., 2008). Sites of upflow and inferred downflow are highly permeable, whereas the central cracking zone exhibits lower permeability (Crone et al., 2011). The blue shading in the upper crust indicates an inferred thermal gradient based on vent temperature data (Scheirer et al., 2006; Tolstoy et al., 2008). The temperature gradient may develop over a decade of localized downflow, leading to the relative cooling of vents closest to the recharge site and warming of vents further away. Red lenses show inferred axial magma chamber (AMC) locations (depth from Kent et al., 1993), with a possible break implied (yellow zone) based on a gap in seismicity and a change in diffuse vent chemistry in this area along-axis (Von Damm and Lilley, 2004). Hydrothermal vents are labeled (see Figure 3a for locations).

cracking and migration of the rock/water reaction zone (Wilcock, 2004) or a dike that did not produce an observed eruption (Germanovich et al., 2011).

Analysis of earthquake activity within the array during the 2003–2004 deployment led to a number of discoveries that integrate well with multidisciplinary observations of vents in the 9°50'N area. An area of hydrothermal recharge was inferred from a pipelike structure of sustained cracking near a kink in the AST at 9°49.4'N (Tolstoy et al., 2008; Figure 9). This interpretation is supported by the observation that the kink area is pervasively fissured and collapsed, but there are no biological communities associated with the fissures, unlike further north along the AST floor (Nees et al., 2009; Moore et al., 2009; Luther et al., 2012, in this issue). In addition, changes in vent temperatures through time (Scheirer et al., 2006) imply the development of a spatial thermal gradient with vents closest to the inferred downflow cooling through time, and vents further from the kink increasing in temperature with time (Tolstoy et al., 2008; Figure 9). A seismically less-well-defined upflow zone is coincident with the location of the greatest number of high-temperature vents active during the OBS deployment period. A gap in the seismicity at ~ 9°50.3'N is interpreted as a break between two hydrothermal cells and is coincident with a change in diffuse-flow chemistry (Von Damm and Lilley, 2004; Nees et al., 2009; Moore et al., 2009; Luther et al., 2012, in this issue).

An approximately symmetrical ~ 1.5 km sized hydrothermal cell is thus inferred to be in place, with circulation dominantly occurring in the along-axis

direction (e.g., Haymon et al., 1991). This flow geometry contrasts with previous ideas that flow was dominantly across axis, with hydrothermal recharge occurring on large off-axis faults. The high permeability afforded by abyssal hill faults was believed to be required because smaller cracks in the volcanic carapace of the ridge crest would rapidly close by anhydrite precipitation (e.g., Lowell and Yao, 2002). However, the sustained cracking caused by repeated diking and fissuring in and adjacent to the AST (Fornari et al., 1998a; Soule et al., 2009) and the kink in its along-strike structure provides a mechanism to maintain permeability within a narrow, axial downflow zone. Patterns of tidal triggering support this hypothesis that the inferred downflow zone coincident with the kink is indeed associated with high permeability in the upper crust (Crone et al., 2011).

Elsewhere on the MOR, microearthquakes are also observed to occur preferentially during periods of highest extensional stress (e.g., Wilcock, 2001; Tolstoy et al., 2002; Stroup et al., 2007). Stress levels within the cracking zone directly above the AMC in the 9°50'N EPR area are likely to be highly heterogeneous (Bohnenstiehl et al., 2008), but a consistent pattern of tidal triggering is observed associated with diffusion of the tidal pressure wave (Stroup et al., 2009). The timing of this diffusion led to the first in situ measurement of permeability within a ridge axis hydrothermal system with a one-dimensional bulk permeability estimate of  $10^{-13}$  to  $10^{-12}$  m<sup>2</sup>. Two-dimensional modeling of the data provided a more detailed picture of the permeability structure of the cell with the upflow and downflow areas having

higher permeability ( $\sim 10^{-9} \text{ m}^2$ ), and the center of the cell having lower permeability ( $\sim 10^{-13} \text{ m}^2$ ; Crone et al., 2011). This modeling result supports the notion that permeability structure is a primary driver controlling the location and intensity of hydrothermal venting.

## DEDUCING MAGMATIC PROCESSES THROUGH LAVA GEOCHEMISTRY

The volcanic eruptions in 1991–1992 and again in 2005–2006 in the 9°50'N area of the EPR axis (see Perfit et al., 2012, and Rubin et al., 2012, both in this issue) have allowed researchers to place important constraints on the extents and timescales of magmatic processes at a fast-spreading MOR. Detailed mapping and geochemical analyses of lavas from the 2005-2006 eruptions show that the northern and southern limits of the new lava flow field are chemically more evolved than the central portion. A similar pattern occurs in lavas of the 1991–1992 eruptions and in prehistoric flows in the region, indicating that these geochemical patterns have existed for many decades (Goss et al., 2010; Perfit et al., 2012, in this issue). This chemical carryover from eruption to eruption is consistent with only about one-tenth of the magma available in the axial magma lens having erupted in 2005-2006 (Soule et al., 2007).

Of particular note are the changes in magma composition that have occurred since the 1991–1992 eruptions at the 9°50'N site. Lavas from the 2005–2006 eruption collected from on and off the ridge axis, including samples that were attached to two of the OBSs that were stuck in the new lava flow (recovered by the remotely operated vehicle *Jason* in

2007), have lower contents of MgO and higher FeO concentrations than 1991-1992 flows (see Perfit et al., 2012, in this issue), indicating that the molten rock stored in the AMC or crystal-melt mush zone beneath the ridge changed composition by some igneous processes that led to the formation of chemically different melts. Although somewhat chemically modified, they have comparable radiogenic isotopic ratios to the 1991–1992 lavas, suggesting that the mantle source of the parental magma has not appreciably changed. Based on measurements of the short-lived isotopes of Pb and Ra in the lavas, Rubin et al. (2005) estimate that repeat magma injections from the mantle occur every 15 to 20 years at this site. Calculations using both major and trace elements suggest between 7 and 30 weight percent fractional crystallization of the least differentiated 1991 EPR eruption parental magma within the AMC could produce some of the compositional range observed in the 2005-2006 EPR flows (Goss et al., 2010). This chemical difference is consistent with an average 10-30°C cooling of the regional melt lens underlying the ridge axis in this area over the 13-year period since the last eruption. However, such a small amount of cooling is inconsistent with heat loss expected from the observed hydrothermal activity and supports the hypothesis that frequent magma replenishment of the AMC melt lens is required to keep it from freezing and to maintain high hydrothermal vent temperatures (Liu and Lowell, 2009). It appears that although some crystallization likely occurred, the AMC has also been replenished by other melts that cooled and crystallized deeper in the crust during the 13-year period of repose between eruptions. Mineralogical, textural, and glass data from a gabbroic xenolith entrained in a basalt from the 1991 EPR eruption support the viability of the process, and point to magma mixing and crystal-melt interactions in the lower crust below the AMC melt lens (Ridley et al., 2006).

Microearthquake studies provide some insight into magma replenishment processes. Analysis of composite focal mechanisms from the 2003-2004 microearthquake data show primarily compressional focal mechanisms (Waldhauser and Tolstoy, 2011), consistent with on-going injection of magma into the AMC (Wilcock et al., 2009) for several years before the 2005-2006 eruptions. An overall picture, therefore, emerges, suggesting that the most recent eruption was not driven by the injection of hotter, more primitive melt directly into the AMC from the mantle, but rather by episodic addition of somewhat more differentiated magma that had resided deeper within the crust, such as in the crystal mush zone beneath the axis (Goss et al., 2010).

#### DISCUSSION AND CONCLUSIONS

Ridge 2000 Program studies conducted at the EPR ISS have made significant contributions to multiple disciplines, and, more importantly, to crossdisciplinary understanding of the flow of material, energy, and life between the mantle, crust, seafloor, and deep ocean. For instance, the detailed marine hydrothermal studies that have been performed at the EPR ISS (and the other ISSs, too) have documented the effects of subseafloor magmatic and tectonic processes on changes in vent fluid

chemistry, and demonstrated clear links to biological and geophysical processes (see ISS articles by Kelley et al., 2012, and Tivey et al., 2012, both in this issue). Integrated multidisciplinary investigations at the EPR ISS have included monitoring and manipulative experiments that documented vent temperatures, time-series fluid chemistry, and biological colonization patterns (Shank et al., 1998; Von Damm and Lilley, 2004). Successful in situ voltammetric studies conducted by Luther et al. (2001), Nees et al. (2008), and Moore et al. (2009) have led to the recognition that variability in the composition or flux of hydrothermal fluids can directly affect the establishment and distribution of microbial and faunal communities. These results are superimposed upon the knowledge that the relative importance of biological interactions may also vary along the hydrothermal fluid flux gradient (Micheli et al., 2002; Mullineaux et al., 2003). Interdisciplinary studies linking the dynamics of the deep ocean to larval dispersal and colonization (e.g., the LADDER project) are placing studies of vent faunal diversity and gene flow in a broader, oceanographic context.

Although the nearly continuous annual record of change in vent fluid chemistry at the EPR ISS since 1991 has contributed fundamental insight into the effects of temperature and pressure on hydrothermal alteration processes, these data would have been difficult or impossible to interpret in the absence of advances in theoretical reaction models involving heat and mass transfer that have developed directly or indirectly from the Ridge 2000 Program (Lowell and Germanovich, 1997; Fontaine and Wilcock, 2006; Fontaine et al., 2007).

Similarly, it would not have been possible to establish the links that are now known to occur among magmatic, tectonic, and hydrothermal processes at the EPR and elsewhere without the long-term coverage and deployment of OBS instruments, in situ continuous temperature loggers (HOBOs), chemical sensors, and fluid chemical sampling that have proved so valuable in constraining the timing of magmatic events, hydrothermal alteration processes, and the permeability structure of the ocean crust (e.g., Fornari et al., 1998b; Sohn et al., 1999; Scheirer et al., 2006; Ding and Seyfried, 2007; Tolstoy et al., 2008; Stroup et al., 2009; Crone et al., 2011). Indeed, a well recognized strength of the RIDGE and Ridge 2000 Programs has been their great emphasis on the need for technology development and interdisciplinary perspectives to achieve a fundamental understanding of the inherently complex links among magmatic, hydrothermal, and biological processes at MORs.

Microearthquake monitoring has proven valuable in defining the dynamics and geometry of a hydrothermal cell at the EPR 9°50'N as well as providing insight into the state of stress in the crust through an eruptive cycle. Hydrothermal circulation appears to be dominantly along axis with focused on-axis recharge, where upflow and downflow zones are marked by high permeability. A < 2 km diameter hydrothermal circulation cell is inferred within the highly heterogeneous seismic Layer 2B (lower oceanic crust) in which permeability varies by several orders of magnitude on spatial scales of hundreds of meters. Increasing levels of earthquake activity over a time period of years, in conjunction with discrete

sampling of hydrothermal vents and monitoring of chemical and temperature changes, appear to be extremely useful signals for forecasting and preparing for future eruptions at fast-spreading ridges.

Although the EPR has been well mapped with ship-based multibeam sonar, near-bottom multibeam and side-scan sonar data and near-bottom imagery have brought new insights about lava emplacement processes, with the near-bottom bathymetric data providing well-constrained quantitative details of structural and lava morphology that are otherwise difficult to ascertain. To date, these data have systematically been acquired only along small portions of the EPR. Advances in autonomous underwater vehicle technologies and sensors have yielded high-resolution co-registered mapping products (side scan and bathymetry) that are critical to establishing spatial relationships among seafloor features, and have enabled quantitative analyses of seafloor morphology that are key to understanding the complex interplay of volcanic, tectonic, and hydrothermal processes on the seafloor. More high-resolution data sets will be needed to fully test current ideas of relationships between ridge crest volcanic and tectonic structures and hydrothermal vent distributions and patterns of chemical variability.

With a full eruption-to-eruption cycle captured at the EPR 9°50'N area, it is clear that the succession of the biological communities from microbial mats to tubeworm-dominance to mussel-dominance follows a trend of decreasing temperatures and hydrothermal chemical input and variability with time following an eruption. One important result of the linked biological

and geochemical studies at the EPR ISS is that both microbial and faunal communities respond to rapid changes in fluid chemistry fluxes in their habitats. Examination of the influence of fluid chemistry and microbial community structure through biofilm development on macrofaunal colonization (see Sievert et al., 2012, in this issue) will be key to future insights. Changes in the composition of microbial communities over time and over gradients in hydrothermal fluid flux may provide important cues that ultimately control settling of invertebrate larvae, colonization, and faunal distribution in vent habitats. The documentation of invertebrate colonization and succession at new vents following a volcanic eruption, and a series of manipulative

questions concerning the ecology of deep-sea hydrothermal systems. The EPR ISS and the close-knit community of researchers who work there are poised to continue to make significant contributions to this field of study for many decades to come.

#### **ACKNOWLEDGEMENTS**

We acknowledge our many collaborators both at sea and in the lab during the past decade of research involved in EPR ISS experiments, and the many seagoing technicians, crewmembers, ships' officers, and deep-submergence vehicle crews that were key to obtaining the field data. We dedicate this contribution to Karen Von Damm, a close friend and colleague, who was a driving force

RIDGE 2000 PROGRAM STUDIES CONDUCTED AT THE [EAST PACIFIC RISE INTEGRATED STUDY SITE] HAVE MADE SIGNIFICANT CONTRIBUTIONS TO MULTIPLE DISCIPLINES, AND, MORE IMPORTANTLY, TO CROSSDISCIPLINARY UNDERSTANDING OF THE FLOW OF MATERIAL, ENERGY, AND LIFE BETWEEN THE MANTLE, CRUST, SEAFLOOR, AND DEEP OCEAN.

field experiments, provide considerable insights into the relative roles of abiotic conditions and biotic interactions in structuring vent communities. Recent and emerging technological developments, such as in situ chemical analyzers, observatory approaches, and laboratory-based pressure culture systems, should provide invaluable new experimental tools for tackling many remaining

in EPR and global hydrothermal vent research over nearly two decades before her untimely death in 2008 (obituary online at: http://www.whoi.edu/page. do?pid=7400&tid=282&cid=48066). We are grateful for the comments and reviews by Ed Baker, Susan Humphris, and William Wilcock, which greatly improved the manuscript. Jim Holden and Stace Beaulieu also provided useful

editorial comments. DJF gratefully acknowledges his 25+ years of collaboration with Rachel Haymon who first got him interested in EPR hydrothermal studies. Grants that supported EPR ISS field and laboratory studies for our research programs include: DJF, SAS, and VF: OCE-9819261, OCE-0525863, OCE-0838923, OCE-0096468, OCE-0732366, and OCE-0112737. KVD, JB, and FP: OCE-0327126, OCE-0937387, and OCE-0525894. JC: OCE-0222069. MDL: OCE-0701196. GWL: OCE-0308398, OCE-0326434, and OCE-0937324. LM: OCE-0424953, OCE-0425361, and OCE-0647948. MRP: OCE-0138088, OCE-0819469, OCE-825265, OCE-638406, OCE-527077, and OCE-535532. TMS: NSF OCE-0327261, OCE-0328117, and OCE-0451983. KHR: OCE-0636439, OCE-0732761, and OCE-0937409. WES: OCE-0751771, OCE-0813861, and OCE-0961188. MT: OCE-0961594, OCE-0732569, OCE-0649538, and OCE-0327283. SW: OCE-0639601 and OCE-0525872.

#### REFERENCES

- Adams, D.K., D.J. McGillicuddy Jr., L. Zamudio, A.M. Thurnherr, X. Liang, O. Rouxel, C.R. German, and L.S. Mullineaux. 2011. Surface-generated mesoscale eddies transport deep-sea products from hydrothermal vents. Science 332:580–583, http://dx.doi.org/10.1126/ science.1201066.
- Adams, D.K., and L.S. Mullineaux. 2008. Supply of gastropod larvae to hydrothermal vents reflects transport from local larval sources. *Limnology and Oceanography* 53:1,945–1,955, http://dx.doi.org/10.4319/lo.2008.53.5.1945.
- Alain, K., N. Callac, M. Guegan, F. Lesongeur, P. Crassous, M.A. Cambon-Bonavita, J. Querellou, and D. Prieur. 2009. Nautilia abyssi sp. nov., a thermophilic, chemolithoautotrophic, sulfur-reducing bacterium isolated from an East Pacific Rise hydrothermal vent. International Journal of Systematic and Evolutionary Microbiology 59:1,310–1,315, http://dx.doi.org/10.1099/ijs.0.005454-0.

- Alain, K., J. Querellou, F. Lesongeur, P. Pignet, P. Crassous, G. Raguenes, V. Cueff, and M.A. Cambon-Bonavita. 2002. Caminibacter hydrogeniphilus gen. nov., sp nov., a novel thermophilic, hydrogen-oxidizing bacterium isolated from an East Pacific Rise hydrothermal vent. International Journal of Systematic and Evolutionary Microbiology 52:1,317–1,323, http://dx.doi.org/10.1099/ijs.0.02195-0.
- Baker, E.T., W.W. Chadwick Jr., J.P. Cowen, R.P. Dziak, K.H. Rubin, and D.J. Fornari. 2012. Hydrothermal discharge during submarine eruptions: The importance of detection, response, and new technology. *Oceanography* 25(1):128–141, http://dx.doi. org/10.5670/oceanog.2012.11.
- Baker, E.T., R.A. Feely, M.J. Mottl, F.T. Sansone, C.G. Wheat, J.A. Resing, and J.E. Lupton. 1994. Hydrothermal plumes along the East Pacific Rise, 8°40' to 11°50'N: Plume distribution and relationship to the apparent magmatic budget. *Earth and Planetary Science Letters* 128:1–17, http://dx.doi.org/10.1016/0012-821X(94)90022-1.
- Barth, G.A., and J.C. Mutter. 1996. Variability in oceanic crustal thickness and structure: Multichannel seismic reflection results from the northern East Pacific Rise. *Journal of Geophysical Research* 101:17,951–17,975, http://dx.doi.org/10.1029/96JB00814.
- Berndt, M.E., and W.E. Seyfried Jr. 1997.
  Calibration of Br/Cl fractionation during subcritical phase separation of seawater;
  Possible halite at 9° to 10°N East Pacific Rise. *Geochimica et Cosmochimica*Acta 61:2,849–2,854, http://dx.doi.org/10.1016/S0016-7037(97)00134-8.
- Bohnenstiehl, D.R., F. Waldhauser, and M. Tolstoy. 2008. Frequency-magnitude distribution of microearthquakes beneath the 9°50'N region of the East Pacific Rise, October 2003 through April 2004. *Geochemistry Geophysics Geosystems* 9, Q10T03, http://dx.doi.org/10.1029/2008GC002128.
- Bowles, J., J.S. Gee, D.V. Kent, M.R. Perfit, S.A. Soule, and D.J. Fornari. 2006. Paleointensity applications to timing and extent of eruptive activity, 9°–10°N East Pacific Rise. *Geochemistry Geophysics Geosystems* 7, Q06006, http://dx.doi.org/10.1029/2005GC001141.
- Butterfield, D., I.R. Jonasson, G.J. Massoth, R.A. Feely, K.K. Roe, R.W. Embley, J.F. Holden, J.R. McDuff, M.D. Lilley, and J.R. Delaney. 1997. Seafloor eruptions and evolution of hydrothermal fluid chemistry. *Philosophical Transactions of the Royal Society of London A* 355:369–386.
- Carbotte, S., R. Arko, D. Chayes, W. Haxby, K. Lehnert, S. O'Hara, W. Ryan, T. Shipley, L. Gahagan, K. Johnson, and T.M. Shank. 2004. New integrated data management system for Ridge 2000 and MARGINS research.

- Eos, Transactions, American Geophysical Union 82:425–433, http://dx.doi.org/10.1029/2004EO510002.
- Carbotte, S.M., J.P. Canales, M.R. Nedimović, H. Carton, and J.C. Mutter. 2012. Recent seismic studies at the East Pacific Rise 8°20′–10°10′N and Endeavour Segment: Insights into mid-ocean ridge hydrothermal and magmatic processes. *Oceanography* 25(1):100–112, http://dx.doi.org/10.5670/oceanog.2012.08.
- Carbotte, S.M., and K.C. Macdonald. 1992. East Pacific Rise 8°–10°30'N: Evolution of ridge segments and discontinuities from SeaMARC II and three-dimensional magnetic studies. *Journal of Geophysical Research* 97:6,959–6,982, http://dx.doi.org/10.1029/91JB03065.
- Childress, J.J. and C.R. Fisher. 1992. The biology of hydrothermal vent animals: Physiology, biochemistry and autotrophic symbioses. *Oceanography and Marine Biology* 30:337–441.
- Cowen, J.P., D.J. Fornari, T.M. Shank, B. Love, B. Glazer, A.H. Treuch, R.C. Holmes, S.A. Soule, E.T. Baker, M. Tolstoy, and K.R. Pomraning. 2007. Volcanic eruptions at East Pacific Rise near 9°50'N. *Eos, Transactions, American Geophysical Union* 88:81–83, http://dx.doi.org/10.1029/2007EO070001.
- Craddock, C., R.A. Lutz, and R.C. Vrijenhoek. 1997. Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. *Journal of Experimental Marine Biology and Ecology* 210:37–51, http://dx.doi.org/10.1016/S0022-0981(96)02701-3.
- Crone, T.J., M. Tolstoy, and D. Stroup. 2011. The permeability structure of young ocean crust from poroelastically triggered earthquakes. *Geophysical Research Letters* 38, L05305, http://dx.doi.org/10.1029/2011GL046820.
- Detrick, R.S., P. Buhl, E. Vera, J. Mutter, J. Orcutt, J. Madsen, and T. Brocher. 1987. Multi-channel seismic imaging of a crustal magma chamber along the East Pacific Rise. *Nature* 326:35–41, http://dx.doi.org/10.1038/326035a0.
- Dietz, R.S. 1961. Continent and ocean basin evolution by spreading of the sea floor. *Nature* 190:854–857, http://dx.doi.org/ 10.1038/190854a0.
- Ding, K., and W.E. Seyfried Jr. 2007. In-situ measurement of pH and dissolved H<sub>2</sub> in mid-ocean hydrothermal fluids at elevated temperatures and pressures. *Chemical Reviews* 107:601–623, http://dx.doi.org/10.1021/cr050367s.
- Dreyer, J.C., K.E. Knick, W.B. Flickinger, and C.L. Van Dover. 2005. Development of macrofaunal community structure in mussel beds on the northern East Pacific Rise. *Marine Ecology Progress Series* 302:121–134, http://dx.doi.org/ 10.3354/meps302121.

- Dunn, R.A., and D.R. Toomey. 1997. Seismological evidence for three-dimensional melt migration beneath the East Pacific Rise.

  Nature 388:259–262, http://dx.doi.org/10.1038/40831.
- Dunn, R.A., and D.R. Toomey. 2001. Crackinduced seismic anisotropy in the oceanic crust across the East Pacific Rise (9°30'N). *Earth* and Planetary Science Letters 189:9–17, http:// dx.doi.org/10.1016/S0012-821X(01)00353-3.
- Dunn, R.A., D.R. Toomey, and S.C. Solomon. 2000. Three-dimensional seismic structure and physical properties of the crust and shallow mantle beneath the East Pacific Rise at 9°30'N. *Journal of Geophysical Research* 105:23,537–23,555, http://dx.doi.org/10.1029/2000JB900210.
- Dziak, R.P., D.R. Bohnenstiehl, H. Matsumoto, M.J. Fowler, J.H. Haxel, M. Tolstoy, and F. Waldhauser. 2009. January 2006 seafloor-spreading event at 9°50'N, East Pacific Rise: Ridge dike intrusion and transform fault interactions from regional hydroacoustic data. Geochemistry Geophysics Geosystems 10, Q06T06, http://dx.doi.org/ 10.1029/2009GC002388.
- Escartín, J., S.A. Soule, D.J. Fornari, M.A. Tivey, H. Schouten, and M.R. Perfit, 2007. Interplay between faults and lava flows in construction of the upper oceanic crust: The East Pacific Rise crest 9°25'–9°58'N. *Geochemistry Geophysics Geosystems* 8, Q06005, http://dx.doi.org/10.1029/2006GC001399.
- Ferrini, V.L., D.J. Fornari, T.M. Shank, J.C. Kinsey, M.A. Tivey, S.A. Soule, S.M. Carbotte, L.L. Whitcomb, D. Yoerger, and J. Howland. 2007. Submeter bathymetric mapping of volcanic and hydrothermal features on the East Pacific Rise crest at 9°50'N. *Geochemistry Geophysics Geosystems* 8, Q01006, http:// dx.doi.org/10.1029/2006GC001333.
- Fontaine, F.J., and W.S.D. Wilcock. 2006. Dynamics and storage of brine in mid-ocean ridge hydrothermal systems. *Journal of Geophysical Research* 111, B06102, http://dx.doi.org/10.1029/2005JB003866.
- Fontaine, F.J., W.S.D. Wilcock, and D.A. Butterfield. 2007. Physical controls on the salinity of midocean ridge hydrothermal vent fluids. *Earth and Planetary Science Letters* 257:132–145, http://dx.doi.org/10.1016/j.epsl.2007.02.027.
- Fontaine, F.J., W.S.D. Wilcock, D.I. Foustoukos, and D.A. Butterfield. 2009. A Si-Cl geothermobarometer for the reaction zone of hightemperature, basaltic-hosted mid-ocean ridge hydrothermal systems. *Geochemistry Geophysics Geosystems* 10, Q05009, http://dx.doi.org/ 10.1029/2009GC002407.
- Fornari, D.J., R.M. Haymon, M.R. Perfit, T.K.P. Gregg, and M.H. Edwards. 1998a. Axial summit trough of the East Pacific Rice 9°–10°N: Geological characteristics and evolution of the axial zone on fast spreading

- mid-ocean ridge. *Journal of Geophysical Research* 103:9,827–9,855, http://dx.doi.org/10.1029/98JB00028.
- Fornari, D.J., T. Shank, K.L. Von Damm,
  T.K.P. Gregg, M. Lilley, G. Levai, A. Bray,
  R.M. Haymon, M.R. Perfit, and R. Lutz. 1998b.
  Time-series temperature measurements at hightemperature hydrothermal vents, East Pacific
  Rise 9°49'–51'N: Evidence for monitoring a
  crustal cracking event. Earth and Planetary
  Science Letters 160:419–431, http://dx.doi.
  org/10.1016/S0012-821X(98)00101-0.
- Fornari, D.J., M.A. Tivey, H. Schouten, M. Perfit, D. Yoerger, A. Bradley, M. Edwards, R. Haymon, D. Scheirer, K. Von Damm, and others. 2004. Submarine lava flow emplacement at the East Pacific Rise 9°50'N: Implications for uppermost ocean crust stratigraphy and hydrothermal fluid circulation. Pp. 187–218 in *Mid-Ocean Ridges: Hydrothermal Interactions Between the Lithosphere and Oceans*. C.R. German, J. Lin, and L.M. Parson, eds, Geophysical Monograph Series, vol. 148, American Geophysical Union, Washington, DC.
- Fornari, D.J., and the WHOI TowCam Group. 2003. A new deep-sea towed digital camera and multi- rock coring system. *Eos, Transactions, American Geophysical Union* 84(8):69, http:// dx.doi.org/10.1029/2003EO080001.
- Fournier, R.O. 1983. A method of calculating quartz solubilities in aqueous sodium chloride solutions. *Geochimica et Cosmochimica Acta* 47:579–586, http://dx.doi.org/10.1016/0016-7037(83)90279-X.
- Foustoukos, D.I., and W.E. Seyfried Jr., 2007a. Fluid phase separation processes in submarine hydrothermal systems. Pp. 213–233 in *Fluid-Fluid Interactions*. A. Liebscher and C.A. Heinrich, eds, Mineralogical Society of America and The Geochemical Society, Chantilly, VA.
- Foustoukos, D.I., and W.E. Seyfried Jr. 2007b.

  Quartz solubility in the two-phase and critical region of the NaCl-KCl-H<sub>2</sub>O system:

  Implications for submarine hydrothermal vent systems at 9°50'N East Pacific Rise. *Geochimica et Cosmochimica Acta* 71:186-201, http://dx.doi.org/10.1016/j.gca.2006.08.038.
- Fox, P.J., and D.G. Gallo. 1989. Transforms of the eastern central Pacific. Pp. 111–124 in *The Eastern Pacific Ocean and Hawaii*. E.L. Winterer, D.M. Hussong, and R.W. Decker, eds, Geology of North America, vol. N, Geological Society of America, Boulder, CO.
- Francheteau, J., and R.D. Ballard. 1983. The East Pacific Rise near 21°N, 13°N, and 20°S: Inferences for along-strike variability of axial processes of the mid-ocean ridge. *Earth and Planetary Science Letters* 64:93–116, http://dx.doi.org/10.1016/0012-821X(83)90055-9.
- Francheteau, J., H.D. Needham, P. Choukroune, T. Juteau, M. Séguret, R.D. Ballard, P.J. Fox, W. Normark, A. Carranza, D. Cordoba, and

- others. 1979. Massive deep-sea sulphide ore deposits discovered on the East Pacific Rise. *Nature* 277:523–528, http://dx.doi.org/10.1038/277523a0.
- Fundis, A.F., S.A. Soule, D.J. Fornari, and M.R. Perfit. 2010. Paving the seafloor: Volcanic emplacement processes during the 2005–06 eruption at the fast-spreading East Pacific Rise, 9°50'N. *Geochemistry Geophysics Geosystems* 11, Q08024, http://dx.doi.org/10.1029/2010GC003058.
- Fustec, A., D. Desbruyères, and S.K. Juniper. 1987. Deep-sea hydrothermal vent communities at 13°N on the East Pacific Rise: Microdistribution and temporal variations. *Biological Oceanography* 4:121–164.
- Germanovich, L.N., R.P. Lowell, and P. Ramondenc. 2011. Magmatic origin of hydrothermal response to earthquake swarms: Constraints from heat flow and geochemical data at 9°50'N, East Pacific Rise. *Journal of Geophysical Research* 116, B05103, http://dx.doi.org/10.1029/2009JB006588.
- Goss, A.R., M.R. Perfit, W.I. Ridley, K.H. Rubin, G.D. Kamenov, S.A. Soule, A. Fundis, and D.J. Fornari. 2010. Geochemistry of lavas from the 2005–2006 eruption at the East Pacific Rise, 9°46'N–9°56'N: Implications for ridge crest plumbing and decadal changes in magma chamber compositions. *Geochemistry Geophysics Geosystems* 11, Q05T09, http:// dx.doi.org/10.1029/2009GC002977.
- Govenar, B. 2012. Energy transfer through food webs at hydrothermal vents:
  Linking the lithosphere to the biosphere. *Oceanography* 25(1):246–255, http://dx.doi.org/10.5670/oceanog.2012.23.
- Govenar, B., and C.R. Fisher. 2007. Experimental evidence of habitat provision by aggregations of *Riftia pachyptila* at hydrothermal vents on the East Pacific Rise. *Marine Ecology* 28:3–14, http://dx.doi.org/10.1111/j.1439-0485.2007.00148.x.
- Govenar, B., M. Freeman, D.C. Bergquist, G.A. Johnson, and C.R. Fisher. 2004. Composition of a one-year old *Riftia pachyptila* community following a clearance experiment: Insight to succession patterns at deep-sea hydrothermal vents. *The Biological Bulletin* 207:177–182. Available online at: http://www.biolbull.org/content/207/3/177.full (accessed January 7, 2012).
- Govenar, B., N. Le Bris, S. Gollner, J. Glanville, A.B. Aperghis, S. Hourdez, and C.R. Fisher. 2005. Epifaunal community structure associated with Riftia pachyptila aggregations in chemically different hydrothermal vent habitats. *Marine Ecology Progress Series* 305:67–77, http://dx.doi.org/10.3354/meps305067.
- Harding, A.J., G.M. Kent, and J.A. Orcutt. 1993.

  A multichannel seismic investigation of upper crustal structure at 9°N on the East Pacific Rise:

- Implications for crustal accretion. *Journal of Geophysical Research* 98:13,925–13,944, http://dx.doi.org/10.1029/93JB00886.
- Haymon, R.M., D.J. Fornari, M.H. Edwards, S. Carbotte, D. Wright, and K.C. Macdonald. 1991. Hydrothermal vent distribution along the East Pacific Rise Crest (9°09'–54'N) and its relationship to magmatic and tectonic processes on fast-spreading mid-ocean ridge. *Earth and Planetary Science Letters* 104:513–534, http://dx.doi.org/10.1016/0012-821X(91)90226-8.
- Haymon, R.M., D.J. Fornari, K.L. Von Damm,
  M.D. Lilley, M.R. Perfit, J.M. Edmond,
  W.C. Shanks III, R.A. Lutz, J.M. Grebmeier,
  S. Carbotte, and others. 1993. Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9°45–52'N: Direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. Earth and Planetary Science Letters 119:85–101, http://dx.doi.org/10.1016/0012-821X(93)90008-W.
- Heezen, B.C., M. Tharp, and M. Ewing. 1959. The floors of the oceans: Part I. The North Atlantic.
  Text to accompany the physiographic diagram of the North Atlantic. *Geological Society of America Special Paper 65*. Geological Society of America, Boulder, CO, 122 pp.
- Hekinian, R., M. Fevrier, F. Avedik, P. Cambon,
  J.L. Charlou, H.D. Needham, J. Raillard,
  J. Boulegue, L. Merlivat, A. Moinet, and
  others. 1983a. East Pacific Rise near 13°N:
  Geology of new hydrothermal fields. Science 219:1,321–1,324, http://dx.doi.org/10.1126/science.219.4590.1321.
- Hekinian, R., J. Francheteau, V. Renard, R.D. Ballard, P. Choukroune, J.L. Cheminee, F. Albarede, J.F. Minster, J.C. Marty, J. Boulegue, and J.L. Charlou. 1983b. Intense hydrothermal activity at the axis of the East Pacific Rise near 13°N: Submersible witnesses the growth of sulfide chimney. *Marine Geophysical Research* 6:1–14, http://dx.doi.org/10.1007/ BF00300395.
- Hess, H.H. 1960. Nature of great oceanic ridges.
  Pp. 33–34 in Preprints of the 1<sup>st</sup> International
  Oceanographic Congress (New York, August 31–September 12, 1959). American Association for the Advancement of Science, Washington, DC.
- Hooft, E.E.E., H. Schouten, and R.S. Detrick. 1996. Constraining crustal emplacement processes from the variation in seismic layer 2A thickness at the East Pacific Rise. *Earth and Planetary Science Letters* 142:289–309, http://dx.doi.org/10.1016/0012-821X(96)00101-X.
- Hurtado, L.A., R.A. Lutz, and R.C. Vrijenhoek. 2004. Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Molecular Ecology* 13:2,603–2,615, http:// dx.doi.org/10.1111/j.1365-294X.2004.02287.x.

- Kelemen, P.B., N. Shimizu, and V.J.M. Salters. 1995. Extraction of mid-ocean-ridge basalt from the upwelling mantle by focused flow of melt in dunite channels. *Nature* 375:747–753, http:// dx.doi.org/10.1038/375747a0.
- Kelley, D.S., S.M. Carbotte, D.W. Caress, D.A. Clague, J.R. Delaney, J.B. Gill, H. Hadaway, J.F. Holden, E.E.E. Hooft, J.P. Kellogg, and others. 2012. Endeavour Segment of the Juan de Fuca Ridge: One of the most remarkable places on Earth. *Oceanography* 25(1):44–61, http://dx.doi.org/10.5670/oceanog.2012.03.
- Kim, S.L., and L.S. Mullineaux. 1998. Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. *Deep-Sea Research Part II* 45:423–440, http://dx.doi.org/ 10.1016/S0967-0645(97)00042-8.
- Kent, G.M., A.J. Harding, and J.A. Orcutt. 1993.

  Distribution of magma beneath the East Pacific Rise between the Clipperton Transform and the 9°17'N deval from forward modeling of common depth point data. *Journal of Geophysical Research* 98:13,945–13,969, http://dx.doi.org/10.1029/93JB00705.
- Kurras, G.J., D.J. Fornari, M.H. Edwards,
  M.R. Perfit, and M.C. Smith. 2000. Volcanic morphology of the East Pacific Rise Crest 9°49′–52′N: Implications for volcanic emplacement processes at fast-spreading mid-ocean ridges.
  Marine Geophysical Research 21(1–2):23–41, http://dx.doi.org/10.1023/A:1004792202764.
- Langmuir, C.H., J.F. Bender, and R. Batiza. 1986. Petrological and tectonic segmentation of the East Pacific Rise, 5°30′–14°30′N. *Nature* 322:422–429, http://dx.doi.org/ 10.1038/322422a0.
- Lavelle, J.W., A.M. Thurnherr, J.R. Ledwell,
  D.J. McGillicuddy, and L.S. Mullineaux. 2010.
  Deep ocean circulation and transport where
  the East Pacific Rise at 9–10°N meets the
  Lamont seamount chain. *Journal of Geophysical Research* 115, C12073, http://dx.doi.org/
  10.1029/2010JC006426.
- Lavelle, J.W., A.M. Thurnherr, L.S. Mullineaux, D.J. McGillicuddy Jr., and J.R. Ledwell. 2012. The prediction, verification, and significance of flank jets at mid-ocean ridges. *Oceanography* 25(1):277–283, http://dx.doi. org/10.5670/oceanog.2012.26.
- Le Bris, N., B. Govenar, C. Le Gall, and C.R. Fisher. 2006. Variability of physio-chemical conditions in 9°50'N EPR diffuse flow vent habitats. *Marine Chemistry* 98:167–182, http://dx.doi. org/10.1016/j.marchem.2005.08.008.
- Lenihan, H.S., S.W. Mills, L.S. Mullineaux, C.H. Peterson, C.R. Fisher, and F. Micheli. 2008. Biotic interactions at hydrothermal vents: Recruitment inhibition by the mussel Bathymodiolus thermophilus. Deep Sea Research Part I 55:1,707–1,717, http://dx.doi.org/ 10.1016/j.dsr.2008.07.007.

- le Roux, P.J., S.B. Shirey, E.H. Hauri, M.R. Perfit, and J.F. Bender. 2006. The effects of variable sources, processes and contaminants on the composition of northern EPR MORB (8–10°N and 12–14°N): Evidence from volatiles (H<sub>2</sub>O, CO<sub>2</sub>, S) and halogens (F, Cl). *Earth and Planetary Science Letters* 251:209–231, http://dx.doi.org/10.1016/j.epsl.2006.09.012.
- Lilley, M.D., J.E. Lupton, D.A. Butterfield, and E. Olson. 2003. Magmatic events produce rapid changes in hydrothermal vent chemistry. *Nature* 422:878–881, http://dx.doi.org/10.1038/ nature01569.
- Liu, L., and R.P. Lowell. 2009. Models of hydrothermal heat output from a convecting, crystallizing, replenished magma chamber beneath an oceanic spreading center. *Journal of Geophysical Research* 114, B02102, http://dx.doi.org/ 10.1029/2008JB005846.
- Lonsdale, P. 1977. Abyssal pahoehoe with lava coils at the Galapagos rift. *Geology* 5:147–152, http://dx.doi.org/10.1130/0091-7613(1977)5 <147:APWLCA>2.0.CO;2.
- Lonsdale, P. 1983. Overlapping rift zones at the 5.5°S offset of the East Pacific Rise. *Journal of Geophysical Research* 88(B11):9,393–9,406, http://dx.doi.org/10.1029/JB088iB11p09393.
- Lonsdale, P. 1985. Nontransform offsets of the Pacific-Cocos plate boundary and their traces on the rise flank. *Geological Society of America Bulletin* 96(3):313–327, http://dx.doi.org/10.1130/0016-7606(1985)96<313: NOOTPP>2.0.CO;2.
- Lowell, R.P., and L.N. Germanovich. 1997.
  Evolution of a brine-saturated layer at the base of a ridge-crest hydrothermal system. *Journal of Geophysical Research* 102:10,245–10,255, http://dx.doi.org/10.1029/97JB00264.
- Lowell, R.P., and Y. Yao. 2002. Anhydrite precipitation and the extent of hydrothermal recharge zones at ocean ridge crests. *Journal of Geophysical Research* 107, 2183, http://dx.doi.org/10.1029/2001JB001289.
- Lundstrom, C.C., D.E. Sampson, M.R. Perfit, J. Gill, and Q. Williams. 1999. Insights into mid-ocean ridge basalt petrogenesis: U-series disequilibria from the Siqueiros Transform, Lamont Seamounts, and East Pacific Rise. *Journal of Geophysical Research* 104(B6):13,035–13,048, http://dx.doi.org/10.1029/1999JB900081.
- Luther, G.W. III, A. Gartman, M. Yücel,
  A.S. Madison, T.S. Moore, H.A. Nees,
  D.B. Nuzzio, A. Sen, R.A. Lutz, T.M. Shank,
  and C.R. Fisher. 2012. Chemistry, temperature, and faunal distributions at diffuseflow hydrothermal vents: Comparison of
  two geologically distinct ridge systems.

  Oceanography 25(1):234–245, http://dx.doi.
  org/10.5670/oceanog.2012.22.
- Luther, G.W. III, B.T. Glazer, S. Ma, R.E. Trouwborst, T.S. Moore, E. Metzger, C. Kraiya, T.J. Waite, G. Druschel, B. Sundby,

- and others. 2008. Use of voltammetric solidstate (micro) electrodes for studying biogeochemical processes: Laboratory measurements to real time measurements with an in situ electrochemical analyzer (ISEA). *Marine Chemistry* 108:221–235, http://dx.doi.org/10.1016/ j.marchem.2007.03.002.
- Luther, G.W. III, T. Rozan, M. Taillefert, D. Nuzzio, C. DiMeo, T.M. Shank, R.A. Lutz, and S.C. Cary. 2001. Chemical speciation drives hydrothermal vent ecology. *Nature* 410:813–815, http:// dx.doi.org/10.1038/35071069.
- Lutz, R.A., T.M. Shank, and R. Evans. 2001.
  Life after death in the deep sea. American
  Scientist 89(5):422–431, http://dx.doi.org/
  10.1511/2001.5.422.
- Lutz, R.A., T.M. Shank, D.J. Fornari, R.M. Haymon, M.D. Lilley, K.L. Von Damm, and D. Desbruyeres. 1994. Rapid growth at deep-sea vents. *Nature* 371:663–664, http:// dx.doi.org/10.1038/371663a0.
- Lutz, R.A., T.M. Shank, G.W. Luther III, C. Vetriani, M. Tolstoy, D.B. Nuzzio, T.S. Moore, F. Waldhauser, M. Crespo-Medina, A. Chatziefthimou, and others. 2008. Interrelationships between vent fluid chemistry, temperature, seismic activity and biological community structure at a mussel-dominated, deep-sea hydrothermal vent along the East Pacific Rise. *Journal of Shellfish Research* 27:177–190, http://dx.doi.org/10.2983/0730-8000(2008)27 [177:IBVFCT]2.0.CO;2.
- Macdonald, K.C., and P.J. Fox. 1983. Overlapping spreading centers: New accretion geometry on the East Pacific Rise. *Nature* 302:55–58, http://dx.doi.org/10.1038/302055a0.
- Macdonald, K.C., and P.J. Fox. 1988. The axial summit graben and cross-sectional shape of the East Pacific Rise as indicators of axial magma chambers and recent volcanic eruptions. *Earth and Planetary Science Letters* 88:119–131, http://dx.doi.org/10.1016/0012-821X(88)90051-9.
- Macdonald, K.C., P.J. Fox, S. Miller, S. Carbotte,
  M.H. Edwards, M. Eisen, D.J. Fornari,
  L. Perram, R. Pockalny, D. Scheirer, and others.
  1992. The East Pacific Rise and its flanks
  8–18°N: History of segmentation, propagation and spreading direction based on SeaMARC II and Sea Beam studies. *Marine Geophysical Research* 14:299–344, http://dx.doi.org/10.1007/BF01203621.
- McCollom, T.M. 2000. Geochemical constraints on primary productivity in submarine hydrothermal vent plumes. *Deep-Sea Research Part I* 47:85–101, http://dx.doi.org/10.1016/ S0967-0637(99)00048-5.
- McGillicuddy, D.J. Jr., W. Lavelle, A.M. Thurnherr, V.K. Kosnyrev, and L.S. Mullineaux. 2010. Larval dispersion along an axially symmetric

- mid-ocean ridge. *Deep Sea Research*Part I 57:880–892, http://dx.doi.org/10.1016/
  j.dsr.2010.04.003.
- Menard, H.W. 1960. The East Pacific Rise. *Science* 132:1,737–1,742, http://dx.doi.org/ 10.1126/science.132.3441.1737.
- Menard, H.W. 1964. *Marine Geology of the Pacific*. International Series in the Earth Sciences, McGraw Hill, 271 pp.
- Micheli, F., C.H. Peterson, L.S. Mullineaux, C. Fisher, S.W. Mills, G. Sancho, G.A. Johnson, and H.S. Lenihan. 2002. Predation structures communities at deep-sea hydrothermal vents. *Ecological Monographs* 72:365–382, http://dx.doi.org/10.1890/0012-9615 (2002)072[0365:PSCADS]2.0.CO;2.
- Moore, T.S., T.M. Shank, D.B. Nuzzio, and G.W. Luther III. 2009. Time-series chemical and temperature habitat characterization of diffuse flow hydrothermal sites at 9°50'N East Pacific Rise. *Deep Sea Research Part II* 56:1,616–1,621. http://dx.doi.org/10.1016/j.dsr2.2009.05.008.
- Mullineaux L.S., D.K. Adams, S.W. Mills, and S.E. Beaulieu. 2010. Larvae from afar colonize deep-sea hydrothermal vents after a catastrophic eruption. *Proceedings of the National Academy of Sciences of the United States of America* 107:7,829–7,834, http://dx.doi.org/10.1073/pnas.0913187107.
- Mullineaux, L.S., C.R. Fisher, C.H. Peterson, and S.W. Schaeffer. 2000. Vestimentiferan tubeworm succession at hydrothermal vents: Use of biogenic cues to reduce habitat selection error. *Oecologia* 123:275–284.
- Mullineaux, L.S., S.W. Mills, and E. Goldman. 1998. Recruitment variation during a pilot colonization study of hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research Part II* 45:441–464, http://dx.doi.org/10.1016/ S0967-0645(97)00045-3.
- Mullineaux, L.S., S.W. Mills, A.K. Sweetman, A.H. Beaudreau, A. Metaxas, and H.L. Hunt. 2005. Vertical, lateral and temporal structure in larval distributions at hydrothermal vents. *Marine Ecology Progress Series* 293:1–16, http://dx.doi.org/10.3354/meps293001.
- Mullineaux, L.S., C.H. Peterson, F. Micheli, and S.W. Mills. 2003. Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. *Ecological Monographs* 73:523–542, http://dx.doi.org/ 10.1890/02-0674.
- Murray, J., and A.F. Renard. 1891. Deep-sea deposits. *Report of the* Challenger *Expedition*. London.
- Nees, H.A., R.A. Lutz, T.M. Shank, and G.W. Luther III. 2009. Pre- and post-eruption diffuse flow variability among tubeworm habitats at 9°50' north on the East Pacific Rise. Deep Sea Research II 56:1,607–1,615, http://dx.doi.org/10.1016/j.dsr2.2009.05.007.

- Nees, H.A., T. Moore, K.M. Mullaugh, R.R. Holyoke, C.P. Jansen, S. Ma, E. Metzger, T.J. Waite, M. Yucel, R.A. Lutz, and others. 2008. Hydrothermal vent mussel habitat chemistry, pre- and post-eruption at 9°50' North on the East Pacific Rise. *Journal of Shellfish Research* 27(1):169–176, http://dx.doi.org/10.2983/0730-8000(2008)27[169:HVMHCP]2.0.CO;2.
- Nelson, D., R.M. Haymon, M. Lilley, and R. Lutz. 1991. Rapid growth of unusual hydrothermal bacteria observed at new vents during the ADVENTURE Dive Program to the EPR Crest at 9°45′–52′N. Eos, Transactions, American Geophysical Union 72:481.
- Neubert, M., L.S. Mullineaux, and M.F. Hill. 2006. A metapopulation approach to interpreting diversity at deep-sea hydrothermal vents. Pp. 321–350 in *Marine Metapopulations*. J. Kritzer and P. Sale, eds, Elsevier Academic Press.
- Oosting, S.E., and K.L. Von Damm. 1996. Bromide/ chloride fractionation in seafloor hydrothermal fluids from 9–10°N East Pacific Rise. *Earth and Planetary Science Letters* 144:133–145, http:// dx.doi.org/10.1016/0012-821X(96)00149-5.
- Orcutt, J.A., B.L.N. Kennett, and L.M. Dorman. 1976. Structure of the East Pacific Rise from an ocean bottom seismometer survey. *Geophysical Journal of the Royal Astronomical Society* 45:305–320, http://dx.doi.org/10.1111/j.1365-246X.1976.tb00328.x.
- Perfit, M.R., J.R. Cann, D.J. Fornari, D.K. Smith, W.I. Ridley, J. Engels, and M.E. Edwards. 2003. Interaction of seawater and lava during submarine eruptions at mid-ocean ridges. *Nature* 426:62–64, http://dx.doi.org/10.1038/ nature02032.
- Perfit, M.R., and W.W. Chadwick Jr. 1998.
  Magmatism at mid-ocean ridges: Constraints from volcanological and geochemical investigations. Pp. 59–115 in Faulting and Magmatism at Mid-Ocean Ridges. W.R. Buck, P. Delaney, and J.A. Karson, eds, Geophysical Monograph Series, vol. 92, American Geophysical Union, Washington, DC.
- Perfit, M.R., D.J. Fornari, M.C. Smith, J.F. Bender, C.H. Langmuir, and R.M. Haymon. 1994. Small-scale spatial and temporal variations in mid-ocean ridge crest magmatic processes. *Geology* 22:375–379, http://dx.doi.org/10.1130/0091-7613(1994)022 <0375:SSSATV>2.3.CO;2.
- Perfit, M.R., V.D. Wanless, W.I. Ridley, E.M. Klein, M.C. Smith, A.R. Goss, J.S. Hinds, S.W. Kutza, and D.J. Fornari. 2012. Lava geochemistry as a probe into crustal formation at the East Pacific Rise. *Oceanography* 25(1):89–93, http://dx.doi.org/10.5670/oceanog.2012.06.
- Plouviez, S., D. Le Guen, O. Lecompte, F.H. Lallier, and D. Jollivet. 2010. Determining gene flow and the influence of selection across the equatorial barrier of the East Pacific Rise in the

- tube-dwelling polychaete *Alvinella pompejana*. *BMC Evolutionary Biology* 10:220, http://dx.doi. org/10.1186/1471-2148-10-220.
- Pockalny, R.A., P.J. Fox, D.J. Fornari, K.C. Macdonald, and M.R. Perfit. 1997. Tectonic reconstruction of the Clipperton and Siqueiros Fracture Zones: Evidence and consequences of plate motion change for the last 3 Myr. *Journal of Geophysical Research* 102:3,167–3,181, http://dx.doi.org/ 10.1029/96JB03391.
- Reynolds, J.R., C.H. Langmuir, J.F. Bender, K.A. Kastens, and W.B.F. Ryan. 1992. Spatial and temporal variability in the geochemistry of basalts from the East Pacific Rise. *Nature* 359:493–499, http://dx.doi.org/ 10.1038/359493a0.
- Ridley, W.I., M.R. Perfit, D.J. Fornari, and M. Smith. 2006. Magmatic processes in developing oceanic crust revealed in a cumulate xenolith collected at the East Pacific Rise, 9°50'N. Geochemistry Geophysics Geosystems 7, Q12O04, http://dx.doi.org/ 10.1029/2006GC001316.
- RISE Project Group. 1980. East Pacific Rise: Hot springs and geophysical experiments. Science 207:1,421–1,433, http://dx.doi.org/ 10.1126/science.207.4438.1421.
- Rouxel, O., W.C. Shanks, W. Bach, and K.J. Edwards. 2008. Integrated Fe- and S-isotope study of seafloor hydrothermal vents at East Pacific rise 9–10°N. *Chemical Geology* 252:214–227, http://dx.doi.org/ 10.1016/j.chemgeo.2008.03.009.
- Rubin, K.H., and D.J. Fornari, 2011.
  Multidisciplinary collaborations in mid-ocean ridge research. Eos, Transactions, American Geophysical Union 92(17):141, http://dx.doi.org/10.1029/2011EO170002.
- Rubin, K.H., J.D. Macdougall, and M.R. Perfit. 1994. <sup>210</sup>Po/<sup>210</sup>Pb dating of recent volcanic eruptions on the sea floor. *Nature* 368:841–844, http://dx.doi.org/10.1038/368841a0.
- Rubin, K.H., S.A. Soule, W.W. Chadwick Jr.,
  D.J. Fornari, D.A. Clague, R.W. Embley,
  E.T. Baker, M.R. Perfit, D.W. Caress, and
  R.P. Dziak. 2012. Volcanic eruptions in the deep
  sea. *Oceanography* 25(1):142–157, http://dx.doi.
  org/10.5670/oceanog.2012.12.
- Rubin, K.H., M. Tolstoy, D.J. Fornari, R.P. Dziak, S.A. Soule, F. Waldhauser, and K.L. Von Damm, 2008. Integrating radiometric, geophysical and thermal signals of volcanic unrest and eruption in 2005–06 at 9°50'N EPR. Eos, Transactions, American Geophysical Union 89(53):Fall Meeting Supplement Abstract B23F-07.
- Rubin, K.H., I. van der Zander, M.C. Smith, and E.C. Bergmanis. 2005. Minimum speed limit for ocean ridge magmatism from <sup>210</sup>Pb-<sup>226</sup>Ra-<sup>230</sup>Th disequilibria. *Nature* 437:534–538, http:// dx.doi.org/10.1038/nature03993.

- Sancho, G., C.R. Fisher, S. Mills, F. Micheli, G.A. Johnson, H.S. Lenihan, C.H. Peterson, and L.S. Mullineaux. 2005. Selective predation by the zoarcid fish *Thermarces cerberus* at hydrothermal vents. *Deep-Sea Research Part I* 52:837–844, http://dx.doi.org/10.1016/ j.dsr.2004.12.002.
- Scheirer, D.S., T.M. Shank, and D.J. Fornari. 2006. Temperature variations at diffuse and focused flow hydrothermal vent sites along the northern East Pacific Rise. *Geochemistry Geophysics Geosystems* 7, Q03002, http:// dx.doi.org/10.1029/2005GC001094.
- Schouten, H., M.A. Tivey, D.J. Fornari, and J.R. Cochran. 1999. Central anomaly magnetization high: Constraints on the volcanic construction and architecture of seismic Layer 2A at a fast-spreading mid-ocean ridge, the EPR at 9°30'–50'N. Earth and Planetary Science Letters 169:37–50, http://dx.doi.org/10.1016/S0012-821X(99)00063-1.
- Shank, T.M., D.J. Fornari, K.L. Von Damm, M.D. Lilley, R.M. Haymon, and R.A. Lutz. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents along the East Pacific Rise. *Deep Sea Research Part II* 45:465–515, http:// dx.doi.org/10.1016/S0967-0645(97)00089-1.
- Shank, T.M., B. Govenar, K. Buckman, D.J. Fornari,
  S.A. Soule, G.W. Luther III, R.A. Lutz,
  C. Vetriani, M. Tolstoy, K.H. Rubin, and others.
  2006. Initial biological, chemical, and geological observations after the 2005–6 volcanic eruption on the East Pacific Rise. *Eos, Transactions, American Geophysical Union* 87(52): Fall
  Meeting Supplement Abstract V13C-04.
- Shank, T.M., and K.M. Halanych. 2007. Toward a mechanistic understanding of larval dispersal: Insights from genomic fingerprinting of deep-sea hydrothermal vent populations. *Marine Ecology* 28:25–35, http://dx.doi. org/10.1111/j.1439-0485.2007.00146.x.
- Sievert, S.M., and C. Vetriani. 2012. Chemoautotrophy at deep-sea vents: Past, present, and future. *Oceanography* 25(1):218–233, http://dx.doi. org/10.5670/oceanog.2012.21.
- Soule, S.A., J. Escartín, and D.J. Fornari. 2009.

  A record of eruption and intrusion at a fast-spreading ridge axis: Axial summit trough of the East Pacific Rise at 9°–10°N. *Geochemistry Geophysics Geosystems* 10, Q10T07, http://dx.doi.org/10.1029/2008GC002354.
- Soule, S.A., D.J. Fornari, M.R. Perfit, W.I. Ridley, M.H. Reed, and J.R. Cann. 2006. Incorporation of seawater into mid-ocean ridge lavas during emplacement. *Earth and Planetary Science Letters* 252:289–307, http://dx.doi.org/10.1016/ j.epsl.2006.09.043.
- Soule, S.A., D.J. Fornari, M.P. Perfit, and K. Rubin. 2007. New insights into mid-ocean ridge volcanic processes from the 2005-06

- eruption of the East Pacific Rise, 9°46'-56'N. *Geology* 35:1,079–1,082, http://dx.doi.org/10.1130/G23924A.1.
- Soule, S.A., D.J. Fornari, M.R. Perfit, M.A. Tivey, W.I. Ridley, and H. Schouten. 2005.

  Channelized lava flows at the East Pacific Rise crest 9°–10°N: The importance of off axis lava transport in developing the architecture of young oceanic crust. *Geochemistry Geophysics Geosystems* 6, Q08005, http://dx.doi.org/10.1029/2005GC000912.
- Sohn, R.A., D.J. Fornari, K.L. Von Damm, J.A. Hildebrand, and S.C. Webb. 1998. Seismic and hydrothermal evidence for a cracking event on the East Pacific Rise crest at 9°50'N. *Nature* 396:159–161, http:// dx.doi.org/10.1038/24146.
- Sohn, R.A., J.A. Hildebrand, and S.C. Webb. 1999. A microearthquake survey of the hightemperature vent fields on the volcanically active East Pacific Rise (9°50'N). *Journal of Geophysical Research* 104:25,367–25,377, http:// dx.doi.org/10.1029/1999JB900263.
- Spiess, F., K.C. Macdonald, T. Atwater, R. Ballard, A. Carranza, D. Cordoba, C. Cox, V.M. Diaz Garcia, J. Francheteau, J. Guerrero, and others. 1980. East Pacific Rise: Hot springs and geophysical experiments. *Science* 207:1,421–1,433, http://dx.doi.org/ 10.1126/science.207.4438.1421.
- Stroup, D., D.R. Bohnenstiehl, M. Tolstoy, F. Waldhauser, and R.T. Weekly. 2007. The pulse of the seafloor: Tidal triggering of microearthquakes at 9°50'N East Pacific Rise. *Geophysical Research Letters* 34, L15301, http://dx.doi.org/ 10.1029/2007GL030088.
- Stroup, D., M. Tolstoy, T.J. Crone, A. Malinverno, D.R. Bohnenstiehl, and F. Waldhauser. 2009. Systematic along-axis tidal triggering of microearthquakes constrains crustal permeability. *Geophysical Research Letters* 36, L18302, http:// dx.doi.org/10.1029/2009GL039493.
- Thurnherr, A.M., J.R. Ledwell, J.W. Lavelle, and L.S. Mullineaux. 2011. Hydrography and circulation near the crest of the East Pacific Rise between 9° and 10° N. *Deep-Sea Research Part I* 58:365–376, http://dx.doi.org/10.1016/j.dsr.2011.01.009.
- Thurnherr, A.M., and L.C. St. Laurent. 2012. Turbulence observations in a buoyant hydrothermal plume on the East Pacific Rise. *Oceanography* 25(1):180–181, http://dx.doi. org/10.5670/oceanog.2012.15.
- Tivey, M.K., E. Becker, R. Beinart, C.R. Fisher, P.R. Girguis, C.H. Langmuir, P.J. Michael, and A.-L. Reysenbach. 2012. Links from mantle to microbe at the Lau Integrated Study Site: Insights from a back-arc spreading center. *Oceanography* 25(1):62–77, http://dx.doi. org/10.5670/oceanog.2012.04.

- Tolstoy, M., J.P. Cowen, E.T. Baker, D.J. Fornari, K.H. Rubin, T.M. Shank, F. Waldhauser, D.R. Bohnenstiehl, D.W. Forsyth, R.C. Holmes, and others. 2006. A sea-floor spreading event captured by seismometers. *Science* 314:1,920–1,922, http://dx.doi.org/10.1126/science.1133950.
- Tolstoy, M., F.L. Vernon, J.A. Orcutt, and F.K. Wyatt. 2002. The breathing of the seafloor: Tidal correlations of seismicity on Axial volcano. *Geology* 30:503–506, http://dx.doi.org/10.1130/0091-7613(2002) 030<0503:BOTSTC>2.0.CO;2.
- Tolstoy, M., F. Waldhauser, D.R. Bohnenstiehl, R.T. Weekly, and W.Y. Kim. 2008. Seismic identification of along-axis hydrothermal flow on the East Pacific Rise. *Nature* 451:181–187, http://dx.doi.org/10.1038/nature06424.
- Toner, B.M., S.C. Fakra, S.J. Manganini, C.M. Santelli, M.A. Marcus, J. Moffett, O. Rouxel, C.R. German, and K.J. Edwards. 2009. Preservation of iron(II) by carbon-rich matrices in a hydrothermal plume. *Nature Geosciences* 2:197–201, http://dx.doi.org/ 10.1038/ngeo433.
- Toomey, D.R., S.C. Solomon, and G.M. Purdy. 1994. Tomographic imaging of the shallow crustal structure of the East Pacific Rise at 9°30'N. *Journal of Geophysical Research* 99:24,135–24,157, http://dx.doi.org/10.1029/94JB01942.
- Turnipseed, M., K. Knick, R. Lipcius, J. Dreyer, and C.L. Van Dover. 2003. Diversity in mussel beds at deep-sea hydrothermal vents and cold seeps. *Ecology Letters* 6:518–523, http://dx.doi.org/10.1046/j.1461-0248.2003.00465.x.
- Van Dover, C.L. 2003. Variation in community structure within hydrothermal vent mussel beds of the East Pacific Rise. *Marine Ecology Progress Series* 253:55–66, http://dx.doi.org/10.3354/ meps253055.
- Van Dover, C.L., and R.A. Lutz. 2004. Experimental ecology at deep-sea hydrothermal vents:

  A perspective. *Journal of Experimental Marine Biology and Ecology* 300:273–307, http://dx.doi.org/10.1016/j.jembe.2003.12.024.
- Vera, E.E., J.C. Mutter, P. Buhl, J.A. Orcutt, A.J. Harding, M.E. Kappus, R.S. Detrick, and T. Brocher. 1990. The structure of 0- to 0.2-m.y.old oceanic crust at 9°N on the East Pacific Rise from expanded spread profiles. *Journal of Geophysical Research* 95:15,529–15,556, http:// dx.doi.org/10.1029/JB095iB10p15529.
- Vetriani, C., Y.S. Chew, S.M. Miller, J. Yagi, J. Coombs, R.A. Lutz, and T. Barkay. 2004b. Mercury adaptation among bacteria from a deep-sea hydrothermal vent. *Applied and Environmental Microbiology* 71:220–226, http:// dx.doi.org/10.1128/AEM.71.1.220-226.2005.
- Vetriani, C., M.D. Speck, S.V. Ellor, R.A. Lutz, and V. Starovoytov. 2004a. *Thermovibrio ammonificans* sp. nov., a thermophilic, chemolithotrophic, nitrate ammonifying bacterium from

- deep-sea hydrothermal vents. *International Journal of Systematic and Evolutionary Microbiology* 54:175–181, http://dx.doi.org/10.1099/ijs.0.02781-0.
- Von Damm, K.L. 1995. Controls on the chemistry and temporal variability of seafloor hydrothermal fluids. Pp. 222–248 in Seafloor Hydrothermal Systems:

  Physical, Chemical, Biologic and Geologic Interactions. S.E. Humphris, R.A. Zierenberg, L.S. Mullineaux, and R.E. Thompson, eds, Geophysical Monograph Series, vol. 91, American Geophysical Union, Washington, DC.
- Von Damm, K.L. 2000. Chemistry of hydrothermal vent fluids from 9°–10° N, East Pacific Rise: "Time zero," the immediate posteruptive period. *Journal of Geophysical Research* 105:11,203–11,222, http://dx.doi.org/10.1029/1999JB900414.
- Von Damm, K.L. 2004. Evolution of the hydrothermal system at East Pacific Rise 9°50'N: Geochemical evidence for changes in the upper oceanic crust. Pp. 285–305 in *Hydrothermal Interactions Between the Lithosphere and Oceans*. C.R. German, J. Lin, and L.M. Parson, eds, Geophysical Monograph Series, vol. 148, American Geophysical Union, Washington, DC.
- Von Damm, K.L., J.L. Bischoff, and R.J. Rosenbauer. 1991. Quartz solubility in hydrothermal seawater: An experimental study and equation describing quartz solubility for up to 0.5 M NaCl solutions. *American Journal of Science* 291:977–1,007, http:// dx.doi.org/10.2475/ajs.291.10.977.
- Von Damm, K.L., and M.D. Lilley. 2004. Diffuse flow hydrothermal fluids from 9°50'N East Pacific Rise: Origin, evolution, and biogeochemical controls. Pp. 245–268 in The Subseafloor Biosphere at Mid-Ocean Ridges. W.S. Wilcock, E.F. DeLong, D.S. Kelley, J.A. Baross, and S.C. Cary, eds, Geophysical Monograph Series, vol. 144, American Geophysical Union, Washington, DC.
- Von Damm, K.L., M. Lilley, W.C. Shanks, M. Brockington, A. Bray, K.M. O'Grady, E. Olson, A. Graham, and G. Proskurowski. 2003. Extraordinary phase separation and segregation in vent fluids from the southern East Pacific Rise. Earth and Planetary Science Letters 206:365–378, http://dx.doi.org/10.1016/ S0012-821X(02)01081-6.
- Vrijenhoek, R.C. 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19:4,391–4,411, http://dx.doi.org/10.1111/j.1365-294X.2010.04789.x.
- Waldhauser, F., and M. Tolstoy. 2011. Seismogenic structure and processes associated with magma upwelling and hydrothermal circulation beneath the East Pacific Rise at 9°50'N. *Geochemistry Geophysics Geosystems* 2, Q08T10, http://dx.doi.org/10.1029/2011GC003568.

- White, S.M., R. Haymon, and S.M. Carbotte. 2006. A new view of ridge segmentation and near-axis volcanism at the East Pacific Rise, 8°–12°N, from EM300 multibeam bathymetry. *Geochemistry Geophysics Geosystems* 7, Q12O05, http://dx.doi.org/10.1029/2006GC001407.
- White, S.M., R.H. Haymon, D.J. Fornari, M.R. Perfit, and K.C. Macdonald. 2002. Correlation between volcanic and tectonic segmentation of fast-spreading ridges: Evidence from volcanic structures and lava flow morphology on the East Pacific Rise at 9°–10°N. *Journal of Geophysical Research* 107(B8), 2173, http://dx.doi.org/10.1029/2001JB000571.
- Wilcock, W.S.D. 2001. Tidal triggering of microearthquakes on the Juan de Fuca Ridge. *Geophysical Research Letters* 28:3,999–4,002, http://dx.doi.org/10.1029/2001GL013370.
- Wilcock, W.S. 2004. Physical response of mid-ocean ridge hydrothermal systems to local earthquakes. *Geochemistry Geophysics Geosystems* 5, Q11009, http://dx.doi.org/ 10.1029/2004GC000701.
- Wilcock, W.S.D., E.E.E. Hooft, D.R. Toomey, P.R. McGill, A.H. Barclay, D.S. Stakes, and T.M. Ramirez. 2009. The role of magma injection in localizing black-smoker activity. *Nature Geoscience* 2:509–513, http://dx.doi.org/10.1038/ngeo550.
- Wilcock, W.S.D., S.C. Solomon, G.M. Purdy, and D.R. Toomey. 1995. Seismic attenuation structure of the East Pacific Rise near 9°30'N. *Journal of Geophysical Research* 100(B12):24,147–24,165, http://dx.doi.org/10.1029/95JB02280.
- Williams, C., M.A. Tivey, H. Schouten, and D.J. Fornari. 2008. Central anomaly magnetization high documentation of crustal accretion along the East Pacific Rise (9°55'–9°25'N). Geochemistry Geophysics Geosystems 9, Q04015, http://dx.doi.org/10.1029/2007GC001611.
- Wirsen, C.O., J.H. Tuttle, and H.W. Jannasch. 1986. Activities of sulfur-oxidizing bacteria at the 21°N East Pacific Rise vent site. *Marine Biology* 92:449–456, http://dx.doi.org/10.1007/ BF00392504.
- Won, Y., C.R. Young, R.A. Lutz, and R.C. Vrijenhoek. 2003. Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiolus*) from eastern Pacific hydrothermal vents. *Molecular Ecology* 12:169–184, http://dx.doi.org/10.1046/j.1365-294X.2003.01726.x.
- Wright, D.J., R.M. Haymon, and D.J. Fornari. 1995. Crustal fissuring and its relationship to magmatic and hydrothermal processes on the East Pacific Rise crest (9°12' to 54'N). *Journal of Geophysical Research* 100:6,097–6,120, http:// dx.doi.org/10.1029/94JB02876.