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however, only a fraction of image sequences with exposure times optimized for observation at 5.0 μm were obtained at high spatial resolution for the polar region.

26. The local time coordinate, which is cyclical, has been linearized by adding 24 hours whenever a cycle was completed (for example, the sequence [-5, 10, -1, -8] turns into [-5, 10, 23, 40]).

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Surface-Generated Mesoscale Eddies Transport Deep-Sea Products from Hydrothermal Vents

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Atmospheric forcing, which is known to have a strong influence on surface ocean dynamics and production, is typically not considered in studies of the deep sea. Our observations and models demonstrate an unexpected influence of surface-generated mesoscale eddies in the transport of hydrothermal vent efflux and of vent larvae away from the northern East Pacific Rise. Transport by these deep-reaching eddies provides a mechanism for spreading the hydrothermal chemical and heat flux into the deep-ocean interior and for dispersing propagules hundreds of kilometers between isolated and ephemeral communities. Because the eddies interacting with the East Pacific Rise are formed seasonally and are sensitive to phenomena such as El Niño, they have the potential to introduce seasonal to interannual atmospheric variations into the deep sea.

Hydrothermal vents are hot spots for geological, geochemical, and biological activity that alter the global oceanic heat and chemical budgets (1, 2) and support unique chemosynthetic communities (3, 4). The disjoint distribution and transient nature of vents pose challenges for exporting vent-derived heat and chemicals into the global ocean and transporting propagules between distant vent fields. On short time scales, vent-derived products can remain close to the ridge axis. Chemical tracers can be used to locate hydrothermal vents (5), and larval supply to established vents is predominantly from local sources (6, 7). However, larvae and much of the seawater chemically altered at vents are eventually transported to distant locales. Hydrothermal seawater alterations contribute to the removal and addition of major chemical constituents (1), such as Ca and Mg, as well as trace metals, such as Fe (8, 9) which may affect local and global biogeochemical cycling (10–12). Vent larvae must, at least episodically, undergo long-distance dispersal to maintain observations of

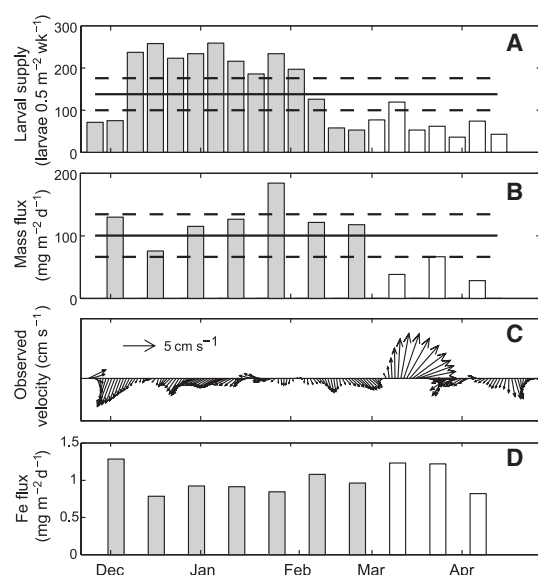
high gene flow (13, 14) and rapid colonization of disturbed and nascent vents (7, 15). Ridge-trapped jets (16, 17) and hydrothermally induced flows (18) have the potential to transport material near the ridge. Yet after decades of research at hydrothermal vents, the mechanisms by which heat, chemicals, and larvae are transported throughout the global ocean and between distant vent fields remain poorly resolved.

To investigate mechanisms that transport vent fluids and larvae, we performed time-series observations of hydrodynamics and larval, chemical, and mass fluxes in the 9°50' N area of the

East Pacific Rise (EPR) (fig. S1). Dramatic decreases in the larval supply of vent gastropods (Fig. 1A and figs. S2 and S3) and in mass flux associated with settling particles (Fig. 1B) were observed near the end of the time series and corresponded to a period of anomalous current velocities. Current velocities both on-axis (Fig. 1C and fig. S4, A and B) and off-axis (fig. S4C) reached speeds exceeding 15 cm s^{-1} during the anomaly, compared with the mean speed of 5.5 cm s^{-1} (at 170 m above bottom). Using a permutation test, larval and mass fluxes were significantly lower than expected post-anomaly (during and after the velocity anomaly): $P = 0.0007$ and $P = 0.008$, respectively. The biological and geochemical changes appear to have been driven by anomalous low-frequency currents (Fig. 1C) because the magnitude of high-frequency motions was relatively stable during this time (fig. S5).

The concurrent decreases (19) in larval supply and mass flux were most likely due to hydrodynamic transport away from the ridge rather than changes in source production. Both larval supply and mass flux are derived from independent pools built up over time, so changes in production would be observed as dampened or lagged changes in flux. Additionally, it is unlikely that mass flux sources and multiple species' reproduction changed concurrently. Hydrothermal vent gastropods typically exhibit continuous or quasi-continuous reproduction (20, 21) with pre-competency periods. Therefore, we assume our samples come from a continuously produced larval pool that integrates reproductive output over time.

Fig. 1. Observations at the EPR ridge crest, East Wall. (A) Supply of vent gastropod larvae and (B) mass flux. Solid line indicates the mean flux. Dashed lines indicate the 95% confidence interval (CI). (C) Current velocities recorded at 170 m above bottom (2350 m depth). Shown are the strong currents and rapid changes in direction in March 2005. (D) Variability of Fe flux over the time series. Solid bars indicate samples analyzed as before (pre-) the current anomaly. Open bars indicate samples during or after (post-) the current anomaly.



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In close proximity to vents that are distant from continents, mass flux is typically dominated by mineral particulates settling from the neutrally buoyant plume supplied by high-temperature “black-smoker” venting and the biogenic fluxes from adjacent chemosynthetic communities associated with low-temperature hydrothermal flow [supporting online material (SOM) text includes detailed geochemical analysis of the mass flux] (22, 23). Consistent temperatures and chemistry of vent fluids in November 2004 and April 2005 (24, 25) indicate that changes in high-temperature and low-temperature hydrothermal flow cannot account for the decreases in mass flux at the end of the time series. Instead, we suggest that the hydrodynamic event displaced the resident water

mass with its accumulated biogenic and mineral particulates, resulting in decreased mass flux. Although a reduction in mineral particulates from high-temperature venting [for example, Fe, Cu, and Zn (Fig. 1D and table S1)] was not observed during the hydrodynamic event, this does not necessarily imply that minerals and vent-altered seawater were not transported. Rapid production by vigorous venting, followed by prompt precipitation through quenching by cold, oxygenated bottom water, could replenish transported material over time scales that are short as compared with our sampling interval, thus masking any changes attributable to transport in the observed metal fluxes. Production of biogenic material from low-temperature vent communities would be mark-

edly slower so that displacement by the hydrodynamic event would be followed by delayed reestablishment of pre-anomaly fluxes. Thus, the observed variation in mass flux (Fig. 1B) and elemental fluxes (Fig. 1D and table S1) was probably due to transport of vent-derived mineral and biogenic material followed by swift replenishment of minerals by high-temperature venting but slower replenishment of the biogenic material.

The rapid changes in direction and coherence between current meters (Fig. 1C and fig. S4) separated by a few kilometers (fig. S1) are consistent with the inference that the hydrodynamic event observed on the ridge was due to the passage of a mesoscale feature. Daily objective analysis of satellite-observed sea-level anomalies revealed multiple eddies, including a ~375-km-diameter anticyclone originating in the Gulf of Tehuantepec in September 2004 that crossed the study site from February to March 2005 (Fig. 2 and movie S1), just before the anomalous bottom current velocities were significantly negatively correlated with the inferred geostrophic flows associated with the eddy (Pearson correlation for the full 5-month record, $R_u = -0.20$, $P_u = 0.010$; $R_v = -0.21$, $P_v = 0.0073$). Given the potential for offset between the surface and deep flows and deformation and delay due to the ridge (26), we also allowed for a lag between the geostrophic (Fig. 2A) and near-bottom velocities (Fig. 1C), which improved the meridional correlation to $R_v = -0.57$ and $P_v < 0.0001$, with an 8-day lag. Although we cannot rule out the possibility of a jet on the ridge flanks sweeping across the site (16), the significant correlations between the observed deep currents and the surface geostrophic currents suggest a relationship between the anomalous current velocities at depth and the passage of the anticyclonic eddy.

Simulations with the $1/12^\circ$ HYCOM ocean model (27) also showed intensified bottom current velocities associated with the passage of anticyclones at the end of the observational time series. As eddies formed off the coast of Central America and propagated westward, bottom-current velocities developed from weak, incoherent flows at the beginning of 2005 into coherent features with increased velocities by February (Fig. 3 and movie S2) and extending through the end of the time series. Simulated currents near the ridge and at the surface (fig. S6) were significantly correlated over 90 days ($R_u = 0.33$, $P_u = 0.0015$; $R_v = -0.54$, $P_v < 0.0001$). Including a lag further improved the meridional correlation [$R_v = -0.62$, $P_v < 0.0001$ (lagged 5 days)]. The strength of the cross-correlations and lag for the simulated currents are roughly consistent with those for our observations. Cross-correlations between near-bottom observed and simulated velocities from January through March 2005 were significant for the meridional component ($R_v = 0.51$, $P_v < 0.0001$) (fig. S6) but not for the zonal component ($R_u = 0.16$, $P_u = 0.14$). Eddy-associated meridional flows may have been intensified along the north-south trending

Fig. 2. Surface and deep expression of a mesoscale eddy. **(A)** Inferred geostrophic velocities at the surface and the associated time series of sea-level anomalies (SLAs) from November 2004 to May 2005. Two eddies pass during this time period: one in February to March during the period of bottom observations and a second from the end of April to May, just after the period of near-bottom observations. **(B)** Map of SLA on 21 February 2005 when an anticyclonic eddy made impact with the study site (white star). The track of the center of the eddy from birth on 10 September 2004 until exit from the study region on 1 May 2005, marked every 4 weeks (black circles), is superimposed on the map.

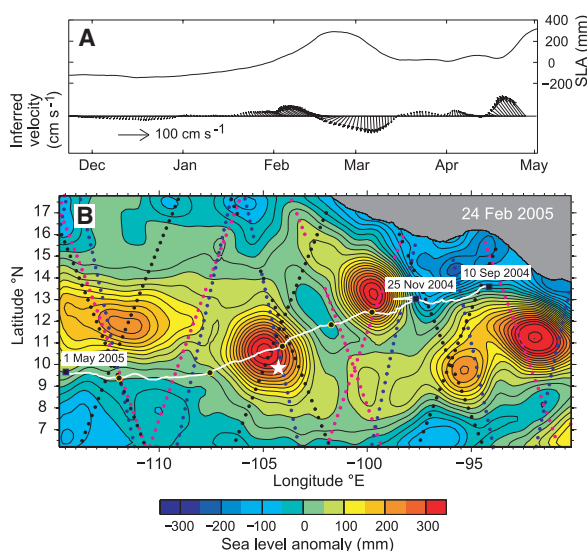
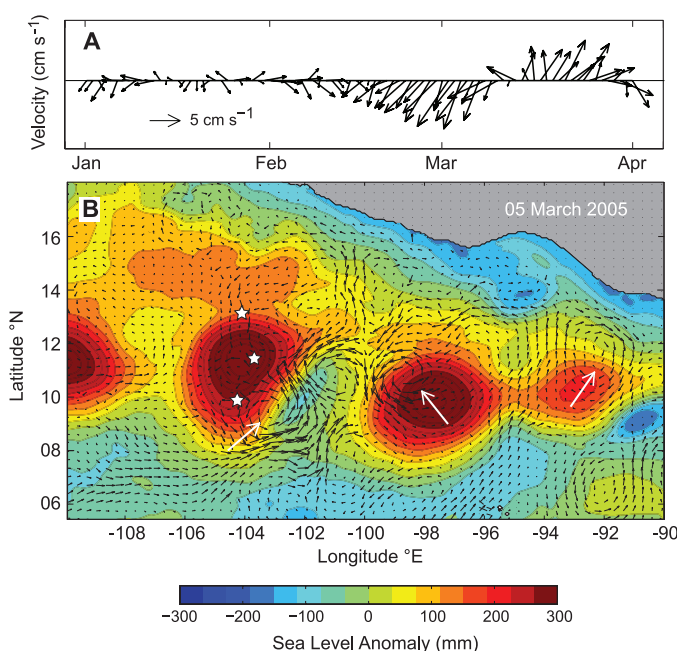


Fig. 3. HYCOM model simulation of anticyclone-induced current velocities at depth. **(A)** Simulated bottom currents at East Wall at 2350 m depth from January to April 2005. **(B)** Simulated sea-surface height variations for 5 March 2005 (color shading) consistent with assimilated satellite observations of a Tehuantepec eddy over hydrothermal vent fields (white stars), including our study site (southern-most white star). The model also predicts intensified and coherent near-bottom currents (black arrows) associated with the eddy field. For clarity, every fourth vector is plotted. The induced near-bottom currents are complex but often include deep cyclones associated with anticyclones (indicated by white arrows) consistent with the significant negative lagged correlations between the inferred geostrophic velocities and observed near-bottom velocities.



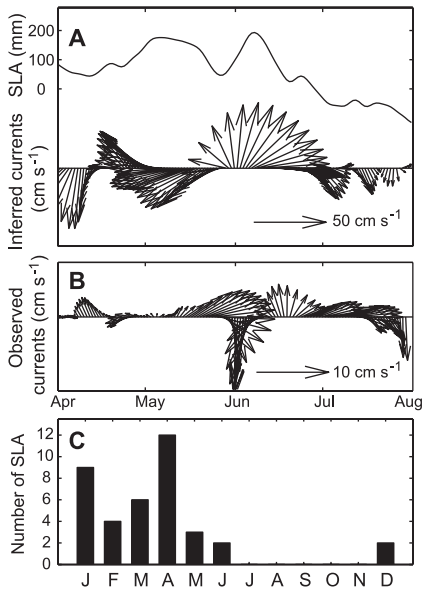


Fig. 4. Multiple eddies interact with the EPR at depth. **(A)** SLAs and inferred geostrophic currents show the passage of two anticyclonic eddies over the 9–10°N vent field from May through June 2007. **(B)** Coincident with the SLA, near-bottom current anomalies in the opposite direction were recorded on the EPR at 9°50.0' N, 104°17.4' W at 2430 m depth. Plots of SLAs and inferred currents were lagged 8 days relative to the observed near-bottom current velocities. **(C)** Mesoscale eddies cross the EPR seasonally. Analysis of satellite altimetry from January 1993 to December 2009 indicates that an average of 2.2 ± 0.9 (SD) eddies crossed the EPR each year, predominantly during the first half of the year.

ridge through topographically induced, meridional eddy elongation (26) or topographically rectified flows (16), whereas the zonal flows may have diminished into the background flows during deformation by the ridge axis or been influenced by fine-scale topography not included in the model, resulting in lower correlations. Still, these comparisons suggest that eddy-induced current velocities at depth were present during the period of observed current velocity anomalies and associated decreases in mass and larval fluxes.

Our findings suggest that eddy-driven impacts extend beyond the upper ocean and main thermocline (28) to include deep-sea benthic environments. Eddies at depth could play a major role in transporting hydrothermal vent-derived heat, chemicals, and biota in a relatively low-energy environment. Transport could occur wherever mesoscale eddies interact with ridges—including the Mid-Atlantic Ridge, the Southwest Indian Ridge, and the East Scotia Ridge (29, 30)—and the surrounding deep ocean. The observed strong decreases in larval and mass fluxes, together with a change in chemical compositions of the settling flux, during and after the current anomaly suggest that the passage of the eddy over the study site removed vent-altered seawater, larvae, and

associated biogenic matter. The observed local removal of larvae would be followed by inevitable loss to unsuitable habitat but could also result in the delivery of those larvae to distant vent fields. Complex interactions within the simulated eddy field created an intensified deep northward current that extended nearly 8° of latitude and interacted with the ridge for weeks (Fig. 3B and movie S2), potentially providing a conduit for larval transport between vent fields. The deep-water expression of large and/or interacting eddies could thus disrupt more persistent pathways of larval supply, such as local retention (6, 7) and transport by rectified mean flows (16, 17). However, the eddies provide a hydrodynamic mechanism to facilitate long-distance dispersal events, such as that of *Ctenopelta porifera* observed at nascent vents over 300 km away from the nearest known source (7). A few long-distance dispersal events driven by these eddies could produce high gene flow among vent fields and, more broadly, in the deep sea in general.

There is the potential for multiple eddies to interact with the EPR each year (31–33). A second instance of a strong negative correlation ($R_u = -0.56$, $P_u < 0.0001$; $R_v = -0.86$, $P_v < 0.0001$ with an 8-day lag) between a current anomaly observed on the ridge crest and inferred geostrophic velocities at the surface was detected from May through June 2007 (Fig. 4, A and B), lending further support for eddy-induced current velocities at depth. In the eastern Pacific, an average of 3.5 ± 1.2 (SD) Tehuantepec and 2.2 ± 1.0 (SD) Papagayo eddies (31) form each year during the late fall to early spring (31–33); a subset of these eddies, 2.2 ± 0.9 (SD) per year, cross the EPR during the winter and spring (Fig. 4C). In addition to the seasonal production of these eddies, Tehuantepec eddies strengthen and increase in frequency during El Niño years (31–33). Although the deep sea and hydrothermal vents in particular are often naively thought of as being isolated from the surface ocean and atmosphere, the interaction of surface-generated eddies with the deep sea offers a conduit for seasonality and longer-period atmospheric phenomena to influence the “seasonless” deep sea. Thus, although hydrothermal sources of heat, chemical, and larval fluxes do not exhibit seasonality, there is potential for long-distance transport and dispersal to have seasonal to interannual variability.

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and current records from 2004–2005 have been deposited in the Marine Geoscience Data System: RIDGE 2000 Data Portal. The authors declare no competing financial interests.

Supporting Online Material

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Materials and Methods

SOM Text
Figs. S1 to S6
Table S1
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Movies S1 and S2

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Brain Evolution Triggers Increased Diversification of Electric Fishes

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Luke J. Harmon,² Matthew E. Arnegard³

Communication can contribute to the evolution of biodiversity by promoting speciation and reinforcing reproductive isolation between existing species. The evolution of species-specific signals depends on the ability of individuals to detect signal variation, which in turn relies on the capability of the brain to process signal information. Here, we show that evolutionary change in a region of the brain devoted to the analysis of communication signals in mormyrid electric fishes improved detection of subtle signal variation and resulted in enhanced rates of signal evolution and species diversification. These results show that neural innovations can drive the diversification of signals and promote speciation.

Although we assume that sensory processing is fundamentally important for the detection of species-specific communications, or “signals” (1), we know relatively little about how brain evolution might affect signal divergence and speciation. African electric fishes within the family Mormyridae provide an ideal model system for relating brain evolution to diversification. The >200 described species in this family are phylogenetically and phenotypically diverse (2–8); communicate using brief, species-specific, and easily quantified electric signals (9); and process these signals in a well-defined sensory pathway devoted solely to the analysis of electric communication signals (10–12) (fig. S1).

Mormyrids generate electric signals to communicate and to actively sense their environment (11). These signals have evolved more rapidly than body shape, size, and trophic ecology, suggesting that electric communication behavior has played a key role in the radiation of mormyrids (3). Further, playback experiments in a few species suggest that these signals are critical for species recognition during mate choice (13–16). Electric signals are generated by an electric organ in the tail, which consists of electrically excitable cells called electrocytes (17). Electrocyte stalks evolved with the origin of mormyrids, and developmental flexibility in stalk morphology arose with the origin of the subfamily Mormyriinae (2). This evolutionary change in the Mormyriinae es-

tablished enhanced capacity for signal variation that is lacking in the Petrocephalinae, the only other mormyrid subfamily (Fig. 1).

Mormyrids have three types of electroreceptors: ampullary organs, mormyromasts, and

knollenorgans (18). Communication behavior is mediated exclusively by knollenorgans (10). In a region of the midbrain called the extero-lateral nucleus (EL; fig. S1), the timing of responses of knollenorgans located on different parts of the body is compared to extract information about electric signals (10–13). Despite the importance of the EL for signal analysis, EL anatomy has only been characterized in a few species (10–12). To investigate the role of brain evolution in mormyrid diversification, we performed a comparative analysis of EL anatomy. We obtained serial sections from the brains of 26 species (table S2). After standard histological processing, we delineated the borders of the EL in each section using established criteria (12). We then calculated total EL volume normalized to brain mass [see supporting online material (SOM)].

Previous studies identified distinct anterior and posterior subdivisions in the EL, referred to as ELa and ELp, respectively (10). Sixteen of the species that we studied clearly have separate ELa/ELp subdivisions (Fig. 2A). However, the

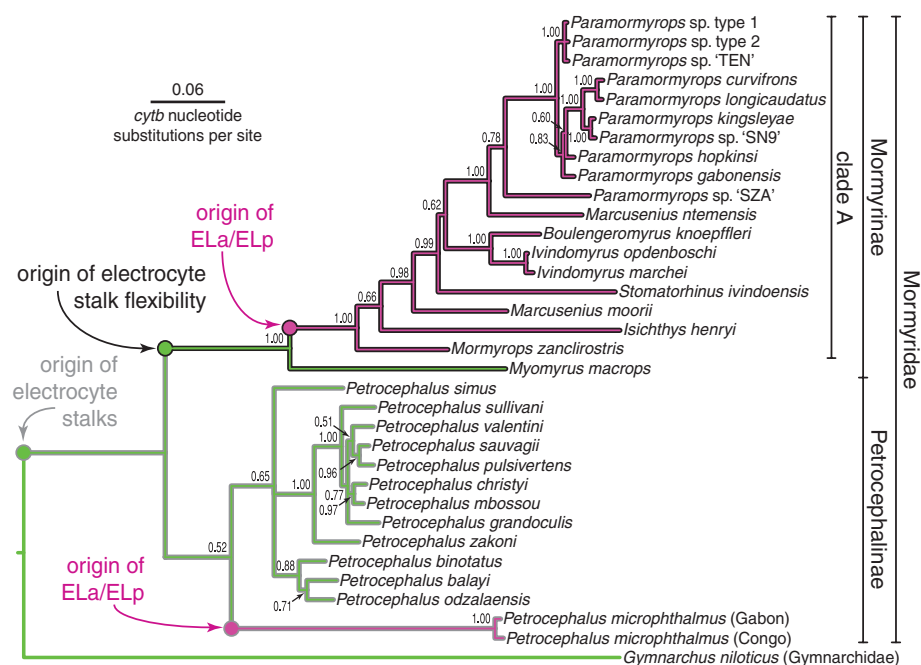


Fig. 1. Inferred tree of phylogenetic relationships among mormyrid species and morphs. The phylogeny was estimated by Bayesian analysis of *cytb* sequences (values at nodes are posterior probabilities). A sequence from the closest outgroup to the Mormyridae (*Gymnarchus niloticus*) was used to root the tree. Green branches represent a small extero-lateral nucleus (EL) and magenta branches represent an enlarged EL divided into anterior and posterior subdivisions (ELa/ELp); we reconstructed ancestral states using parsimony (see text). Gray outline represents electric organs with electrocyte stalks, and black outline represents electric organs with developmentally labile stalks, based on a previous study (2).

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