PERSPECTIVES: HYDROTHERMAL SYSTEMS

Stirring the Oceanic Incubator

Robert P. Dziak and H. Paul Johnson

Hydrothermal fluid circulates through the porous and permeable rocks of the uppermost 600 m of oceanic crust. Fluid is constantly transferred between this reservoir and seawater, with residence times in the crust of only a few thousand years. The warm circulating fluid reacts with volcanic rocks, strongly influencing the elemental composition of seawater, and the porous upper crustal rocks provide an incubator for a microbial biosphere of as yet unknown proportions.

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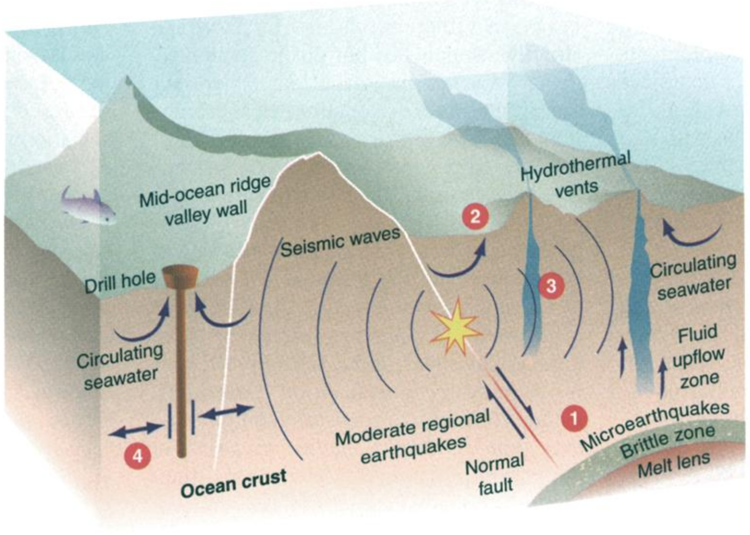
Pressure variations due to tides and atmospheric storms can modulate fluid circulation in oceanic crust at the ridge and on its flanks. Earthquakes also appear to influence this normally quiescent environment. In the eastern Pacific Ocean, earthquakes directly below (*1*, *2*) and tens to hundreds of kilometers distant (*3*, *4*) from active marine hydrothermal systems can change the temperature and flow rate of hydrothermal circulation, altering the biological and geochemical environment of the ocean crust. However, understanding of these processes remains limited.



Shaking the seafloor. Microearthquakes result from cracks propagating into a previously isolated region of lower crust, causing release of high-temperature fluid (**1**). Shaking and crustal stress changes from nearby earthquake(s) remove precipitates that block the vent nozzle (**2**) or alter precipitates that block flow pathways/conduits (**3**); both can induce changes in crust pore pressure and increase fluid flow. Changes to pore pressure and fluid levels in drill holes and hydrothermal vents may be due to crustal stress changes or seismic wave shaking from regional (**4**) or distant earthquakes.

In contrast, the impact of earthquakes on terrestrial hydrothermal systems is well established. The effects are usually instantaneous and widespread (*5*, *6*). Within a few minutes of the 1992 magnitude 7.3 earthquake in Landers, California, hydrological changes occurred at subaerial geothermal sites throughout the western United States, including changes in reservoir level, fluid temperature, and discharge rate (*6*). Earthquake-induced hydrologic changes to terrestrial systems may also occur hours to months before the earthquake (*5*).

Current models suggest that earthquakes induce these hydrologic changes in land-based systems by rapidly changing the pore-fluid pressure and geometry of the rock matrix that hosts the hydrothermal circulation. The shaking of passing seismic surface waves caused by distant earthquakes (100 to >1000 km) can remove obstructions to fluid flow (e.g., bubbles, chemical precipitates, and biofilms), allowing rapid readjustment of pore pressure (*7*, *8*). Earthquakes nearer the hydrothermal system (about 10 to 100 km) can produce rapid adjustments in crustal pore pressure due to induced regional tectonic stress (*8*, *9*). Earthquake rupture less than 10 km from the hydrothermal systems produces strong ground shaking, changing local rock permeability and directly altering fluid circulation and reservoir capacity. All of these effects have been observed after large earthquakes in Iceland (*9*), Japan (*10*), and Turkey (*11*).

In marine systems, the impact of earthquakes appears to be very different (see the figure). A swarm of microearthquakes on the East Pacific Rise increased fluid temperature by 7°C at a hydrothermal vent located directly above the swarm—but only after a delay of 4 days (*1*). Vertical cracks propagated into a previously isolated high-temperature region of lower crust, and it took days to transfer this heat upward to the seafloor.

In June 1999, an off-axis earthquake swarm near the Juan de Fuca Ridge in the northeast Pacific increased fluid temperature and flow rate at several on-axis vents 15 km from the center of the swarm. The temperature increases by 2° to 12°C were delayed by 4 to 11 days (*2*). The pore pressure increased instantaneously at drill holes 25 to 100 km distant (*4*), and after an 8-hour delay, temperature and fluid flow rates increased at vents 220 km away (*3*).

Substantially delayed earthquake-induced hydrologic changes seem to be unique to marine hydrothermal systems. Oceanic earthquakes do not, however, uniformly increase vent fluid temperatures. A magnitude 6.2 earthquake on the Blanco Fracture Zone on the Juan de Fuca Ridge caused both instantaneous and delayed (by 7 days) temperature decreases at vents located 42 km away on the ridge axis (*12*).

Changes in oceanic hydrothermal circulation after an earthquake can also dramatically affect the two large but distinct biological communities at mid-ocean ridges. First, seismicity can substantially increase the effluent thermal flux of hydrothermal vents over an entire ridge segment. This enhanced heat output changes the size and temperature of the thermal boundary layer, a region just above the axial valley floor that supports an abundant and diverse macrofauna. Any change in the thermal flux strongly affects the biota. After the June 1999 Juan de Fuca Ridge earthquake swarm, observations of dramatically increased biological activity were the first indication that something unusual had occurred. Evidence included the recent formation of large bacterial mats, abundant water-suspended bacterial floc and particles, and vent-specific animal communities that were visibly expanded in size since the previous year (*2*).

The microorganisms that reside in the porous upper crustal rocks are also affected by earthquakes. This subseafloor mi-

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crobial community is extremely sensitive to temperature, oxygen content, pH, and other environmental variables. It thrives in subsurface zones where the hot hydrothermal fluid mixes with entrained seawater (*13*). Changes in crustal fluid temperatures of only a few degrees, or a minor alteration of crustal permeability, can cause the prevailing microbial species to weaken and encourage new species to thrive and become dominant (*14*). In crustal fluids, the temperature elevation due to seismic activity can last for months or even years, implying that the species distribution in the oceanic crustal biosphere can shift substantially with every large earthquake or earthquake swarm.

The impact of earthquakes on biological communities associated with terrestrial hydrothermal systems is largely unexamined. However, most terrestrial microbial populations rely on photosynthetic energy, and the impact of changes in fluid temperature and flow rate may hence be greatly reduced. In contrast, ocean-crust hydrothermal fluid provides the primary thermal and chemical energy that fuels the microbial subsurface biosphere and most of the vent-specific macrofauna. Earthquake-induced changes in this circulation, which can occur over areas much wider than previously expected (*3*), will strongly affect these communities.

The dissimilarity in oceanic and terrestrial responses probably results from differences in crustal architecture. On land, where geological structure and fluid reservoir geometries are diverse, the primary response of hydrothermal systems appears to be immediate as temperature and volume changes coincide with the passage of seismic waves that compress or dilate the pore space of the reservoir (*6*). In contrast, hydrothermal fluid circulation in the porous ocean floor is a thermally driven process within an aquifer that is more uniform and can be continuous over thousands of kilometers (*15*, *16*).

The response of marine systems to earthquakes can be complex, even oscillatory (*3*), with delay times of days or weeks before a reaction is observed, and a far wider spatial impact than expected from the amount of seismic energy involved. We do not yet understand the physical processes that link crustal strain, earthquakes, and hydrothermal circulation in the oceans, but we can predict with some certainty that seismic activity has a major impact on the biological communities that inhabit the seafloor.

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PERSPECTIVES: GENETICS

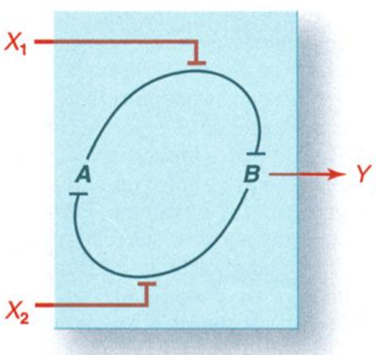
Wild by Nature

Michael Wigler and Bud Mishra

Much of modern biology has centered on dissecting the series of molecular events that we call signal transduction. Typically, the response to a singular event—such as the binding of a hormone, growth factor, neurotransmitter, or some other small chemical moiety to its receptor—is depicted in a wiring diagram of molecules that in temporal order become altered, some acting to propagate the signal, others acting to inhibit it. As these pathways ramify, interconnect, and incorporate components such as feedback inhibition, we begin to speak of regulatory networks. And as the diagrams grow, they reach their apotheosis as office wall decorations, ever-present reminders of the complexity of living things.

But do we really need complex diagrams to generate biological complexity? Can we achieve the imponderable by simpler means? What if we studied cellular responses not to a single signal, but to two signals, which may not necessarily even arrive at the same time? The study by Guet *et al.* (*1*) on page 1466 of this issue describes the creation of very simple pathways that respond to two inputs with a range of unpredictable behaviors.

Guet *et al.*, using DNA fragments as cassettes, constructed a library of plasmids. Every plasmid contained three genes encoding transcription regulators (LacI, TetR, and lambda CI) of the bacterium *Escherichia coli*, and each gene was driven by one of five promoters. The promoters were chosen so that each was controlled by one of the three regulators. In this way, a total of 125 possible combinatorial "circuits" are contained within this plasmid library. The LacI and TetR gene products are responsive to the small molecule inducers isopropyl β-D-thiogalactopyranoside (IPTG) and anhydrotetracycline (aTc), respectively. The two inducers act as the two "inputs." The entire circuit reads out through green fluorescent protein (GFP)—the "output"—which is under the control of a promoter inhibited by lambda CI. Each combinatorial network resembles a binary logic circuit with two inputs and one output. Guet *et al.* introduce these plasmids into two different *E. coli* hosts and then monitor the response of the bacteria to different concentrations of IPTG and aTc. Plasmids that induce interesting behaviors in the bacterial hosts are rescued



A simple metastable biological circuit. The combinatorial genetic network depicted consists of two mutually inhibiting repressor genes, *A* and *B*, which are modulated by two small molecule inducers, X_1 and X_2. The gene products encode the state of the system, and the inducers act as inputs to the network. The state of *B* encodes the output (*Y*). This network has two stable states (output is "high" or "low"), but also a metastable state (output assumes an intermediate state between "high" and "low") that is achieved by withdrawing both inputs simultaneously. For these reasons, the network is also extremely sensitive to the relative order in which the inputs arrive and, thus, is unpredictable.

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