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The Quantum Event of Oceanic Crustal Accretion: Impacts of Diking at Mid-Ocean Ridges

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REVIEW

Seafloor diking-eruptive events represent the irreducible, quantum events of upper oceanic crustal accretion. They record events by which a large portion of the oceanic crust has formed through geological history. Since 1993, the U.S. Navy's real-time Sound Surveillance System has allowed location of ongoing acoustic signatures of dike emplacement and basalt eruptions at ridge crests in the northeast Pacific. These diking-eruptive events trigger a sequence of related, rapidly evolving physical, chemical, and biological processes. Magmatic volatiles released during these events may provide nutrients for communities of seafloor microorganisms, some of which thrive in high-temperature anaerobic environments. Many of the organisms identified from these systems are Archaea. If microorganisms can thrive in the water-saturated pores and cracks within deep, volcanically active portions of our planet, other hydrothermally active planets may harbor similar life forms.

The ocean basins cover nearly 60% of Earth's surface. They are underlain by 5 to 6 km of oceanic crust formed through solidification

of molten basalt along the global spreading center network (Fig. 1). The basalt is generated by partial melting in the rising mantle beneath mid-ocean ridges. Annually, about 20 km³ (*I*) of basaltic magma is buoyantly emplaced along the spreading centers where it cools to form the trailing edges of large tectonic plates. Rates of plate divergence vary from 10 to nearly 200 mm per year. Upon rising into the young crust bounding the zone of divergence, the melt commonly collects in crustal chambers located 1 to 2 km below the seafloor. A significant fraction of the magma solidifies slowly in the chamber to form coarse-grained gabbros, but the remaining magma episodically breaks through the crystalline roof of the chamber, rises to the seafloor through planar, ridge-parallel conduits, and produces submarine eruptions of basaltic lava flows. The conduits are known as dikes, a term that also applies to the rapidly cooled rock that fills the conduit after magma transfer ceases.

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Observations of eroded oceanic crust on land and tectonically exposed crust on the seafloor confirm that at depths of about 1 to 2 km, the entire oceanic crust comprises a dense complex of ridge-parallel dikes about 1 m in width, up to 1 km or so in vertical extent, and tens of kilometers long (2). The dikes represent a virtually endless series of impulsive magma transfer episodes from chamber to seafloor as the ocean basins open along the suture of the spreading center. Dike formation is a discrete extensional event. All submarine lava flows require some type of diking event to supply the magma to the seafloor, but not all dikes reach the seafloor or produce lava flows. Viewed in this context, diking represents the quantum event of upper oceanic crustal accretion, recording the myriad small events by which the oceanic crust has been augmented through geological history (3).

Seafloor diking and eruptive events unleash a series of processes that trigger vigorous hydrothermal output to the ocean and they significantly perturb existing vent systems (Fig. 2). New techniques of detecting and responding to such events provide unparalleled oppor-

tunities to examine directly this most essential process of crustal accretion. By studying such events over the past decade, major new insights have been gained into submarine hydrothermal activity and into chemical and biological fluxes from the subseafloor to the overlying ocean. These studies have begun to influence perceptions of the role that volcanically supported microbial habitats may play in planetary systems in general. In this paper we examine evidence from a series of recent seagoing field programs that have responded to submarine volcanic activity in time to observe the rapidly unfolding changes attendant on such natural perturbation experiments. The interlinked geophysical, geochemical, and microbial activities triggered by diking may have been an integral component of oceanic crustal formation throughout much of Earth history.

Summary of Ridge Biology and Chemistry

The scientific community was astounded by the discovery in 1977 (4) of rich and unusual colonies of animals that owed their existence to

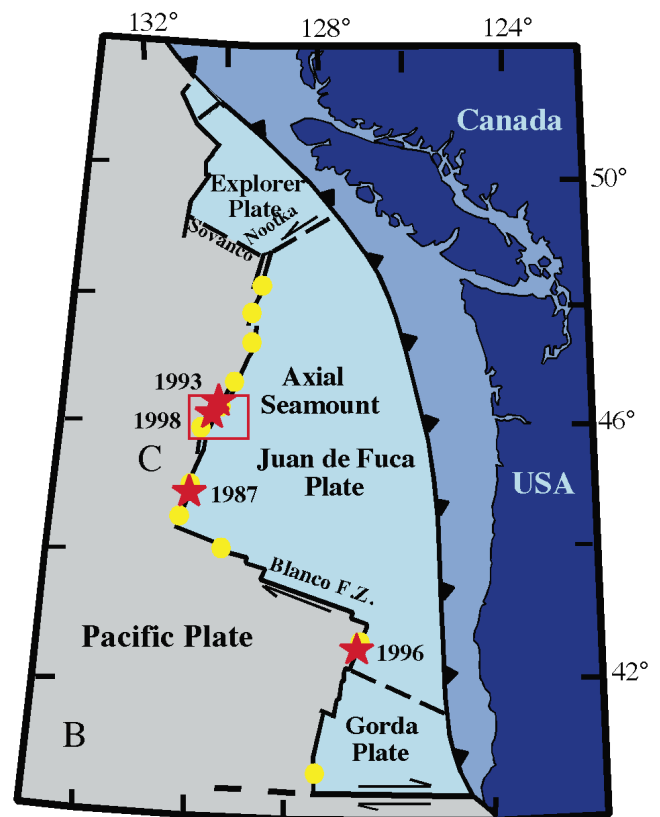
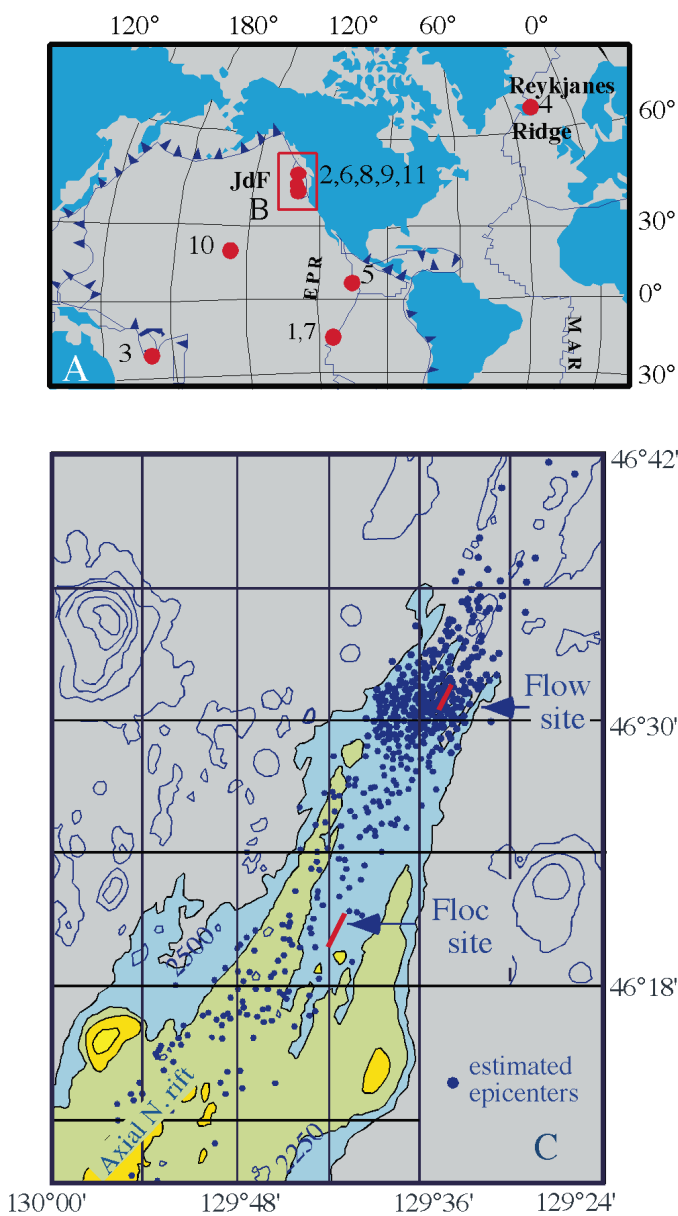


Fig. 1. (A) Location of diking-eruptive events in submarine environments detected since 1983 (red dots). The spreading centers are marked by thin black lines and show the location of the Mid-Atlantic Ridge (MAR), the East Pacific Rise (EPR) and the Juan de Fuca Ridge (JdF; see inset B). There is evidence for 11 eruptive events, six of them detected since 1993 through access to the SOSUS. Specific sites and detection dates of eruptions are as follows: 1. 17°S, EPR, 1983, 1984; 2. Cleft Segment, JdF, 1987; 3. MacDonald Seamount, 1988; 4. Iceland, MAR, 1990; 5. 9°N, EPR, 1991; 6. CoAxial Segment, JdF (2 eruptions), 1981–1993; 7. 17°S, EPR, 1993; 8. North Gorda Ridge, 1996; 9. Axial Seamount, JdF, 1998; 10. Loihi Seamount, Hawaii, 1996. Specifics of each eruptive event are listed in Table 1. **(B)** Location map for northeastern Pacific spreading centers, showing the Gorda and Juan de Fuca Ridges. Locations of active hydrothermal sites are indicated by circles, and eruptions are denoted by stars. Also shown are dates of specific eruptions along the ridges. **(C)** Bathymetric map of the northern rift zone of Axial Seamount and the CoAxial Segment showing the locations of the "Floc" and "Flow" sites. In 1996, a seismic swarm laterally propagated subparallel to the ridge axis a distance of 40 km ending near an eruption at the Flow site. Blue dots represent estimated epicenter locations [after (29)].

seismic swarm laterally propagated subparallel to the ridge axis a distance of 40 km ending near an eruption at the Flow site. Blue dots represent estimated epicenter locations [after (29)].

chemosynthetic microorganisms fueled by the products of magmatic degassing and water-rock reactions associated with hotwater convection along the Galápagos Rift. These hydrothermal vent communities were initially viewed as isolated, widely spaced oases on an otherwise barren seafloor. However, in the past 15 years the discovery rate of vent sites has been high in response to maturation of search strategies and improved detection techniques (5–8). Numerous expeditions indicate that significant lengths of ridge crest are hydrothermally active and that these highly productive, complex biological communities are common wherever hydrothermal venting occurs along the ridge system (9, 10). These flourishing macrofaunal vent communities consist of highly localized clusters of tube worms, clams, mussels, limpets, crabs, and fish (9, 11–13). Many of the macrofaunal communities are sustained by symbiotic microorganisms that derive energy from chemical gradients sustained at the seafloor through mixing of relatively reducing vent fluids with the frigid deep ocean water charged with atmospherically derived oxygen (14). Symbiotic and other microorganisms at the base of the food chain are capable of directly utilizing inorganic carbon and other nutrients in the rising fluids derived through alteration of the underlying volcanic rocks.

Hyperthermophilic microorganisms (microbes that grow between 50° to 113°C) have been documented in 5° to 30°C fluids from the Juan de Fuca Ridge, but they are not detectable in ambient seawater (15). The enhanced levels of microbes in fluids with temperatures below their growth range indicate that there was a warm, stable habitat below the seafloor. Although hyperthermophilic microbes are not the only inhabitants of these subseafloor microbial communities, they provide a convenient tracer (15, 16).

Movement of heated seawater through the ocean crust is the major pathway of geochemical exchange between the oceanic lithosphere and the hydrosphere. Hydrothermal circulation occurs in hot, newly formed crust on the mid-ocean ridge (MOR) axis, in a variety of other submarine volcanic centers, and in the cooler ridge flanks in crust up to ~65 Ma

(17–19). Even before the first MOR hot springs were discovered, it was concluded that high-temperature venting could have a significant impact on the chemistry of seawater (20) by uptake of some elements into secondary minerals, and release of others (for example, transition metals, alkalis, and rare earth elements) from primary igneous minerals. Metals transported by hot hydrothermal fluids are concentrated in seafloor sulfide deposits and underlying stockwork zones (21). MOR hydrothermal circulation is one of the major factors controlling the variation of seawater strontium isotope composition over geologic time (22, 23). Lower temperature fluid circulation in ridge flanks transports more heat and many times more water than on-axis circulation, and plays a major role in the alteration of the upper oceanic crust (18, 24–27).

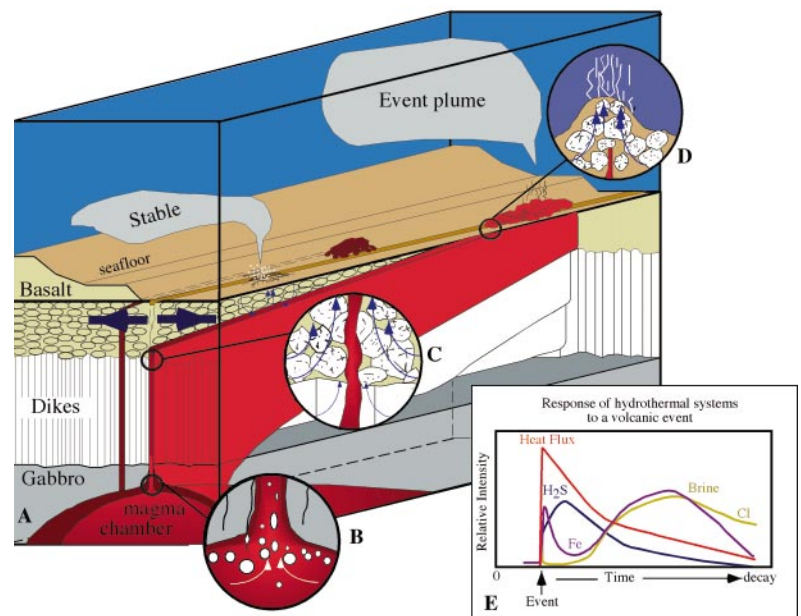
Study of Diking Events

Despite the fundamental role submarine diking plays in the evolution of our planet, until recently, it was not possible to actually investigate the specific processes involved. Once it became possible to conduct such studies we discovered that submarine diking events are tightly linked to previously unrecognized microbial processes within the oceanic crust. Ridge-axis diking-eruptive events are frequent perturbations that trigger a sequence of related, rapidly evolving physical, chemical, and biological processes.

Beginning in late June 1993, access to real-time Sound Surveillance System (SOSUS) information allowed temporal and spatial tracking of the acoustic signatures associated with diking-eruptive events at ridge crests in the northeast Pacific (8, 28–30). It was then possible to respond quickly to the transient events associated with active submarine volcanoes and to study the covariation of processes that are key interactions endemic to oceanic crustal formation.

Since 1986, 11 submarine diking-eruptive events have been inferred or directly observed (Table 1), but the first remote detection of a rapidly migrating submarine linear earthquake swarm was on the CoAxial Segment of the Juan de Fuca Ridge (Fig. 1). In three cases, there are direct

Fig. 2. A schematic model for geological and geochemical processes impacted by a diking-eruptive event. **(A)** Idealized stratigraphy for the oceanic crust. The uppermost crust is a 500- to 600-m-thick extrusive layer of basaltic flows fed by underlying dikes, which form the plumbing system along which melt is transported from the magma chamber to the seafloor. Drilling of submarine rocks by the Ocean Drilling Program and studies of oceanic crust exposed on land show that the dikes form a 1- to 1.5-km-thick layer. This layer is composed of subparallel sequences of individual dikes, each dike representing a separate subseafloor intrusion of lava along a 1-m-wide, several kilometers long fracture. During a diking event, the melt-filled fractures commonly propagate laterally away from the chamber and parallel to the ridge axis; breaching of the seafloor results in the formation of a lava flow (shown in red). The melt lens is encased in a 3- to 4-km-thick section of gabbro, the fully crystallized product of magma chambers. **(B)** All mid-ocean ridge magmas are saturated with carbon dioxide (CO₂), which forms small bubbles within the melt. Buildup of the melt-volatile pressure may result in fracturing of the lens cap; volatiles and melt stream up through the opening fracture. **(C)** Injection of 1200°C melt into the newly formed conduit causes superheating of the interstitial, seawater-derived fluids that saturate the highly porous shallow portion of the oceanic crust. Fluids are entrained near the dike boundary due to large temperature gradients. There is a strong permeability contrast between the dikes and permeable basalts such that flow within in the pillow section is likely to be much more dynamic than in the dikes. Fluids are rapidly expelled into the overlying water column forming a buoyant, volatile-enriched event plume. Vigorous venting flushes microbial material from the subseafloor into the water column, resulting in clouds and drifts of white flocculated material (fine white dots). **(D)** Fluids rapidly circulate and cool the new lava flow, resulting in short-lived periods of very high heat flux. Volatiles and chemical species leached from the rock provide nutrients to microorganisms,



resulting in microbial blooms. **(E)** The response of hydrothermal venting to a diking event is shown. Note that in the impulsive early stage of venting, the fluids are characterized by having high hydrogen sulfide (H₂S) and iron (Fe) concentrations, but are low in chlorinity (Cl) owing to phase separation. Concentrations of hyperthermophiles entrained from the subseafloor biotope are initially high, but decay with aging of the system (Fig. 4). This cycle is repeated endlessly along the global ridge system.

observations of massive effusions of microbial products in close spatial and temporal proximity to the onset of the seafloor volcanic activity. Hyperthermophilic microbes were detected in event-associated low-temperature or plume fluids, indicating that these microbes were released from warmer subsurface habitats (15, 16). We focus on the data from six of the best studied events to develop a model of the mechanisms and consequences of submarine dike-eruptive episodes. Although the Co-Axial evolution was the most thoroughly examined of the group, we begin by describing two earlier events at the southern Juan de Fuca Ridge and at 9°N because insights from these studies set the tone for the CoAxial Response and subsequent events.

Cleft Segment, southern Juan de Fuca Ridge—1986–1987. In 1986

and 1987, event-plume activity along the Cleft Segment of the Juan de Fuca Ridge was detected by water column surveys (31). This type of plume evidently forms when a dike event releases large volumes (~0.1 km³) of heated water from the ridge system (31, 32). Subsequent work has shown that these plumes, containing more heat than the annual output of a large hydrothermal field, are a common aspect of dike-eruptive events and are clearly different from the more typical stable or chronic plumes that are found 100 to 200 m above distinct seafloor sources (5, 7). Event plumes are found from several hundred to nearly 1000 m above the seafloor, are generally disk shaped, and have not been directly traced to a seafloor source. Ocean currents rapidly advect event plumes away from their source site and their study requires an oceanographic field response

Table 1. Diking-eruptive events and associated microbial observations. Temperatures cited from fluids taken for microbial analysis.

Site	Date	Eruption Indicators	Temperature	Chemistry	Floc observed	Thermophiles identified	Comments
17°S, East Pacific Rise (96)	Observed in 1983, 1984		150°C fluid at one site		No observations	No observations	Shimmering water out flow
Cleft Segment, Juan de Fuca Ridge (31–34)	1986	Megaplume 1986; new lava photographed, 1987, seabeam anomalies	5°C at Pipe Organ		Camera observations of probable Floc deposit	No growth detected at 55°C or 90°C (as measured in 1994)	First detection of a megaplume
MacDonald Seamount, SE Pacific (97)	1988		No temperature measurements of source fluids	High concentrations of CH ₄	No observations	Diverse assemblage hyperthermophiles from plume and surface slick, H ₂ -oxidizers	Seamount reaches 40 m below surface
Iceland (98)	October 1990		Temperature anomaly in water column		No observations		Teleseismic events detected
9°N, East Pacific Rise (46–48, 50)	1991	Lava flow, submersible observations	30°C vent sampled (1994)	Rapid changes in fluid chlorinity and volatile concentration	Abundant, formed drifts and coated seafloor, filamentous organisms	Hyperthermophiles and methanogens cultured	Hydrovolcanic explosion, filamentous bacterial mats flourished after eruption
CoAxial segment, Juan de Fuca Ridge (5–7, 12, 15)	Eruption late June–July 1993	1-km long pillow flow, submersible observations	18°C at Floc site; 22° to 51°C at Flow site	Rapid changes in fluid chlorinity and volatile concentration	Copious quantities at Floc site; minor at Flow; diverse assemblage of microbial forms, iron, silica preserve forms	Hyperthermophiles and diverse thermophiles cultured from Floc, none from Flow, sulfur-reducing and methanogens	Teleseismic event, earthquake swarms migrate 50 km, bacterial mats and filamentous bacteria abundant on new flow surface
17°S, East Pacific Rise (99)	1993	Shimmering water out of basaltic pillars			No observations		
North Gorda Ridge (16, 63–65, 68)	February to April 1996	Eruption of pillow lava ridge, diffuse flow from pillars, submersible observations	No temperature measurements of source fluids	Enriched volatiles (H ₂ , CH ₄) in megaplume	Bacterial mats observed coating flow	Thermophiles and hyperthermophiles isolated from 2°C plume water	Teleseismic events, flow imaged with camera, both by topographic anomalies
Loihi Seamount (70–74)	July to August 1996	Pele's Pit deepened by 300 m, submersible observations	3° to 4°C vent, 180°C vent	Enriched volatiles (H ₂ , CH ₄), rapid change in fluid chemistry and venting style	Pervasive	Thermophiles and hyperthermophiles cultured (>50,000 per liter)	Teleseismic events, over 4000 earthquakes
Axial Seamount (54)	January to February 1998			Enriched volatiles (H ₂ , CH ₄) in plumes	No observations	Hyperthermophiles isolated from plume	Teleseismic events migrate to south, glass shards in water column

immediately after an event is detected.

The 1986 Cleft event plume discovery was the first indication of a probable volcanic event on the MOR and it triggered a series of related geological studies of the underlying seafloor. These studies (33, 34) showed that there was a large diking event at North Cleft accompanied by sheet flow and pillow mound eruptions. When all the evidence was assembled, Embley *et al.* (35) proposed that event plume formation was associated with diking and eruption of pillow mounds. Important consequences of the North Cleft eruption include event plumes, chronic plumes with changing ^3He /heat ratios (32, 36), and widespread diffuse venting of low-chloride fluids lasting at least 2 years before becoming more saline than seawater (37). The overall level of venting and the density of animal communities decreased over the next several years. Although there was no explicit study of bacterial activity at the Cleft site, flocculated deposits were seen during *Alvin* dives in 1988 (38). Because direct seafloor observations and sampling at North Cleft followed the diking event by at least 1 or 2 years, the immediate effects of diking and eruption on hydrothermal systems were not fully appreciated.

East Pacific Rise at 9° north—1991. In 1991, a crustal diking event began on the East Pacific Rise at 9°N in an area that had already been well mapped (39, 40). The freshly erupted lava was explored and sampled shortly after the eruption during an *ALVIN* dive program (40, 41–43). During this event 4×10^6 to 6×10^6 m³ of lava was emplaced over a 1 to 2 hour period at an average rate of 10^3 to 10^6 m³ s⁻¹ (44). These rates are comparable to magma emplacement in Hawaii at the East Rift Zone of Kilauea. Dating of basaltic samples from this area, using the ^{210}Po – ^{210}Pb chronometer, show that the two eruptive episodes were separated by about 7 months with the first eruption ending shortly before the 1991 dive program (41). No information was available on any associated event plume.

The Cleft and 9°N events showed that immediately after a diking-eruptive event, pore water in and beneath the vents was generally heated to boiling. Phase separation produced fluids with low Cl^- concentrations, high concentrations of volatiles and metals in fluids with low pH and low $f\text{O}_2$ (42, 43). An excellent example of this behavior was the “A” vent at 9°N. This vent was visited three times (at weekly intervals) in April 1991. Water efflux temperatures increased from 390°, 396°, to 403°C; H_2S increased from 34, 66, to 71 mmol/kg, and Cl^- decreased from 80, 32.6, to 45.2 mmol/kg. Eleven months later this vent had cooled to 332°C, and Cl^- and H_2S concentrations were 286 and 30 mmol/kg, respectively. By 1994, the Cl^- concentration had reached 453 mmol/kg (42). This vent appears to have been influenced by hydrothermal circulation along a shallow dike (40). As the dike rapidly cooled, circulation moved progressively deeper in the crust. Continued cooling is typically associated with further increases in Cl^- concentrations. For example, at F-Vent at 9°N the Cl^- concentration increased from 46 to 846 mmol/kg (0.1 to 1.5 times seawater) between 1991 and 1994 (43).

Rapid and substantial effusion of flocculent material early in this event (40) formed swirling white clouds up to 50 m above the seafloor, and reached distances at least 100 m outside of the axial summit caldera. Extensive filamentous microbial mats lined previously uncolonized fissures and collapse pits and they covered thousands of square meters of the ridge crest (40).

All evidence indicates that a vigorous hydrothermal system existed in the 9°N area before the eruption of April 1991, presumably driven by heat from the underlying magma chamber inferred from multi-channel seismic evidence (45). It appears that the diking-eruptive event did not cause major disruption to many of the established patterns of hydrothermal activity along the axis, but some vents were significantly affected (40, 42, 43, 46–49). Continuous temperature measurements of the Bio9 vent near 9°50N showed an abrupt 8°C increase in fluid temperatures a few days after a seismic swarm (50).

CoAxial Segment on the Juan de Fuca Ridge—1993. On 26 June 1993, the acoustic signature of a migrating seismic swarm was

detected with the SOSUS network on the CoAxial Segment of the Juan de Fuca Ridge (JdF) (8, 29, 51). This area of the ridge is dominated by a large on-axis shield volcano, Axial Seamount, which shoals to a depth of 1500 m (Fig. 1). CoAxial Segment is marked by a zone of local spreading activity centered in a broad valley that encloses a subducted, but distinct ridge lying 2 to 3 km east and north of the northern rift zone of Axial Seamount.

Over a 2-day period, the seismic activity migrated laterally about 40 km along the trend of the ridge axis from a latitude of about 46°11.5' N to a latitude of about 46°31' N (8, 29), terminating near a site of basaltic extrusion on the seafloor (Flow Site). The character of the seismic events is reminiscent of the types of diking activity recorded in Iceland at Krafla and in Hawaii at Kilauea, where it is commonly associated with summit inflation of the volcanoes, followed by harmonic tremor, summit deflation, and flank eruption (26, 52, 53). Similar seismic activity was again detected in February 1998 on the southern flank of Axial Seamount attesting to the robust nature of the magma supply in this area (54).

In July and August of 1993, rapid response surveys of the water column above the axis of the CoAxial Segment delineated large hydrothermal plumes up to 800 m above the seafloor, extending 17 km along the axis of the rift valley (5–7). The plumes, which had a maximum temperature anomaly of nearly 0.20°C and a ^3He /heat ratio of $\sim 0.3 \times 10^{-12}$ cm³ STP cal⁻¹, exhibited a distinct layered structure inferred to form from multiple injections of buoyant hydrothermal fluid (5–7). The plumes were ephemeral in nature and were not observed 2 weeks after the initial surveys, indicating that they were a direct result of the diking-eruption process. Numerical modeling of their rise height requires that they formed in a matter of hours (55). Associated with these event plumes were steady-state or stable plumes, which rose 150 to 200 m above the seafloor and extended for 39 km along the axis. The deeper plumes had temperature anomalies as high as 0.07°C above background values, elevated ^3He /heat ratios of ~ 0.6 to 4.5×10^{-12} cm³ STP cal⁻¹ and reflect longer lived venting of hydrothermal fluids along the CoAxial Segment (5, 7).

Diving operations at the Flow Site using the Canadian Remotely Operated Vehicle ROPOS and the submersible *ALVIN* show that the 1993 lava flow was the product of a fissure eruption that formed a ridge parallel to the JdF ridge axis ~ 2.5 km long and up to 300 m wide (56). The flow has an estimated volume of 5.4×10^6 m³, roughly an order of magnitude less than that of the Cleft eruption (56). Another pillow basalt mound about 700 m to the east, is believed to have erupted between 1982 and 1991 (56). If this interpretation is valid, the 1993 event was the second in a decade. By analogy to land-based volcanoes, the 1993 event was part of a cluster of diking episodes along a volcanically active fissure (57). The rapid, short-lived northward migration of the seismic swarm, coupled with the effusion of basalt near the downslope terminus of the CoAxial spreading axis, is consistent with diking and hydraulically driven transport of the melt.

Shortly after the eruption, water was observed rising from the interstices of fresh pillow and lobate flows at temperatures up to 51°C in a 50-m wide zone centered over the crest of the flow (6). Extensive venting was documented for at least 4 km south of the flow along the southern part of the fissure. Temperatures of fluids venting from the flow decreased from 50°C to 36°C between July and October 1993. By July 1994, venting at the Flow Site had virtually stopped except in one area issuing 9°C water (57). Hydrogen sulfide was undetectable in these waters, CH_4 concentrations were low in October, and Fe and Mn concentrations were elevated (57, 58). No hyperthermophilic bacteria were isolated from samples collected at lava flow sites. However, extensive surfaces of the fresh pillow ridge (up to 10 cm thick) were coated with yellow-orange bacterial matting produced by iron-oxidizing bacteria (12, 15). ROPOS observations over the new lava and the active fracture system revealed no evidence of preexisting vent animal communities (13).

Roughly 20 km south of the Flow Site (Fig. 1), widespread evidence of massive ejection of flocculated microbial material was encountered in July and October of 1993 (the Floc Site) (6, 13, 15, 59–60). The blizzard-like “storm” of flocculated mat fragments penetrated 200 m into the water column for hundreds of meters on either side of the axis of the valley. Extensive bacterial mats covered the local seafloor. This site lies in a gentle axial depression characterized by a freshly broken, braided network of fissures. Observations with *ALVIN* showed that floc-laden fluids were issuing from openings tens of centimeters across within the fissure network. In some locations, intense effusions of flocculated material exhibited very high buoyancy flux, most likely caused by the massive low temperature venting. All venting temperatures observed at the Floc Site in 1993 were below 23°C. Cell morphologies indicative of sulfide-, iron-, and methane-oxidizing microorganisms and protozoa were also found in the hydrothermal fluids (15).

Continued diffuse, low-temperature venting at the Floc Site of water containing culturable hyperthermophiles showed that a microbial community had developed in this area. Several physiological types of thermophilic and hyperthermophilic microorganisms were isolated from the fluids (15, 60). Temperatures of the fluids sampled were more than 50°C lower than the minimum growth temperature of some of the hyperthermophiles cultured, suggesting a higher temperature biotope below the seafloor from which the organisms became entrained in cooler vent fluid. Microbes from Floc were cultured at temperatures in excess of 90°C; they include sulfur-reducers and methanogens (15).

Colonization by animals at the Flow Site was not observed in the years immediately following the eruption. However, vestimentiferans, alvinellid polychaetes, and nemerteans had colonized the Floc Site within 2 years after the eruption, with one-third of the regional vent species represented (13). Colonization was from a distal source and the recruitment was exceedingly rapid with tube worm arrivals about 7 months after the eruption. It is likely that the microbial populations played an important role in animal recruitment as the greatest populations occurred where microbial concentrations were the highest (13). Rapid recruitment of vent animals (vestimentifera) has also been recorded at 9°N (49, 61).

Venting fluids at Floc had methane concentrations of >120 $\mu\text{mol/kg}$ (62). This level is significantly higher than the value of 2 to 4 $\mu\text{mol/kg}$ expected if the methane in these diffuse vents was produced exclusively by sea water dilution of typical high temperature vent fluids (62). Similar anomalous methane concentrations have also been documented in diffuse fluids from 9°N, EPR (47). These data are consistent with a biological source of methane within the plumbing systems of newly formed diffuse vents by diking at both CoAxial and 9°N; high-temperature methanogens were cultured from both systems.

Gorda Ridge—1996. On 28 February 1996 intense seismicity in the northern region of the Gorda Ridge was detected by T-phase monitoring with the SOSUS array (63). Seismic activity reached a peak of 40 events per hour, lasted about 3 weeks, and was similar in character to that of the CoAxial diking-eruptive event. Three field programs responded to this event. On 10 March 1996 a major event plume was detected rising nearly 1500 m above the seafloor (64). Subsequent work showed that the plume was roughly 1 km thick and extended 15 km along axis and at least 8 km across axis, with temperature anomalies up to $\sim 0.12^\circ\text{C}$ and a $^3\text{He}/\text{heat}$ ratio of $0.3 \times 10^{-12} \text{ cm}^3 \text{ STP g}^{-1} \text{ }^\circ\text{C}^{-1}$ (64–66). Stable plumes were distinguished as well. In April 1996 a second distinct event plume was mapped above the western valley wall between depths of 1800 and 2400 m (64).

Rapid field response allowed the first investigation of the concentration of volatiles released immediately after the event. The Gorda event plume was enriched in H_2 by about 235 times (47 nM) background ocean water values (0.2 nM) and in CH_4 by 16 times background (0.4 nM) (65). Roughly 1 month later H_2 concentrations, although still elevated, had dropped drastically to 40 times background values (8 nM).

Hydrogen is rapidly consumed by bacteria in these plumes (67) and its presence in high concentrations implies that a plume is young. Distinct internal layering within the plume, coupled with the extremely high H_2 concentrations show that the plume had been generated within a few days of discovery (64–66). Camera surveys documented a new lava flow and bathymetric anomalies indicated that the flow was at least $\sim 0.02 \text{ km}^3$, roughly twice that of the Coaxial eruption (68).

Anaerobic thermophiles were cultured from 17 of 22 plume samples, whereas thermophiles were not detected in any of the 12 samples of background ocean water (16) (Fig. 3). Some of the thermophiles cultured are novel heterotrophic Archaea that are nutritionally and phylogenetically distinct from previously described marine species (16). The presence in the highly dilute plume fluids of organisms that require high temperature and anaerobic conditions for growth provides strong evidence that the microorganisms were derived from a subsurface biotope and that they were entrained in event plume fluids released from a pre-existing crustal reservoir (16, 69).

Loihi Seamount—1996. Between 16 July and 9 August 1996 over 4000 seismic events were measured at Loihi Seamount by the U.S. Geological Survey Hawaiian Volcano Observatory (70). The seismic swarm, which initiated near the summit of the seamount, migrated along a trend roughly paralleling Loihi’s rift zone. A rapid field response to this event showed the development of a 260 m wide, 300 m deep pit crater, the inward collapse of volcanic cones into the crater, and severe disruption of the hydrothermal site at Pele’s Vent (71). Temperature anomalies of up to 3.5°C were measured in fluids within the caldera and diffuse venting occurred from fissures within the newly formed caldera depression (71, 72). Maximum volatile concentrations were 17 nM TCO_2 , 280 nM CH_4 , and 20 nM H_2 , with the highest levels occurring in the pit crater (67, 71, 73). High concentrations of thermophiles and hyperthermophiles were cultured from the plume fluids, but no such organisms were cultured from samples of the surrounding seawater (74).

Axial Seamount—1998. Beginning 25 January 1998 to February 1998, intense seismicity was detected at Axial Seamount from SOSUS monitoring (54). A rapid response to this site in February detected evidence for extensive new venting at the volcano. Hydrothermal discharge was roughly an order of magnitude greater than before the eruption; event plumes were not found (54). Temperature anomalies of 0.2°C were measured in plumes 200 m above the bottom and gas concentrations were elevated within the plume; methane and hydrogen concentrations were 600 nM and 200 nM, respectively (75). Strong light attenuation anomalies were detected and scanning elec-

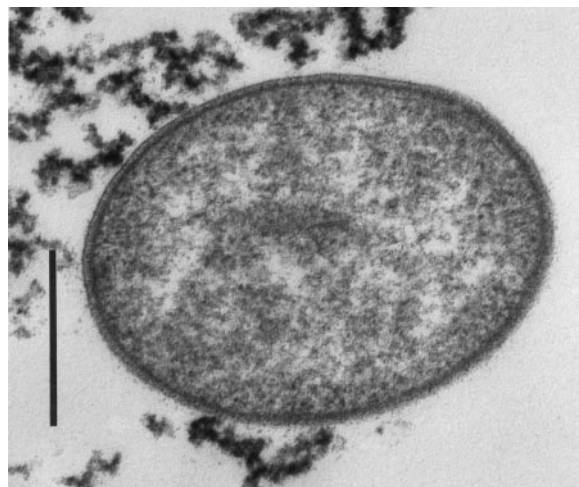


Fig. 3. Transmission electron photograph of a hyperthermophilic archaeon isolated from North Gorda event plume water (16). Hyperthermophiles were not found in background ocean water. Scale bar = 0.4 μm .

iron microscope analyses of the particulates indicate the presence of angular glass shards coated with variable amounts of halite precipitates, particles with high iron concentrations, and abundant elemental sulfur consistent with a seafloor eruption at this site (54). Similar to the CoAxial, Gorda, and Loihi events, hyperthermophiles were cultured from plume fluids at Axial (15).

General Consequences of Diking-Eruptive Events

A remarkable feature of event plumes, which are clearly associated with diking, is their nearly constant ratio of ^3He to heat (76). Although the total amount of heat in the event plumes over Cleft, CoAxial, and northern Gorda segments in the northeast Pacific varies by a factor of 10 and is roughly proportional to the volume of lava erupted (5). The ^3He /heat ratio in each is $0.3 (\pm 15\%) \times 10^{-12} \text{ cm}^3 \text{ STP cal}^{-1}$ (7, 32, 65, 76). The range of ^3He /heat in event plumes is similar to that in a mature or stable vent fluid. In areas recently affected by diking, chronic plumes have elevated ^3He /heat ratios that progressively return to values like stable plumes (7, 36).

The uniformly low ^3He /heat ratios from the seven distinct event plumes in three different geological settings (7, 32, 57, 76) provide strong evidence that event plume formation is caused by diking. One explanation is that event plumes represent a sudden release of a mature hydrothermal fluid (31) (hence the common ^3He /heat ratio of event plumes) followed by a transient recovery phase (36). A number of mechanisms have been advanced to temporarily accelerate deep (1 to 2 km) circulation (77–79) or to eject mature fluids from deep within the crust (80, 81), but it is unclear whether any mechanism alone can explain both the size and short formation times of event plumes without recourse to extremely high permeabilities at depth. Event plume Mn/heat ratios are consistently lower than is typical of high-temperature vent fluids, which argues against rapid emptying of a mature, high-temperature reservoir, but may point to a low-temperature or immature high-temperature reservoir (64, 82, 83).

Because all event plumes have been found near erupted lavas and their documented heat content is similar to the heat in the lava flows, the heat content of event plumes may be derived from direct interaction between seawater and near seafloor magma (57). The low ^3He /heat ratios in event plumes may simply reflect the slow diffusion rate of helium relative to heat through the solidifying lava resulting in most of the helium being released after the event plume has formed. Direct seawater interaction with erupted lavas is probably not the sole source of fluids in all event plumes because hyperthermophiles have been cultivated from one event plume (69), implying a contribution from some pre-existing fluid reservoir. Nonetheless, the event plume chemical (58, 64, 82) and biological (69) data do not preclude surface lavas from being the dominant heat source, and the issue of reservoir release versus direct heating of seawater remains unresolved.

The CoAxial event has the most extensive time series of chronic plume observations. Heat fluxes estimated from the rise heights decayed with a characteristic time of a few months (64, 84). A simple model (84) that considered the convective cooling of a dike injected into a cold porous medium with permeabilities in the range 10^{-11} to 10^{-12} m^2 [values typical of both the uppermost oceanic crust and black smoker systems (85)] was able to reproduce the heat flux decay, although the estimates of the absolute heat flux are not sufficiently accurate to constrain the depth extent of cooling. If event plume formation involves cooling of the near surface portions of the dike (79) then the chronic plumes may be a result of extracting heat from the dike at greater depths. Alternatively, the chronic plumes at CoAxial may have formed by cooling the dike in the upper extrusive layer. At sites such as Cleft and the EPR at 9°N where elevated heat fluxes have persisted for years after eruptive events, the chronic plumes clearly require a subsurface heat source larger than a 1-m-wide dike. Here the fluids must be circulating near a magma body.

A Model for Diking-Eruptive Events

A model that integrates the geological, geochemical, and microbiological activity triggered by a diking-eruptive event is illustrated in Figs. 2 and 4. At depths of 2 to 4 km below the seafloor, a thin horizontal lens of basaltic melt is encased in crystalline material. Overpressuring by rapid accumulation of melt from below and volatile exsolution (CO_2 , H_2O , SO_2 , H_2S , He) within the magma chamber lead to breaching of the carapace and the rapid vertical and lateral injection of a dike along the axis (Fig. 2B) (78). Active magma transport and fracturing of the wallrocks associated with dike injection results in localized seismicity in the form of harmonic tremor and discrete events (29, 81). This activity propagates laterally along the axis for distances up to 40 km; the zone of dike injection is typically 1 m wide and the leading edge of dikes may propagate at speeds of about 1 km/hour (Fig. 2C) (29). When magma supply is sufficient dikes breach the seafloor, forming pillow lava flows, mounds, and sheet flows (Fig. 2D).

Injection of melt into the cooler, seawater-saturated shallow crust may result in heating of the pore fluids and vigorous flushing of interstitial fluids from the crustal reservoir. Event plumes rise many hundreds of meters into the overlying water column. Ratios of ^3He /heat in the plumes are low (0.3 to $0.5 \times 10^{-12} \text{ cm}^3 \text{ STP g}^{-1} \text{ }^\circ\text{C}^{-1}$) (6). A component of the event plume may be derived from supercritical heating of seawater within the newly formed lava flow. The event plumes contain volatiles derived from the melt and from high-temperature reaction of fluids with unaltered crust. During the initial stage of cooling, when heat flux is very high and hydrothermal circulation is intense, phase separation results in expulsion of low chlorinity, vapor-dominated fluids (Fig. 2E). This short-lived, high-temperature stage is followed by a period of sustained venting when fluids become brine-rich and exhibit elevated ^3He /heat ratios (2 to $4 \times 10^{-12} \text{ cm}^3 \text{ STP g}^{-1} \text{ }^\circ\text{C}^{-1}$), which progressively decrease with time (7, 36). High permeabilities in the shallow crust allow rapid removal of heat by circulating fluids, cooling the extrusion and shallowest portion of the dike in a matter of weeks to months (84). At locations that do not overlie the magma source, the heat supply is exhausted in 1 to 3 years. The cycle is renewed with the next diking-eruptive event.

Biological responses to submarine diking events are not yet well understood. But, by combining what we now know about habitats in more stable hydrothermal systems such as the Endeavour Segment on the Juan de Fuca Ridge (15, 86, 87), with what we have learned about transient systems recently perturbed by diking events (15, 16, 88), a general model for microbiological responses can be outlined (Fig. 4).

The strong thermal, chemical, and porosity-permeability gradients in submarine environments directly influence the habitats and types of microorganisms living on or below the seafloor. Within young shallow crust to porosities can be as high as 12 to 36% (89). These systems are water-dominated with ample void space for microbial habitats (Fig. 4A). In the uppermost extrusive layers of these systems, fluids are likely to be oxygenated and have temperatures less than 20°C. With increasing depth, fluid temperatures generally rise and the system may be either aerobic or anaerobic, depending on the conditions of fluid circulation (90). In deeper, higher temperature environments, anaerobic conditions are likely to dominate, bulk permeabilities are generally lower, and hyperthermophilic habitats are stable. In this setting, reductive reactions involving methanogenesis and sulfate and sulfur reduction are likely sources of energy for microorganisms. In the absence of an intrusive event, these environments may remain stable for extended periods of time (Fig. 4A).

During an event, subseafloor biotopes may be strongly disrupted (Fig. 4B). Organisms carried by interstitial fluids entrapped in the void spaces of the basalts and older dikes are released into the water column within hours to days following intrusion of the dike (16, 91) (Fig. 4E). Diffuse flow at the CoAxial sites harbored high numbers of thermophiles when sampled at 3 weeks and at 3 months following the eruption. When these same sites were sampled a year or more after the eruption, either no hyperthermophiles were cultured or their numbers were greatly reduced (15). Diking events may temporarily destroy, or

enrich, thermophilic biotopes within subsurface zones. Either way, flushing of thermophiles into the event plume is followed by decreasing concentrations in the plume over time (Fig. 4E).

Within days to weeks of an event, volatile energy sources blend and hydrothermal fluids are mixed in the high porosity layer with oxygen, sulfate, and nitrate from seawater (90). This blend results in the enrichment of a metabolically diverse group of mesophilic microorganisms (growth between 5° and 45°C) (Fig. 4C) including sulfur, iron, and methane oxidizers (51). This is manifested as massive amounts of white flocculated material resembling “snow” that has been observed at four of the new eruption sites [Table 1 (6, 15, 40, 60)]. Similar material from the CoAxial vent on the Juan de Fuca Ridge contained iron-encrusted sheaths (15, 60). Filamentous sulfur that is morphologically similar to the Floc material collected at 9°N can also be produced by mesophilic, aerobic, hydrogen sulfide-oxidizing microorganisms (92). These oxidative microbes are responsible for the mats that coat the surface and interstices of the new pillow flows. Within a year macrofaunal communities (tube-worms, polychaetes, and crabs) colonize sites of diffuse flow, thriving on chemical energy sources and diverse microbial populations that now inhabit the area (13) (Fig. 4). Macrofaunal assemblages and microorganisms die off or become dormant with loss of a heat and nutrient source.

Although the source of organic carbon necessary to support the

abundant thermophilic heterotrophs is unknown, we hypothesize (Fig. 4) that organic carbon accumulated within the crust from previous microbial oxidative metabolism might be a reasonable source. Depending on the rate of supply of hydrothermal nutrients to the extrusive layer between diking events, slowly growing or dormant oxidative mesophilic organisms could survive within the upper crust, providing both the source of organic carbon for heterotrophs and the seed organisms for the massive microbial blooms that follow seafloor eruptions.

The zone in the crust occupied by thermophiles may be extensive. Diking events, which occur on time scales of years to decades in magmatically active fast- to intermediate-spreading environments, may provide the mechanisms for replenishing thermophilic biotopes with organic carbon and nitrogen. Tests of this model could include drilling through the extrusive layer of the crust at a site not known to have had a recent eruption event and determining if the zone between 50° and 150°C harbors high numbers of thermophiles.

Ramifications

Over the past decade we have learned a great deal about seafloor diking events but many processes remain poorly understood. By the time scientists reach the scene of eruptions, magma transport and event plume

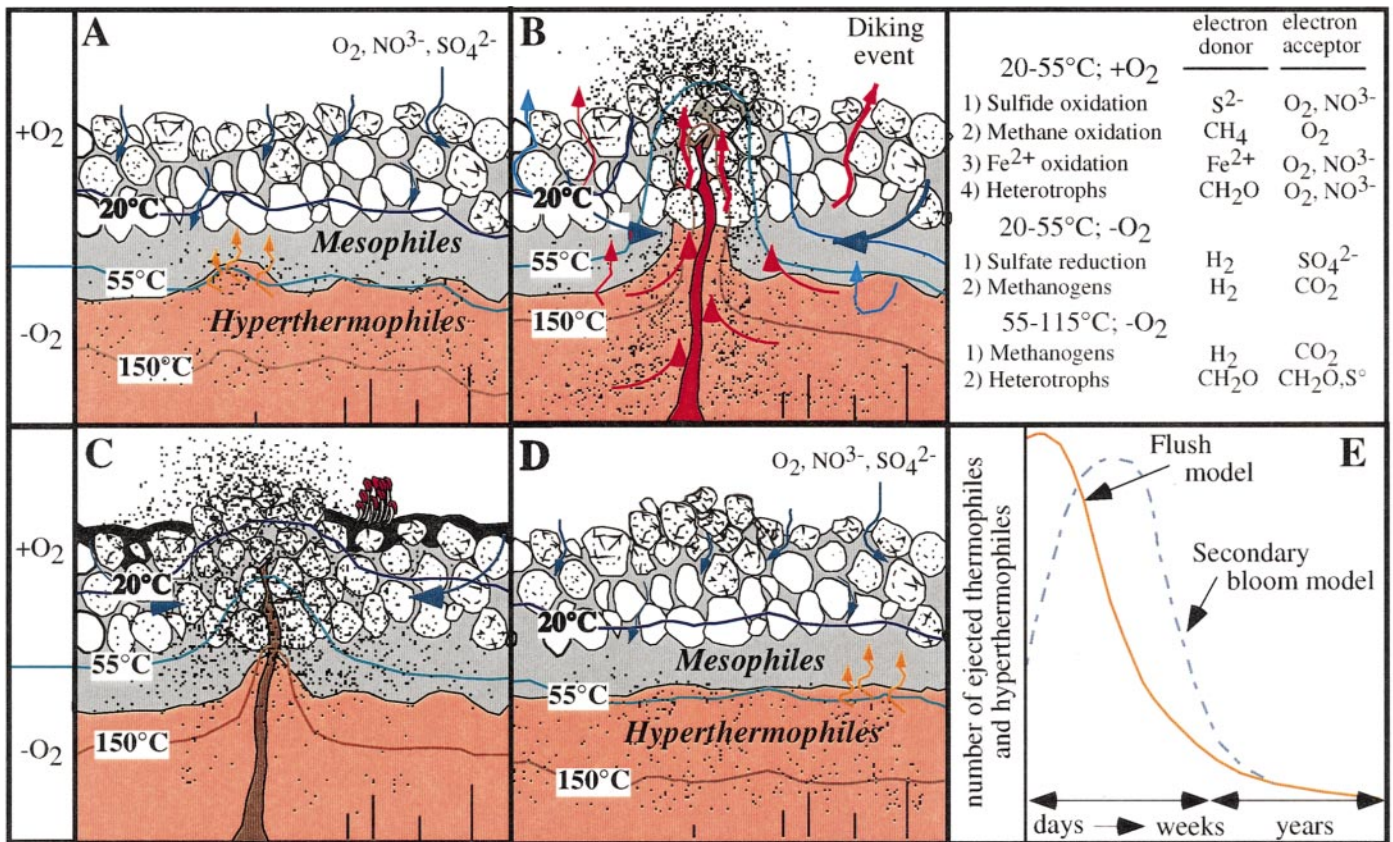


Fig. 4. Model of microbiological responses to submarine diking-eruptive events. (A) Hypothetical isotherms and the location of stable zones conducive to the growth of mesophiles and hyperthermophiles are shown for a system that has not been recently perturbed by a diking-eruptive event. (B) Upon injection of a dike, very strong chemical and temperature gradients are introduced, resulting in transient high heat fluxes and intense periods of circulation. Deep fluids are flushed out of the system, contributing to event plume formation, and these fluids carry microbes from all thermal zones into the water column. (C) As the system cools, volatiles and other sources of energy are progressively extracted from the fresh rock, feeding microbial populations in both shallow, aerobic habitats and deeper, anaerobic habitats. Possible reactions, metabolic processes, and electron donors and acceptors are shown

in the far right panel. Heterotrophic organisms may feed directly on autotrophic organisms or on external carbon sources. Again, organisms from all thermal zones are carried out of the system via the prevailing fluid circulation and appear in the low-temperature, diffuse vents at the surface. (D) Once the dike has completely cooled, the perturbation is removed and the system returns to initial conditions. Excess biomass created during the event may be flushed from the system or settle to deeper habitats, depending on the vigor of the remnant circulation. (E) The initial ejection of subsurface microorganisms and subsequent bloom and decay versus time. The relative heights of the two maxima in numbers of thermophiles and hyperthermophiles ejected is unknown, as is the exact timing of the bloom.

emissions have generally ceased, most of the seismicity has occurred, and chronic plumes have reached or passed their peak intensity. The physical configuration of the intrusion and of the hydrothermal circulation which follows is often only weakly constrained. Much of what we know about the chemical and biological processes which accompany diking has been deduced from highly diluted plume samples obtained well above the seafloor. The point of origin of these samples on the seafloor (let alone in the subsurface) is generally not known. At present, we do not know whether diking events flush active thermophilic and hypothermophilic biotopes or enhance the growth of dormant communities. To address these issues, it will be necessary to obtain extensive suites of coordinated seafloor measurements and samples before and over the entire lifetime of diking events.

Many microorganisms recovered to date are Archaea, believed to be the most ancient of extant hyperthermophilic organisms (93). During the time of the origin of life and development of the first microbial ecosystems (4.3 to 3.8 Ga) the Earth was subject to relentless bombardment by large asteroidal bodies. Some of these bolides may have been large enough to evaporate a 3 km ocean (94). Deep benthic, and especially subseafloor habitats, would have been the least impacted environments on the early Earth. Subsurface organisms sampled from diking events may represent the most ancient lineage of extant microorganisms. Systematic studies of the Archaea and the environments from which they issue could yield more understanding about conditions surrounding the origin and evolution of early life processes.

Massive and sustained output of microbial products associated with diking lend support to recent postulates (86, 87, 95) of a significant deep hot biosphere within the Earth. It may be especially well developed in the subseafloor associated with volcanism. If microbial communities thrive in water-saturated pores and cracks within deep, volcanically active portions of our planet, then perhaps other hydrothermally active planets may harbor similar life forms. By designing innovative strategies to explore linkages between active volcanoes and the life they support here on Earth, we gain essential knowledge about fundamental processes on our own planet. We also obtain critical insights about how and where to explore other planets for metabolizing organisms.

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