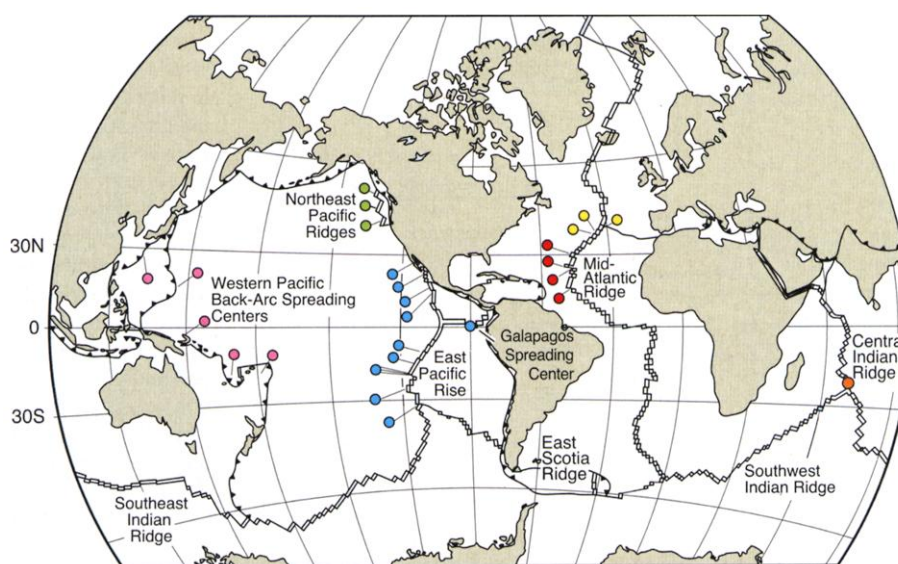REVIEW: MARINE BIOLOGY

Evolution and Biogeography of Deep-Sea Vent and Seep Invertebrates

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Deep-sea hydrothermal vents and cold seeps are submarine springs where nutrient-rich fluids emanate from the sea floor. Vent and seep ecosystems occur in a variety of geological settings throughout the global ocean and support food webs based on chemoautotrophic primary production. Most vent and seep invertebrates arrive at suitable habitats as larvae dispersed by deep-ocean currents. The recent evolution of many vent and seep invertebrate species (<100 million years ago) suggests that Cenozoic tectonic history and oceanic circulation patterns have been important in defining contemporary biogeographic patterns.

Deep-sea hydrothermal vents and their attendant invertebrate communities were discovered in 1977 during exploration of the Galapagos Spreading Center. Vents are now known to occur along all active mid-ocean ridges and back-arc spreading centers (Fig. 1) and at some seamounts. Vent fluids are geothermally heated and enriched in energy-yielding reduced compounds during circulation of seawater through the upper ocean crust. Deep-sea vents were the first complex ecosystems (i.e., involving metazoans) discovered to be based on microbial chemoautotrophic production [reviewed in (*1*)], and their discovery greatly expanded our understanding of the limits to life on Earth (*2*). Microorganisms that extract energy from reduced inorganic compounds (chemoautotrophs) concentrated in vent effluents were found to be primary producers in these deep-sea ecosystems, and they in turn are fil-tered or grazed upon by invertebrates (e.g., barnacles and limpets). Many of the invertebrates (e.g., vestimentiferan tubeworms, bivalve mollusks, provannid gastropods, and bresiliid shrimp) host chemoautotrophic microorganisms as either epi- or endosymbionts.

by microbes to release energy for the fixation of organic carbon from CO_2 (or methane). A complete distinction between vent and seep ecosystems may be inappropriate, as evidence for shared evolutionary histories and even some shared species suggests that there are links between the invertebrate taxa of vents and seeps on evolutionary and ecological time scales (*4–6*).

Evolutionary History of Vent and Seep Invertebrates

Since 1977, taxonomists have described more than 400 morphological species from vents (*7*) and 200 more from seeps (*6*). This corresponds to a species description every 2 weeks throughout the past 25 years. Some vent and seep invertebrate species are immigrants from the surrounding deep sea, whereas others may be derived from shallow-water species. Many of the invertebrate taxa found at vents and seeps have undergone evolutionary radiations at the species level (*7*). Other species have a longer history of endemicity, having diversified within vent and seep habitats at generic, familial, and higher ranks. Where high taxonomic levels of endemism are observed, origins may be ancient, extending back to the Paleozoic [540 to 248 million years ago (Ma)] (*8*). Genera of stalked barnacles and a superfamily of primitive gastropods endemic to vents are thought to be Mesozoic (245 to 65 Ma) relics or living fossils (*8, 9*). Chemosynthetic environments have thus been posited as stable refugia from global extinction events that devastated biological diversity in euphotic zones (*7, 10*).

Fossil evidence for the antiquity of extant vent and seep faunas is mixed. Massive sulfide deposits formed in back-arc spreading systems during the Silurian (438 to 408

Fig. 1. Map of known hydrothermal vent biogeographic provinces and major mid-ocean ridges. Provinces: Pink, western Pacific; green, northeast Pacific; blue, East Pacific Rise; yellow, Azores; red, Mid-Atlantic Ridge; orange, Indian Ocean.

Ecosystems similar to those of vents were subsequently found at cold seeps (*3*). Seeps are areas where chemically modified fluids derived from hydrocarbon reservoirs, methane hydrates, pore waters in sediments, and sites of organic enrichment such as whale skeletons are released into the ocean. Most seeps occur along continental margins and trenches in association with accumulated sediment. The common requirement of vent and seep communities is the presence of a reduced compound (typically hydrogen sulfide or methane) that can be oxidized

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Ma) contain fossils of monoplacophoran mollusks and inarticulate brachiopods (*11*, *12*), organisms that are not common or abundant in modern vent communities. Devonian vent communities do include bivalves belonging to an extinct Paleozoic group (*12*). Fossilized tubes from these deposits resemble modern vestimentiferan tubes, but many wormlike invertebrates make similar tubes. Convincing fossils of modern vent taxa may be limited to Late Cretaceous (~92 Ma) and Cenozoic (<65 Ma) deposits. These include vesicomyid bivalve shells from the late Eocene and Oligocene cold-seep deposits and whale falls (40 to 24 Ma) (*13–15*) and casts of vestimentiferan-like tubes from Late Cretaceous hydrothermal sulfide deposits (*16*).

Molecular clocks (*17*) have been used to infer evolutionary ages of radiations that led to modern vent and seep taxa. Gastropods of the superfamilies Neomphaloidea and Lepetodriloidea may extend to the mid-Cretaceous (~100 Ma) (*18*), although these gastropods have not been found in Cretaceous fossil vent deposits (*19*). Several other families that dominate extant vents and seeps may have also appeared in the Late Cretaceous and Cenozoic. Examples include vestimentiferan tubeworms (<100 Ma) (*20*), vesicomyid clams (<50 Ma) (*21*), bathymodiolid mussels (<22 Ma) [inferred from (*22*)], and bresiliid shrimp (<20 Ma) (*23*). Acknowledging the problems associated with molecular clocks (*24*), we cautiously interpret these estimates to suggest that important groups of vent and seep invertebrates are relatively young.

If groups of extant vent and seep taxa evolved recently (≤100 Ma), they must be derived from other deep-sea or shallow-water ancestors. Molecular phylogenetic studies reveal that modern vestimentiferan tubeworms diversified in cold seeps (Fig. 2). It is possible that earlier radiations of vestimentiferan-like tubeworms arising from polychaete stem ancestors produced the tubes found in fossilized Silurian vent deposits. Bathymodiolid mussels diverged more recently from shallow-water, suspension-feeding mussels and diversified first as decomposers of wood and bone (*22, 25*). Subsequent species invaded progressively deeper environments, including cold seeps and hydrothermal vents (*25–27*). Similarly, vesicomyid clams diversified first in cold seeps (*21, 28*), generating a number of opportunistic species that also exploit sedimented hydrothermal sites and decomposing whale bones (*29*). Not all evolutionary

progressions have been from seep to vent. Bresiliid shrimp appear to have diversified primarily within vent habitats (*23*), and polychaetes in the family Alvinellidae so far are known only from vents. Nevertheless, phylogenetic studies point to seeps and other organically enriched environments as the ancestral habitat for several vent taxa. Evolutionary relationships of other taxa shared between vents and seeps remain to be determined (e.g., polynoid polychaetes, provannid, and neolepetopsid gastropods).
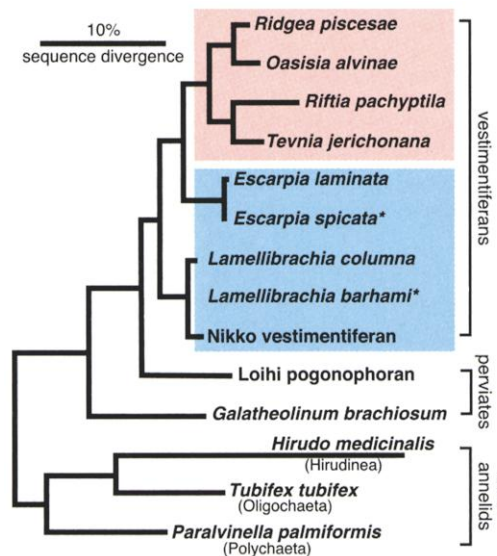
Some species are generalists that can exploit vents, seeps, and other sites of organic enrichment distributed across large distances (*28, 29*). At least one vesicomyid lineage may have spread recently around

Fig. 2. Vestimentiferan tubeworm phylogeny based on a portion of the mitochondrial COI gene (*20*). Once considered a distinct phylum, vestimentiferans are close relatives of perviate pogonophorans, tiny threadlike worms that live in anoxic basins. Vestimentiferans and perviates are now subsumed in the polychaetous family Siboglinidae (*84*). The pink box encompasses hydrothermal vent species, and the blue box encompasses cold-seep species. Two seep species (asterisks) also occur in soft sediments near hydrothermal vents.

the globe: A clam species from West Florida Escarpment seeps, Barbados seeps, and Mid-Atlantic Ridge vents is related to *Calyptogena kaikoi* found off Japan [sequence divergence (d) = 1 to 2% of the mitochondrial cytochrome oxidase subunit I gene (COI) (*28*)]. Likewise, the vestimentiferan tubeworm *Escarpia spicata*, which exploits cold seeps and whale falls off southern California and sedimented hydrothermal vents in the Gulf of California, is genetically similar to *E. laminata* from West Florida Escarpment seeps in the Gulf of Mexico (d = 0.2%, mitochondrial COI) (*30*). Direct dispersal between the eastern Pacific and Gulf of Mexico has been unlikely since the closure of the

Isthmus of Panama to deep-water exchange (~10 Ma) (*31*).

Dispersal and Gene Flow in Contemporary Deep-Sea Hydrothermal Vent Environments

Knowledge of dispersal capabilities and extent of gene flow in contemporary species may aid in identification of biogeographic barriers or filters to dispersal that act on evolutionary time scales. Much of what we know about dispersal of deep-sea organisms comes from studies of vent species. Rapid colonization and population growth at nascent hydrothermal fields (*32, 33*) point to long-distance dispersal capabilities and prodigious reproductive capacities of vent invertebrates. These life-history traits are characteristic of weedy species that live in perennially disturbed environments (*34*). Although it is difficult to assess directly the dispersal abilities of deep-sea invertebrates (*35*), estimates of gene flow provide a measure of rates and modes of dispersal. For example, genetic evidence reveals that *Ventiella sulfuris*, an amphipod that broods its young and has no larval stage, is limited in its ability to cross habitat gaps separating the East Pacific Rise and the Galapagos Spreading Center (*36*). In contrast, high rates of gene flow across thousands of kilometers [reviewed in (*37*)] occur among disjunct East Pacific Rise populations of species that have planktonic larval stages (e.g., vent mussels, clams, limpets, tubeworms, and polychaetes). Developmental arrest at cold temperatures has been implicated in extending the duration and dispersal capabilities of larval life; empirical evidence for arrested development is now available for a vent-endemic polychaete species (*38*). Mussels and clams exhibit no evidence for isolation by distance across thousands of kilometers. For these bivalve mollusks, larvae from distant source populations probably mix in the water column before they settle at hydrothermal sites. Tubeworm populations exhibit genetic signatures of stepping-stone dispersal between neighboring vent habitats, indicating that average dispersal distances of tubeworm larvae (< 100 km) (*35*) may be considerably shorter than those of the bivalves.

Dispersal in open, turbulent systems seems trivial for marine species with large reproductive outputs and prolonged planktonic larval stages (*39*). More problematic is how dilution of larval propagules is kept low enough to account for large numbers of juvenile recruits found at extant vent habitats (*40*). One solution may be optimization of larval life-span to correspond with oscillatory deep-water circulation regimes, as proposed for the vestimentiferan tubeworm *Riftia pachyptila* (*35*). The likely average dispersal range of most vent larvae is 35 to 55 km,

assuming larval durations of 2 to 3 weeks and average along-axis velocities of <3 cm s^{-1} (35).

Chaotic advection by turbulent ocean currents and megaplumes associated with sea floor volcanic eruptions could open intermittent and coherent pulses of communication between vent invertebrate populations along ridge segments (41, 42). Another solution might involve larval behaviors that favor retention at their natal sites (e.g., demersal eggs and epi-benthic behaviors), with some long-distance dispersal of larvae to account for gene flow. Fundamental but missing ingredients are detailed knowledge of the worldwide distribution of vent and seep environments and of deep-ocean circulation patterns and the roles of variation in sea floor topography as barriers or filters to dispersal.

Biogeography

The global mid-ocean ridge system represents a nearly continuous, ~55,000- to 60,000-km-long volcanic chain that hosts a range of hydrothermal settings. Most of this volcanic chain remains unexplored for hydrothermal activity, but wherever systematic searches have been conducted along the mid-ocean ridge, signals of hydrothermal venting have been found, even along the slowest spreading ridge crests (43, 44). To date, six biogeographic provinces are recognized along mid-ocean ridges and back-arc spreading centers (Fig. 1), and more are likely to be discovered as exploration extends to higher latitudes. Known provinces correlate well with ocean basins and degrees of isolation along the mid-ocean ridge system (45). Differences in sedimentation rates and delivery of photosynthetically derived organic material, in geochemistry of venting fluids, and other habitat variables along the global mid-ocean ridge system influence the biogeography of vent faunas, but their effects are poorly quantified. Cold seeps are distributed globally along continental margins and subduction zones, but biogeographical relationships among seep faunas are not well understood because seeps have been studied less extensively than hydrothermal vents (6, 7).

Vicariance probably played an important role in the differentiation of hydrothermal vent provinces. For example, the East Pacific Rise and the northeast Pacific ridge system (Gorda, Juan de Fuca, and Explorer) once formed a continuous plate boundary

that was split ~28 Ma by the over-riding North American plate (46). The two modern ridge systems support related taxa (45). Potential vent habitats along the Cayman Rise in the Caribbean Sea may have become isolated from the Pacific ridges after closure of the Isthmus of Panama (~10 Ma), and closure of the Tethys Sea severed connections between Atlantic and Indian Ocean Ridge systems ~90 Ma (47). On the Mid-Atlantic Ridge, formation of the Azores Plateau was a relatively recent vicariant event (20 Ma) (48) that may have served to isolate deep hydrothermal systems to the north and south.
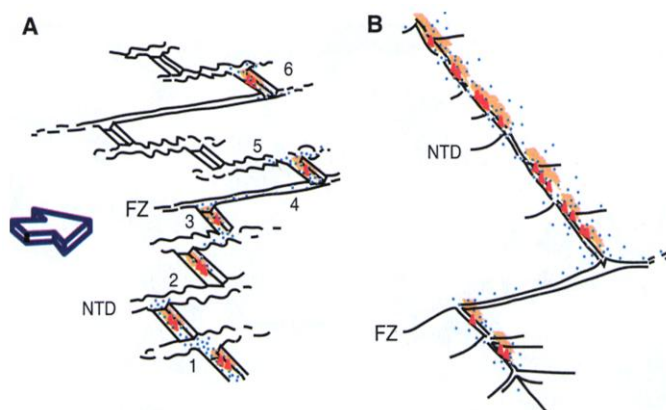
Fig. 3. (A) Schematic representation of a slow- to medium-spreading ridge system (e.g., Mid-Atlantic Ridge), including fracture zone (FZ) offsets and nontransform discontinuities (NTD). Active high-temperature venting is indicated by red triangles. Hydrothermal plumes (orange) are retained within steep-walled rift valleys. Distributions of larvae of vent taxa are indicated by blue dots. The large arrow signifies prevailing bottom-water current direction. Examples of potential biogeographic filters or conduits for northerly dispersal of larvae are as follows: (i) NTD offset is short, allowing effective dispersal, (ii) constricted and/or irregular NTD path hinders dispersal, despite favorable bottom current regional flow, (iii) dispersal between adjacent segments is aided by prevailing flow direction along interconnecting NTD, (iv) FZ links active segments, and exchange of propagules is relatively unrestricted, (v) barren segments and adverse flow direction constrain dispersal, and (vi) isolated community is prevented from wider dispersal by FZ and inactive adjacent segments. (B) Schematic representation of a fast-spreading ridge axis (e.g., East Pacific Rise); symbols as for (A). Note that hydrothermal plumes are not contained within rift valleys, there is a higher spatial frequency of venting, and there are no apparent topographic barriers to dispersal along axis, other than a major fracture zone offset.

Differences in sea floor spreading rate and topographic features also are likely to influence the biogeography of vent faunas (49, 50), but the effects of these variables on dispersal of plankton and nekton are largely unknown. Fracture zones (Fig. 3) disconnect actively spreading ridge segments (51). In areas with reduced fracturing, passive waterborne particles and larvae should be able to be transported far along a ridge axis (52). Pronounced transform valleys may also support hydrothermal activity (53) that might serve as stepping stones for dispersal.

The observed effects of segmentation are nonsystematic. For example, Mid-Atlantic

Ridge mussel species (Bathymodiolus azoricus and B. puteoserpentis) are separated by several large transforms and at least on intermediate ridge segment within which the two species hybridize (54). Some fracture zones with large offsets along the East Pacific Rise also limit gene flow, as observed in the polychaete Alvinella pompejana (55). Other topographic discontinuities may serve as barriers; for example, the Hess Deep between the East Pacific Rise and Galapagos Spreading Center may limit gene flow between populations of the alvinellid Paralvinella grasslei (55) and nearly eliminate gene flow in the amphipod Ventiella sulfuris (36). In contrast, large fracture zones on the Mid-Atlantic Ridge do not appear to limit gene flow in the shrimp, Rimicaris exoculata (56, 57). The tremendous dispersal capacity of the shrimp may be linked to the ability of juveniles to exploit photosynthetically derived resources (58), to the strong swimming abilities of its juvenile and adult stages, and to enhanced dispersal in fracture zone flows.

On a finer scale, mid-ocean ridge magmatic systems are broken or segmented by nontransform discontinuities every few tens of kilometers or so (59) (Fig. 3). Studies of gene flow in eastern Pacific vent species provide no evidence for barriers associated with these second-order segments (37). On the Mid-Atlantic Ridge, however, deeper ridge valleys with sills at either end of second-order discontinuities may serve to contain larvae and inhibit their transport.

Elevated sections of the mid-ocean ridge produced by volcanic hot spots (e.g., Iceland, the Azores Plateau) can restrict or divert deep-water currents. Isolation of Arctic and Atlantic deep waters by sills between Greenland and Iceland and between Iceland and Norway suggests that Arctic vent and seep provinces may be distinct from those of the Atlantic basin. Bathymetric differences along a ridge system can alter the chemistry of vent fluids in local ecosystems (60) and impose physiological constraints on the distribution and dispersal of constituent taxa (61). Such bathymetric effects may account for the presence of two biogeographic provinces along the Mid-Atlantic Ridge (62, 63).

Hydrothermal systems of back-arc basins in the western Pacific are geographically isolated from vents along mid-ocean ridges (47). Despite the potential for geo-

graphic isolation, a *Bathymodiolus* mussel species from western Pacific vents may be shared with vents along the Central Indian Ridge (*57*). Other back-arc hydrothermal settings—e.g., those of the East Scotia Ridge (southern Atlantic Ocean) (*64*) and the Andaman Ridge (northeast Indian Ocean)—remain unexplored. Seamounts may also support hydrothermal systems (*65*), but they also are largely unexplored.

Fundamental differences exist in the spacing and longevity of vent habitats along fast- versus slow-spreading ridge axes. On the fast-spreading East Pacific Rise, frequent volcanic eruptions engulf existing vent communities and create opportunities for new ones (*66*). East Pacific Rise species must be adapted for an ephemeral existence (*67*), with effective dispersal among closely spaced habitats and rapid population growth (*68*). Hydrothermal activity along the slow-spreading Mid-Atlantic Ridge frequently occurs under tectonic control, with venting dependent on deep faults and fissures that tap large, persistent reservoirs of hot rock rather than small pockets of molten lava (*69*). Mid-Atlantic Ridge vents may exist for longer periods at more distant spacing than East Pacific Rise fields (Fig. 3) (*49*, *69*). Temporal and spatial frequencies of hydrothermal vents suitable for colonization by vent-endemic organisms remain poorly known for most of the global mid-ocean ridge system (*69*, *70*).

Deep-Ocean Circulation

Deep-ocean circulation, which is driven by wind and by thermohaline effects that produce differences in density of water masses, has a global reach and helps exchange water among the ocean basins (Fig. 4) (*71*). Two strong constraints on deep circulation are the vertical component of Earth's rotation and topography of the ocean basin. The two constraints are merged as potential vorticity (*PV*, also known as planetary topog-

raphy) (*72*), measured by the ratio *H/f*, where *H* is ocean depth and *f* is the Coriolis parameter. Deep currents tend to follow contours of *PV* (*73*, *74*) except along western boundaries or in areas of turbulent diffusion driven by geothermal heating or mixing near topographic features. For example, deep western boundary currents in particular are important directional controls on the biogeography of seep faunas along ocean basin margins, especially in the Atlantic.

PV-following longitudinal circulation near the equator in the Atlantic Ocean may be implicated in the distribution of a vesicomyid clam species, *Calyptogena* aff. *kaikoi*, shared among seeps on the West Florida Escarpment and the Barbados accretionary prism and the Logatchev vent field on the Mid-Atlantic Ridge (*28*). A mussel species, *Bathymodiolus heckerae*, is shared between the West Florida Escarpment seeps and Blake Ridge seeps off the North Carolina coast; its closest relatives are *B. azoricus* and *B. puteoserpentis* from Mid-Atlantic Ridge vents (*75*). Longitudinal flow and movement of North Atlantic deep water through fracture zones near the equator (Romanche and Chain Fracture Zones) and 23°S (Rio de Janeiro Fracture Zone) may provide faunal linkages between the Gulf of Mexico seeps and seep communities recently discovered off the western coast of Africa (*76*). The hydrographic linkage is on a decadal scale, requiring intermediate stepping stones to connect populations. In the Pacific, the Galapagos Spreading Center, an east-west–trending plate boundary that branches off of the East Pacific Rise at the equator and lies within the region of strongest longitudinal flow at the equator, shares its hydrothermal vent fauna with that of the East Pacific Rise. The extensive biogeographic province of the East Pacific Rise (from ~20°N to 18°S) lies within a region of cross-cutting turbulent diffusion generated by ridge-crest topography and geothermal activity, which permits latitudinal dispersal despite the strong longitudinal flow constraint defined by *PV*.

Among the deep-circulation links suggested by the *PV* map (Fig. 4) is one between the eastern Pacific and the southern Atlantic. This raises the prospect that shared components may exist between southern segments of the East Pacific Rise, the East Scotia Ridge, and the southern Mid-Atlantic Ridge vent faunas, despite the disjunct nature of these ridges. If true, this result would be an exception to the hypothesis put forth by Tunnicliffe and Fowler (*45*) that dispersion of hydrothermal vent taxa occurs primarily along mid-ocean ridges. The *PV* field regions surrounding the Juan de Fuca Ridge and Azores Plateau are relatively isolated, which is consistent with biogeographic provinces defined by these regions. But as already noted, other explanations exist for the isolation of the Juan de Fuca Ridge (vicariance) and the Azores Plateau (depth) faunas. Biogeographic isolation due to vicariance, depth, and current regimes may reinforce one another.

The longitudinally connected regime near the equator switches to a circumpolar west-to-east regime near 25°S in the eastern Pacific (*77*, *78*). Ongoing studies are testing the relationship between the current regime shift and genetic discontinuities in this region (*79*).
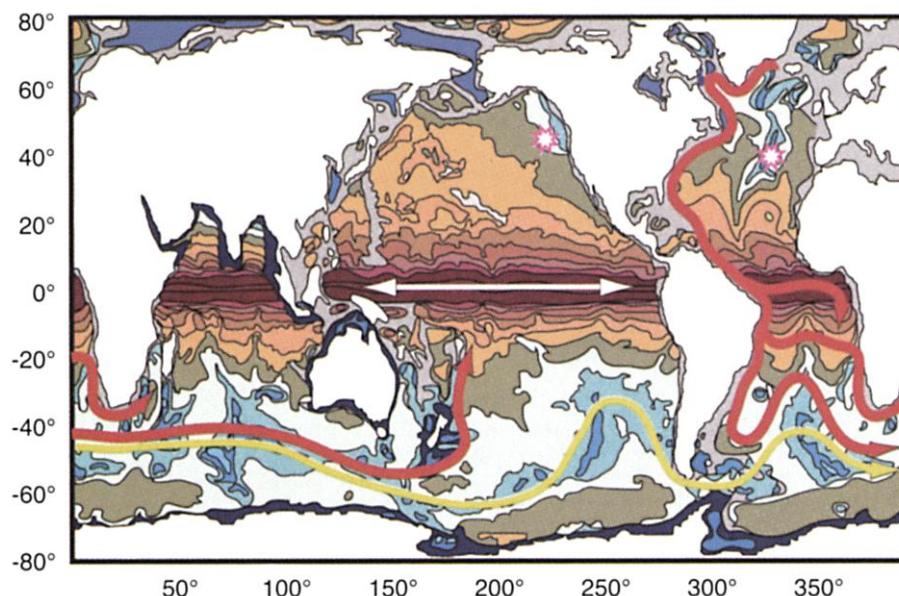
Fig. 4. Plot of *PV*, large-scale potential vorticity (see text for explanation). Values near the equator, where *f* is zero, are set to a constant. Color scale ranges from red, where the Coriolis effect is strongest, to blue, where topography dominates, and ignores the change in sign of *f* across the equator. Longitude is wrapped to display ocean basins clearly. In general, ocean currents tend to follow contours of *PV*, leading to longitudinal motions in the tropics (25°N to 25°S; white flow line illustrated only for Pacific) and circumpolar connections in the Southern Ocean. The Circumpolar Current (yellow flow line) spans the globe. Deep water formed in the northern North Atlantic flows into neighboring ocean basins in a system of swift, narrow, western boundary currents and interior zonal flows (red lines). In these western boundary currents, frictional terms in the equation of motion become important, allowing them to break the constraint of following *PV*. Isolated regimes of nearly uniform *PV* (pink and white stars) occur in ocean basins of the northern hemispheres.

Our understanding of biogeographic relationships among deep-sea chemosynthetically based ecosystems remains incomplete. For example, recent explorations of Indian Ocean vents revealed a fauna that is evolutionarily related to the fauna of western Pacific vents, with the notable exception of a shrimp that is closely related to a Mid-Atlantic Ridge species (*57, 80*). It is difficult to interpret these and other biogeographic observations with our present incomplete knowledge of deep-ocean currents and habitat distribution. Strategic selection of new study sites has the potential to resolve a global map of vent and seep biogeographic provinces and to identify contemporary processes and historical factors that help to define biogeographic boundaries. If the recent past is our guide, the bounty from such explorations is certain to include discovery of new animal and microbial taxa capable of physiological and ecological feats that we cannot yet imagine.

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