Gene Flow and Genetic Diversity in Naturally Fragmented Metapopulations of Deep-Sea Hydrothermal Vent Animals

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The ephemeral nature of deep-sea hydrothermal vents is expected to favor species with good colonization abilities, high dispersal rates, and rapid individual growth rates. Studies of gene flow in vent-endemic species provide glimpses into modes and patterns of dispersal. For some species, gene flow occurs without geographical bias (i.e., island model); their dispersal capabilities probably exceed the sampled geographical range. For other species, genetic differentiation increases with geographical distance (isolation-by-distance model) and suggests a stepping-stone mode of dispersal between neighboring vents. Genetic subdivision in a third group of species is associated with geographical offsets between contiguous segments of a ridge axis. These species all possess a free-living larval stage and average rates of gene flow (Nm) exceeding the critical value of one. In contrast, an amphipod that broods its young shows evidence for isolation-by-distance along a ridge axis and nearly complete isolation between distinct ridge axes. Early successional species (i.e., those that rapidly establish populations at nascent vents) also have high levels of genetic variability that probably results from a larger global population size. Bivalve species, which are restricted to a few of the known vent sites, appear at a later successional stage and have lower levels of variability. The relative successional position (early versus late) and overall abundance of a species may play significant roles in determining the retention of genetic diversity in populations inhabiting these ephemeral environments.
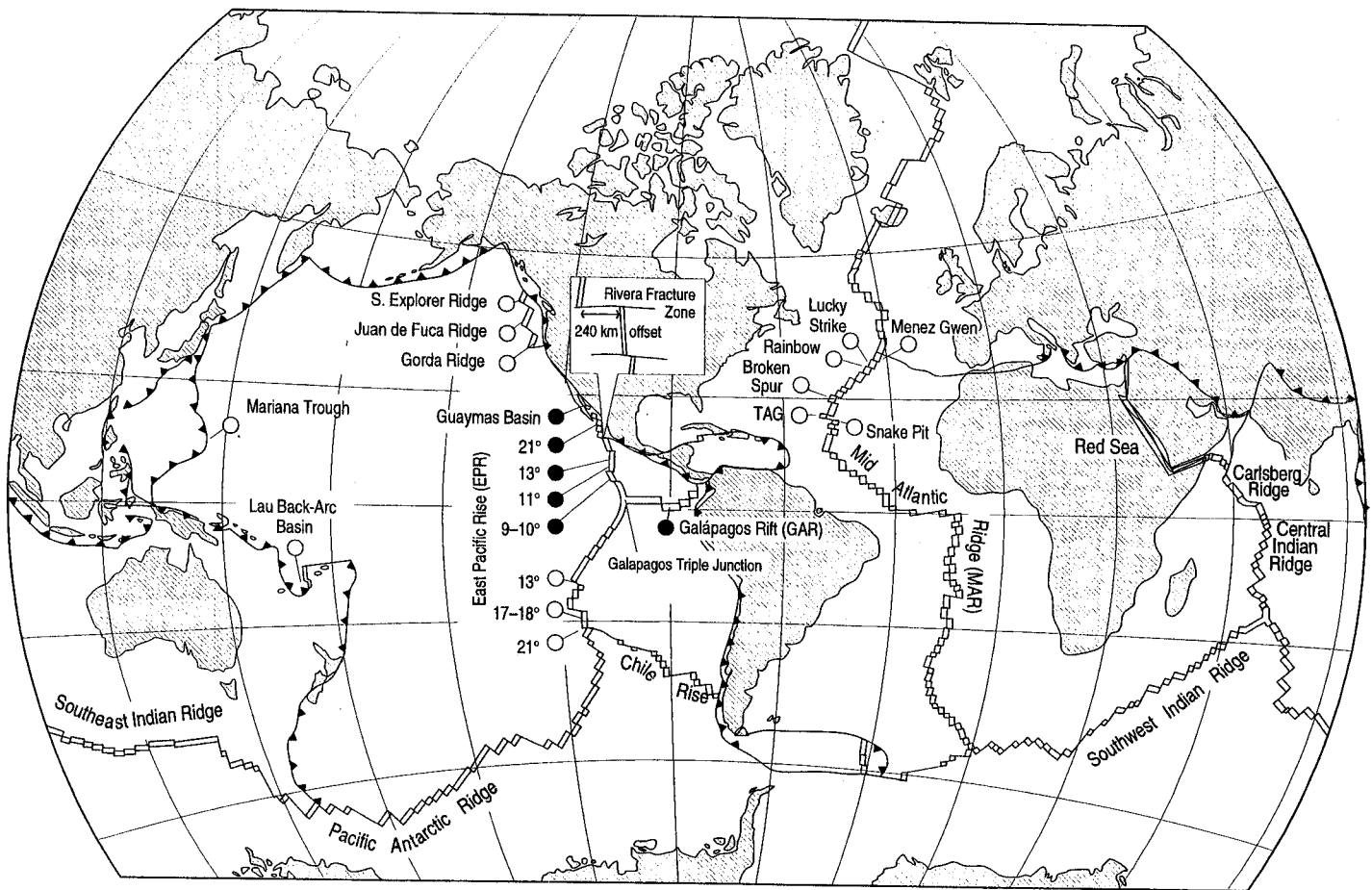
Specialized communities of animals associated with deep-sea hydrothermal vents were first discovered in 1977 along the Galapagos Rift, a spreading center that is part of the global oceanic ridge system (Figure 1). Dense island-like clusters of metazoan animals thrive in a sparse benthic realm that lacks sunlight or photosynthesis. The high biological productivity of these communities depends on chemoautotrophic bacteria that oxidize hydrogen sulfide emitted from submarine hot springs (Jannasch and Mottl 1985). Discrete vent habitats in the eastern Pacific tend to persist for only a few decades before venting diminishes and the sulfide-dependent organisms die (Fustec et al. 1987; Hessler et al. 1988a; Lalou and Brichet 1982; Tunnicliffe and Juniper 1990). Dead, or dying, habitats are commonly encountered along fast-spreading ridge segments. The ephemeral nature of these habitats should favor species with fast growth, early reproduction, and good dispersal abilities (Gaill and Hunt 1991; Grassle 1985b; McHugh 1987; Tunnicliffe and Juniper 1990). Mechanisms used by vent-endemic species to colonize new vents and disperse among existing habitats remain a subject of considerable interest to oceanographers (Tunnicliffe 1991). Herein I review studies aimed at assessing dispersal modes and rates of gene flow in 14 species of deep-sea hydrothermal vent animals. I have organized these studies in four sections according to theoretical models of population structure and observed topological constraints imposed by the oceanic ridge system.

The branching pattern of the oceanic ridge system (Figure 1) creates a hierarchical topology that may affect the genetic structure of vent-endemic organisms. On a local scale, active ridge segments often contain multiple hydrothermal fields, each composed of numerous high-temperature vents (80°C–350°C) and diffusely venting warm springs (0°C–30°C). However, due to the sporadic nature of volcanic and tectonic activity, the next active vent area may be tens to hundreds of kilometers distant. If the walls of the rift valley constrain bottom currents along the main axis, each spreading segment may act as a discrete

Figure 1. The mid-ocean ridge system. Double lines are spreading centers. Single lines with pointers are subduction zones showing the direction of subduction. The black dots mark known vent areas of the GAR and EPR that comprise most of the studies reviewed herein. Open circles mark other known vent sites. The inset displays a portion of the EPR encompassing the Rivera Fracture Zone. Modified from the RIDGE base map, courtesy of the Woods Hole Oceanographic Institution.

corridor for dispersal. For species with limited dispersal capability, populations occupying sites along a spreading segment should be more similar genetically than populations on discrete segments. Transform faults and horizontal offsets between contiguous ridge segments may act as barriers to dispersal for species that cannot rise above the walls of a rift valley. Even greater divergence is expected between populations occupying disjunct ridge axes.

Distinct faunal assemblages are associated with isolated ridge systems in the Pacific Ocean and between different ocean basins. Diversification of these communities may be linked to the regional history of sea-floor spreading (Van Dover 1990, 1995). Intermediate and fast spreading ocean ridges (spreading rates of 7–12 cm/year) in the eastern Pacific support vent communities dominated by vestimentiferan tube worms, alvinellid polychaetes, bathymodiolid mussels, and vesicomyid clams. Following a tectonic or volcanic event, free-living microbes are the first or-

ganisms to exploit sulfide-rich waters at a nascent vent field (Lutz and Haymon 1994). In the eastern Pacific, grazing and predatory Crustacea immediately follow these bacteria. Subsequently, grazing species of limpets and suspension-feeding polychaete worms, and vestimentiferan tube worms that harbor endosymbiotic sulfur-oxidizing bacteria colonize the vent habitats (Lutz et al. 1994). In a later stage of community development, symbiont-bearing mussels and clams replace the tube worms (Fustec et al. 1987; Hessler et al. 1988b); however, the rapid cycle of tectonic and volcanic events along fast-spreading systems can prevent communities from reaching this stage.

Dispersal Patterns

The first studies of dispersal modes in vent organisms focused on mollusks and applied Thorson's (1950) rules. Sizes of the first and second larval shells (e.g., the protoconch-I and protoconch-II stages in gastropods) reflect egg size and growth

prior to metamorphosis, respectively. Species with a small (ornately sculptured) protoconch-I and large protoconch-II have small eggs and actively feeding (planktotrophic) larvae that may contribute to dispersal potential. On the other hand, species with a large protoconch-I and small (or absent) protoconch-II have large yolky eggs, nonfeeding (nonplanktotrophic) larvae, and presumably limited dispersal potential. Lutz et al. (1986) examined larval shells and egg sizes of 30 species of vent mollusks; 27 had nonplanktotrophic development. The limited dispersal capability associated with this mode of development was unexpected for species that are restricted to these ephemeral environments. Lutz et al. (1986) speculated that the nonplanktotrophic species maintain their widespread distributions in the eastern Pacific by dispersing in a stepwise manner between disjunct hydrothermal sites along a ridge axis.

Caution is warranted, however, because Thorson's rules were based on studies of shallow-water species, and exceptions are

(A) Stepping-stone model
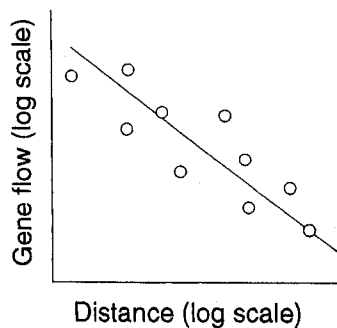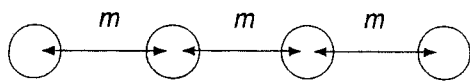
(B) Island Model
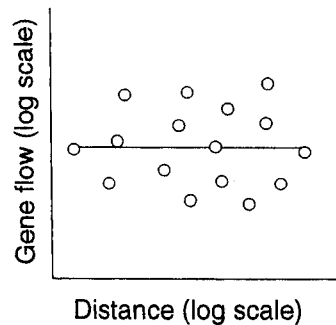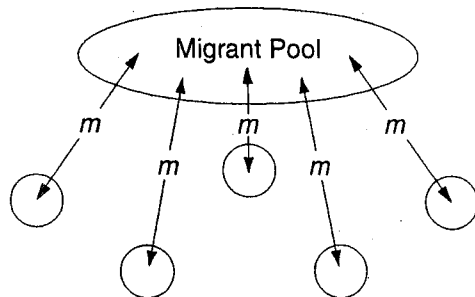
Figure 2. Models of population structure and gene flow. **(A)** The "stepping-stone model" is appropriate for species with limited dispersal capability—the rate of gene flow between colonies declines with increasing geographical distance. **(B)** The "island model" is appropriate for species with long-distance dispersal capability—the rate of gene flow between colonies is independent of geographical distance.

known (Hadfield and Strathmann 1990; Johannesson 1988). Facultative planktotrophy, absorption of dissolved amino acids, and delayed metamorphosis can extend the larval life span of some mollusks (Manahan 1990; Miller 1993; Pechenik 1990). Inferences about dispersal potential based on egg sizes and larval shell morphology may not accurately represent realized dispersal in the deep sea (reviewed by Young 1994). Away from the hydrothermal habitats, cold bottom temperatures ($\approx 2°C$) may lower or arrest larval development and permit dispersal over vast distances. We know even less about the life histories of most nonmolluscan species, for example, the alvinellid polychaetes and vestimentiferan tube worms. These reservations motivated our studies of gene flow as an indicator of realized modes and rates of dispersal.

Indirect Methods for Estimating Gene Flow

If dispersal occurs predominantly in a stepwise manner (i.e., along roughly linear systems as would be expected for ridge-associated vent species), it should be possible to identify a genetic signature associated with the "stepping-stone model" (Figure 2A). When dispersal occurs predominantly between neighboring colonies, the correlation in gene frequencies (or

genic similarity) between colonies is expected to decline monotonically with the number of steps between colonies (Kimura and Weiss 1964). The steepness of this decline increases with the number of dimensions in the stepping-stone model. A similar decline in genic correlation is expected under "isolation by distance" in continuously distributed species (Wright 1943). Under both models, species with limited dispersal capabilities are expected to show a decline in estimated rates of gene flow with increasing geographical distance (Slatkin 1993).

Population structure that is unbiased by geographical distance (Figure 2B) may be described by the classical island model of Wright (1931). This model is appropriate if dispersing individuals are drawn from a well-mixed pool of migrants. Estimated rates of gene flow between such colonies are not expected to vary with geographical distance (Slatkin 1993). Species with long-lived planktotrophic larvae and presumably long-distance dispersal capabilities should exhibit a pattern of population structure consistent with the island model.

The most commonly used method for inferring historical rates of gene flow is based on Wright's (1951) formula $F_{ST} = s_p^2 / [\bar{p}(1 - \bar{p})]$, where s_p^2 is the variance and $\bar{p}$ is the mean frequency of a particular allele

across populations. F_{ST}, the standardized variance in allelic frequencies, is inversely related to the historical rate of gene flow, approximately as $F_{ST} \approx 1/(4Nm + 1)$, where N is the variance effective population size and m is the average proportion of migrants in each population. For multiallelic gene frequency data, the average F_{ST} can be estimated by θ or G_{ST} methods (Nei and Chesser 1983; Weir and Cockerham 1984). Gene flow between colonies is inferred from the relationship $Nm \approx (1/\bar{F}_{ST} - 1)/4$. We typically do not know N or m separately, but we can interpret the product Nm as an average of the number of migrants exchanged per generation. Nm is not an actual number of individuals, it is a virtual number reflecting the historical number of migrants necessary to produce the observed F_{ST} under an island model. We assume that the genetic markers used for this estimate are selectively neutral and that colonies have reached equilibrium between gene flow and drift. Although equilibrium is rapidly achieved under most scenarios (Crow and Aoki 1984), nonequilibrium conditions may persist in regularly disturbed environments such as vent habitats. Slatkin and Barton (1989) examined a variety of methods for estimating Nm and found the F_{ST} method be relatively insensitive to violations of its assumptions (i.e., equilibrium, island model, and selective neutrality) and robust for the datasets typically obtained from allozyme studies. Some nonequilibrium conditions, such as recent range expansions, tend to produce signatures that can be revealed with these analytical methods (Slatkin 1993). The F_{ST} method has been extended to hierarchical population structures, stepping-stone dispersal, and isolation-by-distance models (Slatkin 1993; Slatkin and Voelm 1991).

France et al. (1992) provided the first application of these indirect methods to study dispersal in deep-sea organisms. In this and subsequent publications (Table 1), my colleagues and I have primarily used the DIST program (Slatkin 1993) to discriminate between island model and stepping-stone patterns of dispersal. DIST calculates $\hat{M}$, an estimate of Nm between all pairs of populations, and provides a regression of $\hat{M}$ values on pairwise geographical distances. Because the regression is based on nonindependent pairwise comparisons, we tested the significance of these relationships with Mantel's permutation test (see Manly 1991). Other indirect methods for assessing gene flow have been used in hydrothermal vent research.

Table 1. Allozyme diversity and gene flow in deep-sea hydrothermal vent organisms

Species	Range sampled	Occu-pancy	No. of loci	Nm^a	Slope[b]	Inter-cept[b]	P_{95}	F_{IS}	F_{ST}	H_S	H_T	Ref.[c]
Vestimentiferans												
R. pachyptila	3,960	1.00	14	5.4	−0.362	2.078	52.4	0.056	0.044	0.137	0.143	1
R. piscesia	270	1.00	15	3.3	0.043	2.085	46.7	0.191	0.070	0.154	0.166	2
T. jerichonanae	340	0.50	15	2.4	neg, in[d]	in	24.5	−0.120	0.094	0.058	0.064	3
O. alvinae	1,330	0.67	15	1.2	−0.396	1.409	28.4	0.126	0.168	0.126	0.151	3
Polychaetes												
P. grasslei	~4,000	na[d]	17	3.4	neg	na	63.5	0.011	0.068	0.253	0.271	4
A. pompejana	~1,200	na	17	5.7	neg	na	36.4	0.069	0.042	0.107	0.112	4
A. caudata	~900	na	17	6.7	neg	na	31.7	0.015	0.036	0.118	0.122	4
Bivalves												
C. magnifica	3,340	0.50	17	11.7	−0.027	1.245	5.9	−0.001	0.021	0.031	0.032	5
B. thermophilus	2,370	0.67	26	5.0	0.037	0.848	6.9	0.135	0.048	0.017	0.018	6
Limpets												
E. vitrea	3,340	0.83	10	1.0	0.020	0.346	17.5	0.063	0.204	0.059	0.074	7
L. pustulosus	2,370	0.67	16	2.5	−0.052	0.980	18.8	−0.036	0.090	0.046	0.051	7
L. elevatus	1,360	0.67	16	1.8	neg	in	20.3	0.081	0.121	0.066	0.075	7
L. galriftensis	1,360	0.50	16	1.4	neg	in	16.7	0.035	0.153	0.051	0.060	7
Amphipods												
V. sulfuris	3,340	0.83	13	0.3	−0.563[e]	1.764[e]	39.6	0.211	0.498	0.151	0.301	8

[a] Overall Nm estimated from multilocus F_{ST}.

[b] Isolation by distance: slope and intercept of log-log regression.

[c] References: (1) Black et al. 1994; (2) Southward et al. 1996b; (3) Black 1995; (4) Jollivet et al. 1995a; (5) Karl et al. 1996; (6) Craddock et al. 1995; (7) Craddock et al. 1997; (8) France et al. 1992.

[d] Abbreviations: neq = negative slope; in = insufficient data to estimate; na = not available.

[e] Slope for all populations (see Figure 3).

(A) Riftia pachyptila

(B) Bathymodiolus thermophilus
— mtDNA
— allozymes

(C) Ventiella sulfuris
EPR sites
all sites

log (DISTANCE)

Figure 3. Gene flow and geographical distance. (A) *Riftia pachyptila* and isolation-by-distance across eight discrete vents (least squares regression $y = 1.937 − 0.317x$; correlation coefficient $r = 0.752$). (B) *Bathymodiolus thermophilus* and island model dispersal as determined from allozymes ($y = 0.848 + 0.037x$; $r = 0.126$) and mtDNA ($y = 0.733 + 0.094x$; $r = 0.227$). (C) *Ventiella sulfuris* and ridge-based isolation: all localities ($y = 1.764 − 0.563x$; $r = 0.721$); EPR localities only ($y = 1.546 + 0.249x$; $r = 0.774$). Original data from Black et al. 1994; Craddock et al. 1995; and France et al. 1992.
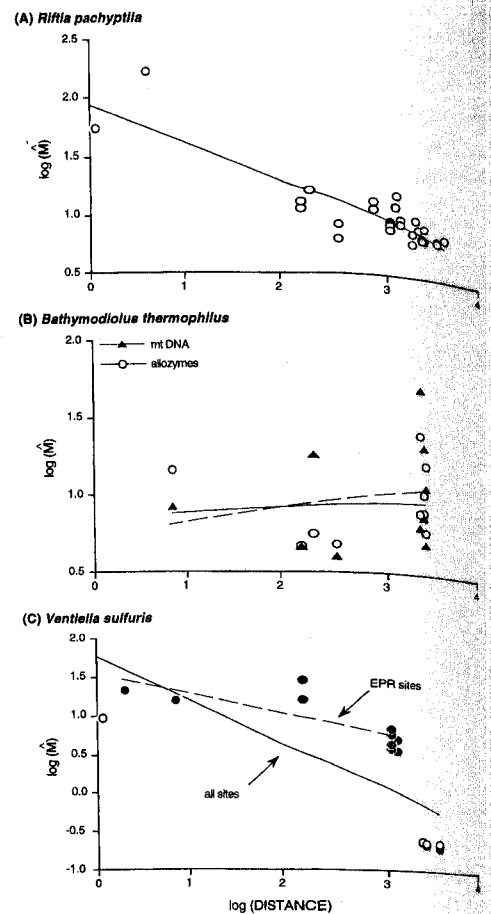
Jollivet et al. (1995a) applied the "private alleles" method (Slatkin 1985) to alvinellid polychaetes, but we were unable to use this method because insufficient numbers of rare alleles were found in the vestimentiferans, amphipods, and mollusks we examined. Rare alleles should be uncommon in species that inhabit ephemeral environments, since they are eliminated rapidly following frequent population bottlenecks and founder events (Fuerst and Maruyama 1986).

The confidence placed in these indirect methods depends mostly on the number of polymorphic loci used to infer gene flow and heterozygosity at these loci (Hellberg 1994). Allozymes provide the most economical method for obtaining such information for multiple independent gene loci. Restriction analysis of mitochondrial DNA and anonymous single-copy nuclear DNAs, as well as DNA sequences from nuclear and mitochondrial genes have been used to expand the suite of loci available for population genetic studies of vent organisms (Black 1995; Craddock et al. 1995; Karl et al. 1996; Kojima et al. 1995). To date, hierarchical patterns of genetic divergence and rates of gene flow have been examined in 14 species (Table 1). I focus on four patterns of differentiation and dispersal that have emerged from these studies.

Isolation by Distance

The giant vestimentiferan tube worm *Riftia pachyptila* (Vestimentifera: Obturata: Riftiidae) occurs at all the known vent areas along the Galapagos Rift (GAR) and northern East Pacific Rise (EPR). It often is highly abundant in young vent habitats and represents one of the early successional species of the EPR (Hessler et al. 1988b; Lutz et al. 1994). This sessile worm depends on endosymbiotic bacteria for nutrition and dies quickly when local sulfide emissions diminish or cease. Dispersal is presumed to occur through a free-swimming trochophore-like larval stage (Jones and Gardiner 1989).

Bucklin (1988) performed the first genetic study of *R. pachyptila* populations. She examined allozymes in samples taken from sites 3340 km apart on the GAR and 21°N latitude on the EPR (Figure 1). A high degree of genetic similarity between the samples suggested effective dispersal between these distant areas. Subsequently Black et al. (1994) examined allozymes in samples from six vent areas along the GAR, northern EPR (9°N, 11°N, 13°N, 21°N), and in the Gulf of California (27°N). We found polymorphism at 52.4% of the loci examined (Table 1) and identified a pattern of genetic divergence consistent with isolation by distance (Figure 3A). Estimated rates of migration ($\hat{M}$) among the six

hydrothermal areas decreased with distance (slope = −0.362) and was significant (Mantel test $P = .018$). Black et al. (1994) pooled subsamples taken from neighboring vents at both the 21°N and 13°N areas. To expand the geographical axis (X axis) and make it consistent with other studies reviewed herein, I separated these subsamples and reexamined the relationship between $\hat{M}$ and distance. The negative slope (−0.317) was similar and still significant (Mantel test $P = .002$). The two shortest distances (between subsamples within the 21°N and 13°N areas) did not strongly influence the relationship illustrated in Figure 3A. The decline in $\hat{M}$ was robust whether we measured distances along rift axes or as linear distances between sites. This declining pattern suggests an underlying isolation-by-distance

process that likely results from stepping-stone dispersal.

The average rate of gene flow (from F_{ST}; Table 1) among *R. pachyptila* populations was approximately 5.4 individuals per generation. Dispersal rates of $Nm > 1$ are sufficient to maintain genetic continuity throughout a species' range (Wright 1951). Allelic frequencies may vary, but discrete populations will tend to share the same suite of alleles (Allendorf 1983). We can interpret the Y intercept pictured in Figure 3A as the genetically effective neighborhood size under an isolation-by-distance model (Slatkin 1993). This value (approximately 2) suggests a neighborhood size of about 100 individuals/km. This estimate appears to be low as local populations often contain thousands of adult worms. However, the census number of adults undoubtedly varies immensely over time, and the effective number is the harmonic mean across these fluctuations (Crow and Kimura 1970). Biased sex ratios and unequal reproductive contributions may further reduce the effective number, especially in growing or declining populations (Gliddon and Goudet 1994). Thus the effective number of reproducing adults is likely to be substantially less (perhaps by an order of magnitude) than the census number at any point in time.

Based on morphological criteria, Jones (1985) hypothesized that Guaymas Basin (Gulf of California) populations of *Riftia* might constitute a discrete species. The allozyme data of Black et al. (1994) refuted this hypothesis. Although the Guaymas sample exhibited slight divergence in allelic frequencies, the difference was consistent with isolation by distance from other EPR populations. The elongated gills of Guaymas Basin *R. pachyptila* may be a consequence of phenotypic plasticity or adaptation to local chemical conditions. A high degree of phenotypic plasticity also appears to be a characteristic of *Ridgeia piscesia* in the northeastern Pacific (Southward et al. 1996a).

Weak evidence for stepping-stone dispersal also was found in other vestimentiferans (Table 1). The number of population samples was limited for both *Tevnia jerichonana* and *Oasisia alvinae,* and the apparent negative slopes of migration on geographical distance were not statistically significant (Black 1995). *Ridgeia piscesia* exhibited no evidence for isolation by distance along a short 240 km portion of the Juan de Fuca Ridge (Southward et al. 1996b). To adequately test dispersal hypotheses for this species, samples should

be collected from more distant sites in the northeastern Pacific, if they exist. *Escarpia spicata* and *Lamellibrachia barhami* may provide the best opportunity to examine isolation by distance as these species appear to have ranges that span ocean basins (Black 1995).

Island Model Dispersal

The mussel [*Bathymodiolus thermophilus* (Mollusca: Bivalvia: Mytilidae)] is abundant at several vent sites between the GAR and 13°N latitude on the EPR. Based on larval shell morphology, Lutz et al. (1986) hypothesized that *B. thermophilus* has a potentially long-lived planktotrophic stage that might mix thoroughly in the water column. Isolation by distance was not expected for this species, but the first genetic study of a vent species produced a contradictory result. Grassle (1985a) examined allozyme polymorphism at seven loci and identified fixed allelic differences that distinguished samples from the GAR and 13°N sites. She also identified differences in allelic frequencies between size classes and argued that founder events and restricted dispersal may be responsible for this differentiation. Ten years later, Craddock et al. (1995) examined allozymes (26 loci) and mitochondrial DNA variation in new samples from the same localities and intervening sites along the EPR (9°N–11°N). Unlike Grassle's result, our analysis provided no evidence for strong differentiation or divergence throughout this species' known range (Figure 3B). The overall effective rate of gene flow between populations was approximately five individuals per generation. As predicted by Lutz et al. (1986), the planktotrophic larvae of this species appear to be capable of dispersing hundreds of kilometers along a continuous ridge system and across gaps separating noncontiguous spreading centers. Although statistically significant heterogeneity (represented as F_{ST}) exists among *B. thermophilus* populations, we found no evidence for stepping-stone dispersal or hierarchical subdivision by ridge segments or axes.

Following a report on balancing selection in the American oyster (*Crassostrea virginica*; Karl and Avise 1992), we were concerned that allozymes might provide biased information about geographical heterogeneity in *B. thermophilus*. Thus we examined RFLP variation in whole mitochondrial DNA extracts from the same mussel populations (Craddock et al. 1995). We obtained pairwise G_{ST} values from mitochondrial haplotype frequencies and es-

timated gene flow from the relationship $\hat{M} \approx (1/G_{ST} - 1)/2$. The result obtained with mtDNA closely paralleled the allozyme data (Figure 3B). Two common mtDNA haplotypes occurred at similar frequencies in each population and provided no evidence for geographical subdivision or barriers to gene flow across this species' known range. However, these mtDNA haplotypes also may be subject to stabilizing selection; sex-biased transmission of mtDNA haplotypes occurs in an unrelated mytilid (Skibinski et al. 1994; Zouros et al. 1994). Notwithstanding, the strong concordance of nuclear (allozymes) and cytoplasmic (mtDNA) markers raised our confidence in the conclusion that high rates of gene flow and no isolation by distance characterize *B. thermophilus* populations.

Contrary to prior expectations, we obtained a similar result for the eastern Pacific clam [*Calyptogena magnifica* (Mollusca: Bivalvia: Vesicomyidae)]. Lutz et al. (1986) predicted that *C. magnifica* should have more limited dispersal capability than *B. thermophilus* because the clam has large yolky eggs and presumably nonplanktotrophic larvae. An allozyme study revealed too little genetic polymorphism to permit inferences about gene flow in *C. magnifica* (Vrijenhoek et al. 1994). To remedy this problem, Karl et al. (1996) designed species-specific DNA primers to amplify anonymous, single-copy, nuclear DNA markers in *C. magnifica*. Although polymorphism also was low for DNA markers, the combined allozyme and DNA data were sufficient to estimate gene flow. These markers revealed the highest estimated levels of gene flow ($Nm \approx 11.7$) for any vent species examined to date and no evidence for isolation by distance (Table 1). Despite its large yolky eggs and presumably nonplanktotrophic larvae, *C. magnifica* disperses effectively throughout its known range in the eastern Pacific. Nevertheless, it has a spotty occurrence within this range, a subject to which I return.

Several archaeogastropod limpets (Mollusca: Gastropoda) common to eastern Pacific hydrothermal vents also failed to provide evidence for isolation by distance (Craddock et al. 1997). Examination of larval shell morphology suggested these limpets possess nonplanktotrophic modes of development that may limit long-distance dispersal. Although we expected to find evidence for stepping-stone dispersal, two relatively widespread species, *Eulepetopsis vitrea* and *Lepetodrilus pustulosus*, pro-

vided no evidence for isolation by distance. Two species with limited distributions along the EPR, *L. elevatus* and *L. galriftensis*, exhibited significant divergence that may be consistent with stepping-stone dispersal, but the number of samples was inadequate to reject the null hypothesis ($\hat{M}$ is independent of distance). *L. elevatus* and *L. galriftensis* warrant further investigation with additional samples and molecular markers. The most pertinent lesson provided by these mollusks, however, is that we cannot predict modes of dispersal from cursory examinations of egg sizes or larval shell morphology (see also, Young 1994).

Segment-Scale Divergence

Alvinellid worms (Annelida: Polychaeta: Alvinellidae) are important constituents of eastern Pacific hydrothermal vent fauna. These worms possess large (lecithotrophic) eggs and presumably have limited long-distance dispersal capability. Jollivet et al. (1995a) examined hierarchical population structure and gene flow in three alvinellid species. They expected stepping-stone dispersal with increasing degrees of divergence at higher geographical scales, that is, demes within segments < demes on different segments < demes on different ridge axis. *Alvinella caudata* and *A. pompejana* were examined at the within- and between-segment scales. Both species exhibited significant subdivision, but only *A. pompejana* showed increased divergence at the between-segment scale. A more widely distributed species, *Paralvinella grasslei*, did not show increased divergence between ridge segments, but divergence doubled at the between-ridge scale. Jollivet et al. (1995a) also used Slatkin's (1993) isolation-by-distance method, but they did not report values that could be used in the subsequent comparative analyses (Table 1). Nevertheless, they suggest that bathymetric and edaphic gaps between ridge axes may have a greater effect on dispersal of *P. grasslei* than isolation by distance. I discuss an accentuated version of this effect below.

Ridge-Scale Isolation

All of the preceding studies involved species with a free-swimming larval stage. *Ventiella sulfuris* (Crustacea: Malacostraca: Lysianassidae) is a small amphipod that broods its eggs in a marsupium and releases free-swimming juveniles. It is a scavenger and suspended particle feeder that occurs in dense swarms. Juveniles and adults swarm near venting water, and

typically they do not occur more than 1 m from the bottom. France et al. (1992) hypothesized that dispersal should follow a stepping-stone pattern, as *V. sulfuris* lacks a specialized larval phase to facilitate long-distance dispersal in the water column. To test this hypothesis, we examined allozyme variation among populations ranging from 21°N latitude on the EPR to the GAR. Dispersal appears to be unimpeded along a 1200 km portion of the EPR from 10°N to 21°N latitude (Figure 3C). The mean of the $\hat{M}$ values between EPR populations was high, 11.6 individuals per generation (Table 1). An isolation-by-distance effect is apparent for EPR populations (black dots on Figure 3C), but this results from differences between populations separated by the Rivera Fracture Zone, a transform fault that offsets the ridge axis by 240 km between the 13°N and 21°N sites. Dispersal across the Rivera Fracture Zone dropped by approximately one-half, to 5.6 individuals per generation.

France et al. (1992) identified significant divergence between populations of *V. sulfuris* from the EPR and GAR (Figure 3C). The mean $\hat{M}$ between EPR and GAR populations was 0.23 individuals per generation (range: 0.21–0.25). This sharp decline in $\hat{M}$ values is decidedly nonlinear on a log-log scale, as expected under simple isolation by distance. The Hess Deep (a 5000 m deep and 50 km wide depression at the Galapagos Triple Junction) may act as a barrier to dispersal if it lacks suitable habitat for these amphipods. Alternatively, diverging bottom currents may deflect dispersal between these ridge axes—bottom water flows eastward near the Triple Junction and 8°N latitude (Lonsdale 1988). Approximately 50% of the total genetic diversity in *V. sulfuris* is contained in the differences between EPR and GAR populations (Table 1). A similar degree of ridge-based genetic subdivision was not observed in vent-endemic species that possess a free-swimming larval stage.

Metapopulations and Genetic Diversity

The rapid cycle of extinctions and recolonization events along a fast-spreading axis like the EPR should affect the genetic structure of vent populations. Frequent founder events during colonization can inflate F_{ST} (Wright 1940, 1977), and depending on the mode of colonization—"migrant pool" (equally representing all populations) versus "propagule pool" (representing one or a few extant populations)—may
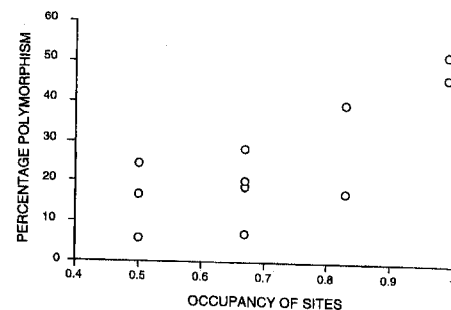

Figure 4. Relationship between levels of polymorphism (P_{95}) and the proportion of sites occupied by vent-endemic species (from Table 1, not including alvinellid polychaetes).

increase or decrease F_{ST} beyond the expectations of Wright's classical island model (Slatkin 1977; Wade and McCauley 1988). On the other hand, very high rates of extinction and recolonization will reduce the overall effective size of a metapopulation, thereby reducing both the within-population (H_S) and between-population (F_{ST}) components of genetic diversity (Gilpin 1991; Maruyama and Kimura 1980).

The levels of genetic diversity maintained in populations of vent-endemic organisms may directly reflect these metapopulation processes. Establishment of a species at a particular vent site represents a balance between local probabilities of colonization and extinction. Herein I define *occupancy* as the proportion of sampled sites at which a particular species was found (Table 1). Species with high occupancy should have a high probability of colonization and low probability of extinction, and vice versa for species with low occupancy. Based on the Maruyama–Kimura effect (Maruyama and Kimura 1980), we expect high-occupancy species to retain more genetic diversity than low-occupancy species.

Among the vent animals studied to date, polychaetes, vestimentiferans, and amphipods maintain high levels of genetic polymorphism (P_{95} range = 24.5–63.5% of the loci examined; Table 1). Limpets maintain intermediate levels of genetic diversity (P_{95} range = 16.7–20.3%), and bivalve mollusks have the lowest levels (P_{95} range: 5.9–6.9%). Overall the mean percentage of polymorphic loci within populations of these species was highly correlated with occupancy ($r = 0.787$, $P = .004$; Figure 4), as was average heterozygosity, H_S ($r = 0.732$, $P = .010$). However, H_S was correlated with P_{95} ($r = 0.927$, $P = .000$), and partial correlation analysis essentially eliminated the H_S relationship once P_{95} was taken into account. Other genetic vari-

bles also were internally correlated, as expected from their mathematical relationships. Total diversity (H_T) was correlated with H_S ($r = 0.889$, $P = .000$), F_{ST} ($r = 0.758$, $P = .007$), and F_{IS} ($r = 0.638$, $P = .035$). Homozygosity indices, F_{IS} and F_{ST}, were not correlated with one another.

The relationship between polymorphism and site occupancy probably depends on the stage of ecological succession and the disturbance regime experienced by each species. For each species, establishment at a site may require a specific set of physical, chemical, and biotic conditions. Long-term studies of a nascent vent habitat at 9°50′N on the EPR are beginning to provide insight in this regard (Lutz and Haymon 1994; Lutz et al. 1994). A disruptive volcanic event in April 1991 covered an active vent habitat with fresh lava. By March 1992, numerous discrete vents were colonized by the vestimentiferan *Tevnia jerichonana*, dense groups of limpets (*Lepetodrilus* spp.), and brachyuran crabs. One year later, adult *R. pachyptila* were established and spawning. Growth rates of these *R. pachyptila* are the highest known for any marine animal (Lutz et al. 1994). The spring of 1996 witnessed a thriving community composed of tube worms, limpets, crabs, and alvinellid polychaetes. Although populations of the bivalve mollusks *B. thermophilus* and *C. magnifica* occurred nearby (<0.5 km), only a few *B. thermophilus* and no *C. magnifica* were found in the nascent area (Shank TM, personal communication). *C. magnifica* and *B. thermophilus* have among the highest rates of gene flow estimated for vent-endemic species (Table 1). Dispersal ability undoubtedly does not limit the establishment of these bivalves. A similar pattern of succession observed along the GAR led Hessler et al. (1988b) to suggest that these bivalves represent the late successional community at eastern Pacific vents. What prevents their establishment at nascent vents remains unknown, however.

The rapidity of tectonic and volcanic events may be responsible for the low occupancy of eastern Pacific sites by these bivalves. If the cycle of disturbance is too rapid, many vent areas may fail to reach the physical/chemical/biological stage of succession required by these bivalves. Although local populations can be very large, their globally effective population size is a product of local population size (N) and the number (n) of extant populations. With high extinction and recolonization rates, the product nN will determine the retention of selectively neutral genetic diversity (Maruyama and Kimura 1980). It is likely that nN is relatively small for these bivalves. However, the occupancy/diversity relationship may be influenced by phylogenetic constraints acting on these organisms. For example, the two bivalves have low occupancy and the lowest genetic diversity, while tube worms have high occupancy and high polymorphism. Clearly, large differences in life history, physiology, and genealogical history also exist between these taxa. The observed relationship is tantalizing but only tentative, until an adequate number of within-clade studies have been conducted. During the next 2 years, we plan to conduct parallel studies of what appear to be the same species from the southern EPR (13°S to 21°S latitude) (see Geistdoerfer et al. 1995) and a distinct suite of species (mostly shrimp and mussels) from the Mid-Atlantic Ridge (9°N to 27°N latitude) (see Van Dover 1995). These contrasts should be informative because habitat turnover is expected to be fast along the super-fast-spreading, southern EPR and very slow along the Mid-Atlantic Ridge where hydrothermal activity may persist for many thousands of years (Rona et al. 1993).

The multilocus estimator of deviation from Hardy–Weinberg equilibrium, F_{IS}, also was marginally correlated with occupancy ($r = 0.604$, $P = .049$) and its partial correlation increased (0.759) when other factors (e.g., P_{95}) were taken into account. High F_{IS} values occurred in *V. sulfuris* and *R. piscesia*, high-occupancy species that rapidly colonize vents. Rapid colonization by propagules from several divergent sources might create initial Wahlund effects that are reflected in these high F_{IS} values. Nevertheless, such nonequilibrium effects at individual loci would be eliminated after one generation of random mating. Nonequilibrium conditions would leave a more persistent signature in two-locus genotypic combinations. Unfortunately, present sample sizes were not large enough to test this hypothesis. Such conditions might also affect the reliability of inferences about gene flow (Nm) in these species, as the estimation procedure assumes the diversifying effects of genetic drift and homogenizing effects of gene flow have reached equilibrium (Slatkin 1993).

Wahlund effects also might result from sampling across local-scale genetic subdivision in time or space. Grassle (1985a) reported shifts in gene frequencies between age classes of *B. thermophilus*—this warrants reinvestigation. Jollivet et al. (1995b) identified a patchy genetic substructure in local populations of alvinellid polychaetes. They provided evidence that differential selection in a thermally heterolgeneous environment might be responsible for the microspatial differentiation observed at some loci. Perhaps the retention of polymorphism in high-occupancy species occurs because they are capable of living in more heterogeneous environments, or vice versa. Unfortunately, experimental studies of the physical tolerances of most deep-sea species are not feasible. Genetic analyses of more species on smaller spatial scales and with larger sample sizes will be necessary to address these issues.

Conclusions

Of the 14 vent-endemic species examined to date, all but one have a free-swimming larval stage, an amphipod that broods its young and apparently does not disperse high in the water column. Although the amphipod exhibits high rates of dispersal along the EPR, little mixing occurs with GAR populations. The remaining species all exhibit rates of gene flow (Nm) exceeding the critical value of one. Two species of bivalve mollusks and two limpet species exhibit high rates of gene flow that are unimpeded by the topology of the ridge system or geographical distance. Several vestimentiferan tube worms exhibit evidence for isolation by distance, and some alvinellid polychaetes exhibit weak genetic subdivision based on ridge-segment versus ridge-axis geographical scales.

For deep-sea mollusks, inferences about larval life history based on egg sizes or shell morphologies do not provide useful guides to dispersal patterns or rates. Factors other than planktotrophy versus nonplanktotrophy play a role in determining realized dispersal abilities of these deep-sea species. We need studies of oceanic currents at various depths, larval positions in the water column, settlement cues, and the physical, chemical, and biotic requirements of settled juveniles and adults. We also need studies of the geological histories and stability of these vent areas.

High rates of disturbance and position in ecological successions may determine levels of genetic diversity retained in metapopulations of vent-endemic species. For the organisms examined to date, species that occur at most of the sampled

sites (high occupancy) tend to occur earlier in vent communities and have higher levels of genetic variability. Species with low occupancy occur late in succession and have very low levels of variability. It will be interesting to see if this pattern persists as we add more species to the analysis. The planned comparative studies involving species from super-fast-spreading systems versus slow-spreading systems will provide a useful test of the occupancy/diversity hypothesis raised by this review.

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