



Gene flow and dispersal in deep-sea hydrothermal vent animals

Robert C. VRIJENHOEK, Timothy SHANK, and Richard A. LUTZ

Center for Theoretical & Applied Genetics, and Institute of Marine and Coastal Sciences

Rutgers University 71 Dudley Road New Brunswick, New Jersey 08901-4521 USA

Fax: (1) 732 932 6557 - email: vrijen@ahab.rutgers.edu

The fragmented and ephemeral nature of hydrothermal vents in the eastern Pacific suggests that endemic organisms should possess well-developed dispersal capabilities. Early attempts to infer dispersal rates of vent species focused on mollusks, because egg sizes and larval shell-remnants reflect larval life-span and feeding mode (Lutz et al., 1986). Reservations exist, however, about such indirect methods to infer dispersal "potential"; consequently, a number of investigators have begun to examine larval development, growth, and longevity more directly, with the goal of determining the limits to dispersal potential (Young, 1994).

Recently researchers have applied genetic approaches to infer dispersal modes and estimate rates of gene flow among populations of hydrothermal vent organisms (reviewed by Vrijenhoek, 1997). Herein, we relate these genetic studies to a parallel study of colonization of a nascent vent habitat (9°50'N latitude on the East Pacific Rise; Shank et al., 1998). We used the F_{ST} method to estimate migration rates (i.e., Nm values) from gene frequency data (see Vrijenhoek, 1997, for a discussion of methods and the "island" and "stepping-stone" models of population structure). Nm is the virtual number of migrants per generation required to explain the observed degree of diversification (F_{ST} values) among colonies.

I - Patterns of dispersal and rates of gene flow

1- Stepping-stone dispersal – Lutz et al. (1986) examined larval shell structure in 30 species of vent mollusks and found that 27 probably have nonplanktotrophic development, a surprising result given the assumption that this developmental mode limits dispersal. Consequently, they hypothesized that the nonplanktotrophic species maintain wide-spread distributions by dispersing in a stepwise manner between disjunct hydrothermal sites along a ridge axis. If dispersal occurs in such a stepping-stone

fashion, estimates of Nm between colonies should decline with the distance between colonies.

We observed such a declining pattern in two of the four vestimentiferan species examined to date (Black et al., 1994, 1998). *Riftia pachyptila* Jones, 1981 populations showed a declining pattern of gene flow (Fig. 2a) across 4000 km, involving segments of the northern East Pacific Rise (NEPR) and Galapagos Rift (GAR). Lateral offsets (e.g., the Rivera Fracture Zone) and gaps between the NEPR and GAR (e.g., the Hess Deep), did not appear to influence this pattern. *Oasisia alvinae* Jones, 1985 showed a similar decline along a 1330 km portion of the NEPR; however, the range (340 km) and number of samples of *Tevnia jerichonana* Jones, 1985 were not sufficient to reveal evidence for stepping-stone dispersal. Although a sufficient number of *Ridgeia piscesae* Jones, 1985 samples were examined, this species exhibited no decline in Nm along a 400 km portion of the Juan de Fuca Ridge; however, the sampled range may be within the average dispersal distance of its trochophore larvae (see Young, 1994).

2 - Island model dispersal – Lutz et al., (1986) hypothesized that the vent mussel, *Bathymodiolus thermophilus* Kenk & Wilson, 1985 has a long-lived planktotrophic stage, and consequently, long-distance dispersal capabilities. The genetic structure of such a species may be predicted by the island model. If dispersing larvae are thoroughly mixed into a migrant pool, population structure will be unbiased by geographical distance. As expected, examination of allozymes and mitochondrial DNA variation in *B. thermophilus* samples from the GAR and NEPR (9-13°N) revealed a high rate of dispersal ($Nm \approx 5$ individuals per generation) and no evidence for a decline of Nm with geographical distance across a 2400 km range (Fig. 2b; Craddock et al., 1995). The larvae of this species appear to be capable of dispersing hundreds of kilometres

along a ridge system and across gaps separating non-contiguous spreading centres.

However, predictions based on larval shell morphology are not always accurate. For example, Lutz et al., (1986) hypothesized that the vent clam *Calyptogena magnifica* Boss & Turner, 1980 has nonplanktotrophic larvae and more limited dispersal abilities than *B. thermophilus*. Nevertheless, genetic analysis revealed that this clam has more than twice the realized dispersal rate ($Nm \approx 12$) of the mussel (Karl et al., 1996). Its high Nm value seems anomalous, given *C. magnifica*'s spotty occurrence along the NEPR/GAR; however, this clam is a late colonizer of nascent vents (Shank et al., 1998). Although the gene flow study showed dispersal abilities of *C. magnifica* are not limited, adults may fail to populate sites that experience a high frequency of disturbance.

Larval shell-structures also suggested that archaeogastropod limpets are nonplanktotrophic (Lutz et al., 1986). Compared to the bivalves and tube-worms, four species of limpets from the NEPR/GAR had relatively low rates of gene flow (average Nm values ranged from 1 to 2.5, Craddock et al., 1996). Nevertheless, rates of gene flow in two species (*Eulepetopsis vitrea* McLean, 1990 and *Lepetodrilus pustulosus* McLean, 1988) were unbiased by geographical distance. Although we observed declines in Nm with distance in two other limpets, *Lepetodrilus elevatus* McLean, 1988 and *L. galrifitensi* McLean, 1993, the samples were not sufficient in number to test the stepping-stone hypothesis. Clearly, it is risky to infer modes of dispersal from examinations of egg sizes or larval shell morphology in hydrothermal vent mollusks.

3 - Divergence between ridge segments – If the walls of rift valleys constrain bottom currents, each spreading segment may act as a separate dispersal corridor. Transform faults and lateral offsets between contiguous segments may act as barriers to dispersal for species that do not rise above the walls of a rift valley. Consequently, more gene flow should occur among colonies along a segment than between populations on disjunct segments. Jollivet et al., (1995) hypothesized that the large lecithotrophic eggs of alvinellid polychaetes may limit long-distance dispersal between offset segments, and more so, between separate spreading centres. *Alvinella pompejana* Desbruyères et Laubier, 1980 exhibited the expected pattern of greater divergence with an increasing scale of topographical separation, but *Alvinella caudata* Desbruyères et Laubier, 1986 did not. Although the widely distributed species, *Paralvinella grasslei* Desbruyères et Laubier, 1982 showed no increase in divergence between disjunct segments, divergence doubled between the NEPR and GAR. Bathymetric and edaphic gaps between these spreading centres appear to have a greater influence on dispersal of *P. grasslei* than geographical distance alone.

4 - Ridge-scale isolation – All the preceding vent species possess a free-swimming larval stage. In contrast, a study of the amphipod, *Ventiella sulfuris* Barnard & Ingram, 1990 revealed that topographical gaps provide significant barriers to the dispersal of species lacking such larvae (Fig. 2c; France et al., 1992). This amphipod broods its eggs and releases juveniles that live within a few meters of the bottom. Genetic analysis revealed that dispersal was unimpeded along a ridge segment ($Nm \approx 12$), but dispersal across the Rivera Fracture Zone was half as great ($Nm \approx 6$). Furthermore, dispersal between the NEPR and GAR was negligible (less than one migrant every four generations). The Hess Deep may act as a nearly complete barrier to dispersal of these amphipods, or perhaps, diverging bottom currents deflect dispersal between the two spreading centres. The more relevant point, however, is that the 11 other vent-endemic species with free-swimming larvae did not show a similarly large ridge-scale effect.

II - Vent metapopulations, colonization order, and genetic diversity

High rates of habitat disturbance at eastern Pacific vents and a species' position in the temporal sequence of vent community development (i.e., succession) affect levels of genetic diversity. Species with established populations at most of the known vent areas (e.g., *Riftia pachyptila*, *Paralvinella grasslei*, and *Eulepetopsis vitrea*) have higher levels of genetic diversity than species that occupy fewer areas (e.g. *Bathymodiolus thermophilus* and *Calyptogena magnifica*) (Vrijenhoek, 1997). The latter species with "low occupancy" would have smaller metapopulation sizes (a product of the number and size of individual populations), and thus be more prone to the loss of selectively neutral genetic polymorphisms due to population bottlenecks and founder events. Levels of genetic diversity in the 12 species examined to date were unrelated to their estimated migration rates.

Nevertheless, the likelihood of a species visibly occupying a site is confounded with the order in which species colonize nascent vents. A long-term study (Shank et al. 1998) of colonization at the 9°50'N site on the NEPR permitted a closer look at this potential relationship. We categorized the species as early colonizers (appearing within 2 years of vent formation: *R. pachyptila*, *Ridgeia piscesae*, *Tevnia jerichonana*, *Paralvinella grasslei*, *Alvinella pompejana*, *A. caudata*, *Lepetodrilus elevatus* and *Ventiella sulfuris*) or late colonizers (after 2 years: *Oasisia alvinae*, *C. magnifica*, *B. thermophilus*, and *E. vitrea*). Using the genetic data summarized in Vrijenhoek (1997), we found that the early colonizers have more than twice the genetic diversity (mean percentage of polymorphic loci = 39.4% ± 4.73% se) of the late colonizers

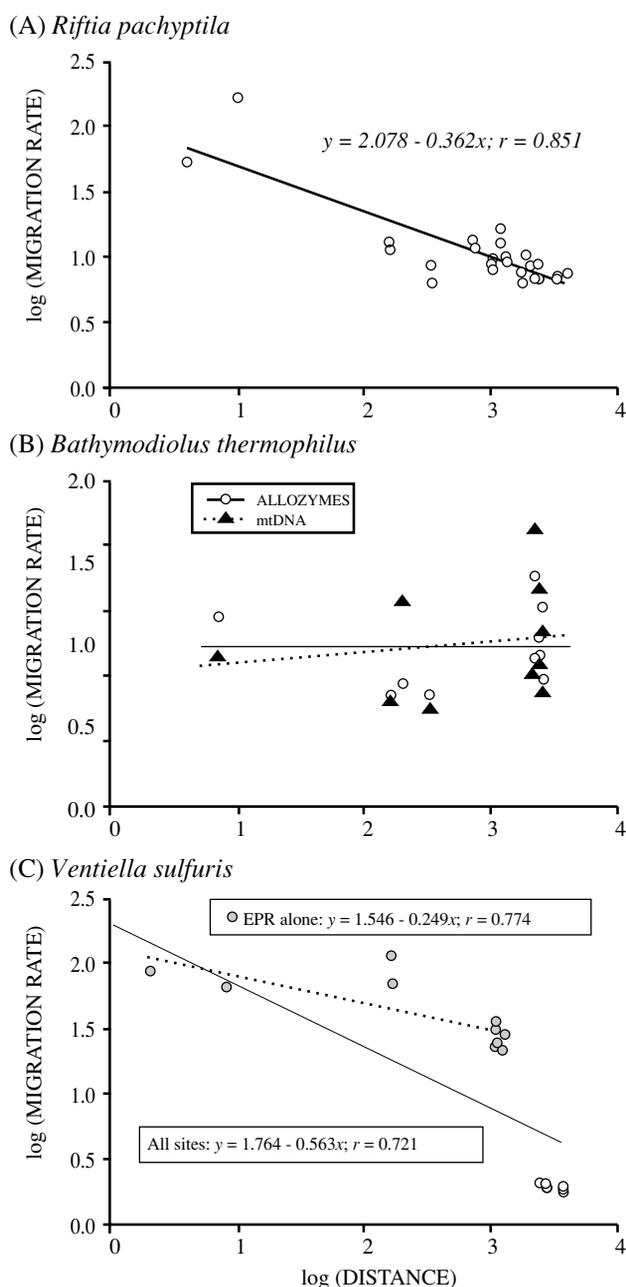


Figure 1. Relationships between gene flow and geographical distance in three species of hydrothermal vent organisms. **A.** *Riftia pachyptila* and stepping-stone dispersal (from Black et al. 1994; based on an allozyme study). **B.** *Bathymodiolus thermophilus* and island model dispersal (from Craddock et al., 1995; based on allozymes and mtDNA). **C.** *Ventiella sulfuris* and ridge-based isolation (from France et al., 1992; based on allozymes). The *V. sulfuris* data are separated into relationships among EPR populations alone (dashed line) and all populations (EPR and GAR) together (solid line).

(14.7% \pm 6.69%; one-way ANOVA $F_{1,10} = 9.09$; $P < 0.013$). With high levels of disturbance, as occurs in the

eastern Pacific, community development at some venting areas may never present opportunities for establishment of some of these late-appearing species. Under such disclimax conditions, late colonizers probably maintain smaller metapopulation sizes than the early colonizers. Rapid establishment and persistence at nascent vents, not migration rates per se, appear to be critical factors affecting the retention of genetic diversity under conditions of frequent local extinctions, recolonization events, and migration among fragmented metapopulations.

Our goals over the next several years are to determine whether these apparent relationships between colonization order, site occupancy, and genetic diversity are exacerbated along a super fast-spreading ridge axis (e.g., the southern East Pacific Rise) or diminished along a slow-spreading ridge system (e.g., the Mid-Atlantic Ridge). Rates of habitat turn-over are expected to have significant effects on the retention of genetic diversity, and perhaps on rates of molecular evolution and speciation in hydrothermal vent organisms.

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