

Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 1. Influence of vent site distribution, bottom currents, and biological patterns

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Abstract

Deep-sea hydrothermal-vent habitats are typically linear, discontinuous, and short-lived. Some of the vent fauna such as the endemic polychaete family Alvinellidae are thought to lack a planktotrophic larval stage and therefore not to broadcast-release their offspring. The genetic evidence points to exchanges on a scale that seems to contradict this type of reproductive pattern. However, the rift valley may topographically rectify the bottom currents, thereby facilitating the dispersal of propagules between active vent sites separated in some cases by 10s of kilometers or more along the ridge axis. A propagule flux model based on a matrix of intersite distances, long-term current-meter data, and information on the biology and ecology of Alvinellidae was developed to test this hypothesis. Calculations of the number of migrants exchanged between two populations per generation (N_m) allowed comparisons with estimates obtained from genetic studies. N_m displays a logarithmic decrease with increasing dispersal duration and reaches the critical value of 1 after 8 d when the propagule flux model was run in standard conditions. At most, propagule traveling time cannot reasonably exceed 15–30 d, according to the model, whereas reported distances between sites would require longer lasting dispersal abilities. Two nonexclusive explanations are proposed. First, some aspects of the biology of Alvinellidae have been overlooked and long-distance dispersal does occur. Second, such dispersal never occurs in Alvinellidae, but the spatial-temporal dynamics of vent sites over geological time-scales allows short-range dispersal processes to maintain gene flow.

Deep-sea hydrothermal-vent habitats are characterized by temperatures higher than ambient for the deep sea, lower oxygen concentration, higher levels of toxic compounds (metals, sulfide), and extreme spatial and temporal variability (Tunnicliffe 1991). The biology and life history of the vent fauna are closely linked with these features, which are stable over geological time on a large spatial scale. In contrast, vent sites seem to be ephemeral on short temporal scales (Lalou 1991). Hydrothermal activity indeed shifts along the ridges, generating numerous short-lived spots and consequently forcing the endemic fauna to colonize new vents as they appear. In the eastern Pacific, hydrothermally active venting areas are restricted to a few portions of oceanic ridges. The continuity between the sediment-covered ridge in the Gulf of California (Guaymas Basin), the East Pacific Rise (EPR), and the Galápagos Rift is of particular interest to biologists. Segmentation of the ridge by transform faults and the great distance separating the main hydrothermal areas raise the question of dispersal processes. This

question is important for understanding the population dynamics, population genetics, phylogeny, and biogeography of the hydrothermal-vent fauna.

One expected consequence of such an ephemeral and patchy habitat would be that hydrothermal-vent species have a very restricted distribution. Unexpectedly, most species seem to be distributed almost all along this whole system of connected ridges. Animals would therefore be expected to largely disperse their offspring and to display indirect development with planktotrophic larvae. However, dispersal strategies inferred so far from deep-sea hydrothermal taxa seem to follow phylogenetic rather than habitat constraints—some species seem to have planktotrophic larvae, whereas others do not (Lutz et al. 1984; Van Dover et al. 1985). Despite these inconsistencies, hydrothermal taxa apparently all succeed in maintaining species' identity over great distances (Black et al. 1994; Craddock et al. 1995; Jollivet et al. 1995).

One explanation for this phenomenon is that larvae (or other developmental stages) might be entrained along the rift axis by the strongly topographically rectified near-bottom currents and colonize new vents via a stepwise pattern. This assumption first requires that individuals are neutrally buoyant or light enough to be carried away by a neutrally buoyant fluid lens. Kim et al. (1994) showed that vertical entrainment by plumes is strong enough to carry larvae several hundred meters above the bottom, and Mullineaux et al. (1991) suggested that even some juveniles could be entrained. Second, transport by currents requires that the traveler withstand non-vent conditions for a certain period. Although this could be the case for some larval stages, it seems unlikely for the juveniles and adults of those species strictly dependent on hydrothermal conditions (temperature, H_2S). Finally, the dispersal efficiency depends on the probability of finding a suitable habitat. Because vent sites are distributed in clusters,

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this probability is high when the propagule travels within a cluster but will dramatically decrease outside the boundaries of a vent field or vent area. Such constraints seriously limit the dispersal capabilities of the vent fauna between well-separated venting areas, especially for those species supposed to have a direct development or lecithotrophic larvae. Thorson (1961), however, indicated that planktonic larval life and lecithotrophy can sometimes co-occur. Furthermore, Lutz et al. (1980, 1984) and Zottoli (1983) suggested that the dramatic difference between the thermal conditions at vents and the cold ambient seawater in which propagules would travel might delay metamorphosis and prolong the dispersal stage of vent larvae.

Alvinellid polychaetes are endemic to deep-sea vents in the Pacific, and the species generally have wide geographic distributions (Desbruyères and Laubier 1991). However, species that have been studied in detail (e.g. *Paralvinella grasslei*) are thought to have lecithotrophic larvae, and direct development has even been hypothesized (Zal et al. 1995). Alvinellidae is closely related to the Terebellidae and Ampharetidae (Desbruyères and Laubier 1991; Féral et al. 1994) and dominates "smoker" habitats, i.e. the walls of active high-temperature (200–400°C) sulfide spires, where it dwells in tubes at intermediate temperatures of 10–50°C or occasionally higher (Chevaldonné et al. 1991, 1992). As a consequence, some alvinellid species restricted to vent chimneys have strict ecological requirements and adults or juveniles are highly sensitive to nonvent conditions (pers. obs.). At vents of the Guaymas Basin, EPR, and Galápagos Rift, five species are found, three of which are conspicuous and abundant—*Alvinella pompejana*, *Alvinella caudata*, and *P. grasslei* (Desbruyères and Laubier 1991; Chevaldonné and Jollivet 1993). Jollivet et al. (1995) recently demonstrated that genetic differentiation is high between neighboring populations of alvinellid species but does not increase with increasing distance along the ridge. According to gene flow estimates, exchanges between populations must therefore be high enough to maintain genetic homogeneity along the species' range despite the evidence of high rates of extinction and recolonization in populations. Dispersal abilities and larval exchange should therefore be in agreement with the level of gene flow estimated so far under the neutral assumptions of the one-dimensional stepping-stone model (Kimura and Weiss 1964).

We propose a preliminary model that addresses three main questions. Given the present knowledge of the spatial distribution of hydrothermal-vent areas, what is the order of magnitude of the distances to be covered by propagules exchanged between two populations? Bottom currents topographically rectified by the ridge axis are often thought to be the primary vector for the dispersal of hydrothermal-vent benthic invertebrates, but can currents alone explain species dispersal? Given the known hydrothermal sector distribution, and assuming bottom currents are the main dispersal vector, how do the biology and ecology of the Alvinellidae fit with gene flow data?

Distribution of venting areas

Distance between populations is of crucial importance in patchy habitats such as vents. Accurate reference to spatial

scales is therefore essential, but only a few attempts have been made to standardize the terms used (Van Dover and Hessler 1990; Tunnicliffe 1991). Because we do not entirely subscribe to previous definitions (especially for site), the terms relative to the spatial scales discussed in the present work must be introduced. "Vent" describes a single localized emission of hydrothermal fluid; "vent site" refers to a spatially continuous venting area made of several emissions only a few meters apart, emerging from a common network of fissures; "vent field" refers to a cluster of vent sites located a few 100s of meters apart that are linked by subterranean ducts and that undergo the same temporal variations. Finally, vent fields can be grouped within larger spatial units termed "venting sectors," which can be at least several 10s of kilometers apart.

With the exception of some off-axis seamounts, hydrothermal sites are mainly confined to the axial graben, which on the EPR is typically 200–500 m wide (Geocyarise Expedition 1984), but can be considerably narrower (40–70 m) in areas such as 9°50'N (Haymon et al. 1991). Vent sites are therefore aligned along the rift axis in a one-dimensional fashion. However, frequent exceptions exist as transform faults offset the ridge axis by as much as several 100s of kilometers. The shortest distance a propagule would have to travel before being able to settle in favorable environmental conditions (i.e. the intersite distance) has often been considered with reference to well-known venting areas such as the distance between 13°N and the Galápagos. The spatial distribution of venting has therefore been assessed in detail at the scale of vent sites for the total portion of the EPR between 14°N and 7°N. Along this 800-km stretch of ridge, each of the 198 vent sites reported in the literature was taken into account. The distribution of vent sites on this part of the EPR is reported on Fig. 1. The average intersite distance over this 800-km portion of the EPR is 4,033 ($\pm 1,399$) m. The very active and best known sectors at 13°N and 9°50'N display the very close intersite distances of 508 (± 119) and 492 (± 122) m. We can therefore safely consider 500 m as a good estimate of the average intersite distance within a very active hydrothermal sector.

Apart from these well-surveyed areas, the information available is usually too scarce to provide good estimates of intersite distances. A thorough review of the literature on the EPR allowed us to produce a checklist of the known or suspected venting sectors along the ridge and to calculate distances between them (Table 1).

Venting sites have been grouped within the same sector when two successive sites are separated by <18.5 km (10' of latitude). Thirty sectors have been identified, including sites from the Guaymas Basin and the Galápagos Rift. All areas where active venting has been evidenced by direct observations, bottom photographs, or vent fauna collections are reported as confirmed in Table 1. In some cases, venting is only suspected after hydrothermal plumes have been detected in the water column, sulfides of recent hydrothermal origin have been dredged, or dense aggregations of nonvent fauna have been found in relation to temperature anomalies. Venting is then reported as not confirmed.

Figure 2 shows the position of each sector, together with the intersector distances. Two main zones (9°–14°N and

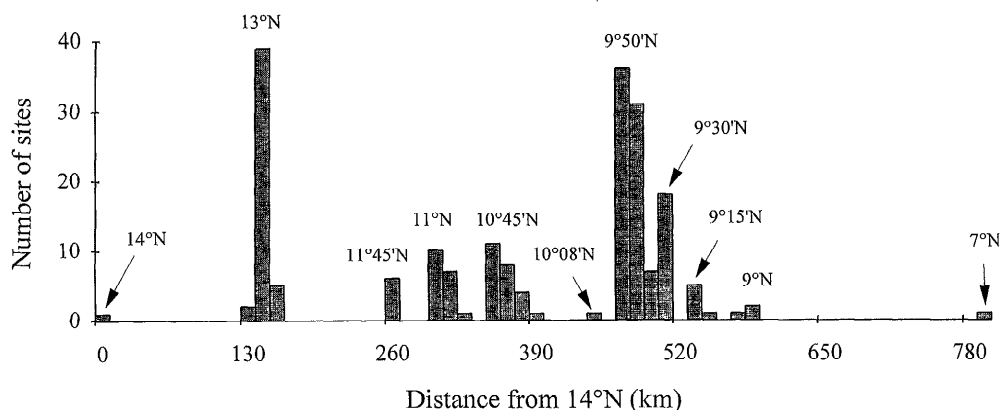


Fig. 1. Distribution of hydrothermal vent sites between 14°N and 7°N on the East Pacific Rise, forming 10 discrete hydrothermal sectors (9°50'N–9°30'N is considered a single sector because of its continuity). Sources of information were (from north to south): Vanko et al. (1991), Geocyarise Expedition (1984), Fouquet et al. (1988), Fustec (1985), Hékinian et al. (1985), Hékinian and Fouquet (1985), ARGO-RISE Group (1988), Lutz (1992), Feely et al. (1994), McConachy et al. (1986), Van Dover et al. (1987), Kastens et al. (1986), Haymon et al. (1991), Baker et al. (1994), Boulègue et al. (1984), and personal observations resulting from the Hydronaut and HERO 91 cruises at 13°N and 9°50'N.

16°30'S–22°30'S) show a higher density of venting sectors, possibly because they have been more intensively explored, they are more active, or both. Note that both zones are nearly the same length (~5–6° of latitude) and that within each zone the mean intersector distance is similar (63 vs. 53 km). If grouping is made with sites <500 km apart, again a similar mean distance is found (118 vs. 109 km). Outside these two zones, the longest distance between sectors is 1,850 km (Galápagos to EPR 3°55'N). However, when the Galápagos sector is not taken into account, the maximum distance drops down to 1,000 km (21°N–14°N).

This checklist demonstrates that there are many more hydrothermally active sectors than is usually thought. The detection of new vents between 4°N and 14°S, along the Galápagos rift, and between 21°N and 14°N will depend on additional submersible dives and deep-tow photographic or plume detection surveys. Unexplored sectors probably exist within these large gaps; hence, the average frequency of hydrothermal sectors cannot be less than one every 1,000 km, and is most likely closer to one every 100 km.

Current flow

To evaluate the hydrodynamic conditions in and over the axial graben, we positioned current meter moorings at several locations in the 13°N sector of the EPR during two French-American cruises (HERO '91 and HERO '92). A long-term mooring was deployed on 27 October 1991 a few hundred meters from active sites with two Aanderaa RCM5 current meters placed 100 and 200 m above the bottom (mab). The mooring was retrieved 159 d later (on 3 April 1992). Fig. 3 shows the progressive vector diagram of the current recorded every hour during the whole period at 100 mab. Such diagrams represent the theoretical trajectory of a particle given the assumption of a homogeneous current field. Tidal effects consisted mostly of semidiurnal oscilla-

tions in a direction roughly perpendicular to the ridge axis (roughly east–west).

During the 159-d period, the residual speed of the current was 2.2 cm s^{-1} toward SSE. The diagram in Fig. 3 shows reversals in the direction of the flow, but motion was always parallel to the rift axis. For most of the duration, the current was heading SSE; it was heading NNW during 28 d, between reversals. Apparently, other reversals had occurred just before the long-term record and right after it at the end of March 1992, i.e. 2 months after the end of the NNW-trending period. A late October 1991 reversal is confirmed by a dataset obtained just before the long-term mooring was deployed (3–25 October 1991), which seems to indicate a 1-month-long NNW-trending period during October 1991 (A. Khripounoff pers. comm.). An early April 1992 reversal is also confirmed by the data obtained from a current meter moored 6 mab on the same site from 7 to 20 April 1992 (P. Chevaldonné unpubl. data), just after the long-term mooring was retrieved. Data indicate a mean NNW flow after the reversal was definitely established by 9 April.

It therefore seems that 1-month-long periods of NNW flow (residual speed, 5.2 cm s^{-1}) alternate with 2-month-long SSE-trending periods (residual speed, 4.2 cm s^{-1}), although our data cover too brief a period and are too heterogeneous to confirm this hypothesis. At 200 mab on the long-term mooring (not shown), currents closely resemble those at 100 mab—the two reversals occur at the same time at both depths, are of the same amplitude, and last as long. At 200 mab, the current axis is shifted from NNW–SSE to north–south and residual speed during the 159 d is only slightly stronger ($2.4 \text{ vs. } 2.2 \text{ cm s}^{-1}$ at 100 mab). On the other hand, residual current speeds and headings at 6 mab are also similar to data obtained for similar durations (~2 weeks) at 100 mab— 4.6 cm s^{-1} (vs. 4.5 at 100 mab) heading NNW. There was therefore no evidence of strong vertical shear in the first 200 m over the ridge, so we did not account for it in our subsequent modeling approach.

Table 1. Checklist of the known or suspected hydrothermal venting areas of the eastern Pacific (Gulf of California, East Pacific Rise, and Galápagos Rift) found in the literature. Conf—direct evidence for venting (*see text*); HT—occurrence of high-temperature smokers; Alv—occurrence of *Alvinella pompejana* or *Alvinella caudata*; Pg—occurrence of *Paralvinella grasslei*.

Sector No.	Location	Name	Reference	Conf	HT	Alv	Pg	Observations
1	27°03'N 27°00'N	Guaymas	Desbruyères and Laubier 1991; Peter and Scott 1988	Y	Y	N	Y	
2	24°00'N	Pescadero	Vorobyev et al. 1990	N	?	?	?	Plume detected
3	22°58'N 22°56'N		Gallo et al. 1984	Y	N	N	?	Two small communities of large clams sighted in sediment and hydrothermal deposit
4	20°52'N 20°48'N	21°N	Spiess et al. 1980; Lonsdale et al. 1982; Desbruyères and Laubier 1991	Y	Y	Y	Y	
5	14°09'N		Vanko et al. 1991	N	?	?	?	Sulfides dredged from a seamount 15 km west of East Pacific Rise
6	12°53'N 12°41'N	13°N	Geocyaris Expedition 1984; Fustec 1985; Hékinian et al. 1985; Fouquet et al. 1988	Y	Y	Y	Y	
7	11°47'N 11°42'N		ARGO-RISE Group 1988	Y	N	?	?	
8	11°27'N 11°08'N	11°N	Hékinian et al. 1985; ARGO-RISE Group 1988; Van Dover and Hessler 1990; Lutz 1992; Jollivet 1993; Feely et al. 1994	Y	Y	N	Y	
9	10°56'N 10°38'N		McConachy et al. 1986; Van Dover et al. 1987; ARGO-RISE Group 1988	Y	Y	?	?	
10	10°08'N		Kastens et al. 1986	Y	N	?	?	At 10°08'N, temperature anomaly + hydrothermal fauna observed with serpulids and <i>Calyplogena</i> clams
11	9°53'N 9°30'N	9°50'N	Haymon et al. 1991	Y	Y	Y	Y	
12	9°17'N 9°11'N		Haymon et al. 1991	Y	Y	?	?	
13	9°00'N 8°50'N		Baker et al. 1994	N	?	?	?	Plume
14	7°00'N		Boulègue et al. 1984	N	?	?	?	
15	3°55'N		Lonsdale 1989	Y	?	?	?	Dense populations of anemones sighted
16	0°48'N, 86°14'W 0°47'N, 86°01'W	Galapagos	Ballard et al. 1982	Y	N	N	Y	
17	3°26'S		Lonsdale 1977	N	?	?	?	Dense populations of anemones, temperature anomaly
18	7°00'S		Dill et al. 1992	Y	?	?	?	Grab samples of anemones, fish, crabs, mussels, worms
19	14°00'S		Fujioka et al. 1995	Y	Y	?	?	
20	15°00'S		Dill et al. 1992	Y	?	?	?	Grab sampling of anemones, crabs, and fish
21	16°35'S		Baker and Urabe 1996	N	?	?	?	Plume detected
22	17°08'S 17°30'S	17°S	Renard et al. 1985; Desbruyères and Laubier 1991; Auzende et al. 1994; pers. obs.	Y	Y	Y	Y	
23	17°45'S		Baker and Urabe 1996	N	?	?	?	Plume detected
24	18°00'S 19°00'S		Marchig and Gundlach 1987; Sinton et al. 1991; Auzende et al. 1994; pers. obs.	Y	Y	Y	Y	
25	20°00'S 20°23'S	20°S	Renard et al. 1985; Macdonald et al. 1988	Y	Y	?	?	
26	20°50'S 21°00'S		Macdonald et al. 1988; Dill et al. 1992	Y	?	?	?	

Table 1. Continued

Sector No.	Location	Name	Reference	Conf	HT	Alv	Pg	Observations
27	21°24'S 22°00'S		Renard et al. 1985; Marchig and Gundlach 1987; Dekov and Gurvich 1991; Hartmann-Schröder 1992; Krasnov et al. 1992	Y	Y	Y	?	Not confirmed from 21°40'S to 22°S; only plume detection and sulfide deposits
28	22°30'S		Dill et al. 1992	Y	?	?	?	Grab sampling of fish, crabs, anemones, mussels, serpulids
29	23°20'S, 111°39'W 23°33'S	23°S	Marchig and Gundlach 1987; J. Francheteau pers. comm.	Y	Y	Y	?	
30	26°12'S	26°S	Marchig and Gundlach 1987	Y	Y	?	?	

Biology of Alvinellidae

The third type of data essential for estimating larval fluxes are the biological and ecological characteristics of hydrothermal taxa. We provide such data here for alvinellid species.

Reproduction—Few data are available on the reproductive biology of the hydrothermal fauna. However, some data have been published for ampharetid polychaetes (McHugh and Tunnicliffe 1994) and Alvinellidae (McHugh 1989; Zal et al. 1994, 1995). Alvinellid species studied to date (*Paralvinella pandorae pandorae*, *Paralvinella palmiformis*, and *P. grasslei*) and the ampharetid *Amphisamytha galapagensis* are all gonochoric with a sex ratio of 1. The maximum observed oocyte size varies from 215 μm (*P. p. pandorae*) to 275 μm (*P. grasslei*), which in Polychaeta in general and in the closely related families Terebellidae and Ampharetidae usually corresponds to species having lecithotrophic larvae or a direct development through brooded embryos (Blake 1991; McHugh and Tunnicliffe 1994). Furthermore, fertilization is thought to be internal and fecundity is relatively low (2,700–18,000 oocytes female⁻¹). Such types of development, which often imply limited dispersal capabilities, might not allow offspring to disperse away from the local area of the vent site without an external vector. However, alvinellid larvae have not yet been observed, so their dispersal abilities remain uncertain. Recent observations on *A. pompejana* and *A. caudata* (P. Chevaldonné unpubl. data) indicate that these species have a much higher number (mean, 80,000; max, 230,000) of slightly smaller (max size, $\sim 200 \mu\text{m}$) oocytes. Continuous reproduction has been suggested for *A. galapagensis* and *P. p. pandorae*, whereas a discrete, possibly synchronized breeding cycle is thought to occur in *P. grasslei* and *P. palmiformis* (McHugh 1989; Zal et al. 1995).

Population structure—Reports on population structure have been published for the alvinellids *P. p. pandorae*, *P. palmiformis* (McHugh 1989), *Paralvinella pandorae irlandei*, *A. pompejana*, *A. caudata* (Jollivet 1993), and *P. grasslei* (Jollivet 1993; Zal et al. 1995). In all but one case (*P. p. pandorae*), recruitment is unambiguously discontinuous and seems to be synchronized within vent fields. In the case of *P. grasslei*, it is even suggested that reproduction occurs several times a year, with an apparent periodicity.

Population size—Although many reports exist on hydrothermal taxa density or biomass estimations, only a few thoroughly estimate these population parameters. Chevaldonné and Jollivet (1993) studied and quantified the spatial distribution of *A. pompejana*, *A. caudata*, *P. grasslei*, and *P. p. irlandei*. Density values range from 50 to 1,200 ind. m⁻² and the populated surface area often reaches 5 m² on a single chimney. Vent sites usually comprise several chimneys, over a total surface area in the range of 10–500 m² (Fustec 1985; Jollivet 1993). Total surface area actually covered by alvinellids within a single vent site can reach a maximum of $\sim 25 \text{ m}^2$. Estimates of population size are ~ 50 –45,000 individuals.

Propagule flux model (PFM)

Definition—A model was set up to assess the level of propagule migration between alvinellid populations in order to compare the fluxes obtained from environmental and biological data with indirect estimates obtained from population genetic studies. Gene flow estimates are often expressed as N_m , the number of migrants (sexually mature adults) exchanged between two randomly chosen populations during one generation. This parameter is usually calculated from the Wright's fixation index (F_{ST}) obtained by means of genotype frequency data according to the infinite island model (Wright 1965). When N_m falls below the critical value of one individual exchanged per generation, gene flow is not sufficient to counteract genetic drift and speciation may occur. Following an ecological approach, N_m would depend on the probability $P_1(t)$ for a propagule to encounter a hydrothermally active site while traveling on the ridge during a time t (in days) and the probability $P_2(t)$ for a propagule to reach a site alive after traveling this same time. $N_m(t)$ can then be expressed as

$$N_m(t) = \frac{2 \times P(t) \times N\omega}{\delta},$$

where

$$P(t) = [P_1(t) \times P_2(t)]^2.$$

$P(t)$ is the probability resulting from the co-occurrence of $P_1(t)$ and $P_2(t)$, which is squared to account for the exchange of a propagule from one site to the other and vice versa. $P(t)$

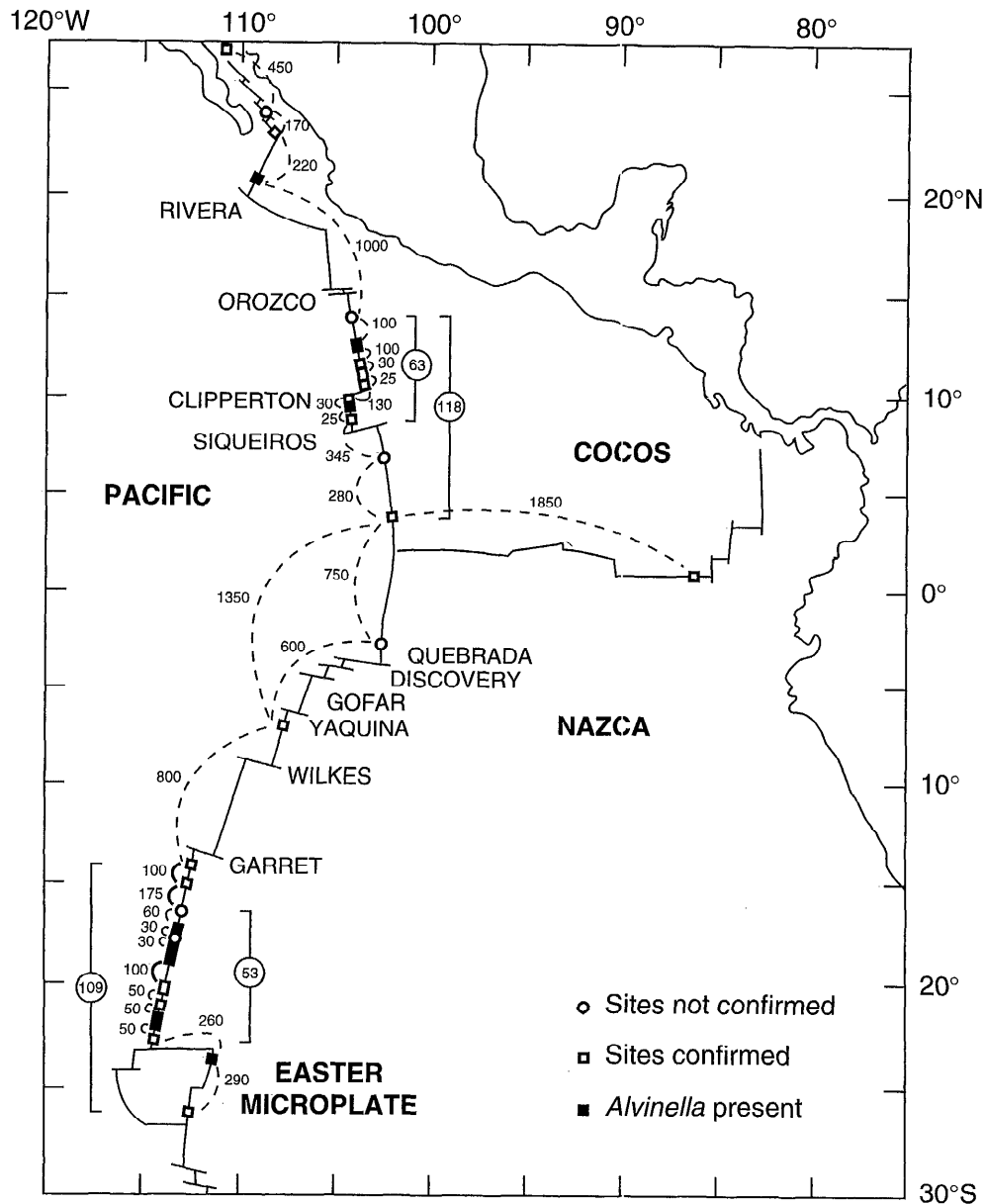


Fig. 2. Distribution of hydrothermal sectors in the eastern Pacific, including those from the Gulf of California, East Pacific Rise, and Galápagos Rift. Numbers indicate intersector distances; circled numbers are the mean intersector distances over corresponding bracketed areas. Distances are in kilometers.

is then multiplied by the population spawning potential or the number of eggs produced in one generation ($N\omega$) for each of the two sites and divided by δ , the recruit-to-mature adult ratio (to convert larvae into migrants). Fertilization was assumed to be 100% efficient, as it is thought to be internal in Alvinellidae (Zal et al. 1994); therefore, the number of fertile eggs was considered equal to the number of oocytes. The loss of propagules between the egg and the recruit stages is accounted for in $P_2(t)$.

$N\omega$ is calculated as

$$N\omega = 0.5 \times f \times N_e,$$

where

$$N_e = r \times S \times d$$

and 0.5 is the proportion of females in the population, f is the female fecundity, and N_e is the effective population size (i.e. the total number of mature individuals in the population estimated through r , the proportion of mature individuals in a population; S , the surface covered by a population; and d , the population density).

When extinction and recolonization processes occur, N_e is a parameter used in population genetics as an average over generations. We here assumed that our estimates of r , S , and d correspond to such an average situation. The probability $P_1(t)$ is calculated as

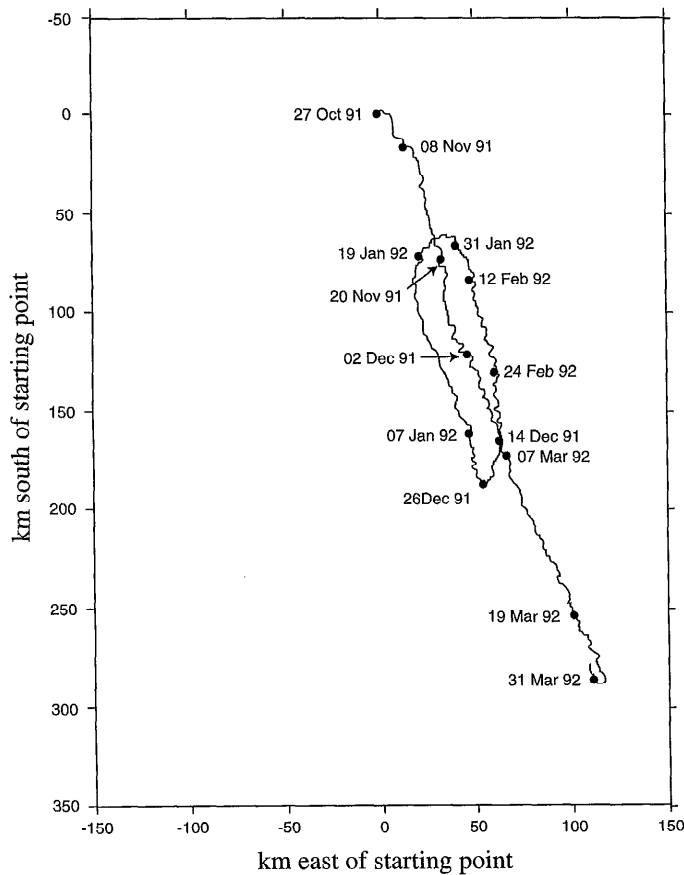


Fig. 3. Progressive vector diagram of currents recorded at 13°N on the East Pacific Rise, 100 m above the bottom of the axial graben, between 27 October 1991 and 3 April 1992.

$$P_1(t) = \frac{a(t)}{A(t)}$$

$a(t)$ is the average number of sites a propagule might encounter during the traveling time t . $A(t)$ is the theoretical maximum number of nonoverlapping sites that could occupy the area covered by the propagule during the same amount of time (i.e. the total rift area corresponding to time t divided by the average size of an active site):

$$A(t) = \frac{L_m \times D(t)}{S_m},$$

where

$$D(t) = v \times t$$

and L_m is the average width of the axial graben, $D(t)$ is the distance traveled by the propagule during t , v is the average transport by currents, and S_m is the average surface area of an active site. S_m was preferred to S (the surface covered by a population) because we assumed that a propagule might be attracted to populated areas by the physical-chemical gradient when entering a site, or passively entrained by convective currents generated by the vent outflow, or both (Lonsdale 1977; Lutz et al. 1980). For simplification pur-

poses, the axis was considered one-dimensional and therefore did not account for diffusive effects in the cross-axis dimension. A simple way to include this effect was to consider the graben width (L_m) in the PFM calculations. Indeed, the wider the axial valley, the more important is diffusion and the lower is the probability of encounter. This significant two-dimensional parameter can therefore be included in our one-dimensional approach under the simple assumption that cross-axis diffusion of propagules is homogeneous and constrained within the valley.

Traveling time (t)	20	30	36	40	50	60	80
Moving avg of v (n)	4.5 (19)	3.9 (16)	3.5 (15)	3.3 (14)	2.5 (11)	2.1 (9)	1.5 (4)
v (model)	4.5		3.5		2.5		1.5

Finally, the probability $P_2(t)$ is

$$P_2(t) = (1 - Z_m)^t,$$

where Z_m is the mortality rate of propagules per day during the journey in the water column.

Parameter choice—The average number of sites encountered, $a(t)$, was computed from the entire matrix of site-to-site distances of the EPR section from 14°N to 7°N. For a traveling time t , the total number of distances in the matrix that are lower than $D(t)$ is divided by 198, the number of sites considered on this section.

Lacking any evidence for vertical shear, we derived transport by currents from the long-term mooring residual speed data at 100 mab, assuming the current field is homogeneous. Transport has been divided into four categories depending on the value of t to take into account the phenomenon of current heading reversal. On the basis of the long-term mooring data, average transport has been calculated for different traveling durations (Table 2) and dispatched into the following homogeneous categories: when $t < 30$ d, $v = 4.5$ cm s^{-1} ; when $30 \text{ d} \leq t < 40$ d, $v = 3.5$ cm s^{-1} ; when $40 \text{ d} \leq t < 60$ d, $v = 2.5$ cm s^{-1} ; and when $t \geq 60$ d, $v = 1.5$ cm s^{-1} .

Other biological and nonbiological parameters that influence propagule flux and are therefore needed to run the model are detailed in Table 3. There are no data available on r , Z_m , or δ . We propose to estimate r from the density ratio of alvinellids visible on video records to total sampled densities ($N_{\infty}:N$; cf. Chevalloné and Jollivet 1993). Accordingly, r was considered close to 0.8. Mortality, which is accounted

Table 3. Values of the parameters used in the propagule flux model. Values were compiled from the literature and personal observations. Min indicates the values that minimize N_m the most, Max those that maximize it, and Std the values that are the most probable given current knowledge. For *Alvinella* and *Paralvinella*, different sets of parameters have been designed based on biological and ecological differences observed or inferred between these two genera.

	Min	<i>Alvinella</i>	Std	<i>Paralvinella</i>	Max
L_m (m)	400	100	100	100	50
S_m (m ²)	10	100	250	500	500
N_e	50	1,125	7,200	15,750	27,000
Calculated from					
S (m ²)	1	5	15	30	30
d (m ⁻²)	100	250	600	750	1,000
r	0.5	0.9	0.8	0.7	0.9
f	2,700	80,000	10,000	3,500	230,000
Z_m (d ⁻¹)	0.1	0.05	0.01	0.005	0.001
δ	10,000	1,000	1,000	1,000	100

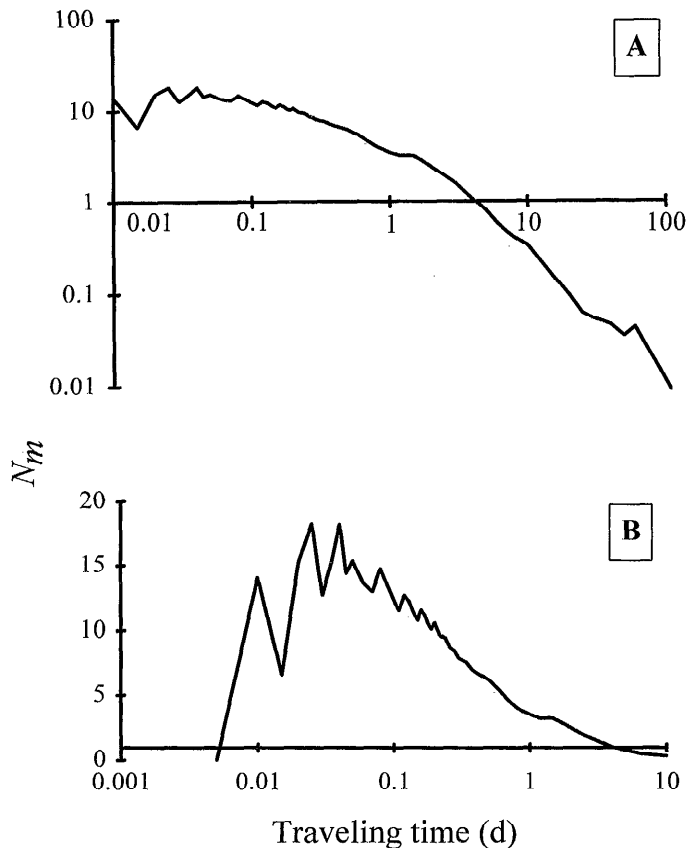


Fig. 4. Propagule flux model. Evolution of the number of migrants exchanged during one generation by two populations of Alvinellidae (N_m) according to the traveling time of a propagule. A. Log-log representation of the results from a model run using most probable values of the parameters (see Table 3). B. Semilog representation of the results as detailed for traveling times < 10 d.

for both by Z_m and δ , is another unknown. It is generally thought that important mortality occurs after settlement of invertebrate larvae (Ólafsson et al. 1994) and that losses can reach several orders of magnitude. According to M. Bhaud (pers. comm.), the recruit-to-mature adult ratio might range from 10^2 to 10^4 . These values, combined with data on fecundity and population structure, allowed the calculation of the first-order estimates of Z_m reported in Table 3, assuming that in a steady-state population one mature female must produce two juveniles attaining maturity. Owing to differences in habitat range and instability, *Alvinella* was assigned a higher mortality rate than was *Paralvinella*. For the same reason, lower values of S and S_m have been considered for this genus. As in most models of larval mortality, we assumed an exponential decay of larval abundance, with Z_m constant over time although it is reported to decrease with age following a logistic equation (Fortier and Leggett 1985; Rumrill 1989).

Results—The model was first run using the most probable values (Std) of the parameters (Table 3). Sixty-six different traveling times were tested (from 5 min to 1 yr). The results are plotted on Fig. 4. N_m displays a logarithmic decrease with increasing time, as forecasted by stepping-stone models (Kimura and Weiss 1964). N_m never exceeds 45.6 ind. generation⁻¹ and reaches the critical value of 1 after 8 d (Fig. 4A). The decrease in migrant numbers is not regular, but rather displays oscillations around the trend that are directly related to the level of patchiness of the vent site distribution. Such fluctuations are progressively damped out as more sites are taken into account (Fig. 4B). Note that given the sampling interval of the current meters (1 h), the PFM does not adequately characterize phenomena occurring at time scales shorter than a few hours (~ 0.1 d). At short time scales, diffusion processes driven by tidal effects and turbulence are likely to be most important. Results for time scales shorter than 0.1 d, however, were displayed to show the behavior of the PFM near its limits.

The influence of the biotic and abiotic parameters on the N_m plots has been tested. For each parameter, the full range (see Table 3) of values was applied, whereas other param-

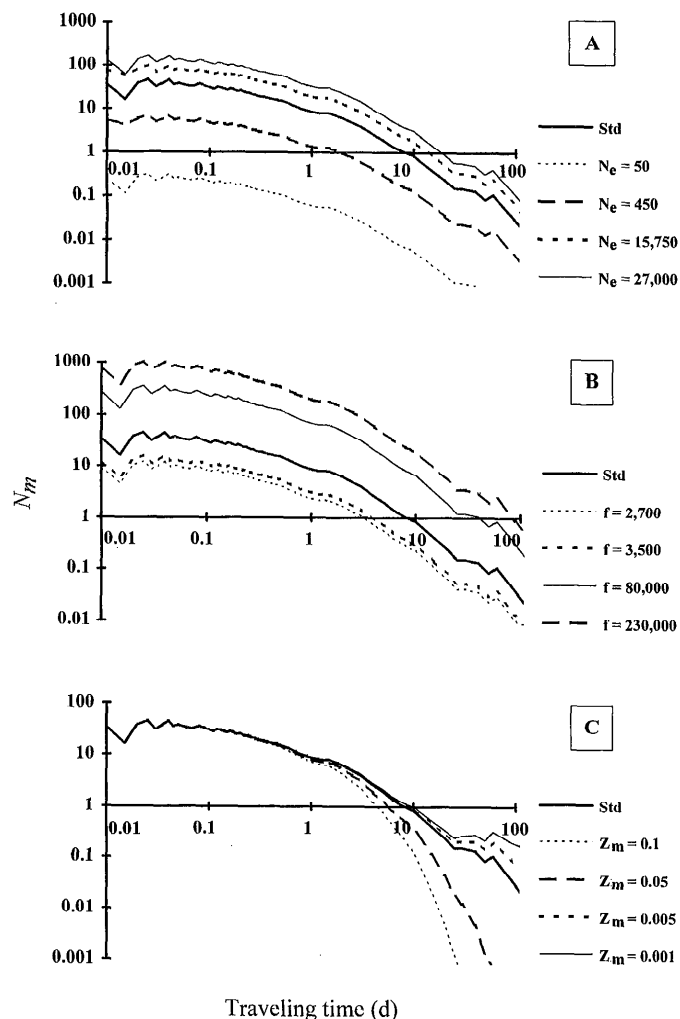


Fig. 5. Propagule flux model. Effects of the effective population size N_e (A), fecundity f (B), and mortality rate Z_m (C) of Alvinellidae on the model. Other parameters are maintained at their most probable value. Std—reference curve with all parameters at their most probable values (see Table 3).

eters were kept at their most probable (Std) levels. Most parameters have a simple direct effect on the position of the origin of the N_m curve relative to the t axis. Z_m , however, does not act on this position, but on the shape of the curve. Testing S_m indicates that 10 m^2 is far too low a value to allow an efficient larval flux even between the closest populations. Conversely, low values of the graben width L_m and of the δ ratio do not produce aberrant levels of exchange. High values of S_m , L_m , and δ also provide realistic plots in which N_m reaches 1 for durations in the range of 15–30 d and never exceeds $250 \text{ ind. generation}^{-1}$. Figure 5 shows how N_e (i.e. S , r , and d), f , and Z_m affect the N_m estimates. As expected, f has a strong direct effect on N_m . With high values of f , N_m reaches 1 after 1–3 months. The PFM was also run with all parameters set at their values for *Alvinella* and *Paralvinella*, according to Table 3. The plots show that N_m reaches 1 after 2 d for *Alvinella* and after 20 d for *Paralvinella* (Fig. 6).

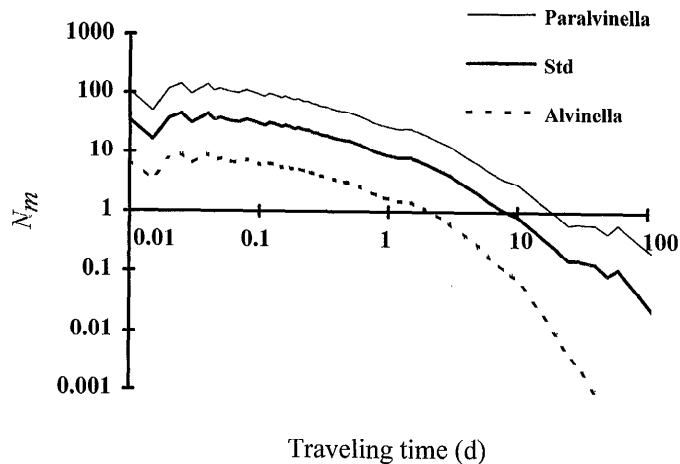


Fig. 6. Propagule flux model run in standard (Std), *Alvinella*, and *Paralvinella* conditions (see Table 3 for parameter values).

Discussion

Modeling approach—Modeling larval dispersal can follow two main pathways. The most widely used modeling approaches are designed to understand microscale variations in the recruitment and fertilization patterns of benthic invertebrates or to evaluate stock-recruitment relationships in fisheries ecology (Fortier and Leggett 1985; Black et al. 1991; Babcock et al. 1994; Petersen and Svane 1995). Such models are usually termed advection/diffusion models because they simulate the tracking of a two- or three-dimensional cloud of particles emitted from a single source. Particles are not only entrained by a current (advection) but are also subjected to turbulence (diffusion), which induce slightly different trajectories and hence the cloud. Particle density can be calculated for any given set of time and space coordinates and compared with actual sampling surveys. This approach requires a good knowledge of the physical-chemical processes involved and the possibility of conducting extensive sampling programs.

For the PFM presented here, an alternative more simplistic and probabilistic approach was adopted. The point of view is that of a single particle, for which the probability of successful migration is assessed. From simple but realistic postulates, the limiting conditions to larval exchanges between steady-state populations can be estimated. Both advective and diffusive processes were accounted for in the PFM because we used transport estimates derived from the progressive vector diagrams, not from mean speeds only. Furthermore, tidal diffusion might not play a very significant role compared to advection, because it is perpendicular to the ridge axis. Consequently, we only considered dispersal in one dimension. A very similar approach was used by Scheltema (1972) to estimate the probability for a teleplanic larva to disperse across the Atlantic.

Limits of the model—The PFM is clearly a preliminary attempt to describe the effects of bottom currents on the dispersal of Alvinellidae, with special reference to patchiness in population distribution. The model is not intended to ac-

curately address small-scale physical and biological phenomena, but rather attempts to consider simple general patterns. There are virtually no data on the life history of Alvinellidae between spawning and recruitment, and the long-term behavior of water masses in the axial valley and across ridge discontinuities remains to be described. However, one of the most important features of the PFM is the small number of unknown parameters for which estimates are required. Assumptions mainly need to be made for the determination of the mortality rate of the propagule (Z_m) and the recruit-to-mature adult ratio (δ). Mortality is the most difficult life-history variable to measure (Hines 1986), but our Z_m calculation is consistent with published data. In studies where calculation of the daily mortality rate of invertebrate larvae is possible, Z_m estimates are close to 10^{-3} – 10^{-1} d $^{-1}$ (see examples in Dorsett 1961; Scheltema 1986; Rumrill 1989; Zea 1992; Petersen and Svane 1995). Importantly, most estimates found in the literature concern species from shallow waters, where predation is thought to be a major source of larval mortality. In the deep sea, predation pressure is likely to be much lower, even though carnivorous macrozooplankton and large actiniaria are frequently observed at the ridge axis near 13°N (pers. obs.). Figure 6 shows that in spite of a lower fecundity, *Paralvinella* species may be slightly more successful at achieving long-range dispersal than are *Alvinella* species. However, given the distribution ranges of known species, this difference might come from the uncertainties of estimation of biological parameters.

Our data on residual current speeds can also be regarded with confidence, because the long-term measurements obtained at 100 m seem to be representative of bottom currents, at least for our purposes and for the area near 13°N. Vertical shear is thought to be important over oceanic ridges (Kim et al. 1994). Thomson et al. (1990) obtained data suggesting that current shear might be significant within 500 m of the top of the Juan de Fuca Ridge, but other published studies have not clearly substantiated such shear. In the comprehensive survey of current circulation over the Juan de Fuca Ridge by Cannon et al. (1991), vertical shear is only demonstrated for water masses circulating more than 200 km from the ridge axis. No clear pattern could be drawn from Cannon et al.'s measurements over the ridge itself where circulation seems more complex.

Our observations on flow direction and speeds also compare well with the data found in the literature on bottom currents of the EPR ridge crest. Crane et al. (1988) published measurements from current meters moored at several latitudes on the northern EPR (12°50'N–10°43'N). Their data confirm that over long periods (>3 months) the residual current heading at 40 mab follows the rift axis at 13°N and is directed southward. These data also fit in our classification of transport speeds according to duration (Table 2). Crane et al. (1988) indeed reported a residual speed of 1.2 cm s $^{-1}$ for 8 months. They also presented two sets of 40-d-long data from the same area at 200 mab. One of these datasets is not relevant to our study because it was moored over a seamount. Seamounts are known to generate very particular and poorly understood hydrodynamic conditions (Rogers 1994). The other 40-d series shows a northward flow at 2.5 cm s $^{-1}$, which exactly fits in our classification (Table 2). Other time

series presented by Crane et al. (1988) only last 1–4 d at depths of 14–210 mab, where current flow is 3.1–4.5 cm s $^{-1}$, which is again consistent with our data.

Additionally, Lonsdale (1977) documented a current flow of 3.9 cm s $^{-1}$ over 21 d on the Galápagos Rift, which compares well with Table 2. More data exist (from the Juan de Fuca Ridge) in a very different context (latitude, depth, topography), which are not as consistent as for the EPR. Cannon et al. (1991) did not find a clear pattern for circulation over the ridge itself near venting sites—the residual speeds obtained from 6–13-month-long series ranged from 0 to 3.7 cm s $^{-1}$ for different settings (e.g. ridge axis, 200 km off axis, seamounts). Although most other studies show a long-term (1–9 months) flow oriented mostly along the ridge axis with typical net advective transport values of 1–2 cm s $^{-1}$ (Baker and Massoth 1986, 1987; Thomson et al. 1990; Baker and Cannon 1993), the most recent observations indicate that currents at 250–300 mab can also flow across (NW–SE) the Juan de Fuca Ridge for periods of up to 8 months (Cannon et al. 1995).

To run the PFM, we assumed a periodic pattern of reversal in the current flow. If reversals never occurred, the residual current speed would be the same whatever the time scale and would be close to the maximum value of 4.5 cm s $^{-1}$ (Table 2). It would also lead to a unidirectional pattern of dispersal. However, our data demonstrate that reversals do occur; therefore, on a long time scale (several months), $v < 4.5$ cm s $^{-1}$. If reversals occur in a nonperiodic manner, then $0 \leq v < 4.5$ cm s $^{-1}$. The assumption made for the PFM of a periodic pattern in the current flow reversal with a long-term value of 1.5 cm s $^{-1}$ is thus an intermediate solution that is strongly supported by our data and by a review of the literature. The probability of having residual speeds of ~ 0 cm s $^{-1}$ is very low; therefore, if our assumption is wrong, v is either < 1.5 cm s $^{-1}$ (but close to that value) or it is in the range of 1.5–4.5 cm s $^{-1}$ (close to the median value of 3 cm s $^{-1}$). In the first case, it means that alvinellid dispersal is even more enigmatic than what we report; in the second case, it means that we have underestimated traveling times and distances by only half, which would not affect our conclusions.

Intersite distances have been considered between 14°N and 7°N, an area that represents the best surveyed and probably one of the most active parts of the EPR. This maximizing bias is expected to counteract the minimizing effects of the probable existence of undetected vent sites. It might thus provide a somewhat realistic picture of the actual vent site distribution. Although more sectors are likely to exist than those reported on Fig. 2, the average number of sites encountered outside 7°N–14°N by a propagule for a given traveling time $a(t)$ is expected to be lower than in the present study.

Another limitation of the PFM is that we considered average situations, whereas dispersal might depend on exceptional or catastrophic events, such as the occasional production of longer lasting propagules, higher velocity currents, or the formation of megaplumes following seafloor volcanic eruptions, which might provide an episodic successful dispersal of large patches of vent larvae. Finally, the model provides information on how vent site patchiness acts as a

barrier to exchanges between populations, but not on the effects of dispersal processes on the genetic structuring of populations over generations. The vent site distribution has indeed been considered as static, whereas vents and sites have a limited lifespan (Lalou 1991). Hydrothermal activity is shifting along the ridges and generates vent site displacements and population extinctions. These processes of birth, death, and coalescence of vent sites have been modeled by Watremez and Kervevan (1990). Over long periods such processes may represent significant evolutionary force producing contact zones between previously isolated populations. The success of hydrothermal-vent invertebrate dispersal might considerably be enhanced by such dynamic aspects, which have been accounted for in the modeling approach by Jollivet et al. (unpubl.).

Comparison with genetic studies—A primary objective of our study was to compare estimates of the number of migrants exchanged between two populations per generation (N_m) generated by the model to existing genetic indirect estimates of N_m derived from Wright's fixation index (F_{ST}). Estimates are available from genotype frequency data from the three dominant alvinellid species of the EPR by use of allozyme electrophoresis and ribosomal DNA restriction fragment-length polymorphism (Jollivet et al. 1995, 1997). There is a good agreement between the data produced by the model and genetic estimates. N_m values derived from multiloci G_{ST} , an estimator of F_{ST} resulting from pairwise comparisons of 13°N/EPR populations, ranged from 0.6 to 22.1 ind. generation⁻¹. F_{ST} estimates from multiple comparisons over the same populations do not exceed 15 ind. generation⁻¹. Jollivet et al. indicated that in the case of *A. pompejana*, N_m might reach the critical value of 1, beneath which genetic differentiation of conspecific populations may occur only by random processes (genetic drift) when the distance between populations is >3–50 km (depending on estimation procedures). This result fits well with the critical traveling times obtained with our model for *Alvinella* or standard conditions (i.e. 2–10 d), which correspond to distances of 8–40 km. However, pairwise genetic comparisons of populations from different vent sectors were not clear enough to support the hypothesis of isolation with distance in alvinellid species studied so far. Indeed, N_m values estimated between populations of 13°N and 21°N always exceeded 1. Such intersector exchanges could only be modeled when the PFM was run under maximizing conditions (Fig. 7).

Gene flow estimates used as reference have been obtained from genetic markers whose neutral behavior is not guaranteed. In recent years, allozymes and even ribosomal DNA have indeed been suspected of being under stabilizing selection (Flavell et al. 1986; Karl and Avise 1992). Balancing selection could mask genetic differences between populations and indicate gene flow when there is none. However, there are many indications of actual gene flow in Alvinellidae—comparisons of populations of alvinellid species from widely separated vent sectors do not present any indication (morphology, allozymes, or rDNA) of isolation with distance (Jollivet et al. 1997); wide species range is not only a characteristic of Alvinellidae but of most hydrothermal invertebrates from the EPR (see Tunnicliffe 1991); and speciation

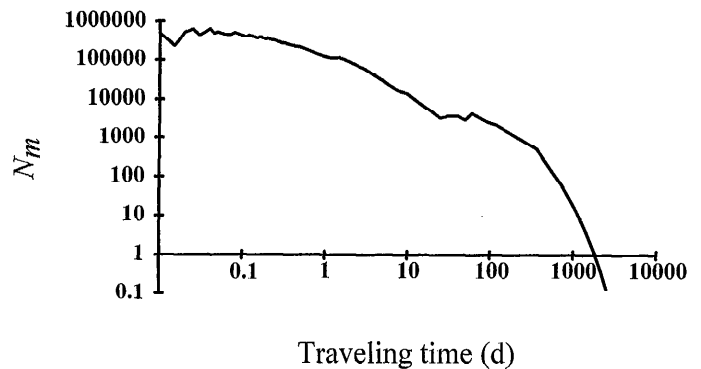


Fig. 7. Propagule flux model run under conditions maximizing N_m , the number of migrants exchanged between two populations during one generation (see Table 3 for parameter values).

occurred within several taxa such as alvinellids and vestimentiferans after the Juan de Fuca Ridge and the EPR became isolated, but not over very distant parts of the EPR. For instance, the closest populations of *P. grasslei* and its northern sibling species *P. palmiformis* are 2,000 km apart (21°N/EPR to Gorda Ridge), whereas the range of *P. grasslei* spans >5,000 km (Guaymas Basin to 19°S/EPR).

Traveling time—According to our modeling approach, the time spent by an alvinellid propagule in the water column is most likely 2–30 d (i.e. traveling distance of ~10–100 km). How long an alvinellid egg, larva, or juvenile can stay in ambient seawater is therefore a key issue. The longest planktonic period recorded for the larvae of Ampharetidae, a polychaete family related to Alvinellidae, is 3–5 d (Nyholm 1951). In the PFM, such a larval lifespan would only ensure Alvinellidae a dispersal range of up to 20 km. However, for such short periods, current transport can be significantly higher than the average value of 4.5 cm s⁻¹. The fastest transport inferred from Fig. 3 for a 12-d interval is 10 cm s⁻¹, which more than doubles the maximum dispersal range to ~58 km. This value is very close to the mean intersector distance of very active zones (see Fig. 2). Outside such zones, traveling time would have to be longer or traveling speed higher.

Transport by bottom current cannot reasonably exceed 10 cm s⁻¹, especially over long periods because the current direction episodically reverses (Fig. 3). However, if we consider that even benthic developmental stages could be entrained by the currents, we must take longer periods into account, and not just those referring to the “planktonic stage.” Ampharetid species are reported to have an entire larval life (i.e. planktonic and nonplanktonic) of 2–5 weeks (Hutchings 1973; Zottoli 1974). Within such a timespan, average current transport is estimated to be 3.5 cm s⁻¹ in the PFM (Table 2), which would provide larvae with a 140-km dispersal range. Exchanges would then be possible within the two main zones reported on Fig. 2, but still not over longer distances. However, Thorson (1961) reported that polychaetes are among the invertebrates that can delay their metamorphosis the most and cited a maximum pelagic larval life of 18 weeks for polychaetes. In our calculations, this

would allow traveling distances up to 220 km, which is consistent with our estimate of the intersector distance range (100–1,000 km), but it seems unlikely. Additionally, some terebellids are known to metamorphose and subsequently feed as juveniles in the plankton while still drifting (Levin and Greenblatt 1981). This behavior could extend dispersal potential substantially if the juvenile Alvinellidae could utilize foods not specific to vents while in the plankton.

Another mode of transportation has been suggested as a possible vector for alvinellid dispersal—the transport by brachyuran or anomuran crabs (Tunnicliffe and Jensen 1987; Zal et al. 1995; Chevaldonné and Olu 1996). Phoretic processes still have to be ascertained, but they would provide a much more accurate way of traveling from site to site, thereby increasing genetic exchanges at a small geographical scale. Such processes are however unlikely to provide a much quicker way of traveling than near-bottom currents.

There are two main hypotheses to explain the discrepancy between the apparent genetic homogeneity of alvinellid populations and their highly discontinuous distribution. The first one is that long-range dispersal of propagules does occur, which would require that almost all the upper limits of assumptions in our model are realized in nature. Although this seems unlikely, it must be stressed that nature is much more flexible and variable than are Thorson's (1950) basic categorizations of developmental modes, and polychaetes are known for their tremendous plasticity (mixed strategies, poecilogony, teleplanic larvae, delayed metamorphosis) as far as developmental strategies are concerned (Mileikovskiy 1971; Hines 1986; Scheltema 1986; Bhaud 1994; Levin and Bridges 1995). It is therefore particularly difficult to predict developmental patterns of polychaetes from small samples, oocyte observations, and comparisons with related nonvent species. Under this hypothesis, currents alone would be strong enough to allow, for example, dispersal of species lacking planktotrophic larval stages but able to develop in the water column and delay their metamorphosis.

A second hypothesis, which we think is more probable, is that long-distance dispersal might never occur in Alvinellidae. The conjunction of several factors would maintain genetic homogeneity of widely separated populations only by short-range (at the interfield scale, exceptionally intersector) stepwise dispersal. It seems likely that active hydrothermal venting occurs within the large gaps presented on Fig. 2. Additionally, the present-day distribution pattern of hydrothermal activity does not reflect its dynamic nature within the timespan that is relevant to maintain gene flow. Processes of vent site birth, death, and coalescence along the ridge could be important enough to allow species with nonplanktonic larvae to be widely distributed (Watremez and Kervan 1990; Jollivet et al. unpubl.). Hence, maintaining gene flow would not only involve a migration of propagules but also a movement of the sites themselves. Between two successive episodes of effective genetic exchange, the selective pressure exerted by the harsh hydrothermal environment on the genetic markers studied so far might be sufficiently directed to compensate for genetic drift in alvinellid populations (Jollivet et al. 1995). Scheltema (1986) indicated that larval exchange between populations does not need to be high or continuous to maintain gene flow. It is now thought

(Strathmann 1980) that long-range dispersal might confer no advantages on a short time scale (10s–100s of generations). As is the case in some littoral colonial invertebrates (Yund 1990), gene flow over great distances might be a highly unusual event within one generation of Alvinellidae. The temporal instability of the hydrothermal activity might therefore be the key to the persistence of species highly constrained by spatial parameters, which illustrates well the intricate relationships that exist between temporal and spatial processes at deep-sea hydrothermal vents.

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