



Implications of cross-axis flow for larval dispersal along mid-ocean ridges

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Introduction

Dispersal processes play an important role in the structure and dynamics of many terrestrial and marine communities, and they are especially critical in deep-sea hydrothermal vent ecosystems. These systems are patchy and transient, and most of the species inhabiting them cannot survive elsewhere, so successful dispersal (usually via a larval stage) is essential for maintaining viable populations and species ranges.

To understand the mechanisms of larval dispersal, we need to know larval life spans and the transport dynamics of deep-water flows near vent habitats. When these values are measured for a species in a given region, a maximum dispersal distance can be calculated and compared to the geographic spacing between vent fields in that region. This approach gives a first-order answer to the questions of how far a larva can disperse and whether a species has the potential to migrate between any two given vent sites. However, to understand the effects of dispersal on population dynamics, gene flow and population genetic structure, we need to know the number of migrants among sites. This calculation requires estimates of fecundities and mortality rates that are very difficult to verify for vent species (e.g., Chevaldonné et al., 1997), and are outside the scope of our study.

The objective of the present study is to focus on the first-order question of how far larvae of a given lifespan can disperse in the flow environments near vent sites at different mid-ocean ridges. We follow the approach that Marsh et al. (2001) used to calculate dispersal potential of larvae of the vestimentiferan tubeworm *Riftia pachyptila* Jones, 1981, near 9°N on the East Pacific Rise (EPR). They conducted physiological measurements on larvae cultured at ambient deep-sea pressure to calculate a *R. pachyptila* lifespan of roughly 38 days, and incorporated a current-meter record

(Fig 1a) into a dispersal model to estimate a maximum larval dispersal distance of 103 km along the ridge in flows in that region. They noted, however, that most *R. pachyptila* larvae released over a 5-mo period did not travel that far during their 38-day life span. The majority of larvae were instead lost off-axis during the sustained episodes of across-ridge flow, or remained close to their natal site due to periodic reversals in along-ridge flows. One conclusion of Marsh et al. (2001) was that the dispersal of *R. pachyptila* larvae near 9°N EPR is limited not by the physiological performance of its larvae, but rather by the local flow regime. In our present study, we explore whether that conclusion holds generally across different locations on mid-ocean ridges. We also discuss the limitations of using current meter records (an Eulerian approach) for dispersal studies, and the value of incorporating alternative Lagrangian approaches such as drifter studies and numerical modeling.

Materials and methods

To calculate larval dispersal potential at 13°N EPR, a current meter record was used from the French-American cruises HERO '91 and HERO '92 (Fig. 1b). The current data had been recorded hourly from 27 October 1991 to 3 April 1992 with an Aanderaa RCM5 current meter placed 100 m above the bottom along the ridge axis (see Chevaldonné et al., 1997 for additional detail). Components of the velocity were calculated along and across the ridge axis, which was oriented NNW/SSE at 10° from geographic North. Following the methods in Marsh et al. (2001), larval dispersal was modeled by releasing neutrally buoyant 'larvae' at hourly intervals into the observed current regime. The trajectory of each released particle was followed for a specified lifespan or until the particle had moved > 25 km off axis. In the dispersal model, the along-axis distance

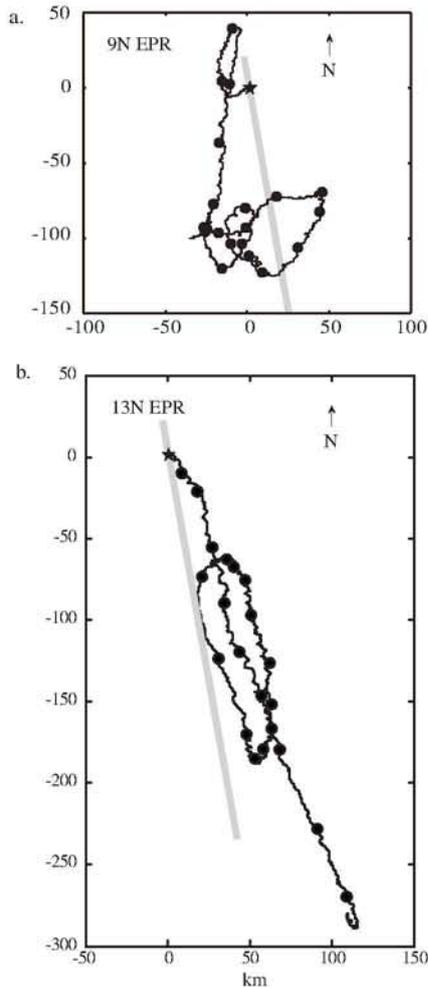


Figure 1. Progressive vector diagrams showing currents at two locations on the East Pacific Rise. Gray lines denote approximate position of ridge axis, additional bathymetric detail can be found in Crane et al. (1988). Diagrams assume lateral homogeneity of flow in order to track the trajectory of a water parcel originating at the location of the current meter (filled star), with filled circles at 7-day intervals: a) currents from 9°50.9'N, 104°17.6'W (9°N), measured at 175 m above bottom, (from Marsh et al. 2001); b) currents from 12°48.9'N, 103°56.6'W (13°N) measured 100 m above bottom (from Chevaldonné et al., 1997).

x_i (in m) traveled by an individual larva released at time step i was calculated as

$$x_i = dt \sum_{j=i}^{i+1} u_j \quad \text{for } i = 1 \text{ to } (n - 1 + 1)$$

where dt is a 1-hr time step, u_j is the mean along-axis velocity (m h^{-1}) during j^{th} 1-hr time step, n is the number of 1-hr intervals in the current record, and 1 is the larval lifespan (hr). The cross-axis distance y_i was calculated similarly, substituting the cross-axis velocity v_j for u_j . A distance of 25 km was set as the maximum that a larva could travel off-axis and still be capable of colonizing the

ridge. This distance corresponds roughly to the outer limit of the ridge base, and was selected because the ridge-affected flows tend to extend roughly to this distance (e.g. for Juan de Fuca Ridge, Thomson et al., 1990).

The dispersal calculations made for 9°N in Marsh et al. (2001) and for 13°N in the present study require the (untested) assumption of lateral homogeneity and linearity of flow over the duration of the current measurements to be applicable. Although this assumption appears reasonable for locales where topography is relatively simple and consistent along the ridge, it is likely violated at regions with complex topography, such as those near fracture zones, offsets or collapses. Current records from the Rainbow vent site on the Mid-Atlantic Ridge (Thurnherr et al., 2002) provide an example of topographically steered flow that is laterally inhomogeneous on scales as small as a few kilometers. For such sites, drifter studies likely provide a better model for dispersal.

As an example of using drifters to calculate dispersal potential, transport along the Mid-Atlantic Ridge (MAR) was estimated using 21 float tracks from the Eurofloat experiment (Speer et al., 1999). The floats had been placed at 1750 m depth, near the ridge crest level north of the Azores Plateau, and followed daily for four years with an acoustic network. For each float that moved within 25 km of the ridge crest, we recorded the time and along-axis distance that the float traveled before it moved off axis (i.e., > 25 km from crest). Because the ridge crest is not linear at this latitude, and the Azores Plateau is a major topographic feature, we considered a float to be 'on-axis' as long as it was less than 25 km horizontally from the 2000 m bathymetric contour of the ridge. Along-axis distance was measured along a contour, not as a linear distance between the start and end point of a trajectory.

Results

The current records at 9°N and 13°N EPR both show that residual currents are aligned along-axis and reversed episodically (Fig. 1), and that semidiurnal and diurnal tidal variations occur across- and along-axis (R. Thomson, analyses not shown for 9°N; Chevaldonné et al., 1997 for 13°N). However, the 13°N record does not show the sustained cross-axis residual flows observed at 9°N. This difference in measured flow leads to very different results from the dispersal model between the two EPR sites. At 9°N, the maximum along-axis dispersal distance for a larva of any life span was 103 km, and the percentage of larvae remaining on axis (survivors) decreased below 70% for larvae with life spans > 12 days (Fig. 2a). Note that we use the term 'survivor' to refer to any larva remaining within 25 km of the ridge crest, and we do not invoke any other sources of mortality. Dispersal distance increased with life span, but only up to a life span of 20 days. This 20-day interval corresponds to the longest period of sustained along-axis flow in one direction. In contrast, at 13°N, the maximum dispersal distance was 241 km and survivors decreased below 70% only for larvae with >64 day life spans (Fig. 2b; longer life spans not shown). Dispersal distance increased with life span up to a life span of 64 days,

corresponding to the longest period of along-axis unidirectional flow, as at 9°N.

For relatively short larval life spans (< 20 days), maximum dispersal distances are similar at the two sites (Fig. 2), because daily averaged currents are similar. For longer larval life spans (20 - 64 days), dispersal distances are greater at 13°N than 9°N. For example, a *Riftia pachyptila* larva with a lifespan of 38 days would have a maximum dispersal distance of approximately 200 km, and if it increased its life span, it could migrate even farther.

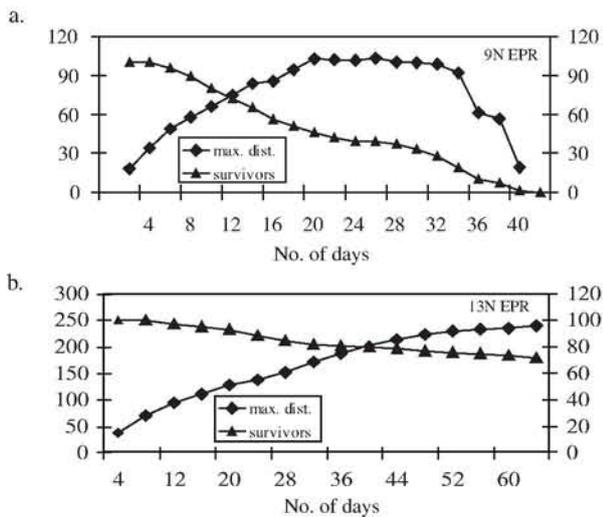


Figure 2. Maximum dispersal distance and survivors (% larvae remaining within 25 km of ridge axis) calculated from dispersal model for larvae of different life spans at two locations on East Pacific Rise: a) at 9°N for larval life span of 2 - 42 days (from Marsh et al., 2001); b) at 13°N for larval life span of 4 - 64 days.

Of the 21 floats released on the Mid-Atlantic ridge as part of the Eurofloat experiment, nine were transported to within 25 km of the 2000 m bathymetric contour of the ridge, and three of those nine moved off axis and then on again (Table 1). The along-axis excursion times of floats ranged from 91 to 833 days, resulting in along-axis dispersal distances of up to 812 km.

Discussion

The results from the dispersal model at 13°N on the East Pacific Rise indicate that dispersal potential of a larva with relatively long life spans (> 20 days) may vary substantially even among neighbouring segments along an individual ridge. Larvae of *R. pachyptila* (life span 38 days) appear to have the potential to disperse farther at 13°N than 9°N EPR, even though daily averaged current speeds are roughly comparable at the two sites. The reason is that during our measurement intervals, along-axis residual flows at 13°N reversed less frequently than at 9°N, allowing larvae longer intervals to disperse in a single direction. Furthermore, the across-axis residual flows at 13°N were not sustained for multi-day intervals as they were at 9°N, and off-axis loss of

Table 1. Along-axis excursion times and distances of floats released at 1750 m depth near Azores Plateau (Mid-Atlantic Ridge) as part of Eurofloat experiment. Shown are the start and end positions of float during interval(s) when it was within 25 km of the 2000 m depth contour of the ridge.

Float	Start position		End position		Excursion	
	Lon (°W)	Lat (°N)	Lon (°W)	Lat (°N)	Time (d)	Dist (km)
1	25.95	47.93	26.51	45.17	336	170
	28.08	40.99	29.15	40.34	96	72
9	26.48	40.70	23.94	37.14	168	296
	26.38	40.52	24.62	38.29	91	178
3	24.45	38.41	27.58	37.69	599	304
	28.23	43.61	28.79	42.72	245	66
4	26.58	40.62	29.47	36.72	350	528
	26.27	40.57	35.78	34.62	787	804
7	27.07	45.23	27.13	45.39	91	34
8	26.94	40.26	26.82	39.84	185	50
	26.33	39.26	27.46	35.60	364	360
9	25.72	39.38	35.82	35.26	833	812

larvae occurs only occasionally during the 5-month record. Because our modeled larval dispersal potential increases with life span up to a value of 64 days, we suggest that dispersal of species with larval life spans such as *R. pachyptila*'s (38 days) is limited at 13°N EPR by physiological performance of the larvae, rather than by flow regime.

However, the dispersal distances calculated in our model are realistic only for regions of a ridge segment where currents are similar to those recorded at the location of the current meter, and our model does not take into account the possibility of geographic or oceanographic barriers. We cannot, for instance, assume that larvae continue to disperse in an along-axis direction as they cross transform faults or other major topographic features. This limitation raises the point that dispersal calculations made using the Eulerian approach are based on the assumption of homogeneity of flow. Although we think this is a reasonable assumption within a ridge segment (as long as currents are measured away from anomalous topographic features) and for larval life spans of roughly 1 month, we are not able to test it with our data. We expect the error in the current meter-based larval trajectories to increase with time from their release, so they are more reliable for the shorter excursions than the longer ones.

The dispersal estimates made from drifter tracks on the Mid Atlantic Ridge (the Lagrangian approach) suggest that dispersal distances could be long (many hundreds of km) for very long-lived larvae (life span > 100 days). They also indicate that most larvae released at the ridge crest could remain along the ridge for intervals of 100 days or more, resulting in high survival (defined as on-axis retention). The conformity of these trajectories to ridge contours is unrelated to the presence of rift-valley walls, which can channel currents within the rift valley and limit off-axis transport (e.g., Khripounoff et al., 2000; 2001). Mean daily averaged speeds of the drifters appear low relative to current speeds on the EPR, and a larva with a 38-day life span

would have a maximum dispersal distance much less than 100 km along the Mid Atlantic Ridge (Table 1). The combination of relatively slow along-axis mean currents with infrequent off-axis loss suggest that larval dispersal potential may be limited by larval life span for most larval types in this region of the Mid Atlantic Ridge. However, the number of drifter trajectories analysed was low (9), and comparisons of these trajectories with EPR dispersal results are difficult to analyse statistically.

An alternative Lagrangian approach that avoids the problem of low numbers of floats is use of a general circulation model (GCM) to estimate dispersion rates. For example, Speer et al. (2002) used the Parallel Ocean Program (POP), set up essentially as described in Maltrud et al. (1998), to quantify off-ridge dispersion. RMS zonal displacement of trajectories in the POP model was calculated along the mid-ocean ridges of the Pacific, Atlantic and Indian oceans. These zonal dispersal distances suggested that off-axis dispersal of larvae varies in a predictable way among ridges and with latitude on an individual ridge. For instance, on the northern Mid-Atlantic Ridge, dispersion is maximal at high latitudes and decreases poleward, whereas on the Juan de Fuca Ridge, dispersion at similarly high latitudes is relatively low (Fig. 9 in Speer et al., 2002). Model-based diagnostics can address sampling problems associated with limited numbers of floats; however, they will require careful comparison with observations to be useful. Thus, future work should combine both modeling and observational assessments of dispersion.

In summary, we have presented three different ways to use information on ridge-related flows to estimate larval dispersal distances along-axis, and larval losses off-axis. The Eulerian approach using current meter data has the advantage of providing numerous trajectories over long time intervals, but is limited by the assumption of homogeneity of flow. The Lagrangian approach using field observations of floats provides trajectories that are directly relevant to larval dispersal paths, but is limited by the number of floats available. The Lagrangian approach using a general circulation model provides numerous trajectories, but their relevance to dispersal distances on time scales of larval life spans is still being evaluated. We suggest that although each of these approaches is valuable on its own, they are likely to provide more reliable and robust estimates of larval dispersal when used in combination.

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