

## Supply of gastropod larvae to hydrothermal vents reflects transport from local larval sources

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### *Abstract*

Variation in larval supply to disjunct marine populations can provide insight into larval transport and delivery mechanisms, especially when compared with observations of physical transport. Daily variability in larval supply at two mussel-dominated hydrothermal vents, East Wall and Choo Choo, near 9°50'N, East Pacific Rise, was quantified concurrently with hydrodynamic observations to investigate local dispersal processes. The magnitude and temporal variation in supply differed between the two vent sites despite their close proximity, 1.6 km. Larval supply was relatively high and uninterrupted at East Wall compared to low and episodic at Choo Choo. Observed variation in larval supply was compared to predictions based on advective transport from larval sources at neighboring vents. Variation in larval supply at Choo Choo correlated with along-axis southward currents, consistent with larval transport from a northern larval source. Larval supply to East Wall appeared to be independent of current velocities, suggesting that larvae came from multiple sources north of and south of and possibly including East Wall. Transport of larvae from discrete local sources can explain differences in larval supply to vent communities, even on spatial scales of kilometers.

Understanding the biological and physical transport mechanisms involved in the dispersal, retention, and delivery of larvae is essential to the study of marine benthic population dynamics and structure, gene flow, and connectivity. Larval supply contributes to shaping population and community structure and dynamics and the strength of postsettlement benthic interactions: competition, facilitation, and predation (Gaines and Roughgarden 1985; Menge 1991; Underwood and Keough 2001).

The timing and spatial extent of larval supply to benthic habitats can be governed by physical processes. Recent research has focused on larval delivery on tidal scales (Roegner 2000; Underwood and Keough 2001), especially in regard to bay–ocean exchange. However, larval delivery

has also been correlated with wind-driven and mesoscale events, such as wind reversals (Epifanio 1995; Bertness et al. 1996), storms (Reed et al. 1988; Etherington and Eggleston 2000), upwelling relaxation (Roughgarden et al. 1988; Shanks and Brink 2005), and eddies (Rodríguez et al. 2004; Sponaugle et al. 2005). In many of these studies, correlations between observed physical transport and larval supply have provided insight into larval transport and delivery mechanisms.

Disturbed and dynamic communities, such as hydrothermal vents, may be particularly sensitive to variation in larval supply. Hydrothermal vents along the East Pacific Rise (EPR) undergo successional processes (Shank et al. 1998) reset by eruptive and/or tectonic events on a decadal time scale (Fornari and Embley 1995; Tolstoy et al. 2006). Initial colonization of nascent vents after a disruptive event will be determined, in part, by the availability and delivery of larvae. Larval supply in conjunction with the environment and benthic interactions determine the community composition and the successional sequence. While environmental effects (Shank et al. 1998; Luther et al. 2001) and benthic interactions (Mullineaux et al. 2003) have been studied on the EPR, the role of larval supply remains largely unknown because of infrequent larval collections and a poor understanding of larval dispersal and delivery.

Larval transport and recruitment processes at vents along the EPR have been inferred from only a few physical and biological studies. Physical observations suggest that passive advective transport in currents would carry larvae tens to hundreds of kilometers within a 30-d larval life span (Chevaldonné et al. 1997; Marsh et al. 2001). Population genetic studies also suggest extensive dispersal over

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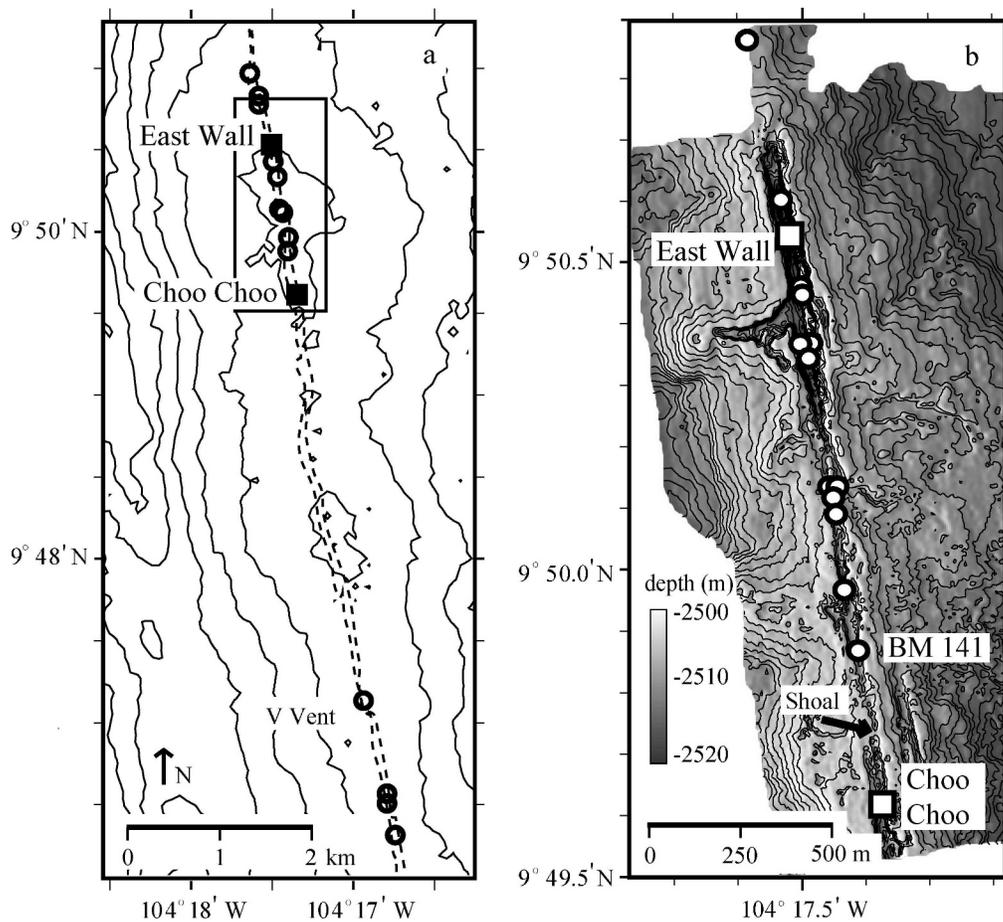


Fig. 1. The 9°50'N area of the East Pacific Rise. Collection sites (squares) at East Wall and Choo Choo and the known vent communities (circles) are identified. (a) Distribution of known vent sites between 9°46'N and 9°51'N along the axial summit trough (dashed line). Contour lines are 25 m; the ridge axis depth near 9°50'N is 2,500 m. (b) Expanded view of area in rectangle in panel (a) to show detail in axial summit trough topography; contours are 1 m. The strike of the axis is approximately 8° counterclockwise from north.

hundreds to thousands of kilometers for many vent species (e.g., Vrijenhoek et al. 1998; Hurtado et al. 2004). Larval retention in buoyancy-driven flows trapped within the axial summit trough (AST) has been proposed for the Juan de Fuca Ridge (Thomson et al. 2003) but may be less likely to occur on the EPR, where the AST is shallower. Despite the evidence for extensive larval dispersal, local exchange processes may also be important on the EPR, as larval abundances are typically greatest in the vicinity of vents (Mullineaux et al. 2005).

We investigate variability of gastropod larval supply to hydrothermal vent communities near 9°50'N, EPR, on small temporal (days) and spatial (kilometers) scales in order to better understand local dispersal processes. Gastropods are used as a model group because of their diversity, abundances, range of physiochemical tolerances, and relative ease of identification for vent species. Continuous records of currents and of daily gastropod larval supply to two hydrothermal vents are compared to predictions based on a simplified model of advective transport from different larval sources. Our intent is to

characterize whether larval supply in the field correlates with physical transport near bottom and/or at the height of the neutrally buoyant plume.

## Methods

*Study sites*—The study was done at two mussel-dominated vent sites, East Wall and Choo Choo, in the 9°50'N area on the EPR in November 2004. East Wall and Choo Choo communities had similar species compositions based on qualitative macrofaunal sampling in 2004 (D. K. Adams unpubl.) and quantitative sampling in 1999 and 2001 (Dreyer et al. 2005; Choo Choo referred to as Train Station). In 2004, the diffuse-flow hydrothermal community at East Wall was located within the northern portion of an active section of the AST on the ridge axis (Fig. 1), draping the ~13-m relief of the east wall of the AST. Numerous other high-temperature and diffuse-flow vent sites were located within a few hundred meters to the north and south of East Wall within a continuous section of the AST (Fig. 1). The northernmost vent sites known on the

9°N segment were just to the north (<1 km) of East Wall. Choo Choo was 1.6 km south of East Wall along the ridge axis in a small section of the AST encompassing no other vent communities. The AST at Choo Choo was shallower (~5 m) than at East Wall and was separated from the northern section by a shoal 200 m to the north (Fig. 1b). The closest larval source to Choo Choo was the Biomarker 141 community, approximately 400 m to the north (Fig. 1). Tubeworm Pillar and Y Vent were the closest vents to Choo Choo, tens of meters south, but had shut down as of the spring of 2004 (T. Shank and K. Von Damm pers. comm.) and thus were not considered a source of larvae for this study. The closest known active larval source to the south of Choo Choo was the V Vent community in the 9°47'N area, approximately 4.5 km away (Fig. 1a). We think it is unlikely that other, unknown larval sources existed in this region of the EPR at the time because it has been mapped intensively (e.g., Haymon et al. 1991; Ferrini et al. 2007) and visited frequently prior to our study.

*Experimental design*—Moorings were deployed from 12 to 22 November 2004, one each near East Wall and Choo Choo, to collect time-series samples of larvae and to measure current velocities. The Choo Choo mooring was deployed a day after the East Wall mooring because of ship time constraints, causing the Choo Choo records to be a day shorter. Each mooring was equipped with a PAR-FLUX Mark 78H-21 time-series sediment trap (McLane Research Laboratories, Inc.) with the opening positioned at 4 m above bottom (mab) to collect larvae. Each trap had a sampling area of 0.5 m<sup>2</sup> covered with a baffle (cell diameter 2.5 cm, aspect ratio of cells 2.5) to reduce eddy generation and sample bias. The traps sampled continuously, collecting discrete daily (24-h interval) samples until day 8 (19 November 2004). The last two days were sampled in 4-h intervals in an attempt to capture diurnal and semidiurnal tidal variability. The number of larvae collected in each 4-h interval was too low for statistical analyses, and samples were subsequently pooled into daily intervals.

Each mooring was also equipped with two current meters positioned near bottom (at 10 mab) and within the level of the neutrally buoyant vent plume (at 170 mab) as mapped by Baker et al. (1994). Aanderaa RCM11 acoustic current meters were used except for the instrument at 170 mab on the Choo Choo mooring, which was a vane and rotor RCM8 model. The current meters on the Choo Choo mooring recorded at 10-min intervals, and the current meters on the East Wall mooring recorded at coincident 30-min intervals because of lower battery capacities. Moorings were positioned within 10 m of the center of each of the venting areas. Exact positioning was accomplished by lowering the mooring from the ship's hydrowire and navigating it into an acoustic network on the seafloor (Hunt et al. 1974) using the ship's dynamic positioning capabilities. A transponder on the wire communicated acoustically with the long baseline navigational network used by DSV *Alvin* and allowed positioning directly above the target drop site. After placement on the seafloor, the positions of the moorings at East Wall, 9°50.54'N, 104°17.53'W, and at Choo Choo, 9°49.60'N,

104°17.37'W, were verified using slant range surveys and visual observation from DSV *Alvin*.

*Larval sample processing*—Larvae were preserved in the sediment traps in situ and processed in the laboratory after trap recovery. We used a saturated-salt–20% dimethylsulfoxide solution (Khrifounoff et al. 2000) to preserve sediment trap samples for morphological identification and to preserve DNA for future studies. The fraction retained on a 63- $\mu$ m sieve was sorted for larvae (gastropods, bivalves, polychaetes, and crustaceans) under a dissecting microscope at  $\times 25$ . Gastropod larvae were further identified to the lowest possible taxonomic level under dissecting and compound microscopes, often to the species level, based on shape, size, and sculpture of the larval shells (Protoconch I and II) (Mullineaux et al. 1996, 2005). Larval identifications, groupings, and nomenclature were based on Mullineaux et al. (2005), except for Benthic Gastropod A, which was previously named Unknown Benthic sp. A, and *Planorbidella planispira* (Unk. W), which was previously referred to as Unknown neomphalid W. Gastropod larvae unequivocally identified as of vent origin were grouped as vent gastropod larvae for subsequent analyses. Gastropod larval morphotypes found in high abundance in present samples and in past larval collections (Mullineaux et al. 2005) but not definitively identified as of vent origin were grouped and treated separately as probable vent gastropods.

*Spatial and temporal variability in larval supply*—Sampling was designed to characterize spatial and temporal variability of larval supply at two sites. Capture rate of larvae in the sediment trap samples was considered as a proxy for larval supply to the benthos. We acknowledge that this serves only as an approximation of larval supply since it assumes the larvae were competent to settle. Little information exists on the development of competency in vent larvae. Many vent gastropod larvae may be competent on release or shortly thereafter because the majority are nonfeeding and have no detectable development stages (Lutz et al. 1986), but times to competency are unknown. Sediment traps also collect particles of different sizes and weights differently (Butman 1989; Knauer and Asper 1989). Therefore, sediment trap collections of larvae do not necessarily reflect the relative abundances of different species. To avoid bias due to particle fall velocity, only spatial and temporal patterns within a single species and for predefined species groups are considered here. Time series of grouped and species-specific larval supply were not autocorrelated ( $p > 0.05$ ) (Systat version 10, Systat Software Inc.); therefore, larval supply data were treated as independent for spatial comparisons. Differences in larval supply between the two sites were tested using Bonferroni corrected paired  $t$ -tests in Systat version 10. Temporal variability in gastropod larval supply was assessed using a 95% confidence interval (CI) to identify anomalous supply compared to the mean.

*Current meter records*—Current velocities were transformed onto a coordinate system oriented along the strike

of the axis ( $8^\circ$  counterclockwise from true north and  $16^\circ$  from magnetic north), such that  $v$  is along-axis flow and  $u$  is cross-axis flow. Tidal analyses were performed in MATLAB version 7.1 (The MathWorks, Inc.) using the program `t_tide` (Pawlowicz et al. 2002). Current records from Choo Choo were low-pass filtered (Alessi et al. 1985) with a cutoff of 50 min (five data points) and then subsampled every third record to make records of equal sampling intervals from both sites for correlations of current velocities between sites. Pearson correlations were determined for the cross-axis and along-axis components of the current velocities between heights and between sites using MATLAB version 7.1.

*Correlation between advective transport and larval supply*—Predictions of temporal variation in larval supply at the collection sites, based on horizontal advective transport from a continuous discrete larval source, were constructed for comparison with sediment trap collections of larvae. The assumption of continuous larval gastropod production for the predictive model is based on the known reproductive biology of vent gastropod species from the EPR (Pendlebury 2005) and the observation that most species are present in the plankton throughout the year (Mullineaux et al. 2005). Analyses were additionally simplified to consider transport only along the ridge axis. The cross-axis component was ignored because hydrothermal vent communities are found typically along the north–south trending ridge axis (Haymon et al. 1991) (Fig. 1). The possible sources of larvae were placed north of, south of, in between, or directly at the two collection sites, East Wall and Choo Choo. Measured current velocities were used to calculate horizontal advective transport at 10 and 170 mab. The along-axis component of velocity determined the potential for transport of larvae from a given source to each collection site. For example, when currents became northward, transport to East Wall was expected to increase if the larval source was at a more southern site and to decrease if the source was at a more northern site. In contrast, when currents became southward, transport to East Wall should have decreased if the larval source was to the south but increased if the source was to the north. If the larval source was directly at East Wall, larval transport was not expected to vary with current direction. The predictions for transport to Choo Choo followed the same reasoning and depended on the direction of currents and location of source sites of larvae. Correlations between larval supply and advective transport were used to determine which vents were likely sources of larvae collected at the two study sites.

A measure of daily advective transport, derived from measured current velocities, was needed for correlation with daily larval supplies. Total or net transport during each 24-h period was not adequate because the flows were not unidirectional. Changes in the direction of flow could have caused sustained transport in one direction to be obscured by transport in the opposite direction. As an alternative, sustained transport distance in a single direction during each 24-h period was calculated as follows to yield estimates of along-axis northward and southward transport. Intervals of continuous (sustained) unidirectional

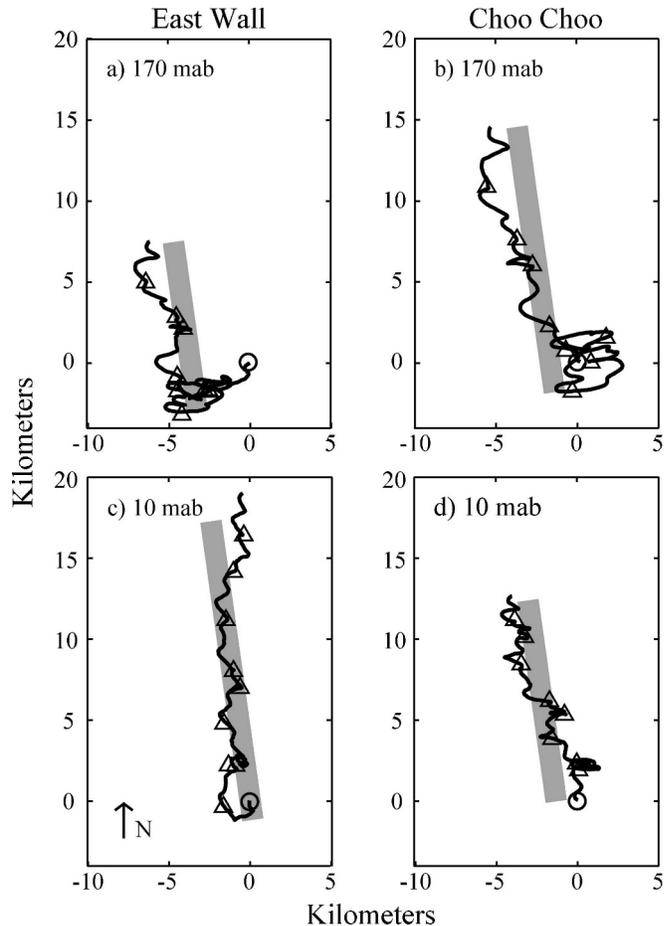


Fig. 2. Progressive vector diagrams from measured current velocities. The orientation of the ridge axis is shaded. The open circles indicate initial start date, and the triangles designate subsequent 24-h intervals. East Wall: (a) 170 mab and (c) 10 mab. Choo Choo: (b) 170 mab and (d) 10 mab.

al along-axis transport during each day were identified by filtering out high-frequency variation (cutoff 6 h) (Alessi et al. 1985). Transport distances for each interval were calculated by integrating the unfiltered velocity ( $v$ ) over time. If multiple periods of, for example, northward flow (interrupted by intervals of southward flow) occurred during a day, the period of furthest transport was used to calculate the northward transport value for that day. Only intervals that corresponded to transport distances exceeding 100 m were included. This distance represents sufficient transport to exchange material between most neighboring vents—the average distance between vents clustered near  $9^\circ 50' N$  was 138 m. These transport calculations are based on the assumption that larvae are lost from the system when currents reverse directions so that only the larvae produced during a particular interval of sustained unidirectional flow are available for transport during that interval.

Daily larval supply for pooled groups and selected species were cross correlated with daily along-axis northward, southward, and net transport using MATLAB version 7.1. We tested for autocorrelation in the larval supply and transport time series to determine whether a

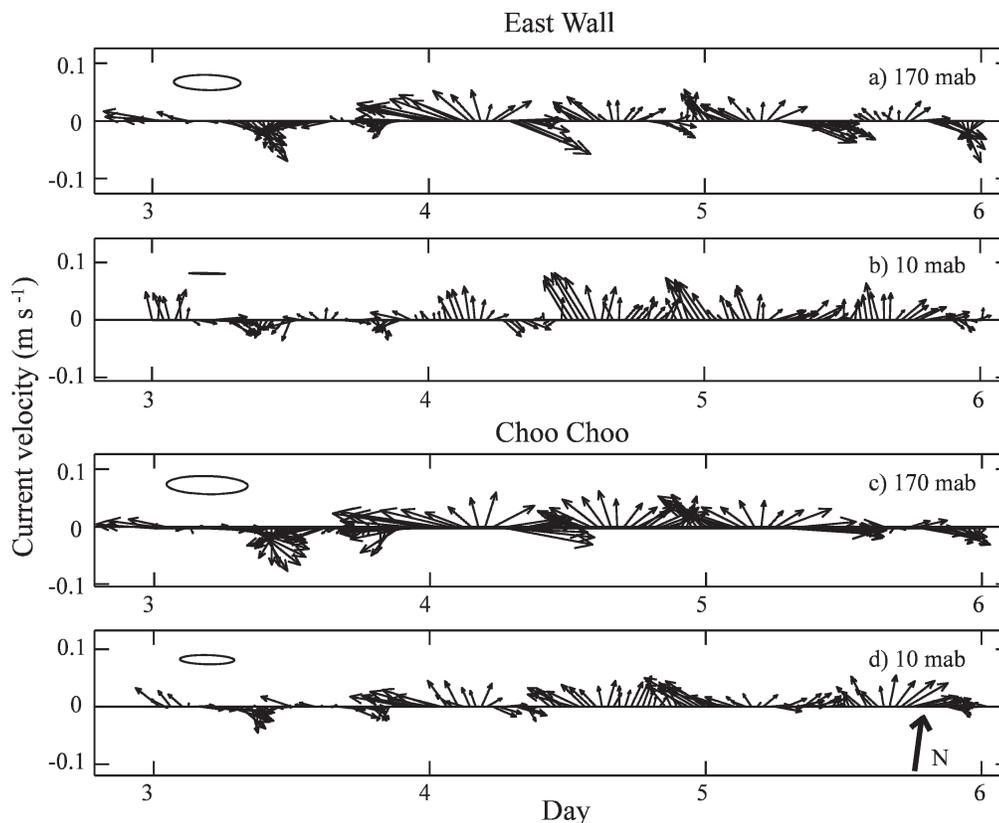


Fig. 3. Representative current velocities from days 3 to 6 of the 10-d time series. Current velocities are transformed onto a coordinate system oriented along the ridge axis (strike  $+8^\circ$  relative to true north). This subset allows visualization of the predominantly cross-axis diurnal and semidiurnal tidal fluctuations. Tidal ellipses of the dominant tidal frequency, M2, are presented in the upper left corner of each time series on the same scale as the vectors. East Wall: (a) 170 mab and (b) 10 mab. Choo Choo: (c) 170 mab and (d) 10 mab.

correction would be necessary for the cross correlations. We found no evidence for significant autocorrelation (MATLAB version 7.1; results not shown) at the  $\alpha = 0.05$  level. We also found no evidence of lagged correlations in the cross correlations between supply and transport (analyses not shown). We, therefore, present the uncorrected Pearson correlation coefficients (cross correlation at 0 lag).

*Evaluating trap collection efficiency*—Collection efficiency of a sediment trap can change if eddies form within the trap at high Reynolds numbers (Knauer and Asper 1989). Eddies may lead to under- or overcollection of particles, including larvae. Current speeds less than  $0.1 \text{ m s}^{-1}$  are

Table 1. Correlation coefficients of along-axis,  $v$ , and cross-axis,  $u$ , current velocities between sites at the same height and between heights within a site. All correlations were significant at the  $\alpha = 0.001$  level.

	Between sites		Between heights	
	170 mab	10 mab	East Wall	Choo Choo
Along-axis	0.7801	0.6971	0.6894	0.6117
Cross-axis	0.8806	0.7531	0.7407	0.8557

thought not to induce collection bias (Honjo and Doherty 1988; Butman 1989; Knauer and Asper 1989). Therefore, periods with current speeds greater than  $0.1 \text{ m s}^{-1}$  were reviewed qualitatively for coincidences with peaks and deficits ( $>95\%$  CI) in larval supply. The daily mean and maximum current speeds at 10 mab, near the trap opening, were also cross correlated with larval supply to determine if temporal variations in larval supply were caused by changes in Reynolds number due to current speed variation.

## Results

*Currents*—Current velocities at both sites and both heights generally trended north-northwest, nearly aligned along the ridge axis (Fig. 2). Near-bottom currents at East Wall were an exception and trended approximately due north (heading  $005^\circ$ ) rather than along the general strike of the axis (heading  $352^\circ$ ) (Fig. 2), possibly because of local topographic steering. Diurnal and semidiurnal tides were the dominant frequencies (analyses not shown). Tidal currents were aligned cross axis (east–west) as shown by M2 tidal ellipses (Fig. 3). Tidally driven cross-axis current velocities were apparent in the 170-mab current records but were less pronounced near bottom.

Table 2. Total number of gastropod larvae collected over 10 d at East Wall and 9 d at Choo Choo on the East Pacific Rise. V, species endemic to vents; PV, probable vent species; ?, not determined or unknown.

Taxa	Origin	East Wall	Choo Choo
Gastropoda			
<i>Bathymargarites symplector</i>	V	5	3
<i>Clypeosectus delectus</i>	V	2	1
<i>Cyathermia naticoides</i>	V	242	25
<i>Echinopelta fistulosa</i>	V	1	0
<i>Eulepetopsis vitrea</i>	V	12	0
<i>Gorgoleptis spiralis</i>	V	11	1
<i>Gorgoleptis emarginatus</i>	V	15	2
<i>Laeviphitus</i> sp.	PV	54	12
<i>Lepetodrilus</i> spp.	V	73	9
<i>Neomphalus fretterae</i>	V	4	0
<i>Pachydermia laevis</i>	V	2	0
Peltospirid (240 $\mu$ m)	V	5	1
Peltospirid (215 $\mu$ m)	V	2	1
<i>Planorbidella planispira</i> (Unk. W)	V	1	0
Benthic Gastropod A	PV	50	7
Unknown slit limpet	PV	2	1
Unknown neomphalid sp. 5	PV	18	1
Unknown neomphalid (290 $\mu$ m)	PV	1	0
Unknown	?	1	0
Vent gastropods		375	43
Probable vent gastropod		126	21

Along-axis and cross-axis current velocities were significantly correlated ( $p < 0.001$ ) between heights at a site and at the same height between sites (Table 1), but the correlation between sites was lower near bottom, where the currents were likely influenced by bottom friction and the topography of the AST. The correlation between the heights was higher at Choo Choo than at East Wall possibly because the AST was shallower at Choo Choo.

Current speeds varied with height above bottom and between sites. Mean current speeds were  $0.052 \text{ m s}^{-1}$  (max  $0.144 \text{ m s}^{-1}$ ) at 170 mab and  $0.039 \text{ m s}^{-1}$  (max  $0.097 \text{ m s}^{-1}$ ) at 10 mab at East Wall. Mean current speeds were  $0.064 \text{ m s}^{-1}$  (max  $0.182 \text{ m s}^{-1}$ ) at 170 mab and  $0.043 \text{ m s}^{-1}$  (max  $0.114 \text{ m s}^{-1}$ ) at 10 mab at Choo Choo.

**Larval supply**—Larvae were collected over 10 d at East Wall and over 9 d at Choo Choo. We identified 19

gastropod taxa, 5 polychaete taxa, 1 bivalve taxon, and 1 crustacean taxon (*Bythograea thermydron*) of probable vent origin. Of these, the crustacean and 12 gastropod taxa were unequivocally of vent origin and have been observed in mussel-dominated benthic communities from this region of the EPR (Van Dover 2003; Dreyer et al. 2005).

We focused analyses and discussion on gastropod larvae (Table 2), which were relatively well preserved and abundant in the samples. Some taxa were not identifiable to species but could be assigned to genus or a familial group and thus could be assigned as having a vent, probable vent, or nonvent origin. Taxa considered of probable vent origin had morphological characteristics common to families known to occur at vents. Analyses focused on pooled vent gastropods; pooled probable vent gastropods; two vent gastropod taxa, *Cyathermia naticoides* and *Lepetodrilus* spp.; and two gastropod taxa of

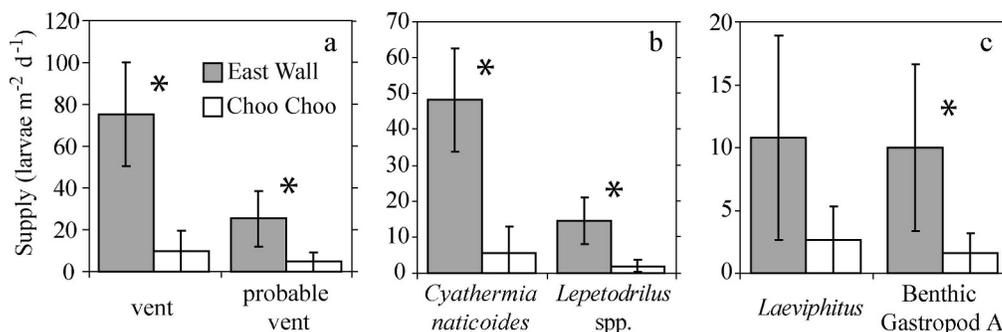


Fig. 4. Mean daily supply of gastropod larvae at East Wall and Choo Choo for the 9 d of concurrent collection; (a) pooled groups, (b) individual vent taxa, and (c) individual probable vent taxa. Asterisk denotes significant differences between sites detected by paired  $t$ -tests after Bonferroni correction ( $p < 0.05$ ). Error bars are one standard deviation.

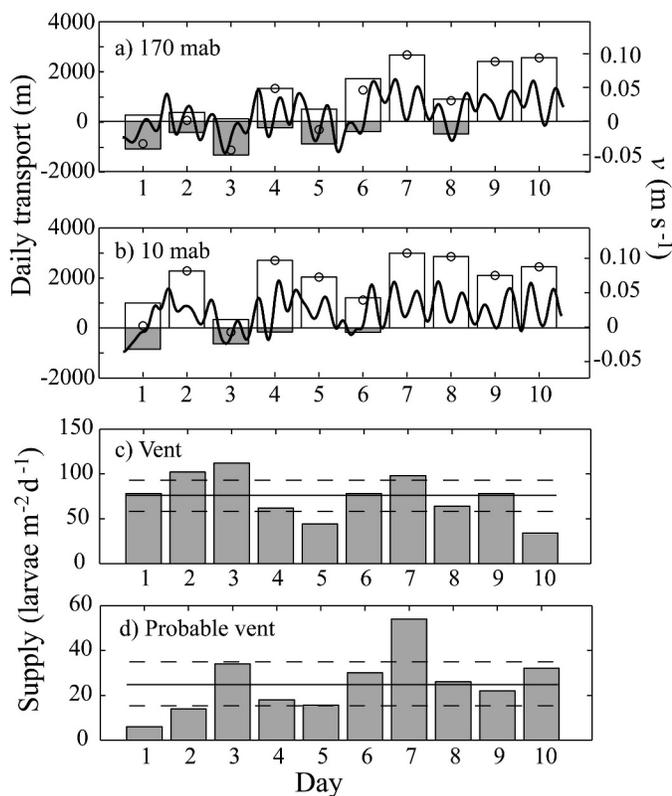


Fig. 5. Along-axis current velocities and transport at (a) 170 mab and (b) 10 mab compared to the supply of (c) pooled vent and (d) pooled probable vent gastropod larvae at East Wall. Bars (a and b) denote the northward (open bars) and southward (gray bars) transport over each 24-h period of larval collection. Open circles denote the daily net along-axis transport. The solid line is the smoothed along-axis,  $v$ , current velocity (low-pass filtered 6 h). Supplies of (c) vent and (d) probable vent gastropod larvae are presented with a solid horizontal line denoting the mean and dashed horizontal lines denoting the 95% confidence interval.

probable vent origin, *Laeviphitus* sp. and Benthic Gastropod A, which were relatively abundant.

All gastropod taxa had greater mean supply at East Wall than at Choo Choo (Fig. 4; Table 2). Daily supply at East Wall was 2–18 times higher than at Choo Choo for individual taxa. Supply was significantly greater at East Wall than at Choo Choo ( $p < 0.05$ ) for both pooled groups (Fig. 4a) and the dominant gastropod taxa (Fig. 4b,c), except for *Laeviphitus* sp., which was not significant after Bonferroni correction.

Temporal patterns of daily gastropod larval supply differed between East Wall and Choo Choo. East Wall received an uninterrupted yet variable supply of larvae (Fig. 5). Daily supply varied from the mean, exceeding the upper 95% CI on days 2, 3, and 7 and falling below the 95% CI on days 5 and 10. Supply of probable vent gastropod larvae exceeded the upper 95% CI only on day 7 and fell below the 95% CI on days 1 and 2. On the other hand, Choo Choo received comparatively low larval supply with only one episode of elevated larval supply (Fig. 6). Vent gastropod supply to Choo Choo deviated from the 95% CI only on day 3, with a peak (Fig. 6) coincident with the peak

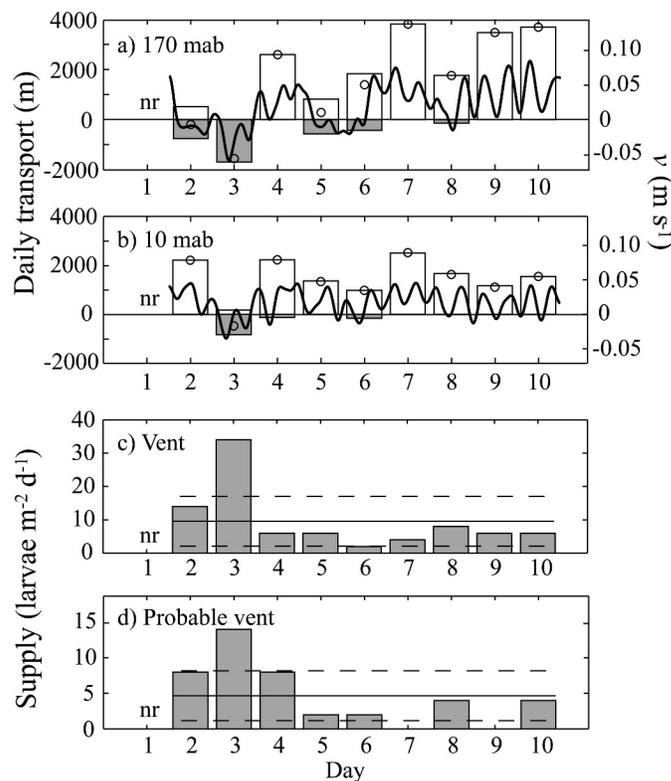


Fig. 6. Along-axis current velocities and transport at (a) 170 mab and (b) 10 mab compared to the supply of (c) pooled vent and (d) pooled probable vent gastropod larvae at Choo Choo. Bars (a and b) denote the northward (open bars) and southward (gray bars) transport over each 24-h period of larval collection. Open circles denote the daily net along-axis transport. The solid line is the smoothed along-axis,  $v$ , current velocity (low-pass filtered 6 h). Supplies of (c) vent and (d) probable vent gastropod larvae are presented with a solid horizontal line denoting the mean and dashed horizontal lines denoting the 95% confidence interval. Larval supply and transport were not recorded (nr) on day 1.

at East Wall (Fig. 5). Although larval supply peaked on day 3 at both East Wall and Choo Choo, temporal variation in supply was not significantly correlated ( $p < 0.05$ ) between sites for pooled vent gastropods ( $r = 0.574$ ) or probable vent gastropods ( $r = -0.207$ ).

Individual taxa generally followed the same patterns as the groups to which they were assigned (Fig. 7). At East Wall, supplies of *C. naticoides*, *Lepetodrilus* spp., and Benthic Gastropod A were higher than the 95% CI on day 3. *Cyathernia naticoides* also had elevated supply on days 2 and 7. *Lepetodrilus* spp. had elevated supply on days 2, 6, and 7, whereas *Laeviphitus* sp. supply peaked only on day 7. At Choo Choo, supplies of *C. naticoides*, *Lepetodrilus* spp., *Laeviphitus* sp., and Benthic Gastropod A also exceeded the 95% CI only on day 3 (Fig. 7). Supplies of *Lepetodrilus* spp., *Laeviphitus* sp., and Benthic Gastropod A to Choo Choo were intermittent with few or no larvae collected many days. Temporal variation in supply was not significantly correlated ( $p > 0.05$ ) between sites for any of the individual gastropod taxa ( $r = 0.485$  for *C. naticoides*,  $r$

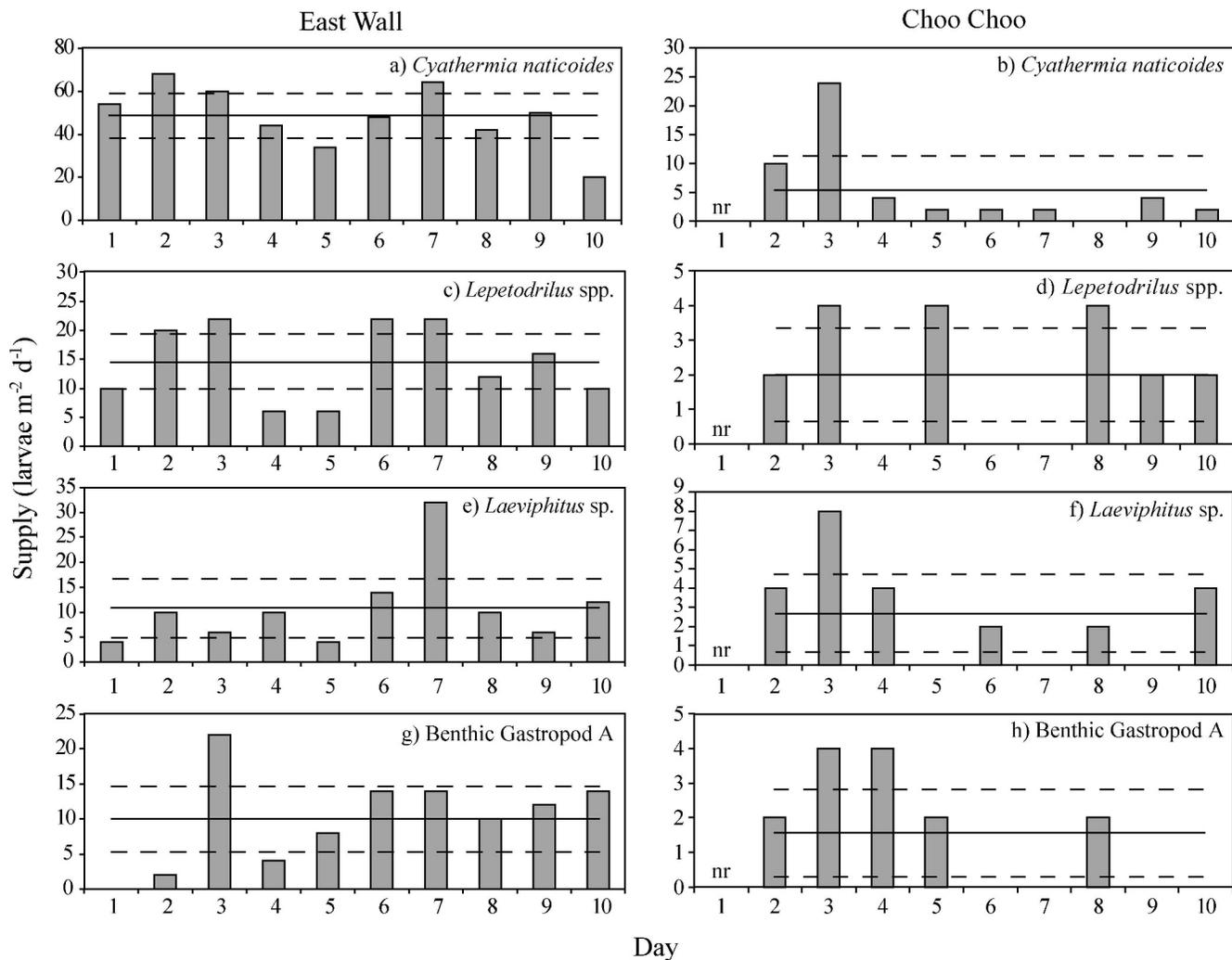


Fig. 7. Daily larval supply of vent gastropod taxa, *Cyathermia naticoides* (a and b) and *Lepetodrilus* spp. (c and d), and probable vent gastropod taxa, *Laeviphitus* sp. (e and f) and Benthic Gastropod A (g and h), at East Wall (a, c, e, and g) and Choo Choo (b, d, f, and h). The solid line denotes the mean, and dashed lines denote the 95% confidence interval. Larval supply was not recorded (nr) at Choo Choo on day 1.

=  $-0.213$  for *Lepetodrilus* spp.,  $r = -0.304$  for *Laeviphitus* sp., and  $r = -0.144$  for Benthic Gastropod A).

**Larval supply and hydrodynamics**—Daily along-axis transport during the study was sufficient to advect water parcels—and presumably larvae—between the vent sites in the  $9^{\circ}50'N$  area. Mean net along-axis transport at East Wall and Choo Choo was  $1.3$  and  $0.9$   $\text{km d}^{-1}$  at 10 mab, respectively, and  $1.5$  and  $1.8$   $\text{km d}^{-1}$  at 170 mab, respectively. Advective transport to the north was greater and more frequent than transport to the south (Figs. 2, 5, 6). Focus on along-axis transport was justified as net cross-axis transport during the study period was minimal compared to net along-axis transport (Fig. 2). Furthermore, larval supply was not significantly correlated with cross-axis transport at East Wall or Choo Choo (analyses not shown).

Supply of gastropod larvae to East Wall was not significantly correlated at the  $\alpha = 0.05$  level with along-

axis advective transport at either height (Table 3). Pearson correlation coefficients for both groups and all taxa analyzed were generally low ( $r < 0.5$ ). The only notable relationships were the positive associations of the probable vent group and *Laeviphitus* sp. with net and northward along-axis transport at 170 mab, though neither were significant.

Supply of gastropod larvae was significantly correlated with along-axis southward transport at Choo Choo at the  $\alpha = 0.05$  level (Table 4). Pooled vent gastropods, probable vent gastropods, and *C. naticoides* were significantly correlated with southward transport at 10 and 170 mab. Both the vent and the probable vent groups and *C. naticoides* showed the same trends of negative correlation with net along-axis transport (where positive was northward) and with northward transport and positive correlation with southward transport. Analyses for *Lepetodrilus* spp., Benthic Gastropod A, and *Laeviphitus* sp. were not performed because of the low magnitude of larval supply

Table 3. Correlation between daily advective transport and larval supply at East Wall. Pearson correlation coefficients are shown comparing measured larval supply and predicted along-axis advective transport during 24-h periods at East Wall. Larval values were from pooled groups and individual taxa; transport was calculated as net, northward, and southward advection at heights of 10 and 170 m above bottom. Correlations were not significant at the  $\alpha = 0.05$  level.

	Net transport	North transport	South transport
170 mab			
Pooled vent	-0.289	-0.257	0.275
Pooled probable vent	0.544	0.600	-0.381
<i>Cyathernia naticoides</i>	-0.280	-0.282	0.210
<i>Lepetodrilus</i> spp.	0.069	0.128	-0.034
<i>Laeviphitus</i> sp.	0.616	0.623	-0.561
Benthic Gastropod A	0.214	0.324	-0.005
10 mab			
Pooled vent	-0.385	-0.384	0.360
Pooled probable vent	0.287	0.246	-0.306
<i>C. naticoides</i>	-0.246	-0.221	0.285
<i>Lepetodrilus</i> spp.	-0.229	-0.291	0.039
<i>Laeviphitus</i> sp.	0.484	0.492	-0.372
Benthic Gastropod A	-0.162	-0.261	-0.061

for most days. Qualitative comparison (Fig. 6) of along-axis flow to pooled larval supply shows that the peak supply of both vent and probable vent larvae occurred on day 3, when currents were predominantly southward at 10 and 170 mab.

*Trap collection efficiency*—If trapping efficiency changed with current velocity, then one might expect to see a correlation between larval supply and current speed. Speeds directly above the trap openings did not exceed  $0.1 \text{ m s}^{-1}$  at East Wall and rarely exceeded  $0.1 \text{ m s}^{-1}$  at Choo Choo (only seven 10-min intervals). These high-speed intervals occurred at Choo Choo on days 3, 4, and 5, during periods of relatively high and low larval supply. Higher current speeds could have been due to the shorter

Table 4. Correlation between daily advective transport and larval supply at Choo Choo. Pearson correlation coefficients are shown comparing measured larval supply and predicted along-axis advective transport during 24-h periods at Choo Choo. Larval values were from pooled groups and *Cyathernia naticoides*; transport was calculated as net, northward, and southward advection at heights of 10 and 170 m above bottom. Bold indicates significance at the  $\alpha = 0.05$  level.

	Net transport	North transport	South transport
170 mab			
Pooled vent	<b>-0.740</b>	-0.657	<b>0.897</b>
Pooled probable vent	<b>-0.701</b>	-0.656	<b>0.756</b>
<i>C. naticoides</i>	<b>-0.720</b>	-0.621	<b>0.901</b>
10 mab			
Pooled vent	<b>-0.685</b>	-0.570	<b>0.879</b>
Pooled probable vent	-0.453	-0.343	<b>0.778</b>
<i>C. naticoides</i>	<b>-0.670</b>	-0.558	<b>0.895</b>

Table 5. Correlation between larval supply and current speeds. Pearson correlation coefficients comparing larval supply and current speeds during 24-h periods at East Wall and Choo Choo. Larval values are presented as pooled groups and individual taxa; speeds are presented as means and maxima at height of 10 m above bottom. Correlations were not significant at the  $\alpha = 0.05$  level.

	East Wall		Choo Choo	
	Mean	Maximum	Mean	Maximum
Pooled vent	-0.136	-0.043	0.366	0.424
Pooled probable vent	0.345	0.447	0.573	0.433
<i>Cyathernia naticoides</i>	-0.218	-0.120	0.310	0.371
<i>Lepetodrilus</i> spp.	0.150	0.175	0.099	0.250
<i>Laeviphitus</i> sp.	0.068	0.165	0.407	0.320
Benthic Gastropod A	0.495	0.528	0.731	0.624

recording interval at Choo Choo (averaged over 10 min) compared to East Wall (averaged over 30 min). However, when the Choo Choo record was averaged over 30-min intervals, speeds still peaked on days 3, 4, and 5 at greater than  $0.095 \text{ m s}^{-1}$ . Only one instance of currents greater than  $0.090 \text{ m s}^{-1}$  occurred at East Wall, on day 4, when larval supply was within the 95% CI. Additionally, observed daily larval supply was not correlated with either mean or maximum current speed during each 24-h collection at 10 mab ( $p > 0.5$ ) (Table 5). Therefore, we conclude that observed spatial and temporal variability in larval supply reflected changes in larval transport to the vents and not changes in collection efficiency of the traps caused by hydrodynamic bias.

## Discussion

Variations in larval gastropod supply to the two study sites conformed to a scenario of advective transport from local sources located at or near East Wall and north of Choo Choo. Variation in vent gastropod larval supply to East Wall did not correlate with along-axis transport at either height and thus did not appear to result from immigration from a single neighboring larval source. Instead, the East Wall community itself and/or multiple sources to the north and south may have contributed larvae, resulting in uninterrupted supply that did not vary strongly with current direction. Numerous vent communities were located near East Wall during the study (Fig. 1), providing multiple potential larval sources. The positive correlation between gastropod larval supply and southward transport to Choo Choo was consistent with a larval source north of the vent site. Again, this result is consistent with the distribution of vent communities: many vents to the north within 1 km of Choo Choo and no known vents to the south of Choo Choo within 4.5 km. We suggest that directional advection of vent larvae from these discrete sources created differences in larval gastropod supply between two vent communities in close proximity.

Diffusion, cross-axis advection, and topographic barriers could have also contributed to the decreased supply of gastropod larvae to Choo Choo during northward flows.

Assuming lateral homogeneity of flow, northward advection over a couple of days (e.g., days 7 and 8 at 170 mab or any three of days 4–10 at 10 mab) would have been sufficient to transport larvae from V Vent to Choo Choo. The very low larval gastropod supply,  $<10$  larvae  $m^{-2} d^{-1}$  during northward flows, suggests that gastropod larvae from a southern source did not reach Choo Choo, at least not in high abundances, during the study period. The well-defined AST near East Wall may have facilitated transport between vents by providing a connecting conduit, whereas larvae may have been more easily lost because of diffusion and cross-axis transport south of Choo Choo, where the AST was discontinuous and shallower. Topographic breaks in the AST may have further impeded near-bottom transport from V Vent to Choo Choo by allowing larvae to “leak” off the ridge axis. Any retention mechanisms would also reduce long-distance transport of larvae. Separation by more than a few kilometers appears to substantially reduce larval exchange of gastropods between vent sites, indicating that larval gastropod supply was primarily from neighboring vent communities (within ~1–2 km). Based on these observations, we expect that the supply of gastropod larvae would be intermittent and correlated with along-axis currents at sites isolated from other communities in this region of the East Pacific Rise by as little as 5 km, whereas sites within the center of a vent cluster would receive relatively uninterrupted supply.

Larval behavior or spatial and temporal variation in larval production also could have contributed to the observed spatial variation in larval supply. East Wall and its neighboring vents supported larger and spatially more extensive metazoan populations than the isolated Choo Choo site. Therefore, East Wall might be more likely than Choo Choo to have settlement cues such as conspecifics. Additionally, more larvae could have been produced and thus collected at or near East Wall. It is possible that an abrupt spawning event at Choo Choo caused the 1-d peak in larval supply recorded there, but we have no reproductive data to support that proposition. Given the significant correlation between southward transport and larval supply, we think that advection of gastropod larvae from nearby sources is a more plausible explanation for the temporal variability of larval supply observed at Choo Choo.

Our observation that supply of gastropod larvae to vents on the EPR appears to be influenced by transport from local sources is in contrast to previous studies that indirectly inferred extensive larval dispersal of various vent species along the northern EPR using genetics (e.g., Vrijenhoek et al. 1998; Hurtado et al. 2004) and simple physical transport models (Chevaldonné et al. 1997; Marsh et al. 2001). However, the observations presented here do not preclude the exchange of a few individuals and/or dispersal events (e.g., Reed et al. 1988) that could maintain the observed high gene flow and facilitate recolonization and successional processes over long periods of time (i.e., years to decades). We suggest that local populations were an important source of potential colonists to vents near 9°50'N EPR during the 10-d interval of our study. Evaluating the importance of localized dispersal

over longer time scales will require more extended observations.

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