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# Deep-Sea Research II

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ABSTRACT

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The vertical position of larvae of vent species above a mid-ocean ridge potentially has a strong effect on their dispersal. Larvae may be advected upward in the buoyant vent plume, or move as a consequence of their buoyancy or by active swimming. Alternatively, they may be retained near the bottom by the topography of the axial trough, or by downward swimming. At vents near 9°50'N on the axis of the East Pacific Rise, evidence for active larval positioning was detected in a comparison between field observations of larvae in the plankton in 2006 and 2007 and distributions of non-swimming larvae in a two-dimensional bio-physical model. In the field, few vent larvae were collected at the level of the neutrally buoyant plume (~75 m above the bottom); their relative abundances at that height were much lower than those of simulated larvae from a near-bottom release in the model. This discrepancy was observed for many vent species, particularly gastropods, suggesting that they may actively remain near the bottom by sinking or swimming downward. Near the seafloor, larval abundance decreased from the ridge axis to 1000 m off axis much more strongly in the observations than in the simulations, again pointing to behavior as a potential regulator of larval transport. We suspect that transport off axis was reduced by downward-moving behavior, which positioned larvae into locations where they were isolated from cross-ridge currents by seafloor topography, such as the walls of the axial valley-which are not resolved in the model. Cross-ridge gradients in larval abundance varied between gastropods and polychaetes, indicating that behavior may vary between taxonomic groups, and possibly between species. These results suggest that behaviorally mediated retention of vent larvae may be common, even for species that have a long planktonic larval duration and are capable of long-distance dispersal.

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## 1. Introduction

Deep-sea hydrothermal vents are oases of productive and unusual faunal communities that rely on microbial chemosynthesis as the base of the food web. Most vent invertebrates are capable of moving from one vent to another only in a planktonic larval stage. This mobile stage is particularly important because vent habitats are transient, sometimes on time scales as short as decades. In regions where vent fields are disturbed frequently, larval dispersal is essential for regional persistence of a population. Larval retention at a natal site, however, may be necessary to sustain a local robust population. Metacommunity theory emphasizes the importance of this balance between retention and dispersal in shaping patterns of species diversity and distributions (Holyoak et al., 2005), particularly in disturbed systems like vents (Neubert et al., 2006). Larval culturing studies have revealed a potential for long distance transport in vent species (Epifanio et al., 1999; Marsh et al., 2001; Watanabe et al., 2004; Hamasaki et al., 2010; Miyake et al., 2010), but long-distance dispersal events may be rare. Larval abundances tend to be greater near vents than away from them (Metaxas, 2004; Mullineaux et al., 2005), and most of the recruitment into an established vent appears to be from nearby populations (Adams and Mullineaux, 2008). Nevertheless, colonization by larvae dispersing hundreds of kilometers has been observed, on occasion, in the field (Mullineaux et al., 2010). These studies indicate that both long-distance dispersal and larval retention are possible at vents, but leave unresolved the questions of how often, and by what mechanism, the long-distance events occur.

Field studies indicate that transport in deep currents plays an important role in vent larval dispersal (Adams and Mullineaux, 2008; Adams et al., 2011), but numerous coastal studies show that vertical larval swimming behavior can alter transport trajectories and speeds (Dekshenieks et al., 1996; North et al., 2008; Cowen





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and Sponaugle, 2009), especially in sheared flows, such as those observed above mid-ocean ridges (Cannon and Pashinski, 1997; Thurnherr et al., 2011). Vent larvae may move vertically by entrainment into, and advection in, the buoyant vent plume (Kim et al., 1994), or as a consequence of their buoyancy or swimming behaviors. The potential for larval entrainment is substantial, as field measurements show that roughly 10% of tracer released near the bottom became entrained into the plume of a nearby vent (Jackson et al., 2010). In a biophysical model of vent larval transport along an axially symmetric ridge, McGillicuddy et al. (2010) demonstrated a strong effect of larval vertical position on dispersal away from the ridge axis. In the model, numerical larvae were released at five heights between 10 and 225 m above the bottom. Lateral transport distance of these larvae decreased systematically with height above the bottom because individuals rising 100 m or more were less influenced by topographically intensified currents near the bottom. A surprising consequence of transport in these sheared currents was that larvae released near the seafloor appeared less likely to recolonize their natal vent than those released at the level of the neutrally buoyant plume.

Our main objective in the present study is to determine whether field distributions of vent larvae show evidence for active vertical positioning, and to evaluate how this behavior may affect their dispersal or retention at vents. We compare distributions of vent larvae collected in plankton samples near 9°50'N along the East Pacific Rise (EPR) to positions of neutrally buoyant larvae in simulations using the same hydrodynamic configuration as the model in McGillicuddy et al. (2010). The comparisons evaluate differences in abundance vertically on a scale of ~100 m (near the bottom and at plume level), and laterally on the scale of 100-1000 m off axis. We use multiple species to look for individualized behaviors and to explore whether related taxa behave similarly. We also compare vent larval distributions to those of the strongly swimming vent amphipod, Halice hesmonectes, which is known to form swarms and hold position in active vent effluent (Kaartvedt et al., 1994), and to a common non-vent barnacle cyprid larva. We hypothesize that larvae of some vent species will aggregate more tightly to the ridge crest (i.e., their source vent) than simulated neutral 'larvae', and that the degree of straying from the vent, both vertically and cross-ridge, will be a function of swimming ability (with strong swimmers holding position at the vent). We expect the distribution of non-vent species to show no aggregation at the ridge crest. The 9°-10°N segment of the EPR is a good model system for this study because the geological and hydrodynamic settings (a linear ridge crest with axial valley and anticyclonically sheared boundary currents; Thurnherr et al., 2011) are common features of seafloor spreading centers globally.

# 2. Methods

# 2.1. Field collections

Specimens were collected in high-volume water filtration systems (McLane WTS 6-1-142LV), fitted with a large (50 L min<sup>-1</sup>) pump head and a 63  $\mu$ m mesh filter, as in Beaulieu et al. (2009). Pumps were suspended on autonomous moorings at heights of 3 and 75 m above the bottom (mab). The 3 m height was as close to the seafloor as possible, given the geometry of the mooring release system, and 75 m was at the lower margin of the neutrally buoyant vent plume. Moorings were lowered from the R/V *Atlantis* on the hydrographic wire and navigated into position on the seafloor using a relay transponder at the end of the wire that interrogated the submersible Alvin's Long Baseline (LBL) net. A wire-mounted Edgetech acoustic release was used to release the mooring from the wire. Pumps were scheduled to run for 24 h at a rate of 30 L min<sup>-1</sup>, starting before

#### Table 1

Location, start date and start time (GMT) for pump samplers on paired on/off axis moorings in 2006 and 2007. Paired samplers operated synoptically, except when constrained by ship operations (in 2006) or instrument malfunction (L15).

Mooring	Site	Start date	Start time
L1, L2 L3, L4 L5, L6 L15 L16 L17, L8	Ty/lo Tica Riftia Field Tica Tica	1st Nov. 2006 5th Nov. 2006 8th Nov. 2006 18th Nov. 2007 17th Nov. 2007 21st Nov. 2007	17:30, 15:30 17:30, 15:30 17:30, 15:30 17:30 15:30 15:30
L19, L20 L21, L22	Tica Tica	25th Nov. 2007 29th Nov. 2007	15:30 15:30

noon, local time (LT). This timing allowed for the submersible to survey the on-axis mooring (and reposition if necessary), and for recovery of both moorings mid-day when the ship was not involved in submersible deployment or recovery. An Edgetech acoustic release was used to release each mooring from the seafloor.

Samples were collected on cruises in November 2006 and December 2007 (Table 1). In 2006, three pairs of on/off-axis moorings were deployed. The on-axis moorings were located at three different vents, Riftia Field, Tica, and Ty/Io, all within 1.2 km of each other. Ty and Io were originally described as two neighboring vents, but only one was apparent when we visited in 2006. The two northern sites, Riftia Field and Tica were situated in a well-defined axial trough with 15 m high walls, whereas the Ty/Io vent was on a section of the ridge axis without a well-defined trough (Fornari et al., 2012). The off-axis mooring of each pair was positioned 100 m directly east of each vent. The bottom depth for both on- and off-axis moorings was 2505 m. Off-axis pumps started sampling at 15:30 GMT (09:30 LT) and on-axis ones at 17:30 GMT (11:30 LT). In 2007, four pairs of moorings were deployed. All four on-axis moorings were at Tica, and off-axis moorings were 1000 m directly east. The bottom depth for the offaxis moorings was 2530 m. On- and off-axis pumps started sampling at 15:30 GMT (except L15 which started at 17:30). Sample volumes for a 24-h pump period were approximately 40 m<sup>3</sup>. In a few cases, a pump stopped early, resulting in a smaller sample (Table 2), and one pump failed to start (L4, Tica, off-axis, 75 mab).

When plankton samples were recovered on board ship, they were cold (typically < 5 °C), and in good condition, with some of the specimens still alive. Samples were placed immediately in a 4 °C cold room, examined briefly under a dissecting microscope, and preserved in 95% ethanol. In the laboratory, larvae in the samples were sorted under a dissecting microscope and identified to species, or to the lowest taxonomic group possible. Species identifications, and affinities of taxa to vent species, were assigned based on morphology, as done by Mills et al. (2009). Selected juvenile and adult vent zooplankton were also quantified, as well as non-vent larvae.

Larval abundance patterns in vertical and cross-ridge dimensions were evaluated with a separate 2-way ANOVA (Systat v. 11) for each year, adjusted with a Bonferroni correction when necessary for multiple testing. Abundance data were log transformed, ln (x+1), to reduce unequal variance. Larvae of individual vent species were the focus of these ANOVAs, but we also analyzed non-larval (amphipod) and non-vent (cyprid) groups for comparison, as well as pooled vent larval groups (all larvae, all gastropods, all polychaetes) to look for overall or taxon-specific patterns.

#### 2.2. Model simulations

Larval trajectories were simulated using velocities extracted from a primitive equation model (Lavelle, 2006) implemented in a Download English Version:

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