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Larval Dispersal

VENT LIFE IN THE WATER COLUMN

BY DIANE K. ADAMS, SHAWN M. ARELLANO, AND BREEA GOVENAR

ABSTRACT. Visually striking faunal communities of high abundance and biomass cluster around hydrothermal vents, but these animals don't spend all of their lives on the seafloor. Instead, they spend a portion of their lives as tiny larvae in the overlying water column. Dispersal of larvae among vent sites is critical for population maintenance, colonization of new vents, and recolonization of disturbed vents. Historically, studying larvae has been challenging, especially in the deep sea. Advances in the last decade in larval culturing technologies and more integrated, interdisciplinary time-series observations are providing new insights into how hydrothermal vent animals use the water column to maintain their populations across ephemeral and disjunct habitats. Larval physiology and development are often constrained by evolutionary history, resulting in larvae using a diverse set of dispersal strategies to interact with the surrounding currents at different depths. These complex biological and oceanographic interactions translate the reproductive output of adults in vent communities into a dynamic supply of settling larvae from sources near and far.

INTRODUCTION

Since the discovery of life at hydrothermal vents, a prevailing question has been how the endemic vent fauna colonize suitable habitats in the vast deep sea. Most vent animals are sedentary (benthic) as adults, but they produce tiny offspring, many of which are free-living larvae that can travel with ocean currents as plankton (Figure 1). Because larvae have different morphological and physiological characteristics than their adult counterparts, they can withstand environmental differences between the natal habitat and the water column in order to find locations to settle and develop into adults. Larval dispersal is responsible for (1) the exchange of individuals necessary to maintain populations and genetic connectivity over space and time, and (2) the colonization of new habitats or immigration into existing communities that can influence community structure and species diversity. Thus, the dispersive larval phase is separated from the adult phase in space and time, yet it can buffer, connect, and drive dynamics of the adult populations on the seafloor. So, although these two phases of the life cycle are inherently separated, they are also inextricably linked.

In order to understand how population dynamics and species diversity are maintained at hydrothermal vents, a mechanistic understanding of larval dispersal among vent sites is critically important. Levels of exchange between vent sites have traditionally been evaluated through population genetic studies (reviewed in Vrijenhoek, 2010), but genetic measures do not reveal dispersal mechanisms and can be further complicated by historic events that do not reflect current levels of exchange. Although studying larvae in the deep sea is difficult due to limited access and sampling constraints, in the past decade, advances in culturing techniques and continued integrated, interdisciplinary time-series monitoring of larvae and currents have provided new insights into vent life in the water column. Some of the most useful developments for predicting larval dispersal mechanisms have been hydrodynamic observations and modeling. However, to accurately predict dispersal by currents, larval biology must also be considered. The reproductive efforts of adults determine the timing and number of larvae in the water column. During their planktonic journey, the biology and behavior of larvae interact with oceanic circulation, ocean ridge topography, and ridge flows to influence the timing, distance, and trajectory of larval transport among hydrothermal vent habitats (Figure 2). Finally, the supply of larvae, their settlement behaviors, and recruitment dynamics ultimately affect benthic population structure and community interactions.

In this paper, we review reproductive patterns and known larval durations, behaviors, and vertical distributions, and suggest how these biological features couple with vent topography and hydrodynamics to affect dispersal. Finally, we suggest some areas to focus efforts on, especially in light of conservation issues recently arising at hydrothermal vents.

Larvae of vent animals (insets) ensure the persistence of life at vents by tying together distant communities such as these giant tubeworms huddled around a chimney vigorously gushing hot, chemically laden hydrothermal fluids. *(top inset) Image of shrimp larva courtesy of H. Miyake (Miyake et al., 2010). Images of (middle inset) gastropod larva, (bottom inset) polychaete larva, and (main photo) tubeworm community*

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ON THE RISE

The timing of larval release and the planktonic larval duration (PLD), the amount of time larvae take to develop to the settlement stage, affect when and for how long currents will transport larvae. In the simplest scenario, larval dispersal distance could be estimated by the duration of larval life combined with the direction and magnitude of prevailing currents. However, many larvae are not simply particles being passively carried by currents. Instead, larvae may adjust their vertical positions in the water column in order to influence which water masses transport them.

Reproduction

Because hydrodynamic conditions in the water column vary with time, dispersal patterns initially depend on when larvae enter the water column. This timing is controlled by reproductive patterns in vent animals (e.g., when they become sexually mature, how many times they reproduce, when they reproduce) and timing of spawning (release of eggs and sperm) or brooding embryos for release of later-stage larvae. Specific spawning events are rarely observed at deep-sea chemosynthesis-based ecosystems (but see Hilário et al., 2011; Bright and Lallier, 2010); thus, inferences about spawning time are often made from scrutinizing patterns in population structure or, more directly, reproductive cycles. Reproductive patterns in the deep sea are diverse and complex (Young, 2003). While individuals typically reproduce periodically and spawn in synchrony with other individuals to ensure fertilization, population-wide breeding tends to be continuous throughout the year in the deep sea (Gage and Tyler, 1991; Young, 2003) and at hydrothermal vents (reviewed in Tyler and Young, 1999; Van Dover, 2000). Continuous reproduction has been shown for many populations of hydrothermal vent gastropods (e.g., Tyler et al., 2008; Matabos and Thiébaut, 2010) and several caridean shrimp (Llodra et al., 2000). Intensive time-series studies of reproductive development are not yet available for any gutless tubeworms (Hilário et al., 2011). However, "snap-shot" analyses in *Riftia pachyptila* and other tubeworms indicate that fertilization is internal and sperm is stored in the female until eggs are mature. Sperm storage may provide tubeworm populations a mechanism for continuously reproducing in

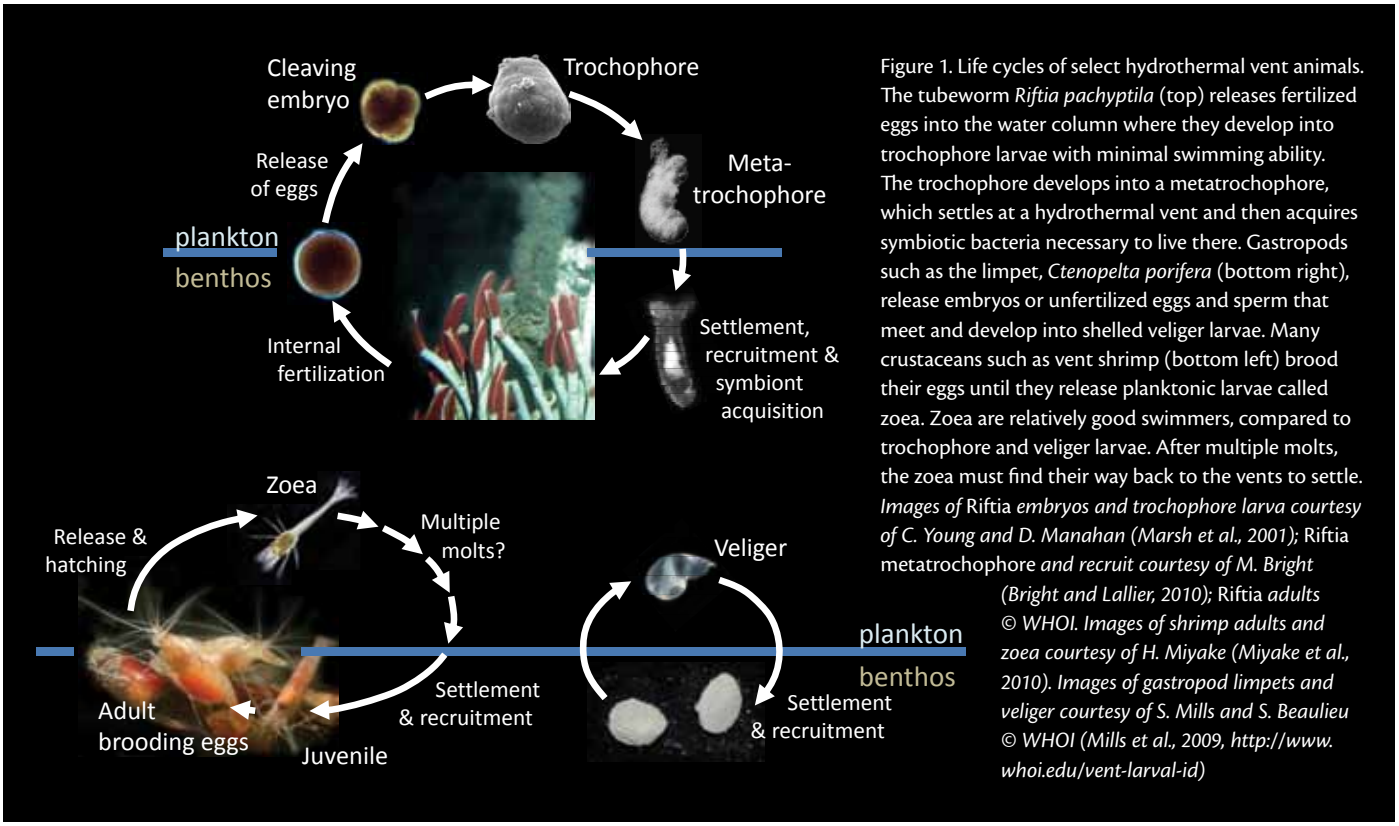

Figure 1. Life cycles of select hydrothermal vent animals. The tubeworm *Riftia pachyptila* (top) releases fertilized eggs into the water column where they develop into trochophore larvae with minimal swimming ability. The trochophore develops into a metatrochophore, which settles at a hydrothermal vent and then acquires symbiotic bacteria necessary to live there. Gastropods such as the limpet, *Ctenopelta porifera* (bottom right), release embryos or unfertilized eggs and sperm that meet and develop into shelled veliger larvae. Many crustaceans such as vent shrimp (bottom left) brood their eggs until they release planktonic larvae called zoea. Zoea are relatively good swimmers, compared to trochophore and veliger larvae. After multiple molts, the zoea must find their way back to the vents to settle. *Images of* Riftia *embryos and trochophore larva courtesy of C. Young and D. Manahan (Marsh et al., 2001);* Riftia metatrochophore *and recruit courtesy of M. Bright (Bright and Lallier, 2010);* Riftia *adults © WHOI. Images of shrimp adults and zoea courtesy of H. Miyake (Miyake et al., 2010). Images of gastropod limpets and veliger courtesy of S. Mills and S. Beaulieu © WHOI (Mills et al., 2009, http://www.whoi.edu/vent-larval-id)*

environments devoid of obvious cues that would entrain population-wide reproductive or spawning synchrony (reviewed in Hilário et al., 2011).

Population-wide "periodic" or "seasonal" patterns of reproduction have not been expected in chemosynthetic environments, where the primary carbon and energy sources are not closely coupled to seasonal variation at the ocean surface. Yet, periodic reproduction that is seemingly correlated with surface productivity is known for populations of the mussel *Bathymodiolus azoricus* from the Menez Gwen vent field (~ 840 m deep) on the Mid-Atlantic Ridge (MAR; Dixon et al., 2006). Periodic reproduction in the deep sea is often attributed to surface-derived pulses of organic nutrients to the seafloor, leading to an entrainment of gamete development cycles in deep-sea species (Gage and Tyler, 1991; Eckelbarger and Watling, 1995). Variation in surface production over the East Pacific Rise (EPR) may also indirectly affect the seasonal reproductive activity in populations of the vent crab *Bythograea thermydron* by providing a food source for their feeding larvae (reviewed in Dittel et al., 2008). Other cues may also induce periodic reproduction in hydrothermal vent organisms. Although two species of alvinellid polychaetes (*Paralvinella sulfincola* and *P. pandorae*) reportedly reproduce continuously, two other species, *P. grasslei* and *P. palmiformis,* reproduce periodically at the vent scale, possibly in response to tidal variations in environmental factors (reviewed in Pradillon and Gaill, 2007).

Time to Develop

The amount of time from fertilization to metamorphosis determines the PLD, or the time that a larva spends in the water column dispersing. A significant stumbling block in understanding the developmental dynamics that control PLDs of hydrothermal vent larvae is the difficulty in culturing embryos and larvae in the laboratory. Some invertebrates that reside at relatively shallow hydrothermal vents can be cultured at

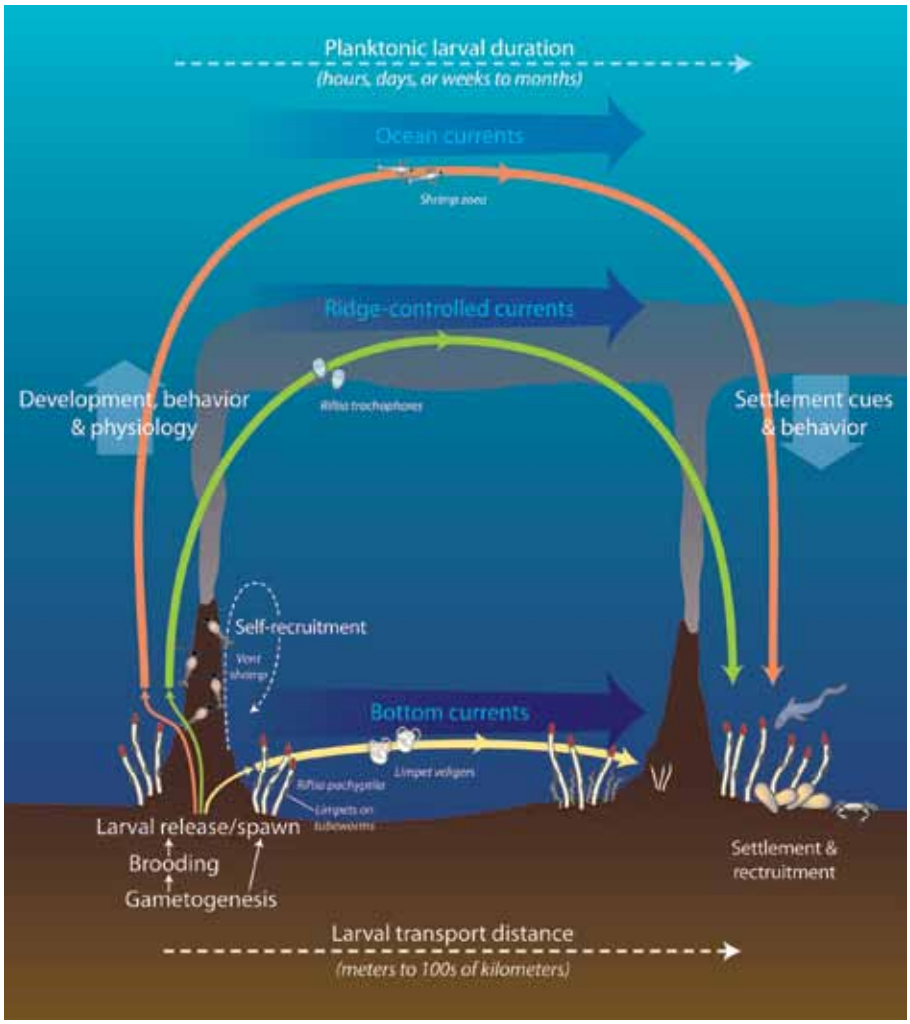

Figure 2. A simple model depicting how the interaction between larval biology and currents may affect dispersal among hydrothermal vent communities. Larval physiology, development, and behavior influence the vertical distance above the vent that a larva may travel, as well as the amount of time it spends in the water column. Planktonic larval duration and position interact with currents to alter transport distance. Then, larval behavior in response to an intrinsic or extrinsic cue triggers the transport of larvae back to the seafloor where they settle and recruit into a hydrothermal vent community. This example shows three larval types. The veliger larvae of many gastropods such as limpets (e.g., *Lepetodrilus* spp.) tend to remain near the bottom (Mullineaux et al., 2005) where they are more likely to be retained in slower currents close to home. The embryos of the tubeworm *Riftia pachyptila* are buoyant and cannot tolerate the high temperatures where the adults thrive (Brooke and Young, 2009); thus, they are likely to be transported above the bottom. Strong-swimming larvae, such as shrimp or crab zoea, migrate up into the oceanic currents far out of the influence of the hydrothermal vent plume or ridge-controlled currents (Dittel et al., 2008).

atmospheric pressure, including vent crabs, shrimp, barnacles, mussels, and tubeworms (e.g., Miyake et al., 2010). Most vent organisms, however, cannot develop in the absence of high pressure. The larvae of deep-sea vent tubeworms *Riftia pachyptila* and *Alvinella pompejana* have been reared through early stages of development in high-pressure systems in the laboratory (Marsh et al., 2001; Pradillon et al., 2001; Brooke and Young, 2009). Still, no single hydrothermal vent species has been cultured through the entire planktonic stage, from fertilization or larval release through settlement, to allow direct estimation of PLD.

Without culturing through the complete planktonic stage, estimates of how long larvae remain in the water column have been made through inferences based on developmental mode (feeding or nonfeeding larvae) and physiology. Developmental modes may be phylogenetically constrained in deep-sea and hydrothermal-vent species, with feeding as a likely ancestral rather than derived condition for deep-sea species (Bouchet and Warén, 1994). In shallow-water invertebrates, feeding larvae are generally presumed to remain in the planktonic stage for longer periods and to disperse farther than nonfeeding larvae or brooded embryos, which have finite energy reserves (Thorson, 1950; Wray and Raff, 1991). However, in the deep sea and in Antarctica waters, this pattern does not always hold true because low metabolic rates at cold temperatures tend to increase PLDs of even nonfeeding larvae (Lutz et al., 1984; reviewed by Young, 2003). The estimated mean larval duration for the nonfeeding larvae of the tubeworm *Riftia pachyptila* is 38 days, based on physiological modeling of metabolic rates at low temperatures (Marsh et al., 2001). With a 38-day PLD, Marsh et al. (2001) predicted that dispersal distances of *R. pachyptila* larvae would more likely be limited by hydrodynamics than by PLD due to periodic reversals in the currents (but see McGillicuddy et al., 2010).

Additionally, developmental arrests and delays of metamorphosis can confound estimates of PLD. Pradillon et al. (2001) suggested that nonfeeding embryos of *Alvinella pompejana* arrest their development while dispersing at 2°C between vents until warm water is encountered, at which time embryos may quickly develop and settle out of the water column near vents. Also, the extraordinarily long estimated PLD of the closely related cold-seep mussel *"Bathymodiolus" childressi* might indicate that bathymodiolin mussels can delay metamorphosis, allowing longer dispersal times (Arellano and Young, 2009).

Where Are the Larvae?

The horizontal and vertical distribution of larvae determines the hydrodynamic regime in which they disperse. Although most larvae are poor horizontal swimmers, they can alter their vertical positions actively through vertical swimming and/or passively through differential buoyancy. Unfortunately, quantifying larval distributions in the field is difficult. Once larvae of hydrothermal vent animals enter the water column, they are extremely difficult for researchers to find; small larvae can quickly be diluted in the large ocean. Concentrations of vent gastropod larvae decrease exponentially with increasing vertical and horizontal distance away from the vents along the northern EPR (Mullineaux et al., 2005), raising the possibility of retention near vents (Figure 2). However, larval abundances even very near vents are low compared to shallow waters (e.g., Mullineaux et al., 2005; Metaxas, 2004). Once in the pelagic environment, larvae are captured in low numbers, even with extraordinary sampling effort. Difficulties in species-level identification of the larvae (see Box 1) further hamper quantifying distributions. New ocean observatories will increase access and temporal sampling of the plankton, but development of high-volume samplers with sequential sampling capabilities (for time series and/or depth profiling) will be essential to fully characterize the dynamics and distributions of hydrothermal vent larvae.

Without many direct observations of larval distributions, the examination of indirect biological indicators has led to inferences about vertical distributions of hydrothermal vent larvae. The feeding history of deep-sea molluscan larvae can leave an "imprint" on their larval shells by changing their size and sculpturing once feeding on plankton begins; thus, larval shell morphology can be a good indicator of whether larvae are feeding or nonfeeding (Lutz et al., 1984). However, just as feeding mode does not necessarily correlate with PLD, it may not be a reliable indicator of whether larvae migrate vertically toward the surface to take advantage of higher food supplies. The larval shell morphology of many hydrothermal vent mussel species suggests that they feed, but there is no evidence that they do so in the photic zone. For example, isotopic studies on the MAR vent mussel *Bathymodiolus azoricus* and the related seep mussel

One of the many challenges of studying hydrothermal vent larvae, and larvae in general, is identifying them from a mixed larval pool. In ephemeral hydrothermal vent ecosystems, the arrival of species through larval exchange drives benthic community composition and dynamics, including recolonization of disturbed habitat and succession. Species from the same family and even genus can occupy different habitats and drive different benthic biological interactions (e.g., Mullineaux et al., 2003), making species-level identification of larvae critical. But larvae collected near hydrothermal vents do not look like the adult organisms living there. Larvae in the water column face different challenges than the adults on the seafloor and thus have different selective pressures on larval development and morphology. Although there are evolutionary constraints on the larval form that usually enable identification to phylum and even to family level, species-level identifications are difficult, yet essential.

Traditionally, larvae are described from laboratory cultures reared from identified adults or by raising wild larvae until they metamorphose into identifiable juveniles. These techniques have been successful for identifying only a handful of vent larvae (e.g., Dittel et al., 2008; Miyake et al., 2010). Unfortunately, most vent species are difficult to keep in culture, and species composition of the larval pool does not necessarily reflect that of the nearest benthic adult community (Mullineaux et al., 2005; Adams and Mullineaux, 2008), so other morphological and molecular identification techniques must be used.

The larval shell is sometimes preserved on the shell of juvenile or adult mollusks (e.g., limpets, snails, and mussels), allowing for species identification by examining unique shell characters such as size, sculpturing, and shape (Lutz et al., 1984; Mullineaux et al., 1996; Mills et al., 2009). However, even shell characters can lack species-level differences. What's more, identification of larvae through morphology requires a good understanding of the diversity of larval characteristics and is labor intensive.

Molecular identification techniques are being rapidly developed to provide species-level identifications of embryos and larvae with the potential for high-throughput processing. Sequenced "barcodes," such as cytochrome oxidase I (COI) and 16S mitochondrial genes, from unidentified individuals can be compared to known sequences to provide identification (Hebert et al., 2003) irrespective of morphological information. The only limiting factor is the sequence database, which is rapidly expanding but still incomplete for hydrothermal vent species (Vrijenhoek, 2009; Adams et al., 2010). Restriction fragment length polymorphisms provide an inexpensive alternative to sequencing to identify a well-defined group of species (Adams et al., 2010). One of the main complaints about molecular identification is the destruction of morphological information. Whole mount in situ hybridization with species-specific probes can also provide identification of specific species while preserving the morphology (Pradillon et al., 2007).

As identification techniques continue to be developed and applied to hydrothermal vent species, our ability to identify vent larvae constantly improves, but may remain hindered by incomplete sampling of vent fauna and overall taxonomic progress describing new vent species.

Examples of mollusk, crustacean, and polychaete larvae of hydrothermal vent species. Larvae come in various shapes and sizes that may not look like the adults. *Images of crustacean zoea courtesy of H. Miyake (Miyake et al., 2010); all other images courtesy of http://www.whoi.edu/vent-larval-id, © WHOI*

B. heckerae do not provide any record of photosynthetically derived food in recently settled juveniles (Salerno et al., 2005). Absence of evidence of feeding on phytoplankton, however, does not mean larvae do not vertically migrate to take advantage of other food sources in the upper ocean.

Although feeding may not be a very good predictor of vertical migration of larvae in some deep-sea mollusks, other morphological features in crustaceans may be better indicators. For example, the zoea (larval form) of the crab *Bythograea thermydron* from the EPR has an image-forming eye with visual pigmentation sensitive to blue light characteristic of a water depth no deeper than 1,000 m (reviewed in Dittel et al., 2008). Moreover, isotopic signatures in *B. thermydron* megalopae are consistent with a phytoplankton diet, while later juvenile and adult stages have isotopic signatures that reflect chemosynthetically based food (Dittel et al., 2008). Similarly, Pond et al. (2000) have argued that larvae of hydrothermal vent shrimp must feed during their planktonic phase in order to accumulate essential unsaturated fatty acids required for maturation and breeding. Combined with the fact that crustacean larvae are generally strong swimmers, there is considerable evidence that development of many hydrothermal vent crustaceans may occur high in the water column (Figure 2).

For some species, physiological tolerances provide the best indications of a larva's potential for ontogenetic vertical migration. In culturing experiments at the EPR, embryos of the thermophilic tubeworm *Alvinella pompejana* could not tolerate the high temperatures found immediately near the adults, and development was reversibly arrested at cold temperatures (2°C; reviewed in Pradillon and Gaill, 2007). Thus, it is suggested that larvae of *A. pompejana*, which have yet to be found in plankton samples, could potentially disperse in the water column until they encounter a heat pulse or could be retained near their natal vent, taking advantage of moderate temperature microhabitats. Comparable conclusions have been drawn for another hydrothermal vent archetypal species. Using a similar experimental approach, Brooke and Young (2009) showed that the high temperatures found around hydrothermal vents would inhibit normal development of embryos of the tubeworm *Riftia pachyptila*, suggesting these buoyant embryos and larvae must not be retained in or among the adult tubes and, instead, should disperse above the seafloor (Figure 2).

Finally, it is worth noting that empirical analyses of swimming behaviors of hydrothermal vent larvae are rare, but useful. Although observations of larval swimming behaviors provide insights into vertical migration behaviors and later settlement behaviors, quantitative measures are also necessary to parameterize energetic and biophysical dispersal models. To our knowledge, direct quantifications of swimming behaviors have only been made for hydrothermal vent crustaceans (reviewed in Dittel et al., 2008). Currently, videos of various polychaete larvae that were abundant in the plankton near the southern Mariana back-arc are being analyzed for vertical displacement and swimming speeds (Recent work of Stace Beaulieu, Thomas Sayre-McCord, and Susan Mills at Woods Hole Oceanographic Institution). As we continue to develop methods to culture and maintain larvae in the laboratory, as well as to identify planktonic larvae (see Box 1), we are optimistic that quantitative measurements of larval development, physiology, and swimming behavior can soon be incorporated with hydrodynamics into larval transport models for hydrothermal vent organisms.

WAFTING IN THE FLOW

As larvae of hydrothermal vent species rise through the water column (Figure 2; up to 5,000 km!), they are exposed to a wide range of current directions and speeds that influence their transport potential.

Close to Home in the Valley

Larvae positioned very close to the seafloor, a few meters above bottom (mab), experience slower currents. Interaction of the flow with the seafloor slows, and can even reorient, current velocities along the ridge axis (e.g., Thomson et al., 2003; Thurnherr et al., 2011). The majority of vents are positioned within an axial valley whose walls further slow and steer the flow (Figure 3; Thomson et al., 2003). At the EPR, mean axial currents between the height of the neutrally buoyant plume (170 mab) and the inside of the ridge valley (≤ 10 mab) can be reduced by over 30% (Adams and Mullineaux, 2008; Thurnherr et al., 2011). Because the axial valleys at the Juan de Fuca Ridge (JdFR) in the Northeast Pacific are deeper (~ 100 m), the overlying water column has less influence on the current velocities within the valley. Instead, hydrothermally induced circulation can dominate the flow (Thomson

et al., 2003, 2009), and consequently larval transport, on a regional scale. Buoyant hydrothermal fluids rise and spread within (and outside) the valley of the JdFR. The rise of the hydrothermal fluids draws in cold water along the bottom, creating a recirculation within the valley (Figure 3; Thomson et al., 2003, 2009). Currents may also be constrained by valley bathymetry along the MAR. At vent fields on the MAR, the exit of hydrothermal fluids is hydraulically controlled by flow through a small number of sills (e.g., Thurnherr et al., 2008). The relative contribution of hydrothermally driven circulation within the shallower EPR valleys has not been determined; however, models suggest that bottom currents rather than rising hydrothermal fluids dominate larval transport near vents (Kim et al., 1994; Bailly-Bechet et al., 2008). Irrespective of the mechanism driving the dynamics, observed mean current velocities within the valleys at the JdFR, MAR, and EPR typically are relatively weak, 5 cm s^{-1} or less. Thus, the potential for dispersal is lower, favoring retention within the valley at local (< 5 km for the EPR; Adams and Mullineaux, 2008) or basin scales (tens of kilometers for the JdFR; Thomson et al., 2003). However, larvae that are swept upward or cross-axis outside the axial valley will encounter stronger currents resulting from hydrodynamic interactions with the overall ridge topography.

Ridge-Dominated Flow

The ridge itself can greatly influence the overlying flow. Influences on the current regime are related to the shape and structure of the ridge, which can vary substantially, depending on the magmatic supply. However, intensification of along-axis and cross-axis current velocities at the ridge crest (e.g., Thomson et al., 1990; Thurnherr et al., 2011) occurs at multiple ridges and may be a common hydrodynamic feature near hydrothermal vents. Thus, larvae that rise above the axial valley should immediately experience a period of increased transport.

Ridge topography rectifies the current direction, so the flow intensifies along the ridge (Figure 3; Thomson et al., 1990; Lavelle et al., 2010; Thurnherr et al., 2011). At the EPR, interactions with the ridge force the formation of along-axis jets on the ridge flanks extending ~ 600 m deep and ~ 10 km zonally (see Lavelle et al., 2010, and 2012, in this

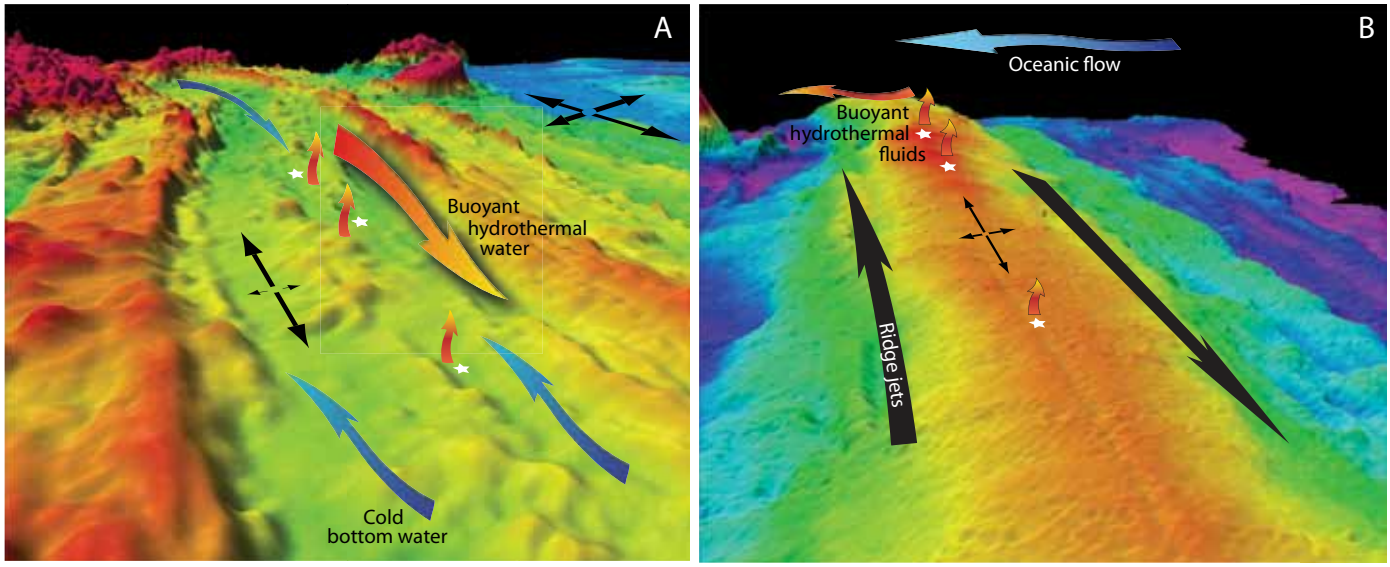

Figure 3. The shapes of the ridge and axial valley direct the currents that transport larvae near the Juan de Fuca Ridge (A) and the East Pacific Rise (B). (A) Intermediate- and slow-spreading ridges like the Juan de Fuca have deep valleys that trap hydrothermal outflow and rectify oceanic currents. Warm fluids (red arrows) rise from the vents (stars) and flow along the axis toward the southwest above cooler water (blue arrows) entering the valley. Tidal cross currents are rectified by the topography within the axis (black arrows). (B) Fast-spreading ridges like the East Pacific Rise have shallow valleys with low or no walls. This morphology allows much of the warm hydrothermal outflow to leave the axis and become entrained into the overlying oceanic flow (blue arrow). Cross currents can be stronger due to weaker protection and rectification (thin black arrows). The ridge topography still aligns the flow, producing two jets on either side of the ridge axis that flow in opposite directions. *Three-dimensional bathymetric perspectives courtesy of Adam Soule, WHOI*

issue; Thurnherr et al., 2011). The ridge-trapped jet on the western flank moves poleward while the jet on the eastern flank moves equatorward at velocities up to 10 cm s^{-1}. When simulated larvae were entrained into these jets, the dispersal potential nearly doubled to ~ 200 km, but the settlement density decreased threefold (McGillicuddy et al., 2010). Similar sheared currents observed at other ridges (Cannon and Pashinski, 1997) suggest that these jets may be another common feature near hydrothermal vents. Thus, transport of larvae outside of the axial valley, even if still close to the bottom (e.g., ~ 10 mab, as observed for many gastropod larvae; Mullineaux et al., 2005; Figure 2), could result in enhanced bi-directional movement along the axis in the flank jets. These jets could reduce larval transport away from the ridge axis in the slow westward background flow at the EPR and JdFR. It is important to note that the length of the continuous ridge segment probably limits the jets, so 200 km may be an overestimate for a given segment. At the segment ends, the possible fates of larvae are unknown, as the hydrodynamics across transform faults remain woefully understudied.

Open Ocean

Multiple species of vent larvae rise above it all and bypass the confines of ridge topography. Larvae that vertically migrate into the upper ocean (Figure 2) would be subjected to stronger mid-oceanic and upper-layer oceanic currents and, thus, have a higher potential for being transported away from suitable habitats. However, as a larva rises through the ocean, currents can change direction. For example, background flow at the Endeavour Segment, JdFR, is predominantly westward, counter to the prevailing southeasterly currents in the upper ocean. These countercurrents may provide a mechanism for larval transport back toward the ridge(s) closer to the time of settlement, similar to the processes thought to occur in upwelling zones (reviewed in Sponaugle et al., 2002). Near 9°50'N on the EPR, the North Equatorial Countercurrent and the Equatorial Countercurrent could form a loop in the upper ocean to return vent larvae closer to the ridge even without vertical migration. A scenario of transport and return of vent larvae in the upper ocean is speculative at best, but worth future investigation. Nevertheless, sophisticated sensory systems and swimming abilities may help larvae find vents again after prolonged dispersal periods. How vent larvae ultimately find their way back to suitable habitat remains an open question.

Going the Distance

Episodically, vent larvae may be subjected to upper-ocean and atmospheric processes independent of their position in the water column. Off the coast of Central America, wind-driven eddies at the surface can reach all the way to the seafloor to transport gastropod larvae away from the EPR (Adams et al., 2011). Most of these larvae are undoubtedly transported into inhospitable habitat, but a few may be transported long distances to new vent fields hundreds of kilometers away, even across transform faults. The presence of surface eddies in close proximity to, and interacting with, other mid-ocean ridges suggests that this mechanism may not be unique to the northern EPR.

Hydrothermal Plumes

Early in studies of larval transport between hydrothermal vents, it was hypothesized that larvae might be packaged and dispersed within the hydrothermal plume (Mullineaux et al., 1991). This transport mechanism would have different implications at sites with deep axial valleys (e.g., JdFR) compared to sites with shallow axial valleys (e.g., EPR). At the JdFR, the plume rises to just above the ridge axis where hydrothermally driven circulation still dominates (Thomson et al., 2009; see Di Iorio et al., 2012, in this issue). On the other hand, the buoyant plumes exiting vents along the EPR (Thurnherr and St. Laurent, 2012, in this issue) rise to similar heights, but quickly exit the axial valley and are subjected to ridge- and oceanic-forced currents. Although larval buoyancy may cause some larvae to be transported within the plume, overall larval abundances are higher near bottom than at plume level (Kim et al., 1994; Metaxas, 2004; Mullineaux et al., 2005). Furthermore, modeling efforts demonstrate that plumes may entrain only a small fraction of the larval pool (Kim et al., 1994) and entrainment primarily occurs when bottom currents are negligible (Bailly-Bechet et al., 2008). Although plumes were suggested to be "larval highways" (Mullineaux et al., 1991), recent modeling of larval transport at the EPR suggests that larvae positioned at the height of the plume are approximately three times more likely to remain near the ridge crest compared to larvae positioned near the bottom (McGillicuddy et al., 2010). Thus, establishing even a small number of larvae at plume level that would otherwise be positioned near

the bottom might alter the probability of their remaining close to home or being swept away.

GETTING TO THE BOTTOM OF IT ALL

Like larval transport, the movement of larvae from the water column back to the seafloor is also an inherently complex interaction between biology and the environment. Since the discovery of hydrothermal vents, many investigators have suggested that chemical and physical cues such as temperature and seawater chemistry, and cues from adult colonies (reviewed in Van Dover, 2000), must be important signposts to guide some larvae back to hydrothermal vents, while in other species, larvae may simply settle after they reach a certain stage. Once they make contact with substrata, larvae select specific settlement sites within the substrata based on flow, surface texture, or chemical cues from conspecifics, competitors, predators, or microbial biofilms (Underwood and Keough, 2001). Although recognized as important, settlement cues are rarely studied at hydrothermal vent sites. In a single brief report on settlement selection at the JdFR, Rittschof et al. (1998) showed a significant number of vent polychaetes burrowing into alginate gels impregnated with sulphide after only 24 hours. Hydrothermal vent chemistry may seem to be the most obvious settlement cue for vent larvae, but hydrothermal vent organisms with obligate chemoautotrophic symbionts may cue instead to microbial distributions (see Sievert and Vetriani, 2012, in this issue) to ensure the acquisition of their symbionts post-settlement (e.g., Nussbaumer et al., 2006). After larvae have selected settlement sites and undergone metamorphosis, then post-settlement pressures (e.g., mortality due to physiological stresses, competition, predation) weed out individuals until some ultimately join the community as adults (known as "recruitment").

The dynamics of the larval stage can lead to temporal and spatial disconnects between the initial reproductive output of a benthic community and the recruitment of larvae back to that substratum. The journey from the initial release into the water column back to a vent site could last days to months and span the axial valley or the depth of the water column. During the dispersal process, many larvae are lost—either consumed as prey or transported by currents to inhospitable habitat (Thorson, 1950). The supply of larvae may originate from distant vent sites (hundreds of kilometers; e.g., Marsh et al., 2001; Mullineaux et al., 2010), local sources (< 1 km; e.g., Adams and Mullineaux, 2008), or both. The total abundance, the relative species abundance, and the temporal flux of larvae can vary significantly among hydrothermal vents, depending on vent location (Adams and Mullineaux, 2008) and community composition (Metaxas, 2004), on top of any variation in larval supply caused by variance in PLDs between individuals and hydrodynamics (Adams and Mullineaux, 2008; Adams et al., 2011).

Variation in the supply of larvae can directly affect community dynamics through spatial and temporal variations in settlement and recruitment. In general, most vent invertebrates exhibit gregarious settlement, discontinuous recruitment, and high juvenile mortality (e.g., Metaxas and Kelly, 2010). Gregarious settlement and discontinuous recruitment might suggest that larval supply is episodic and that the larval pool can be temporally or spatially variable at the scale of a vent field (1–10 km). However, high mortality after settlement confounds direct correlations between larval supply and recruitment. Abiotic and biotic environmental factors can facilitate larval settlement and recruitment by providing settlement cues and habitat provisioning, or they can inhibit recruitment through post-settlement predation, competition, and interference (e.g., Govenar, 2010; Metaxas and Kelly, 2010). Still, it is clear that the larval supply and the post-settlement (benthic) environment interact to shape vent communities through variable recruitment. Successional dynamics at the EPR Integrated Study Site following seafloor eruptions exemplify the importance of and interplay between the larval supply and the benthic environment (Govenar, 2012, in this issue). In vent systems, this variation in recruitment has been shown in ecological models to have a greater effect on population growth than either adult survival or fecundity (Kelly and Metaxas, 2010).

THE WAY FORWARD

Larvae of vent animals tie together distant communities, ensuring persistence of life at vents (Figure 4). Understanding the dynamics that lead to maintenance and recovery of communities at hydrothermal vents has become increasingly important as pressure rises to exploit vents through mining and bioprospecting (Ramirez-Llodra et al., 2011). Predicting larval transport and estimating population connectivity are central to estimating

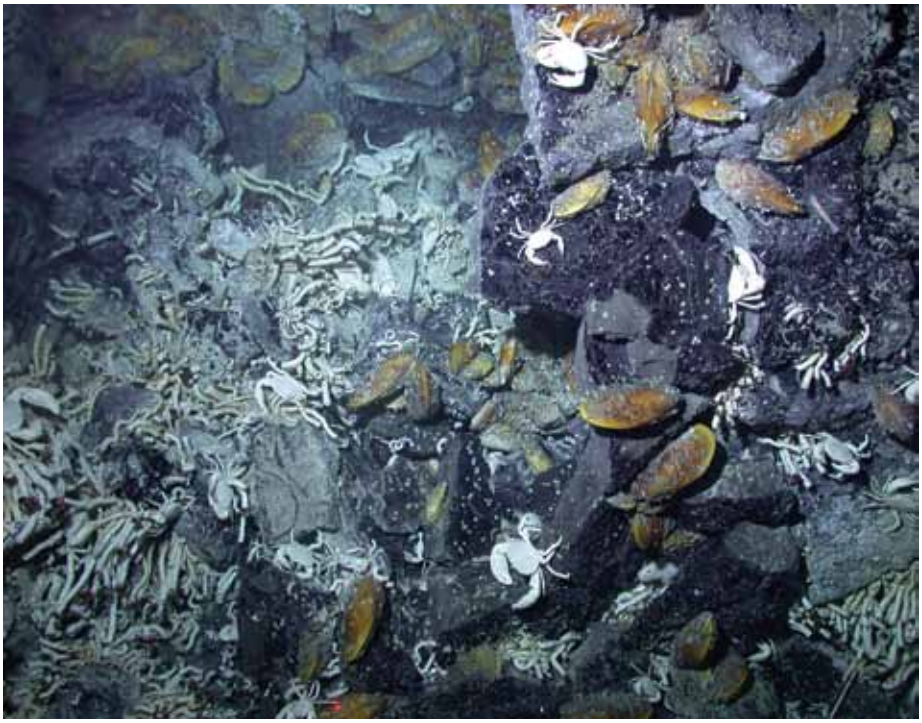

Figure 4. Shortly after an eruption on the East Pacific Rise, vent life replenishes itself through the settlement of larvae sometimes from distant sources. Small tubeworms (*Tevnia*) and limpet gastropods begin to cover the new glassy basalt crust. © *Woods Hole Oceanographic Institution*

population resilience and determining future conservation methods (Van Dover, 2011).

To illuminate the mechanisms driving dispersal and connectivity, accurate hydrodynamic modeling coupled to larval biology and ecology is essential. New understanding of the processes controlling current velocities along ridges, especially at the EPR and JdFR Integrated Study Sites, have led to better hydrodynamic models. A need remains, however, to characterize hydrodynamics at the scales of a vent within a shallow axial valley, which may be important to local retention, and of regional vent fields (e.g., northern EPR), which is necessary for understanding long-distance dispersal across transform faults and to new vent fields. Incorporating multiple scales of oceanographic processes with complex topography into larval transport models will be challenging (Werner et al., 2007) but critically important to understanding dispersal of vent organisms.

Moreover, advances in our understanding of vent larval biology—especially PLD, vertical distribution, and settlement-inducing behaviors—would lead to better parameterization of biophysical larval transport models, resulting in more realistic predictions of dispersal. Quantification of PLD and swimming behaviors should become possible for more vent species as the use of high-pressurization techniques to culture larvae becomes more widespread. Sampling systems that are spaced through the water column and used for time-series collecting would allow direct observations of distribution of hydrothermal vent larvae. New collection devices at ocean observatories coupled with larval identification by high-throughput genetic techniques could be the future of larval monitoring at hydrothermal vents.

Finally, integrating larval transport models with in situ recruitment and population dynamic studies would allow for direct analysis of the consequences of larval transport for population connectivity on ecological timescales. While extensive population genetic studies have led to a good understanding of gene flow, genetic diversity, and evolutionary patterns at hydrothermal vents (reviewed in Vrijenhoek, 2010), these patterns can be complicated by historic events that do not reflect current levels of larval exchange. As managing hydrothermal vents becomes a priority, conservation efforts in these ephemeral habitats will be best informed by using larval transport models that have been ground truthed with larval collections and by incorporating knowledge of how transport and supply of larvae translate into population dynamics.

The integrated, interdisciplinary efforts must continue near vents, off axis, and in the lab to shed light on the dynamics that result when planktonic larvae recruit into the benthic community (Govenar, 2012, in this issue). Discoveries made at the Integrated Study Sites and through advances in methodologies have provided valuable insights, but there is still much to learn about the evolution and ecology of life at hydrothermal vents. Thus, we must continue to look at life not only in the immediate vicinity of the hydrothermal flow but also at vent life in the water column. As we move forward with hydrothermal

vent research past the Ridge 2000 Program, it is essential to appreciate that the larvae in the water column are a key component to the dynamics and ultimately survival and conservation of hydrothermal vent communities.

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