Oceanographic and topographic influences on dispersal of hydrothermal vent species

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SUMMARY

When hydrothermal vent communities were first discovered 25 years ago, biologists immediately recognized the key role of dispersal in the dynamics and persistence of the populations. Despite substantial progress on this topic over the past 10 years, some very important questions remain unanswered about the mechanisms of dispersal and their effects on population dynamics, population genetics and community structure. Investigators have hypothesized that larval dispersal is driven largely by physical transport processes. The primary objectives of the present proposal are to investigate how larval behaviors interact with topographically-influenced flows on mid-ocean ridges, and determine how these interactions affect dispersal trajectories, maximal dispersal distances, and relative probabilities of supply to natal versus remote vents.

We have identified three specific ecological questions to address:

1. What are the influences of advection and eddy diffusion on the maximal dispersal distance of vent species with given larval life spans?;
2. What are the effects of ontogenetic changes in larval behavior (i.e., vertical positioning) on species' dispersal distances; and
3. How are the probabilities that larvae will be lost from the ridge system influenced by topography and flow? Might the axial summit trough inhibit off-axis transport of larvae, and serve as a conduit between habitable vent sites?

Our proposal also addresses several issues of interest to the physical oceanography community, including:

1. What are the mean and temporally varying flows in the vicinity of a mid-ocean ridge crest, and what is their spatial structure and coherence?;
2. What is the magnitude of the diapycnal diffusivity near the ridge crest?;
3. How rapid is lateral dispersion, and how effective is lateral homogenization by eddy diffusion near the ridge crest?

Our dispersal questions cannot be answered without an integrated set of physical and biological approaches. We have assembled a diverse team of observationalists and modelers to investigate relevant aspects of ridge-associated oceanography and biology, and to combine them into a quantitative model of dispersal. The approach includes a tracer release in the field, current meter measurements, a hydrodynamic/transport model, measurements of larval positions and stages in the field, and a coupled biological/physical model. We have chosen to study the region near 9°50'N on the East Pacific Rise (EPR), a site that has been the focus of much interdisciplinary research in the past and has been selected as an Integrated Study Site by the NSF Ridge 2000 program.

Broad impact of this result will be achieved through several different activities. The approaches and results from the proposed studies will be incorporated into graduate courses, and into presentations given to local K-12 classes. Two graduate students will be supported, and undergraduates will be integrated through the WHOI Summer Student Fellowship program and the NSF REU program. We will link our research with web-based outreach efforts including Dive and Discover (www.divediscover.whoi.edu) and Women Exploring the Oceans (http://wexo.whoi.edu/).

The long-term benefits of the proposed activity to society will be achieved by contributing to a general understanding of retention, dispersal, and connectivity of marine populations, and to a better understanding of seafloor topographic effects on flows and mixing. Vent systems are subject to increasing use by researchers, tourists and industry (e.g., extracting polymetallic minerals, and sampling fauna for natural products discovery and pharmaceutical applications). Our results will inform efforts to develop plans for sustainable use of vent ecosystems.

1. Introduction

When hydrothermal vent communities were first discovered 25 years ago, biologists immediately recognized the key role of dispersal in the dynamics and persistence of the populations. It was clear that frequent migration was the only way for vent species to maintain their populations and geographic ranges in the patchy, transient vent environment. Because adults of most vent species are attached or have minimal migratory capabilities, it was assumed that vent species dispersed through the water via larval stages. However, the dispersal mechanisms and their population consequences were not easily predicted. Over the past 10 years, important advances have been made in understanding mechanisms of larval dispersal and the effects of dispersal on population dynamics, gene flow and community structure of vent species. For instance, life spans have been calculated for cultured larvae (Marsh et al. 2001), dispersal distances estimated from currents (Chevaldonné et al. 1997; Mullineaux et al. 2002) and swimming behaviors observed (Epifanio et al. 1999). Population genetic studies have constrained the spatial scales over which larvae are frequently exchanged (reviewed in Vrijenhoek 1997).

Despite this progress, some very important questions about dispersal of vent species remain unanswered. Larval culture has been attempted only for the tubeworm *R. pachyptila*, leaving us to infer dispersal potential of most species from egg size and larval morphology (Tyler and Young 1999). Larval swimming behaviors for most species are unknown, and their influences on dispersal have been addressed only for the final megalopa stage of the bythograeid crab (Epifanio et al. 1999). Furthermore, physical transport processes in vent larval dispersal models are calculated from individual current meter measurements, and require the assumption of lateral homogeneity of flow. This assumption is likely violated in areas with complex topography (e.g., Thurnherr et al. 2002) and at increasingly large distances from the measurement location. Thus, our present dispersal estimates may be limited in applicability, and questions such as how far larvae can disperse, what oceanographic and geographic features constitute dispersal conduits or barriers, and what features of life history and behavior allow pioneer species to colonize quickly, remain open for most vent species.

A more subtle question about vent population dynamics also remains unsolved – the problem of how vent species recolonize existing populations in sufficient numbers to maintain them over the life time of a vent. This question is particularly perplexing for larvae that have a precompetent period, and may disperse away from the source habitat before they are ready to settle. However, an ability to recolonize a natal environment has important consequences for benthic populations in general (Strathmann et al. 2002). It has been suggested that secondary flows set up by the buoyant hydrothermal plume may entrain larvae (i.e., when they are negatively buoyant or downwardly swimming) and bring them in toward the venting source (e.g., Mullineaux and France 1995). Alternatively, larvae of some species may be fully competent on release, and resettle immediately, or may remain very near the seafloor in order to avoid export.

Analysis of population genetic structure in hydrothermal vent communities has supplied additional insight into dispersal of vent species and provides us with some testable hypotheses. For instance, along the East Pacific Rise, populations of the polychaete *Alvinella pompejana* are genetically very similar at vents within a ridge segment (Jollivet at al. 1995). Similarly, populations of the amphipod *Ventiella sulfuris* are genetically similar within a segment, but distinct between the East Pacific Rise and the Galapagos spreading center (France et al. 1992). These results, and studies showing other species along the East Pacific Rise are genetically similar within ridge segments (reviewed in Vrijenhoek 1997) but dissimilar between them (Won et al. 2003), have led many researchers to suggest that larvae can disperse extensively within segments of a mid-ocean ridge, but not across transform faults and other large topographic discontinuities in the ridge system (Tunnicliffe et al. 1998).

The primary objective of the present proposal is to investigate oceanographic and topographic influences on larval retention and dispersal in hydrothermal vent communities. The focus will be on processes occurring on relatively short spatial O(10-100km) and temporal O(1 mo) scales (corresponding roughly to invertebrate larval life spans) because those can be approached using current technologies. We do not intend to study processes at the scale of individual vents. We have identified three main ecological questions to address in detail:

1. What are the influences of advection and eddy diffusion on the maximal dispersal distance of vent species with given larval life spans?

2. What are the effects of ontogenetic changes in larval behavior (i.e., vertical positioning) on species' dispersal distances?

3. How are the probabilities that larvae will be lost from the ridge system influenced by topography and flow? Might the axial summit trough inhibit off-axis transport of larvae, and serve as a conduit between habitable vent sites?

In addition, we will explore whether transform faults at the ends of ridge segments act as barriers to dispersal. We include this question because it is of broad interest to vent ecologists, but we are able to address it only in an exploratory manner.

Our proposal also addresses several issues of interest to the physical oceanography community, including: 1) What are the mean and temporally varying flows in the vicinity of a mid-ocean ridge crest, and what is their spatial structure and coherence?; 2) What is the magnitude of the diapycnal diffusivity near the ridge crest?; 3) How rapid is lateral dispersion, and how effective is lateral homogenization by eddy diffusion near the ridge crest?

2. Justification of Approach

Our dispersal questions cannot be answered without an integrated set of physical and biological approaches. We have assembled a diverse team of observationalists and modelers to investigate relevant aspects of ridge-associated oceanography and biology, and to combine them into a quantitative model of dispersal. J. Ledwell (WHOI) will coordinate tracer releases to characterize dispersion of neutral particles, and measure diapycnal diffusivity and lateral homogenization. A. Thurnherr (LDEO) will deploy an array of current meters to characterize the flow field near the crest and over the flanks of the ridge, and investigate the effects of ridge crest topography on flow. W. Lavelle (PMEL) will employ a primitive equation hydrodynamic/transport model to aid in experimental design, to help interpret field observations and to provide a framework for evaluating what aspects of the circulation most influence the transport of larvae along the ridge. L. Mullineaux (WHOI) will sample larvae in the plankton to determine their vertical positions at different stages in their larval life histories, and will help constrain estimates of larval life span. D. McGillicuddy (WHOI) will integrate information on species-specific larval positioning and life spans into the transport model in order to determine how larval behaviors and physiology affect dispersal trajectories, maximal dispersal distances, and relative probabilities of colonizing natal versus remote vents. We are well aware that this interdisciplinary approach results in a hefty budget, but we think it is the only way to do this project effectively.

We have chosen to study the region near 9°50'N on the East Pacific Rise (EPR), because the topography and location of vents are well mapped (e.g., Haymon et al. 1991), the species composition and recent history of vent communities are well characterized (e.g., Shank et al. 1998), and the region supports numerous and species-rich vent communities. This site has been the focus of much interdisciplinary research in the past and has been selected as an Integrated Study Site by the NSF Ridge 2000 program. Complementary studies of biology, chemistry and heat flux along the EPR are planned by other Ridge investigators.

We've elected to study the process of dispersal at hydrothermally active ridges for two different reasons. One is that we cannot understand fundamental aspects of the ecology of these systems – i.e., their population dynamics and genetics, community structure, and biogeography – until we have characterized their dispersal dynamics. The second is that vent systems represent a metapopulation (as defined in Hanski 1999) because the habitat is patchy, the inhabitants disperse, and the populations undergo extinctions. Most current metapopulation theory, however, assumes a static landscape, whereas along mid-ocean ridges, the habitability of a site (i.e., presence or absence of venting) varies temporally, as do the population sizes within habitable vents. The study of vent populations will likely bring a unique perspective to metapopulation studies, and will provide a testing ground for the generality of theory conceptualized largely for terrestrial ecosystems.

3. Background

3.1 Dispersal and colonization in deep-sea hydrothermal vent ecosystems

Larvae of most vent species are small (Berg and VanDover 1987; Mullineaux et al. 1995), and appear to be relatively weak swimmers, suggesting that their dispersal may be determined largely by oceanic circulation. Larvae of most dominant vent species do not feed on particulates in the plankton (Lutz et al. 1980; Tyler and Young 1999). Similar larvae in shallow water have short dispersal times (hours to days). However, physiological studies of Antarctic asteroids have shown that non-feeding larvae may remain viable in the plankton for months, due to lowered metabolism in cold water (Hoegh-Guldberg et al. 1991). The vent tubeworm *Riftia pachyptila*, has been cultured to obtain direct estimates of life span (Marsh et al. 2001); the larvae can live on the order of 30-40 days without feeding. If the larvae are transported as passive neutrally-buoyant particles, they have the potential to disperse distances up to 100 km in typical East Pacific Rise flows (Mullineaux et al. 2002). Using inferred larval life spans, a dispersal model of the vent polychaete *Alvinella* suggests that this species should be able to traverse the distances necessary to migrate between neighboring vent sites along the East Pacific Rise (Chevaldonné et al. 1997).

Despite limited swimming capabilities during most or all of their planktonic life, larvae may affect their dispersal through behaviors that alter their position above the seafloor. Larvae of species living in shallow water exhibit a variety of behaviors that result in stratification of their populations in the water column (reviewed in Sulkin 1984; Young and Chia 1987; Forward 1988). Migrations of coastal larvae may occur daily in response to light, tidally in response to salinity or temperature, or ontogenetically (i.e., over the life span of the larva). Ontogenetic migrations typically involve upward floating or swimming during early larval stages (when lipid reserves are replete), maintenance of position during mid stages, and sinking or downward swimming at late stages, when the larva has depleted lipids (and possibly grown a shell) and is ready to settle. This sort of ontogenetic migration appears to enhance retention of larvae in estuarine environments, since the late stages avoid the strong seaward flows at the surface (e.g., Dittel and Epifanio 1990; Thiebaut et al. 1992). Alternatively, some larvae, termed demersal, stay near the seafloor during their full planktonic life. In deep water, we do not expect larvae to migrate in response to light, temperature or salinity cues, but we do think that ontogenetic migrations or demersal behaviors are possible, given their general prevalence in invertebrate larvae. We suggest that the behaviors most likely exhibited by larvae in deep water are ‘passive’ (little directional larval swimming), ‘demersal’ (maintenance of proximity to seafloor), or ‘balloonist’ (upward movement shortly after fertilization and downward movement shortly before settlement). The ‘balloonist’ larva may achieve ontogenetic change in vertical position behaviorally, or through changes in buoyancy during larval development.

The unique geological and hydrological framework within which vents exist places fundamental constraints on the abilities of vent fauna to disperse from one vent to another. Vents are typically distributed linearly along mid-ocean ridges and are separated by tens-of-meters to tens-of-kilometers along fast-spreading ridges (*e.g.*, East Pacific Rise), and up to hundreds of km along slow-spreading ridges (*e.g.*, Mid Atlantic Ridge). Thus, successful colonization requires that a species’ dispersal distance be greater than the distance between neighboring habitable vents. Furthermore, the vent habitats are transient, and theoretical considerations indicate that variation in the frequency and duration of active venting substantially affects the probabilities of migration success and gene flow (Jollivet et al. 1999). Such barriers to dispersal can set boundaries to a species' range and permit genetic differentiation between previously interbreeding populations. The range and frequency of larval dispersal influence how quickly a species can colonize a new vent habitat (i.e., will it be an opportunistic pioneer colonist or a later arrival), and constrain the amount of genetic exchange among existing vent populations.

Although colonization of new vent sites can occur rapidly when established communities are nearby (Tunnicliffe et al. 1997; Shank et al. 1998), the remote site at Loihi Seamont has remained sparsely colonized for years (Grigg 1997) indicating that larval supply may be limiting. Our ability to relate larval supply to recruitment has improved recently with the advent of high-volume pumps and refined morphological and molecular methods for identifying larvae to species. Identification of most vent gastropod and bivalve larvae can be accomplished by examining the morphology and sculpturing of the larval shell (Mullineaux et al. 1996; Fig. 1), and the two most abundant larval crustacean species also are

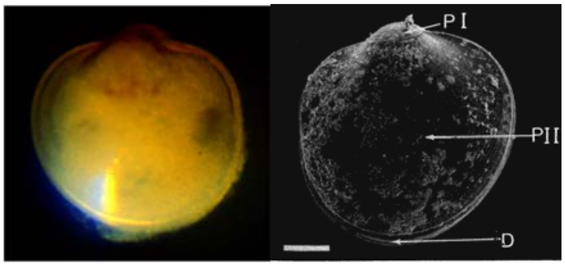

Fig. 1. A. Photo of a late-stage larva (0.4 mm in diameter) of the vent mussel *Bathymodiolus thermophilus* collected near 9ºN EPR; B. Scanning electron micrograph of a postlarva (scale bar = 0.1 mm) of a deep-sea mussel, showing relative sizes of early-stage (PI), and late-stage (PII) larval shells (from Turner and Lutz 1984; D marks edge of larval shell).

distinguishable by morphology. However, molecular genetic techniques are required for other groups, including polychaetes (alvinellids, vestimentiferans, etc) and even some mollusk species (Comtet et al. 2000).

3.2 Oceanic circulation near mid-ocean ridges

The flow field near mid-ocean ridges is often complex. Processes associated with topography, such as blocking, channeling, hydraulics, flow rectification, and boundary mixing act in conjunction with rotation and stratification to control the regional circulation. As a result, flow near mid-ocean ridges is intensified in comparison to the velocities typically encountered away from topography. On a large scale, enhanced diapycnal mixing associated with the roughness of the ridge flanks and/or vertical advection cause isopycnals to dip downward toward the crest; in conjunction with the effects of the Earth's rotation, this leads to along-flank boundary currents (e.g. Thompson and Johnson, 1996), as well as cross-flank secondary circulations (Thurnherr and Speer, 2003). Doming of the isopycnal surfaces immediately above the ridge crests is commonly observed (e.g. Joyce 1981). Both effects are apparent in a cross-ridge hydrographic section at the central latitude of our proposed current-meter array (9°30'N, Fig. 2). Tidal and longer-period oscillations are often prominent at ridge sites (e.g. Lavelle and Cannon 2001), and these can also drive substantial cross-flank flows, as well as contribute, through rectification, to along-flank mean flows.

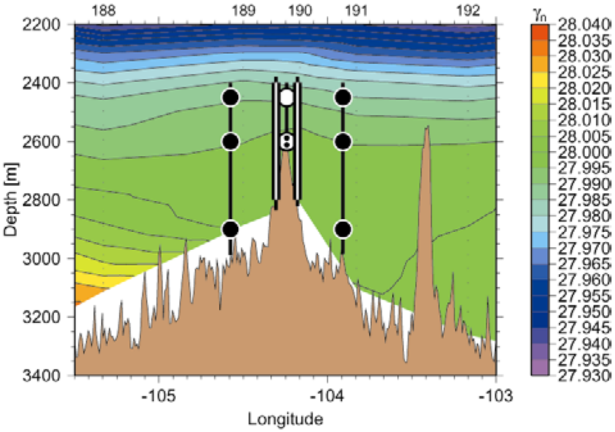

Fig. 2. WOCE neutral-density section across the EPR crest at 9° 30'N (see Fig.3 for station positions). Bathymetry is taken from Macdonald et al. (1992). Aanderaa RCM11 current meters (black and white circles) will be used on the outer flank moorings and on the axial moorings at 2400m. Current meters (double dots) will also sample two closely-spaced levels on the ridge axis, one instrument in and the other just above the rim of the Axial Summit Collapse Trough (ASCT). Two moored velocity profilers (black and white columns) will sample the flows over the ridge flanks 7km off axis.

Of particular interest in the context of larval dispersal is the flow field at and below the level of the neutrally buoyant hydrothermal plumes (~2450m; Baker et al. 1994). Assuming geostrophy, the hydrographic section of Fig. 2 suggests horizontally sheared along-axis flow at this depth. Plume-depth current-meter records from 9°51'N indicate high variability over a 5-month sampling period, with along-axial advection dominated by a single period of southward flow (Marsh et al. 2001). For a different time, Baker et al. (1994) conclude, on the basis of hydrothermal plume-dispersal observations, that advection from the EPR crest between 9° and 10°N was dominated by westward flow during their sampling. These two inferences indicate that near-crest velocities observed during weeks to months may not be representative on longer time scales. The along-axial velocities of Marsh et al. (2001) can be used to estimate how long current meters need to be deployed in order to detect mean flows of a given magnitude. Considering only the subdiurnal frequency band, the integral time scale is 3.55 days and the velocity standard deviation 4.5 cm s^{-1}. In order to sample a 0.5 cm s^{-1} flow (e.g. the along-ridge boundary currents inferred by Thompson and Johnson 1996) 81 degrees of freedom (287 days) are required. Therefore, we plan to deploy our current-meter array for a full year.

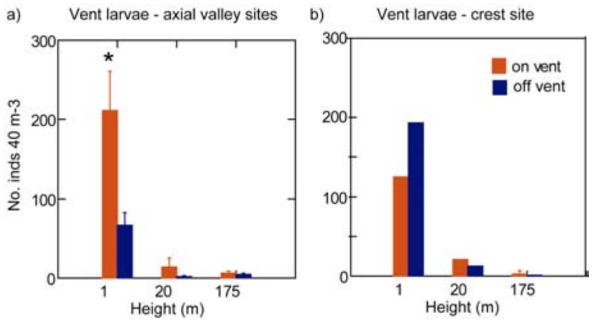

Fig. 3. Larval abundance at vent sites in the axial valley (a) and up out of the valley on the ridge crest (b) in comparison to abundances outside the vent boundaries. At vent sites within the valley, larvae at 1 m above bottom were significantly more abundant on-vent than off-vent (*ANOVA; $p<0.05$). The pattern is not seen at a site where the vent is up out of the valley (b), nor is it significant at heights of 20 or 175 m above bottom. One explanation for these patterns is that larvae at 1 mab are retained in the axial valley.

Larval-abundance data indicate that larvae are concentrated on the ridge axis (Fig. 3), where the Axial Summit Collapse Trough (ASCT), a narrow (<200m) and shallow (~15m) depression runs along the otherwise comparatively smooth ridge crest (Fornari et al. 1998). Most known hydrothermal sources in this region (triangles in Fig. 4) are located either inside or close to the edge of the axial trough (Haymon et al. 1991). It is therefore possible that dispersal from axial hydrothermal sources on the EPR near 9°30'N may be influenced by the presence of the ASCT. How this is possible is somewhat of a mystery, though, because the ASCT is shallow enough to be flushed each tidal cycle. (There are, however, no velocity measurements in the trough to support or disprove this inference.) Entrainment of seawater into buoyant hydrothermal plumes has the potential to drive horizontal currents along the seafloor (e.g., Speer and Rona 1989), especially within submarine valleys (Thomson et al., 2003). In the relatively open topographic situation at the EPR with its shallow axial valley, hydrothermally driven flows are expected to be minor compared to the tidal and residual flows of the type shown in Fig. 5a.

Potentially important for larval dispersal are residual currents (e.g. Fig 5a) caused by rectification of oscillatory, stratified flow of over a ridge. These rectified flows are localized and anti-symmetric about the ridge at crest depth, with the strength and period of subtidal forcing important in setting maximum core speed. Preliminary model results for the topography, hydrography, and forcing conditions estimated for our EPR –9^{o}N site suggest that a similar pattern of residual flow can be expected.

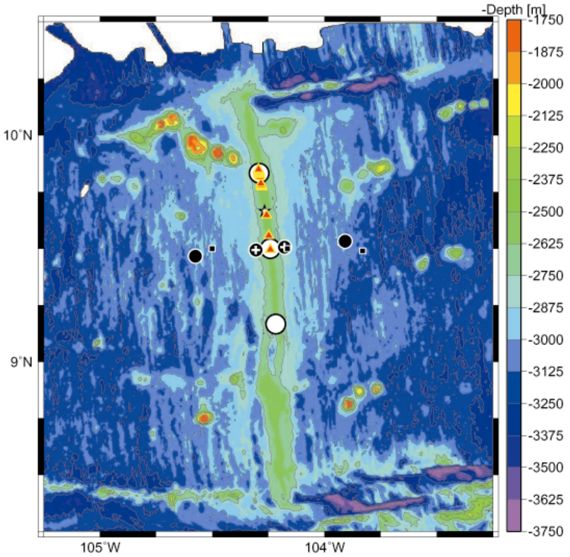

Fig. 4. SeaBeam bathymetry of Macdonald et al. (1992) of the study site near 10ºN EPR. Small black squares show the WOCE CTD stations (c.f. Fig. 2). Red-and-yellow triangles show locations of known hydrothermal sources. Deployment locations for current meters (RCM11's) are shown as circles. The star indicates the location of the bottom mounted ADCP near the tracer release site. White circles show the location of moorings with RCM11's, that are to be anchored within the ASCT. Black circles with white crosses show the locations of the moored velocity profilers. The remaining black circles represent the flank moorings

Flow near topography is commonly associated with significant vertical shear. At the Juan de Fuca Ridge, for example, the velocities a few hundred meters above the ridge are often greater and in different directions than those directly above the seafloor (Thomson et al. 1989; Thomson et al. 1990; Cannon et al. 1991). Such shear implies that the vertical position of a particle such as a larva will have a strong influence on its trajectory. Thus, deviation of larval behavior from neutral and passive, such as that described for demersal and balloonist larvae, may have a significant impact on an individual's dispersal path and its probability of colonizing natal versus remote habitats.

Biologists have speculated that cross-axis flows at fracture zones (e.g. those near 8°20'N and 10°15'N in Fig. 4) impede larval dispersal and are responsible for genetic differentiation of vent species between ridge segments (Van Dover et al. 2002; Won et al. 2003). Measurements carried out in Atlantic fracture zones suggest that the flows across the ridges are often persistent and strong (e.g., Speer et al. 2002; Ledwell et al. 2000a,b). Characterization of flows and larval distributions across EPR fracture zones is outside the scope of the present study, but we will examine tracer distributions for evidence of a barrier to transport.

4. Objectives and Methods

4.1 Tracer Release Experiment

The main objectives of the tracer release experiment are to characterize dispersion of neutral particles, and to measure diapycnal diffusion and lateral homogenization near the ridge crest. The resulting measures of advection, and isopycnal and diapycnal dispersion will be combined with the current-meter measurements to constrain the hydrodynamic/transport model. Thus, they will contribute directly to questions of dispersal distance and barriers (Ecology Question 1) and provide input on subgrid-scale processes needed for the model to address effects of behavior and cross-axis flow (Ecology Questions 2 and 3). As a passive tracer, SF_6 provides important information about, but does not mimic, the dispersal of larvae that are able to adjust their depth. All of the components of the project must be used together to model larval disperison.

Tracer will be released in a 1-km streak in the axial trough, about 60 km south of the Clipperton FZ. The distribution of the patch will be surveyed after approximately 40 days. It is anticipated that the tracer patch will probe a layer about 200 meters thick, where the thermal plumes from the vents are found. The tracer will also measure rates of lateral homogenization and dispersion relative to the center of mass – information that will be of general use for estimating dispersion probabilities for larvae. Movement of the center of mass of the tracer patch and the final overall shape of the patch will give one 40-day realization of the effects of the larger scale flow on particles originating in the axial trough and drifting in the layer just above it. Comparison of the tracer displacement with the current meter data over the same period will give a measure of the spatial coherence of the flows at scales of tens of kilometers. The one-year current measurements will determine the variability of the larger scale flow from one 40-day period to another.

In addition to the ship survey at 40 days, tracer samples will also be taken every week for a year from a 50-chamber sampler moored during the release cruise about 20 km north of the Clipperton FZ (near 10°15’N) on the crest of the next ridge segment. The concentrations in these samples will help determine the probability of larvae crossing a fracture zone interrupting the ridge to colonize sites nearly 100 km away from their place of birth.

The Tracer. Sulfur hexafluoride (SF_6) is a gas at normal temperature and pressure, but a liquid at the conditions of the tracer release. It is a nearly inert compound in the ocean environment. Particle scavenging and settling of SF_6 were unnoticeable in a multiyear experiment below the sill of particle-rich Santa Monica Basin (Ledwell and Watson, 1991; Ledwell and Hickey, 1995). Settling of SF_6 in the open ocean, due possibly to transport on particles, has been at most 10 m/year (Ledwell et al., 2000a), far too slow to affect the present 40-day experiment. SF_6 is not hazardous, except for a risk of suffocation if it is allowed to displace air in an enclosed space. Although it is a powerful greenhouse gas, the radiative effect of the amount to be used in the present experiment is negligible compared with that of the diesel fuel to be burned during a typical research cruise. Because of a strong affinity for free electrons, SF_6 is detectable in amounts as low as 0.01 femtomoles with a gas chromatograph and electron capture detector (Law et al., 1994). For deep ocean mixing experiments, samples are taken from Niskin bottles or special samplers and transferred to glass vessels for analysis on board the ship, about 6 minutes being required for each sample analysis.

Release and Initial Condition. Ten moles of SF_6 will be released from the DSV Alvin about 10 meters off the bottom, along the axial trough near 9° 41’N, near the moored ADCP shown in Fig. 4. The release system will be similar to that used for past experiments in the North Atlantic pycnocline (North Atlantic Tracer Release Experiment; NATRE) and the deep Brazil Basin (Brazil Basin Tracer Release Experiment; BBTRE), described by Ledwell et al. (1998), repackaged for Alvin. Sixty liters fluorescein dye solution will be released with the SF_6 to enable documentation of the initial condition. Four neutrally buoyant floats will also be released with the SF_6 to guide sampling of the tracer patch, which will commence about 35 days after the release. The release will be performed in 60 minutes, with the vehicle moving about 900 meters along the axis of the trough at cruising speed of 0.25 m/s to avoid affecting the density of the water with the tracer or with the thermal wake of the vehicle. The turbulent wake of the vehicle will homogenize and spread the tracer into an initial plume that will be no more than 20 meters deep after the turbulence of the wake subsides. The initial condition of the plume will be surveyed with fluorometers on board Alvin in the 2 to 3 hours immediately following the release.

SF_6 Survey. Sampling the tracer patch would commence about 35 days after the release, guided by the floats, which will have surfaced a few days before. Stations would be occupied at 5- to 10-km spacing, with the details of the sampling lines suggested initially by the float positions, and adjusted as needed. The tracer patch will be much less streaky at 40 days at the present site than the patch was at 6 months in NATRE (Ledwell et al. 1998), because of the shorter time and the greater diapycnal diffusivity and tidal dispersion, both of which will enhance the cross-streak dispersion. Hence the approach of standard rosette casts will be effective, as it in fact was even for the much more severely streaky case at 6 months in NATRE (Ledwell et al. 1998).

CTD/Rosette casts for tracer at 2400 meters depth can be done at 5 to 10-km spacing at a rate of about 12 per day with the fast system that has been designed for deep tracer experiments. A total of 240 hours would be dedicated to sample the tracer patch. A rough estimate is that the plume will occupy an area about 50 km wide by 100 km long. Such an area could be covered in 6 days with 5-km x 10-km resolution. If the main survey proceeds well, then the other days would be used to sample at 2-km resolution to determine the spatial covariance of the patch at finer scales, if desired, and to delimit outlying regions of the patch. Tracer surveying can be interrupted by Alvin operations to some extent, but 4 consecutive days (without dives) should be allocated for tracer sampling in order to avoid the patch moving too much during the main survey.

Moored Sampler. The moored sampler will be deployed north of the Clipperton FZ during the release cruise. Every week for 50 weeks it will fill a 1-liter sample bag by pumping water out of the canister in which the collapsed bag is mounted, the sample entering the bag through its inlet valve. The system would be assembled from equipment that has been used in a towed system in previous experiments (Ledwell et al. 1998; Polzin et al. 1997). Samplers of very similar design, built by McLane Research Laboratories, have recently been used successfully in a year-long deployment in the North Pacific upper ocean (K. Hayashi, personal communication). The mooring will be recovered during the cruise one year after the release, and the samples will be analyzed on board immediately after recovery. The minimum detectable level will be 0.01 fM with 1-liter samples, low enough to be able to detect tracer more than 200 km away from the center of the patch after one year, if it were distributed in a similar way to that in the Brazil Basin (Ledwell et al., 2000a,b). Samples will also be taken by rosette during the recovery cruise along the ridge between the release site and the mooring, to tell us if tracer has lingered at all, and, if so, to determine the spatial correlation scale of the tracer at that time. These measurements comprise our one exploratory attempt to determine whether the fracture zone constitutes a barrier to transport. If tracer is detected at the time predicted from currents and extrapolation of the 35-day dispersion observations, then we will infer that the FZ poses no barrier. If tracer is detected significantly later than expected, or not at all, then we can speculate that the FZ poses at least a partial barrier.

Shear and stratification measurements. This experiment will be one of a series of deep ocean studies of diapycnal mixing with a tracer release. No such study is complete without measurements of the forcing of the mixing. The moored current meter profilers placed 5 to 10 km to the east and west of the ridge crest (see below) will give current shear and stratification once per hour for the 40 days of the tracer experiment at a resolution of approximately 1 meter over a 400-meter interval. The gradient Richardson number Ri down to this scale will be calculated from these data, as well as the vertical and temporal structure of the flow field responsible for events of likely shear instability ($Ri < 1/4$), in order to gain insight into the processes governing the diapycnal mixing experienced by the tracer. The bottom mounted ADCP in the axial trough (see below) will also provide measurements of finescale shear at the ridge crest to help with this effort, as will profiles obtained with CTD/ADCP. Shear at the ridge crest may be quite different from that at the location of the moored profilers.

Analysis. Diapycnal diffusivity in the region of the tracer patch will be estimated from application of the vertical advection-diffusion equation for the tracer concentration, integrated on isopycnal surfaces over an area encompassing the patch. Ledwell et al. (2000a) gives a recent example of the technique applied to a deep ocean site – the flanks of the Mid Atlantic Ridge in the Brazil Basin. The measurement in the present experiment would complement that prior measurement, since it will be on the axis of a fast spreading center, while the Brazil results apply to the flanks of a slow spreading center.

We will obtain the size, shape, and smoothness of the tracer distribution 40 days after release, an important time scale for *Riftia* larvae. Of particular interest to the question of larval recolonization of a natal site or nearby sites will be the concentration of tracer in the ASCT at and near the release site at this time. The tracer distribution will be combined with the statistics of the low-frequency velocity field determined from the current meters to estimate dispersal probability functions for larvae originating at the vent sites in the axial trough. The current meter results, the shape of the patch and the model will help us to determine the mechanism for the growth of the patch area at 0 to 40-day time scale, and a growth law, e.g. linear with time (Fickian), or, more likely, something stronger. Such a growth model, and also various vertical migration behaviors of larvae, will be used to refine these estimates of settlement probability fields for larvae.

4.2 Current meter measurements

The primary objective of the current-meter measurements is to determine the temporal and spatial characteristics of the flow field near the EPR crest, particularly the cross-axial structure, the vertical shear between the crest and the plume level, and the coherence of the axial flow along the ridge for length scales over which tracer dispersion is expected to occur. Additionally, the current meters will yield a time-series of flow sufficiently far away from the topography so that it can be used to force the numerical model. A further objective consists in measuring the currents in and just above the axial summit trough. The resulting flow observations will be the first long-term velocity data near the EPR, except for a few axial point measurements near hydrothermal vent fields (e.g. Marsh et al. 2001). The data will help interpret the measured distribution of tracer, constrain model parameters, and ultimately help predict pathways of larvae along-, across-, and off-axis (Ecology Questions 1-3). The axial flow measurements will ensure that we have a good characterization of flows where the tracer and most larvae are released, and will contribute to evaluating whether the flows in the axial trough channel larvae between vent sites by inhibiting cross-axis transport (Ecology Question 3).

The current-meter array will be in the shape of a cross with five moorings forming a cross-axial transect and one additional axial mooring each north and south of the transect (Figs 2 and 4). The separation between the axial moorings (~35 km) was chosen with the estimates of Marsh et al. (2001) in mind that the dispersal distance over a 30-day life span for Riftia larvae has a typical value of ~50 km. The cross-axial mooring line will be deployed near the latitude of the WOCE P04 hydrographic section (Fig. 2). The two outer flank moorings will be deployed ~30km off axis. All moorings will have instruments at the depth of the hydrothermal plumes (nearly continuous between 9°30 and 10N at ~2450m; Baker et al. 1994) and at crest depth (~2600m). On the axial moorings there will be two instruments each near crest depth, one half way down inside the ASCT (5-10 mab) and one immediately above the lip of the trough. This configuration allows comparing the flow regime within the trough to that immediately above. On the outer flank moorings there will be instruments at 2900m, deep enough to sample the along-ridge flows inferred by Thompson and Johnson (1996). Based on the height of the steep part of the EPR crest and hydrographic data, the deformation radius is 5-10km, i.e. the crest-level instruments on the outer flank moorings are several Rossby radii away from topography. It is therefore anticipated that we will be able to calculate a time series of velocities with which we can force the numerical model. Aanderaa RCM11 acoustic doppler current meters will be used at all positions in the array.

Between the central axial mooring and the outer-flank moorings, one moored velocity profiler will be deployed on each ridge flank between 5 and 10km off axis. The moored profilers will carry an acoustic current meter and a CTD, both made by Falmouth Scientific, Inc. Details on specifications and performance can be found at http://www.mclanelabs.com/mmp.html. There are two reasons for deploying moored velocity profilers there. First, during the tracer-release experiment the profilers will sample once per hour between 2400m and 2800m, providing vertical-shear and stratification data that will be used to provide the dynamical context of the diapycnal diffusivity measured with the tracer, as described earlier. With a single battery the profilers can sample approximately one million meters. Second, the profilers will be turned around during the tracer-survey cruise and re-deployed in order to measure the near-crest flow during the remainder of the year. We plan to re-program the profilers to collect one profile per hour for one five-day period every three weeks after re-deployment. The profiler locations coincide with strong along-crest jets that are found in preliminary model runs with EPR-relevant parameters (topography and stratification) and will allow us to measure these flows if they exist in the ocean. Before deploying the moored velocity profilers a cross-ridge LADCP section with 5km horizontal resolution will be carried out in order to determine the locations of the along-crest velocity cores that are predicted by model runs (e.g., Fig. 5a).

In addition to the moored current meters, a bottom-mounted ADCP will be deployed near 9°40'N ('star' in Fig. 4) during the 1.5 mo tracer experiment. The resulting data will characterize the vertical shear in the velocity field near the tracer release site and will supplement the measurements from the profiling moorings on the flank. The ADCP sampling range depends on the acoustic scattering properties of the particles in the water. On Juan de Fuca Ridge, similar ADCPs deployed near the seabed are capable of measuring to a vertical distance of 75 m (S. Hautala, pers. comm), and we expect similar performance in the particle-rich environment of the EPR crest (Baker et al., 1994). The shallow depth of the ASCT (~15 m) and the narrowness of the ADCP beam (20 degrees) imply that even where the trough is narrow (50m), there should be no reflections off the walls for an instrument deployed in the trough axis. The distance between the ADCP and the two neighboring axial moorings is ~15km; i.e. sampling of the flow between the hydrothermal vent fields inside and above the ASCT is comparatively fine.

The current-meter moorings will be deployed conventionally from shipboard, with modifications for precise positioning within the axial trough. The three main axial moorings will be repositioned by submersible after deployment, a process that takes approximately 1.5 hours of dive time per mooring, including time to survey the trough topography, locate the mooring and move it. All moorings will be released acoustically and retrieved at the surface. The ADCP will be both deployed and recovered by submersible (~1.5 hr to survey trough and deploy; 0.5 hr to recover).

4.3. Larval distribution and stage structure

The objective of this component is to characterize vertical and lateral distributions of target vent species through their larval life spans. These data will be used to build an ontogenetic profile for each species, describing where it resides at various stages of its larval life. We anticipate that these profiles will correspond roughly to ‘passive’, ‘demersal’ or ‘balloonist’ behaviors, but we can accommodate whatever results are obtained. The larval profiles will be used as input into the biological/physical model to answer the question of how behavior affects dispersal trajectory and speed (Ecology Question 2) and explore the potential effects of transform faults as barriers. We also will obtain information on the stages of larvae (i.e., early or late in life span) at increasing distances from source vent populations. Although our most recent study on larval distributions (Mullineaux et al., submitted) provides valuable information on larval vertical abundances, horizontal scales of variation, and temporal patterns, it was not designed to provide the stage-specific information necessary for modeling dispersal in an interdisciplinary context.

Larvae will be collected quantitatively in high-volume plankton pumps. These pumps (McLane WTS-LV series), were developed specifically for deep-sea larval collections, and filter 40 m^3 of water in a single 20-hr deployment. Resulting samples have tens to hundreds of larval individuals (Fig. 3) many of which are alive on recovery due to thermal insulation and low shear in the filter compartment.

Pumps will be attached to autonomous moorings at positions just above the seafloor (within 5m), and at the level of the neutrally

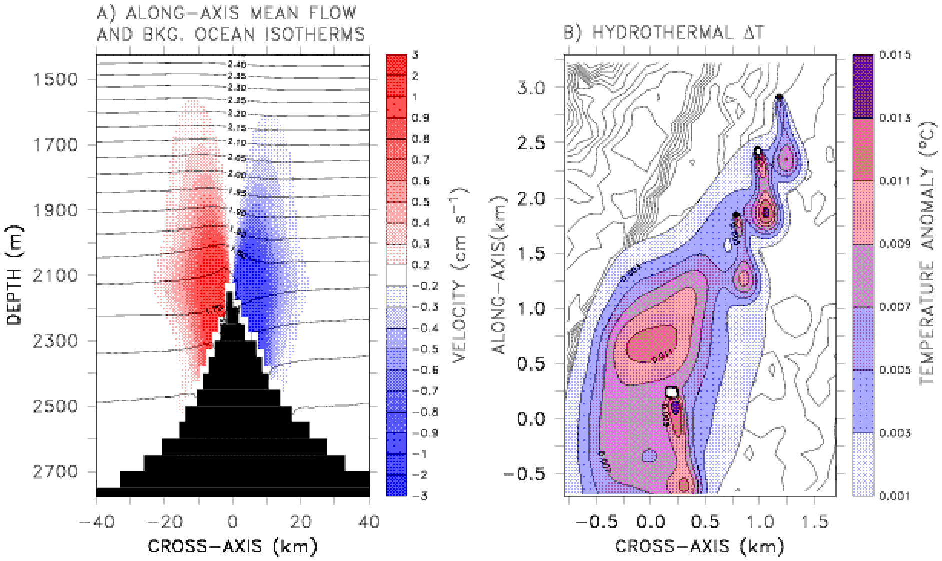

Fig. 5. A) Model residual flow (color contoured) over the Juan de Fuca Ridge when background forcing is oscillatory at a period of 5 days. Flow is northward to the west and southward on the east at speeds upward of 3 cms^{-1}. The off-axis pattern and magnitudes are similar to residual flows measured across the JdFR. Vertical motion related to oscillatory cross-ridge flow forces isotherms (black curves) downward below ridge crest depth alternately on each side of the ridge. Isotherms plunging below the JdF Ridge crest have been observed by Cannon and Pashinski (1997); B) Heat and other tracers released from vent sources along the ridge are subject to time variable currents. When currents are fast, plumes stream away from source regions, and when currents are weak, plumes pool above vents. Weak followed by strong currents result in boluses of elevated concentration downstream. Larvae entrained into the ascending flow at vents will be subject to the same effect. This snapshot of a model thermal plume from four sources at and near Pipe Organ Vent shows the results of that pooling and streaming.

buoyant plume (roughly 200 mab). The lower height corresponds to the expected strata where we would find demersal larvae of all stages, neutral larvae of all stages, and early- or late-stage balloonist larvae; the upper height should contain neutral larvae and mid-stage balloonists.

Seven pump moorings will be deployed during each cruise to quantify vertical and lateral distributions of larvae. Three moorings will be repositioned directly at active vent sites between 9°45' to 9°50'N where faunal communities are vigorous and abundant. These will ensure that we have sufficiently high larval numbers to characterize vertical distributions of the dominant 4 to 6 vent species. The remaining moorings will be positioned along the ridge axis at distances of 5 and 20 km away from the nearest inhabited vent. These distances were selected to be greater than one semidiurnal tidal excursion O(1 km), but less than the maximal spacing between vents sites on this segment (as displayed in Haymon et al. 1991). Because the dominant species vary over time (Mulineaux et al., submitted), the sample array will be repeated on each cruise to increase the number of species available for statistical analysis.

Larval individuals will be preserved in 95% EtOH immediately on recovery, and dominant taxa identified to species. Most of these identifications will be accomplished morphologically, but some (e.g., polychaetes) will require molecular genetic analysis. We are collaborating with Tim Shank (WHOI) and Nicole Dubilier and Florence Pradillon (Max Plank, Bremen) to develop PCR/RFLP and in-situ hybridization probes for the problematic species. Molecular identifications of larvae will be conducted as part of those collaborations (funded by international and internal WHOI sources), and are not detailed here due to space constraints

Larvae will be categorized into relative stages (early, late), based on characteristics such as shell morphology of planktotrophic molluscs (e.g., presence of PII; Fig. 1), lipid stores of lecithotropic forms (using flame-ionization detection as in Miller et al. 1998) or size and segmentation of polychaetes. Ethanol preservation will ensure that larval tissues are suitable for molecular identification and future population genetic studies.

Our field data will address questions about how larval positioning interacts with hydrodynamics near ridges to affect dispersal trajectories and speeds. We will not attempt to calculate larval lifespans (requires culturing), larval fluxes (requires estimates of reproductive output and larval mortality), or number of migrants (requires information on recruitment success). To determine maximal dispersal distances, we will use accurate measures of life span when available (e.g., *Riftia pachyptila*), and will constrain the life span estimates used in the model to realistic ranges (i.e., days to months) based on the limited data available for related species at temperatures similar to those in the deep sea.

4.4. Numerical Model of Flow and Larval Dispersal

A primitive equation hydrodynamic-transport model will be employed to aid experimental design, to help interpret field observations of flow and transport of SF_6, and to provide a framework for evaluating what aspects of the circulation most influence the distribution and transport of biota along the ridge. The model will be used directly to evaluate dispersal distances (Ecology Question 1), in an exploratory mode to evaluate transform faults as barriers, and will be combined with larval positioning results into a coupled biological/physical model to determine the effect of larval behavior on dispersal potential (Ecology Question 2).

The model has already been used to describe flow over ridge topography (Lavelle and Cannon 2001), around Axial (Lavelle et al. 2003) and Irving (Lavelle et al., 2004) seamounts, and has been tested against laboratory data for non-linear, baroclinic, time dependent flow in a canyon (Perenne et al. 2001). Consider, for example, Fig. 5a depicting model distributions of residual flow over the Juan de Fuca Ridge (JdFR) subject to monochromatic oscillatory forcing at a weather-band (5 day) frequency. Rectified mean flow moves northward to the west and southward to the east of the ridge (Fig. 5a), just as the long-term mean observations at the JdFR show (Cannon and Pashinski 1997). That flow is in the same directional sense as the anticyclonic rectified flow around the summit of a seamount. Oscillatory flow across the ridge causes substantial vertical motion along the ridge's upper flanks, and this motion cyclically depresses isotherms below crest depth on alternating sides of the ridge. Cross-ridge CTD transects at the JdFR (Cannon et al. 1995; Cannon and Pashinski 1997) show comparable downward depression of isotherms. Preliminary model experiments for the EPR that include subinertial forcing show rectified flows with similar distributions (Fig. 5a).

Consider the model results in Fig. 6 for flow over and around Axial seamount, a much different topographic setting. Here the anticyclonic mean circulation caused by diurnal forcing takes the form of a toroid near the top of the seamount, while mean flow caused by longer period oscillations move down the seamount's flanks. Observations (Lavelle et al. 2003) showing intensified anticyclonic mean flow at Axial from just above the summit to 500 m below support the model results, even though observed flows cannot be separated into tidal or weather-band forced means. A second consequence of the oscillations is, in the absence of hydrothermal forcing, a persistent distortion of isotherms (Fig. 6). That redistribution takes the form of a cold dome-shaped temperature anomaly above and a warm toroidal anomaly around the sides of the seamount. Cold domes are known features of many seamounts (as reported, for example, by Brink 1995). In light of the successes of the model in these topographies, we propose to use the same numerical model for the ridge at 9ºN.

The hydrodynamic/transport model uses finite-differenced equations for momentum, salt, heat, tracer, and turbulent mixing intensities and, along with a density equation, solves them using methods detailed in Williams (1969), Arakawa and Lamb (1977), Smolarkiewicz and Clark (1986), Briggs (1987) Dukowicz and Smith (1994), and Wang and Ikeda (1997). The equations are written in generalized x-y but level z, rather than sigma, coordinates; sigma coordinates are not used because of their limitations in steep topography (e.g. Berntsen 2002). Well above or away from the influence of the ridge, the momentum balances are relatively simple, involving acceleration, Coriolis and pressure-gradient forces F_R. Background current time series taken over the duration of the experiment can consequently be used to evaluate F_R. That gives the forcing a fuller spectrum (Fig. 7) than might otherwise be achieved. Background hydrography will come from regional

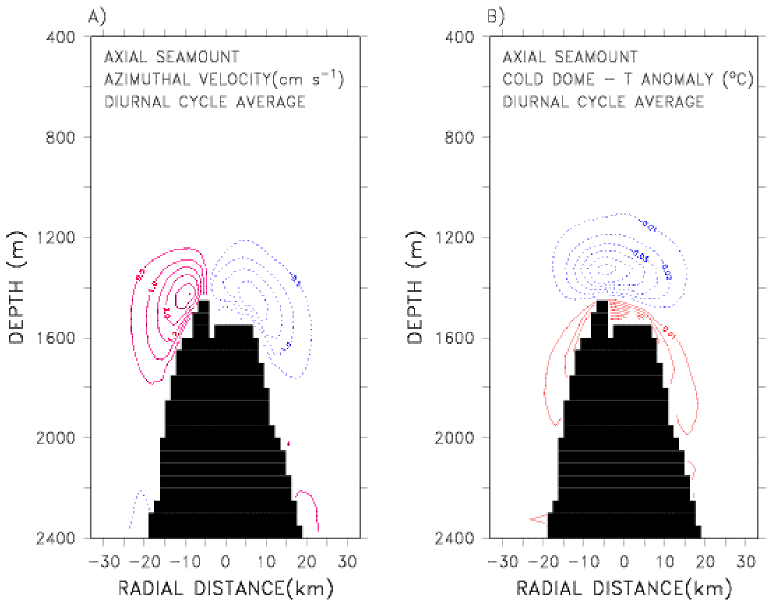

Fig. 6. Model results for an experiment in which flow was forced over Axial Volcano topography at diurnal period. A) Cycle averaged flow is confined to a toroidal region around the top of the seamount, with maximum mean flow four times larger than the amplitude of oscillatory forcing. Anti-cyclonic residuals of 5-10 cm s^{-1} have been observed at Fieberling and Axial seamounts, among others. B) The thermal anomaly predicted by the model, excluding effects of hydrothermal or volcanic discharges, takes the form of a cold dome and a warm apron. Observations at numerous seamounts have documented the presence of cold domes. The model suggests that the existence of that dome does not depend on mean vertical circulation. The transport and fate of larvae at seamounts, on the hand, must depend heavily on the non-zero instantaneous vertical (model observed), horizontal, and the pronounced residual flow surrounding seamount summits.

measurements. Rayleigh damping near model lateral boundaries (e.g., Kar and Turco 1995) is used to suppress the reflection of outgoing superinertial baroclinic waves scattered from the ridge topography. We have tested and can demonstrate the effectiveness of this method. Velocity shear determines both horizontal and vertical turbulent mixing intensities (e.g., Lavelle et al. 2004), which will be compared with mixing results inferred from SF_6 and from vertical shear profiler measurements. Additional details about hydrodynamic model design are available in Lavelle and Cannon (2001) and Perrene et al. (2001).

The model's transport module for passive tracers allows for localized and time-dependent sources (Fig. 6b). A line source of tracer can thus be introduced into the flow field, simulating the introduction of tracer in the SF_6 field experiments. The model will be used to simulate but not assimilate the SF_6 data—a necessary first step before proceeding with the more complex problem of larval transport and dispersal. The same three-dimensional transport model will be used for coupled physical-biological simulations, in which we will examine the impact of different larval behaviors in the hydrodynamic fields prescribed from the circulation model. Incorporation of organism behavior into the hydrodynamic model is straightforward, and we have done so in several previous studies of physical-biological interactions using various model architectures (e.g., McGillicuddy et al. 1995a,b; Lynch et al. 1998; McGillicuddy et al. 2003; Hetland et al. 2003). Because the flows in this area are time-dependent and strongly sheared in both horizontal and vertical directions, we expect the three canonical larval behaviors (passive, demersal, and balloonist) to result in distinct patterns of transport and dispersal. Large ensembles of numerical experiments will be required to span the range of reasonable physical and biological parameter values. This parameter dependence and sensitivity analysis will provide quantitative constraints on the probability density functions of larval dispersal for the various species-specific scenarios to be investigated.

Observations of larval stage structure (section 4.3) will provide important information about transport and dispersion pathways.

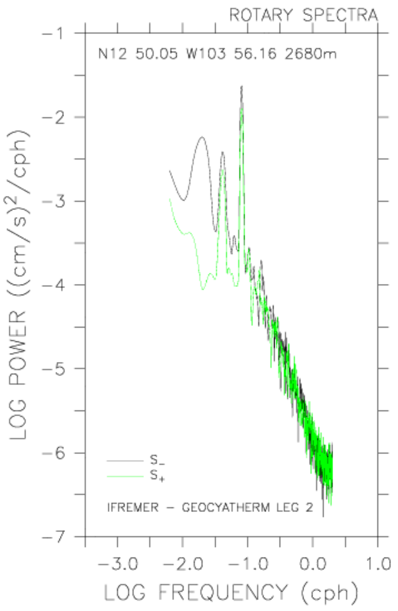

Fig. 7 Tidal frequencies dominate the spectra of currents measured several hundred of kms north of the proposed tracer release site. Data courtesy of IFREMER/SISMER, Plouzane, France.

Specifically, we expect to see younger larvae near the spawning area, and older larvae downstream in the sense of the ambient currents. As such data become available, we will undertake individual based model (IBM) simulations that allow for explicit representation of age structure in the larval population. The IBM approach relies on large ensembles of Lagrangian particle tracking experiments from which the underlying statistics of the population can be gleaned. The software required to conduct such simulations is readily available (Lynch et al. 2001; Werner et al. 1996), and it will be straightforward to use the velocity and diffusivity fields from the EPR hydrodynamic model to drive the Lagrangian IBM integrations.

Initially the EPR hydrodynamic model will be configured for a single ridge segment, and will span distances of approximately 200 km along and across axis. The limited latitudinal extent allows the use of an f-plane approximation. The first set of experiments will be directed at studying the time dependence and cross-ridge structure of flow and hydrographic fields. Based on JdFR results and anecdotal information on currents at 9ºN, we expect substantial vertical motions on the ridge flanks and along-ridge mean transport, both of which likely are factors in larval distributions and transport. Away from the ends of the ridge segment, the dominant features of the flow are expected to be invariant in the along-ridge (y) direction. The three dimensional transport of SF_6 and biota will therefore be calculated by specifying the 2-D hydrodynamic fields assuming along-axis invariance (with cyclic boundary conditions). This component of the modeling work is process-oriented, directed at understanding the space and time scales of cross-axis flow and the impact of larval life history strategies on dispersal.

We note that SF_6 released at 9º 41' N may come under the influence of circulation at the northern ridge end. It seems likely that tracer advected northward on the west of the ridge will turn southward, which when coupled with cross-ridge tidal currents, will lead to a broad across-ridge distribution typical of shear dispersion. To compare actual SF_6 measurements with model results, time-dependent hydrodynamic and transport fields will both likely need to be calculated in three-dimensions, i.e. over ridge topography of finite segment length.

It is our intention to intertwine observational and modeling efforts as much as possible. Current meter measurements least affected by the ridge will be used to specify the time-dependent forcing for the hydrodynamic model. The remainder of the current meter array will provide the information necessary to evaluate the cross-ridge structure of the simulated currents. Comparison of the vertical and cross-ridge tracer distributions with the simulated tracer field will constrain isopycnal and diapycnal diffusion in the model, and the coefficients of the subgridscale mixing parameterizations will be specified accordingly. Knowledge of the model's successes and shortcomings in matching the current meter and tracer measurements will set the stage for estimating the uncertainty in our coupled physical-biological predictions. Ultimately, we wish to test these predictions of dispersal with population genetic data that define the geographic characteristics of various species. Our model simulations should thus provide information about the degree to which the observed patterns can be explained by species-specific larval dispersal.

5. Submersible and Ship Use

We are requesting three cruises; two in Fall 2006 and a third a year later. During the first cruise, we will release tracer, release and survey dye, sample larvae and deploy the current meter array and tracer sampling mooring (15 d ship time, 8 submersible dives). On the second cruise, we will survey tracer, sample larvae, recover the ADCP and turn around the profiling moorings (21 d ship; 6 dives). The tracer surveying needs to take place at roughly 40 d after its release. During the third cruise, roughly 1 yr after tracer release, we will survey tracer, recover the tracer mooring, recover the current meter array and sample larvae (17 d ship; 6 dives). The submersible Alvin is ideal for our purposes because of its ability to maneuver within a moored array to position moorings and deploy tracer. However, we could modify our approach to use a large ROV (Jason) if the submersible is not available. On all cruises we need more ship days than submersible days and anticipate that we will be combined with another research group.

6. Significance

This study addresses a long-standing and important question at hydrothermal vents – how populations are maintained in the patchy transient environment. We go beyond previous attempts to model dispersal by investigating dispersal directly using Lagrangian approaches. We also go beyond modeling larvae as passive particles by incorporating vertical positioning behaviors that can strongly affect dispersal. In addition to informing our biological questions, the physical measurements address fundamental questions about circulation and dispersion near topography. Our direct dispersal estimates can be used to evaluate conclusions from past population genetic studies, and will provide testable hypotheses for future studies in phylogeography and biogeography of vent species and communities. Estimates of dispersal also contribute to efforts to manage hydrothermal vent resources, and establish marine reserves, by providing information on connectivity among vent populations. And finally, the results will be useful in testing the generality of new metapopulation models which currently are derived primarily from terrestrial perspectives.

7.Relevance to other NSF programs

The objectives in this proposal are complementary to those of the Ridge2000 program, and efforts to quantify ecological connectivity in marine systems. The Ridge2000 program has designated 9°49' - 9°51' N on the East Pacific Rise as the bull's eye for an Integrated Study Site. Our flow and larval investigations center in this area, and the dye survey will extend to the outermost concentric ring of interest. Our scientific objectives relate directly to one of the key questions identified for the 9ºN EPR site: '*How and to what extent are hydrothermal products (heat and material) and organism larval stages dispersed to the ocean?'* The results of the project will contribute to attainment of the five-year goals, including: '*New information on flow paths of hydrothermal fluids.'* The dispersion and advection measurements will contribute to the identified community data need of '*Water column parameters*' for understanding mixing and transport of vent-derived chemicals, production and organisms. Our project is complementary to studies of colonization and succession currently funded for EPR (Lutz, Shank, Von Damm), and to a study of reproduction proposed by Van Dover and colleagues. In addition, the present project will provide an opportunity for complementary studies of small-scale turbulence using a new microstructure measurement capability under development at Florida State University (see letter of support from K. Speer)

8. Broader Impact

Results of the project will be disseminated broadly to enhance scientific understanding. The approaches and results from the proposed studies will be incorporated into graduate courses taught by Mullineaux and McGillicuddy in the MIT/WHOI Joint Program in Oceanography, and Speer at FSU, and into presentations given to local K-12 classes through the Woods Hole Science and Technology Education Partnership (WHSTEP). This project is associated with research featured in the NSF-funded web site Women Exploring the Oceans (http://wexo.whoi.edu/), designed as an outreach effort to inspire high-school and undergraduate students (particularly females) to investigate careers in ocean sciences. Two graduate students will be directly involved in all aspects of the research as part of PhD thesis projects. Undergraduates will be integrated through the WHOI Summer Student Fellowship program and the NSF REU program. We will coordinate our research with the web-based outreach effort Dive and Discover (www.divediscover.whoi.edu). We also will associate our outreach efforts with the Ridge 2000 Education and Outreach Coordinator.

The long-term benefits of the proposed activity to society will be achieved by contributing to a general understanding of retention, dispersal, and connectivity of marine populations. This topic has direct relevance to management of hydrothermal vent resources in the face of increasing disturbance by scientists, documentary film crews, and tourists. Vents also are subject to renewed interest in drilling for research, extracting polymetallic minerals, and sampling of fauna for natural products discovery and pharmaceutical applications. Our results will inform efforts to establish marine reserves, such as those designated by the Canadian government at Endeavour vent and the Portuguese at Rainbow vent.

9. Results from Prior Support

Mullineaux - *Community development and structure at hydrothermal vents* (OCE 9712233): $200,169 for 15 Dec. 1997 to 30 Nov. 2000. Mullineaux has collaborated with Pete Peterson and Chuck Fisher to conduct in situ experiments on colonization and predation at vents near 9-10°N along the EPR. We showed that faunal interactions (facilitation, competition, predation) play a large role in the structure, zonation and succession of vent communities. This is a new perspective on these communities, which for 20 years were assumed to be structured by their physical and chemical environment. Broader impacts have included research opportunities for 2 graduate students, 4 postdocs and 4 undergraduates. Results have been incorporated into MIT/ WHOI graduate courses and into local K-12 presentations, and museum exhibits. Publications from this grant are listed in References[1].

Ledwell - James R. Ledwell has led a series of tracer studies of mixing that have been funded by the National Science Foundation. Most pertinent is A Tracer Release Experiment in the Brazil Basin, OCE-9415598 ($1,800,000), and OCE-9906685 ($835,000), which found enhanced mixing in the abyssal Brazil Basin on the flanks of the Mid-Atlantic Ridge (Polzin et al., 1997; Ledwell et al, 2000a,b). The tracer component of that experiment quantified diapycnal and isopycnal diffusivities for a passive tracer at 4000 meters depth, 1000 meters above the bottom of the local fracture zones, about 500 meters above the tops of the abyssal hills, and hundreds of km west of the axis of the ridge, over a period of several years. The present experiment, on the axis of a ridge, will complement the Brazil experiment. Publications from this project are listed in References[2].

McGillicuddy - *U.S. GLOBEC: Maintenance of Pseudocalanus spp. Populations on Georges Bank* (OCE-9806591,11/1/1998–10/31/2003, $120,394). Dr. McGillicuddy's major contribution in this area has been the development and application of inverse methods to quantify the influences of coastal circulation and population dynamics processes on the distribution and abundance of keystone zooplankton species. Two general conclusions have emerged from these studies: first, species-specific population dynamics are necessary to resolve the underlying physical-biological interactions; second, advection plays a critical role in determining the seasonal biogeography of these organisms, with fundamental implications with respect to long-term regional maintenance of these populations. Publications from this project as well as Dr. McGillicuddy's NSF-sponsored work in the JGOFS and ECOHAB programs are listed in the References section[3].

Thurnherr - Deep Basin Experiment Synthesis OCE-0220407 ($105,964; 09/01/02-08/31/03). Andreas Thurnherr has collaborated with Kevin Speer on the continued analysis of hydrographic, tracer, and float data in the Brazil Basin. Two refereed papers (listed in References[4]) have so far resulted from this study (a third one is in preparation). The first shows the effects of topography on the ridge-flank hydrography; one important consequence is that along-ridge flows that feature prominently in forward as well as in inverse models are actually blocked within the deep canyons on the ridge flank. The other paper assesses the representativeness of repeat hydrographic sections and shows that the large-scale temporally varying zonal flow field in the South Atlantic is of the same order as the mean flows, which has important consequences for inverse models. Broader impacts include a new online hydrographic and tracer climatology of the South Atlantic (http://www.oean.fsu.edu/SAC).

Lavelle – no prior NSF support

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