Vol. 293: 1–16, 2005

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 2

Vertical, lateral and temporal structure in larval distributions at hydrothermal vents

L. S. Mullineaux[1,*], S. W. Mills[1], A. K. Sweetman[2], A. H. Beaudreau[3], A. Metaxas[4], H. L. Hunt[5]

[1]Woods Hole Oceanographic Institution, MS 34, Woods Hole, Massachusetts 02543, USA
[2]Max-Planck-Institut für marine Mikrobiologie, Celsiusstraße 1, 28359 Bremen, Germany
[3]University of Washington, Box 355020, Seattle, Washington 98195, USA
[4]Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada
[5]University of New Brunswick, PO Box 5050, Saint John, New Brunswick E2L 4L5, Canada

ABSTRACT: We examined larval abundance patterns near deep-sea hydrothermal vents along the East Pacific Rise to investigate how physical transport processes and larval behavior may interact to influence larval dispersal from, and supply to, vent populations. We characterized vertical and lateral distributions and temporal variation of larvae of vent species using high-volume pumps that recovered larvae in good condition (some still alive) and in high numbers (up to 450 individuals sample^{-1}). Moorings supported pumps at heights of 1, 20, and 175 m above the seafloor, and were positioned directly above and at 10s to 100s of meters away from vent communities. Sampling was conducted on 4 cruises between November 1998 and May 2000. Larvae of 22 benthic species, including gastropods, a bivalve, polychaetes, and a crab, were identified unequivocally as vent species, and 15 additional species, or species-groups, comprised larvae of probable vent origin. For most taxa, abundances decreased significantly with increasing height above bottom. When vent sites within the confines of the axial valley were considered, larval abundances were significantly higher on-vent than off, suggesting that larvae may be retained within the valley. Abundances of all vent species varied significantly among sample dates; the variation was not synchronized among taxa, except for consistently low abundances during November 1998. Lateral distributions did not vary among major larval groups (gastropods, polychaetes and bivalves), although polychaetes showed anomalously high abundances off-vent at 1 m above bottom. Lateral patterns also did not vary among species of gastropods, indicating that hydrodynamic processes may be transporting diverse species in similar ways. However, the species-level differences in temporal patterns indicate that there is substantial discontinuity in the abundance of individual species at vent communities, possibly due to timing of spawning and/or behavioral interactions with flow.

KEY WORDS: Hydrothermal vent · East Pacific Rise · Larva · Dispersal · Connectivity · *Bathymodiolus thermophilus* · *Lepetodrilus*

INTRODUCTION

Hydrothermal vent communities are unique among deep-sea faunas, not only because of their chemosynthetically based food web, but also in the dynamics and distribution of their habitat. Venting of the heated, chemical-rich fluids is transient; vents may remain active for only decades or years in regions where new crust is being formed quickly (e.g. East Pacific Rise, Haymon et al. 1993), or for 100s of years in areas where crust formation is slow (Mid-Atlantic Ridge, Lalou et al. 1993). Initiation and cessation of venting may occur abruptly during volcanic eruptions or tectonic events (reviewed in Fornari & Embley 1995). Supply of vent fluids to the seafloor is spatially disjunct along oceanic ridges, resulting in patchy distribution of the associ-

---

*Email: lmullineaux@whoi.edu

ated communities. Individual vent communities typically extend less than 100 m (e.g. Hessler et al. 1985, Van Dover 1995), and can be separated from neighboring vent sites by 100s of meters to 100s of kilometers. Vent species must have life histories that accommodate the patchy and transient nature of their environment.

The majority of invertebrate species inhabiting vents are endemic to vents (Tunnicliffe et al. 1998), so a capability for dispersal is essential for maintenance of regional populations, given the transience of individual vent sites. Many vent species are sessile as adults or have limited swimming ranges, and appear to disperse via planktonic larval stages. Lutz et al. (1980) predicted that most vent species should have planktotrophic larvae in order to maintain energy reserves necessary for long-distance dispersal, but an examination of egg sizes and larval shell types did not support this prediction (Turner et al. 1985). Subsequent studies showed that reproduction and larval type of vent species were highly constrained by phylogenetic affinity (reviewed in Tyler & Young 1999), i.e. species appear to retain the life-history attributes of their shallow-water relatives, even if they do not appear optimal for the vent environment. For instance, alvinellid polychaete larvae are presumed to be planktonic for 3 to 5 d, during which time they would be expected to disperse distances of 10s of kilometers (Chevaldonné et al. 1997). However, some larvae have prolonged life spans in cold water (e.g. Shilling & Manahan 1994), and it has been suggested that larvae of vent species may be capable of dispersing long distances in cold deep waters even without feeding in the plankton (Lutz et al. 1984). Marsh et al. (2001) maintained unfed larvae of the vestimentiferan tubeworm *Riftia pachyptila* in laboratory culture, and calculated a larval stage duration of roughly 40 d based on metabolic rates and energy stores. During this period, larvae may disperse 10s to 100s of kilometers in near-bottom flows along mid-ocean ridges (Marsh et al. 2001, Mullineaux et al. 2002).

Interactions between hydrodynamic transport processes and larval behaviors may enhance dispersal or act to retain larvae near source populations (e.g. Cowen et al. 2000). Despite limited swimming abilities during most or all of their planktonic life, some larvae exhibit ontogenetic behavior that alters their position above the seafloor (Sulkin 1984 [review], Young & Chia 1987, Forward 1988, Epifanio & Garvine 2001). In vent environments, topographically-enhanced mixing (Ledwell et al. 2000) or entrainment in the buoyant hydrothermal vent plumes (Kim et al. 1994) also may transport larvae 100s of meters above a ridge (Mullineaux et al. 1995). The vertical position of a larva will probably influence its dispersal trajectory due to the vertical shear in currents within 200 m of oceanic ridges. Current velocities 200 m above the ridge may be an order of magnitude faster than, or in the opposite direction of, those directly above the bottom (Cannon & Pashinski 1997, Thurnherr et al. 2002, Thomson et al. 2003). Thus, species-specific differences in larval vertical positioning will probably result in differences in species' dispersal patterns.

Vertical swimming or sinking behaviors also may influence the probability of larvae being retained near their natal vent. Tidal flows in the deep sea are enhanced near topography, and semidiurnal tidal excursions of 1 km or more have been estimated from current-meter records on ridges (Kim & Mullineaux 1998, Lavelle & Cannon 2001). This mixing should move vent-derived particles away from their source habitats in a matter of days, and would seem to generate a dynamic system in which return to a source site would be exceedingly rare. However, vent-specific hydrodynamic and behavioral processes may counteract this transport. The buoyant hydrothermal plume theoretically can drive local secondary circulation (Speer 1989, Helfrich & Speer 1995) and retain particles and larvae near their source populations. Such a circulation cell is expected to extend roughly a few kilometers from a vent, with focused upward velocities at the center, diffuse downward velocities at the perimeter, and inward velocities along the seafloor (Fig. 1). The residence times of neutrally-buoyant, non-swimming larvae would not be affected by this circulation, but any larvae that sink, swim downward, or have

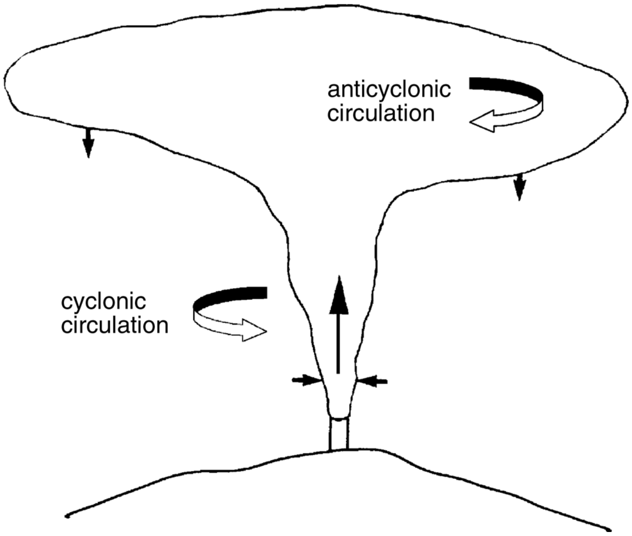

Fig. 1. Circulation in buoyant hydrothermal vent plume, showing upward flow at vent orifice, outward at level of neutrally buoyant plume, downward at periphery of neutral plume, and inward along seafloor. Rotation is anticyclonic in neutrally buoyant plume and cyclonic below. Downward swimming or sinking larvae would be expected to accumulate at seafloor near vent orifice. (Redrawn from Helfrich & Speer 1995)

a positive tactic response to vent fluids would tend to accumulate near the vent. Such a retention mechanism would inhibit dispersal, and potentially enhance settlement back into the local population (Mullineaux & France 1995). The buoyant plume also can interact with local topography to influence circulation. Thomson et al. (2003) observed channeled flow within the axial valley of Juan de Fuca Ridge and suggested that these buoyancy-driven flows should enhance larval supply to vent communities. Finally, a demersal larva with a consistent affinity for benthic surfaces might be able to maintain position near its natal vent simply by staying in the relatively slow flows of the benthic boundary layer.

Large temporal variations in abundance have long been noted for many species (e.g. Thorson 1950) both within years and between them. Much of this observed intra-annual variability is due to seasonal periodicity in spawning, but differential larval mortality and aggregation processes also introduce discontinuity in supply to benthic habitats (e.g. Pineda 1999, Shanks et al. 2000, Garland et al. 2002). For instance, fronts and eddies have been observed to aggregate larvae and supply them in pulses to benthic environments (Limouzy-Paris et al. 1997), or alternatively prevent their shoreward transport (Shanks et al. 2003). Similar aggregative mechanisms may be occurring in deep-water mesoscale eddies and in the buoyant hydrothermal plume. Such temporal variation in larval supply, and subsequent variation in recruitment success, has substantial impacts on population dynamics and community structure (e.g. Gaines et al. 1985, Menge 2000).

Very little direct information is available on larval dispersal distances, retention and periodicity of supply at vents, although larvae of many prominent vent species have been observed in the vicinity of vent habitats (Berg & Van Dover 1987, Kim & Mullineaux 1998, Comtet et al. 2000, Metaxas 2004). However, inferences can be made from studies of colonization and population genetics. Many vent species colonize new habitat within weeks to months (Tunnicliffe et al. 1997, Shank et al. 1998), indicating that they are efficient dispersers. However, these studies were conducted at sites quite close (<10 km) to active neighboring vent communities, and provide little constraint on maximal dispersal distances. Similarly, in colonized vent habitats, subsequent recruitment of vestimentiferan tubeworm species occurs consistently at time intervals of 5 to 8 mo (Mullineaux et al. 2000), indicating that interruptions in larval supply do not persist over those durations. Genetic structure of vent populations shows evidence of extensive gene flow for most species of tubeworms and mollusks on the scale of a typical ridge segment (100 km) (Vrijenhoek 1997, Won et al. 2003). The lack of evidence for the 'isolation by distance' pattern on scales of 100 km has led researchers to speculate that larvae are supplied to vent communities as a well-mixed pool of potential colonists (Vrijenhoek 1997, Van Dover 2000). This expectation of a larval pool differs substantially from the situation in coastal environments, where patchiness and temporal variation in larval abundances are well documented (e.g. Garland et al. 2002, Shanks et al. 2003, Wing et al. 2003)

The present study documents spatial distributions and temporal variation in larvae of vent species and uses these patterns to address questions of how physical transport processes and larval behaviors may interact to influence dispersal from and supply to vent communities. We start with a conceptual null model of expected larval distributions, based on simplified assumptions about spawning (continuous), transport (via eddy diffusion that is greater in the vertical than horizontal direction), and behavior (passive, neutrally buoyant). Given this scenario, larval abundances would decrease monotonically away from source communities, vertical gradients in abundance would be steeper than horizontal gradients, and abundance patterns would remain constant over time. The patterns result from larvae emigrating away from the source, which are expected to be numerically dominant over other larvae immigrating from remote populations. Immigrating larvae would not necessarily conform to these patterns. We used this conceptual framework to design the spacing and timing of sampling and as a starting point for interpreting larval patterns. Deviations of observed patterns from these expectations may provide insight into spawning schedules, larval behavior, or non-diffusive physical transport processes (e.g. retention in eddies or episodic supply due to mesoscale flows). Although determination of larval competency is outside the scope of this study, determination of larval developmental stage enables speculations as to whether larval distribution patterns reflect supply to benthic communities. A species-level approach is critical for these analyses, in order to ensure that only vent species are included, and to avoid obscuring patterns by pooling species that exhibit different behaviors and dispersal dynamics.

MATERIALS AND METHODS

We used high-volume pump systems designed specifically by McLane Research Laboratories, East Falmouth, Massachusetts, USA for collecting larvae in the deep sea. The standard McLane WTS 6-1-142LV system was fitted with a high-volume (50 l min^{-1}) pump head and an expanded, insulated compartment upstream from the filter (63 µm mesh-size) to reduce damage to specimens. Sampling intervals lasted up to 24 h, with a pump rate of 30 l min^{-1} providing the maximum volumes filtered (battery power was the ultimate limit to sample size). Resulting sample volumes were usually >40 000 l water filtered, and temperatures in the filter compartment typically were <5°C, despite recovery from tropical (~26°C) surface waters. This sampling strategy recovered larvae in good condition (some still alive), and in sufficiently high numbers (up to 450 individuals) to examine details of their distribution and abundance. Sample volumes were lower (17 000 to 36 000 l) for 9 samples collected on the 1998 cruise when we were still resolving the optimal intake flow rate, and on 5 subsequent occasions when an individual pump underperformed (12 000 to 36 000 l) due to friction in the rotor or a blockage at the intake.

Moorings supporting 3 pumps each at heights of 1, 20 and 175 m above bottom (mab) were dropped from the ship 'Atlantis' to the seafloor near vent sites in the region of 9° 50′ N along the East Pacific Rise at depths of approximately 2500 m. The heights were chosen to sample environments close to the benthic community (1 mab), within the bottom boundary layer (20 mab), and at the level where the hydrothermal plume was expected to be neutrally buoyant (175 mab). Pairs of moorings were deployed synoptically, with 1 mooring positioned directly above a vent community by the submersible 'Alvin'. Due to limited 'Alvin' time, the other mooring was left where it landed as long as it was outside the community and away from detectable hydrothermal venting. This procedure resulted in off-vent moorings located anywhere from 5 to 300 m away from the vent community in a direction (E or W) perpendicular to the axis of the ridge. The variation in off-axis distances was regrettable, as it constrained our lateral analyses to a comparison of larval abundances on- and off-vent rather than along a distance gradient. Sampling was conducted on 4 different cruises, during December 1998, April 1999, December 1999 and May 2000 as part of the Larvae At Ridge Vents (LARVE) project. During each cruise, we attempted to collect paired samples (on- and off-vents) at 3 or more vent sites. At the end of each 24 h sampling interval, moorings were released acoustically and were recovered at the surface within 40 min.

The sampling setup was designed to test the effects of height above bottom, proximity to vent and sampling date on larval abundance. Multiple vent sites were sampled, but not all sites on all cruises and only rarely with replication within a cruise. We were curious about site-specific patterns, but did not have the resources to test them as part of the formal experimental design. Therefore, site location was included in the main analyses as a random factor and sites were examined individually in subsequent tests. The benthic fauna of each of the sites appeared to be in mid-to-late stages of succession as described in Shank et al. (1998). Some of the sites were within 50 m of each other (Fig. 2), so that a mooring positioned 40 m away from one vent might be <100 m away from a neighboring vent. One of the sites, Biovent, differed from the others in topographic setting — the smoker and vent community at this site are located on the ridge crest rather than in the axial valley. After completing the study, we realized that it was possible that the walls of the axial valley might 'channel' flows and impede off-axis larval emigration, as proposed for vent communities along the Juan de Fuca Ridge (Thomson et al. 2003). Therefore, Biovent was excluded from subsequent analyses to address possible effects of the valley walls.

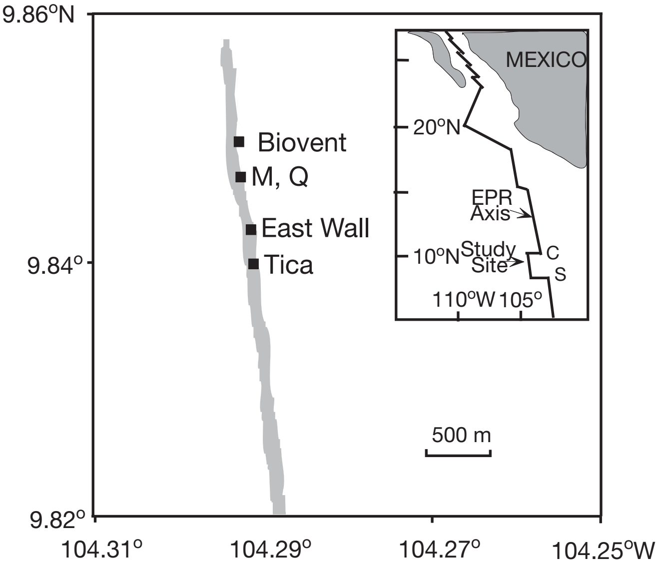

Fig. 2. East Pacific Rise (EPR) axis (shaded corridor) near 9° 50′ N, showing vent sites sampled with plankton pumps (on-vent sites only shown). Sites located in axial valley of ridge between Clipperton (C) and Sequieros (S) fracture zones, except for Biovent which is located outside the valley. M and Q vents are located within 10 m of each other

Our optimal sampling objectives were attained only in the spring 2000 cruise, when a set of samples at all 3 heights was collected on- and off-vent at 3 different sites (Biovent, East Wall and Tica; Table 1). In fall 1998 and spring 1999, only 2 pumps were available, so no samples were collected at the 175 mab level. In fall 1999, pump malfunctions resulted in missing samples in the 20 mab, off-vent category. Technical issues with the pump systems had been resolved by the time of the final cruise.

Immediately after recovery of the pump moorings on the deck of the ship, the filter chambers were immersed in cold filtered seawater and taken to a cold room (4°C) for initial processing. Larvae were sorted and observed live under a dissecting microscope at 12× magnification to assist in identification and to make morphological and behavioral observations prior to preservation. Predatory zooplankton were observed only rarely in samples and were not expected to have reduced larval abundances. After initial observation (<1 h), samples and specimens were rinsed in freshwater and preserved in 95% ethanol. After each cruise, the preserved samples were re-examined at 25× under a dissecting scope in the laboratory, and all larvae were removed and identified to the lowest taxonomic category possible.

Species-level identification was possible for many of the gastropod larvae because of the distinctive size, shape and sculpturing of their shells (Protoconchs I or II). We used a modification of the light-microscope protocol described by Mullineaux et al. (1998) to make an image of the larval shells. To mount the shells for observation, we positioned them on a depression slide in 1 of 2 ways: by lining the slide with either Parafilm® (American National Can), or by using superglue, and puncturing small wells (150 µm diam.) to hold each individual shell. The shell morphology was examined under a Zeiss Stemi SV 6 transmitted light microscope at 50× or 100× magnification. Specimens were photographed under an Olympus SZX9 Zoom stereomicroscope fitted with a digital camera. Protoconch morphologies were compared to those in taxonomic publications (McLean 1981, 1988, 1989a,b, 1990, Warén & Bouchet 1989, 1993, 2001) to identify specimens. This light-microscope-based protocol was more efficient than our previous techniques based on scanning electron microspopy (Mullineaux et al. 1996), and we were able to identify as many as 20 specimens h^{-1}.

Only taxonomic groups or species identified as being of unequivocal or probable vent origin were used in statistical analyses. Analyses of variance were conducted first on 3 pooled vent species-groups, the gastropods, polychaetes and bivalves (the bivalve group included only the mussel *Bathymodiolus thermophilus* because no other vent bivalve larvae could be identified). Pooling individual species into taxonomic groups decreased variability among replicate samples, increased the power of statistical tests and revealed general patterns shared among related species. Analysis of these groups was performed with 3-way multivariate analysis of variance (MANOVA) (Systat Version 10), testing effects of height, date and proximity. Because of missing samples in fall 1998 and spring 1999 at 175 mab, the 3-way MANOVAs were conducted in 2 different ways. The initial analysis included all 3 levels of height (1, 20, 175 mab), but was limited to the 2 later cruises (fall 1999 and spring 2000). To analyze the complete temporal sequence, a separate analysis was performed with all 4 dates (including fall 1998 and spring 1999), but limited to 2 levels of height (1 and 20 mab). Both analyses included 2 levels of proximity, on- and off-vent. Although this approach is not as elegant as a single analysis, it was the only way to avoid excluding samples and evaluate all possible interaction effects.

MANOVAs were conducted before univariate ANOVAs of the 3 taxonomic groups (gastropods, polychaetes, bivalves) because detection of a significant effect eliminated the need for multiple-comparison adjustments (e.g. Bonferroni) in the ANOVAs (Zar 1999). We selected this approach to maintain power in the statistical tests despite the low number of repli-

Table 1. Sites of larval pump samples collected during each cruise directly above (On-vent) and outside (Off-vent) vent communities at 3 heights above bottom (1, 20 and 175 m above bottom, mab). (2): duplicate samples; pa: limited availability of pumps, pf: pump failure, both of which resulted in gaps in experimental design. Locations of sites in Fig. 2

Date		On-vent			Off-vent	
	1 mab	20 mab	175 mab	1 mab	20 mab	175 mab
1998						
Fall (Nov)	Biovent	Biovent	pa			
	Q	Q	pa	Q	Q	pa
	East Wall	East Wall	pa	M	M	pa
1999						
Spring (Apr)	Biovent	Biovent	pa	Biovent	Biovent	pa
	East Wall	East Wall	pa	East Wall (2)	East Wall	pa
Fall (Dec)	Biovent	Biovent	Biovent	Biovent (2)	pf	Biovent (2)
	East Wall	East Wall	East Wall	East Wall	pf	East Wall
	Q	Q	pf	Q	Q	Q
	Tica	pf	Tica	Tica	pf	Tica
2000						
Spring (May)	Biovent	Biovent	Biovent (2)	Biovent	Biovent	Biovent
	East Wall	East Wall	East Wall	East Wall	East Wall	East Wall
	Tica	Tica	Tica	Tica	Tica	Tica

cates. Similarly, for the gastropod group, which comprised 9 abundant species or genera, significant effects in a MANOVA were used to avoid multiple-comparison adjustments in ANOVAs of individual species. As in the MANOVAs, missing samples in fall 1998 and spring 1999, required the ANOVAs be conducted in 2 different ways: one with all 3 levels of height but only the 2 later dates, and the other with only 2 levels of height but all 4 dates.

An additional focused analysis was conducted to determine whether our results were consistent with the hypothesis that valley walls impede lateral dispersion. We re-examined lateral patterns in total larval abundance using vent sites only within the valley. Biovent was excluded from the analysis because it is outside the axial valley; heights of 20 and 175 mab also were excluded because they are above the level of the 15 m high walls. The analysis was restricted to the spring 2000 cruise, when sampling was most extensive and balanced.

Prior to statistical analysis, the data distributions were evaluated with Cochran's tests ($\alpha = 0.05$) for homogeneity of variances. Logarithmic transformations, $\ln(x + 1)$, were performed when necessary to achieve homogeneity of variance. Treatment means for date and height effects were compared using Tukey's post-hoc comparisons.

RESULTS

Larvae of benthic invertebrates collected in 59 pump samples comprised representatives of all major groups inhabiting hydrothermal vents, including gastropods, bivalves, polychaetes and crustaceans (Table 2). We identified 22 gastropod taxa, 1 bivalve species (*Bathymodiolus thermophilus*), 5 polychaete taxa and 1 crustacean species (*Bythograea thermydron*) to a sufficient taxonomic level to determine that they were of probable vent origin. Other groups that were of mixed vent and non-vent origin or of unknown origin are enumerated in Table 2, but not included in subsequent quantitative analyses. In addition, we included in our categories, but not in our analyses, some groups that are larvae of planktonic species or are benthopelagic postlarvae or adults (e.g. amphipods, tanaids, leptostracans). Other morphological groups that were observed in the samples but not sorted or identified included copepod adults (which were numerous, but not a main focus of this study), copepod nauplii, euphausids, ostracods, chaetognaths, tomopterid polychaetes, kinorhynchs, gelatinous zooplankton, planktonic foraminiferans, pteropod shells, planktonic gastropod shells, and various eggs.

Species identification

The vent gastropod larvae were identified conservatively and were assigned to species only if the protoconch morphology was an unequivocal match with the larval shell on an identified adult known to occur on the East Pacific Rise (EPR). For instance, we suspect that the *Lepetodrilus* spp. group comprises predominantly *L. elevatus*, but it may also include specimens of *L. ovalis*, *L. pustulosus* or *L. cristatus*. The protoconch morphology of our taxon '*Laeviphitus* sp.' is very similar to *Laeviphitus desbruyeresi* (as pictured in Warén & Bouchet 2001), but that species has not been recorded as an adult at 9°N EPR. Our '*Peltospira* spp.' are probably either *P. operculata* or *P. delicata* (McLean 1989b) or both, but we cannot yet distinguish between the two. 'Unknown peltospirids' were identified to family by their distinctive linear protoconch sculpture, size and shape, and may include a variety of species such as *Ctenopelta porifera*, *Echinopelta fistulosa*, *Hiropelta hirta*, *Nodopelta heminoda*, *N. rigneae*, and *N. subnoda*. We determined that 2 gastropod larval specimens (1 *Bathymargarites symplector* and 1 *Phymorhynchus ? major*) had developed into a planktotrophic stage, because they had formed a Protoconch II shell. Larval developmental stage could not be determined for any of the other species.

Species-level identification of selected bivalve and polychaete larval specimens was possible because they were sufficiently developed to exhibit diagnostic morphological characters. The mussel *Bathymodiolus thermophilus* could be identified to species because of its distinctive Prodissoconch II larval shell. These larvae were considered to be in a late stage of development, and competent to settle because their larval shell had reached the size (400 µm) of a newly-settled recruit. A second group of small (D-stage) bivalve larvae was not identifiable to species. Identifiable polychaetes included larvae of the vent-endemic species *Archinome rosacea*. *Amphisamytha galapagensis* and *Ophryotrocha akessoni* were found only as juveniles or adults. Other polychaete larvae could be identified to genus or family (e.g. *Nereis* sp., *Glycera* sp., polynoids) and were considered of probable vent origin because of the presence of these groups at the 9°N vents. The 'nectochaete' group of small, early-stage polychaete individuals was considered of probable vent origin because a subset of individuals was matched to known vent species using molecular techniques (R. Jennings unpubl. data). It is possible that some non-vent nectochaete larvae were mistakenly included in the probable-vent category, but we do not think they affected the overall patterns.

Among the less abundant taxa, selected crustacean and foraminiferan specimens could be identified as vent-endemic species. The brachyuran megalopae were identified as *Bythograea thermydron* (as in Epifanio et al. 1999), and the zoeae were morphologically similar to zoeae harvested from adults of that species (A. Dittel pers. comm.). Specimens of the vent-endemic foraminiferan *Abyssotherma pacifica* appear to be a planktonic dispersive phase, as they are small and have thin tests. The foraminiferal taxon designated '*Tretomphalus*-like' has an inflated ultimate chamber and also appears to be a dispersive phase, but not necessarily of vent origin.

Spatial distributions

The vent gastropod, polychaete and bivalve groups all were more abundant at 1 mab than higher in the water column (Fig. 3). This height effect was significant ($p < 0.05$) in the MANOVA, and for the gastropod and polychaete groups in the ANOVAs, when fall 1999 and spring 2000 were considered (Table 3). Bivalves were rare on all dates except spring 1999; when this date was included in the analysis (Table 3), a signifi-

Table 2. Total abundance (N) of larvae of benthic vent species and other plankton, collected in 59 plankton pump samples from 1998 to 2000 near 9° 50′ N on the East Pacific Rise. V: species endemic to vents; PV: probable vent species (identified to genus or higher-level taxon that includes vent species); mixed: vent and non-vent species; juvenile or adult: post-larval forms; plankton: planktonic species; ?: identification unsure

Vent larvae of benthic species	N	Habitat	Other larvae, juveniles + adults	N	Habitat/category
Mollusca, Gastropoda			**Mollusca, Gastropoda**		
Bathymargarites symplector	1	V	Unknown 7	8	Undetermined
Clypeosectus delectus	20	V	Other benthic unknowns	60	Mixed
Cyathermia naticoides	559	V	Unknown benthic sp. A	159	Undetermined
Eulepetopsis vitrea	15	V	Unknown 8	5	Plankton
Gorgoleptis emarginatus	3	V	Unknown 9660	17	Plankton
Gorgoleptis spiralis	19	V	**Mollusca, Bivalvia and Aplacophora**		
Laeviphitus sp.	44	PV	?*Teredo* sp.	1	Non-vent
Lepetodrilus spp.	1266	V	Other bivalve, including D-stage	21	Mixed
Lirapex granularis	7	V	Aplacophoran	1	Undetermined juvenile
?*Lirapex* sp.	1	V	**Polychaeta**		
Melanodrymia aurantiaca	18	V	?Spionid	3	Mixed
?*Melanodrymia galeronae*	1	V	?Chaetosphaera	197	Mixed
Neomphalus fretterae	52	V	Polychaete (miscellaneous)	205	Mixed
Pachydermia laevis	9	V	Syllid epitoke	1	Undetermined
Peltospira spp.[a]	189	V	*Amphisamytha galapagensis*	4	V, juvenile
Phymorhynchus ?major	1	V	*Ophryotrocha akessoni*	6	V, juvenile
Rhynchopelta concentrica	42	V	Hesionid	3	Mixed, juvenile
Unknown peltospirids	29	V	Unknown polychaetes	18	Mixed, ?plankton
Unknown slit limpet	75	PV	**Crustacea**		
Unknown neomphalid 5	24	PV	Cyprid (barnacle)	14	Undetermined
Unknown neomphalid W	15	PV	Copepods	>2000	Mixed juveniles and adults
Unknown neomphalid B	3	PV	Amphipods	1693	PV adult
Mollusca, Bivalvia			Cumacean	3	PV adult
Bathymodiolus thermophilus	77	V	Isopods	16	Undetermined adult
Polychaeta			Tanaid	1	PV adult
?*Nereis* sp.	9	PV	Caridean shrimp	1	PV adult
Polynoid	13	PV	*Dahlella calderiensis* (leptostracan)	51	V adult
Archinome rosacea	14	V	**Miscellaneous**		
Nectochaete larvae	137	PV	?Trochophores	4	Undetermined
Glycera sp.	7	PV	Cyphonautes	43	Undetermined
Crustacea			Unidentified larvae	9	Undetermined
Bythograea thermydron megalopa	1	V	Eggs (90–110 µm)	44	Undetermined
Bythograea thermydron zoea	7	V	Mite	1	Undetermined adult
Protista			?Hydroid stalk	3	Undetermined adult
Abyssotherma pacifica[b]	19	V	?Planula	1	Undetermined adult
			Flatworm	1	Undetermined adult
			Unsegmented worm	1	Undetermined adult
			Forams (?benthic)	299	Undetermined adult
			Forams (*Tretomphalus*-like)	29	Undetermined adult
			Octopod	1	Undetermined juvenile
			Fish	1	Undetermined juvenile

[a] *P. operculata* and/or *P. delicata*

[b] Apparent dispersive form

cantly greater abundance at 1 mab was observed for this group as well.

When analyzed as individuals, the 9 gastropod species all showed significantly higher abundances at 1 mab than at 20 or 175 mab (Fig. 4; Table 4), and this pattern was generally consistent over the 4 sample dates (Table 4). Although interaction effects of height × date were found for *Cyathermia naticoides*, *Lepetodrilus* sp. and *Neomphalus fretterae*, in each case the height pattern was anomalous only in the fall 1998 sample, when abundances of these 3 species were 1 order of magnitude lower than at other times.

When all sites were considered, the gastropod, polychaete and bivalve groups showed no significant pat-

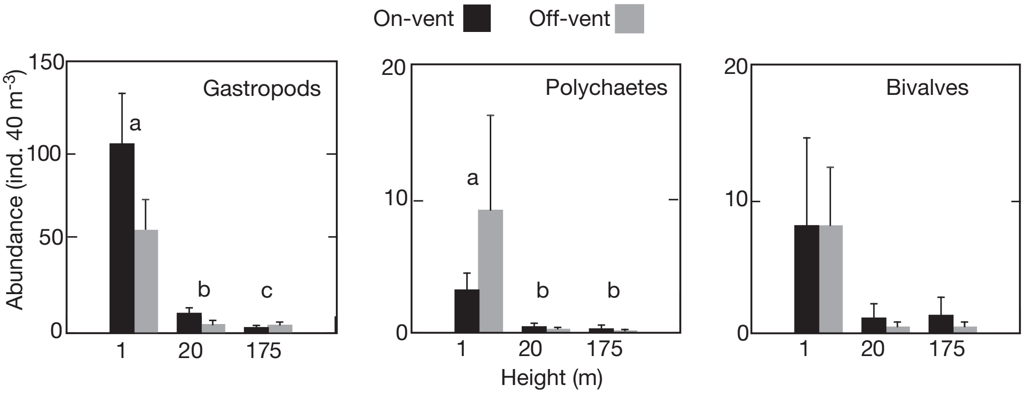

Fig. 3. Larval distributions by height and proximity (i.e. on- or off-vent), over all sites. Abundance of vent larvae from gastropod, polychaete and bivalve groups in plankton pump samples collected on- and off-vent at heights of 1, 20 and 175 m above bottom (mab). Data are means (+SE) for all 4 sampling dates, except at 175 mab, for which data were available only for fall 1999 and spring 2000. N = 3 for most combinations of height, date and proximity (exceptions shown in Table 1). Letters above bars: significant differences among heights detected by 3-way ANOVA of height, proximity and date (fall 1999 and spring 2000 data only; Table 3) and post-hoc Tukey tests ($p < 0.05$). Effects of proximity were not significant

Table 3. MANOVAs comparing vent larval abundance and univariate ANOVAs comparing vent gastropod, polychaete and bivalve larval abundances among all heights (1, 20, 175 mab) and among all dates (1998F, 1999S, 1999F, 2000S). 'All heights' comparison included only later dates (1999F, 2000S) and both proximities (prox: on-vent, off-vent); 'all dates' comparison included only the lower heights (1, 20 mab), and both proximities. N = 3 sites in most cases; exceptions in Table 1. Logarithmic transformations $\ln(x+1)$ were performed on data when necessary to obtain homogeneity of variances. Post-hoc Tukey tests are shown in Fig. 3 for significant height effects in 'all-heights' comparison, and in Fig. 6 for significant date effects in 'all-dates' comparison. Boldface indicates significant p-values (<0.05, except p <0.017 for ANOVAs corrected for multiple comparisons)

Source	df	MANOVA			ANOVA, Gastropods			ANOVA, Polychaetes			ANOVA, Bivalves		
		Wilks λ	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
All heights													
Height (H)	2	0.46	11.61	**<0.01**	47.11	29.21	**<0.01**	6.58	7.22	**0.01**	0.01	0.06	0.81
Date (D)	1	0.73	5.08	**0.01**	1.20	0.74	0.40	2.76	3.03	0.09	0.67	4.22	**0.05**
Proximity (P)	1	0.84	1.97	0.14	3.93	2.44	0.13	0.03	0.03	0.86	0.13	0.84	0.37
H × D	2	0.98	0.22	0.88	0.01	0.01	0.93	0.40	0.44	0.51	0.01	0.06	0.81
H × P	2	0.83	2.10	0.12	3.53	2.19	0.15	0.07	0.07	0.79	0.19	1.21	0.28
P × D	1	0.97	0.28	0.84	0.09	0.05	0.82	0.24	0.27	0.61	0.13	0.84	0.37
H × D × P	2	0.92	0.83	0.49	0.38	0.24	0.63	0.20	0.22	0.64	0.19	1.21	0.28
Error	32				51.609			29.13			5.11		
Total SS					107.29			17.51			1.76		
All dates													
Height	1	0.38	14.00	**<0.01**	46.62	42.84	**<0.01**	6.42	7.74	**0.01**	2.93	8.59	**0.01**
Date	3	0.14	8.84	**<0.01**	11.86	10.90	**<0.01**	1.88	2.27	0.10	4.49	13.19	**<0.01**
Proximity	1	0.94	0.55	0.65	1.10	1.01	0.32	0.04	0.05	0.83	0.00	0.00	0.96
H × D	3	0.57	1.84	0.08	1.93	1.77	0.18	0.51	0.62	0.61	1.12	3.28	0.04
H × P	1	1.00	0.05	0.99	0.09	0.08	0.78	0.07	0.08	0.78	0.03	0.10	0.76
P × D	3	0.76	0.86	0.57	1.00	0.92	0.45	0.14	0.17	0.92	0.12	0.34	0.80
H × D × P	3	0.78	0.75	0.67	0.74	0.68	0.57	0.22	0.27	0.85	0.11	0.31	0.82
Error	28				30.47			23.23			9.54		
Total SS					94.40			14.79			20.45		

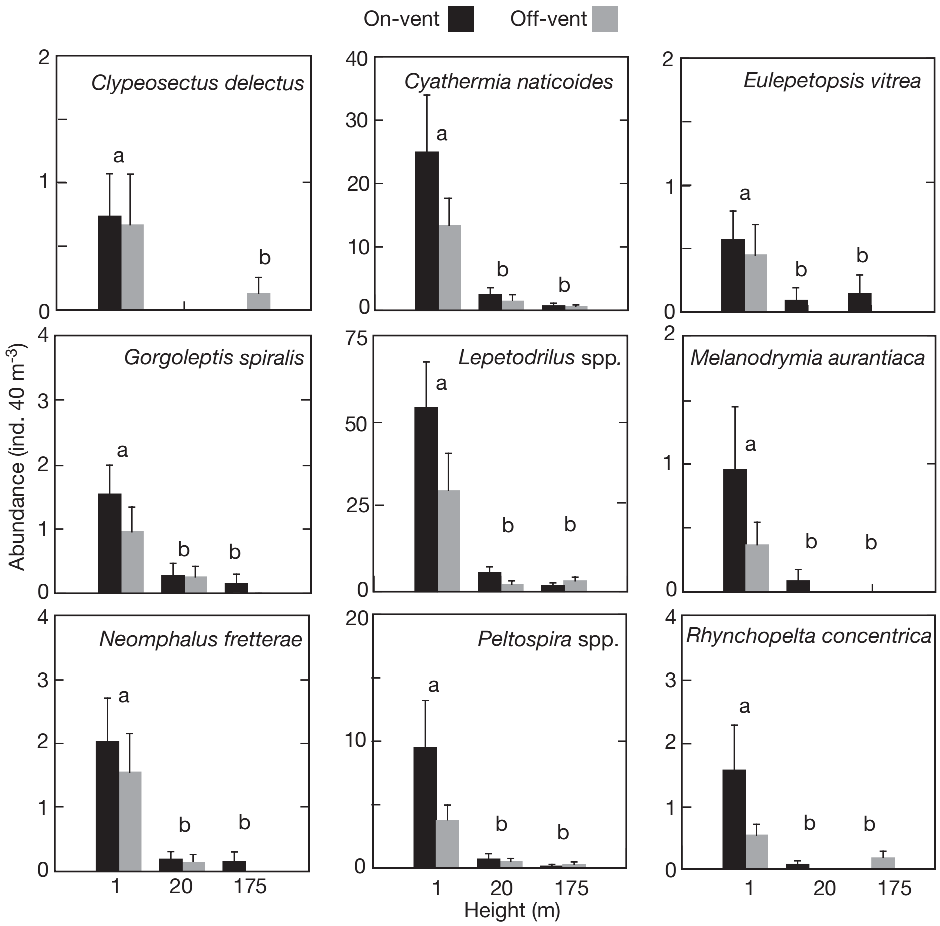

Fig. 4. Gastropod larval distributions by height and proximity over all sites. Abundance of larvae of vent gastropod species in plankton pump samples collected on- and off-vent at heights of 1, 20 and 175 mab. Further details as in Fig. 3 legend. Letters above bars: significant differences among heights as detected by 3-way ANOVA of height, proximity and date (fall 1999 and spring 2000 data only, Table 4) and post-hoc Tukey tests ($p < 0.05$). Effects of proximity were not significant

terns in their lateral distributions (Table 3). Gastropods tended to be more abundant on-vent than off-vent, especially at 1 mab (Fig. 3), and polychaetes showed the opposite pattern, but the differences were not significant. Abundances of individual larval gastropod species tended to be greater on-vent than off-vent (Fig. 4), but this proximity effect was not significant in any of the individual ANOVAs when corrected for multiple comparisons (Table 4).

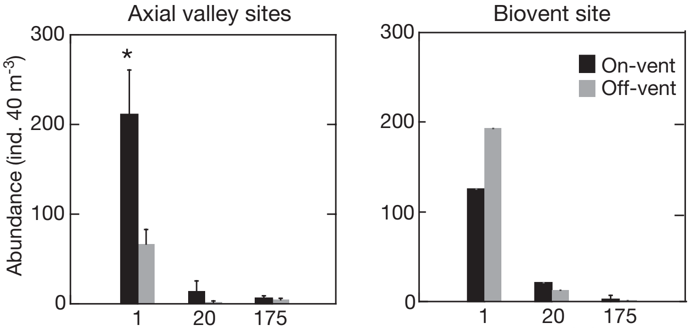

Fig. 5. Larval distribution at axial valley sites (excluding Biovent) and at Biovent alone. Abundance of all vent larvae in plankton pump samples collected on- and off-vent in spring 2000 at axial valley sites (Tica and East Wall) and Biovent, which is located outside valley. Means (+SE) (N = 2) are presented for axial valley sites; *: significantly greater abundances on-vent than off-vent (1-way ANOVA; $p < 0.05$) at 1 mab

When only vent sites within the valley were considered (East Wall and Tica during spring 2000; 1 mab only) total larval abundance was higher on-vent than off-vent (Fig. 5; 1-way ANOVA of proximity, df = 1, $F = 52.9$; $p = 0.018$). The opposite pattern was apparent at Biovent, but lack of replication prevented statistical analysis. This result suggested that we might see a stronger proximity effect in our larval data if Biovent was excluded from the analysis. MANOVA of vent gastropod, polychaete and bivalve group abundances, identical to those in Table 3 but exclusive of Biovent, showed a significant proximity effect when all dates were included (df = 1, Wilks $\lambda = 0.49$, $F = 4.20$, $p = 0.03$). Proximity effects were significant in the ANOVA of bivalves (df = 1, $F = 4.91$, $p = 0.04$), nearly significant for gastropods (df = 1, $F = 4.10$, $p = 0.06$), but not significant for polychaetes (df = 1, $F = 0.02$, $p = 0.88$). Significance of the height and date effects remained largely unchanged (results not shown).

Table 4. MANOVAs and univariate ANOVAs comparing abundance of larvae of 9 gastropod species among all heights (1, 20, 175 mab) and among all dates (1998F, 1999S, 1999F, 2000S). 'All heights' comparison included only later dates (1999F, 2000S) and both proximities (prox: on-vent, off-vent); 'all dates' comparison included only the lower heights (1, 20 mab) and both proximities. N = 3 sites in most cases; exceptions in Table 1. Logarithmic transformations $\ln(x+1)$ were performed on data when necessary to obtain homogeneity of variances. Post-hoc Tukey tests are shown in Fig. 4 for significant height effects in 'all-heights' comparison, and in Fig. 7 for significant data effects in 'all-dates' comparison. Boldface indicates significant p-values (<0.05, except $p < 0.006$ for ANOVAs corrected for multiple comparisons)

Source	df	MANOVA			*Clypeosectus delectus*		*Cyathermia naticoides*		*Eulepetopsis vitrea*		*Gorgoleptis spiralis*		*Lepetodrilus* spp.		*Melanodrymia aurantiaca*		*Neomphalus fretterae*		*Peltospira* spp.		*Rhynchopelta concentrica*	
		Wilks λ	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p
All heights																						
Height (H)	2	0.52	2.49	**0.04**	4.49	**0.04**	20.78	**<0.01**	4.48	**0.04**	13.26	**<0.01**	17.51	**<0.01**	6.96	**0.01**	13.01	**<0.01**	17.58	**<0.01**	5.89	**0.02**
Date (D)	1	0.62	1.60	0.17	0.00	0.95	0.10	0.75	1.32	0.26	1.53	0.22	2.24	0.15	5.68	**0.02**	0.54	0.47	0.16	0.69	0.00	0.97
Proximity (P)	1	0.71	1.07	0.42	0.03	0.87	1.97	0.17	0.33	0.57	1.04	0.32	4.87	0.04	4.00	0.05	0.35	0.56	4.78	0.04	2.32	0.14
H × D	2	0.85	0.48	0.88	0.07	0.80	0.07	0.80	0.16	0.69	0.23	0.64	0.52	0.48	2.29	0.14	0.64	0.43	0.27	0.61	0.00	0.97
H × P	2	0.77	0.78	0.64	0.23	0.64	1.04	0.32	0.00	0.99	0.22	0.64	3.07	0.09	1.70	0.20	0.01	0.92	2.55	0.12	2.26	0.14
P × D	1	0.68	1.28	0.27	0.30	0.59	0.33	0.57	0.96	0.34	0.61	0.44	0.13	0.72	4.00	0.05	0.26	0.62	0.10	0.75	0.71	0.40
H × D × P	2	0.81	0.63	0.76	0.40	0.53	0.02	0.90	0.05	0.83	0.04	0.84	0.53	0.47	1.73	0.20	0.27	0.61	0.11	0.74	0.42	0.52
Error	32				7.42		36.27		3.97		8.41		53.34		3.95		11.35		19.74		8.29	
SS					248.1		1206.8		138.9		299.8		1757.2		165.5		392.1		677.7		285.6	
All dates																						
Height	1	0.07	3.23	**<0.01**	4.85	**0.04**	27.64	**<0.01**	5.40	**0.03**	9.16	**0.01**	29.75	**<0.01**	6.82	**0.01**	16.79	**<0.01**	23.61	**<0.01**	11.41	**<0.01**
Date	3	0.07	3.23	**<0.01**	3.90	**0.02**	10.85	**<0.01**	2.17	0.11	3.79	**0.02**	10.88	**<0.01**	4.07	**0.02**	7.46	**<0.01**	6.76	**<0.01**	3.34	**0.03**
Proximity	1	0.68	1.03	0.45	0.17	0.69	1.15	0.29	0.73	0.40	2.80	0.11	2.40	0.13	1.69	0.20	2.02	0.17	5.63	0.03	2.96	0.10
H × D	3	0.28	1.19	0.29	1.80	0.17	2.96	0.05	0.07	0.56	1.12	0.36	3.10	0.04	1.05	0.39	3.25	0.04	2.43	0.09	1.67	0.20
H × P	1	0.81	0.54	0.83	0.07	0.79	0.00	0.96	0.11	0.74	0.97	0.33	0.02	0.89	0.35	0.55	0.71	0.41	2.06	0.16	0.95	0.34
P × D	3	0.36	0.93	0.57	0.10	0.96	0.67	0.58	0.25	0.86	0.36	0.78	1.88	0.16	3.23	0.04	0.46	0.71	0.60	0.62	0.63	0.60
H × D × P	3	0.63	0.38	1.00	0.05	0.99	0.25	0.86	0.09	0.96	0.13	0.94	1.11	0.36	0.59	0.63	0.60	0.62	0.05	0.99	0.37	0.78
Error	28				5.14		24.00		3.79		6.45		31.35		3.28		6.68		15.52		3.80	
SS					166.5		745.1		120.2		209.7		960.7		127.4		241.8		495.2		139.7	

Temporal variation

Patterns of temporal variation in abundance differed substantially among the vent gastropod, polychaete and bivalve groups (Fig. 6). The gastropod group was consistently abundant on all sampling dates except fall 1998. In contrast, the bivalve *Bathymodiolus thermophilus* was abundant on only 1 occasion (spring 1999), and rare or absent during all other dates. The polychaetes appeared to be more abundant in fall 1999 than on the other dates, but the difference was not significant (Table 3). None of the groups showed a consistent pattern related to season (i.e. between spring and fall collections). Visual inspection of patterns at individual sites suggested that temporal variation generally was coherent among sites (Fig. 6). A notable exception was the very high abundance of polychaetes at East Wall in fall 1999. These high abundances were detected both on- and off-vent and at all heights at this site, but not at any other site.

Temporal patterns in larval abundance varied among gastropod species (Fig. 7), although all species exhibited their lowest abundances in fall 1998. Variation among dates was significant in the MANOVA ($p < 0.05$) and in the ANOVAs for all species except *Eulepetopsis vitrea* (Table 4). In all cases when post-hoc tests detected differences, abundances in fall 1998 were significantly lower than on at least one other date (Fig. 7). Post-hoc tests failed to find differences in *Clypeosectus delectus* and *Rhynchopelta concentrica*, despite significant date effects in the ANOVAs. Although the time of peak mean abundance differed among species (spring 1999 for *Cyathermia naticoides*, *Peltospira* spp. and *R. concentrica*; fall 1999 for *Melanodrymia aurantiaca*, and spring 2000 for *Clypeosectus delectus*, *E. vitrea*, *Gorgoleptis spiralis*, *Lepetodrilus* spp., and *Neomphalus fretterae*), none of these peaks was distinguishable statistically from any dates, other than fall 1998. Visual inspection of site-specific patterns indicated that temporal variation of the

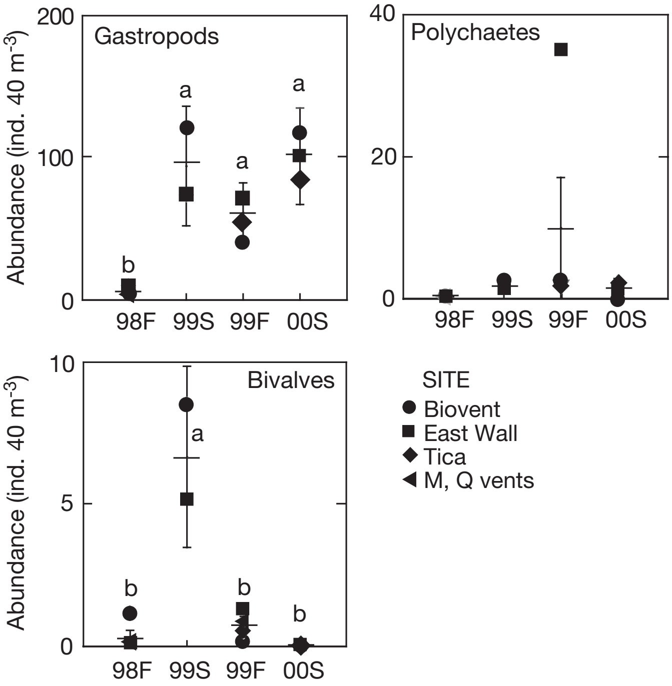

Fig. 6. Temporal variation in abundance of vent larvae from gastropod, polychaete and bivalve groups in plankton pump samples collected on 4 sampling dates: fall 1998 (98F), spring 1999 (99S), fall 1999 (99F) and spring 2000 (00S). Data points: pooled over proximities (on- and off-vent) and lower heights (1 and 20 mab) for each site (for clarity SEs not shown); horizontal and vertical bars: means and SEs respectively, pooled over proximities, lower heights and all sites. N = 3 for most combinations of height, date and proximity, except as shown in Table 1. Letters above symbols: significant differences of means among dates, detected by 3-way ANOVA of height, proximity and date (Table 3) and post-hoc Tukey tests ($p < 0.05$)

more common species (*Cyathermia naticoides*, *Lepetodrilus* spp., *Peltospira* spp.) generally was coherent across sites. A conspicuous exception was the low abundance of *Peltospira* spp. at East Wall in spring 1999. Temporal patterns in several of the less common species (e.g. *C. naticoides*, *G. spiralis*, *N. fretterae*) varied substantially among sites, but low sample sizes make this variation difficult to interpret.

DISCUSSION

Based on our null model of larval dispersal, we expected that vent larval abundance would decrease sharply with increasing height above bottom, and more gradually with lateral distance away from source communities. Spatial patterns of larval abundance conformed generally, but not uniformly, to our expectations. For most species and species-groups, larval abundances decreased roughly exponentially with increasing height above bottom up to the level of the neutrally buoyant plume. Abundances tended to be greater at vent communities than laterally away from them over similar spatial scales (<300 m), but the lateral differences were less intense and were significant only at sites within the axial valley. A curious (but not significant) exception to this pattern was observed in the polychaete group at 1 mab (Fig. 3), which appeared to be more abundant away from the vent community than within it.

We also anticipated that larval abundances would remain consistent over time due to continuous spawning and uninterrupted supply. Temporal patterns in larval abundance did not conform to this expectation. Abundances varied significantly between sampling dates and were not coordinated among taxonomic groups, but whether these differences were due to discontinuous spawning or interruptions in dispersal remains an open question.

Variations in larval distributions can be interpreted in terms of larval supply, but only when the larvae are assumed to be competent to settle. We had hoped to be able to identify early developmental stages that might reflect spawning patterns and late-stage larvae that were supplying benthic communities. However, we were able to assess developmental stage for only 1 common species, the mussel *Bathymodiolus thermophilus*. Thus, the mussel is the only species of use in the present study for evaluating larval supply.

Spatial structure

A decrease in larval abundance with increasing height above bottom is consistent with boundary-layer mixing of larvae away from a benthic source. However, we cannot determine quantitatively whether larval swimming behavior might be influencing the patterns without an appropriate model of passive larval distributions for comparison. Because the vertical patterns were generally consistent between species groups and among gastropod species, they suggest that hydrodynamic processes may be transporting diverse species in similar ways. It is surprising that the late-stage mussel larvae also showed this distinct pattern of decreasing abundance with height, since they are probably planktotrophs (Lutz et al. 1980) with precompetent larval durations of at least several weeks (e.g. Bayne 1965), and would be thought unlikely to remain near the natal vent for that interval (Marsh et al. 2001). It is possible that late-stage mussel larvae return to and aggregate near vents in response to a water-born cue, or that they have swimming behavior that keeps them within a few meters above bottom for their entire larval duration.

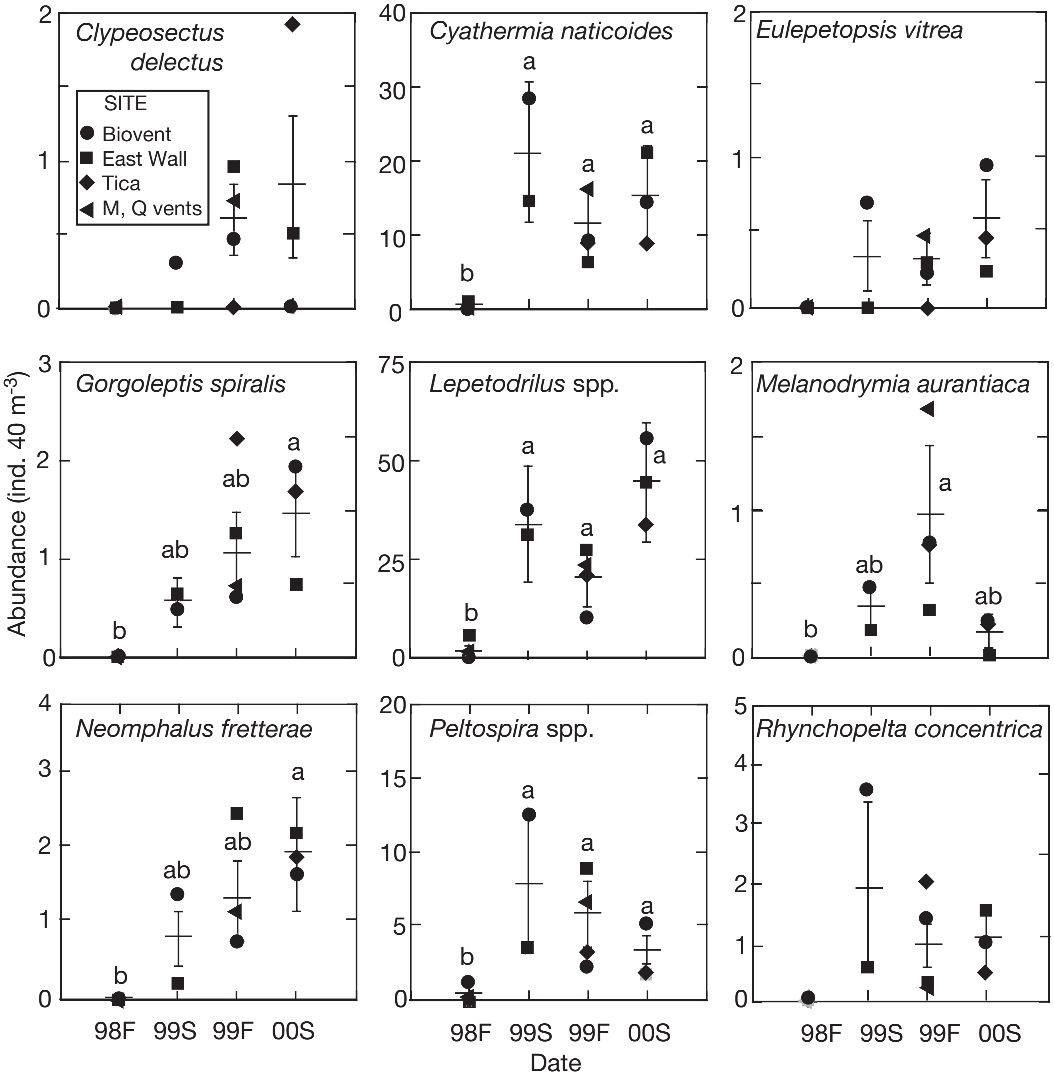

Fig. 7. Temporal variation in abundance of larvae of vent gastropod species in plankton pump samples collected on 4 sampling dates: fall 1998 (98F), spring 1999 (99S), fall 1999 (99F) and spring 2000 (00S). Letters above symbols: significant differences among dates detected by 3-way ANOVA of height, proximity and date (Table 4) and post-hoc Tukey tests ($p < 0.05$). Tukey tests failed to detect variation in *Clypeosectus delectus* and *Rhynchopelta concentrica* despite significant date effects in ANOVAs. Further details and symbols as in Fig. 6 legend

One implication of the greater abundances in near-bottom samples is that the majority of larvae complete their dispersal journey within a few meters of the seafloor. However, we do not know whether settlement success varies with dispersal height, nor whether a near-bottom dispersal strategy is equally advantageous for local or remote colonization. Larvae maintaining a position near the seafloor may be more likely to recolonize a natal vent site because they remain in relatively slow currents and are more likely to experience advection toward a vent in the lower portion of plume-driven circulation. Alternatively, it is likely that successful colonization of distant vents occurs predominantly via larvae dispersing well above the bottom, since currents several 100 meters above the bottom can be more than twice as fast as those within a few meters of the seafloor (Thomson et al. 1990, Cannon & Pashinski 1997). Thus, even though the relative numbers of larvae dispersing 200 m above the bottom are low, they could potentially play an important role in gene flow, population connectivity, and initial colonization of new vents.

The greater on-vent larval abundances at sites within the axial valley indicate that some process may be acting to retain larvae within the valley. A significant difference in abundance was found only at the 1 mab height, which is the only sampling level within the confines of the ~15 m tall valley walls. We think that off-axis advection of larvae may be reduced by impedance of cross-axis flows within the valley walls.

Metaxas (2004) suggested that laterally homogeneous larval abundance in the plankton and larval flux to the benthos at spatial scales of 10s of meters to kilometers may be indicative of retention within the axial valley on the Juan de Fuca and Explorer ridges. Our speculation is consistent with measured flows in the axial valley at Endeavour Segment (Thomson et al. 2003) and Axial volcano (Lavelle et al. 2001) on the Juan de Fuca ridge. However, the axial valley is much deeper at these sites and no comparable flow measurements have been made at sites on the East Pacific Rise.

When sites and heights outside the axial valley walls are considered, no significant decrease in larval abundance is detected laterally away from vents. This pattern suggests that larvae are not actively maintaining position directly in their natal vent community, and are likely to be transported away from their natal vents in near-bottom tidal currents. In flow conditions on the East Pacific Rise, where larvae are advected as far as 1 km across axis in a single tidal excursion (Kim & Mullineaux 1998), larvae would quickly be transported much farther than the distance separating our off-vent collectors from vent communities. Mixing in these tidal currents may cause larval abundance to become relatively homogeneous on scales of 100s of meters. Sampling on larger scales would be necessary to quantify the horizontal distance at which abundances decrease significantly and to determine whether larvae modify their vertical position as they mature.

In the few cases where more larvae were collected off-vent than on-vent (e.g. polychaetes at 1 mab; *Clypeosectus delectus*, *Lepetodrilus* spp., *Peltospira* spp. and *Rhynchopelta concentrica* at 175 mab), the differences were not significant. A plausible explanation for the substantial variation among replicate on-vent and off-vent samples, and the general, but non-significant, trend toward off-axis decrease in abundance, is that larvae are distributed in patches that move with the tidal flow and may or may not be sampled at a particular time by a stationary pump. If the source of the patches is the vent, then a mean abundance gradient may exist, but would be difficult to detect. The spacing of off-axis pumps was not sufficiently large to test the possibility of retention in secondary-flow cells which are expected to extend roughly 1 km in diameter (Helfrich & Speer 1995).

Thus, the question of whether larvae are retained and recolonize their natal vent sites remains open, but our results place some constraints on possible mechanisms. The lack of lateral structure in larval distributions at heights and sites not influenced by topographic barriers suggests that most species are not able to maintain their positions actively within individual vent sites. Exceptions may exist, such as species that spend a substantial portion of their larval life brooded by the adult, or developing in an attached egg capsule (e.g. certain polychaetes or gastropods, respectively). It is also possible that some planktonic larvae remain so low in the bottom boundary layer that they are not exposed to vigorous tidal currents (or our plankton pumps), and spend their entire larval life without leaving the natal site. An example might be the presumed planktotrophic snail *Bathymargarites symplector*, which recruits frequently to adult communities, but was found only once as a larva in our collections. However, our results indicate that many planktonic larvae rise at least 1 m above the seafloor, and would be subject to retention by larger-scale hydrodynamic processes. In situations such as those observed at Juan de Fuca vents, where currents are channeled into the axial valley (Thomson et al. 2003), off-axis loss of larvae is probably reduced and larval abundances potentially enhanced. Whether the source of these larvae is the local vent community, or alternatively another community within the valley, remains unknown. Additional approaches, such as developing geochemical, isotopic or genetic tags of larvae (Levin 1990 [review], Campana 1999) and measuring mixing and residence times of near-bottom water masses, will be required to solve the retention question definitively.

Temporal variation

Differences in abundance of larval species and species-groups among sampling dates were substantial, with some taxa showing order-of-magnitude variation between minimum and maximum abundances. In some groups, such as the bivalves and the *Lepetodrilus* spp. gastropods, temporal patterns were coherent across sites. In others (e.g. polychaetes and the *Peltospira* spp. gastropods), abundances at individual sites deviated on occasion from the regional mean. Many different processes, biological and physical, could be responsible for this temporal variation. If larvae are retained near the natal site, then spawning episodes could result in periods of high larval abundance. If the timing of spawning is driven locally, then larval abundance patterns might vary among sites, whereas if spawning is driven by regional processes, then abundance patterns might be coherent among sites. If larvae are not retained, episodes of local spawning could result in larval patches that remain cohesive during transport, and could be detected as pulses of later-stage larvae at remote vents. Alternatively, even if spawning is continuous, the supply of larvae to particular vents may be interrupted by episodes of off-axis flow (as observed by Marsh et al. 2001) or passage of mesoscale eddies generated elsewhere (e.g. at seamounts, Bograd et al. 1997). Furthermore, if large numbers of larvae are entrained into 'event plumes' (large, discrete, rotating plumes generated by high-volume release of hydrothermal fluids, Baker 1998), they could be transported as a patch for 10s of kilometers, as observed for other vent particulates (Lupton et al. 1998). Clearly, additional studies of adult reproductive status, spawning, and physical influences on transport are needed to evaluate these alternatives.

With the exception of the fall 1998 samples, most of the variation in larval abundance was not synchronized among species. Peak abundances of each of the species groups occurred on different sampling dates, and there was no consistent pattern among the 9 gastropod species. Kim & Mullineaux (1998) and Metaxas (2004) also detected order-of-magnitude differences in abundances of some vent taxa between sampling dates, but no coherence among different taxa. This lack of correspondence suggests that temporal variation may be imparted by species-specific processes such as spawning (for early-stage larvae), differential survival (for planktotrophs), or aggregative behavior during dispersal (for late-stage larvae). We detected no consistent difference between larval abundance in fall and spring collections, indicating that reproductive variation in response to seasonal pulses of phytodetritus such as that observed in deep-sea populations at high latitudes (e.g. Tyler & Gage 1984, Gage & Tyler 1985) was not responsible for the temporal patterns in vent larvae.

Larval abundances during fall 1998 were notable because they were the lowest observed for virtually all species. It is possible that an unusual flow event, such as the passage of an energetic mesoscale eddy, could have swept much of the meroplankton endemic to vents away during that sampling period. Alternatively, a regional tectonic or hydrographic event affecting all the vent sites may have caused a suspension of spawning for some time prior to our sampling in 1998. Although it seems improbable that the 1997/1998 ENSO event could have influenced reproduction of vent species, we cannot rule out the possibility that large perturbations in production at the sea surface could affect the food supply to vent communities. We do not think that these low abundances were due to pump error, because the fall 1998 abundances of strongly swimming adult groups, such as amphipods, were not correspondingly low.

Implications for colonization and gene flow

If larval abundance affects recruitment patterns, then temporal variation in larval supply should cause variations in recruitment. The 2 most abundant gastropod larvae in our samples, *Lepetodrilus* sp. and *Cyathermia naticoides*, were also the most abundant colonists in benthic experiments conducted at these same EPR vents in 1995 to 2000 (Mullineaux et al. 2003), indicating the potential for a close link between supply and colonization. Given the extreme variation in *Bathymodiolus thermophilus* larval abundance, one might expect to see evidence of discrete cohorts in mytilid populations. Comtet & Desbruyères (1998) found large numbers of new recruits of a mytilid bivalve (probably *B. azoricus*) at Mid-Atlantic Ridge vent sites, and suggested that a discrete settlement event had occurred recently. Van Dover et al. (2001) also found a substantial number of new *B. thermophilus* recruits at northern East Pacific Rise vents, but inferred continuous recruitment.

Our results show that larvae of vent species do not occur in an homogeneous pool (patchiness occurs on scales of 10s to 100s of meters), and are not supplied uniformly to vent habitats. Temporal variation in larval supply potentially has important consequences for succession, community structure and population genetic structure in new habitats. For instance, if a particular species settles initially into a new vent, and is capable of excluding other species or functional groups (as in Mullineaux et al. 2003), it may have a large influence on successional processes at that site. In this scenario, the timing of larval supply relative to the timing of the opening of new vent habitat can result in communities with quite different species composition. Furthermore, if the genetic composition of available larval populations varies over time, then colonists may represent only a subset of regional genetic diversity, which complicates interpretation of gene flow. Vrijenhoek (1997) noted that frequent founder events will alter estimates of gene flow and limit the ability to infer number of migrants based on Wright's classical model of population genetic structure (Slatkin 1977). Rigorous quantification of variation in both the number and genetic composition of larval migrants should help refine gene flow interpretations in systems with frequent extinction and colonization events, such as those at vents.

Acknowledgements. We are grateful to BLee Williams for keeping the pumps working at sea, and to the 'Atlantis' and 'Alvin' crews for supporting the mooring operations. Craig Young and Donal Manahan were Co-PIs in the grant that supported this project, served as Chief Scientists on cruises, and provided ideas during numerous discussions on land and at sea. Stace Beaulieu, Ewann Berntson, Erica Goldman, Lara Gulmann, Rob Jennings, Anne Sell and Sheri Simmons all assisted with pump operations and sample processing at sea, and Diane Poehls contributed to the larval identifications. Thanks to all the participants of the Redfield 120 laboratory meeting, who contributed to discussions at various stages of the research and manuscript preparation. The field work was conducted as part of the NSF RIDGE program. Funding was provided by NSF grants OCE-961905 and OCE-9712233 to L.S.M., a WHOI Postdoctoral fellowship through the Doherty Foundation and NSERC Discovery Grant to A.M., and a NSERC postdoctorate fellowship to H.L.H. This is WHOI contribution number 11354.

LITERATURE CITED

Baker ET (1998) Patterns of event and chronic hydrothermal venting following a magmatic intrusion: new perspectives from the 1996 Gorda Ridge eruption. Deep-Sea Res II 45: 2599–2618

Bayne BL (1965) Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2:1–47

Berg CJ, Van Dover CL (1987) Benthopelagic macrozooplankton communities at and near deep-sea hydrothermal vents in the eastern Pacific Ocean and the Gulf of California. Deep-Sea Res 43:379–401

Bograd SJ, Rabinovich AB, LeBlond PH, Shore JA (1997) Observations of seamount-attached eddies in the North Pacific. J Geophys Res C 102:12441–12456

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297

Cannon GA, Pashinski DJ (1997) Variations in mean currents affecting hydrothermal plumes on the Juan de Fuca Ridge. J Geophys Res 102:24965–24976

Chevaldonné P, Jollivet D, Vangriesheim A, Desbruyères D (1997) Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 1. Influence of vent site distribution, bottom currents, and biological patterns. Limnol Oceanogr 42:67–80

Comtet T, Desbruyères D (1998) Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez Gwen hydrothermal vent fields (37° 17'N and 37° 50′ N on the Mid-Atlantic Ridge). Mar Ecol Prog Ser 163:165–177

Comtet T, Jollivet D, Khripounoff A, Segonzac M, Dixon DR (2000) Molecular and morphological identification of settlement-stage vent mussel larvae, *Bathymodiolus azoricus* (Bivalvia:Mytilidae), preserved in situ at active vent fields on the Mid-Atlantic Ridge. Limnol Oceanogr 45: 1655–1661

Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? Science 287:857–859

Epifanio CE, Garvine RW (2001) Larval transport on the Atlantic continental shelf of North America: a review. Estuar Coast Shelf Sci 52:51–77

Epifanio CE, Perovich G, Dittel AL, Cary SC (1999) Development and behavior of megalopa larvae and juveniles of the hydrothermal vent crab *Bythograea thermydron*. Mar Ecol Prog Ser 185:147–154

Fornari DJ, Embley RW (1995) Tectonic and volcanic controls on hydrothermal processes at the mid-ocean ridge: an overview based on near-bottom and submersible studies. Geophys Monogr 91:1–46

Forward RJ (1988) Diel vertical migration: Zooplankton photobiology and behaviour. Oceanogr Mar Biol Annu Rev 26: 361–393

Gage JD, Tyler PA (1985) Growth and recruitment of the deep-sea urchin *Echinus affinis*. Mar Biol 90:41–53

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67: 267–272

Garland ED, Zimmer CA, Lentz SJ (2002) Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. Limnol Oceanogr 47: 803–817

Haymon RM, Fornari DJ, Von Damm KL, Lilley MD and 11 others (1993) Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9° 45–52′ N: direct submersible observations of sea-floor phenomena associated with an eruption event in April, 1991. Earth Planet Sci Lett 119:85–101

Helfrich KR, Speer KG (1995) Oceanic hydrothermal circulation: mesoscale and basin-scale flow. Geophys Monogr 91: 347–356

Hessler RR, Smithey WM, Keller CH (1985) Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. Bull Biol Soc Wash 6: 465–474

Kim SL, Mullineaux LS (1998) Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. Deep-Sea Res II 45:423–440

Kim SL, Mullineaux LS, Helfrich KR (1994) Larval dispersal via entrainment into hydrothermal vent plumes. J Geophys Res 99:12655–12665

Lalou C, Reyss JE, Brichet E, Arnold M, Thompson G, Fouquet Y, Rona PA (1993) Geochronology of TAG and Snake Pit hydrothermal fields, Mid-Atlantic Ridge: witness to a long and complex hydrothermal history. Earth Planet Sci Lett 97:113–128

Lavelle JW, Cannon GA (2001) On sub-inertial oscillations trapped by the Juan de Fuca Ridge, North East Pacific. J Geophys Res 106:31099–31116

Lavelle JW, Wetzler MA, Baker ET, Embley RW (2001) Prospecting for hydrothermal vents using moored current and temperature data: Axial Volcano on the Juan de Fuca Ridge, Northeast Pacific. J Phys Oceanogr 31:827–838

Ledwell J, Montgomery E, Polzin K, St. Laurent L, Schmitt R, Toole J (2000) Evidence for enhanced mixing over rough topography in the abyssal ocean. Nature 403:179–182

Levin LA (1990) A review of methods for labeling and tracking marine invertebrate larvae. Ophelia 32:115–144

Limouzy-Paris CB, Graber HC, Jones DL, Roepke AW, Richards WJ (1997) Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. Bull Mar Sci 60:966–983

Lupton JE, Baker ET, Garfield N, Massoth GJ, Feely RA, Cowen JP, Greene RR, Rago TA (1998) Tracking the evolution of a hydrothermal event plume with a RAFOS neutrally buoyant drifter. Science 280:1052–1055

Lutz RA, Jablonski D, Rhoads DC, Turner RD (1980) Larval dispersal of a deep-sea hydrothermal vent bivalve from the Galápagos Rift. Mar Biol 57:127–133

Lutz RA, Jablonski D, Turner RD (1984) Larval development and dispersal at deep-sea hydrothermal vents. Science 226:1451–1454

Marsh AG, Mullineaux LS, Young CM, Manahan DT (2001) Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411:77–80

McLean JH (1981) The Galapagos Rift limpet *Neomphalus*: relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. Malacologia 21:291–336

McLean JH (1988) New archaeogastropod limpets from hydrothermal vents. Superfamily Lepetodrilacea. Part 1. Systematic descriptions. Philos Trans R Soc Lond B 319: 1–32

McLean JH (1989a) New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. Zool Scr 18:49–66

McLean JH (1989b) New slit limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radular characteristics. Contrib Sci 407:1–29

McLean JH (1990) Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. J Zool 222:485–528

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289

Metaxas A (2004) Spatial and temporal patterns in larval supply at hydrothermal vents in the northeast Pacific Ocean. Limnol Oceanogr 49:1949–1956

Mullineaux LS, France SC (1995) Dispersal of deep-sea hydrothermal vent fauna. Geophys Monogr 91:408–424

Mullineaux LS, Wiebe PH, Baker ET (1995) Larvae of benthic invertebrates in hydrothermal vent plumes over Juan de Fuca Ridge. Mar Biol 122:585–596

Mullineaux LS, Kim SL, Pooley A, Lutz RA (1996) Identification of archaeogastropod larvae from a hydrothermal vent community. Mar Biol 124:551–560

Mullineaux LS, Mills SW, Goldman E (1998) Recruitment variation during a pilot colonization study of hydrothermal vents (9° 50′ N, East Pacific Rise). Deep-Sea Res II 45: 441–464

Mullineaux LS, Fisher CR, Peterson CH, Schaeffer SW (2000) Vestimentiferan tubeworm succession at hydrothermal vents: use of biogenic cues to reduce habitat selection error? Oecologia 123:275–284

Mullineaux LS, Speer KG, Thurnherr AM, Maltrud ME, Vangriesheim A (2002) Implications of cross-axis flow for larval dispersal along mid-ocean ridges. Cah Biol Mar 43: 281–284

Mullineaux LS, Peterson CH, Micheli F, Mills SW (2003) Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. Ecol Monogr 73:523–542

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnol Oceanogr 44:1400–1414

Shank TM, Fornari DJ, Vondamm KL, Lilley MD, Haymon RM, Lutz RA (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9° 50'N, East Pacific Rise). Deep-Sea Res II 45:465–515

Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol Oceanogr 45:230–236

Shanks AL, McCulloch A, Miller J (2003) Topographically generated fronts, very nearshore oceanography and the distribution of larval invertebrates and holoplankters. J Plankton Res 25:1251–1277

Shilling F, Manahan D (1994) Energy metabolism and amino acid transport during early development of Antarctic and temperate echinoderms. Biol Bull (Woods Hole) 187: 398–407

Slatkin M (1977) Gene flow and genetic drift in a species subject to frequent local extinctions. Theor Pop Biol 12: 253–262

Speer KG (1989) A forced baroclinic vortex around a hydrothermal plume. Geophys Res Lett 16:461–464

Sulkin SD (1984) Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar Ecol Prog Ser 15:181–205

Thomson RE, Roth SE, Dymond J (1990) Near-inertial motions over a mid-ocean ridge: effects of topography and hydrothermal plumes. J Geophys Res 95:12961–12966

Thomson RE, Mihaly SF, Rabinovich AB, McDuff RE, Veirs SR, Stahr FR (2003) Constrained circulation at Endeavour ridge facilitates colonization by vent larvae. Nature 424: 545–549

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45

Thurnherr AM, Richards KJ, German CR, Lane-Serff GF, Speer KG (2002) Flow and mixing in the rift valley of the Mid-Atlantic Ridge. J Phys Oceanogr 32:1763–1778

Tunnicliffe V, Embley RW, Holden JF, Butterfield DA, Massoth GJ, Juniper SK (1997) Biological colonization of new hydrothermal vents following an eruption on Juan de Fuca Ridge. Deep-Sea Res I 44:1627–1644

Tunnicliffe V, McArthur AG, McHugh D (1998) A biogeographical perspective of the deep-sea hydrothermal vent fauna. Adv Mar Biol 34:355–442

Turner RD, Lutz RA, Jablonski D (1985) Modes of molluscan larval development at deep-sea hydrothermal vents. Bull Biol Soc Wash 6:167–184

Tyler PA, Gage JD (1984) Seasonal reproduction of *Echinus affinis* (Echindermata: Echinoidea) in the Rockall Trough, northeast Atlantic Ocean. Deep-Sea Res 31:387–402

Tyler PA, Young CM (1999) Reproduction and dispersal at vents and cold seeps. J Mar Biol Assoc UK 79:193–208

Van Dover CL (1995) Ecology of Mid-Atlantic Ridge hydrothermal vents. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes, Spec Publ 87. Geological Society, London, p 257–294

Van Dover CL (2000) The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton

Van Dover CL, Jenkins CD, Turnipseed M (2001) Corralling of larvae in the deep sea. J Mar Biol Assoc UK 81:823–826

Vrijenhoek RC (1997) Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. J Hered 88:285–293

Warén A, Bouchet P (1989) New gastropods from East Pacific hydrothermal vents. Zool Scr 18:67–102

Warén A, Bouchet P (1993) New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zool Scr 22:1–90

Warén A, Bouchet P (2001) Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. Veliger 44:116–231

Wing S, Botsford L, Morgan L, Diehl J, Lundquist C (2003) Inter-annual variability in larval supply to populations of three invertebrate taxa in the northern California Current. Estuar Coast Shelf Sci 57:859–872

Won Y, Young CR, Lutz RA, Vrijenhoek RC (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae:*Bathymodiolus*) from eastern Pacific hydrothermal vents. Mol Ecol 12:169–184

Young CM, Chia FS (1987) Abundance and distribution of pelagic larvae as influenced by predation, behavior and hydrographic factors. In: Giese AC, Pearse JS, Pearse VB (eds) Reproduction of marine invertebrates. IX. General aspects: seeking unity in diversity. Boxwood Press, Palo Alto, CA, p 385–463

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River, NJ

Editorial responsibility: Lisa Levin (Contributing Editor), La Jolla, California, USA

Submitted: May 7, 2004; Accepted: November 21, 2004
Proofs received from author(s): May 13, 2004