

Comparison of a sediment trap and plankton pump for time-series sampling of larvae near deep-sea hydrothermal vents

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Abstract

Studies of larval dispersal and supply are critical to understanding benthic population and community dynamics. A major limitation to these studies in the deep sea has been the restriction of larval sampling to infrequent research cruises. In this study, we investigated the utility of a sediment trap for autonomous, time-series sampling of larvae near deep-sea hydrothermal vents. We conducted simultaneous deployments of a time-series sediment trap and a large-volume plankton pump in close proximity on the East Pacific Rise (2510-m depth). Grouped and species-specific downward fluxes of larvae into the sediment trap were not correlated to larval abundances in pump samples, mean horizontal flow speeds, or mean horizontal larval fluxes. The sediment trap collected a higher ratio of gastropod to polychaete larvae, a lower diversity of gastropod species, and over- or undercollected some gastropod species relative to frequencies in pump sampling. These differences between the two sampling methods indicate that larval concentrations in the plankton are not well predicted by fluxes of larvae into the sediment trap. Future studies of deep-sea larvae should choose a sampling device based on specific research goals. Limited by battery power, a plankton pump in combination with a current meter is useful for estimating horizontal advective fluxes in short-term (days to weeks) studies of larval dispersal. A sediment trap, selecting for larvae with downward trajectories, is more appropriate for studies of larval supply to the benthos. For some species, a time-series sediment trap can collect sequential larval samples for long-term studies (months to years) for correlation to larval settlement and recruitment patterns.

Introduction

For many benthic invertebrate species, local populations are connected by larval dispersal, and temporal fluctuations in larval supply may affect benthic community dynamics. Deep-sea hydrothermal vents, inhabited by endemic fauna, are examples of discrete and ephemeral habitat patches in which larval dispersal and supply are critical to maintaining popula-

tions. However, very little is known about larval dispersal between or larval supply to hydrothermal vents (e.g., Marsh et al. 2001; Tyler and Young 2003). Our study was motivated by the need for an improved method to assess temporal patterns and variability in larval dispersal and supply to these, and other, habitats in the deep sea.

Time-series sampling of larvae is a major challenge in the deep sea. Traditional methods for time-series studies of planktonic larval abundance, such as repeated sampling with nets or pumps, are severely limited by access to the study site, restricting the sampling to a limited number of research cruises. Two other limitations to sampling deep-sea larvae include low abundances and depth, which necessitate greater use of ship time for towing nets and pressure housings to protect pumps and associated electronics. Although pumps have been developed for autonomous time-series sampling of larvae in coastal waters (e.g., Garland and Zimmer 2002), these instruments have not been successfully adapted for the deep sea, mainly due to limitations of battery power necessary to pump large volumes per sample. Larval concentrations in the proximity of hydrothermal vents are on the order of 10/m³, or 1/100 L (Metaxas 2004; Mullineaux et al. 2005). To quantify

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Acknowledgments

We thank S. Manganini, A. Fleer, S. Worrilow, J. Kemp, and R. Trask for providing, respectively, a sediment trap, plankton pump, current meter, acoustic releases, and floats for our moorings. We also thank Chief Scientist M. Lilley, the crew of R/V *Atlantis*, the shipboard scientific support group, and the Alvin group during Cruise AT11-20. We thank V. Starczak for help with statistics, and S. Bayer, I. Garcia Berdeal, N. Reynolds, C. Strasser, D. Thistle, and three anonymous reviewers for comments on the manuscript. Funding for this study was provided by a Woods Hole Oceanographic Institution Deep Ocean Exploration Institute grant to L.S.M. and S.E.B., NSF grant OCE-0424953 to L.S.M., and a National Defense Science and Engineering Grant Fellowship to D.K.A.

larval abundance near specific vent sites, pumps, which collect water at discrete locations, can be preferable to nets because towing a net near-bottom over rough topography can require a submersible or remotely operated vehicle and potentially integrates over the horizontal scale of multiple vent sites.

Several recent studies have used sediment traps for collection of larvae near deep-sea hydrothermal vents, including tube traps which yield single samples per deployment (Metaxas 2004) and time-series sediment traps (Comtet et al. 2000; Adams and Mullineaux 2008; Khripounoff et al. 2008). Tube traps, set into or just above the seafloor, have been used in coastal waters for determining larval supply to the benthos (e.g., Yund et al. 1991; Bertness et al. 1992; Gaines and Bertness 1993; Todd et al. 2006). Time-series sediment traps, used regularly over the past two decades to estimate sinking particulate fluxes to deep water (e.g., Knauer and Asper 1989) and for particulates from hydrothermal plumes (e.g., Khripounoff et al. 2001, 2008), collect a sequence of samples and may be deployed for periods on the order of a year (Honjo and Doherty 1988). Traps are passive collectors, and their shape and configuration in combination with the ambient flow regime influence their collecting properties, sometimes with hydrodynamic biases in the estimation of sinking particulate fluxes (Butman et al. 1986; Knauer and Asper 1989; Jürg 1996). For studies of particulate fluxes, live zooplankton that actively enter sediment traps are called “swimmers,” and very rarely have sediment-trap studies reported on temporal patterns in zooplankton (e.g., Forbes et al. 1992). However, most benthic invertebrate larvae, with the exception of crustacean larvae, can be considered weak swimmers (Chia et al. 1984), and a study in coastal waters could not reject the hypothesis that larvae were collected in sediment traps as if they were passive particles (Butman 1989).

Although researchers are already using sediment traps to collect larvae near hydrothermal vents, it is unclear how downward larval fluxes are related to larval abundances as collected by nets or pumps. A series of studies with tube traps in laboratory and coastal settings indicated that, for some species and stages of larvae, downward fluxes were correlated to larval concentration and horizontal advection in the overlying water (Yund et al. 1991; Bertness et al. 1992). In addition, several studies in shallow water have correlated larval fluxes into tube traps to larval settlement (e.g., Bertness et al. 1992; Gaines and Bertness 1993; Todd et al. 2006), implying that sediment traps might be useful for evaluating temporal changes in larval supply to deep-sea benthic communities. In this article, we compare results for larvae collected during simultaneous deployments of a sediment trap and a plankton pump near a deep-sea hydrothermal vent. The two main questions motivating our study were (1) Are temporal patterns similar in the number of larvae collected in simultaneous deployments of a sediment trap and a plankton pump near a hydrothermal vent? (2) Does the sediment trap selectively collect certain taxonomic groups of larvae relative to frequencies sampled by a plankton pump near a hydrothermal vent? Our

intentions were to evaluate the advantages and disadvantages of these two methods for time-series studies of larval dispersal and supply in the deep sea.

Materials and procedures

Study site—Our study was conducted near East Wall Vent at the Ridge2000 Integrated Studies Site at the East Pacific Rise (9°50'32" N, 104°17'32" W, 2510-m depth). We specifically chose this site due to the well-defined axial summit trough, likely to constrain the flow (Fig. 1; see Ferrini et al. 2007 for a detailed description of the bathymetry at this site). Several nearby, colonized vents within 1 km to the north and to the south likely served as additional local sources of larvae (Adams and Mullineaux 2008). Our study was conducted in November 2004, before the eruption that covered many of these established vent communities (Tolstoy et al. 2006).

Sediment trap samples—For sampling of downward larval fluxes, we used a time-series sediment trap with a sampling aperture of 0.5 m² and 21 cups (McLane Parflux Mark 78H-21; McLane Research Laboratories). The conical shape enables greater collection area than tube traps, and the aperture was baffled to reduce the development of eddies in the trap funnel

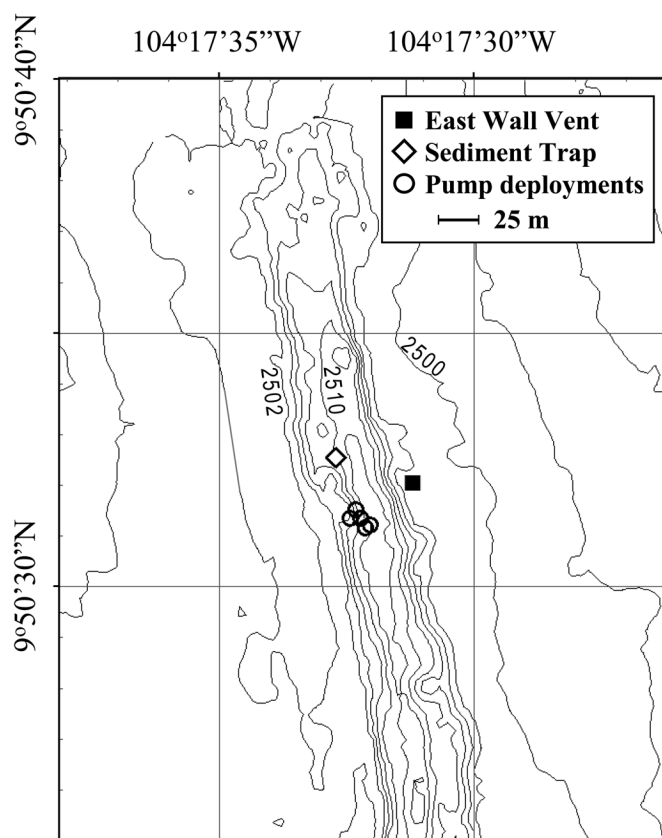


Fig. 1. Study site at the East Pacific Rise. Deployment positions for sediment trap and plankton pump moorings in the axial trough of the ridge near East Wall Vent. Bathymetry available at Ridge Multibeam Synthesis Data Portal (<http://www.marine-geo.org/rmbs>), contour interval 2 m.

Table 1. Sample schedule for the sediment trap and the plankton pump deployments.

Mooring	Start time (GMT)	End time (GMT)	Trap Cup(s)	Volume, L
Sediment trap	12 Nov 2004, 1400	22 Nov 2004, 1800	NA	NA
Pump 1	12 Nov 2004, 1400	13 Nov 2004, 1400	1	41505
Pump 2	14 Nov 2004, 1400	15 Nov 2004, 0730 ^a	3	29840
Pump 3	16 Nov 2004, 1400	17 Nov 2004, 1400	5	41505
Pump 4	18 Nov 2004, 1400	19 Nov 2004, 1400	7	41505
Pump 5	20 Nov 2004, 1400	21 Nov 2004, 1400	9–14	41505

Pump sampling intervals corresponded to specific cup samples from the sediment trap. NA, not applicable.

^aPump stopped prematurely because of low battery (the filter appeared to be clogged by a gelatinous zooplankter).

that might affect trapping efficiency (baffle cell diameter 2.5 cm, height 6.25 cm; Honjo and Doherty 1988; Jürg 1996). Before deployment, cups were filled with a solution of 20% dimethylsulfoxide (DMSO) in ultrapure water saturated with NaCl (e.g., Comtet et al. 2000). We deployed the sediment trap for 10 days, with cups rotating over 1-day or 4-h intervals (Table 1). The sediment trap was deployed on an autonomous subsurface mooring, with the trap opening at 4 m above bottom (mab), as close as possible to the seafloor above the bridles, mooring acoustic release, pull pin release, and anchor (Fig. 2). Above the sediment trap, we attached Aanderaa RCM11 2-D acoustic current meters (Aanderaa Data Instruments) at 10 and 170 mab, recording averages of 30-min intervals (entire data set for these current meters in Adams and Mullineaux 2008). After recovery of the mooring, we photographed the cups and stored them at 4°C for examination at our laboratory.

Plankton pump samples—We collected discrete plankton samples over 1-day periods using a large-volume pump designed for use in deep water (McLane Large Volume Water Transfer System WTS-LV50; McLane Research Laboratories). We pumped at 30 L min⁻¹ over a filter comprised of 63- μ m Nitex mesh, yielding ~40 m³ pumped per day (Table 1). The inlet to the pump apparatus is oriented such that the pump draws down fluid from above; thus, the intake is not isokinetic with the ambient flow field, and plankton may have behavioral interactions with the intake flow field (e.g., escape response; Powlik et al. 1991). However, the intake has a diameter of 3 cm, and intake velocity was ~71 cm s⁻¹, an order of magnitude greater than ambient horizontal flow speed and two to three orders of magnitude greater than larval swimming speeds (e.g., Chia et al. 1984). Many of the collected specimens were alive upon retrieval of the pump, owing to insulation of the filter compartment and placement of the rotor downstream. The pump was deployed on an autonomous subsurface mooring (Fig. 2), located as close as possible to the trap mooring without risking entanglement (~40 m). The pump inlet was positioned at 4 mab to match the altitude of the sediment trap opening, and an Aanderaa RCM11 2-D acoustic current meter at 10 mab was synchronized with the current meters on the trap mooring. After recovery on deck, the filter holder was removed into a 20-L bucket with chilled, filtered seawater. All subsequent handling

of the sample occurred in the cold room (4°C). Samples were rinsed from the filter with chilled, filtered seawater and briefly examined live under a dissecting microscope before being collected onto a 63- μ m sieve, rinsed with fresh water, and preserved in 95% ethanol for examination at our laboratory.

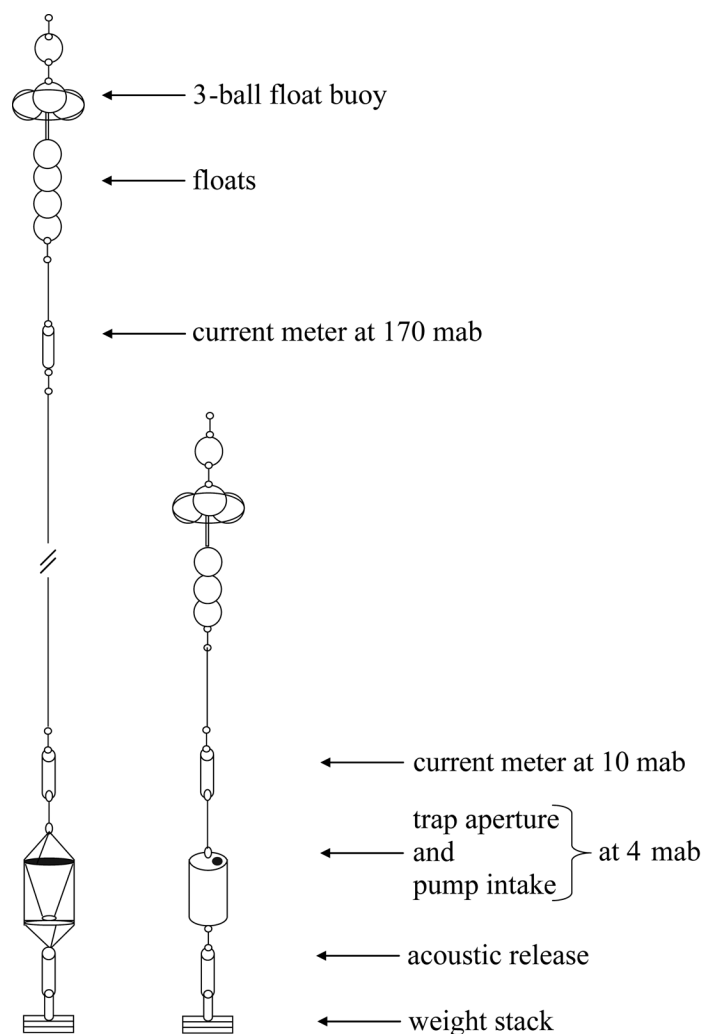


Fig. 2. Sediment trap (left) and plankton pump (right) mooring diagrams. Sampling openings at 4 m above bottom (mab) indicated by shading.

Laboratory sorting of larvae in samples—Within a few months after the cruise, larvae from both sediment trap and pump samples were classified morphologically to species groups or morphotypes. In this region of the East Pacific Rise, many of the larval morphotypes (especially gastropod protoconchs) have been matched to adult forms (Mullineaux et al. 1996; Mills et al. 2007, <http://www.whoi.edu/science/B/vent-larval-id>). All gastropod larvae reported in this study were benthic species known (or likely) to inhabit vents. Some polychaete larvae were identifiable morphologically as vent-endemic species, but most could not be categorized to species level and likely include both vent and nonvent species. Samples, rinsed over nested 300- μm and 63- μm sieves, were sorted under a dissecting microscope at 25 $\times$, with identification at 50 $\times$ or 100 $\times$ under a compound microscope. Larvae sorted from both sets of samples were saved in 95% ethanol and stored in L.S.M.'s laboratory. We do not recommend transfer from DMSO solution to ethanol for future studies because it apparently caused tissue degradation, especially for polychaete larvae. For the remainder of each sample, we counted the copepods (planktonic and benthic) and amphipods, which are strong swimmers relative to gastropod and polychaete larvae, and noted the presence or absence of pteropod shells and large planktonic foraminiferans, which are expected to have greatest sinking velocities. To estimate the total abundance of copepods in each pump sample, we counted at 25 $\times$ at least 300 copepods in combined fields from each quadrant of a divided Petri dish.

Assessment

Experimental design—Our comparative study required repeated deployments of a plankton pump mooring in close proximity to a sediment trap mooring within the axial trough of the ridge (Fig. 1). To maximize the replicate comparisons within the logistical constraints of the cruise, our experiment was conducted during 10 days with simultaneous sampling periods every other day (total $n = 5$ replicates; Table 1). Moorings were deployed anchor-first and positioned within a surveyed long baseline (LBL) navigation net on the seafloor using a relay transponder. All pump deployments were within 7 m of a target deployment position (Fig. 1), within the expected accuracy of the LBL navigation (Soule et al. 2008). Although more precise positioning can be attained by moving a mooring using a submersible (e.g., Mullineaux et al. 2005; Khripounoff et al. 2008), the spatial separation (~ 40 m) between pump and trap moorings was unavoidable because of risk of entanglement. The current experimental design could be improved further by deploying multiple trap/pump pairs at different locations (i.e., to avoid spatial pseudoreplication), but the expense of instrumentation and ship time would likely be prohibitive. An alternative configuration with the trap and pump co-located would have been preferable, but was not possible at the time. In the future, with the design of a high-volume pump system with internal sample preservation,

a platform could be deployed on the seafloor to hold a time-series sediment trap and multiple pumps (or, ideally, a time-series pump system). Such a platform would also enable sampling larvae closer to the seafloor (e.g., 2.5 mab in Khripounoff et al. 2008).

Analysis of the current meter records on the separate moorings indicated that the sediment trap and plankton pump were exposed to very similar horizontal currents during the experiment (Fig. 3). Mean current speeds at 10 mab were generally ≤ 5 cm s^{-1} at both moorings, with maximum speeds at the sediment trap mooring < 9 cm s^{-1} and at the pump mooring < 12 cm s^{-1} (Table 2). Correlation coefficients for the paired records ranged from 0.75 to 0.84, with alignment ranging from 5 to 23 degrees (raw data with zero lag; complex vector correlations as in Kundu 1976); however, because of tides, the reduced number of independent (i.e., not serially autocorrelated) realizations of data within each record reduces the degrees of freedom, and these correlations are not significant. Importantly, the magnitudes of the along-axis component in the paired records did not differ significantly (with the exception of the last several hours in the November 20–21 deployment; paired t tests, $\alpha = 0.05$, $\text{df} = 48$). We might expect current speeds at the level of the sediment trap and pump (4 mab) to be slightly less than at 10 mab (e.g., Garcia Berdeal et al. 2006).

Sediment trap results—Downward fluxes of larvae into the sediment trap ranged more than 2-fold, from 35 to 95 larvae (per $0.5 \text{ m}^{-2} \text{ day}^{-1}$) and were dominated by gastropod larvae and polychaetes (larvae and juveniles), representing an average of 76% and 23% of the total larvae collected, respectively (Fig. 4). Similarly, gastropod and polychaete larvae dominated collections with tube traps in the vicinity of hydrothermal vents on the Juan de Fuca Ridge (Metaxas 2004). During our 5-day experiment, no other benthic invertebrate larvae or postlarvae were collected by the sediment trap, with the exception of one brachyuran crab megalopa. “Swimmers” numbered an average of 18 copepods ($0.5 \text{ m}^{-2} \text{ day}^{-1}$) and a total of three amphipods during the 5-day comparison (Table 3). Each sediment trap sample also contained several pteropod shells (about five per day) and relatively large planktonic foraminiferans (about 40 per day). Current speeds, measured 6 m above the sediment trap (< 9 cm s^{-1} ; Table 2), were not expected to have a significant effect on trapping efficiency for passive particles (e.g., Knauer and Asper 1989; Gardner et al. 1997; Yu et al. 2001). We calculated the product-moment correlation coefficient (r) between downward flux into the trap and daily mean current speed and found no significant correlation ($\alpha = 0.05$) for gastropod larvae ($r = 0.08$) or polychaetes ($r = -0.18$), or for any of the abundant species or morphotypes within these larval groups (MATLAB R2006a software). Adams and Mullineaux (2008) reported that grouped and species-specific larval fluxes into the sediment trap in the entire 10-day time series were not serially autocorrelated.

Larvae of 17 benthic gastropod species were collected by the sediment trap during the 5 days for comparison to the pump

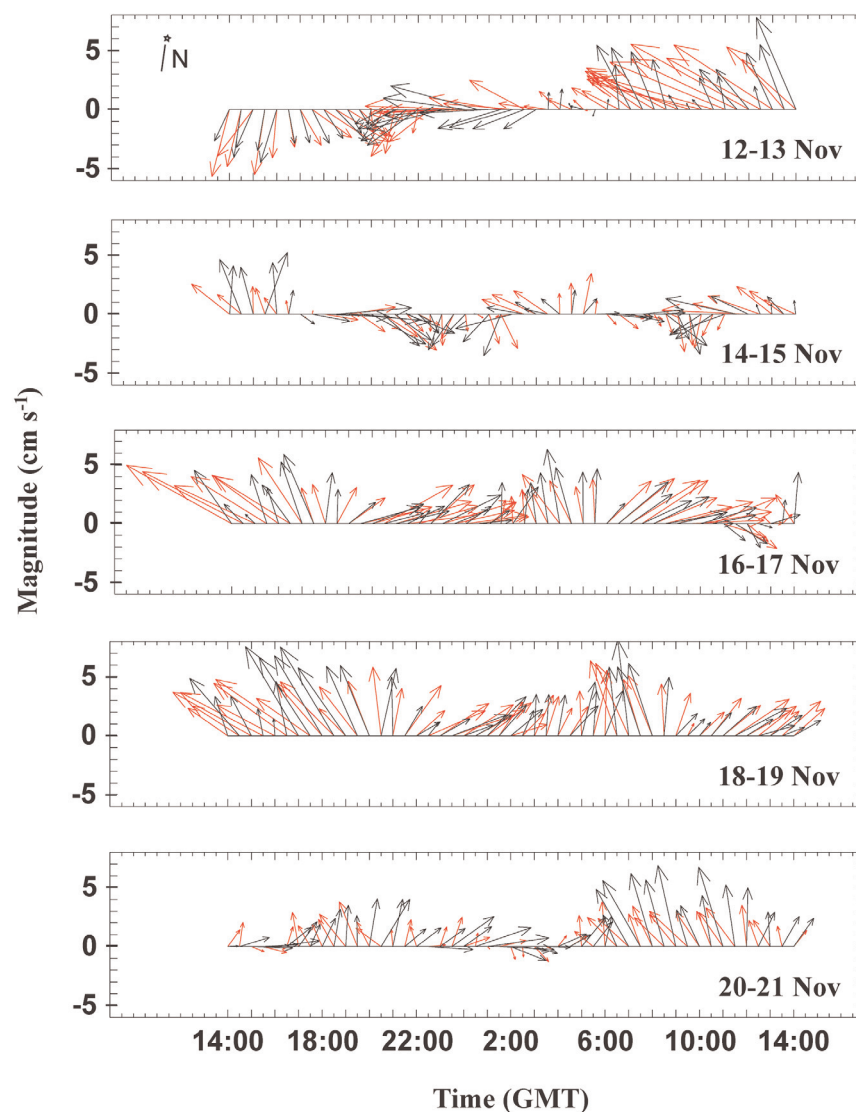


Fig. 3. Current velocities at 10 mab at the sediment trap (black) and plankton pump (red) moorings during the 5 days of simultaneous sampling. Vectors are aligned with ridge axis.

Table 2. Daily mean and maximum current speeds at 10 mab, recorded simultaneously at the sediment trap and pump moorings.

Start date	Current speed, cm s^{-1}			
	Mean		Maximum	
	Sediment trap	Pump	Sediment trap	Pump
12 Nov 04	3.8	5.5	8.5	11.4
14 Nov 04	3.4	2.6	6.5	7.3
16 Nov 04	3.8	5.0	6.5	10.3
18 Nov 04	4.3	4.8	8.8	8.5
20 Nov 04	3.6	2.4	7.0	4.4

deployments (271 of 273 individuals were classified to species groups; Table 3). The dominant species, *Cyathernia naticoides*, accounted for 48% of all gastropod larvae collected by the

sediment trap (Fig. 5A). The second most abundant species group, *Lepetodrilus* spp., accounted for 14%, and overall, the top five species groups in rank abundance accounted for 86%

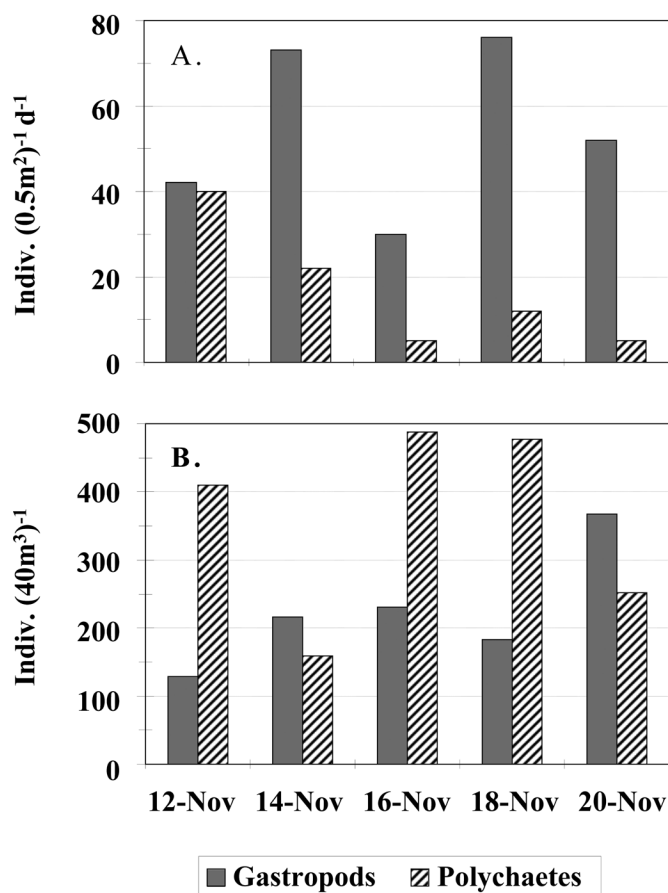


Fig. 4. Time-series sampling of larvae in simultaneous deployments of sediment trap and plankton pump moorings. Total counts include all individuals (classified and unclassified). (A) Downward larval flux into the sediment trap. (B) Larval abundance in plankton pump samples, normalized to 40 m³.

of the total gastropod larvae collected by the sediment trap.

Only six types of polychaete larvae (and juveniles) were collected by the sediment trap during the 5 days for comparison to the pump deployments (59 of 84 individuals were classified to morphotypes; Table 3). The dominant morphotype, representing 33% of the total polychaetes collected by the trap (47% of the classified polychaetes; Fig. 5B), was a larval morphotype that we tentatively assigned to *Ophryotrocha* sp. [previously reported under “polychaete (miscellaneous)” in Mullineaux et al. 2005]. The second most abundant morphotype, accounting for 34% of the total classified polychaetes, was similar to chaetosphaera larvae. The relatively large fraction of individuals classified to the unknown (juvenile) morphotype (12% of classified polychaetes) and unclassified (30% of total polychaetes sampled) likely resulted from degradation of the polychaetes upon transfer from DMSO solution to ethanol.

Plankton pump results—Larval abundances in the 5 days of pump sampling ranged 2-fold, from 377 to 723 larvae (per 40 m³) and were dominated by polychaetes (larvae and juveniles)

and gastropod larvae, representing an average of 61% and 38% of the total larvae collected, respectively (Fig. 4). Dominance by polychaete and gastropod larvae in the vicinity of hydrothermal vents is consistent with previous larval collections by net and pump near this site (Kim and Mullineaux 1998; Mullineaux et al. 2005) and by net at other ridge segments (e.g., Metaxas 2004). Larvae of a few other benthic invertebrate taxa were collected in the pump samples in low numbers, such as barnacle cyprids, trochophores of undetermined phyla, cyphonautes, and bivalve larvae (Table 3). The dominant, nonlarval zooplankton group in the pump samples was copepods (planktonic and benthic), at an average concentration of 8351 individuals (per 40 m³), and amphipods were collected at an average of 69 individuals (per 40 m³). Qualitatively, we observed very few pteropod shells and large planktonic foraminiferans in the pump samples.

Larvae of 29 benthic gastropod species were collected in the pump samples (1077 of 1105 individuals were classified; Table 3). The dominant species group, *Lepetodrilus* spp., accounted for 41% of all gastropod larvae collected by the pump (Fig. 5A). The second most abundant species, *Cyathernia naticoides*, accounted for 14%, and overall, the top five species groups in rank abundance accounted for 74% of the total gastropod larvae collected in the pump samples.

Eleven types of polychaete larvae (and juveniles) were collected in the pump samples (all 1807 individuals classified; Table 3). The two most dominant morphotypes were the same as for the sediment trap samples, with the group consisting mainly of ?*Ophryotrocha* sp. larvae accounting for 40%, followed by ?chaetosphaera larvae at 29% of the total polychaetes sampled by the pump (Fig. 5B). The third most abundant group, at 19% of the total polychaetes, was nectochaetes (unidentified morphotypes), followed by polynoid larvae and *Archinome rosacea* larvae at 4% each. Very few individuals (0.11%) were classified to the unknown (juvenile) morphotype.

Comparison of sediment trap and plankton pump results: temporal correlations—Our first objective in comparing the sediment trap and plankton pump samples was to assess the correlation in temporal patterns in the number of larvae collected. We calculated the product-moment correlation coefficient (r) between downward flux into the sediment trap and abundance measured by the pump in the 5 days of simultaneous sampling. We found no significant correlation ($\alpha = 0.05$) between the numbers of larvae collected by the sediment trap and pump for gastropod larvae ($r = -0.05$) or polychaetes ($r = -0.08$), or for any of the abundant species or morphotypes within these larval groups. Visual inspection of plots for the total and two most abundant species groups of gastropod larvae and morphotypes of polychaetes illustrates the lack of relationship between the two sampling methods (Fig. 6). One pattern that emerged from these correlations for the five most abundant gastropod species in the sediment trap was that larger protoconchs (>200 μ m diameter) had negative whereas smaller

Table 3. Total number of individuals, classified to species groups or morphotypes, collected in 5 days of simultaneous sampling near East Wall Vent.

Taxon	Sediment trap	Plankton pump
Mollusca, gastropoda		
<i>Laeviphitus</i> sp., 400 µm	26	69
<i>Rhynchopelta concentrica</i> , 290 µm, < ^a	0	14
<i>Melanodrymia aurantiaca</i> , 260 µm, < ^a	0	10
Unknown W, 260 µm	1	9
<i>Eulepetopsis vitrea</i> , 250 µm	8	15
<i>Neomphalus fretterae</i> , 250 µm	3	14
<i>Pachydermia laevis</i> , 250 µm, <	1	16
<i>Cyathermia naticoides</i> , 240 µm, > ^a	131	148
Unknown peltospirids, 240 µm, < ^a	0	16
<i>Peltospira</i> spp., 220 µm, < ^a	3	66
Unknown peltospirids, 210 µm, <	1	15
<i>Clypeosectus delectus</i> , 180 µm, < ^a	0	27
<i>Gorgoleptis emarginatus</i> , 180 µm	11	26
<i>Lepetodrilus</i> spp., 180 µm, < ^a	38	438
Unknown 5, 180 µm, < ^a	8	69
Unknown A, 170 µm	28	70
Pointy apex (unknown slit limpet), 160 µm	2	17
<i>Gorgoleptis spiralis</i> , 150 µm	6	19
Rare gastropod species groups ^b	4	19
Classified gastropod larvae totals	271	1077
Number of gastropod species groups, including rare groups	17	29
Unclassified gastropods	2	28
Mollusca, bivalvia		
<i>Bathymodiolus thermophilus</i>	0	1
Other bivalve larvae	0	2
Polychaeta		
<i>Archinome rosacea</i> , <	0	71
Glycerid	0	12
Nereid	1	15
Polynoid	2	73
?Chaetosphaera	20	532
Nectochaete, <	1	344
? <i>Ophryotrocha</i> sp.	28	726
Hesionid (juv.)	0	1
<i>Ophryotrocha akessoni</i> (juv.)	0	3
?Spionid (juv.)	0	28
Unknown polychaetes (juv.)	7	2
Classified polychaete totals	59	1807
Number of polychaete morphotypes	6	11
Unclassified polychaetes	25	0
Crustacea		
Crustacean larvae (excludes nauplii)		
Barnacle cyprids	0	7
<i>Bythograea microps</i> megalopa	1	0
<i>B. thermydron</i> zoea	0	1
Crustacean adults (includes holoplankton)		
Amphipods	3	339
Copepods ^c	92	41084
Cumacean, Isopods, Leptostracan	0	10
Other larvae		
Cyphonautes, Echinoderm larva, Trochophores	0	13

Gastropod species groups are listed in descending order of maximum protoconch diameter. > or <, over- or undercollecting by the sediment trap, relative to the pump. ?, some degree of uncertainty in assigning a morphotype to a particular taxonomic group.

^aSignificant in paired *t* tests at $\alpha = 0.05$, $df = 4$ [both untransformed and log base 10 (proportion + 1) transformed data]. We assumed that there was no covariance in the proportions among the different gastropod species groups.

^b*Bathymargarites symplector*, 350 µm, > ; *Ctenopelta porifera*, 310 µm; Unknown ?neomphalid, 290 µm, > ; *Lirapex granularis*, 220 µm; Unknown *Pachydermia*-like, 220 µm; Unknown U, 200 µm; Unknown *Lepetodrilus*-like, 190 µm; Unknown 9-like, 190 µm, > ; Unknown 8-like, 190 µm; *Gorgoleptis* sp. 3, 185 µm; Unknown 7-like, 175 µm.

^cNumber of copepods in pump samples estimated from subsampling.

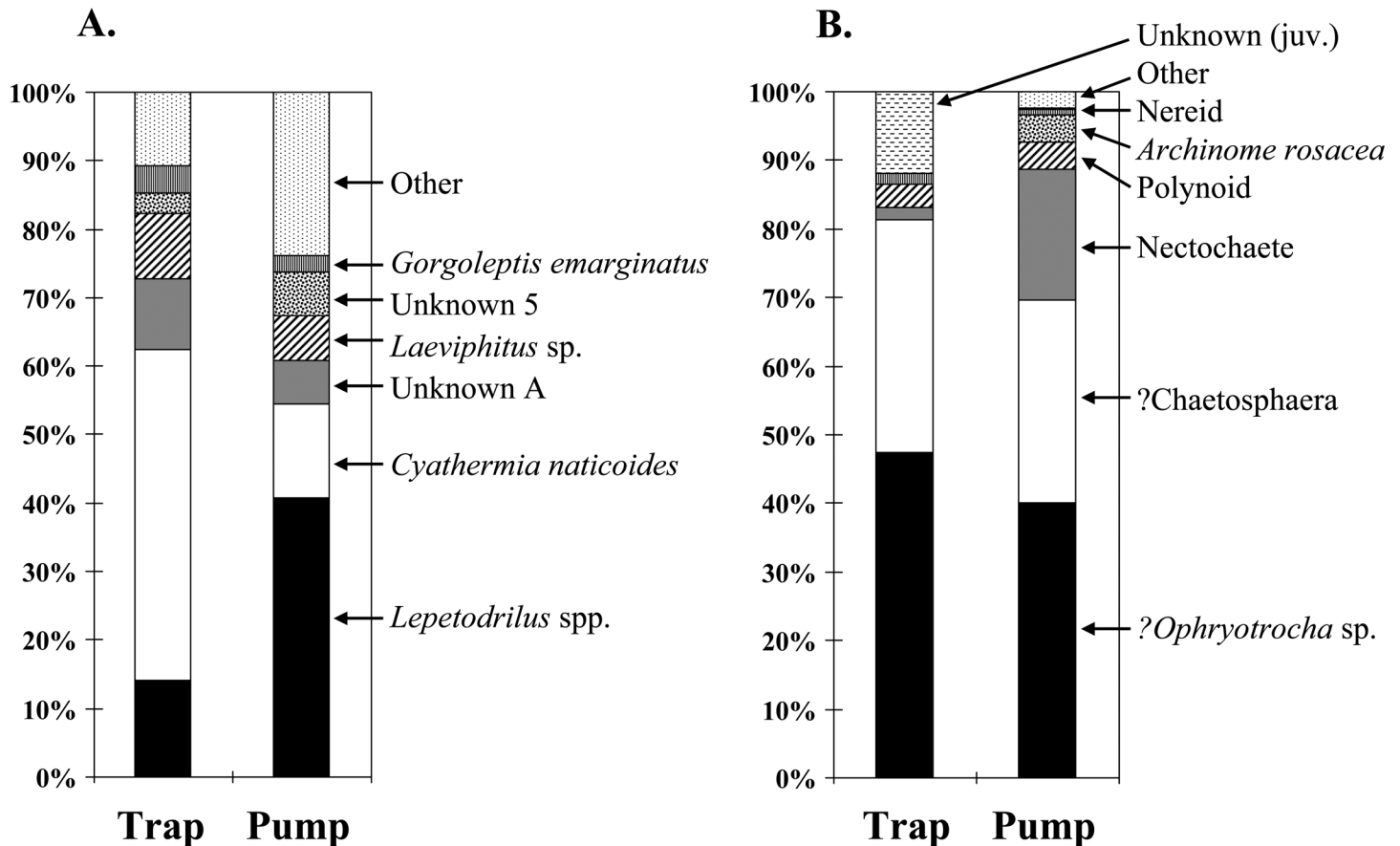


Fig. 5. Relative abundance of larvae collected in 5 days of simultaneous sampling. For pump sampling, the five most abundant species groups or morphotypes are displayed in rank order, from the bottom. (A) Gastropods. (B) Polychaetes (including juveniles). All six morphotypes classified in sediment trap samples are displayed.

protoconchs (<200 μm) had positive correlation coefficients, although none was statistically significant.

We also examined correlations between the downward fluxes into the trap and the mean horizontal fluxes of larvae, as estimated by multiplying larval concentration times daily mean flow speed at the pump moorings. Again, there was no significant correlation ($\alpha = 0.05$) for gastropod larvae ($r = -0.61$) or polychaetes ($r = 0.14$), or for any of the abundant species or morphotypes within these larval groups. Although not statistically significant, all of the abundant gastropod species groups had negative correlation coefficients, indicating that when horizontal fluxes were lower, sediment trap fluxes were higher, and vice versa. Gaines and Bertness (1993, p. 2433) suggested caution in combining concentration and average flow speed to indicate horizontal flux of larvae owing to the potential for covariation. Although not statistically significant for gastropod larvae ($r = -0.75$), we noted that there was a significant, positive correlation between polychaete abundance in the pump samples and daily mean flow speed ($r = 0.89$, $P = 0.05$).

Although all of the above correlations would require $r \geq 0.88$ for significance at $\alpha = 0.05$ ($n = 5$, $df = 3$; Rohlf and Sokal

1981), we think it is unlikely that the lack of correlation between trap and pump collections was due solely to the limited number of replicates. Larval fluxes into the sediment trap were not serially autocorrelated (Adams and Mullineaux 2008) and thus do not reduce the degrees of freedom for the temporal correlation to pump samples. It is possible that the spatial separation between the moorings contributed to the lack of correlation, in particular if there is persistent zooplankton patchiness associated with complex bathymetry. However, we chose this particular study site due to the prominent axial trough, expected to rectify the flow (and passive particle transport), and as expected, the currents were very similar at 10 mab between the moorings (Fig. 3).

The lack of correlation between downward fluxes and larval concentrations or horizontal fluxes is not necessarily surprising, given that the sediment trap and the plankton pump sample quite differently. The sediment trap samples passively, selecting for a subset of particles and plankton with downward trajectories, whereas the pump samples actively, drawing in particles and plankton with trajectories in all directions. Downward trajectories for larvae would result from advection

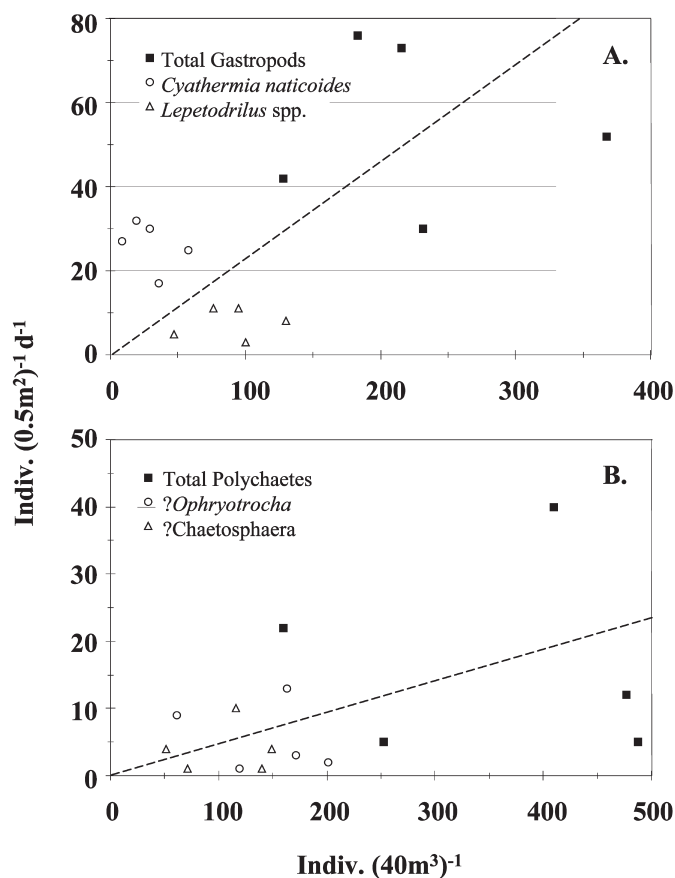


Fig. 6. Downward larval flux into the sediment trap plotted against larval abundance in simultaneous plankton pump samples. Dashed line is drawn through mean number of total collected per sampling method per day. Points above (or below) this dashed line indicate oversampling (or undersampling) by the sediment trap compared to the plankton pump. (A) Total gastropods and two most abundant gastropod species groups. (B) Total polychaetes (including juveniles) and two most abundant polychaete morphotypes.

(sinking, swimming, and vertical component of the ambient flow) and turbulent diffusion. Vertical velocities and turbulence in the near-bottom flow of the axial summit trough might be substantial and vary temporally; for example, downward velocities up to 2 cm s⁻¹ have been measured in near-bottom flows at the Juan de Fuca Ridge, with turbulence dissipation rates up to levels observed in shallow waters (Garcia Berdeal et al. 2006; I. Garcia Berdeal, S.L. Hautala, M.J. Pruis, and H.P. Johnson, unpublished observations). Larvae may exhibit different swimming behaviors in response to different flow conditions (Metaxas 2001), and gastropod larvae, in particular, may exhibit sinking behaviors in response to turbulence (Fuchs et al. 2004). Strong swimmers (i.e., >1 cm s⁻¹), such as copepods, might avoid or be attracted to the sediment trap (e.g., Forbes et al. 1992), and the flux of copepods into the sediment trap was not correlated to abundance ($r = -0.19$) or horizontal fluxes ($r = -0.12$) at the pump moorings.

Our results are similar to a previous deep-water study, specific to passive particulate matter, that showed no effect of horizontal particle fluxes on vertical fluxes into sediment traps exposed to currents up to ~20 cm s⁻¹ (Gardner et al. 1997). Our results are in contrast to the study by Yund et al. (1991), however, which indicated a positive correlation between collection of crustacean larvae in cylindrical tube traps and both larval concentration and rate of horizontal advection. This relationship has been used in coastal field studies to infer concentrations and horizontal fluxes of barnacle cyprids from tube-trap collections (Bertness et al. 1992; Gaines and Bertness 1993). In our study, data for larvae collected by the sediment trap, in combination with current meter data, cannot be used as a proxy for larval concentrations or horizontal fluxes. Reasons for this discrepancy may include that larvae tested by Yund et al. (1991) were much larger, with greater sinking and swimming velocities than expected for larvae in our study (based on similar-sized gastropod and polychaete larvae; e.g., Chia et al. 1984, Butman 1989, Krug and Zimmer 2004). Also, our samples include larvae of all stages, and we might expect the abundance of competent larvae such as cyprids to correlate better to trap collections. In our samples, we might expect that a higher proportion of gastropods collected by the sediment trap would be competent than in simultaneous pump sampling, due to greater sinking velocities or downward-directed swimming in competent gastropod larvae (e.g., Krug and Zimmer 2004). However, we were not able to morphologically determine competency for larvae in our study. We have observed all of the gastropod species groups (Table 3), with the exception of *Laeviphipitus* sp., in benthic samples with no postlarval growth. Tissue degradation precluded enumerating setigers to determine competency of polychaete larvae in trap samples (e.g., Shanks and del Carmen 1997).

Comparison of sediment trap and plankton pump results: relative abundance and diversity—Our second objective in comparing the two sampling methods was to assess the selectivity of the sediment trap for certain types of larvae, relative to the plankton pump. We found clear differences in the relative abundance of larval groups during the simultaneous deployments, with the sediment trap consistently collecting a higher ratio of gastropod larvae to polychaetes than the plankton pump (although we must acknowledge that poor preservation of polychaetes in the trap samples likely resulted in underestimating their numbers). This result is consistent with the expectation that, in the absence of behavior, shelled gastropod larvae would have higher sinking velocities than similar-sized polychaetes, particularly after depleting lipid stores. Selectivity for certain larvae has been reported previously for tube traps of various designs (e.g., Yund et al. 1991; Todd et al. 2006) and suggested for a recent study with sediment traps (Khripounoff et al. 2008). Yund et al. (1991) noted that differences in swimming behavior among taxa, and between larval stages within a species, might influence collection by a passive

sediment trap. As expected, the sediment trap tended to exclude the stronger swimming crustacean zooplankton compared to the pump sampling; the ratio of copepods to total larvae collected in the pump samples (mean 15.00) was almost two orders of magnitude greater than in sediment trap samples (mean 0.29). An additional, qualitative comparison is that the sediment trap collected relatively large shells of pteropods and planktonic forams, expected to be part of the sinking particulate flux, that generally were not found in the pump samples.

The sediment trap appeared to be selective for certain gastropod species groups and polychaete larval morphotypes. *Cyathernia naticoides* was consistently the most abundant gastropod species in the sediment trap samples, whereas *Lepetodrilus* spp. dominated all of the pump samples (Fig. 5A, 6A). To determine whether the proportions of gastropod species groups differed between the simultaneous pump and sediment trap samples, we conducted paired *t* tests for 18 of the 29 groups (11 groups were considered rare, or only occasionally collected by the pump; Table 3). Paired *t* tests were significant for 8 of the gastropod species groups ($\alpha = 0.05$, $df = 4$; Table 3), confirming differences in the proportions sampled by the two methods. Because of the low numbers collected by the sediment trap, χ^2 tests were not an effective way to do pairwise comparisons of the daily gastropod collections. We also explored the pooled counts; approximately four times the number of gastropods and 20 times the total polychaetes were collected per day by the plankton pump (Table 3). Using the pooled expected ratios (4.12 for gastropod larvae and 21.26 for polychaetes), we assigned selectivity for those groups collected by the sediment trap at $>300\%$ or $<33\%$ of the expected count (Table 3). Overall, there did not appear to be a relationship between protoconch size and over- or undercollecting by the sediment trap (Table 3). In addition, of the 12 gastropod species not collected by the trap, six were large-diameter ($>200\ \mu\text{m}$) and six were small-diameter ($<200\ \mu\text{m}$) protoconchs. For the polychaetes, the two dominant morphotypes were collected in similar relative proportions by the pump and sediment trap (Fig. 5B, 6B). However, two polychaete morphotypes, *Archinome rosacea* and nectochaetes, were undercollected by the trap (Table 3). The selectivity did not appear to be related to larval size; nectochaete larvae were intermediate in size (170–380 μm) between the two most abundant morphotypes, *Ophryotrocha* sp. and *Chaetospaera* larvae (160–280 and 200–400 μm , respectively). Results for the proportions of polychaete morphotypes in the sediment trap samples may be biased by degradation upon transfer from DMSO solution to ethanol. We did not evaluate whether polychaete larvae were associated with marine snow, as part of the sinking particulate flux (e.g., Shanks and del Carmen 1997).

To further explore the selectivity of the sediment trap for certain gastropod species groups, we compared species diversity and similarity among the pump and sediment trap samples. All measures of species diversity indicated that the plankton pump samples were more diverse than the sediment trap

samples during the simultaneous sampling, including Fisher's α , Shannon-Wiener's information function H' , and Chao1 and Chao2 total species richness estimators [results not shown; EstimateS (Colwell 2006) and BioDiversity Pro (<http://www.sams.ac.uk/research/software/>)]. Pump samples had about twice the number of gastropod species groups (18–23 compared to 8–11 in sediment trap samples), although this might be expected owing to greater numbers of individuals sampled each day by the pump. We compared individual-based rarefaction curves for sediment trap samples (individually and pooled) against rarefaction curves for pump samples (individually and pooled) and confirmed the lower diversity of gastropod species in the sediment trap samples (Fig. 7). Similarity coefficients (Bray-Curtis and Jaccard) and Pearson correlations indicated strong similarity among pump samples and among sediment trap samples, and a nonmetric multidimensional scaling (nMDS) analysis clearly distinguished between pump and sediment trap samples (Fig. 8; Systat 11). Overall, the implication of these results is that the sediment trap was collecting only a portion of the larval gastropod diversity in the ambient species pool, analogous to the conclusion by Forbes et al. (1992) that lower diversity of zooplankton in sediment trap samples compared to net collections in the same area was partly due to selectivity of the traps.

Discussion

Suitability of the two sampling methods for measuring larval dispersal or supply—Our simultaneous deployments of the sediment trap and plankton pump differed in temporal patterns and types of larvae collected. We conclude that the two methods sampled different portions of the larval pool in the vicinity of East Wall Vent. The lack of correlation and species-specific and, potentially, stage-specific selectivity in collecting larvae preclude using sediment traps as a proxy for collecting larvae via plankton pumps. However, the use of time-series sediment traps for continuous time series of downward larval flux has a potential advantage over plankton pumps in providing insight into larval supply to hydrothermal vent communities. Below, we consider the advantages and disadvantages of each method in time-series studies of larvae near hydrothermal vents.

The major strengths of plankton pump sampling are for assessing larval abundances and diversity on short time scales (<1 day to several weeks). Assessing larval concentration in conjunction with horizontal flow enables estimates of larval horizontal advective flux, important in studies of larval dispersal. Although pumps have some sampling biases (e.g., Powlik et al. 1991; Liu et al. 2005), a large-volume, fast intake rate pump as tested in this study should be far less selective than passive sediment traps in terms of collecting planktonic larvae (see discussion of pump sampling efficiency in Johannsson et al. 1992). Pump sampling is well suited for short time series because multiple deployments can be conducted during a cruise, and far more individuals can be collected in a short time period than with a sediment trap.

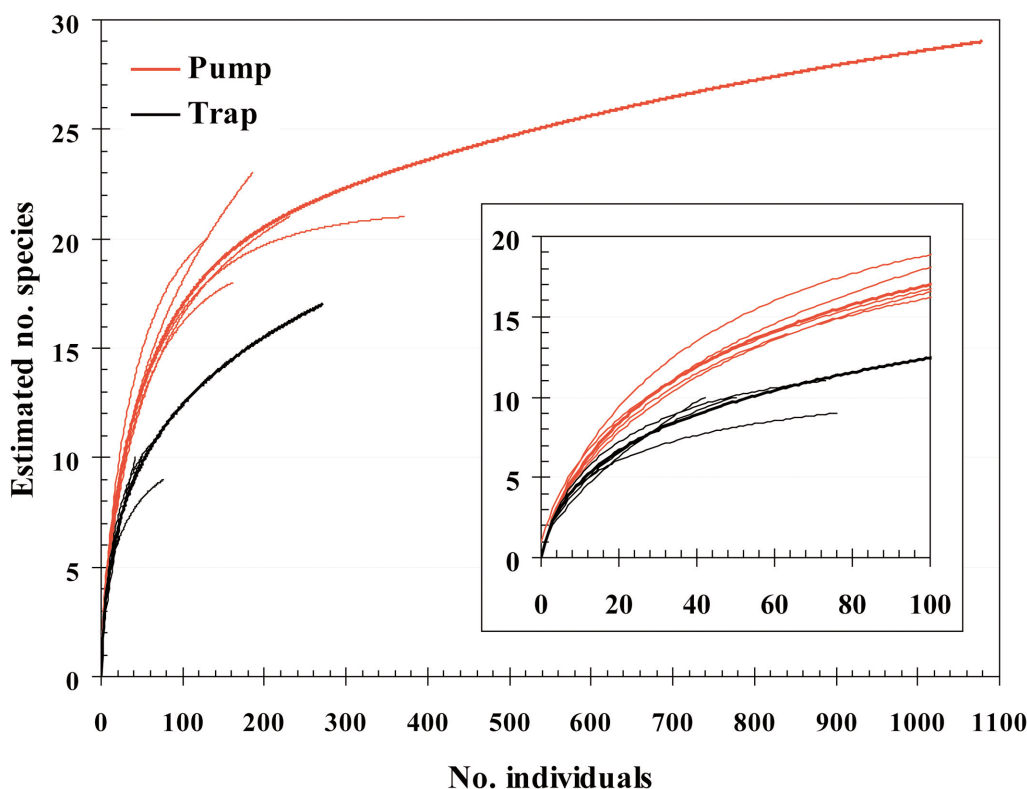


Fig. 7. Individual-based rarefaction curves for gastropod species groups for each day (thin lines) and the pooled 5 days (thick lines) of sediment trap and pump sampling.

In comparison to time-series sediment traps, currently available plankton pumps are not effective for long time-series sampling of deep-sea larvae, because of the battery power required for pumping large volumes. Pump sampling requires repeat cruises for long-term studies of larval abundance, creating very intermittent time series that are not likely to resolve temporal patterns. Even in shallow-water studies, it is often difficult to determine if the lack of correlation between pump (or net) samples and larval settlement is due to intermittent plankton samples versus integrative settlement panel studies (Gaines and Bertness 1993; but see Miron et al. 1995). This disadvantage might be overcome at select sites in the future with power provided through seafloor observatories (e.g., Ocean Observatories Initiative, http://www.joiscience.org/ocean_observing), and with the development of large-volume, time-series pumps with internal sample preservation.

In contrast to plankton pumps, a major advantage of time-series sediment traps is the ability to collect continuous, long time series of larvae autonomously, because of low power requirements and preservative. Sediment traps were deployed to collect larvae for 6-month time series following this study (Adams 2007) and for >1-year time series after the eruption at the East Pacific Rise in 2005/2006 (L.S.M., unpublished data). For preservation of DNA, we recommend a DMSO solution, which does not preclude additional analyses of sediment trap

samples for multidisciplinary studies, such as particulate mineral fluxes (e.g., Khripounoff et al. 2001).

The selectivity of sediment traps in collecting larvae limits their utility for community-level studies, but may provide a useful way to quantify downward fluxes of some species as a proxy for larval supply to the benthos. Studies in shallow waters have indicated a strong correlation between larval supply, as determined by tube traps, and larval settlement (Yund et al. 1991; Bertness et al. 1992; Gaines and Bertness 1993; Todd et al. 2006). The use of time-series sediment traps is likely to lead to new insights into the influence of larval supply on temporal patterns of colonization at deep-sea hydrothermal vents. Selecting for larvae with downward trajectories might exclude or limit collection of larvae that are dispersing or precompetent and enhance the collection of settling and competent larvae that may exhibit behaviors including swimming downward or increased sinking velocity (Metaxas 2001; Krug and Zimmer 2004). Future studies using sediment traps to collect larvae near hydrothermal vents will benefit from simultaneous measurements of hydrodynamics (vertical velocities and turbulence in the ambient flow) and larval developmental stage (e.g., gene expression in competent larvae), as well as knowledge of species-specific and stage-specific behavior.

Short-term variability in larval abundance and downward flux—Although previous studies at the East Pacific Rise have

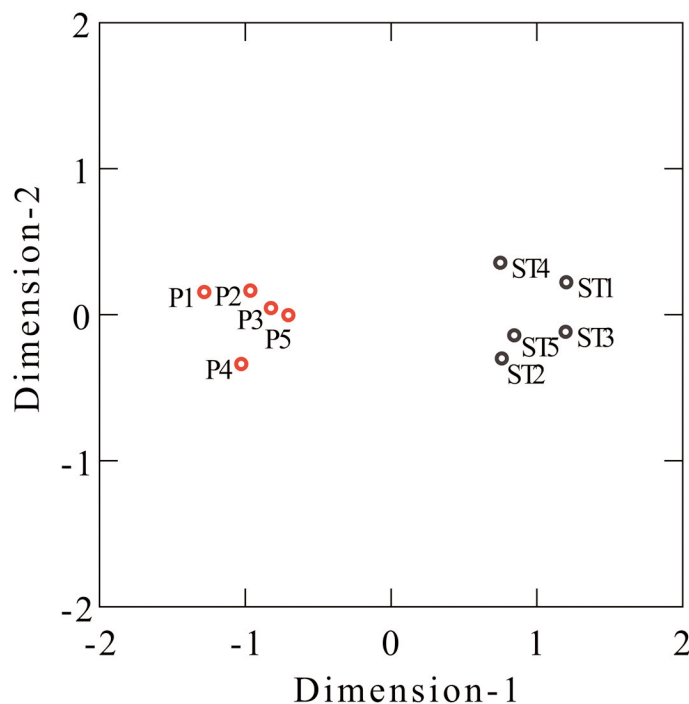


Fig. 8. Nonmetric multidimensional scaling (nMDS) analysis of species composition of gastropod larvae collected in the 5 days of simultaneous sampling by the sediment trap (ST) and pump (P). Analysis conducted on Pearson correlation matrix. Kruskal stress = 0.025; proportion of variance = 0.998.

indicated variability in larval abundance among widely spaced time points (months to years; Kim and Mullineaux 1998; Mullineaux et al. 2005), our study was the first to examine variability in larvae in this region near the same vent site on day-to-week time scales. Both the plankton pump and sediment trap samples were highly variable in the numbers of larvae collected on these short time scales. The overall range in larval abundance during this short-term study equaled (gastropod larvae) or exceeded (polychaetes) that of all previous pump deployments in the axial trough near East Wall Vent during four cruises in 1998–2000 (Fig. 9; Mullineaux et al. 2005). The observation by Mullineaux et al. (2005) that the abundance of some taxa ranged an order of magnitude among samples in 1998–2000, held true on day-to-week time scales for some larval gastropod species and polychaete groups in this study. Comtet et al. (2000) reported an order of magnitude variability in the numbers of bivalve larvae collected in a sediment trap in contiguous 4-day periods at a vent on the Mid-Atlantic Ridge. Adams and Mullineaux (2008) suggest that variation in horizontal transport from local larval sources might have contributed to short-term variability in larval fluxes into sediment traps during our short-term study at the East Pacific Rise.

The daily variability in larval abundance indicates that snapshot sampling (i.e., sampling restricted to intermittent research cruises) is likely to alias higher frequency changes in

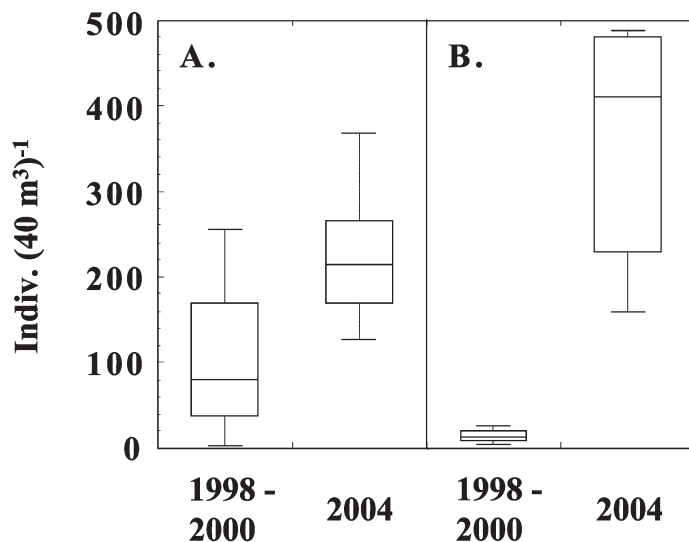


Fig. 9. Box-and-whisker diagrams (box plots) for larval abundance in this short-term study ($n = 5$; single cruise in 2004) compared to previous plankton pump sampling ($n = 4$; one sample per four cruises in 1998–2000) near East Wall Vent. Each box has lines at lower quartile, median, and upper quartile values; whiskers indicate range. (A) Gastropods. (B) Polychaetes (including juveniles).

larval abundance near vent sites. For instance, the variation in numbers of larvae observed on cruises separated by 1 year (Metaxas 2004) or several months (Mullineaux et al. 2005) may reflect variation occurring on much shorter time scales. Finally, to highlight the importance of continuous time-series sampling, we note the difficulty in explaining why the pump samples in November 2004 had a higher mean abundance of gastropod and polychaete larvae than previous pump sampling in 1998–2000 (Figure 9; Mullineaux et al. 2005). Because we lack samples from 2001–2003, we cannot determine whether there was a long-term increase in larval abundance associated with older local communities (i.e., post-1991 eruption) or whether hydrodynamic effects such as local retention caused elevated concentrations of larvae during the Nov 2004 cruise.

Comments and recommendations

Part of our motive for this study was development of a larval sampling program to be used at seafloor observatories planned for mid-ocean ridges. The variability in numbers of larvae collected on day-to-week time scales and the lack of correlation between sampling devices have implications for a sampling design to assess periodicity and long-term changes in larval abundance and supply near deep-sea vents. Currently, because of limited battery power, large-volume pumps are restricted to single samples per deployment; for the future, we recommend the design of a large-volume pump with internal sample preservation for time-series sampling of larval abundance. Pumps are a means to quantify larval concentration that can be combined with current meter data for calculations of horizontal fluxes, important in modeling larval

dispersal. Sediment traps collect downward fluxes that might select for settling larvae, important in larval supply to benthic communities. Overall, sediment traps, which can collect sequential samples during a long-term deployment, are a promising technique for time-series studies of larvae near hydrothermal vents, but more work is required to evaluate species- and stage-specific differences in the traps' sampling efficiency. Either method of collection would benefit from improved techniques to assess larval competency, which would help answer whether larvae are dispersing or settling. Future studies should carefully consider which quantity—larval abundance in the plankton or downward flux of larvae—is most appropriate to address specific research goals.

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Submitted 9 June 2008

Revised 12 January 2009

Accepted 1 February 2009