



Amphipods on a deep-sea hydrothermal treadmill

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Abstract—Conspicuous swarms of a pardaliscid amphipod were observed at about 2520 and 2580 m depth in the East Pacific Rise vent field during dives with the submersible *Alvin*. Swarms occurred in association with mussels, clams and tubeworms, and were located above, and immediately downstream of cracks with emanating hydrothermal water. Numerical density sometimes exceeded 1000 individuals l^{-1} , which is 3 orders of magnitude greater than any previous report on pelagic crustaceans from the deep sea. The amphipods, however, were not obligatory swimmers, and thin-layered shoals and scattered individuals were observed. Orientation of individuals was often polarized as they headed into the venting flow, swimming vigorously at 5–10 $cm\ s^{-1}$ to maintain their position in the current. Retention within the preferred habitat requires an average swimming speed corresponding to the average current speed, suggesting a sustained swimming of >10 body lengths s^{-1} . These observations contrast with the general concept of low swimming activity in deep-sea crustaceans.

INTRODUCTION

HYDROTHERMAL vents are characterized by high biomass of benthic organisms sustained by chemoautotrophic production. There are also some reports of enhanced abundance of plankton associated with vents (SMITH 1985; BERG and VAN DOVER, 1987), but the level of plankton enrichment at vents versus non-vent deep-sea sites is not well established. Furthermore, the nature of the trophic coupling between planktonic and benthic systems is uncertain.

Vents are unique and ephemeral habitats, with life spans on the time scale of decades, and vent fields are isolated from each other, sometimes by as much as 100s to 1000s of kilometers. Larval dispersal is therefore crucial for the survival of sessile vent organisms on an evolutionary time scale (e.g. LUTZ *et al.*, 1984). For endemic vent plankton, however, retention within the vent habitat may be the immediate critical need. Entrainment by the buoyant plumes emanating from the vents (e.g. MULLINEAUX *et al.*, 1991) may conceivably deplete local plankton populations, as may displacement by other currents, although accumulation of particles entrapped in convection cells established around the vents (LONSDALE, 1977; ENRIGHT *et al.*, 1981) has been suggested as a mechanism to raise biomass of zooplankton (BERG and VAN DOVER, 1987). Alternatively to these scenarios of

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passively drifting plankton, adapted vent species may possess behavioral traits to assure retention, equivalent to what has been suggested for plankton in other geographically confined and specialized habitats like estuaries and coral reefs (e.g. SINCLAIR, 1988).

During dives with the deep submersible *Alvin* at the East Pacific Rise in December 1991 (9°50'N, 104°W–9°30'N), we observed conspicuous "plankton" swarms associated with venting water. These swarms caught our attention for two reasons. The concentrations of pelagic individuals apparently surpassed any previous reports from the deep sea, and the swarms maintained strikingly fixed positions in an environment which, with respect to the size of the animals, was highly advective. A brief description of the phenomenon was given by VAN DOVER *et al.* (1992). The swarms consisted of a near monospecific assemblage of a previously undescribed pardaliscan amphipod, 3–5 mm in length. In the present paper, we provide further data on distribution and behavior of the swarming individuals, current velocities, and finally, we discuss possible mechanisms underlying swarm maintenance in the advective field.

AREA DESCRIPTION

The Venture Hydrothermal Fields are located along the East Pacific Rise from 9°11'N to 9°54'N (HAYMON *et al.*, 1991a). Hundreds of geologic and biologic hydrothermal features have been mapped in this region during previous *Argo* and *Alvin* surveys (HAYMON *et al.*, 1991a,b). The region is both tectonically and volcanically active, with evidence of recent lava extrusions during May 1991. Our D.S.V. *Alvin* dives took place in two East Pacific rise study sites: one between 9°46' to 9°51'N at about 104°18'W along the axial ridge in a region of recent volcanism, and the other centered on 9°31'N, 104°14'W, which is an older site where the Ocean Drilling Program has undertaken a survey in preparation of drilling operations. Swarms of amphipods were encountered at both study sites (Fig. 1).

The study areas had shallowest depths of ~2500 m along the ridge crest and increasingly deeper depths down the ridge flanks to the east and west. There was a cleft or depression (axial graben) of 100–200 m width and 30–100 m depth on the crest where active venting and volcanic action was occurring. The seafloor in this region of the ridge was comprised of lava pillow, fractured pillows, lava pillars, and occasional sheet flows. Ambient bottom water was approximately 1.8°C. Plumes of geothermally heated seawater emanated from the vent sites as diffuse flows or buoyant jets (black smokers). The most common hydrothermal effluent was shimmering water that emanated from small cracks (centimeters width) or large fissures (meters width) in the axial graben. Temperatures in these diffuse flows were measured from a few tenths of a degree above ambient up to 20°C. Higher temperatures were measured in flows coming out of holes in the seafloor and from chimneys.

Megafauna of the largest vent communities within the Venture Hydrothermal Fields is typically dominated by the mussel *Bathymodiolus thermophilus* and decapods (galatheid squat lobsters, *Munidopsis subsquamosa* or the brachyuran crab *Bythograea thermydron*). They occur on fields of flat sheet flow and low-relief lobate lavas where shimmering warm water is diffusely venting. Smaller invertebrates, i.e. limpets, coiled gastropods, serpulid worms and anemones, are associated with the larger megafauna. Living and dead clams, *Calyptogena magnifica*, were scattered throughout the area, often in association with the mussel beds. The tubeworm, *Riftia pachyptila*, was less common, but a dense concentration was observed at a basalt pillar in the middle of a small drainback basin. The pillar,

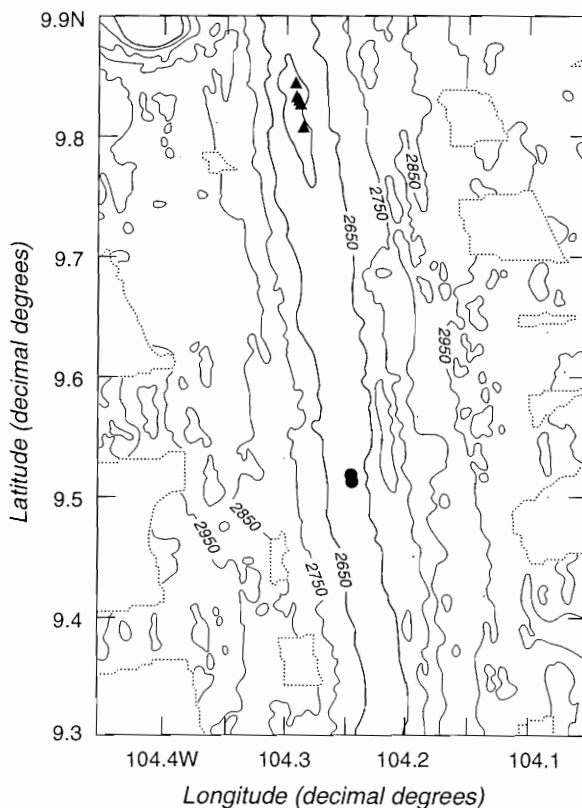


Fig. 1. Locations of dive sites with amphipod swarms at the East Pacific Rise. The dotted lines enclose areas on the flanks of the rise in which there were no topographic data.

10 m in height, was venting hot water at a maximum measured temperature of 124°C. Warm water emerged from between the tubeworms and varied from just above ambient ($\sim 2.0^{\circ}\text{C}$) to 3.7°C . At this site, two other tubeworms co-occurred, *Tevnia jerichonana* and *Oasisia alvinae*.

MATERIALS AND METHODS

Swarm shape and size, and animal swimming behavior and abundance were examined using video records. A total of 2 h of videotape from an Osprey camera mounted on the submersible and a Sony handheld camera has been analysed. Abundance of individuals was estimated from video images. The distance between neighbors was measured, and density (ind. m^{-3}) estimated assuming a closest packing configuration (e.g. NICOL, 1986) where $\text{number m}^{-3} = 1/d^2L$ (both distance between individuals (d) and length of individuals (L) in meters).

Swimming speed was deduced from estimates of current velocity surrounding individuals that maintained a fixed position. At four sites, current velocities within swarms were calculated from time and distance travelled of either (1) passive drifting particles in the flow field, (2) dye injected in the flow, or (3) moving edges of murky venting water.

Distance travelled was estimated using objects of known size as reference, generally the swarming individuals themselves, this minimizing errors related to the depth of field of the video images. Eleven independent observations were made at each site.

Additional measurements of near-bottom flow were done by tracking dye streams as they dissolved from small pellets (0.5–1.0 cm in diameter) of fluorescein dye mixed with beeswax, following the methods used in MULLINEAUX and BUTMAN (1990). The pellets were attached at 10-cm intervals on thin, moored, vertical lines so that they were suspended 10–50 cm above the seafloor. Flow speeds were estimated from video images of the dye streams, recorded at right angles to the flow direction. Dye speeds were corrected for minor deviations in camera angle, and were divided by a factor of 0.9 to compensate for the retarding effect of the mooring wake. When possible, at least five separate dye streams were measured at each height off the bottom. Fewer measurements were recorded when the image quality was not adequate.

Dyestrings were deployed outside direct influence of venting water as well as in locations where speeds were accelerated by vertical velocities in buoyant plumes. In one location (Dive 2480), dye string measurements were done close to an amphipod swarm, concurrent to estimates using drifting particles, as described above.

To evaluate environmental gradients (created by venting water) in the locations occupied by the swarms, temperatures were measured within the center and at the outer fringes of the swarms.

RESULTS

Swarm distribution

Swarms were found close to sources of hydrothermal flow, and were generally associated with mussels, clams and tubeworms, although swarms also were observed at sites devoid of sessile macrofaunal assemblages. Most observations were within mussel beds (e.g. Fig. 2), possibly due to the prevalence of this type of habitat in the vent field. However, at our northern dive site, where a very rich mussel bed was established, swarms were infrequent and hard to locate. At the southern dive site, characterized by more scattered clutches of mussels (e.g. Fig. 3), there was a swarm above most of the clutches.

Swarms associated with mussels and clams were situated above and downstream of the clutches, and very few individuals were found upstream. A leading edge was clearly delineated (e.g. Fig. 2), lining up with the visibly murky venting water. (The trail of the flow could sometimes actually be mapped from the amphipod distribution.) Swarms were generally found within 0.5 m of the bottom and occupied a volume of $<1 \text{ m}^3$.

The appearance and locations of each swarm remained fairly consistent throughout individual observation periods, which spanned up to several hours. There were, however, variations in swarm shape, possibly related to small scale variations in the flow field, and on one occasion, the whole swarm relocated about 1 m in the course of a few minutes.

Swarm size and numerical density of animals varied, and the amphipods were not obligatory swarmers. On the upper extreme, numerical densities could exceed 10^3 ind. l^{-1} in the densest part of the swarms (see legend of Fig. 4). Intermediate concentrations were found in thin shoals of amphipods swimming in mussel beds and above tube worms (e.g. Fig. 5). We made one observation of an assembly of approximately 50 amphipods crowding around a crab, congregating of scales of 10s of centimeters. We could not decide

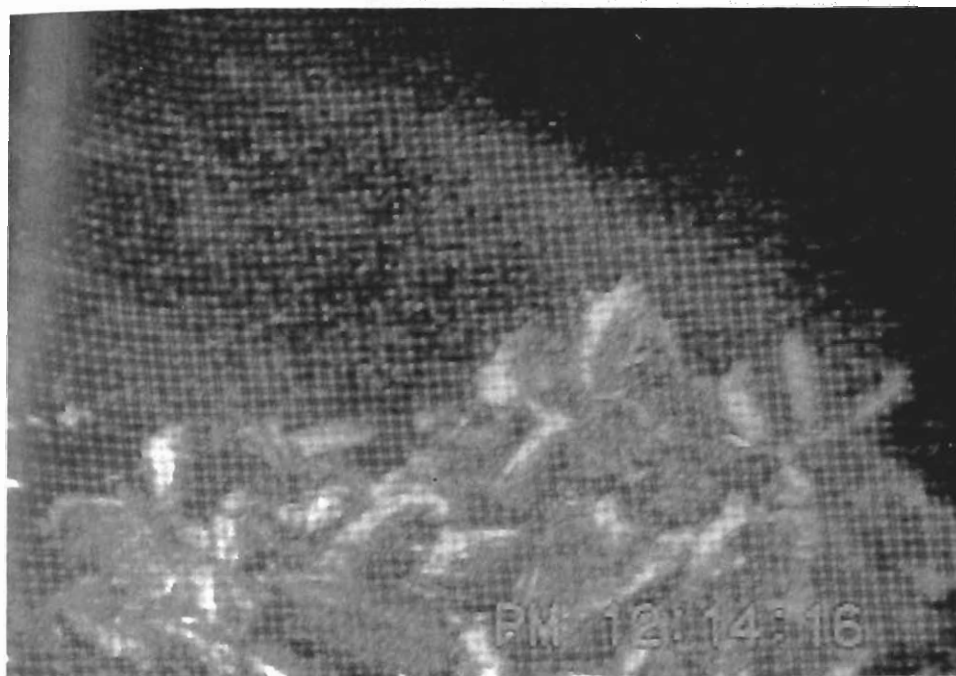


Fig. 2. Swarm of amphipods above a clutch of mussels (photograph taken from a video image). Note the sharp slanting delineation of the swarm in the upstream direction as the animals maintain their position in the emanating water.



Fig. 3. Typical environment at southern dive site consisting of barren pillow lava, crabs and clutches of mussels with amphipod swarms, indicating the extremely patchy plankton distribution encountered in the vent field. The dye patch was injected into the swarm associated with the mussels on the lower right of the picture <30 s earlier (automatic series of pictures taken at 30 s intervals). The dye drifted away while the amphipods remained stationary. When the next picture was taken 30 s later, the dye patch had drifted beyond the photographed region.

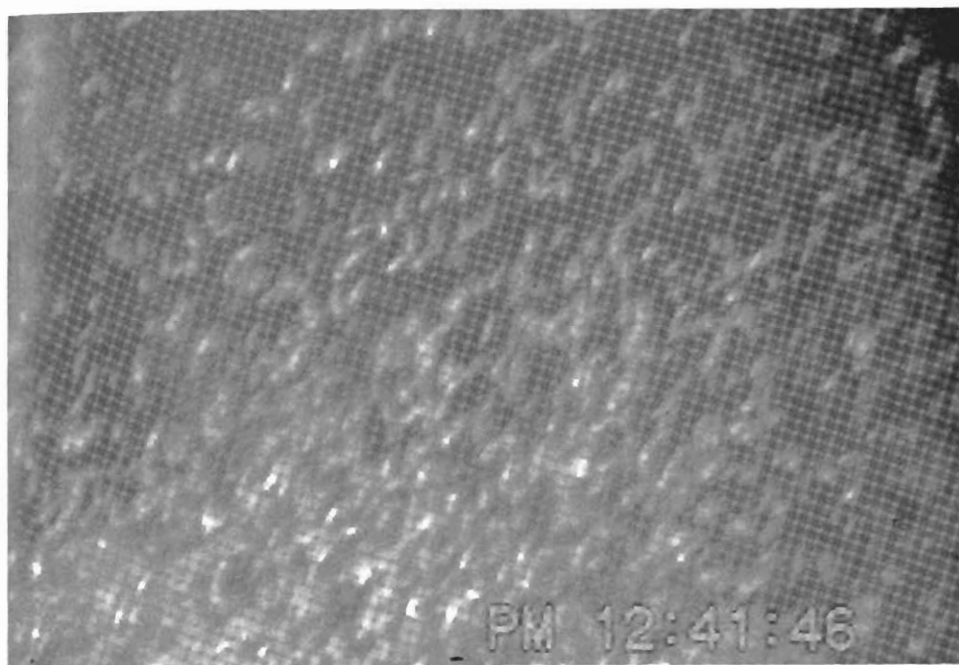


Fig. 4. Individual amphipods heading diagonally into the venting flow (photograph taken from a video image). An accurate distance between neighbors in the three-dimensional swarm may not be obtained from the two-dimensional image due to diffuse focusing, but the picture suggests a numerical density exceeding 1000 ind. l^{-1} as the swarm becomes denser toward the lower part of the photograph. For 1, 2, and 3 body length distances between individuals (assumed body length of 5 mm), a closest packing model estimates 10,000, 2000 and 833 ind. l^{-1} , respectively.

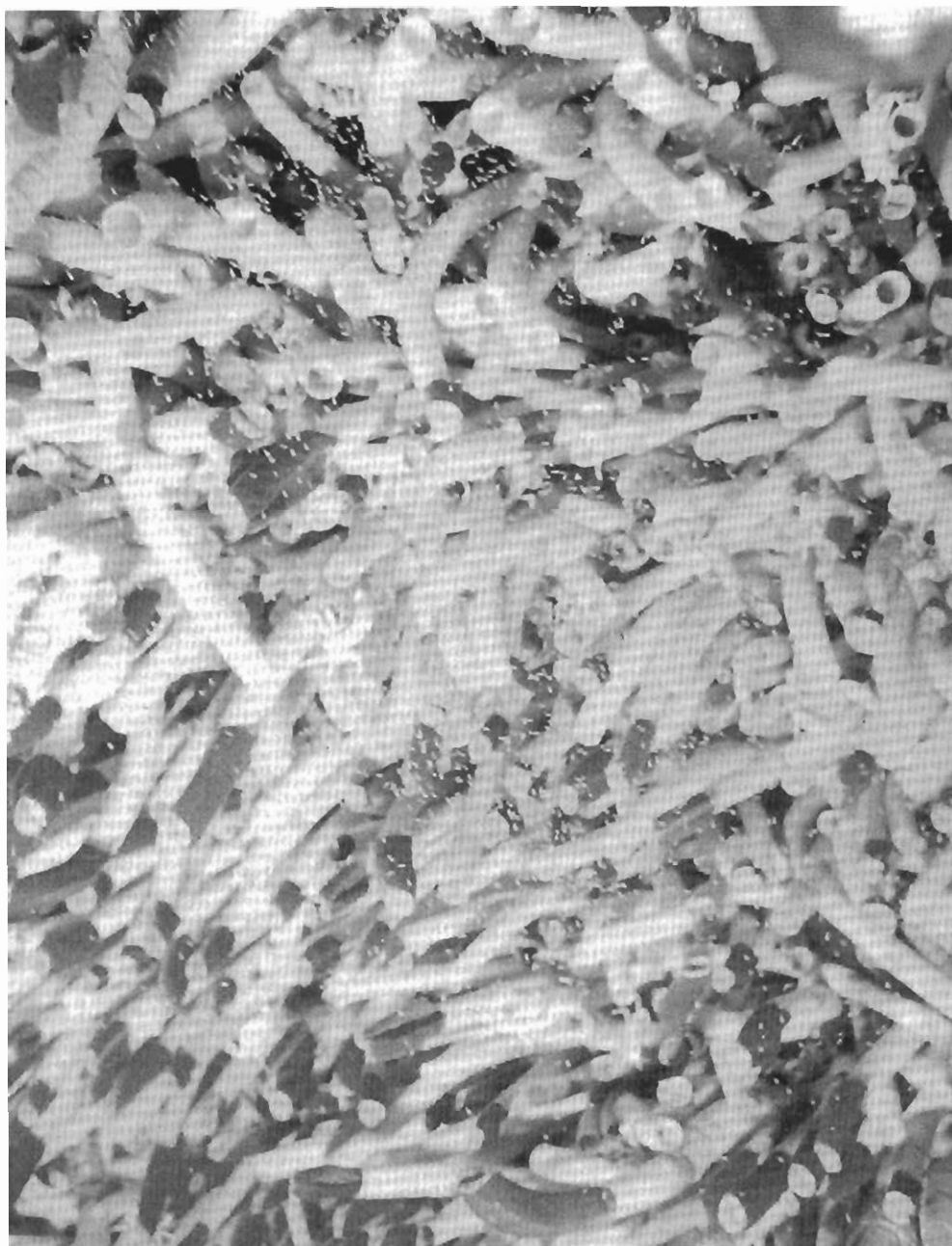


Fig. 5. Shoal of amphipods above tubeworms. Note the mainly polarized distribution as the animals line up swimming against the current.



Fig. 7. High concentrations of amphipods swimming close to a vent opening (photograph taken from a video image). Here orientation appears less polarized than in Figs 4 and 5 as individuals are heading into the source from different directions and several animals are drifting away with the flow. Parts of three mussels and their siphons are seen to the right of the picture.

Table 1. Currents within amphipod swarms at four different sites estimated from time and distance travelled by passively drifting objects (11 observations on each site)

Dive	Location	Depth	Mean speed (cm s ⁻¹)	S.D.* (cm s ⁻¹)
2472	9°49.79'N, 104°17.40'W	2517	7.5	0.92
2479	9°30.85'N, 104°14.50'W	2584	7.3	1.04
2480	9°30.89'N, 104°14.67'W	2583	7.7	1.63
2482	9°30.87'N, 104°14.67'W	2583	6.8	0.95

*S.D. = standard deviation.

whether the crab itself was attracting the amphipods, if it was located at a tiny crack with venting water, or if it had a prey item attracting the amphipods. Single individuals were also observed swimming in areas apparently not directly influenced by venting hydrothermal water, but such observations were underrepresented by our filming procedure, as we selectively focused on conspicuous aggregations.

Temperature measurements revealed small gradients from the fringe to the center of a swarm. At a single site, the amphipods were found in temperatures up to 8°C, compared to ambient temperatures of 1.8°C. However, temperature gradients associated with most swarms were generally small (temperatures in the core of swarms elevated by only a few tenths of a degree), and at outer fringes of the swarms temperatures were always close to ambient.

Current velocities

Video recordings of four amphipod swarms appeared useable for estimates of current velocities using drifting objects. While there was some variation between single measurements, the average current velocities in the venting water were estimated at around 7 cm s⁻¹ at all sites (Table 1).

These current speeds to a large degree are caused by vertical flows from the buoyant vent fluids. One set of profiles with dye strings taken 15 m upstream of a swarm, within a few centimeters of the swarm, and 15 m downstream, showed that current speeds were substantially higher in the swarm environment (Fig. 6). The average velocity at 50 cm above bottom determined from the dye string experiment (7.3 cm s⁻¹) was very similar to the concurrent estimates from drifting particles (average 7.7 cm s⁻¹).

Away from the influence of venting water, horizontal velocities ranged from <1 cm s⁻¹ to almost 6 cm s⁻¹ (Table 2). Horizontal velocities did not show a classic log-linear profile near the bottom, because the bottom roughness elements were on the same order as, or larger than, the height of the profiles.

Our measurements were averaged over less than 10 min and are therefore not necessarily representative of speeds over the range of tidal currents. Preliminary analyses of short-term (2–3 days) current meter records from sites near the amphipod swarms indicate that currents at 5 m above the bottom are strongly tidal, and vary in speed from less than 2 cm s⁻¹ to 15 cm s⁻¹ (S. L. KIM, personal communication). The corresponding current velocities at the height of the amphipod swarms are likely to be lower, but also will be influenced by tidal fluctuations. Given conservative estimates of vertical diffuse vent

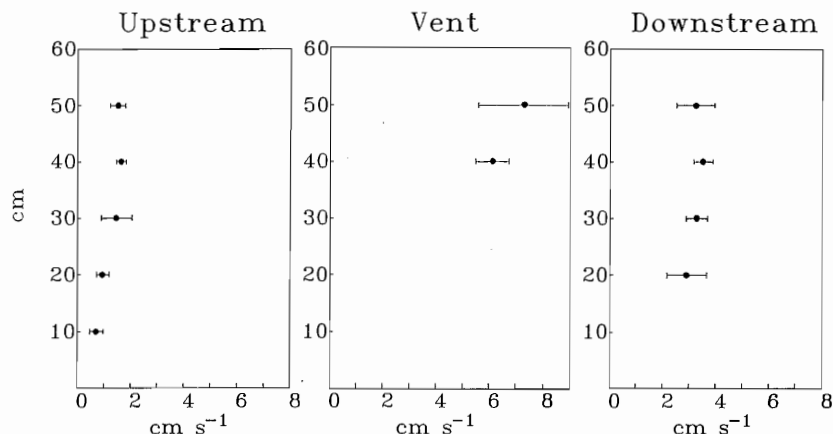


Fig. 6. Flow speeds (mean and standard deviations) from video images of dye streams near amphipod swarm during Dive 2480. Dye strings were deployed at three locations; 15 m upstream of vent, at vent, and 15 m downstream of vent.

flows (5 cm s^{-1}) and horizontal tidal flows within 50 cm of the bottom ($0\text{--}6 \text{ cm s}^{-1}$), the tidal variation in flow speeds at most diffuse vents appears to be relatively moderate ($5\text{--}7.8 \text{ cm s}^{-1}$ by vector addition) due to the prevalence of the buoyant component.

Animal orientation and swimming activity

Swarms were maintained at geographically fixed locations, although exposed to the continuous flow of venting water. Dye injected into the swarms rapidly drifted away, whereas the amphipods remained more or less stationary (Fig. 3) by swimming against the currents. The estimates of current velocities (Table 1, Fig. 6) suggested that a swimming speed of $5\text{--}10 \text{ cm s}^{-1}$ was required for position maintenance, representing >10 body lengths s^{-1} . Close to the outlet of venting water, we observed amphipods heading diagonally down into the stream, swimming vigorously to stay in the flow. In some locations, abundance of animals was low in the lowermost centimeters near outlets, while elsewhere high concentrations were found all the way down to and among the mussels clustering the vent opening (Fig. 7).

Successful position maintenance against the current, however, did not mean that animal location was fixed on scales less than 1 m. At some sites there was an apparent cyclic swimming pattern; animals worked their way towards the source of the flow, drifted back, turned and repeated the cycle. Sometimes single individuals "were lost" at the tail of the swarm, drifting away into the darkness. Usually, there were small scale lateral movements, with animals undulating sideways back and forth in the flow field.

The orientation of the amphipods was primarily, but not exclusively, polarized (e.g. Figs 4, 5 and 7). Polarization was partly broken because vent flow was pulsed and turbulent, and each individual seemingly headed into the prevailing current of their micro-environment. Pulsed flows also caused transient disorder as physical forces temporarily overpowered animal behavior. Cyclic swimming behavior, as described above, was an additional cause for the breakdown of orientation order.

On several occasions, we observed amphipods "colliding" with mussels, crabs and other

Table 2. Mean and standard deviation of flow speeds, calculated from video images of dye eddies released from dye-ball moorings. Speeds represent horizontal velocities in the benthic boundary layer, except on Dives 2476-p and 2480-p, where speeds are influenced by vertical velocities in buoyant plumes

Dive	Location	Depth (m)	Height* (cmab)	Speed (cm s ⁻¹)	S.D. (cm s ⁻¹)	No. obs.
2469	9°47.75'N, 104°17.05'W	2518	10	5.5	0.67	5
			20	5.8	0.85	5
			30	4.4	0.36	5
			40	4.2	0.24	4
			50	4.1	0.54	3
2471	9°49.76'N, 104°17.39'W	2517	40	2.1	0.60	5
			50	4.2	0.38	3
2475	9°50.30'N, 104°17.44'W	2515	40	4.3	0.38	3
			50	5.3	0.57	5
2476-p	9°47.18'N, 104°16.96'W	2521	10	4.1	0.70	5
			20	5.1	1.3	4
2480	9°30.88'N, 104°14.67'W	2582	10	0.7	0.18	7
			20	0.9	0.24	5
			30	1.5	0.57	7
			40	1.6	0.12	5
			50	1.5	0.28	5
2480-p	9°30.89'N, 104°14.67'W	2583	40	6.1	0.61	2
			50	7.3	1.7	7
2480	9°30.89'N, 104°14.67'W	2583	20	2.9	0.75	7
			30	3.3	0.37	4
			40	3.5	0.34	5
			50	3.2	0.69	6
2482	9°30.91'N, 104°14.67'W	2583	10	2.1	0.45	7
			20	2.2	0.33	7
			30	3.0	0.51	7
			40	2.4	0.62	7
			50	2.8	0.74	7

*cmab = centimeters above bottom.

substrate, and immediately altering their swimming direction. We could not decide whether this was accidental, or if the amphipods intentionally searched for the substrate. Infrequently, we observed amphipods settling on mussels.

DISCUSSION

The morphology of the swarming pardaliscid amphipod is well adapted for swimming, with strongly developed pleopods (VAN DOVER *et al.*, 1992). Until our findings, pardaliscids comprised only about 1% of the amphipod individuals collected in vent communities (BARNARD and INGRAM, 1990). The remainder consisted of lysianassids, with an overwhelming dominance of a single species. The lysianassids contain all known deep-sea

necrophagous feeders, but many feeding types occur (THURSTON, 1990). By contrast, most pardaliscids are predators or shallow infaunal detritivores (BOUSFIELD, 1982).

The high numerical density in the swarms exceeds any so far reported in the deep-sea literature. SMITH (1985) reported on a single aggregation of a copepod, *Isaacsicalanus paucisetus*, at another vent site on the East Pacific Rise. Estimates from pump samples were 920 ind. m^{-3} , and according to SMITH (1985) this abundance "is substantially higher than any previously measured in the deep sea". Our estimated density of amphipods exceeds this by 3 orders of magnitude. Dense assemblages of shrimps were found at vents in the Atlantic (RONA *et al.*, 1986; VAN DOVER *et al.*, 1988), but these were mainly crawling on the substrate and did not exhibit swarming in the water column unless disturbed by submersible operations.

Possible adaptive significance of swarm formation

High food supply represents the most apparent adaptive advantage of inhabiting outlets of venting water. Like the high macrofaunal benthic biomass surrounding the vent openings, the aggregates of amphipods evidently rely on some sort of bacterial growth, as the high biomass cannot be accounted for by any other known food source. Increased growth rates in elevated temperatures could possibly represent an alternative explanation (feeding in cooler water outside the flow, digesting in warmer water in the flow; e.g. WURTSBAUGH and NEVERMAN, 1988), but this is unlikely in the present case because of the slight temperature gradients involved (large proportion of individuals in water with temperature only a few tenths of a degree above ambient) and the apparent high metabolic cost of swimming against the emanating water.

At least three food sources are possible: (1) the amphipods forage on bacteria (flocclates) emitted with the venting water; (2) they forage on the vent macrofauna (cf. our observations on "collisions" between amphipods and macrofauna); or (3) they are fuelled by symbionts getting their energy from reduced compounds in the venting water. While the relative importance of these potential sources remains to be determined, our results clearly indicate a coupling between benthic primary production and pelagic production in vent communities.

Mechanism underlying swarm maintenance

The video records show that the amphipods persisted in preferred positions in the flow field by swimming against the current. Actually, these animals should be considered as 3–5 mm nekton in flow of $5\text{--}10 \text{ cm s}^{-1}$. In terms of body length, this swimming capacity surpasses that of the highly mobile antarctic krill (*E. superba*) (KILS, 1979; HAMNER, 1984). Our estimates of sustained swimming speed add up to substantial "distance" travelled on this hydrothermal treadmill. By assuming average swimming at 7 cm s^{-1} (faster when making forward progress against the current, slower when drifting back) we estimate that the amphipods swim 252 m h^{-1} , or about 6 km day^{-1} . LAVER *et al.* (1985) found swimming speeds of larger scavenging deep-sea amphipods of 7 cm s^{-1} , generally representing $1\text{--}3$ body lengths s^{-1} and a maximum of 5 body lengths s^{-1} . These velocities were considered as short term maximum values for highly motivated animals searching food in the odor plume of baits. The metabolic cost for such swimming excursion represents a significant fraction of total stored energy (SMITH and BALDWIN, 1982).

We do not know whether single individuals occupy the same site for days or longer, or if they have resting periods (cf. observations of animals drifting away from swarms and individuals settling on mussels). Amphipods outside the buoyant plume clearly experience lower current velocities (e.g. Fig. 6 and Table 2). However, our observations suggest low "turnover rates" and consequently long residence time (i.e. long activity period) of individuals within a swarm. Filming upstream revealed low flux of animals into the swarms, and the numbers of animals drifting away from a swarm seemingly were low in comparison with the huge number of individuals within a swarm. Regardless, the high amphipod swimming activities suggest a substantial metabolic cost. Reports so far have concluded that deep-living pelagic crustaceans and fishes generally have considerably lower O_2 -consumption (by at least a factor of 10) than do shallower living species (CHILDRESS and MICKEL, 1985; GIBBS and SOMERO, 1990). Pressure apparently has no part in this decline (MICKEL and CHILDRESS, 1982). Rather, CHILDRESS and MICHEL (1985) suggest that lower metabolic activity mainly results from relaxation of selection for strong swimming abilities at greater depth due to changes in predator-prey interactions. Our results apparently are unique in reporting a deep-sea locality providing a strong selection pressure for elevated swimming activity and show that, when required, high swimming power actually is evolved.

The vigorous amphipod swimming, implying a high respiratory rate, likely partly takes place in vent waters containing hydrogen sulfide (cf. observations of amphipods swimming in among mussels at the vent openings; Fig. 7). Hydrogen sulfide is a highly reduced component and an extremely toxic compound that can poison aerobic respiration at very low concentrations (POWELL and SOMERO, 1983; FELBECK *et al.*, 1985). Thus it would appear that these amphipods have some adaption to avoid HS^- toxicity, as found in other vent-living organisms (e.g. SANDERS and CHILDRESS, 1992).

Cue to swarm maintenance

Our observations suggest some possible cues these amphipods may use to regulate their swimming behavior to achieve retention. They seem able to sense currents, as we observed from their escape reactions when sampling them by pump. They accordingly may use the direction and velocity of the turbulent venting flow as stimuli for adjusting swimming behavior. The zone nearest the vent outlet is an environment of strong physical and chemical gradients (e.g. JOHNSON *et al.*, 1986, 1988), which also may serve as stimuli. However, at present we are not able to discriminate between these options. Light radiating from hot smokers (350°C) has been suggested as a clue for orientation of shrimps clustering around black smokers on the mid-Atlantic ridge (VAN DOVER, 1989), but at the EPR dive sites the diffuse venting by hydrothermal water is too cool to produce thermal radiation. The amphipods lack normal eyes (MARTIN *et al.*, submitted), and the strong light from *Alvin* would be expected to influence amphipod behavior if governed by vision, either "confusing" their orientation or damaging visual pigments. The swarms, however, were apparently undisturbed by the light of the submersible.

How do our observations relate to other observations of zooplankton swarms?

Swarming in crustaceans is most commonly reported from shallow water. This may partly be due to methods, as most researchers do not have access to appropriate equipment

for deep-sea observations. Nevertheless, swarm formation actually may be more common in shallow water due to light conditions. For example, copepod swarms apparently always disperse at night, and light seems to be important for their maintenance (AMBLER *et al.*, 1991). Swarming in various taxa has been ascribed to avoidance of visual predators, in which case swarming in darkness is unwarranted. Daylight is not, however, obligatory for organized swarming, and HAMNER *et al.* (1983) reported rigid nocturnal swarm maintenance in euphausiids without the use of bioluminescence.

The literature on crustacean swarms is dominated by reports on copepods, mysids and euphausiids. O'BRIEN (1989) tried to generalize findings on mysids and euphausiids, and concluded that maintenance of contact with conspecific individuals was the primary influence on aggregation structure. Responses to changes in the physical environment were generally statistically insignificant. Our findings do not fit this scheme. The swarms clearly were structured by the venting flow, although it is uncertain whether the swarms *per se* are functional entities, or if their presence only reflects an assemblage of individuals responding to a common factor, much like deep-sea amphipods attracted to bait (e.g. HESSLER *et al.*, 1978).

In an environment characterized by ephemeral point sources of food, the amphipods seem to enjoy the best of two worlds, i.e. capability of harvesting the point source, and mobility to find other locations when the flows die off. Still, corresponding swarms have not been reported outside vents between 9 and 12°N (VAN DOVER *et al.*, 1992). Whether this may be explained by predators, food supply, advective constraints, level of toxicity of the venting flow or perhaps other causes are questions awaiting future studies.

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