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Extensive deep-sea dispersal of postlarval shrimp from a hydrothermal vent

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Abstract

Hydrothermal vent fields on the Mid-Atlantic Ridge (MAR) are small (no more than 0.1–1.0 km²) and widely spaced (a reported average of one field per 175 km between 11°N and 40°N). Their faunas are similar and usually dominated by shrimp of the family Bresiliidae. Little is known about the way these animals (and other members of the vent fauna) disperse and colonize new vents. Vent shrimp juveniles have been taken close to certain vent sites, and in midwater, but their larvae and postlarvae have not been captured. We report here that bresiliid shrimp postlarvae are very widely dispersed around the Broken Spur vent field and extend into the next MAR segment and the Atlantis Fracture Zone beyond. The populations show density gradients declining both vertically and horizontally from the vent site, in contrast to the overall pelagic biomass. This is the furthest recorded dispersal (> 100 km) of identified larvae from a hydrothermal vent and is sufficient to give them access to adjacent vent fields and thus the scope for colonising new sites. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

Numerous hydrothermal vent fields have been identified on the Mid Atlantic Ridge (MAR), notably in the Azores Triple Junction region (36°–38°N) and at the Snakepit, Trans-Atlantic Geotraverse (TAG) and Broken Spur sites further south (23°, 26° and 29°N, respectively) with at least one hydrothermal field every 175 km between 11°N and 40°N (German *et al.*, 1995) and probably every 25–30 km between 36° and 38°N (German *et al.*, 1996). Although vents in the Atlantic are quite long-lived (with

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minimum lifetimes of about 100 yr and vent fields such as TAG have been intermittently active over 15–20,000 yr (Lalou *et al.*, 1993)), venting will eventually cease at any one site and the local fauna must locate a new vent or die.

It is not yet clear how larval dispersal by vent-associated species achieves the colonization of new vents. The biological populations at MAR sites are dominated by shrimp of the family Bresiliidae (Van Dover, 1995). This family may be an artificial assemblage (Chace, 1992); Christoffersen (1986) has separated the vent- and seep-associated species into the family Alvinocarididae, which now includes the four genera *Rimicaris*, *Alvinocaris*, *Chorocaris* and *Iorania* (Vereshchaka, 1996), though this familial separation is still a matter of dispute (Martin and Hessler, 1990; Martin and Christiansen, 1995; Williams and Dobbs, 1995). Recent allozyme data on the populations of *Rimicaris exoculata* from the TAG and Broken Spur vent fields of the MAR (separated by ~370 km) showed no significant genetic differentiation, suggesting frequent migration of adults or larvae between the fields (Creasey *et al.*, 1996). These data accord with the earlier results from the analysis of vent amphipods at hydrothermal sites along the East Pacific Rise (France *et al.*, 1992), which also indicated genetic similarity of populations along the axis. There was significant differentiation, however, between populations on two different ridges, the Galapagos Rift and East Pacific Rise.

Our knowledge of the processes controlling larval dispersal at hydrothermal vents is still rudimentary. This applies particularly to the Atlantic communities, with a different fauna from those in the Pacific (Tunnicliffe, 1991). Early work presumed that the temporal and spatial instability that characterises vents would select for a primarily planktotrophic dispersal strategy. However, it is now apparent that a wide range of reproductive strategies (ranging from brooding to planktotrophy) are employed by different vent-associated species.

The gastropod larvae found abundantly in the Pacific (Mullineaux *et al.*, 1995, 1996) are very small. This makes it necessary to sample with a fine mesh net, which in turn limits the practicable volumes of water that can be filtered and therefore imposes limits on the densities at which the larvae can be detected. Larvae of this size are difficult to assign to particular species, and this has in the past led, for example, to pelagic heteropod larvae being interpreted as derived from vent molluscs, or the Scanning Electron Microscope being a required tool for species identification (Mullineaux *et al.*, 1995). Bresiliid shrimps have larger eggs (ca 1 mm diameter) than vent-associated molluscs and considerably fewer of them (only a few hundred). The larvae are potentially larger and should therefore be easier to recognize. Molluscs are more fecund than shrimp and at equivalent adult densities there will, therefore, potentially be far fewer shrimp larvae in the water column than there would be mollusc larvae. Much larger volumes of water need to be sampled for there to be any reasonable chance of finding them. With these constraints in mind, and previous success in capturing bresiliid adults and juveniles in midwater (Herring, 1989), we undertook a sampling programme using a large midwater trawl over a MAR vent field (Broken Spur, 29°N), in an attempt to determine the distribution of bresiliid larvae in the water column and from this to assess their dispersal potential.

2. Methods

The MAR is dominated by a series of offset segments whose valleys are separated from each other by sills and are enclosed by steep walls that may rise a kilometer or more above the valley floor. We worked in Segment 17 of the MAR (Fig. 1) on RRS *Charles Darwin* Cruise 95 (FLUXES 1) during August and September 1995 in the

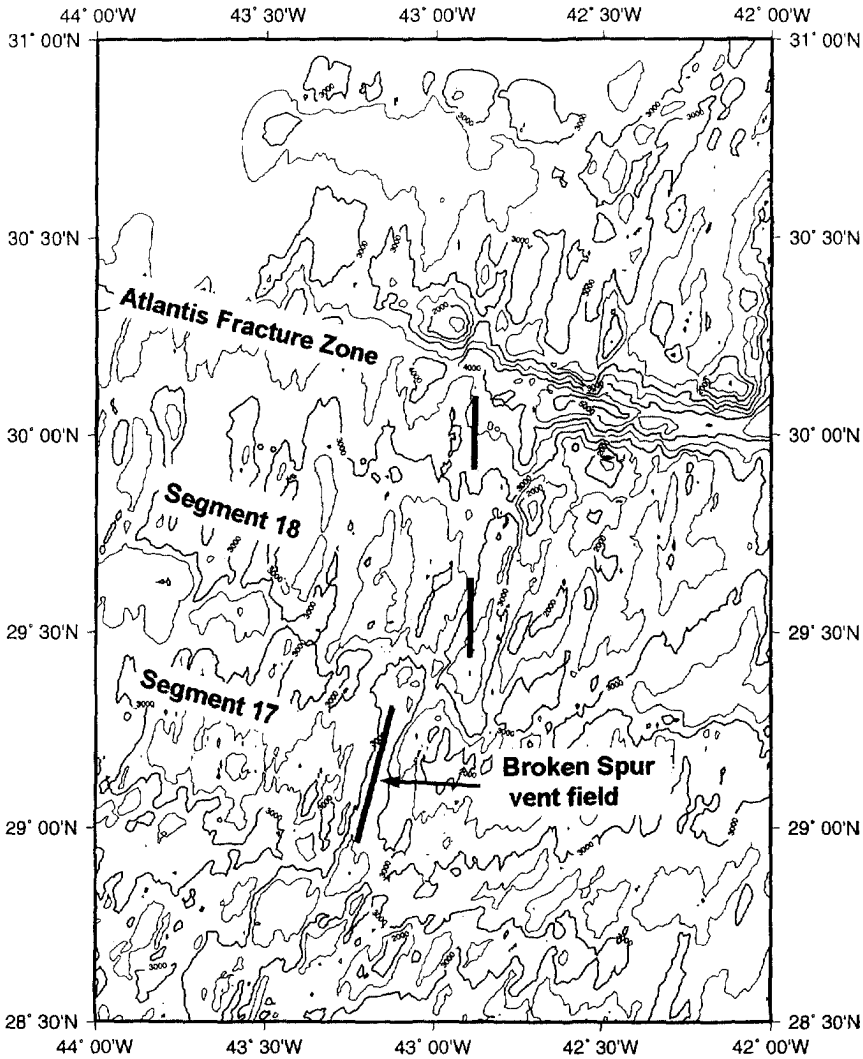


Fig. 1. Approximate trawl lines in Segments 17 (Broken Spur) and 18, and in the Atlantis Fracture Zone. The site of the Broken Spur vent field is indicated by the arrow. Each line comprises three consecutive net hauls, each one filtering $50\text{--}90 \times 10^3 \text{ m}^3$ water, depending on duration.

Broken Spur basin (Murton *et al.*, 1996). This basin has a long central axial valley with a maximum bottom depth of some 3200 m, and the valley is delimited to the west, north and east by walls that rise to a depth of 2400–2000 m (Purdy *et al.*, 1990). The valley contains a single vent region at 29°10'N; the hydrothermal plume rises to a depth of 2850–3000 m and is contained within the basin by the valley walls, except to the south (Murton *et al.*, 1995). There is also a narrow sill at about 2700 m depth leading to Segment 18 at the northeast corner of the basin.

Our sampling was carried out using the acoustically controlled multiple rectangular midwater trawl (RMT) system (Roe and Shale, 1979). This consists of three pairs of nets, each pair comprising one 1 m² (RMT1) and one 8 m² (RMT8) nominal mouth area net, with mesh sizes of 0.33 mm and 4.5 mm, respectively. In a complete tow, consisting of three net hauls, each pair of nets is fished consecutively at a nominal 2kt (1 m s⁻¹). The volume of water filtered by each net is calculated from the speed through the water as measured by the flowmeter on the net (Roe *et al.*, 1980) and for the RMT8 hauls ranged from 32 to 84 × 10³ m³ with distances run of 3.5–12 km.

Eleven tows with this net system were made down the length of the Segment 17 axial valley, six from south to north and five from north to south (i.e. a total of 33 hauls with each pair of nets). Ten of these tows were down the line of the central ridge within which the vent site is situated, and one was offset to the east by 1.5–2 km. The net opening and closing is triggered acoustically and was timed to ensure that the middle of the three pairs was open as the two nets passed over the vent field. Each net pair was held within a limited depth band (min. 95 m, max. 350 m) and fished for 1.5–2.5 h. Hauls were made at depths between 2000 and 3050 m, i.e. up to 1 km above the vents. Of the 30 hauls along the central ridge six were between approximately 2000 and 2500 m, four were between 2500 and 2750 m and 20 were between 2750 and 3050 m. One tow hit the bottom and tore the nets; the three RMT8 codends were recovered intact, and the catches are included in this analysis. The RMT1s were destroyed and their nominal filtration volumes are excluded from the data set (one postlarva was recovered from the shreds). Full trawl data are given in the Appendix.

On retrieval the samples in the codend of the nets were transferred to cold seawater, any obvious bresiliid postlarvae were picked out, and both shrimp and sample residues were then preserved in 5% buffered seawater formalin. A considerable number of the shrimp larvae were prepared for DNA analysis before preservation; the total length of each of these specimens was measured and the abdomen removed for analysis. The cephalothorax was fixed in 5% formalin and stored in 70% ethanol. In the shore laboratory the drained volumes of the RMT8 samples were measured (as a measure of biomass) and the larger crustaceans were then picked out and their volumes measured separately. The carapace lengths and total lengths of other bresiliid postlarvae were recorded to the nearest 0.1 mm, using a micrometer eyepiece. 10 specimens were fixed for study of the eye morphology (Gaten *et al.*, 1998) and 18 specimens deep-frozen for lipid analysis (C. Copley, unpublished).

3. Results

3.1. *Bresiliid* postlarvae

28 of the 30 hauls along the axial ridge caught bresiliid postlarvae. The most useful morphological characters for their identification as Bresiliidae were the size and form of the first and second pereopods and their chelae, the cephalothoracic eye in one type, and the apparent absence of epipods (though this could be a developmental feature) (Holthuis, 1993; Chace, 1992). The term postlarva is used here to designate post-zoeal stages with the full complement of abdominal appendages (*sensu* Gurney 1942; cf. Williamson, 1969). The shrimp postlarvae were of three morphologically very different types (Fig. 2). Two of these appear to belong to the genera *Alvinocaris* and *Chorocaris* (color photographs of adults of related species are presented by Segonzac

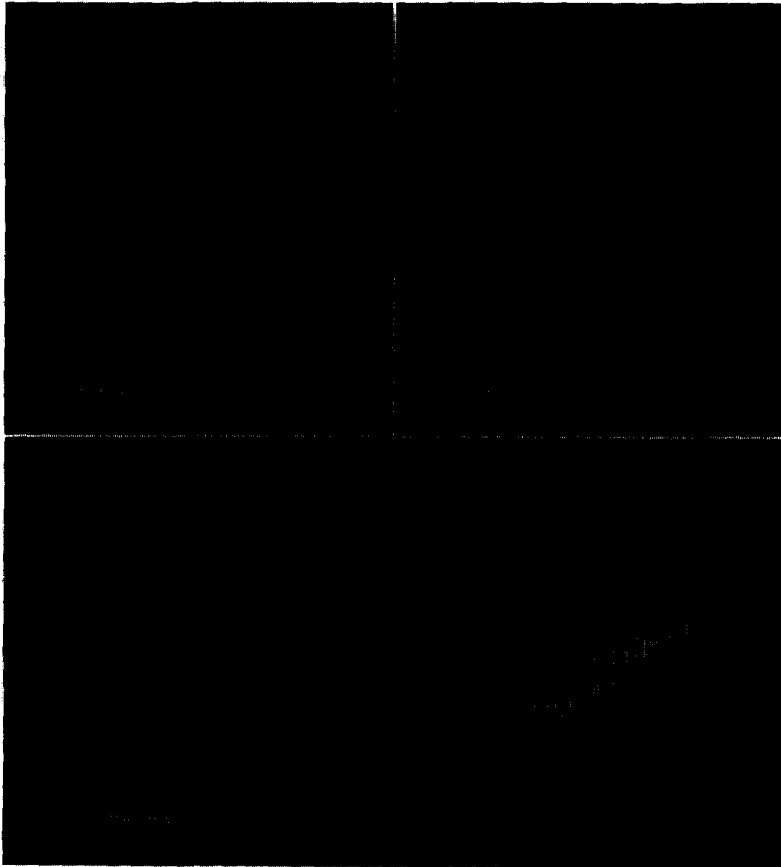


Fig. 2. Photographs of fresh specimens of (A) type A, (B) *Alvinocaris* sp. and (C) *Chorocaris* sp. (arrows indicate the thoracic extension of the eye). Scale bars: 5 mm.

et al., 1993). The third has a superficial resemblance to *Bresilia* adults (Holthuis, 1993). We refer in the text to the first two as *Alvinocaris* sp. and *Chorocaris* sp. and this last as "Type A" (see Discussion for further consideration of their specific identities). *Alvinocaris* sp. has small separate compound eyes, a pterygostomian spine and a toothed rostrum. *Chorocaris* sp. has fused compound eyes extending posteriorly to form a dorsolateral eye in the anterior cephalothorax. It has a very short smoothly rounded rostrum and no pterygostomian spine. Type A has large stalked compound eyes, a short rostrum faintly toothed on both margins, a pronounced dorsal hump on the third abdominal segment, a pterygostomian spine and, in some specimens, a minute orbital spine. The 33 hauls within Segment 17 caught 226 specimens, comprising 50 *Alvinocaris* sp., 42 *Chorocaris* sp. and 134 Type A. Full details of the catch data are given in Table 3. The two highest combined densities in any haul were 38.3×10^{-5} and 37.6×10^{-5} postlarvae m^{-3} . These occurred in two of the three samples in which the net hit the bottom and was damaged. It is likely therefore that even these high values represent a considerable underestimate of the real densities very close to the bottom. In the 10 tows over the central ridge significantly more postlarvae were caught in the middle net pair (which crossed the vent field) than in the north and south pairs (Wilcoxon's Signed Rank test $p < 0.05$, comparing the mean number of postlarvae in the north and south nets with that in the middle net) (Table 1). The same level of significance was obtained whether all the hauls over the central ridge were included ($n = 30$) or only those below 2700 m ($n = 20$).

The individual density distributions of the three larval types follow a similar pattern (Table 2). In the additional tow in Segment 17, offset from the central ridge and at

Table 1

Densities ($\times 10^{-5} m^{-3}$) of all bresiliid shrimp postlarvae in combined RMT1 and RMT8 hauls (number of hauls in parenthesis) taken over different sections of the axial ridge containing the Broken Spur vent field. The middle net pair fishes over the position of the vent field. Densities are calculated as summed numbers of postlarvae/summed water volume filtered for each region and depth horizon

Depth (m)	South	Middle	North	All hauls
2000–2500	0.78 (2)	2.25 (2)	1.53 (2)	1.53 (6)
2500–2750	3.63 (2)	9.10 (1)	4.61 (1)	5.06 (4)
2750–3050	13.33 (6)	19.61 (7)	10.29 (6)	14.83 (20)

Table 2

Densities ($\times 10^{-5} m^{-3}$) of different types of bresiliid shrimp postlarvae in combined RMT1 and RMT8 hauls ($n = 30$) at depths of 2000–3050 m down the axial ridge

Larval type	South	Middle	North	All hauls
<i>Chorocaris</i> sp.	0.83	3.07	0.99	1.69
<i>Alvinocaris</i> sp.	2.00	3.36	1.82	2.43
Type A	5.16	8.77	5.16	6.46
Total larvae	7.99	15.20	7.97	10.58

a depth of 2700–3000 m, all three net hauls also contained postlarvae. These comprised 8 *Chorocaris* sp., 6 *Alvinocaris* sp. and 12 Type A, at a combined density of 12.6×10^{-5} postlarvae m^{-3} .

A single comparative tow (three net hauls) was made in the adjacent Segment 18 (some 30 km to the northeast) at depths between 2875 and 3030 m. This was planned as a control set of samples in a segment with no known hydrothermal site. They contained one each of *Alvinocaris* sp. and *Chorocaris* sp. and six of Type A (total density 4.4×10^{-5} m^{-3}). Another tow in the Atlantis Fracture Zone a further 50 km to the north at similar depths (2870–3010 m) caught 1 *Alvinocaris* sp. and 1 Type A (total density 1.2×10^{-5} m^{-3}) (see the appendix).

The lengths of all of the bresiliid postlarvae taken were within the limited range of 13–23 mm, except one (28 mm). All appeared to be at a similar stage in development, though some showed indications of an imminent moult. A conspicuous feature of all three types was a very characteristic saddle of lipid droplets, which completely encircled the posterior cephalothorax and extended dorsally into the first three abdominal segments. This was colored pale orange in Type A and *Chorocaris* sp. and yellow in *Alvinocaris* sp. The animals were near neutral buoyancy in refrigerated surface seawater (ca 10°C); most specimens sank slowly while a few remained floating. No obvious gut contents were visible in six dissected specimens.

3.2. RMT8 Biomass data

All RMT8 samples were of very small volume, with a biomass range of $0.3\text{--}7.2 \times 10^{-4}$ $ml\ m^{-3}$, and an overall mean value for all 39 hauls (33 in Segment 17, 3 in Segment 18 and 3 in the Atlantis Fracture zone) of 2.2×10^{-4} $ml\ m^{-3}$. Because the overall volumes were so low, larger individuals had a disproportionate effect on the total. The main components were pelagic oplophorid decapods, nemerteans, amphipods and a few large copepods. One large octopod was taken and a large pelagic holothurian and two specimens of the large mysid *Gnathophausia* (the octopod and holothurian are omitted from the biomass calculations; the mysids are included). When the RMT8 biomass data along the axial ridge are tabulated according to the depth of sample and position along the axial valley, as for the bresiliid postlarvae in Table 1, no significant increase in biomass concentration occurs in the deeper samples or in the middle net. Indeed such differences as there are indicate a slight increase in biomass at the shallowest depths sampled (Table 3).

Table 3
Biomass concentration (wet volume, $\times 10^{-4}$ $ml\ m^{-3}$) in all RMT8 samples (30 hauls) down the axial ridge of Segment 17

Depth (m)	South	Middle	North	All hauls
2000–2500	4.0	3.9	5.6	4.5
2500–2750	1.9	2.1	1.2	1.8
2750–3050	1.6	2.0	1.4	1.7

RMT1 catches were very small, often < 1 ml total volume and frequently dominated by net debris (cf. Vinogradov *et al.*, 1997). They were not considered further, although any bresiliid postlarvae present in them were dealt with as described above.

4. Discussion

Our results show that vent shrimp postlarvae are present in midwater and extend to great distances from the vents. All the specimens had huge deposits of lipid in their tissues and must have fed and grown extensively since hatching. If the Segment 18 and Atlantis Fracture Zone specimens originated from the Segment 17 vents, then they must have first ascended above the central valley walls (and out of Segment 17) or crossed the sill, and subsequently descended in Segment 18 to approximately 3000 m, where they were captured. All the postlarvae found were of remarkably similar size and stage of development. This is not a consequence of net selection, because the RMT1-caught specimens are of a similar size to those caught by the RMT8, despite the much smaller mesh size of the RMT1. The postlarvae are at the bottom end of the size of organism efficiently retained by the RMT8 mesh. There may even have been some slight loss from this net, because the density of postlarvae calculated from the RMT8 catches alone in Segment 17 is approximately $10 \times 10^{-5} \text{ m}^{-3}$ whereas when calculated from the RMT1 samples alone it is $15 \times 10^{-5} \text{ m}^{-3}$.

The RMT1 samples do not contain any smaller larvae (i.e. earlier, zoeal stages), so it does not appear that there is a continuous series of developmental stages in the basin water column. If there were, we would expect larvae to be more numerous than postlarvae, unless the larval stages are relatively short and the postlarval ones lengthy. If the postlarvae we caught are derived from adults at the Broken Spur site, then there appears to have been a pulse of larvae dispersed into the water column at some time in the past. The eggs of bresiliid shrimp are small, of the order of 1 mm diameter (Williams and Rona, 1986; M. Segonzac, personal communication). If their embryonic development time is comparable to that of meso- and bathypelagic Ophlophoridae (e.g. *Acanthephyra*) with eggs of equivalent size, and to which the adults are morphologically and phylogenetically related (Christoffersen, 1986), then they are likely to be carried by the female for several months (unless the ovigerous females forage consistently in warm water) (Herring, 1974). Development from hatching to the lipid-rich postlarvae that we obtained is likely to have taken at least as long. Animals carried a long way from the Broken Spur site, for example to the Atlantis Fracture Zone, might be expected to show some differences in size or stage of development, but there is no indication of this in our specimens. This would, however, conform to a short pulse of larval release, resulting in postlarvae present at all ranges from the release area being of equivalent age.

Despite the very low biomass in this near-bottom region (comparable to that recorded on the Madeira abyssal plain by Roe *et al.*, 1990), the observed densities of bresiliid larvae make only a limited contribution. Even assuming that an individual postlarva has a volume of 0.5 ml, their *maximum* contribution to the biomass in any one haul was just over 20%, and the usual level was 5% or less.

Submersible observations and captures in the Broken Spur vent field have shown that species of both *Rimicaris* and *Alvinocaris* are present around the vents, together with the small *Chorocaris fortunata* (Murton *et al.*, 1995; Martin and Christiansen, 1995; Vereschaka and Vinogradov 1996), though none of them were present in particularly large numbers when compared with other surveyed sites. *Rimicaris exoculata* was observed to be the most abundant one by at least an order of magnitude. We have not, however, taken any postlarvae whose morphology suggests they are immediately ascribable to *Rimicaris* (larvae and postlarvae of this species have been reported close to vents (Vereschaka and Vinogradov, 1996)), and our most abundant postlarval type is that of Type A. The taxonomic characteristics of our specimens are currently being studied (M. de St Laurent, personal communication), and genetic analysis is in progress. This should ultimately provide specific identifications and will make clearer the relationships between these postlarvae and the adults identified at the site. The preliminary evidence (Dixon and Dixon, 1996) indicates that our *Alvinocaris* sp. matches *A. markensis*. All but one of our *Chorocaris* sp. match *C. chacei*, but that one (the largest, 28 mm, specimen) matches *R. exoculata*. Type A includes individuals matching either *A. markensis* or *C. chacei*. Only adults of *A. markensis*, *C. chacei*, *C. fortunata* and *R. exoculata* have so far been available for molecular comparison.

We conclude from these preliminary indications that Type A is an early postlarval form of more than one species, which metamorphoses into the more typical *Chorocaris* and *Alvinocaris* postlarvae. We also conclude that *Chorocaris* sp. postlarvae are morphologically very difficult to distinguish from *Rimicaris exoculata* postlarvae at a similar stage of development. This implies that the early developmental stages of *R. exoculata* have typical fused compound eyes similar to those of *C. chacei* and *C. fortunata* (confirmed by M. de St Laurent, personal communication; Gaten *et al.*, 1998), though these were not present in juveniles of 22.2 and 24.7 mm total length included in the original description of the species (Williams and Rona, 1986).

The apparent disparity in the relative abundances of particular species (e.g. *Rimicaris exoculata*) as pelagic postlarvae and as epibenthic adults is remarkable. One possible interpretation is that the postlarvae are *not* derived from the adults at this site. The significant decrease in larval densities with increasing distances away from the Broken Spur vent field is certainly what would be anticipated if this field is where they originate. It would, however, also occur if widely dispersed larvae were specifically attracted to the Broken Spur vent field (e.g. by chemoreception (Renninger *et al.*, 1995)). At the moment we have no means to distinguish whether the larvae are coming or going, although the high densities of well-developed postlarvae close to the bottom suggest that this is their final location. In addition, the relative densities of the notionally younger Type A, compared with those of *Chorocaris* sp. and *Alvinocaris* sp., increases with distance from the vents. The apparent absence of *Rimicaris* postlarvae could alternatively result from a different reproductive strategy (e.g. in timing or extent of pelagic dispersal) compared with that of *Chorocaris* and *Alvinocaris*.

Our results demonstrate that postlarval dispersal occurs over very long distances, certainly far enough to reach several adjacent vent fields, according to recent estimates

of their local occurrence (German *et al.*, 1996). Current velocities on Pacific ridges may reach 40 mm s^{-1} but are highly variable, with mean velocities of up to 30 mm s^{-1} (Cannon *et al.*, 1991). An along-ridge mean current velocity of, say, $10\text{--}20 \text{ mm s}^{-1}$ would transport a shrimp larva between the Atlantis Fracture Zone and the Broken Spur basin ($\sim 100 \text{ km}$) in some 2–4 months. Our specimens have certainly been in the water column at least as long as that.

If the larvae are being dispersed from (rather than aggregating in) Broken Spur, the problem is not so much one of lateral dispersal as of explaining how the larvae first rise above the enclosing basin walls and then sink down again to the habitat depths at other sites. This cannot be explained by plume entrainment, which is elsewhere a probable means of dispersal for smaller larvae (Kim *et al.*, 1994; Mullineaux *et al.*, 1995; Mullineaux and France, 1995), because the Broken Spur plume is largely contained within the basin, except at the southern end. Active vertical swimming, perhaps assisted by changes in buoyancy, seems the most likely explanation. Near-bottom currents on the eastern flank of the MAR are slow ($1\text{--}2 \text{ mm s}^{-1}$) and southerly (Murton *et al.*, 1996). While they could take larvae out of the basin, through the southerly gap in the walls, the Segment 18 and Atlantis Fracture Zone specimens would have had to move against the prevailing current, as well as rise over the sill or walls, if indeed they are derived from Broken Spur adults. The likelihood of this occurring will remain uncertain until details of the currents above these particular basins become available.

Acknowledgements

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Appendix

For station numbers, locations and catch data for all RMT8 and RMT1 hauls, see Table 4

Table 4

Station	Fishing depth (m)	Location	Haul sequence	RMT8			RMT1				
				Volume filtered (m ³)	Choro-caris sp.	No. of specimens Alvino-caris sp.	Type A	Volume filtered (m ³)	Choro-caris sp.	No. of specimens Alvino-caris sp.	Type A
53501 #1	2450–2810	Axial ridge	South	84873			2	7655			
#2	2800–2930		Middle	83207	2	3	12	6736			
#3	2900–2995		North	55954	1	2	4	0			
53502 #1	2795–2980	Axial ridge	South	55920		2	2	5072			2
#2	2750–2920		Middle	88271			12	6998			
#3	2590–2730		North	59477			3	5545			
53503 #1	2350–2495	Axial ridge	South	56582	1			5103			
#2	2470–2700		Middle	60905	1	1	1	4996			3
#3	2700–2930		North	54386			4	5179			
53504 #1	2270–2560	Axial ridge	North	79364			1	7786			
#2	2320–2490		Middle	67906			2	5616			
#3	2480–2630		South	66228		2	2	6347			
53505 #1	2890–3000	Axial ridge	North	64829	2	4	3	6376	1		3
#2	2860–3000		Middle	64835	6	7	8	5526	1	1	2
#3	2970–2880		South	32724		2	5	3185			
53506 #1	2000–2200	Axial ridge	North	39152			1	3691			
#2	1990–2280		Middle	55149			1	4611			
#3	2010–2300		South	59834				5715			
53507 #1	2900–3070	Axial ridge	North	47191	1	2	4	0			1
#2	2900–3050	(Hit bottom)	Middle	50577	4	9	6	0			
#3	2965–3060		South	47004		4	14	0			
53508 #1	2900–2980	Offset	South	54447	1		5	5402			1
#2	2880–2980		Middle	76583	2	1	2	6290			1
#3	2870–3000		North	57420	5	3	4	5417			

Station	Fishing depth (m)	Location	Haul sequence	RMT8				RMT1			
				Volume filtered (m ³)	<i>Choro-caris</i> sp.	No. of specimens <i>Alvino-caris</i> sp.	Type A	Volume filtered (m ³)	<i>Choro-caris</i> sp.	No. of specimens <i>Alvino-caris</i> sp.	Type A
53509 #1	2890–2950	Axial ridge	South	55320	1	1		5062			
#2	2910–3000		Middle	44988	3	1	3	3777			
#3	2880–3025		North	52644	1		3	5050	1		
53510 #1	2710–2875	Axial ridge	South	45714				3461			
#2	2730–2880		Middle	67230			1	5556			1
#3	2880–3000		North	59307		2	4	5547			
53511 #1	2875–3000	Segment 18	South	55920			3	5072			1
#2	2930–3025		Middle	59790			1	4916			1
#3	2955–3030		North	52204	1	1		5015			
53512 #1	2860–2995	Axial ridge	North	47024		1	2	4630			1
#2	2960–3000		Middle	52169	2	2	4	4406	1		2
#3	2850–2995		South	49255	1	1	2	4775	1		1
53513 #1	2900–3010	Atlantis F.Z.	South	46826		1	1	4550			
#2	2890–3020		Middle	52169				4406			
#3	2870–2950		North	53482				5117			