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Spatial and interannual variation in the faunal distribution at Broken Spur vent field (29°N, Mid-Atlantic Ridge)

Abstract Initial ecological observations at Broken Spur in 1993 suggested a low biomass relative to other deep-water vent communities known along the Mid-Atlantic Ridge. The persistence of a low shrimp biomass over 15 mo at Broken Spur vents appears to refute the hypothesis that the community is expanding through reproduction and immigration to occupy habitat vacated during a recent period of hydrothermal quiescence or catastrophe. Although the absence of "swarms" of shrimp similar to those found at the hydrothermal mounds of TAG (26°N) and Snake Pit (23°N) is a visually striking feature of the majority of venting structures known at Broken Spur, the biomass of fauna other than shrimp may not be significantly less than that of other Mid-Atlantic sites. The discovery of "swarms" of shrimp at Bogdanov Site, visited for the first time in 1994, suggests that availability of substratum exposed to the flow of hydrothermal fluids, which is a function of the topography of venting structures, may be a prerequisite for the development of these dense aggregations. Two testable predictions arise from this hypothesis. Firstly, dense aggregations of *Rimicaris exoculata* should occur at any other structures with a morphology similar to Bogdanov Site that may be discovered in the Broken Spur vent field, and should not occur at other isolated chimney structures that may be found. Secondly, "swarms" of shrimp should appear at any Broken Spur chimneys that develop into structures with a morphology more similar to that of Bogdanov Site in future.

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Introduction

Since the discovery of the active TAG and Snake Pit hydrothermal mounds in the mid-1980s, the number of vent communities observed along the Mid-Atlantic Ridge (MAR) has increased to include Menez Gwen, Lucky Strike, Broken Spur and 14°45′N (Van Dover 1995), and there is strong evidence of venting at other locations (German et al. 1996). Return visits to TAG and Snake Pit have found little change in community structure, in contrast to the changes seen at vents on the East Pacific Rise (Van Dover 1995). The dynamics and ecological context of the communites at the other Mid-Atlantic vents have yet to be fully characterised, however, as few of the more recently discovered vents have been revisited to provide an assessment of faunal change. An opportunity for such an assessment at the Broken Spur vent field, first explored by two dives with D.S.V. "Alvin" in June 1993, was provided by submersible dives during the British–Russian Atlantic Vents Expedition 1994 (BRAVEX/94). The 15 mo interval between these two series of dives allows a test of the hypothesis that the community at Broken Spur is responding to a possible change in hydrothermal activity (Murton et al. 1995b). Because of the potential modification of vent ecosystems by scientific activity such as sampling (Tunnicliffe 1990) and ODP (Ocean Drilling Program) drilling (Copley et al. in preparation), it is important that natural temporal variations are determined before anthropogenic influences can be assessed.

The presence of a hydrothermal field at 29°10′N on the Mid-Atlantic Ridge was initially suggested by water-column anomalies detected on 4 March 1993 during Cruise CD76 of the R.R.S. "Charles Darwin" (Murton et al. 1993, 1994). Geophysical imaging revealed the

Table 1 Taxonomic comparison of vent communities at Broken Spur, TAG and Snake Pit based on current observations and those of

Site	Bresiliid shrimp	Brachyuran crabs	Other decapods	Ophiuroids
Broken Spur (29°N)	*Rimicaris exoculata*[a] *Chorocaris fortunata*[b] *Alvinocaris ?markensis*	*Segonzacia mesatlantica*	*Munidopsis* sp.	*Ophioctenella acies*
TAG (26°N)	*Rimicaris exoculata* *Chorocaris chacei* *Alvinocaris markensis*	*Segonzacia mesatlantica*	*Munidopsis* sp.	*?Ophioctenella acies*[c]
Snake Pit (23°N)	*Rimicaris exoculata* *Chorocaris chacei* *Alvinocaris markensis*	*Segonzacia mesatlantica*	*Munidopsis crassa*	*Ophioctenella acies*

[a] Confirmed by allozyme analysis (Creasey et al. 1996)
[b] Martin and Christiansen (1995)
[c] Known from video only

water-column anomalies to be concentrated above a neovolcanic ridge located towards the western margin of the Mid-Atlantic Ridge median valley. Deployment of a submersible camera system within this area indicated seafloor hydrothermal activity, and the site was informally named the Broken Spur vent field.

The Broken Spur vent field was the target of "Alvin" Dives 2624 and 2625 in June 1993. These dives confirmed the presence of an active hydrothermal field at a depth of 3090 m at the axial summit graben of the neovolcanic ridge. Three high-temperature "black smoker" sites were visited by these dives (Saracen's Head, The Spire and Wasp's Nest), in addition to two weathered sulphide mounds emitting diffuse low-temperature fluids (Murton and Van Dover 1993; Murton et al. 1995b).

A further water-column survey to assess the extent of hydrothermal activity at Broken Spur was carried out during R.R.S. Charles Darwin Cruise CD77 (18 March to 18 April 1993; Elderfield et al. 1993). Intense hydrothermal signals were detected with a focus ≃2 km south of Broken Spur, as previously defined by Cruise CD76. These results were interpreted as suggesting the existence of additional vents in this area (James et al. 1995b). Submersible video deployments, however, during Cruise CD95 of the R.R.S. Charles Darwin and exploration by two "Mir" submersible dives failed to find any evidence of hydrothermal activity south of the sites visited by D.S.V. "Alvin" (BRAVEX/94 Scientific Team 1994; Murton et al. 1995a).

Water-column data collected during Cruise CD95 were consistent with the presence of a single point-source of hydrothermal activity at the known Broken Spur vent field, with considerable temporal variability in the direction of plume dispersal. The water-column signal from CD77, previously attributed to a southern source of venting, therefore may have been the result of bifurcation or lateral transport of the Broken Spur plume under the local hydrodynamic regime. A seafloor video survey of the Broken Spur vent field by CD95 found evidence of further hydrothermal activity extending 200 m north of sulphide mounds visited by submersibles (Murton et al. 1995a).

The most striking ecological feature observed at the edifices discovered during the first submersible dives at Broken Spur in June 1993 was the relative paucity of biomass, particularly of shrimp, compared to other Mid-Atlantic sites such as TAG and Snake Pit (Murton et al. 1995b). The sulphide mineralogy (Duckworth et al. 1995), vent fluid geochemistry (James et al. 1995a) and level of hydrothermal activity first observed at Broken Spur, however, were similar to those of other Mid-Atlantic sites (Murton et al. 1995b). The fauna at Broken Spur also displays taxonomic similarities to that of TAG and Snake Pit (Table 1) and a similar general zonation, with bresiliid shrimp close to black smokers, and anemones and other invertebrates situated more peripherally. The high population densities of shrimp found at the black smokers of TAG and Snake Pit were absent from Broken Spur edifices visited in 1993, however, and a high ratio of predators and scavengers to primary consumers was noted and interpreted as indicating ecological instability, possibly as a result of a recent environmental change (Murton and Van Dover 1993).

The size and morphology of the massive sulphide deposits observed at Broken Spur from "Alvin" precluded the possibility that Broken Spur was a "new" site where hydrothermal activity had just begun. In order to reconcile the disparity of a low faunal abundance in an otherwise active and established hydrothermal field, Murton et al. (1995b) proposed that venting at Broken Spur may have undergone a recent reactivation after a period of quiescence, or a catastrophic event sufficient to reduce faunal abundance drastically. The vent community was hypothesised to be still recovering from such a disturbance, with animals only just arriving to recolonise the system (Van Dover 1995). Episodic activity at other Mid-Atlantic hydrothermal vents is well established from radiochronological studies of sulphide deposits. Data from TAG indicate intermittent pulses of hydrothermal activity every 4000 to 6000 yr over the past 20 000 yr, with the present episode of venting beginning ~50 yr ago (Lalou et al. 1993). Similar studies at Snake Pit have also suggested episodic activity over its 4000-yr history, with

Segonzac (1992) and Van Dover (1995)

Bivalves	Gastropods	Polychaetes	Anemones	Fish
Bathymodiolus sp.	*Phymorhynchus moskalevi* ?*Pseudorimula midatlantica*	Ampharetid sp. Chaetopterid sp.	Actinian sp.	Synaphobranchid sp.
	Phymorhynchus moskalevi	Ampharetid sp. Chaetopterid sp.	Actinian sp.	Synaphobranchid sp.
Bathymodiolus puteoserpensis	*Phymorhynchus* sp. *Pseudorimula midatlantica*	Ampharetid sp.	Actinian sp.	Synaphobranchid sp.

the current phase of venting starting around ∼80 yr ago (Lalou et al. 1993).

The presence of mussel populations at Broken Spur in 1993 suggests that any recent interruption of venting was of sufficient magnitude and duration to reduce the abundance of shrimp, but not long or large enough to eliminate the mussel populations (Van Dover 1995). Mussels are believed to be the last faunal survivors at Galápagos vents following a cessation of hydrothermal activity (Hessler et al. 1988), but the longest period that they have been observed to survive in the absence of venting is 5 yr (Fisher 1995). Our interest was to test the hypothesis that the Broken Spur vent community is recovering from an interruption in hydrothermal activity or some other disturbance, by remapping the faunal distribution on subsequent visits (Murton and Van Dover 1993; Van Dover 1995). An increase in biomass would be expected if the hypothesis is correct.

rections for such distortions are possible using isometry ratios (Chevaldonné and Jollivet 1993), such methods depend on the optical properties of the camera, which were not known.

Results

Morphology of Broken Spur vent field

Submersible exploration by BRAVEX/94 more than doubled the number of hydrothermal structures known within the Broken Spur vent field. Although navigational problems hampered systematic mapping, a geographical interpretation of the vent field can be constructed from dive videos and the commentary of dive observers (Fig. 1). Sites of venting are located on the floor and walls of a valley interpreted as the axial summit graben identified by Cruise CD76 (Fig. 1, "Eastern Valley"), and on the crest of the neovolcanic ridge to the west of this graben
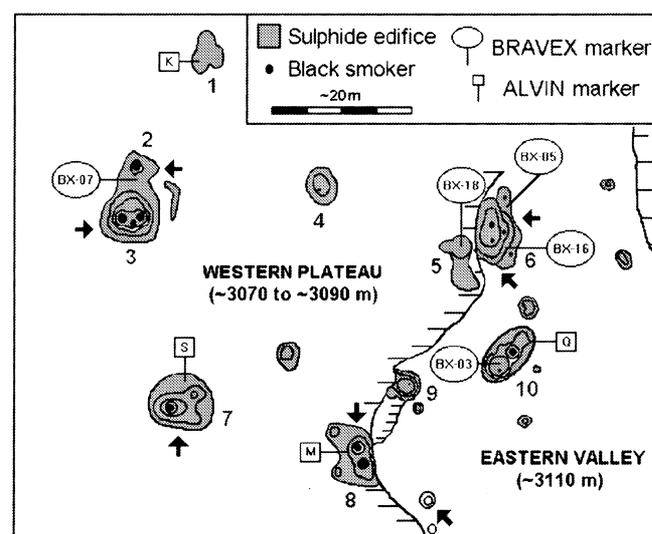
Materials and methods

Eight dives to the Broken Spur vent field were made by the two "Mir" submersibles from R.V. "Akademik Mstislav Keldysh" during September 1994 (BRAVEX/94 Scientific Team 1994). Three transponders were deployed for submersible navigation, but sea-floor topography frequently prevented position-fixing within the vent field, so identification of markers and pilotage were the primary navigational tools during dives. The "Mir" submersibles carried a fixed-focus NTSC video camera and a PAL video with zoom, both mounted on a pan-and-tilt array. Two lasers mounted in parallel 10 cm apart provided a scale on video footage. Additional footage was obtained during two dives from a Hi8 camcorder filming through the portholes from inside the submersibles. Over 60 h of video footage were recorded during the dive series. Footage from the two "Alvin" dives of June 1993 was provided for comparison.

Video images showing clearly identifiable vent fauna were captured onto a PC through a Targa + framegrabber. These images were analysed using Jandel Scientific's "Mocha" image-analysis system. In some close-up frames where the laser dot scale was not visible, the modal size of visible *Rimicaris exoculata* was used as a scale by equating this to the modal size of specimens collected from the vent field. Geometric solids were used to approximate the surfaces occupied by fauna to obtain estimates of faunal density. Images with approximately zero angle of incidence between the camera view and the surface viewed were preferred, to avoid distortions resulting from oblique-angle conditions. Although cor-

Fig. 1 Interpretation of Broken Spur hydrothermal field from BRAVEX/94 videos, showing main structures. *1* Mound 'K'; *2* Judy's Tower; *3* Triple Chimney; *4* White Button; *5* Dog's Head; *6* Bogdanov Site; *7* The Spire; *8* Saracen's Head; *9* White Mushroom; *10* Wasp's Nest; *arrows* indicate view of structures presented in video collages

(Fig. 1, "Western Plateau"). The southernmost active site of high-temperature venting within the vent field is Saracen's Head, situated at the top of the western wall of the Eastern Valley. The previously reported height of 35 to 40 m for this structure (Murton et al. 1995b) may have included the depth of the Eastern Valley. In September 1994, Saracen's Head consisted of an 11 m-high sulphide mound surmounted by two active chimneys, oriented approximately north–south. The northern chimney (Fig. 2) was 4 to 6 m high and the southern chimney 2 to 3 m; both these chimney structures had grown in the 15 mo between the "Alvin" and "Mir" dives (Nesbitt and Murton 1995a).

Three other black-smoker chimney structures are known on the Western Plateau. The Spire (Fig. 3), which was discovered by "Alvin" consists of a sulphide mound topped by a single chimney at least 12 m high. At the Triple Chimney (Fig. 4), a 17 m tall structure branches into two actively-venting slender chimneys oriented approximately E–W, with a smaller inactive chimney between, although venting was re-established from this smaller chimney during geological sampling. Immediately north of Triple Chimney on the same sulphide mound is Judy's Tower (Fig. 5), a single chimney that was 4 m high when discovered by BRAVEX/94 but which was demolished by a collision with a "Mir" submersible. In addition to the black-smoker chimney structures, the Western Plateau also contains an actively-venting platform structure on top of a sulphide mound at White Button.
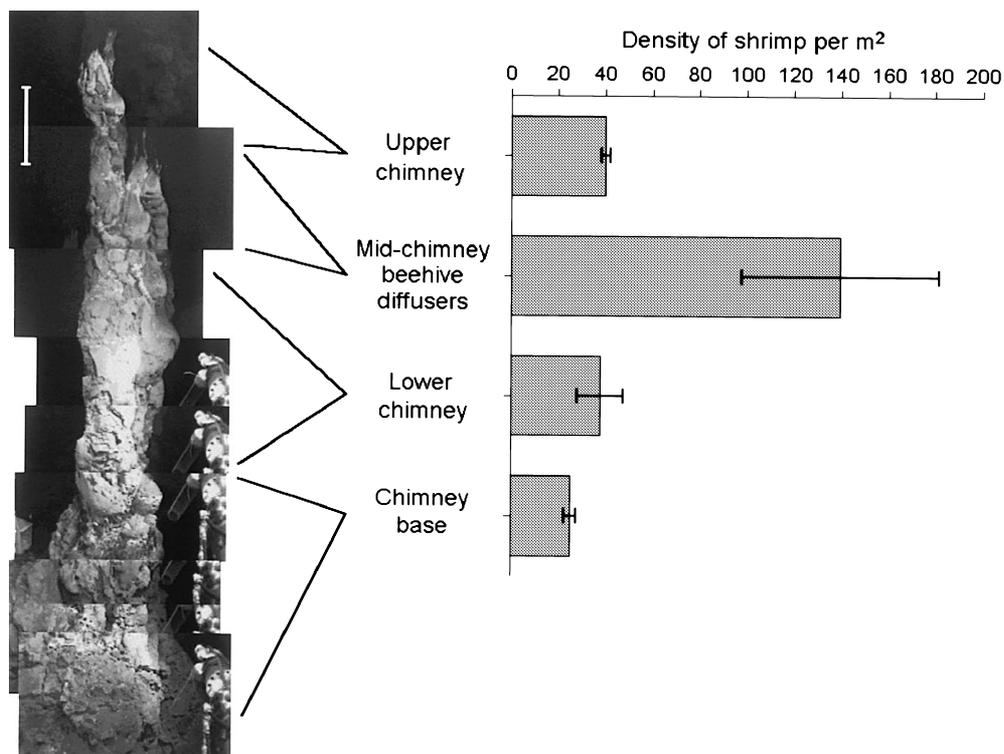
Platforms and ledges are common at active sites in the Eastern Valley. Wasp's Nest consists of a 23 m-high sulphide mound topped by a small black-smoker chimney and a platform large enough to accommodate a "Mir" submersible during sampling. An actively-venting platform jutting out from the western wall to the north of Saracen's Head forms White Mushroom. At Bogdanov Site (Fig. 6), ledges issuing black smoke and vigorous diffuse flow protrude from the western wall to form a 20 m vertical stack, topped with beehive diffusers and small chimneys.

The Broken Spur vent field also contains sites of low temperature venting and inactive, weathered sulphide mounds. At Mound K, shimmering water percolates from cracks in a sulphide outcrop. Weathered sulphides also form the distinctive Dog's Head, where there is little visible evidence of diffuse flow. Plates of weathered sulphides are present south of Dog's Head and north of Saracen's Head, and the base of the sulphide mound at Saracen's Head extends out to the west and northwest towards upstanding, weathered sulphide structures.

Inactive features also lie northeast of The Spire, below White Mushroom, north and south of Wasp's Nest, and in the vicinity of the eastern wall of the Eastern Valley. Sulphide rubble forms a 1.5 m high wall east of the mound carrying Triple Chimney and Judy's Tower and is also present around the periphery of the other sulphide mounds. Elsewhere between the sites of venting the substratum is comprised of pillow basalts, occasionally collapsed, often covered by oxidised sulphide sediments. Basalts also form a vertical stack close to the western wall of the Eastern Valley to the south of Saracen's Head (Fig. 7).

Fig. 2 Video collage of Saracen's Head northern chimney showing vertical distribution and density (mean ± SE) of shrimp *Rimicaris exoculata* (Scale bar ∼1 m)

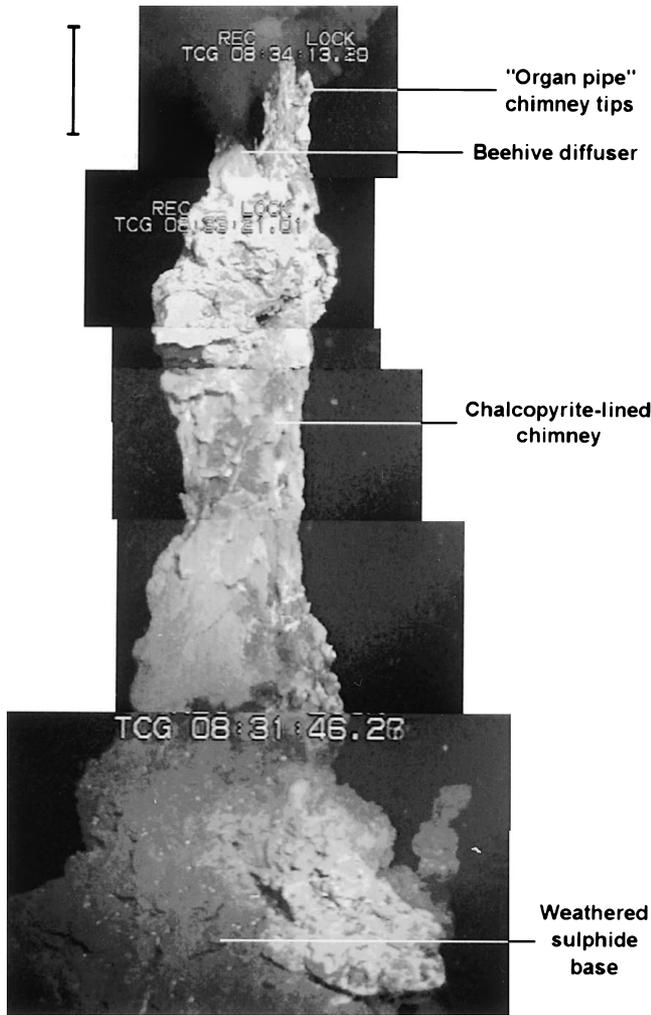**Fig. 3** Video collage of The Spire showing main depositional features (Scale bar ~1 m)

Fig. 4 Video collage of Triple Chimney (Scale bar ~1 m)

Interannual variation in faunal distribution

The distribution of *Rimicaris exoculata* observed by "Alvin" dives and BRAVEX/94 at The Spire shows considerable heterogeneity related to the presence of fissuring, but overall there is no significant difference in population density between 1993 and 1994 (Fig. 8; Mann–Whitney U-test, $U' = 6$, $p = 0.111$, $n = 5$ and $m = 4$). At Saracen's Head, chimney growth over the interval between expeditions (Nesbitt and Murton, 1995a) provided additional substratum for fauna to occupy. However, these new chimney surfaces might represent a different microhabitat to that surveyed in 1993; therefore, comparison of the density of *R. exoculata* between the two years was made over the "homologous" region at the base of the chimneys. No significant difference was found between 1993 and 1994 in this region (Fig. 8; Mann–Whitney U-test, $U' = 8$, $p = 0.365$, $n = 5$ and $m = 4$). Similarly, the density of shrimp at Wasp's Nest shows no evidence of an increase (Fig. 8), although a shortage of close-up and non-oblique video
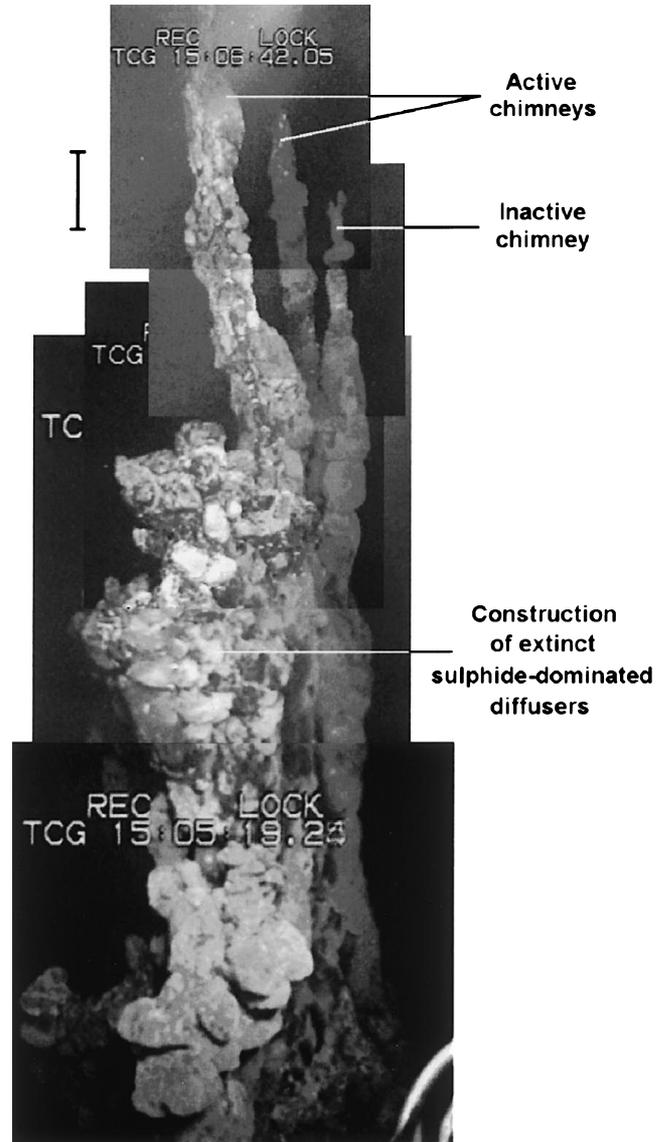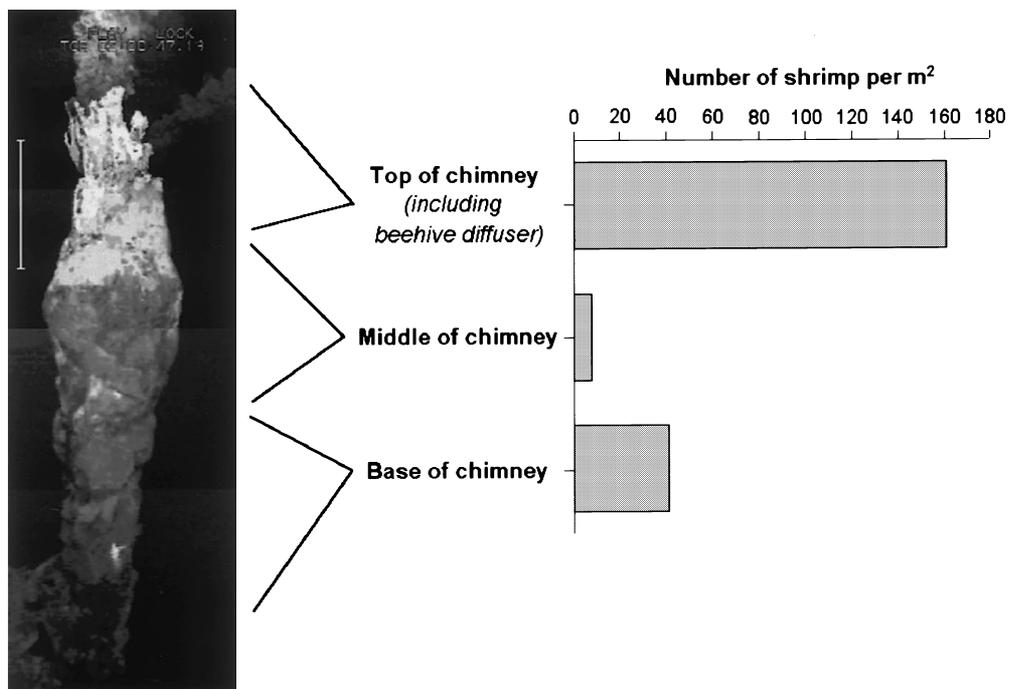
images at this structure prevented a statistical comparison. No increase in population density was shown by the other fauna observed at the high-temperature venting structures visited by "Alvin" and BRAVEX/94 (Table 2). Estimates of faunal densities obtained from image analysis of "Alvin" dive tapes are consistent with those reported by dive observers (Murton et al. 1995b), providing a validation of the analytical technique.

Spatial variation in faunal distribution observed by BRAVEX/94

The population density of shrimp found on the sides of the Triple Chimney (10.75 m^{-2} ± 1.70 SE) was comparable to that observed at The Spire (Mann–Whitney U-test, $U' = 8$, $p = 0.21$, $n = 5$ and $m = 5$). Similar densities of shrimp were also found at White Button

Fig. 5 Video collage of Judy's Tower showing vertical distribution and density of shrimp *Rimicaris exoculata* before accidental demolition (Scale bar ~1 m)

(17.99 m^{-2}) and Mound K (15.61 m^{-2}), but very few shrimp were observed at the inactive Dog's Head structure (3.43 m^{-2}). A bimodal vertical distribution of shrimp was found at Judy's Tower (Fig. 5), where the shrimp population density mid-chimney was similar to that of Triple Chimney. Shrimp densities on the sides of new chimney growth at Saracen's Head were comparable to those found at the base of the chimneys (Fig. 2; Mann–Whitney *U*-test, $U' = 8$, $p = 0.345$, $n = 5$ and $m = 4$), except in proximity to beehive diffusers where they were significantly elevated (Fig. 2; Mann–Whitney *U*-test, $U' = 0$, $p = 0.004$, $n = 5$ and $m = 4$). Dense aggregations of shrimp (~2000 m^{-2}) comparable to the "swarms" observed at the black smokers of TAG and

Fig. 6 Video collage of Bogdanov Site on western wall of central graben showing vertical distribution and density (error bars represent estimated maximum density of aggregations) of shrimp *Rimicaris exoculata*. Lower collage is a view from east of structure and upper collage is a view from the southeast; ≃5 m of intervening sulphides have been omitted (Scale bars ~1 m)
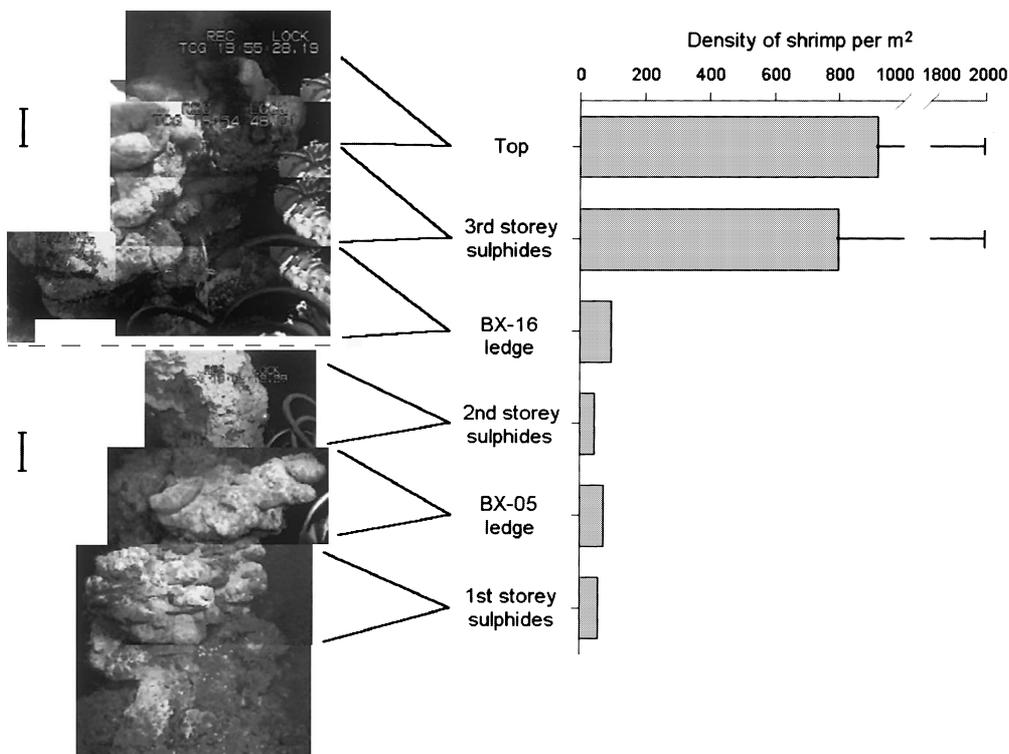
Fig. 8 *Rimicaris exoculata.* Interannual variation (mean ± SE) of population density of on Saracen's Head, The Spire and Wasp's Nest

Table 2 Comparison of densities of fauna other than shrimp observed at Broken Spur in 1993 and 1994. Estimates of faunal densities were calculated from total area of images for each structure, including images where none of a particular faunal group were present

Fauna	1993	1994
Saracen's Head[a]		
Crabs (m^{-2})	0.85	0.80
(*Segonzacia mesatlantica*)		
The Spire		
Crabs (m^{-2})	0.63	0.23
(*Segonzacia mesatlantica*)		
Ophiuroids (m^2)	3.13	2.53
(*Ophioctenella acies*)		
Anemones (m^{-2})	0.31	0.23
Wasp's Nest (platform)		
Crabs (m^{-2})	7.56	5.83
(*Segonzacia mesatlantica*)		

[a] 1994 estimates from "homologous" region at base of chimneys

Fig. 7 Video collage of a basalt pillar (Scale bar ~1 m)

Snake Pit (1500 to 2500 m^{-2}; Van Dover et al. 1988; Segonzac 1992) were observed on the upper surfaces of Bogdanov Site (Fig. 6), although the overall coverage of surfaces by these aggregations was 40 to 50%.
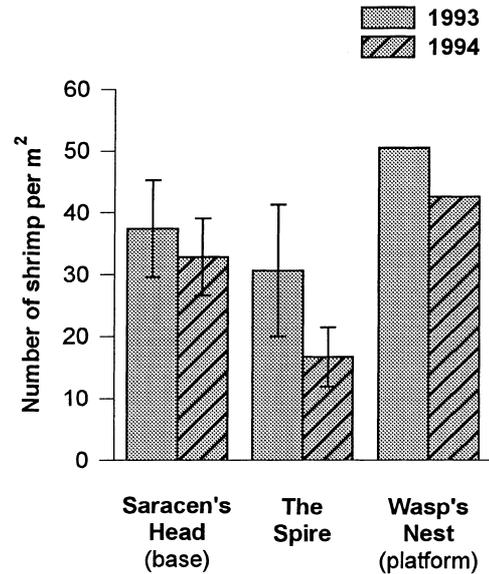
Maximum densities of the crab *Segonzacia mesatlantica* were found at the platform structures of Wasp's Nest, White Button and White Mushroom (6.37 m^{-2} ± 0.54 SE). The brittle star *Ophioctenella acies* was observed on the solid surfaces of chimneys and mounds (Fig. 9). Maximum densities of anemones occurred on the aprons of rubble at the base of sulphide mounds such as The Spire, Triple Chimney and Bogdanov Site (11.41 m^{-2} ± 1.04 SE). Fluted polychaetes (Ampharetidae) were present at the base of the Saracen's Head and Triple Chimney mounds, as well as being found in collapsed pillow lavas further away. Errant polychaetes were observed around the base of sulphide mounds, and a dense aggregation of synaphobranchid "snakefish" (up to
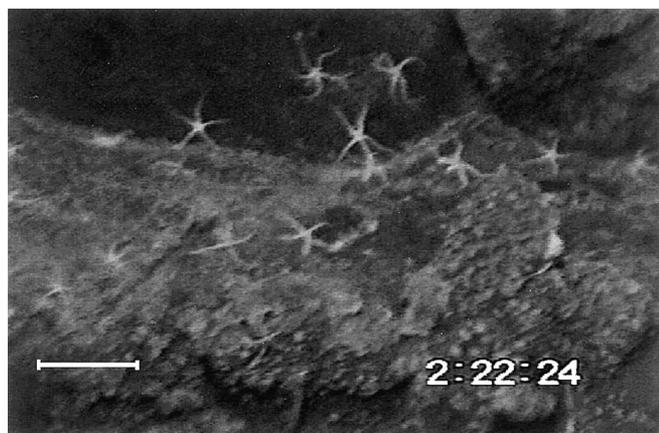
Fig. 9 Dense patch of *Ophioctenella acies* at base of Saracen's Head. Video-image from hand-held video camera (Scale bar ∼50 mm)

5 m⁻², but overall 0.98 m⁻²; Fig. 10) was found immediately east of the Triple Chimney mound. Other fish were also observed throughout the vent field, both in the periphery and close to active sites. BRAVEX/94 dive observers reported seeing octopus, but none were recorded on video. No mussels were observed during BRAVEX/94, but the locations previously described for these animals during "Alvin" dives (under ledges at the base of The Spire; Murton et al. 1995b) were not explored.

Discussion

The general faunal distribution and zonation observed in 1994 at sites of venting visited for the first time at Broken Spur, as well as those visited previously, is similar to that reported for 1993 (Murton et al. 1995b). Bresiliid shrimp are present close to black smokers, ophiuroids are found on solid surfaces of chimneys and mounds, peak densities of anemones occur at the base of

Fig. 10 Dense aggregation of synaphobranchid fish at base of Triple Chimney mound (Scale bar ∼1 m)

sulphide mounds, and peak densities of brachyuran crabs are found at platform structures. The lack of a significant increase in the population density of shrimp over 15 mo at sites visited by "Alvin" and BRAVEX/94 has implications for the hypothesis that the community at Broken Spur is recovering from a catastrophic disturbance. If such a recovery is taking place, then it must be very slow.

The rates of immigration, reproduction and recruitment at Mid-Atlantic hydrothermal vents are unknown, but a significant level of gene flow detected between populations of *Rimicaris exoculata* at TAG and Broken Spur (Creasey et al. 1996) suggests the presence of a metapopulation covering these two sites that should provide a ready source of new colonists following any interruption of venting (Herring 1996). A rapid faunal recovery is known from 9°N on the East Pacific Rise, where the vent community recovered from an absence of sessile metazoa to an abundant faunal assemblage resembling that observed at the Rose Garden in 1979 (Lutz et al. 1994; Hessler and Kaharl 1995) within 31 mo of the catastrophic interruption of venting by a lava flow (Haymon et al. 1993). There may be a substantial disparity in the rates of biological processes at Mid-Atlantic and Pacific vents because of marked faunistic differences (Van Dover 1995). Rates of immigration, reproduction and recruitment at Broken Spur might not be high enough to produce a visible increase in the faunal populations over the time-scale of our observations if a recovery were taking place. An alternative explanation, however, is that no recovery is taking place and the low biomass of shrimp at Broken Spur is a "climax" feature of the community.

Although low population densities of shrimp were observed at the majority of Broken Spur edifices visited during 1994, the "swarms" of shrimp at Bogdanov Site are exceptional and may offer a clue to possible factors controlling shrimp population density. The most obvious difference between Bogdanov Site and other structures at Broken Spur is the topography of the venting structure. Rather than being an isolated, thin, chimney structure like Judy's Tower (Fig. 5), venting at Bogdanov Site occurs across the top of a broad, flat structure and from ledges below (Fig. 6). How might these features influence the population density of vent shrimp?

Stable carbon-isotope ratios of *Rimicaris exoculata* indicate that adult shrimp are dependent on a non-photosynthetic source of organic carbon, whilst their nitrogen isotopes are consistent with a role as primary consumers (Van Dover et al. 1988). A strong but circumstantial case has been developed for the importance of epibiotic chemosynthetic bacteria in the nutrition of this species (Van Dover et al. 1988; Gebruk et al. 1993; Segonzac et al. 1993; Van Dover 1995). If shrimp do feed primarily on epibiotic bacteria occupying the "bacteriophore" setae of their maxillae, then it is important for these bacteria to be exposed to the sulphide in vent fluid in order to sustain chemosynthetic primary production.

Therefore the shrimp must occupy some substratum directly exposed to the flow of hydrothermal fluids. Swimming to maintain a vertical position in a buoyant hydrothermal plume rising at 100 cm s^{-1} from a high-temperature vent source (Nesbitt and Murton 1995a, b) would be energetically expensive, if at all possible. Such behaviour is exhibited by paradaliscid amphipods at Pacific vents, but only in a vertical flow of 5 to 10 cm s^{-1} from diffuse venting (Kaartvedt et al. 1994).

If the shrimp instead feed by dislodging bacteria from sulphides using their walking legs (Van Dover et al. 1988; Segonzac et al. 1993), then these bacteria and therefore the shrimp similarly need to occupy some substratum exposed to the flow of hydrothermal fluids. Whatever the reason, adult *Rimicaris exoculata* are generally found crawling on the substratum (Rona et al. 1986; Segonzac et al. 1993), and maintain high levels of activity on surfaces at the central black smokers of TAG (Van Dover et al. 1988). Sensillae on the second antennae of the shrimp display sensitivity to dissolved sulphide at picomolar levels, which may offer a stimulus over tens of metres from its source (Renninger et al. 1995). When displaced from the substratum, shrimp immediately seek to re-establish themselves near the source of hydrothermal fluid (Van Dover et al. 1988; Renninger et al. 1995), resulting in "lines" of jostling shrimp oriented against the current of vent fluids (Fig. 11). The development of dense aggregations of shrimp may therefore depend on the availability of sufficient substratum exposed to the flow of hydrothermal fluids for the shrimp.

At thin, isolated, chimney structures where venting occurs from a restricted area at the top of the edifice, little or no substratum is available in the flow of hydrothermal fluids for shrimp to occupy. Little diffuse venting occurs below this, and there are few shrimp. Where fissuring occurs at the base of Judy's Tower, the density of shrimp is greater. A similar bimodal vertical distribution is observed in alvinellid polychaetes on a chimney at 13°N on the East Pacific Rise (Chevaldonné and Jollivet 1993). Where active beehive diffusers occur, substratum for shrimp to occupy may be available beside and above the source of venting, and population densities of shrimp are significantly greater in these areas. As most Broken Spur chimneys are thin and isolated, the area of suitable substratum is small and the coverage of shrimp is sparse, but on the broad, flat top of Bogdanov Site, much more substratum washed by vent fluid is available for shrimp to occupy beside and between discrete sources of venting. It is in these regions that the "swarms" of shrimp are found. Black smoke also issues from orifices on the sides of this edifice just below the top, and dense aggregations of shrimp are found above and beside these sources.

At TAG, central black smokers occupied by dense aggregations of shrimp (Fig. 11) form a conical complex of chimneys 30 m in diameter and 25 m high. High-temperature fluids issue from fractures in the sulphides at the base of chimneys as well as from the chimneys themselves (Van Dover 1995), so that the whole area is wreathed in black smoke, prompting Japanese workers to name it "Laputa" after Swift's fictional city built on a cloud (Fujioka et al. 1995). At Snake Pit, dense aggregations of shrimp occur at "Les Ruches", a 50 m-high sulphide mound crowned by two edifices constructed from several chimneys and beehive diffusers (Segonzac et al. 1993). Shrimp "swarms" are present at these two smoker complexes, whilst their density is much lower at an isolated chimney situated lower and more periperally on the mound ("Laussel"; Segonzac et al. 1993). The availability of substratum exposed to the flow of hydrothermal fluids seems to be dependent on the topography of venting structures and is more prevalent at larger, flatter mound structures with chimney/diffuser complexes than at isolated chimneys.

Further exploration of the Broken Spur vent field by seafloor video during R.R.S. Charles Darwin Cruise CD95 (Murton et al. 1995a) did not find any evidence of an increase in shrimp biomass 9 mo after BRAVEX/94. Observations of a redistribution of vent shrimp within 2 mo of a change in the pattern of hydrothermal activity on the TAG mound (Copley et al. in preparation) reinforce the interpretation that the low population densities of shrimp on the Broken Spur chimneys are a "climax" feature. Shrimp would be expected to redistribute rapidly from the local source of Bogdanov Site to fill any vacant habitat available at the other Broken Spur chimneys.

The absence of shrimp from the majority of Broken Spur edifices is a particularly striking feature of the community compared to the "swarms" at TAG and Snake Pit. However, the degree to which other fauna at Broken Spur are depauperate is less clear. The crab *Segonzacia mesatlantica* has a maximum density of 10 individuals m^{-2} at Snake Pit (Guinot 1989) comparable to the maximum observed at Broken Spur (6.66 to
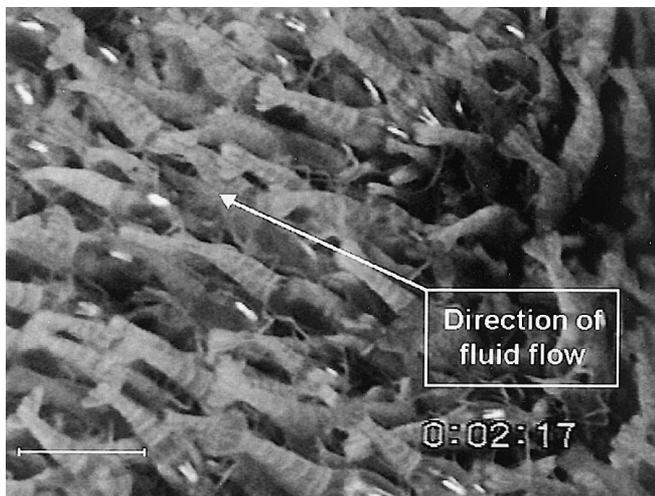

Fig. 11 Dense swarm of *Rimicaris exoculata* at TAG, showing non-random orientation in hydrothermal flow. Video-image from hand-held video camera (Scale bar ~50 mm)

10 m^{-2}, Murton et al. 1995b; 7.56 m^{-2}, this study). Densities of the brittle star *Ophioctenella acies* at Broken Spur (e.g. ~30 dm^{-2} within patches such as that shown in Fig. 9) are comparable to those at TAG and Snake Pit (up to 20 dm^{-2}, Tyler et al. 1995).

The dense aggregation of synaphobranchid fish observed near Triple Chimney (Fig. 10) certainly does not represent a depauperate biomass compared to that observed for this group at TAG and Snake Pit. Video observations of behaviour suggest that the fish in this aggregation are feeding on items on sulphide surfaces, possibly ampharetid polychaetes. Population densities of ampharetids may approach 300 m^{-2} at the base of sulphide mounds and in the hollows of some collapsed pillow basalts. The high ratio of predators and scavengers to primary consumers noted during the first submersible dives at Broken Spur (Murton and Van Dover 1993) is consistent with low populations of shrimp at the majority of Broken Spur structures, but with an abundance of fauna other than shrimp comparable to that of other Mid-Atlantic sites.

Although interannual variation in the faunal distribution at Broken Spur suggests that the community is not immediately recovering from a disturbance such as that imposed by a recent period of hydrothermal quiescence, this does not remove the possibility that Broken Spur has undergone such a period, or several such periods, during its geological past. Current geological models of Broken Spur (Nesbitt 1995; Nesbitt and Murton 1995b) include the hypothesis that Broken Spur was once a continuous sulphide mound like TAG, but that oxidation and mass wasting during periods of inactivity caused dissection of the mound to leave the present isolated sites of venting. Thus, the low population density of shrimp at the chimney structures of Broken Spur only represents a "climax" state in the sense that there is currently little optimal habitat available. Should more habitat become available as a result of the geological evolution of venting structures, then the population density of shrimp would be expected to increase accordingly. Therefore, the shrimp population at Broken Spur may still be recovering from a period of hydrothermal quiescence, if recovery is taken to mean the development of dense "swarms" like those at TAG and Snake Pit. Achieving such a recovery would depend on the geological evolution of venting structures with appropriate topographies, and would require a longer time-scale than if population growth were solely dependent on the immigration, reproduction and recruitment of animals.

References

BRAVEX/94 Scientific Team (1994) BRAVEX/94: a joint British–Russian expedition to the Broken Spur (29°N) and TAG (26°N) hydrothermal vent sites on the Mid-Atlantic Ridge. BRIDGE Newsl (Univ Leeds) 7: 6–9

Chevaldonné P, Jollivet D (1993) Videoscopic study of deep-sea hydrothermal vent alvinellid polychaete populations: biomass estimation and behaviour. Mar Ecol Prog Ser 95: 251–262

Creasey S, Rogers AD, Tyler PA (1996) Genetic comparison of two populations of the deep-sea vent shrimp *Rimicaris exoculata* (Decapoda: Bresiliidae) from the Mid-Atlantic Ridge. Mar Biol 125: 473–482

Duckworth RC, Knott R, Fallick AE, Rickard D, Murton BJ, Van Dover CL (1995) Mineralogy and sulphur isotope geochemistry of the Broken Spur sulphides, 29°N, Mid-Atlantic Ridge. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes. Geological Society, London, pp 175–189 (Spec Pub geol Soc Lond No. 87)

Elderfield H, German CR, Palmer MR (1993) Hydrothermal activity on the Mid-Atlantic Ridge at 29°N: results of *RRS Charles Darwin* Cruise 77 (BRIDGE Cruise No. 8). BRIDGE Newsl (Univ Leeds) 5: 7–10

Fisher CR (1995) Towards an appreciation of hydrothermal vent animals: their environment, physiological ecology and tissue stable isotope values. In: Humphris SE, Zierenberg R, Mullineaux L, Thomson R (eds) Seafloor hydrothermal systems: physical, chemical, biological and geological interactions. American Geophysical Union, Washington, pp 297–316 (Geophys Monogr No. 91)

Fujioka K, Kato K, Kinoshita M, Nishizawa A, Aoki M, Mitsuzawa K (1995) TAG hydrothermal mound of the Mid-Atlantic Ridge, its evolution and long-term change. EOS Trans Am geophys Un 76: p 574 (Abstract)

Gebruk AV, Pimenov NV, Savvichev AS (1993) Feeding specialization of bresiliid shrimps in the TAG site hydrothermal community. Mar Ecol Prog Ser 98: 247–253

German CR, Parson LM, HEAT Scientific Team (1996) Hydrothermal exploration near the Azores Triple Junction: tectonic control of venting at slow-spreading ridges? Earth planet Sci Lett 138: 93–104

Guinot D (1989) Description de *Segonzacia* gen. nov. et remarques sur *Segonzacia mesatlantica* (Williams): campagne HYDROSNAKE 1988 sur la dorsale médio-Atlantique (Crustacea Decapoda Brachyura). Bull Mus Hist nat, Paris (4 sér) 11: 203–231

Haymon RM, Fornari DL, Von Damm KL, Lilley MD, Perfit MR, Edmond JM, Shanks WC, Lutz RA, Grebmeier JM, Carbotte S, Wright D, McLaughlin E, Smith M, Beedle N, Olson E (1993) Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9°45–52′N: direct submersible observations of seafloor phenomena associated with an eruption in April 1991. Earth planet Sci Lett 119: 85–101

Herring PJ (1996) Travelling shrimp. BRIDGE Newsl (Univ Leeds) 11: 6–8

Hessler RR, Kaharl VA (1995) The deep-sea hydrothermal vent community: an overview. In: Humphris SE, Zierenberg R, Mullineaux L, Thomson R (eds) Seafloor hydrothermal systems: physical, chemical, biological and geological interactions. American Geophysical Union, Washington, pp 72–84 (Geophysical Monogr No. 91)

Hessler RR, Smithey WM, Boudrias MA, Keller CH, Lutz RA, Childress JJ (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift: eastern tropical Pacific). Deep-Sea Res 35: 1681–1709

James RH, Elderfield H, Palmer MR (1995a) The chemistry of hydrothermal fluids from the Broken Spur site, 29 N Mid-Atlantic Ridge. Geochim cosmochim Acta 59: 651–659

James RH, Elderfield H, Rudnicki MD, German CR, Palmer MR, Chin C, Greaves MJ, Gurvich E, Klinkhammer GP, Ludford E, Mills RA, Thomson J, Williams AC (1995b) Hydrothermal

plumes at Broken Spur, 29°N Mid-Atlantic Ridge: chemical and physical characteristics. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes. Geological Society, London, pp 97–110 (Spec Publ geol Soc Lond No. 87)

Kaartvedt S, Van Dover CL, Mullineaux LS, Wiebe PH, Bollens SM (1994) Amphipods on a deep-sea hydrothermal treadmill. Deep-Sea Res 41: 179–195

Lalou C, Reyss J-L, Brichet E, Arnold M, Thompson G, Fouquet Y, Rona PA (1993) New age data for Mid-Atlantic hydrothermal sites: TAG and Snakepit chronology revisited. J geophys Res 98: 9705–9713

Lutz RA, Shank TM, Fornari DJ, Haymon RM, Lilley MD, Von Damm KL, Desbruyeres D (1994) Rapid growth at deep-sea vents. Nature, Lond 371: 663–664

Martin JW, Christiansen JC (1995) A new species of the shrimp genus *Chorocaris* Martin & Hessler 1990 (Crustacea: Decapoda: Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge. Proc biol Soc Wash 108: 220–227

Murton BJ, Becker K, Briais A, Edge D, Hayward N, Klinkhammer G, Millard N, Mitchell I, Rouse I, Rudnicki M, Sayanagi K, Sloan H (1993) Results of a systematic approach to searching for hydrothermal activity on the Mid-Atlantic Ridge: the discovery of the "Broken Spur" vent site. BRIDGE Newsl (Univ Leeds) 4: 3–6

Murton BJ, German CR, Herring P, Dixon DR, Rudnicki M, Mullane E, Miller R, Edge D, Boorman B, Bonner R, Holland S, Riches S, Vandermirsch F, Taylor P, Rees D, Booth D, Taylor A, Day C (1995a) Volcanoes, plumes, minerals and life: FLUXES I, a segment-scale study. BRIDGE Newsl (Univ Leeds) 9: 14–19

Murton BJ, Klinkhammer G, Becker K, Briais A, Edge D, Hayward N, Millard N, Mitchell I, Rouse I, Rudnicki M, Sayanagi K, Sloan H, Parson LM (1994) Direct evidence for the distribution and occurrence of hydrothermal activity between 27°–30°N on the Mid-Atlantic Ridge. Earth planet Sci Lett 125: 119–128

Murton BJ, Van Dover CL (1993) *ALVIN* dives on the Broken Spur hydrothermal vent field at 29°10′N on the Mid-Atlantic Ridge. BRIDGE Newsl (Univ Leeds) 7: 11–14

Murton BJ, Van Dover CL, Southward EC (1995b) Geological setting and ecology of the Broken Spur hydrothermal vent field: 29°10′N on the Mid-Atlantic Ridge. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes. Geological Society, London, pp 33–42 (Spec Publ geol Soc Lond No. 87)

Nesbitt RW (1995) The geology of the Broken Spur hydrothermal vent site; a new look at an old field. BRIDGE Newsl (Univ Leeds) 8: 30–34

Nesbitt RW, Murton BJ (1995a) Chimney growth rates and metal deposition at the Broken Spur Vent Field, 29°N, MAR. BRIDGE Newsl (Univ Leeds) 8: 35–37

Nesbitt RW, Murton BJ (1995b) Chimney growth rates and metal deposition at the Broken Spur Vent Field, 29°N MAR: a correction and further speculation. BRIDGE Newsl (Univ Leeds) 9: 38–41

Renninger GH, Kass L, Gleeson RA, Van Dover CL, Battelle B-A, Jinks RN, Herzog ED, Chamberlain SC (1995) Sulfide as a chemical stimulus for deep-sea hydrothermal vent shrimp. Biol Bull mar biol Lab, Woods Hole 189: 69–76

Rona PA, Klinkhammer G, Nelsen TA, Trefry JH, Elderfield H (1986) Black smokers, massive sulphides and vent biota at the Mid-Atlantic Ridge. Nature, Lond 321: 33–37

Segonzac M (1992) Les peuplements associés à l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique; 23°N, 3480 m): composition et microdistribution de la mégafaune. C r hebd Séanc Acad Sci, Paris (Sér 3) 314: 593–600

Segonzac M, de Saint-Laurent M, Casanova B (1993) L'enigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale médio-atlantique. Cah Biol mar 34: 535–571

Tunnicliffe V (1990) Observations on the effects of sampling on hydrothermal vent habitat and fauna of Axial Seamount, Juan de Fuca Ridge. J geophys Res 95: 12961–12966

Tyler PA, Paterson GLJ, Sibuet M, Guille A, Murton BJ, Segonzac M (1995) A new genus of ophiuroid (Echinodermata: Ophiuroidea) from hydrothermal mounds along the Mid-Atlantic Ridge. J mar biol Ass UK 75: 977–986

Van Dover CL (1995) Ecology of Mid-Atlantic Ridge hydrothermal vents. In: Parson LM, Walker CL, Dixon DR (eds) Hydrothermal vents and processes. Geological Society, London, pp 257–294 (Spec Publ geol Soc, Lond, No. 87)

Van Dover CL, Fry B, Grassle JF, Humphris S, Rona PA (1988) Feeding biology of the shrimp *Rimicaris exoculata* at hydrothermal vents on the Mid-Atlantic Ridge. Mar Biol 98: 209–216