Food sources, behaviour, and distribution of hydrothermal vent shrimps at the Mid-Atlantic Ridge

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Five species of bresilioid shrimp were investigated at seven hydrothermal sites on the Mid-Atlantic Ridge: Menez Gwen, Lucky Strike, Rainbow, Broken Spur, TAG, Snake Pit and Logatchev. Samples were prepared for analysis of stable isotopes, elemental composition and lipids. Shrimp behaviour was observed from the submersible 'Alvin' and in the laboratory aboard RV 'Atlantis'. The distribution and zonation of the shrimp species was recorded. Juvenile shrimp of all species arrive at the vents carrying reserves of photosynthetic origin, built-up in the pelagic larval stages. These reserves are used while the shrimp metamorphose to the adult form and, in *Rimicaris exoculata* and *Chorocaris chacei*, while they develop epibiotic bacteria supporting structures, the modified mouthparts and the inside of the carapace. The main food of adult *R. exoculata* is filamentous bacteria that grow on these structures. The intermediate sizes of *C. chacei* also feed on such bacteria, but the final stage gets some food by scavenging or predation. *Mirocaris* species scavenge diverse sources; they are not trophically dependent on either *R. exoculata* or mussels. Adults of *Alvinocaris markensis* are predators of other vent animals, including *R. exoculata*. The dense swarms of *R. exoculata*, with their exosymbionts, can be compared to endosymbiont-containing animals such as *Bathymodiolus* and the vestimentiferan tube-worms of the Pacific vents. Such associations, whether endo- or ectosymbiotic, may be necessary for the development of flourishing communities at hydrothermal vents.

INTRODUCTION

Exploration of hydrothermal vents in the Atlantic Ocean discovered abundant populations of shrimp and there has been much discussion of their role in the community and their food source (Rona et al., 1986; Williams & Rona, 1986). Hydrothermal communities in the Pacific Ocean are supported by invertebrates that harbour endosymbiotic chemosynthetic bacteria, regarded as 'primary producers' (Fisher, 1990, 1996; Childress & Fisher, 1992;). Although deep-water pelagic shrimps are usually carnivores (Omori, 1974), by analogy with Pacific vent communities, it was anticipated that the dominant shrimp at the Mid-Atlantic Ridge (MAR) would harbour endosymbiotic bacteria (Gal'chenko et al., 1989), but no evidence was found. Gut contents, lipopolysaccharide analyses and stable isotope assays suggested that the shrimp ingested bacteria (Van Dover et al., 1988). A particular problem was the high density of the shrimp aggregations compared with the areas of bacterial mats. It is difficult to visualize how large numbers of shrimp could be sustained by grazing on such mats or by filtration of suspended particles. An alternative food source for the shrimp might be bivalve molluscs that rely on endosymbiotic bacteria; these are abundant at some vents, but absent or rare at two sites (TAG, Broken Spur) where shrimp are dominant. The question arises whether the food chain at the MAR is different from other vent ecosystems (Gebruk et al., 1997a).

In reviewing theories of hydrothermal shrimp nutrition, Van Dover (1995), Gebruk et al. (1997a) and Polz et al. (1998) discussed the dietary importance of the bacterial filaments that grow on the mouthparts and the under surface of the carapace, especially in *Rimicaris exoculata*. Casanova et al. (1993) suggested that shrimp might absorb dissolved organic matter (DOM) from the bacteria, while Polz et al. (1998) proposed that autotrophic bacteria in the gut might contribute to nutrition.

Vent animals are difficult to investigate experimentally, and most evidence about MAR shrimp nutrition comes from chemical, biochemical and stable isotope analyses. We are able to contribute to the investigation of this problem, using new data from a unique set of samples obtained from all the known hydrothermal areas on the MAR (Figure 1), in the depth range 750–3700 m. Samples were taken for stable isotope analysis, lipid analysis, and elemental analysis. Observations on behaviour and microscale distribution of shrimp were made *in situ* and in the laboratory. In addition to *R. exoculata*, four other shrimp species were investigated, including different ages. The investigations tested several hypotheses, including the role of epibiotic bacteria, input of photosynthetically derived carbon, effect of age and the influence of depth and differing vent environments.

MATERIALS AND METHODS

Sampling

Collections were made from the submersible 'Alvin', operating from the RV 'Atlantis', from 29 June to 27 July 1997, at seven sites (Figure 1, Table 1). Most samples were taken with a suction sampler that held its catch inside a perspex cylinder, and the shrimps remained alive until
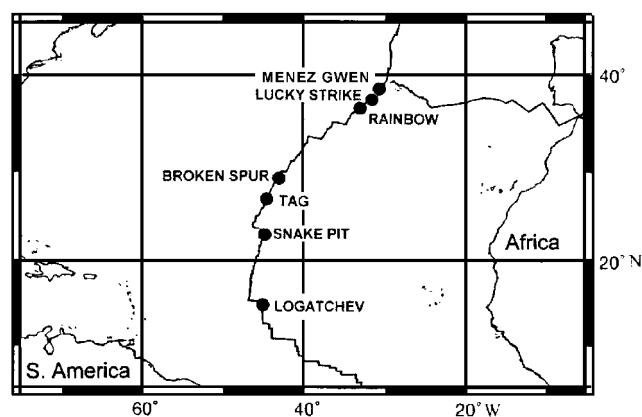
Figure 1. The hydrothermal vent sites along the Mid-Atlantic Ridge, sampled for bresilioid shrimp on cruise MAR 97.

transferred to the ship. The water from the slurp guns at Lucky Strike showed dissolved sulphide of the order of 0.5 to 5 μM, indicating some retention of ambient water during the ascent. A few samples were taken with a small net operated by the manipulator arm, placed in an insulated, but unsealed container (biobox) until return to the ship; these shrimp were less viable. Shrimps were sorted into species, transferred to cooled surface seawater and kept in a cool room at 14°C, or a refrigerator at 4°C. Representative individuals were preserved in 4% formol or 70% ethanol, and the rest measured for total length (rostrum to telson, (TL)). Some workers on *Rimicaris exoculata* (e.g. Polz et al., 1998) have employed carapace length (CL) hence we measured both total length and carapace length of 17 specimens from Broken Spur and

TAG for comparison. The regression of CL over TL was y=0.6417 + 0.3667 x, for a correlation coefficient of 0.95.

Selected tissues, usually abdominal muscle, from measured specimens were divided into three subsamples, for drying, lipid preservation and freezing for genetic analysis. The lipid analyses and the genetic results are being reported elsewhere (Pond et al., 2000a,b; Shank et al., 1998). Some specimens were dissected into body components, analysed separately. Very small specimens were used whole. Tissues and whole shrimp were dried in aluminium foil boats at 60°C, then wrapped in foil and stored in a refrigerator. At Plymouth the dry samples were ground in a ball-mill, and the powder stored in glass vials.

Carbon and nitrogen stable isotope analysis

Subsamples of the dried and ground tissue were acidified in 2N HCl to remove any carbonates and re-dried at 40°C. The samples were loaded into small pre-combusted quartz tubes along with copper, precombusted copper oxide and silver foil. These tubes were then loaded into large precombusted quartz tubes, evacuated and sealed. The samples were combusted at 910°C for 3h and allowed to cool slowly overnight. Resulting CO_2 and N_2 were separated cryogenically. The N_2 collected was analysed immediately, the CO_2 was frozen into small glass tubes and flame-sealed until analysis. Both gases were analysed on a VG SIRA II mass spectrometer. Results are expressed relative to PDB and atmospheric nitrogen standards in the usual notation. Precision of an internal laboratory sub-standard was 0.05‰.

Table 1. *'Atlantis' cruise 3, legs 2 and 3, 1997. Station list for this investigation. Temperature is for ambient seawater.*

Dive station	Date	Site	Latitude	Longitude	Depth m	Isotope samples	Lipid samples	C:N:S samples	Temp. (°C)	Species of shrimp sampled
3114	29.06.97	Lucky Strike	37′17°N	32′16°W	1727	3	nd	nd	4.5	none
3115	30.06.97	Lucky Strike	37′17°N	32′16°W	1719	15	nd	nd	4.5	*C. chacei, M. fortunata*
3117	07.07.97	Menez Gwen	37′50.474°N	31′31.366°W	857	4	4	3	8.8	*M. fortunata*
3118	08.07.97	Lucky Strike	37′17.51°N	32′16.66°W	1719	7	5	3	4.5	*C. chacei, M. fortunata*
3119	09.07.97	Lucky Strike	37′17.394°N	32′16.672°W	1721	2	6	3	4.5	*C. chacei, M. fortunata*
3120	10.07.97	Lucky Strike	37′17.629°N	32′16.532°W	1733	10	11	5	4.5	*R. exoculata, C. chacei, M. fortunata*
3121	11.07.97	Rainbow	36′13.89°N	33′54.15°W	2350	2	2	2	3.7	*M. fortunata*
3122	12.07.97	Rainbow	36′14.030°N	33′54.065°W	2305	6	6	4	3.7	*R. exoculata, M. fortunata*
3123	15.07.97	Broken Spur	29′09.976°N	43′10.394°W	3060	6	9	5	3	*R. exoculata, M. fortunata*
3124	16.07.97	Broken Spur	29′10.015°N	43′10.423°W	3056	4	5	3	3	*R. exoculata, C. chacei, M. fortunata, M. keldyshi*
3125	17.07.97	Broken Spur	29′10.008°N	43′10.400°W	3056	3	3	3	3	*R. exoculata, C. chacei,*
3126	19.07.97	TAG	26′08.141°N	44′49.543°W	3655	4	5	2	2.8	*R. exoculata*
3127	20.07.97	TAG	26′08.184°N	44′49.543°W	3643	4	4	2	2.8	*R. exoculata, C. chacei, M. keldyshi, A. markensis*
3128	21.07.97	Snake Pit	23′22.060°N	44′56.987°W	3560	4	5	4	2.4	*R. exoculata, C. chacei, M. keldyshi, A. markensis*
3129	22.07.97	Snake Pit	23′22.200°N	44′57.042°W	3510	5	10	3	2.4	*R. exoculata, A. markensis*
3131	25.07.97	Logatchev	14′44.937°N	44′58.278°W	3018	6	9	3	2.8	*R. exoculata, C. chacei, M. keldyshi, A. markensis*
3132	26.07.97	Logatchev	14′44.946°N	44′58.278°W	3011	0	1	0	2.8	*M. keldyshi*
3133	27.07.97	Logatchev	14′45.189°N	44′58.829°W	3038	7	8	5	2.8	*C. chacei*

nd, no data.

Elemental analysis

Total carbon and nitrogen in the powdered dried tissues were analysed by R.N. Head, Plymouth Marine Laboratory. Total sulphur was measured by Elemental Microanalysis Ltd, Okehampton, Devon.

Behaviour of shrimps and their micro-scale distribution.

Video images from each dive were examined for shrimp behaviour and distribution. Detailed observations were made during 'Alvin' Dive 3131 at Irina-2, Logatchev and during 'Alvin' Dive 3123 at the Moose site, Snake Pit. Close-up sequences of up to 15 min were recorded. 'Alvin' video equipment included three-chip and digital cameras. The three-chip camera was equipped with a two-beam laser array to indicate scale. Additional records were made with the observers' own Hi-8 video cameras. The distribution of the shrimp was mapped.

Behaviour of shrimps in the laboratory.

Recovered shrimps were maintained alive in a small tank of surface seawater (renewed daily) with a simple aerator to stir the water. The tank was in a cooled room, at 14°C. Indirect lighting from screened fluorescent tubes was used for observation and recording, otherwise the animals were kept in the dark. The activities of the shrimp in the main tank or in smaller plastic boxes were recorded with a Sony Hi-8 video camera with zoom lens. Food items taken from the vent habitat were crushed mussels (*Bathymodiolus* spp.), shrimp tissues and filamentous bacteria on rock fragments. *Artemia* nauplii were hatched from eggs.

Observations with a stereomicroscope were made in the ship's laboratory (temperature about 20°C). An Olympus stereomicroscope was fitted with a video camera and a monitor for viewing, and recordings made on SVHS tape. Observations began with animals at 14°C, but the dishes warmed up and long-term microscopic observation was not possible.

A mixture of glass beads (70–50 μm diameter) and carborundum powder (600 mesh) was used to find out whether the shrimp were picking up particles. This mixture was allowed to settle as an even, light-coloured layer on the bottom of three plastic boxes of seawater. Five juvenile *R. exoculata*, 24–25 mm, long were added to each box and left for 10, 15 and 20 h. As they crawled they left tracks in the particle layer and some of them appeared to be handling the particles with their mouthparts and chelae. The shrimp were then fixed in 4% SW formol and later transferred to 70% ethanol to harden the tissues.

Taxonomic status of MAR hydrothermal shrimps

It is necessary to explain the status of the species investigated, as the taxonomy of some vent shrimp has been confused. There may be at least eight species on the MAR. Experts have agreed on the status of four: *Rimicaris exoculata* Williams & Rona, 1986, *Chorocaris chacei* (Williams & Rona, 1986), *Alvinocaris markensis* Williams, 1988 and *Mirocaris fortunata* (Martin & Christiansen, 1995). Vereschaka (1997a) separated *Mirocaris keldyshi* from *M. fortunata* and we found that fresh specimens could be

distinguished morphologically and by colour. These were prepared separately for analysis. Using the same series of samples, Shank et al. (in press) found little genetic difference at the mitochondrial COI gene level, but we choose to treat them separately here. The 'small orange shrimp', that are often abundant among aggregations of *R. exoculata*, have had their status disputed. As first noted by Segonzac et al. (1993) they have features intermediate between *Chorocaris* and *Rimicaris* (see also Van Dover, 1995; Creasey et al., 1996; Gebruk et al., 1997a). This 'small orange shrimp' was described as *Iorania concordia* by Vereshchaka (1996a), and as *Rimicaris aurantiaca* by Martin et al. (1997). The sample series analysed for isotopes was examined by Shank et al. (1998) using allozymes and mitochondrial DNA sequences (COI and 16S rRNA genes), and no difference was found between adult *R. exoculata* and the 'small orange shrimp'. Dixon et al. (1998) also concluded that this form was genetically identical to *R. exoculata*. Therefore we refer to the small orange form as juvenile *R. exoculata*. There are more species of *Alvinocaris* than first suspected: two new species are being described from MAR '97 cruise material: *Alvinocaris* sp.aff. *stactophila* at Menez Gwen (A.B. Williams & T.M. Shank, personal communication), and *Alvinocaris* sp. aff. *muricola* from Logatchev (A.B. Williams & A.L. Vereshchaka, personal communication). Another species may be present at Logatchev (Vereshchaka, personal communication). Our analyses refer only to *A. markensis*.

The taxonomy of bresilioid shrimps at the family level is somewhat uncertain (Van Dover, 1995; Gebruk et al., 1997a). Recently, experts (A.B. Williams, J.W. Martin, F.A. Chace and A.L. Vereshchaka, personal communication) have agreed on the placing of vent/seep related shrimps in the families Alvinocarididae Christoffersen 1986 (*Alvinocaris, Rimicaris, Chorocaris* and *Opapele*) and Mirocarididae Vereshchaka 1997a (*Mirocaris*), separating them from non-vent genera which remain in the family Bresiliidae Calman. All three families are included in the superfamily Bresilioidea Calman (Vereshchaka, 1997a).

RESULTS

Stable carbon and nitrogen isotope analysis

Results of the stable isotope analyses are set out in Table 2. The values for each species are summarized separately.

Rimicaris exoculata

Adult stage *R. exoculata* show a moderate range of $\delta^{13}C$ values (−9.97 to −14.55‰, mean −11.79; see Table 2), with no significant variations between vents or depths. The most negative values, −14.55 and −14.44‰, were from specimens of 26 and 29 mm length, but a 25 mm specimen had a value of −13.84 and another 26 mm specimen showed −11.05‰, extending the range for the small adult size group. The larger *Rimicaris*, those exceeding 45 mm length, had a narrow range of $\delta^{13}C$, from −9.97 to −12.05‰ (mean −11.01‰). The mouthparts (maxilliped I), densely covered with filamentous bacteria, showed $\delta^{13}C$ values of −11.45 and −10.52‰, within the range for abdominal issues of the large adults, and close to the mean. Corresponding $\delta^{15}N$ values for the maxillipeds with

Table 2. *Five species of hydrothermal vent shrimp. Stable isotope ratios (C:N), and element analysis (C, N, S).*

| Site | Length (mm) | Stable isotopes | | | Elemental analysis | | | |
		Tissue used	δ^{13}C (‰)	δ^{15}N (‰)	Tissue used	Carbon (%)	Nitrogen (%)	Sulphur (%)
Rimicaris exoculata: adult form								
LS	58.00	a	−11.13	7.45		nd	nd	nd
LS	58.00	a	−11.10	7.87	a	35.08	10.57	1.13
LS	58.00	m	−11.45	5.57	c	27.26	6.86	2.00
RB	49.00	a	−10.09	7.43	a	34.84	10.53	1.05
RB	53.00	m	−10.52	6.54		nd	nd	nd
RB	45.00	a	−9.97	7.98	a	34.98	10.69	1.09
BS	57.00	a	−10.75	7.64	c	38.89	10.08	0.84
BS	26.00	a	−14.55	6.18	c	35.68	6.82	2.00
TAG	26.00	a	−11.05	5.55		nd	nd	nd
TAG	52.00	a	−11.47	6.57	c	40.98	8.58	0.53
SP	31.00	a	−12.70	5.93	c	41.00	8.83	1.14
SP	25.00	a	−13.84	6.08	c	41.37	6.45	1.65
SP	57.00	a	−12.05	6.88	c	nd	nd	nd
LOG	29.00	a	−14.44	5.84	c	34.30	8.14	0.68
Rimicaris exoculata: juveniles								
BS	18.00	a	−18.07	5.68	c	34.69	6.84	0.93
BS	26.00	a	−16.81	4.73	c	50.68	5.89	0.56
BS	25.00	a	−15.79	4.48	c	49.85	5.79	0.95
BS	28.00	a	−15.61	nd		nd	nd	nd
TAG	26.00	a	−16.13	4.50		nd	nd	nd
TAG	25.00	a	−17.44	4.69	c	50.16	5.94	0.45
SP	28.00	a	−16.18	3.94	c	54.55	4.17	1.64
LOG	26.00	a	−16.11	5.15	c	53.69	4.75	0.30
Chorocaris chacei								
LS	23.00	a	−12.78	6.07		nd	nd	nd
LS	40.00	a	−12.58	6.79		nd	nd	nd
LS	40.00	m	−13.76	4.07		nd	nd	nd
LS	42.00	a	−12.96	5.99	c	34.30	7.19	2.10
LS	47.00	a	−14.85	4.75	a	32.44	9.6	0.77
LS	49.00	a	−15.14	4.99	a	35.94	11.24	nd
LS	50.00	a	−14.36	5.50	a	37.92	11.12	1.14
LS	50.00	m	−14.38	5.22	c	31.79	7.67	2.52
LS	45.00	a	−12.53	7.07		nd	nd	nd
LS	32.00	a	−11.67	7.31		nd	nd	nd
LS	32.00	c	−11.82	5.72		nd	nd	nd
LS	43.00	a	−14.33	5.88		nd	nd	nd
LS	43.00	c	−14.07	5.34		nd	nd	nd
LS	43.00	ex	−14.31	4.23		nd	nd	nd
LS	43.00	m	−14.35	4.15		nd	nd	nd
LS	43.00	s	−14.61	4.19		nd	nd	nd
BS	48.00	a	−13.02	8.00	c	32.92	9.52	0.85
BS	62.00	a	−13.61	7.98	c	31.90	7.62	1.01
TAG	16.00	t	−15.93	5.58		nd	nd	nd
TAG	43.00	a	−15.56	7.32	c	42.82	9.03	0.71
SP	18.00	t	−18.03	5.40		nd	nd	nd
SP	68.00	a	−13.44	8.03	a	35.66	11.55	0.46
LOG	16.00	t	−16.79	5.82		nd	nd	nd
LOG	54.00	a	−13.28	7.71	a	35.80	11.61	0.55
Alvinocaris markensis								
TAG	58.00	a	−17.89	9.19	a	nd	nd	nd
SP	52.00	a	−15.21	7.54	a	37.34	8.83	0.50
LOG	28.00	a	−21.17	3.65	a	nd	nd	nd

Table 2. *(Continued)*.

Site	Length (mm)	Stable isotopes			Elemental analysis			
		Tissue used	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Tissue used	Carbon (%)	Nitrogen (%)	Sulphur (%)
Mirocaris fortunata								
MG	14		nd	nd	c	36.71	7.28	0.67
MG	14	t	−19.32	6.73		nd	nd	nd
MG	18		nd	nd	t	34.16	9.52	0.88
MG	23	a	−14.82	6.4		nd	nd	nd
MG	29	a	−19.73	4.1	c	36.02	8.24	1.04
LS	17	t	−22.06	2.16		nd	nd	nd
LS	18		nd	nd	t	35.41	9.52	1
LS	28	a	−21.61	1.34	c	30.11	8.02	1.23
LS	26	a	−14.45	6.65	c	37.01	8.04	1.15
LS	31	a	−12.16	7.07	a	34.11	10.56	0.96
RB	17	t	−12.3	8.4		39.37	7.78	1.02
RB	20		nd	nd	a	34.93	10.46	0.98
RB	22	a	−15.89	6.37	c	29.26	6.94	1.27
RB	20	a	−11.66	7.41	a	33.69	7.82	1.68
RB	23	a	−11.13	7.93	c	39.73	8.04	0.88
BS	23	a	−11.68	7.2	c	34.08	7.55	3.37
BS	30	a	−10.46	7.69	c	33.62	7.23	3.86
Mirocaris keldyshi								
BS	24	a	−11.38	7.87	a	29.89	7.12	3.1
BS	28	a	−12.05	7.67		nd	nd	nd
TAG	30	a	−15.50	8.00	a	41.02	6.36	0.57
SP	20	a	−12.12	8.56	c	32.33	8.40	1.06
SP	32	a	−11.89	7.02	c	37.91	8.68	0.94
LOG	14	t	−21.71	6.66		nd	nd	nd
LOG	26	a	−15.45	6.05	c	35.24	7.57	0.61

The vent sites are coded: MG, Menez Gwen; LS, Lucky Strike; RB, Rainbow; BS, Broken Spur; SP, Snake Pit; LOG, Logatchev. Tissues used are noted: a, abdominal muscle; c, cephalothorax; m, mouthparts + bacteria; nd, no data.
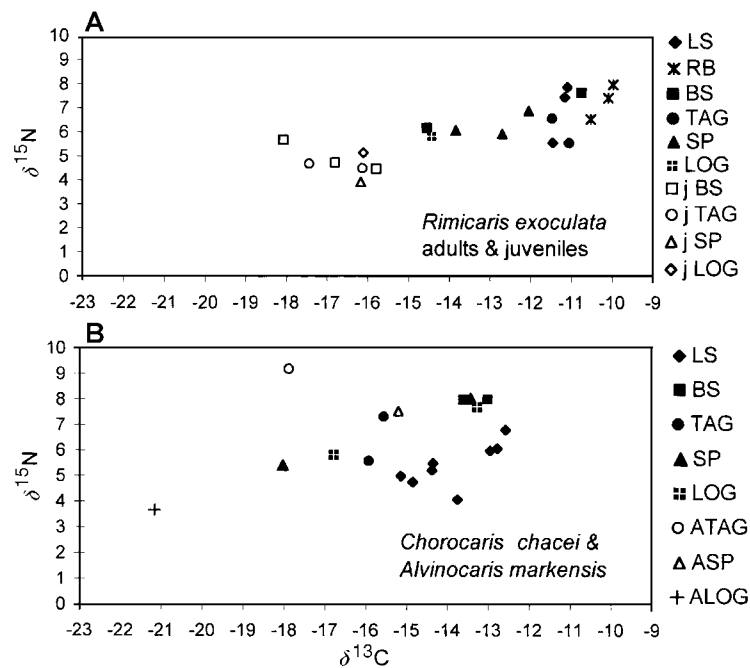
Figure 2. (A) *Rimicaris exoculata*, adults and juveniles. Plot of $\delta^{15}N$ against $\delta^{13}C$ for individual specimens. The juvenile *R. exoculata* are indicated by open symbols and the prefix j to the site abbreviation. (B) *Chorocaris chacei* and *Alvinocaris markensis*. Plot of $\delta^{15}N$ against $\delta^{13}C$ for individual specimens. *Alvinocaris* specimens are indicated by open symbols and the prefix A to the site abbreviation. Vent sites are shown abbreviated: MG, Menez Gwen; LS, Lucky Strike; RB, Rainbow; BS, Broken Spur; TAG, full name; SP, Snake Pit; LOG, Logatchev.

bacteria were 5.57 and 6.54‰, at the lower end of the range for adults (5.55–7.98‰). These values for the maxillipeds and bacterial coatings are from Lucky Strike specimens; surprisingly, the abdominal tissues of the same specimens are less depleted in ^{13}C (−11.1 to −9.97‰) but are enriched in ^{15}N (7.43 to 7.98‰)

Juveniles of *R. exoculata* differed remarkably in δ^{13}C from the adults. There was a narrow range of δ^{13}C, compared to all other shrimp, from −18.07 to −15.61‰ (mean −16.84‰). The difference is highly significant (ANOVA, $P < 0.001$). There is also a significant difference ($P < 0.001$) in the δ^{15}N values of the two groups; the juveniles have the narrowest range of all shrimp analysed, and the mean δ^{15}N (4.96‰) is not far from that for mixed oceanic plankton. The juveniles form a distinct cluster when the δ^{15}N values are plotted against the δ^{13}C results (Figure 2). The strongest sign of photosynthetic material (δ^{13}C−18.07‰) was in the smallest juvenile (18 mm). After arrival at vent habitats the young rapidly change in shape and their mouthparts enlarge (Vereshchaka, 1997b). There is a gradual increase of bacterial abundance on the mouthparts, from a small amount at the 18–21 mm stage to a significant amount at 25–26 mm.

Chorocaris chacei

Chococaris chacei δ^{13}C varied from −12.58 to −18.03‰. (Table 2). Larger specimens (>40 mm) were least depleted (mean −13.88‰), but on average were 2‰ more depleted than large *R. exoculata*. The greatest depletion (−18.03‰) was shown by a specimen of 18 mm length, but the two smallest specimens (16 mm) were less depleted (−16.79 and −15.93‰). The mouthparts carrying filamentous bacteria had δ^{13}C of −13.76 and −14.38‰, more depleted than the same appendages in *R. exoculata*. The δ^{15}N values, from 4.07 to 8.03‰, correspond to the total range for *R. exoculata*, taking into account juveniles as well as adults.

When *Chorocaris chacei* δ^{15}N values are plotted against δ^{13}C some differences from *R. exoculata* can be seen (Figure 2B). The eight specimens from Lucky Strike vary, but form a cluster with generally lower δ^{15}N values than those from the deeper sites, Broken Spur, TAG, Snake Pit and Logatchev. Specimens from these latter sites have a more nearly linear relationship of δ^{15}N to δ^{13}C, and include the four highest δ^{15}N values for *C. chacei* (7.71–8.03). Some additional specimens from Lucky Strike were further dissected (Table 2). The abdominal tissues differ little in δ^{13}C from the rest of the body, but the δ^{15}N values are higher for abdominal tissues than other parts, especially the limbs and the exoskeleton. This must be borne in mind when comparing values for whole specimens with values for abdominal muscle.

Alvinocaris markensis

Only three specimens of *Alvinocaris markensis* were available, each from a different site (Table 2). The carbon and nitrogen results differed slightly in the larger specimens, 58 mm long from TAG (δ^{13}C −17.89‰ and δ^{15}N 9.19‰) and 52 mm long from Snake Pit (δ^{13}C −15.21‰ and δ^{15}N 7.54‰). A greater difference was found for the small specimen (28 mm) from Logatchev (δ^{13}C −21.17‰ and δ^{15}N 3.65‰), indicating a different food source. Inclusion
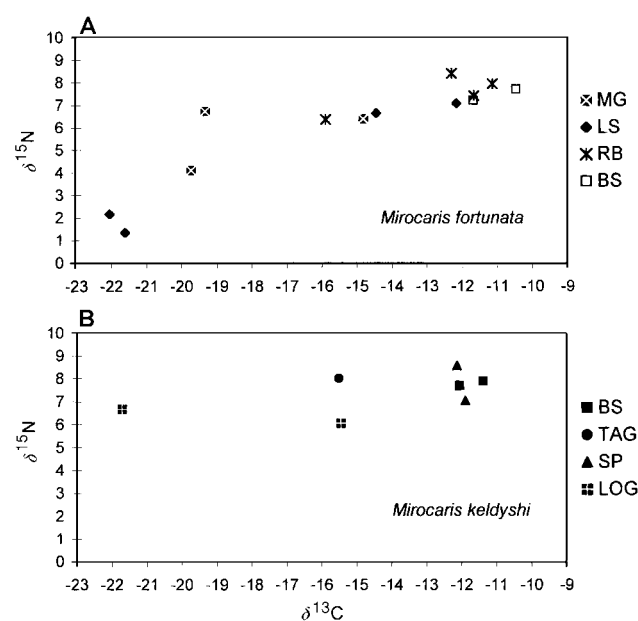
Figure 3. (A) *Mirocaris fortunata*. Plot of δ^{15}N against δ^{13}C for individual specimens. (B) *Mirocaris keldyshi*. Plot of δ^{15}N against δ^{13}C for individual specimens. Vent sites are shown abbreviated: MG, Menez Gwen; LS, Lucky Strike; RB, Rainbow; BS, Broken Spur; TAG, full name; SP, Snake Pit; LOG, Logatchev.

of these values for *A. markensis* in the plot (Figure 2B) emphasizes the great individual variation.

Mirocaris

Both species of *Mirocaris* showed wide ranges of δ^{13}C, −10.46‰ to −22.06‰ for *Mirocaris fortunata* and −11.38‰ to −21.71‰ for *M. keldyshi* (Table 2). There is no significant relationship to size, but a relationship to depth is evident. *M. fortunata* from the two shallower sites, Menez Gwen and Lucky Strike, had mean δ^{13}C values of −17.96 and −17.57‰ respectively. There was much less depletion at the slightly deeper Rainbow site (mean −12.75‰) and the deeper Broken Spur site (mean −11.07‰). *M. keldyshi* co-occurred with *M. fortunata* at Broken Spur and had similar δ^{13}C values there, but individuals from Logatchev showed much more depletion of ^{13}C and lower δ^{15}N values. The slight difference in mean δ^{15}N between the two species, *M. keldyshi* at 7.4‰ and *M. fortunata* at 6.1‰, is not statistically significant.

Plots of δ^{15}N against δ^{13}C (Figure 3) emphasize the different trends in isotope ratios in *Mirocaris* spp. Much of the variation in *M. fortunata* is due to inclusion of depleted specimens from Lucky Strike dive 3118, at a location where samples of the bacterial mats showed greater depletion of ^{13}C and ^{15}N (see section below).

Free-living bacteria

Samples of free-living bacteria that contained enough material for isotope assay were available only for Lucky Strike and Logatchev. They came from mats of filamentous bacteria on the mussel beds, close to aggregations of *R. exoculata* and where there were considerable numbers of *Mirocaris* spp. Two batches from Lucky Strike gave δ^{13}C values of −29.39‰ and −27.64‰, compared with −23.44‰ at Logatchev; these samples were too small to

measure nitrogen isotopes. A larger sample from Lucky Strike, in which the bacteria were mixed with detritus, showed a comparable value for $\delta^{13}C$ (-25.69‰) but an extremely low $\delta^{15}N$ value (-7.11‰). These values for free-living bacteria differ from those established for the bacteria carried by the shrimp.

Other vent fauna

A few bivalves were submitted to stable isotope analysis, to gain some idea of the composition of alternative food available to the shrimp. Specimens of *Bathymodiolus azoricus* from Lucky Strike, had $\delta^{13}C$ values ranging from -32.42 to -32.08‰, and $\delta^{15}N$ values from -13.52 to -12.22‰. The most highly depleted $\delta^{15}N$ value (-13.52‰) was from gill tissue, where the endosymbiotic bacteria live. A mussel from Logatchev differed markedly in isotope ratios ($\delta^{13}C$ -14.86‰ and $\delta^{15}N$ 1.87% for the foot, $\delta^{13}C$ -14.3‰ and $\delta^{15}N$ 1.43‰ for the gill). A vesicomyid from the clam bed at Logatchev had stable isotope ratios close to those found in vesicomyids from other vent areas ($\delta^{13}C$ -34.79‰ and $\delta^{15}N$ 3.64‰ for the foot, $\delta^{13}C$ -36.27‰ and $\delta^{15}N$ 1.53‰ for the gill).

These results need to be judged in the context of data from larger Menez Gwen and Lucky Strike samples studied by Trask & Van Dover (1999) and Pond et al. (1998). There is a species difference between Lucky Strike (*B. azoricus*) and Logatchev (*B. puteoserpentis*), as reported by Von Cosel et al. (1999) and discussed by Maas et al. (1999).

Elemental composition (C:N:S)

Individual results for all shrimps are presented in Table 2. The high content of carbon and low content of nitrogen in juvenile *R. exoculata* (mean C:N ratio 9.18) is striking in comparison to older individuals, which had a mean C:N ratio of 4.3, close to normal for marine life. ANOVA shows this difference to be highly significant ($P < 0.001$). The other species of shrimp show C:N ratios like those of older *R. exoculata* ($\sim$4.3).

Sulphur analyses showed the greatest range (0.5–4.0%) and highest mean value (2.28%) in *M. fortunata*, which also showed a wide range in carbon isotope ratios. The sulphur range was least (0.53–2%) and the mean value lowest (1.06%) in *R. exoculata*, a surprising result in view of the predilection of this species for the hottest, and presumably, most sulphurous parts of the vents. The juveniles showed slightly less sulphur (mean 0.80%) than the older specimens of *R. exoculata* (mean 1.21%), but this was not statistically significant.

Shrimp distribution and behaviour

Rimicaris exoculata and *C. chacei* were found at all sites except Menez Gwen, where *M. fortunata* and *Alvinocaris* sp. aff. *stactophila* were collected. A discontinuity exists at Broken Spur. *Mirocaris fortunata* is present there and at the sites to the north (Menez Gwen, Lucky Strike and Rainbow). *Mirocaris keldyshi* overlaps with *M. fortunata* at Broken Spur, but is the only species of *Mirocaris* farther south at TAG, Snake Pit and Logatchev. *Bathymodiolus* species show a similar discontinuity (Maas et al., 1999).

Shrimp micro-scale distribution patterns depend on the habitat landscape at the various sites.
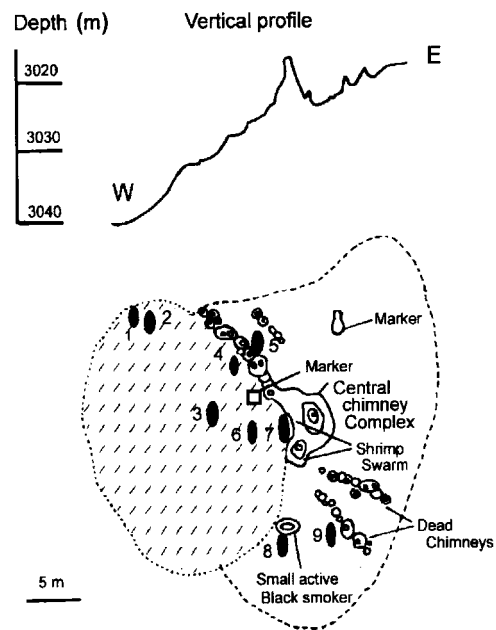
Figure 4. Chart of the Irina-2 complex at Logatchev, with a vertical profile across it. The mussel bed on the west side is shown with diagonal dashes. The chimneys occupy the higher and eastern part of the mound. Places where observations were made on shrimp, as mentioned in the text, are labelled 1–9.

Logatchev

Shrimp distribution was studied at nine locations at Irina-2 where the fauna is most diverse (Gebruk et al., 2000). Figure 4 maps the site. The overall pattern was patchy, but two zones could be discerned: (a) a swarm of *Rimicaris* with strongly pronounced borders, and (b) the mussel bed with *M. keldyshi*.

On the mussel bed *M. keldyshi* was dominant, but patchy, with estimated densities varying from a few individuals per m^2 at the edge of the bed (point 1) to 80–90 ind m^{-2} at point 3, in small groups of 10–12 ind at most. Higher densities occurred at the base of the central chimney complex where biomass was high. The greatest density of *M. keldyshi* was at the thickest part of the mussel bed. There were fewer individuals on mussel clusters (points 4 and 5) and fewer still on the wall of the small black smoker (8) where the temperature was slightly elevated. A few occurred on the wall of a small smoker at the base of the central chimney complex (point 6) where the temperature was 23.1°C. These shrimp were moving actively on the mussel bed, often changing their position.

The central smoker complex was occupied by a swarm of adult *R. exoculata* with distinct patches (0.3–0.5 m in diameter) of the juvenile stage. Groups of juvenile *R. exoculata* occurred in zones of diffuse flow where the temperature was >20°C. Juveniles were not present in zones of high vent flow or close to black smoke. Shrimps in the swarm remained motionless on the substratum but started swimming when entrained by turbulent water; juveniles were usually less active than adults.

Density of *R. exoculata*, estimated from video frames, was at least 3000 ind m^{-2} for adults and up to 3500 ind m^{-2} for juveniles. However, the vertical orientation of the swarm and its thickness (up to 0.4 m on concave surfaces) make the three dimensional structure very complex, so
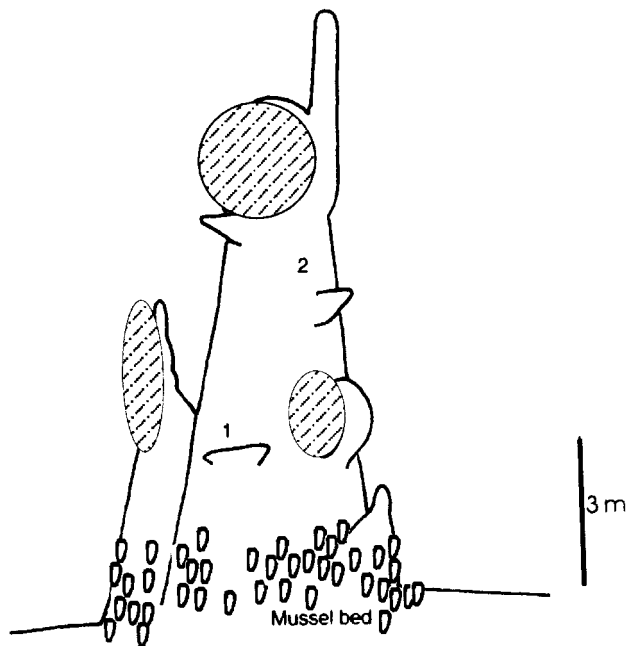
Figure 5. Sketch of the Moose chimney at Snake Pit, with mussels at the base. The swarms of *Rimicaris exoculata* are delineated with diagonal dots and dashes. Places mentioned in the text are numbered 1 and 2.

estimates of density are conservative. The borders of the swarm were pronounced: density changed from thousands to just a few per m² over a few tens of centimetres.

Patches of up to 10–15 juvenile shrimp often occurred on the mussel bed. Slurp-gun samples taken at points 3 and 4 contained mostly *M. keldyshi* and *C. chacei*, with a few *R. exoculata*. Adult *C. chacei* occurred alone or in small groups (3–4 individuals) within the swarm of *R. exoculata* and on the mussel bed. They were seen scavenging on dead *R. exoculata* but sometimes attacking apparently undamaged shrimps.

Snake Pit

The distribution of shrimps was studied on a chimney complex at the Moose site, sketched in Figure 5. The main chimney was 9–10 m high and there was a clear vertical pattern. Swarms of *R. exoculata*, including small groups of juveniles, occurred in regions of diffuse flow on the tops of the main and smaller structures, and on one of the side heads, with densities of about 2500 ind m⁻² for both adults and juveniles. *Alvinocaris markensis* was abundant at the periphery of the swarms, forming groups of 6–8 individuals at points 1 and 2, with a density of up to 30 ind m⁻². Single *C. chacei* and juveniles were present on the wall of the main structure between points 1 and 2, but the mussel bed at the base of the main structure and mussel clusters close to it showed mainly juveniles. A slurp-gun sample contained several species: *C. chacei* (most abundant), *A. markensis*, *R. exoculata* and *M. keldyshi*, the latter two in small numbers. The total shrimp density on the mussel bed was ∼40 ind m⁻².

Lucky Strike

At Lucky Strike *C. chacei* and *M. fortunata* were dominant and *R. exoculata* was uncommon. Recordings from dive 3120 at Sintra chimney showed the shrimp reacting

to mussel sampling. *Chococaris chacei* and *M. fortunata* were moving, separately or in small groups, over the mussels. As the manipulator arm approached, the shrimp kept still or retreated slightly. When a mussel was crushed by the arm and left *in situ*, individuals of both species moved within 10 s to the crushed mussel, investigated the broken shell and appeared to feed.

Behaviour of captive shrimp

Viability

Mirocaris fortunata, *C. chacei* and juvenile *R. exoculata* survived at atmospheric pressure for at least a few hours and swam apparently normally. Some lived two or three days, and a few egg-bearing female *M. fortunata* survived a week or longer. Most large *R. exoculata* died during sorting; survivors lay on their backs or sides moving their limbs weakly and a few lived for 24 h.

Feeding behaviour

When presented with mussel or shrimp tissue *M. fortunata* and *C. chacei* from Lucky Strike touched the material with their antennae, then remained close and appeared to cut it with their chelae. Only one or two individuals at a time were attracted, though there were many in the tank. Pieces of sulphide rock coated with bacterial filaments attracted *M. fortunata* and *C. chacei*, and the shrimp remained for hours in contact with the rough-surfaced rock which was easier to cling to than the aquarium surface. An individual *M. fortunata* partly consumed a polychaete (*Amathys lutzi*) that was attached to one of the rock fragments, but filamentous bacteria did not apparently stimulate a feeding response and the visible filaments remained uneaten. Small *M. fortunata* and *C. chacei* did not attempt to capture living *Artemia* nauplii when these were provided.

Water currents

Microscopic observation and video recordings of the cephalothoracic region showed regular beating of the scaphognathites, large flaps on the second maxillae, at 50–100 beats min⁻¹. Water flowed forward through the space under the carapace. Addition of dye trails showed that in *M. fortunata* and small *C. chacei* water entered under the postero-ventral border of the carapace, to pass over the gills (attached to the bases of the pereiopods), before passing the mouthparts and emerging below the antennal bases. This is the normal ventilatory current in free-swimming shrimps. Suspended carmine particles appeared to be removed by the mouthparts, indicating the feasibility of filter feeding.

Feeding on surfaces

Juvenile *R. exoculata* from Snake Pit, TAG and Logatchev swam in the aquarium only when disturbed and sank when they stopped swimming. They spent much time on the bottom of the aquarium tank. These juveniles have a very narrow stomach (proventriculus) and intestine that traverse a mass of lipid-filled digestive gland, occupying the cephalothoracic region and extending back to the third abdominal segment. The stomach is smaller than that of the adults (cf. Segonzac et al., 1993). In the experiments with films of glass beads and carborundum

powder on the bottom of dishes, none of the glass beads and very few of the sharp edged carborundum particles were seen in the guts of the juveniles, even after 20 h. Their stomachs contained a mixture of granular black particles and amorphous organic material, presumably ingested before capture. The mid gut sometimes held a small quantity of material similar to that in the stomach but the hind gut was empty. Thus, these juvenile *R. exoculata* do have a functional gut, but half of their internal volume is occupied by the lipid-filled digestive gland, which can probably provide most of the nourishment required at this stage.

DISCUSSION

Data are now available on hydrothermal shrimp biology that allow consideration of differences between species and between sites on the Mid-Atlantic Ridge, gained from samples taken on a single cruise and treated in a uniform way for carbon and nitrogen stable isotope ratios, total carbon, nitrogen and sulphur content, local microdistribution, behaviour in the field and in captivity. The results of lipid analyses (Pond et al., 2000a,b), and results from previous publications on MAR shrimp can be combined with the new data to determine their trophic ecology.

The seven sites investigated are spread out along the MAR, ranging from 857 to 3655 m depth, the shallowest to the north (Table 1, Figure 1). Ambient temperature and quantity of organic sedimentation both decrease as the depth increases. The hydrothermal fluids vary in maximum temperature, dissolved sulphide and methane concentrations and these may affect the local distribution of shrimp species and their food organisms.

Stable isotope ratios have been increasingly used to identify food sources and to trace trophic pathways (see Rau et al., 1983; Fry & Sherr, 1984; Owens, 1987; Conway et al., 1994; Vander Zanden & Rasmussen, 1999, for references). Stable carbon isotope ratios ($\delta^{13}C$) usually show little or no enrichment of the heavy isotope (<1‰) for each trophic level and can help to identify food sources whose $\delta^{13}C$ is known. In contrast, stable nitrogen isotopes ($\delta^{15}N$) usually become enriched by 3–5‰ at each trophic level and can show relative trophic position, again with the proviso that the nitrogen isotope ratios are known for the primary producer. This generalization may break down in unusual habitats such as the hydrothermal vents. For example, $\delta^{15}N$ ratios may show enrichment of over 6‰ between tubeworm primary producers and their predators (Rau, 1981) and vent primary producers may have $\delta^{15}N$ values lower than average in the marine environment (Owens, 1987). Moreover, stable carbon isotope ratios may not always agree with deduced food web structures, and there is sometimes little evidence for direct trophic links (Fisher et al., 1994; Southward et al., 1994; Fisher, 1996). In addition, vent ecosystems can contain a preponderance of chemosynthetic bacteria that fix CO_2 by means of type II ribulosebisphosphate carboxylase, which discriminates less than does type I against ^{13}C (Van Dover & Fry, 1989, 1994; Robinson & Cavanaugh, 1995).

The proposed main food sources for the MAR vent shrimp, and their isotope signatures are: (a) bacteria growing on the mouthparts that use the enzyme RubisCo type II to fix CO_2 ($\delta^{13}C$ −8 to −11‰); (b) free-living sulphur-oxidizing bacteria that use RubisCo type I, taken up by grazing or filtration ($\delta^{13}C$ −18 to −29‰); (c) descending pelagic material containing carbon fixed in the euphotic zone by photosynthetic organisms using RubisCo type I ($\delta^{13}C$ −22‰ and $\delta^{15}N$ 6‰, (H. Kennedy, personal data), for large volume net samples taken at 24°N 24°W); (d) benthic particulate organic matter ($\delta^{13}C$ −17 to 20‰); (e) organic matter derived from hydrothermal vent molluscs that harbour symbiotic sulphur-oxidizing bacteria employing RubisCo type I to fix CO_2 ($\delta^{13}C$ −32 to −34‰); (f) organic matter derived from hydrothermal vent bivalves (*Bathymodiolus* spp.) that harbour both sulphur-oxidizing and methanotrophic bacteria ($\delta^{13}C$ varying from −14 to −34‰).

Interpretation of the isotope data is complicated by lack of information on isotope ratios of some of the carbon sources, therefore some caveats need to be expressed. The analyses presented here show not only considerable individual variation, but also covariance between $\delta^{13}C$, $\delta^{15}N$ and the C:N ratio. The relative proportion of lipid, protein and carbohydrate can strongly influence the isotopic composition of bulk samples. This may obscure the expected stepwise increase in $\delta^{15}N$ between first, second and third level consumers (Vander Zanden & Rasmussen, 1999; Vander Zanden et al., 1999; Stapp et al., 1999). As a result, it is not always easy to distinguish dietary differences. It is necessary to allow for enrichment in ^{13}C with decreasing C:N ratio, an effect of decreased lipid content, while animals with high lipid content often have markedly negative bulk $\delta^{13}C$ values, reflecting the isotopic depletion of the lipid component.

The bresilioid shrimps living on the MAR possess a range of morphological, anatomical and physiological adaptations to the hydrothermal environment, as well as different patterns of behaviour and micro-distribution. (Segonzac et al., 1992, 1993; Casanova et al., 1993; Charmantier-Daures & Segonzac, 1997; Gebruk et al., 1997a; Lallier & Truchot, 1997; Negre-Sadargues et al., 1997; Jinks et al., 1998; Lallier et al., 1998). A transitional series has been demonstrated, from *Alvinocaris*, closest in appearance to non-vent bresilioid shrimps, to the highly specialized *Rimicaris*, (Vereshchaka, 1996a,b; Gebruk et al., 1997a). The concept of an evolutionary series is supported by the deduced evolution of eyes in bresilioid shrimps (Gaten et al., 1998). The morphological differences are accompanied by dietary differences, so each species will be discussed separately, after noting some general features.

From evidence now available, all the hydrothermal shrimp species on the MAR pass through a juvenile pelagic phase whose food originates from photosynthetic carbon fixation in the euphotic zone. The length of the pelagic phase and the nature of the feeding mechanism, whether predation or filtration of particles, are unknown. Bathypelagic caridean shrimps generally have non-feeding zoeal stages and their juveniles feed on zooplankton (Omori, 1974). The juvenile vent shrimp colonize the vents at lengths ranging from 14 to 25 mm, carrying abundant stores of lipids. The change in trophic strategy then differs between the species.

Two of the species studied, *R. exoculata* and *C. chacei*, develop 'gardens' of filamentous bacteria on their mouthparts and other surfaces inside the carapace chamber after arrival at the vents. The others investigated, *Mirocaris* spp. and *Alvinocaris* spp. do not develop 'gardens' of bacteria, though they may carry a few bacterial filaments. We discuss these groups separately.

Rimicaris

Rimicaris exoculata is the most specialized vent shrimp (Gebruk et al., 1993; Segonzac, 1992; Segonzac et al., 1993; Van Dover, 1995; reviewed by Gebruk et al., 1997a). Since the first evidence for a bacterial diet (Van Dover et al., 1988) investigations have focused on the role of the epibiotic bacteria vs free-living bacteria. The proposal by Van Dover et al. (1988) of grazing on the surface of sulphide chimneys, where free-living micro-organisms occur, was suggested by the presence of sulphide crystals in the shrimp foreguts, but ingestion of epibionts was also deemed likely. A symbiotic relationship with the filamentous bacteria that colonize the shrimp mouthparts and the undersurface of the carapace was suggested by Gebruk et al. (1992, 1993), and Segonzac et al. (1993) based on morphological and behavioural adaptations. Casanova et al. (1993) suggested that DOM from the bacteria might be absorbed by the maxillipeds. Crustacean cuticular fragments were found in the gut of one *R. exoculata* (Segonzac et al., 1993). An analysis of digestive enzymes (Ravellec & van Wormhoudt, 1997) suggested a low level potential for necrophagy. Recent work has stressed the importance of the epibiotic bacteria to *R. exoculata*, although the idea of symbiotic autotrophic bacteria in the gut was also introduced (Pond et al., 1997b; Polz et al., 1998).

The present results for *R. exoculata* show a graded increase in the proportion of ^{13}C from the juveniles, through the smaller adults, to the older specimens, corresponding to the development of bacterial growths on the maxillipeds. There is also an increase in the proportion of the heavy isotope of nitrogen between the juvenile and adult stages. If these trends are considered together with the data from lipids (Pond et al., 2000a,b), then there is evidently a change in the diet during metamorphosis and maturation. The juveniles reach the vents with reserves from photosynthetic sources which fuel the immediate metabolism of the growing shrimp. Our $\delta^{13}C$ results for mouthparts (maxilliped I) covered with epibiotic bacteria (-10.52 and $-11.45‰$) are close to previously reported values for shrimp epibionts, ($\delta^{13}C$ -9.4 and $-12.3‰$; Polz et al., 1998) and values for bacteria filtered from the water in a slurp-gun container that had been filled with *R. exoculata*, presumed to be detached epibiotic bacteria (-8.6 to $-10.2‰$; Gebruk et al., 1997b). These values indicate that the epibiotic bacteria are sulphur-oxidizers that employ type II RubisCo and the correspondence between their isotope ratios and the ratios in the tissues of adult *Rimicaris* from all of the MAR sites studied underlines the nutritional role of the bacteria. The similarity of $\delta^{13}C$ values for adult *R. exoculata*, from shallower sites (Lucky Strike, $\sim 1700\,m$) and the much deeper sites (Snake Pit, TAG, Broken Spur), where there will be lesser input of photosynthetic detritus, also stresses the

importance of the epibiotic bacteria. Analysis of lipids of adult *R. exoculata*, of their epibiotic bacteria and of free-living bacteria also indicates the role of the epibionts (Rieley et al., 1996; Pond et al., 1997a, in press; Allen Copley et al., 1998).

The similarity of $\delta^{13}C$ values for adults from all sites does not indicate any local restriction in availability of CO_2, as was previously proposed to account for $\delta^{13}C$ values of -9 to $-11‰$ in some vent organisms (Van Dover & Fry, 1989; Fisher, 1990; Fisher et al., 1992; Kennicutt et al., 1992; Childress et al., 1993; Southward et al., 1994). Isotope and lipid data would not distinguish between ingestion of bacterial filaments and trans-epidermal transfer of DOM. However, studies of other Crustacea have shown that active transport of DOM across the chitinous exoskeleton is unlikely (Stephens, 1988).

Polz et al. (1998) used mass balance calculations, based on carbon isotope values of shrimp tissue, organic material from sulphide deposits and the epibionts, to estimate the proportion of carbon from different sources. They calculated that over 80% of the carbon in larger *R. exoculata* was provided by their epibionts, whereas smaller stages were thought to obtain 30% of their carbon by grazing on the sulphide rock surfaces. These authors did not have data for the lipid reserves of photosynthetic origin that were demonstrated subsequently (Pond et al., 1997a,b,c, 1998, 2000a,b). The presence of photosynthetic carbon explains the difference between the smaller and larger animals; partial retention to the adult would explain any difference between the bacterial food source and the tissues.

It is an open question whether adult *R. exoculata* can take up bacteria from the substratum. The chamber formed by the enlarged carapace (Segonzac et al., 1993), is nearly closed ventrally, leaving little space for manipulation of the appendages outside. *Rimicaris exoculata* are not attracted by the coating of filamentous bacteria that may occur within a few metres of the swarms (on rocks, mussel shells, polychaete tubes, etc.), where these occur in areas not exposed to diffuse venting fluid. The free-living bacteria in the micro-habitat favoured by adult *R. exoculata* are usually inconspicuous (Gebruk et al., 1993; Segonzac et al., 1993; Polz et al., 1998), though Polz & Cavanaugh (1995) found filamentous forms comparable to those that grow on the shrimp. We did not see any signs of active grazing by adult *R. exoculata* on the surface of sulphide deposits. The organic material scraped from sulphide deposits at Snake Pit by Polz et al. (1998), had a $\delta^{13}C$ of -22 to $-17.8‰$ (mean $-20.66‰$) and a $\delta^{15}N$ of -1 to $-3.5‰$ (mean $2.0‰$). The results presented here for bacterial mats show a range of $\delta^{13}C$ from -23 to $-29‰$ and a $\delta^{15}N$ of $-7‰$. All these figures are quite different from the stable isotope values of the epibionts and the tissues of *Rimicaris*, indicating that the bacteria on the sulphide rock surfaces are of little nutritional importance to adult *R. exoculata*.

Polz et al. (1998) found that active autotrophic bacteria in the gut of *R. exoculata* were isotopically similar to but genetically distinct from the epibionts and suggested that they might also contribute to nutrition. A bacterial microflora occurs in the guts of many marine organisms, including deep-sea animals (Deming et al., 1981; De Ridder et al., 1985; Temara et al., 1993). However, the main role of

intestinal sulphur-oxidizing bacteria in benthic inverte-brates is detoxification (Plante et al., 1990) or provision of essential dietary components (Pond et al., 1997a).

Adult *R. exoculata* avoid the hottest parts of the black smokers. The temperatures among swarms range from slightly over 10 to 30°C, but at times may reach 40°C (Gebruk et al., 1993; Segonzac et al., 1993; Van Dover, 1995; Segonzac et al., 1997). Wirsen et al (1993) believe that mesophilic temperatures ($>20°C$) are important for CO_2-fixation by the epibiotic bacteria. The shrimp may seek such temperatures, aided by the greatly modified eyes that can detect radiation from the heated effluents and by chemosensory receptors for sulphide (Van Dover et al., 1989; Gaten et al., 1998; Jinks et al., 1998). It is difficult to see how this search for suitable vent fluid flow is driven, even by combined use of visual and chemosensory cues. There would be a lag in growth of the bacterial filaments that could hardly be related by the shrimp to its environment.

Patches of juvenile *Rimicaris* usually occur away from the zones of higher temperature. They are relatively slow moving and may not feed. Pelagic juveniles of *R. exoculata* have been collected both near vent fields and farther away (Herring & Dixon, 1998; Herring, 1998). Their lengths range from 14 to 28 mm. Our $\delta^{13}C$ values for juveniles at vent sites suggest that the critical size for finding vent habitats lies between 18 and 25 mm length.

Chorocaris

Much of the carbon in adult *C. chacei* is derived from chemosynthetic bacteria (RubisCo type II), as in *R. exoculata*. Juveniles arrive at the vents carrying reserves of photosynthetic origin (Pond et al., 1997a), as confirmed by our isotope ratios for 16–18 mm length specimens ($\delta^{13}C$ as low as $-18.03‰$).

Chococaris chacei resembles *R. exoculata* in carrying dense growths of filamentous bacteria on the mouthparts (Casanova et al., 1993), although the area available is smaller than in *R. exoculata*. Bacterial growths are evident on juveniles of *C. chacei* 16–19 mm long. The small adults (23–42 mm) show a mean $\delta^{13}C$ of $-12.77‰$ (Table 2), indicating that there is a strong input of carbon from bacterial sources (type II RubisCo). In contrast, the larger adults of *C. chacei* are often found within (or close to) swarms of *R. exoculata* and can act as predators or scavengers on the latter. This behaviour is confirmed by the presence of mouthparts of *R. exoculata* in the stomach of *C. chacei* (Segonzac et al., 1993; A. Gebruk, personal observations).

In theory, nitrogen isotope ratios might indicate whether *C. chacei* feed on adult *R. exoculata*. *C. chacei* from Lucky Strike are in fact more depleted in ^{15}N than adult *R. exoculata* there. At the deeper stations the *C. chacei* are slightly more enriched in ^{15}N than the *R. exoculata,* but the difference is less than 0.5‰. Thus adult *R. exoculata* cannot be a major source of nitrogenous food for *C. chacei*. However, the juveniles of *R. exoculata* have a mean $\delta^{15}N$ some 1.6‰ lower than the mean for *C. chacei*, leaving open the possibility that this stage of *R. exoculata* is a source of food for adult *C. chacei*.

The carbon isotope ratios for *C. chacei* do not discriminate between feeding on epibiotic bacteria and scavenging

among *R. exoculata* swarms. The trophic changes in growing *C. chacei* are thus more difficult to interpret. The juveniles arrive at the vents with reserves of photosynthetic origin, as does *R. exoculata*. At an intermediate size, before reaching the full adult stage, they must rely heavily on the epibiotic bacteria on the mouthparts. In the adult stages, where scavenging or occasional predation on *R. exoculata* may occur, there is still considerable input from the epibiotic bacteria.

Alvinocaris

Alvinocaris spp. are opportunistic feeders. The distribution of *A. markensis* adults (present study and Segonzac et al., 1993) shows little correlation with that of *R. exoculata*. *Alvinocaris markensis* is most common at the periphery of vent communities where it is likely to use a variety of food, as shown by the carbon and nitrogen isotope results (Table 2). Both *A. markensis* and *C. chacei* were seen at the Logatchev clam bed (Anya's Garden) where *R. exoculata* is absent. In contrast, observations at Snake Pit showed large numbers of adult *A. markensis* close to swarms of *R. exoculata*.

The $\delta^{13}C$ for a small (28 mm) adult from Logatchev ($-21.17‰$) suggests little input of chemosynthetic bacterial carbon. Taken with the large quantity of wax esters reported by Pond et al. (1997b) in post-larval *A. markensis* from Broken Spur, an initial photosynthetic food source is confirmed.

Mirocaris

Mirocaris spp. are opportunists that will ingest tissues of mussels, shrimp and other invertebrates when available. *Mirocaris* spp. are most abundant in zones of high biomass such as mussel beds, but can also be found at the periphery of the vent communities, as noted also by Vinogradov & Vereshchaka (1995) and by Gebruk et al. (1997a). Previous studies reported a mixture of bacterial and mussel-derived material (pseudo-faeces, mucus, etc.) in the diet of *M. fortunata* at Lucky Strike, but the juveniles also contained material of photosynthetic origin (Pond et al., 1997c, 2000a,b). Vereschaka et al. (1997b) noted remains of *R. exoculata* in the stomach of *M. keldyshi* at TAG , where there are no mussels

Both *M. fortunata* and *M. keldyshi* have a wide range of $\delta^{13}C$ values. *Mirocaris fortunata* also showed a very wide range of $\delta^{15}N$. Bacterial carbon (RubisCo type II) occurred in specimens from certain sites, notably Rainbow and Broken Spur. Some *M. fortunata* from Lucky Strike showed distinctive $\delta^{13}C$ values of -22.61 and $-22.06‰$ and $\delta^{15}N$ values of -1.34 and $-2.16‰$. These can be compared with values for free-living bacteria and bacteria plus detritus ($\delta^{13}C$ $-29.39‰$, $-27.64‰$, $-25.69‰$; $\delta^{15}N$ $-7.11‰$) at the site and also with the values for the dominant mussels on which the shrimp might be preying. While not excluding input from photosynthetic sources, as suggested by Pond et al. (1997c) from study of lipids, our isotope values indicate that a proportion of the carbon in *M. fortunata* at Lucky Strike could be derived from bacteria that use type I RubisCo, either by scavenging/predation on mussels, or by grazing on sulphide surfaces and detritus. Previous detailed

investigations on *Bathymodiolus azoricus* from the shallow sites, Menez Gwen and Lucky Strike, show great variation in stable isotope ratios, consistent with varying predominance of two types of endosymbionts, thiotrophs and methanotrophs. Pond et al. (1998) determined lipid $\delta^{13}C$ values ranging from -34.9 to $-24.9‰$ in Menez Gwen mussels. Trask & Van Dover (1999) reported two isotopically distinct communities of *Bathymodiolus* at Lucky Strike, one from Sintra (predominantly methanotrophic) with gill tissue $\delta^{13}C$ of -25.1 to $-14.7‰$ (mean $-22.0‰$), the other from Eiffel Tower, with gill tissue $\delta^{13}C$ of -33.4 to $-28.7‰$ (mean $-31.1‰$), deemed thiotrophic. The corresponding means for $\delta^{15}N$ were $-4.5‰$ and $-10.5‰$. The nitrogen isotope differences between Lucky Strike *M. fortunata* and possible food sources would thus average 11.25 (published data) to 12.95‰ (our data) for thiotrophic mussels and 8.85‰ for bacterial mats. Adult thiotrophic mussels are thus not a major food source for *M. fortunata*. Trask & Van Dover (1999) also examined larval and post-larval stages of *Bathymodiolus*, finding $\delta^{13}C$ values from -19.9 to $-17.3‰$ and $\delta^{15}N$ values from 0.1 to 4.4‰, indicating photosynthetic origin. Feeding on these juvenile mussels might better fit the nitrogen isotope values in *M. fortunata*, but the carbon values do not support the idea.

Ecological implications

Shrimps such as *C. chacei* and *R. exoculata* are highly specialized for carrying and cultivating their symbionts. The grooming behaviour in many decapod crustaceans has probably assisted this form of feeding (Bauer, 1989). Nevertheless, the shrimp community cannot exist on chemosynthetic sources alone. Planktonic larval feeding is needed to allow accumulation of essential unsaturated fatty acids (PUFA) required for maturation and breeding (Pond et al. 1997a,b,c; 2000a). What still remains to be determined is how the larvae obtain enough food to build up these reserves. The MAR vent communities are overlain by relatively oligotrophic surface waters where many other crustaceans, mostly carnivores, are present at depths between 800 and 3000 m, and where the mesoplankton biomass is <1 mg m^{-3} (Foxton, 1970; Vinogradov, 1997). This habitat is the antithesis of the rich feeding available at hydrothermal vents. However, over the hydrothermal vents at the deeper MAR sites there are local increases in plankton and particulate matter below 2000 m (Vinogradov et al., 1996). Corresponding enrichment has been found over vents in the north-east Pacific (Roth & Dymond, 1989; Thomson et al., 1992; Burd & Thomson, 1995). This near-bottom increase in biomass has been attributed to material carried up in the hydrothermal plume, but may be an accumulation of sedimenting particles of photosynthetic origin trapped by the density gradient (Vinogradov, 1997). Particulate matter above the plume could thus be the source of the PUFA required by the larval shrimp, if there is enough of it.

Gebruk et al. (1997a) believe that the large biomasses found at hydrothermal vents are linked to nutritional symbioses that support the community. The evidence reviewed here can be regarded as favouring this hypothesis. However, in several hydrothermal vent communities, the stable isotope data do not always indicate tight trophic coupling between the endosymbiont-containing 'primary producers' and other invertebrates, for example, arthropods and molluscs (Fisher et al., 1994; Fisher, 1996).

The shrimps of the Mid-Atlantic Ridge have radiated since the Miocene (Shank et al., 1999). The symbiotrophy found in *R. exoculata* and *C. chacei* seems necessary to produce the observed high population densities. The absence from the Atlantic vents of other 'primary producers', such as the symbiont-containing tube-worms, may have provided a vacant niche for exploitation by the shrimp.

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