



North Atlantic midwater distribution of the juvenile stages of hydrothermal vent shrimps (Decapoda: Bresiliidae)

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Introduction

The fauna of Mid-Atlantic Ridge hydrothermal vents is dominated by species of bresiliid shrimp, in marked contrast to that of Pacific vents where vestimentiferan and alvinellid worms predominate. The shrimp have small eggs and release planktotrophic larvae into the water column, but the timing of the release and the later development and dispersal of the larvae have not been determined. This paper presents a summary of the work that has been undertaken to sample these animals quantitatively in midwater and discusses particular issues highlighted by the results.

Sampling procedures

Sampling was undertaken in 1986, 1995 and 1997 using the SOC multiple RMT1+8 midwater trawl system. With this system, three pairs of nets were fished consecutively, and the opening and closing of each pair was controlled by acoustic command. Each pair comprised a 1 m² net (mesh 330 µm) for macroplankton and an 8 m² net (mesh 4.5 mm) for micronekton. From 1995 the system was routinely fitted with an altimeter to determine the height of the net above the bottom. The nets were towed horizontally within defined depth horizons for 1-2 hr each. At the end of each set of 3 tows the nets were recovered, any bresiliid shrimp picked out, and the total biomass determined as wet volume. The samples were subsequently sorted and the contributions of different groups determined.

In June 1986, a single net sample was taken at the TAG vent site (RRS Discovery cruise 159). In August 1995, 39 samples were taken in the Broken Spur area (RRS Charles Darwin cruise 95), and in June and August 1997, 53 samples were taken between Lucky Strike and the Rainbow site (RRS Discovery "FLAME" cruise 228, and N.O. *Atalante* "MARVEL" cruise, leg 1).

Results

Several types of bresiliid shrimp were obtained, all post-larvae or juveniles. They were separable into at least four types; three were identified as *Alvinocaris* sp., *Chorocaris* sp. and *Rimicaris* sp. They showed close affinities to the adults of known species of the genera. The fourth type was identified only as "Type A"; it was a postlarval form with stalked compound eyes, a toothed rostrum and a pronounced dorsal hump on abdominal segment 3 (Herring & Dixon, 1998). Subsequent molecular analysis has shown that it is a common larval type with different specimens ascribable to either *Alvinocaris* or *Chorocaris* (Dixon & Dixon, 1996).

The four TAG specimens had carapace lengths of 4.5-9.5 mm and at the time were tentatively identified as *Rimicaris chacei*, now *Chorocaris chacei* (Williams & Rona, 1986). Subsequent examination by M. de St Laurent has shown them to be *Rimicaris exoculata* Williams & Rona, 1986. The net was estimated to have fished some 200 m above the vent site, with a maximum depth of 3460 m.

Within the Broken Spur valley (MAR segment 17), 30 samples were taken in 1995, down the axial ridge where the vent sites are situated (Copley et al., 1997). The fishing operation was arranged so that the middle pair of each of the three pairs of nets was open as the system passed over the vent area. Three other samples were taken in the valley but on a parallel course offset 1-2 km to the east of the axial ridge. Another three samples were taken in the basin of segment 18, some 50 km to the northeast, and another three in the Atlantis Fracture Zone (AFZ), an additional 50 km north. All were taken between 2000 m and 3050 m. Full details of these samples are given by Herring & Dixon (1998). The 30 tows down the axial ridge yielded 200 postlarvae, the 3 offset tows yielded 26 postlarvae, the 3 in segment 18 yielded 8 postlarvae and the 3 in the AFZ yielded 2 postlarvae. The mean density of bresiliids in the

1995 RMT8 catches was 1 specimen per 11000 m³. There was a statistically significant increase in the density of postlarvae in the middle net of the tows down the axial ridge (i.e. the net that fished over the vents). Only four of the 39 RMT8 tows failed to capture any bresiliid postlarvae. The densities of all postlarvae declined with increasing distance from the vents. "Type A" postlarvae were overall twice as abundant as *Chorocaris* sp. and *Alvinocaris* sp. combined, but the proportions of the latter two increased as the fishing depth approached the bottom.

The 1997 tows covered the MAR between the Lucky Strike site and the South Amar basin, just to the south of the Rainbow site (Fig. 1). The depths sampled were between 1200 m and 2700 m, with most tows between 1800 m and 2300 m (vent site depths at Rainbow are about 2000 m and at Lucky Strike about 1700 m). The 29 tows during the FLAME cruise took only four "Type A" postlarvae and the 24 tows during the Marvel cruise only one *Alvinocaris* sp. and five "Type A". Two of these ten specimens were taken in the Rainbow area, one in the Famous/South Lucky Strike offset and the remaining seven in the Lucky Strike region. The mean density in the 1997 RMT8 catches was ≤ 1 specimen per 10⁵ m³.

A single additional specimen of "Type A" was taken in September 1995 on RRS *Challenger* Cruise 122 at an estimated depth of 1500 m (2800 m wire out) about 150 km south of Madeira. Some 30 previous RMT8 samples, taken

from the North Atlantic to the east of the MAR at depths >2500 m, were also re-examined, but no bresiliids were present in them.

Discussion

The sampling programmes have covered a considerable portion of the MAR between 26°N and 32°N (Fig. 2), over at least four hydrothermal fields known to harbour substantial numbers of bresiliid adults. It has not been possible to sample all depths at each site, but the initial experience at the Broken Spur site suggested that juvenile numbers were maximal near the vent depths and that similar sampling strategies would identify their presence elsewhere. Despite this anticipation, the data from positions further north do not support the hypothesis of widespread populations of abundant juveniles above all the regions of the MAR where benthic adults are known to be important components of the vent fauna. Nevertheless the juveniles *are* widespread. Those found in the AFZ were 100 km from the nearest known hydrothermal site (Broken Spur) and the single specimen from south of Madeira was more than 1000 km from the MAR.

All the specimens were small, with carapace lengths of generally no more than 6 mm and total lengths of 14–24 mm. The only exceptions were the largest Broken Spur specimen (8.5 mm c.l., 28 mm total length) which was

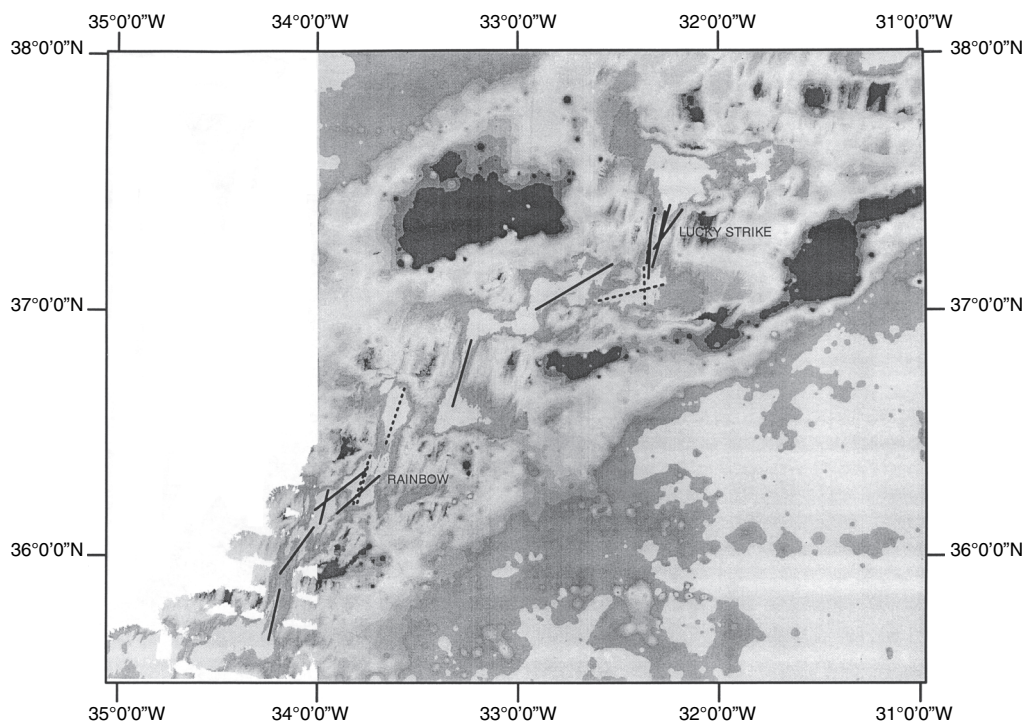


Figure 1. Positions of the tows between Rainbow and Lucky Strike in 1997. Each tow line comprised three consecutive nets. The six which contained bresiliid juveniles are shown as dashed lines.

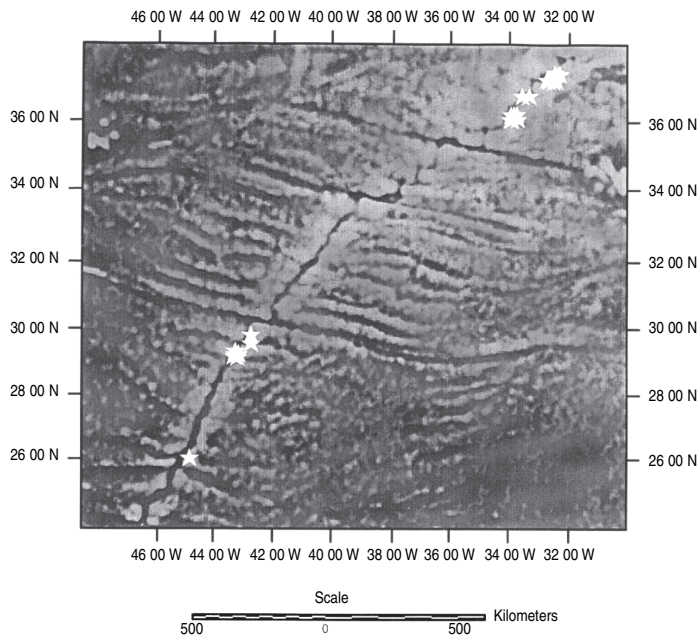


Figure 2. Chart showing the locations of the 93 midwater samples taken between TAG and Lucky Strike.

the only *Rimicaris* identified at that site, and the larger two specimens from TAG, also *R. exoculata*. The relative uniformity of size suggests that the midwater juveniles are all of rather similar age. All the specimens obtained had very substantial reserves of lipid located in the thorax and abdomen. Analyses of specimens from Broken Spur showed lipid levels of 30–40% of the dry weight, and comprising 80–95% wax esters. “Type A” postlarvae had the highest lipid levels. The presence of these large lipid stores indicates substantial pelagic feeding by the animals during their early development. The fatty acid composition of the lipid indicates that it derives from a pelagic rather than a bacterial origin. In most cases the juveniles had small pigmented chromatophores and deep yellow or orange lipid. This carotenoid pigmentation also indicates a diet of photosynthetic rather than chemosynthetic origin. The specimens had clearly been in midwater for some considerable time, certainly many weeks, probably many months.

The eggs are small and negatively buoyant at ambient temperature, as are the first zoeas of *Mirocaris* (*Chorocaris*) *fortunata* (Martin & Christiansen, 1995) and it is not clear how the larvae become entrained high in the water column. Vertical advection in the hydrothermal plume could raise them a few hundred metres, but not to the height of more than 1 km above the bottom, where a number were found. The small size of the larvae probably precludes active vertical swimming to this distance and the only likely explanation would seem to be gradual advection in the water currents within and above the MAR.

Getting up into the water column presents one problem; getting back down to colonize a new or existing site presents another. From the individual samples it is not possible to distinguish the direction in which the animals are travelling. The juvenile stages, at Broken Spur, may be either dispersing from the vent field or converging on it. An associated problem is whether the larvae are released continuously or periodically from the benthic populations of the adults. The almost complete absence of ovigerous females of *R. exoculata* in collections suggests a periodic bout of reproduction (the sampling effort to date has been almost entirely restricted to the summer months). Gravid *M. fortunata*, in contrast, have been quite commonly taken during this sampling period (M. Segonzac, personal communication). It is assumed from the similar sizes of the juvenile stages captured in midwater that they are all of rather similar age. If this assumption is valid then the Broken Spur samples appear to derive from one reproductive pulse, but involving at least two species.

There are two main questions that remain unanswered:

1. Are the juveniles moving away from the vent fields or towards them?
2. Why are the juvenile densities at Broken Spur so much higher than those at the other sites?

Three possible hypotheses could account for the presence of the midwater juveniles:

- A. They are dispersing from the vent sites, either as a pulse or as a continuous process.
- B. They are returning to the vent field from a much more widespread dispersion of earlier stages.
- C. They are stragglers from a local development cycle, normally at or near the vent sites, and have been accidentally entrained into the water column and advected away.

If A is the case, the evidence of few ovigerous females and the similar-sized juveniles suggests a pulsed release. Under this hypothesis large numbers of early larvae should be observed near the vents (the site of release) and the stage of development of the midwater specimens should correlate with distance (= time) from the vents. There is no evidence, however, that the juveniles are larger further away from the vents. Nevertheless “clouds” of larvae have been reported close to the vents (Vereschaka & Vinogradov, 1996) but their identity is still uncertain.

In hypothesis B, very widespread distribution of later developmental stages would be anticipated. The distribution observed is indeed widespread, but there are no clear differences in developmental stages. If the population at Broken Spur is returning to the vent field from wider dispersal, then the youngest (=smallest) specimens captured should be those at the greatest distance from the vent. This

is not observed either. A third prediction of hypothesis **B** is that the densities of juveniles should increase with proximity to the vents. This is certainly the case for the Broken Spur samples.

Under the "midwater stragglers" hypothesis **C**, variable and low densities of juveniles would be expected in midwater and large numbers of *all* developmental stages, including juveniles, should be present close to the vents. The densities of juveniles in the Broken Spur samples do increase with proximity to the vents, but no other larval stages were taken.

The data from the midwater samples do not unequivocally support any particular one of these hypotheses. Molecular data suggest that the "Type A" postlarva is an earlier developmental form of *Alvinocaris* sp. and *Chorocaris* sp. (Dixon & Dixon, 1996). The fact that the densities of the latter two increase relative to that of "Type A" close to the vents at Broken Spur suggests that these animals are moving in towards the vents from midwater, i.e. supports hypothesis **B**. The high levels of lipid in the midwater specimens, and the evidence for extensive midwater feeding, make it unlikely that the midwater presence of these juvenile stages is an accident, as implied in hypothesis **C**.

The second question, as to why the densities at Broken Spur are so different from elsewhere, is also not answered simply. A seasonal difference can be discounted, because the sampling period of the MARVEL cruise at Rainbow/Lucky Strike in 1997 was similar to that at Broken Spur in 1995, yet the number of midwater specimens was trivial by comparison. The 1997 May/June and August data from the Lucky Strike/Rainbow area were very similar. The fact that the single net at TAG caught four specimens implies that pelagic juvenile densities there were high (in June), akin to those at Broken Spur. The dichotomy appears to be between the deep southern vent fields and the shallower northern ones. The densities of adult bresiliids at TAG are much greater than at Broken Spur (Copley et al., 1997) and it is possible that the pelagic specimens from Broken Spur to the AFZ had their origin at TAG. There are no adequate data to show whether adult bresiliid densities at southern and northern locations are consistently and significantly different. Recent observations indicate that large numbers occur at both locations. One major difference between the two pairs of sites is that at the southerly (deep) sites the bathypelagic biomass is very low ($4.5\text{--}1.7 \times 10^{-4} \text{ ml m}^{-3}$ (Herring & Dixon, 1998)), reflecting the oligotrophic nature of the surface waters. At the vent depth of about 2000 m at the Rainbow and Lucky Strike sites the biomass levels are an order of magnitude greater. This difference represents a much greater predatory

pressure on any bresiliid juveniles, with a concomitant reduction in their potential survivorship. Lower numbers of temporary pelagic juveniles would be expected from equivalent numbers of reproducing benthic adults. Nevertheless the benthic populations are very substantial, despite the lower numbers of pelagic juveniles, and recruitment is apparently unaffected.

Widespread larval dispersal of vent shrimp is indicated by the genetic uniformity of *R. exoculata* at different vent sites (Creasey et al., 1996). This is reinforced by the capture of pelagic juveniles at great distances from any known vent site. The timing and scale of this dispersion has yet to be determined and the marked geographic differences in the present data fully interpreted. The sampling opportunities up to now have been largely opportunistic; any future programme needs to target specific questions more closely. Particular attention should be given to increased seasonal coverage, the repeatability at a given site (e.g. Broken Spur) and more extensive sampling at TAG. The ability to age the pelagic juveniles would greatly contribute to an understanding of their dispersal pattern.

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