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Recent advances in our understanding of the life history of bresiliid vent shrimps on the MAR

David R. DIXON[1], Linda R.J. DIXON[1,2] and David W. POND[3]
[1] *Southampton Oceanography Centre, Empress Dock, Southampton SO14 3ZH, UK*
Fax: (44) 1 703 596247 - e-mail: DRD@mail.soc.soton.ac.uk
[2] *Plymouth Marine Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*
[3] *NERC Unit of Aquatic Biochemistry, Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK*

Introduction

Hydrothermal sites on the Mid-Atlantic Ridge (MAR) are dominated by dense communities of bresiliid shrimps. Given the discontinuous nature of venting along the ridge axis, vent shrimp populations are continually faced with the threat of local extinction linked to the ephemeral nature of hydrothermal emissions. During a BRIDGE-funded FLUXES cruise to the Broken Spur vent field (Chief scientist, B. J. Murton), in August 1995, a series of vertical plankton trawls were taken along and across the ridge axis, between 200 and 1000 metres above the bottom using the IOS RMT1+8 net system, in an attempt to collect vent-shrimp larvae which, it was anticipated, would be in the water column above the vents. Details of the sampling programme are to be found in the accompanying paper by P. Herring (1998). Adult vent shrimps and net-collected larvae, representing three distinct morphological types, were subjected to molecular analysis to establish their species identities. The different larval stages contained large amounts of bright-orange coloured (carotenoid pigmented) lipids in their thoracic regions and first three abdominal segments. Given the small egg size (less than 1 mm in diameter), this raised the question of the source of this storage material. To provide an answer to this question, plus a greater insight into the life history of vent shrimps, fatty acid analysis was carried out on the eggs, larvae, small adults and adults, thereby covering virtually all the different life stages.

Materials and methods

Collection details and descriptions of the different larval types are to be found in the references referred to by Herring (1998). The methods used for fatty acid analysis and diene characterization are given in Pond et al. (1997).

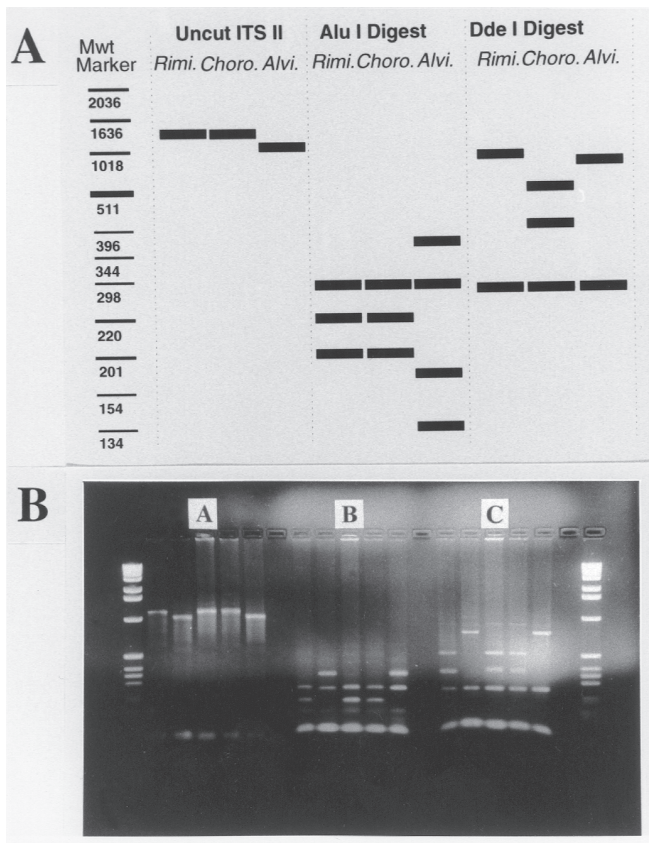

Figure 1. A. Schema showing restriction digest profiles for two diagnostic endonucleases, *Alu*I and *Dde*I, conducted on vent shrimp larvae collected over the Broken Spur vent field. While it was only possible to distinguish *Alvinocaris markensis* from *Rimicaris exoculata* or *Chorocaris chacei* based on the size of the uncut PCR fragments (panel 1), after *Alu*I and *Dde*I digestion (panels 2 and 3) it became possible to separate all three species based on their restriction digest patterns. B. Examples of PCR products from unidentified *type A* bresiliid postlarvae, uncut (A) and cut with restriction enzymes (panel B, *Alu*I; panel C, *Dde*I). This clearly demonstrates that this sample of larval *type A* was made up of a mixture of more than one species: in this case, *A. markensis* and *C. chacei*. The weight marker values are in bp.

Results

Fig. 1a is a schema showing restriction digest profiles for two diagnostic 4-cutter enzymes, *Alu*I and *Dde*I, used to distinguish typed adult specimens of three species of vent shrimps. Panel 1 shows the sizes of the uncut PCR products generated using the ITS2 and PH19 primers, where it was only possible to distinguish *Alvinocaris markensis* Williams, 1988 from the other two species; after *Alu*I digestion (panel 2) it was possible, with greater clarity, to separate *A. markensis* from *Chorocaris chacei* (Williams & Rona, 1986) and *Rimicaris exoculata* Williams & Rona, 1986, whereas digestion with *Dde*I allowed *C. chacei* to be unequivocally separated from *R. exoculata*. Fig. 1b gives examples of PCR products and restriction digest patterns for unidentified *"type A"* bresiliid larvae, collected above the Broken Spur vent field in August 1995. Comparison with species fingerprints similar to those shown in Fig. 1a allowed these 5 larvae to be identified as a mixture of *Chorocaris chacei* (lanes 1, 3 and 4) and *Alvinocaris markensis* (lanes 2 and 5).

Initially, it had been our belief that the net hauls contained postlarvae of just two vent shrimp species, *A. markensis* and *C. chacei* plus an earlier stage larval type of an unknown, eyed, bresiliid, nominally described as *"type A",* for which we had no known adult stage (Herring & Dixon, 1998). Detailed analysis of the front ends of the *"type A"* specimens has so far revealed no taxonomic features which can be used to distinguish species identity (M. Saint-Laurent, unpublished). The results of our DNA comparisons showed the *"type A"* larval cohort was polyspecific, while the *"Chorocaris-type"* postlarva consisted of two species, *Chorocaris chacei* and *Rimicaris exoculata**. Only the *Alvinocaris-type* postlarva was what it appeared to be. Thus, we are in a position to construct a developmental sequence for most of the known vent shrimps on the MAR (Fig. 2). This includes *Mirocaris (Chorocaris) fortunata* (Martin & Christiansen, 1995) but this data arrived too late to be included in the figures. Moreover, recent analysis, using molecular methods, has revealed at least two genetic morphs within the larval subset we identified as *Chorocaris chacei*, which were present

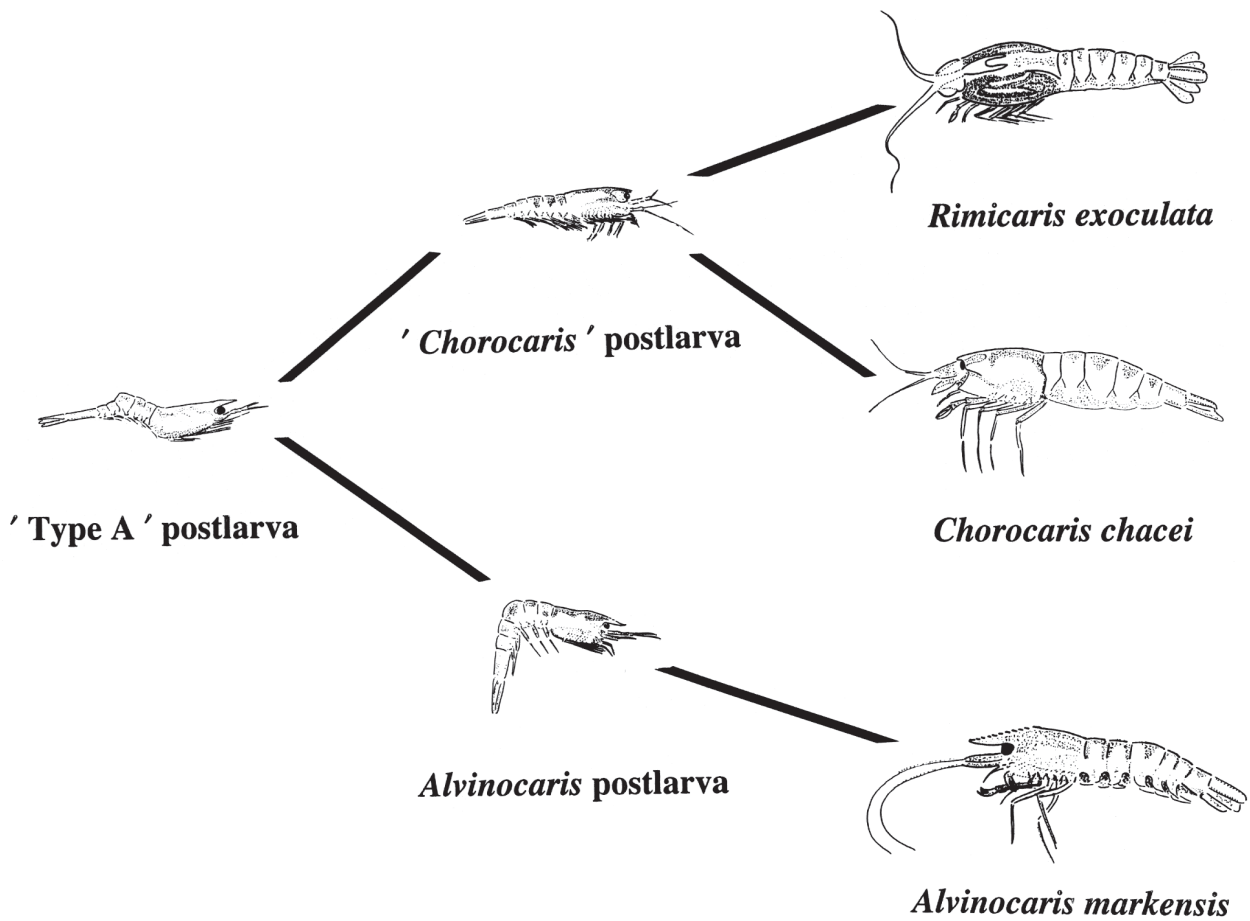

Figure 2. Proposed developmental sequence of vent shrimps sampled at the Broken Spur vent field in August 1995, based on the results of PCR-RFLP analysis.

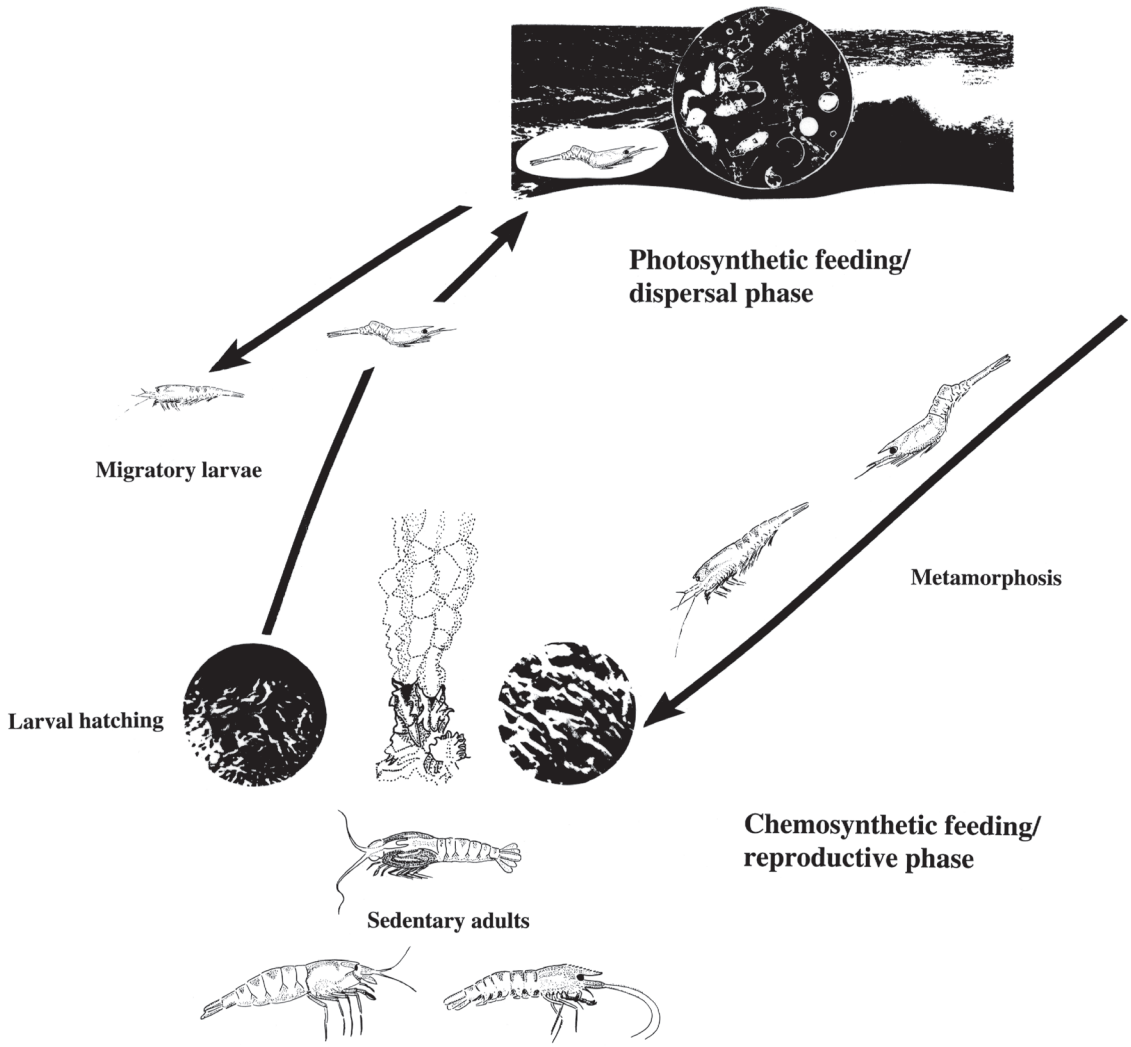

Figure 3. Schema depicting the life history of MAR vent shrimps. The life cycle is divided into two parts: a sedentary adult feeding stage and a planktotrophic larval phase which is largely responsible for dispersal between vents and vent fields.

	Eggs	Late zoeal and early postlarval stages	Small Adults	Adults
SFA	16	10	7	19
MFA	7	52	30	64
16:2 (n-4) 18:2 (n-4)	4	0	1.5	6
NMID	4	0	1	6.5
PUFA	2	38	60.5	4.5

Table 1. Lipid analyses carried out on different life stages of vent shrimps. Results are expressed as percentages of total fatty acid. SFA: saturated fatty acid; MFA: monounsaturated fatty acid; NMID: non-methylene interrupted dienes; PUFA: polyunsaturated fatty acids, i.e. 3 or more double bonds. For further details of methods see Pond *et al*. (1997).

both in the *"type A"* and postlarval samples. The significance of this genetic subdivision is still being assessed, but there is the possibility that an additional bresiliid species, *Mirocaris keldyshi* Vereschaka, 1997, which has only been described from Broken Spur, may also be present in our larval collections (Dixon and Dixon, unpublished).

Table 1 shows results of lipid analyses conducted on a series of life stages of vent shrimps. The main findings are that, while both the large adults and their eggs have lipid signatures which reflect feeding, either directly or indirectly on filamentous vent bacteria, the larvae and small adults (recent vent colonizers) showed a predominance of PUFA which are characteristic of phytoplankton (better photosynthetic microplankton). This demonstrates a clear separation within the life history of these organisms into a chemosynthetic-feeding adult stage and a photosynthetic-feeding larval phase.

Discussion

When dealing with complex developmental patterns, great care must be exercised when describing new taxa based on morphological characters alone. Morphological characters can vary at different stages in the life history making these unreliable as species markers. This points to the need to include molecular markers as part of standard taxonomic practice, particularly when dealing with difficult groups such as the bresiliids, where material is sometimes difficult to obtain and where there are striking changes in morphology throughout development. The sequence, *"Alvinocaris-type"* to *"Rimicaris-type",* reflects a pattern of increasing morphological adaptation and trophic specialization. It was Ernst Haeckel, the German biologist and contemporary of Charles Darwin, who first proposed the principle that ontogeny recapitulates phylogeny (Haeckel's principle). Whether or not one subscribes to this viewpoint (and many present-day biologists do not), it is clear that vent shrimps and their larvae display a sequence of morphological variation which mirrors the changes which must have occurred within the group since they first colonized the vent environment in the distant past.

Armed with the lipid biochemistry information (Table 1), it becomes possible to unravel the life history of the bresiliid vent shrimps on the MAR (Fig. 3). Prior to the CD 95 cruise, our knowledge of vent shrimp reproductive biology was restricted largely to: 1) egg size (less than 1 mm e.g. *Rimicaris exoculata*); 2) the eggs are carried, at least temporarily, beneath the abdomen in typical decapod fashion; and 3) females *(R. exoculata)* undergo several distinct spawning periods in their lifetime (J. Copley unpublished data). Given the size of the newly hatched larva *(Mirocaris fortunata,* 2.5 mm; unpublished), these must become dependent on an external food supply very early on in their development. The strong convection currents generated at sites of hydrothermal activity will rapidly transport newly-hatched larvae to the height of the neutrally-buoyant plume, some 200-300 metres above the sea bed (Mullineaux, 1994), and possibly above. Horizontal transport, meanwhile, will be greatly assisted by deep ocean water currents. Their return to the vent environment may be aided by a sensitivity to low levels of H2S in the surrounding sea water (Renninger et al., 1995). By utilizing materials originating in the photic zone, vent shrimp larvae have the potential to extend their dispersal range almost indefinitely.

*Footnotes:** Morphological examination by M. de Saint-Laurent (Paris, Muséum d'Histoire Naturelle) has since shown this single specimen to be a metamorphosed small juvenile.

Since completing this study we have extended our larval identifications and species comparisons to include *Mirocaris* (formerly *Chorocaris*) *fortunata* (from Lucky Strike and Rainbow) and *Iorania concordia* (Vereschaka, 1996) (from Broken Spur). Interestingly, while *M. fortunata* yielded its own unique pattern of DNA fragments, the pattern for *I. concordia* turned out to be identical to that of *Rimicaris exoculata*. Clearly, the separate species status of *I. concordia* is not supported by these findings.

Acknowledgements

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