



Recruitment and population structure of the vetigastropod *Lepetodrilus elevatus* at 13°N hydrothermal vent sites on East Pacific Rise

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Introduction

Understanding the processes involved in both the persistence of hydrothermal vent populations and the colonization of new vents in such a patchy and ephemeral environment constitute a major goal (Tunnicliffe, 1991). Although the biological life history of most vent species remains poorly documented (Tyler & Young, 1999), the number of studies of various life cycles stages has increased over the last decade. However, gastropods are an important component of the fauna of deep-sea hydrothermal vents and are often overlooked.

The vetigastropod *Lepetodrilus elevatus* MacLean, 1988 is one of the most prevalent species along the East Pacific Rise, reported from 9°N to 21°N on vestimentiferan tubes, bivalve shells and rocks (McLean, 1988; Craddock et al., 1997). From morphological observations on larval shells, Lutz et al. (1986) concluded that *L. elevatus* undergoes nonplanktotrophic development with a free-swimming, but nonfeeding planktonic larval stage. Although they suggested that larval dispersal may be limited and may occur in a stepwise fashion along the ridge system, genetic studies did not confirm this hypothesis (Craddock et al., 1997). Analysing size-frequency distributions of *L. elevatus* at the end of a 3-year colonization experiment, Mullineaux et al. (1998) observed both an episodic recruitment and a maximal size at settlement of 250 µm for protoconch-stage recruits.

This paper presents preliminary results on the population structure of *L. elevatus* collected from one hydrothermal vent field (13°N EPR) through the analysis of length-frequency histograms. Two main questions are addressed in this study: (1) Is the recruitment of *L. elevatus* in their natural habitat discontinuous? (2) What is the spatial

coherence of recruitment? Results are discussed in relation to recruitment processes.

Materials and methods

A hierarchical sampling method involving two spatial scales was undertaken: (i) within the 13°N EPR vent field where 4 sites were sampled: Grandbonum, Julie, Elsa and Genesis, (ii) within a single site where one to four samples were collected (Table 1). Distances between sites varied from 175 m to 1800 m, while distances within a site were <10 m.

All *L. elevatus* individuals were sampled from collections of the giant tubeworm *Riftia pachyptila* Jones, 1981 using the hydraulic arm of the French submersible 'Nautile' during the HOPE'99 cruise in April-May 1999. On board ship, individuals were fixed with 10% neutral formalin in seawater. Because of the large sample sizes, all samples except that from Granbonum were subsampled to establish size-frequency distributions: about 500 limpets were randomly sampled and measured.

To analyse the population structure, the curvilinear shell length (L_{curv}), which is strongly correlated with individual dry weight (W), was used as an index of limpet size ($W = 0.0053L_{\text{curv}}^{2.923}$; $r^2 = 0.9665$; $n = 90$). This measure corresponds to the total curvilinear length from the anterior edge of the shell to the lip of the protoconch. Measurements were achieved to the nearest 0.01 mm using the 'Image Tool' image analysis software (University of Texas, <http://www.uthscsa.edu/dig/download/html>). Measurement error was fixed at 0.14 mm, which is the maximum difference among 10 repeated measures of the curvilinear length determined on a small and a large limpet. Size-

Table 1 : Characteristics of *Lepetodrilus elevatus* samples collected in April-May 1999 on different vent sites at 13°N/EPR. Except for Granbonum where all the individuals were measured, curvilinear length of *L. elevatus* was determined for other samples after random subsampling.

Vent Site	Date	Dive no.	Geographic coordinates	Sample size	Curvilinear length (mm)		
					Range	Mean	SD
Grandbonum	May 2	1371	103° 56.35'W 12° 48.72'N	195	2.3 - 12.55	8.86	1.79
Julie	April 16	1360	103° 56.56'W 12° 49.05'N	531	2.32 - 9.61	6.03	1.28
Elsa	April 15	1359	103° 56.33'W 12° 48.11'N	512	2.41 - 13.29	8.08	1.33
Elsa	May 10	1379	- -	1129	1.14 - 11.44	7.01	2.40
Genesis	April 12	1357	103° 56.43'W 12° 48.67'N	492	2.06 - 11.51	7.01	1.93
Genesis	May 1	1370	- -	490	1.31 - 12.24	6.48	2.34
Genesis	May 12	1381	- -	575	1.43 - 12.23	6.73	2.31
Genesis	May 16	1385	- -	544	1.72 - 11.35	6.17	1.91

frequency histograms were plotted using a size-class interval of 0.25 mm. This interval was chosen according to three criteria (Jollivet et al., 2000): (i) most size-classes must have at least five individuals, (ii) the number of adjacent empty classes must be minimized and (iii) the interval has to be much greater than the error of measurement.

Size-frequency distributions were compared to a normal distribution using a Kolmogorov-Smirnov one-sample test adapted by Lilliefors, while pairwise comparisons of distributions were made using a Kolmogorov-Smirnov two-sample test. Modal decomposition was performed according to the Bhattacharya method using the NORMSEP program adapted by Gros & Cochard (1978), assuming that limpets sizes follow a Gaussian distribution within a single cohort. The program calculated the principal parameters of each component (i.e. mean length, standard deviation and number of individuals) according to the Hasselblad's method with a χ^2 goodness-of-fit test. A hierarchical cluster analysis measuring the Hellinger distance and using an average link (UPGMA) between observations was made in order to group samples as a function of their size-frequency distributions (Legendre & Legendre, 1998).

Results

The curvilinear length of *L. elevatus* ranged from 1.14 mm for the smallest recruits to 13.29 mm for the largest adults (Table 1). All size-frequency distributions except for Genesis 1385 differed significantly from the normal distribution (Kolmogorov-Smirnov one-sample test, $p < 0.05$) and were assumed to be polymodal. Modal decomposition of the size-frequency histograms indicated a great variability in the number of Gaussian components with the occurrence of 2 (i.e. Julie, Elsa 1379) to 6 (i.e. Grandbonum) modal classes (Fig. 1). The four samples collected a few meters apart at Genesis were composed of 4 to 5 modes while those from Elsa contained 2 or 3 modes. Within a site, the main difference between the modal decomposition consisted of the separation of 1 mode into 2, whereas other Gaussian components showed only slightly shifted modal values. Note that results from Granbonum have to be considered with caution: the sample size (i.e.

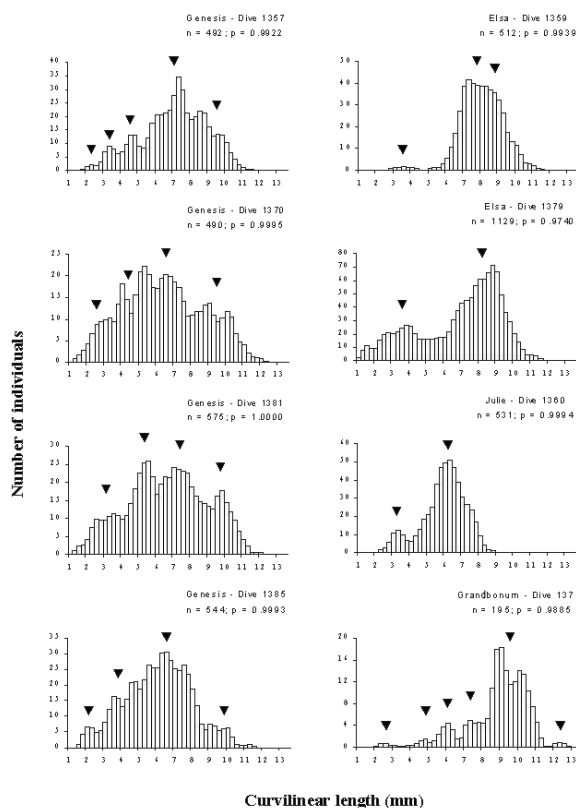


Figure 1: Size-frequency histograms of the curvilinear length of *Lepetodrilus elevatus* from samples collected in April-May 1999 on different vent sites at 13°N EPR. n = sample size ; p = significance level of the modal decomposition according to the χ^2 goodness-of-fit test; ▼ = modal classes determined using the NORMSEP program.

only 195 individuals) may have been too small to perform a reliable analysis of population structure, possibly yielding artificial modes.

All distributions were dominated by a large number of individuals of medium and large sizes (Fig. 1). Thus, Elsa

1359, Julie and Grandbonum samples were mainly composed of individuals ranging from 6 to 10, 5 to 8 and 8 to 11 mm respectively. These individuals belonged to one or two modal classes. Conversely, Genesis and Elsa 1379 samples showed a higher frequency of small individuals (<5mm) although medium and large animals constituted most of the population.

Size-frequency distributions of each sample were significantly different (Kolmogorov-Smirnov two-sample test, $p < 0.05$) except between Genesis 1370 and Genesis 1381 ($0.05 < p < 0.1$). Cluster analysis based on Hellinger distance did not clearly distinguish samples according to their spatial location but showed that inter-site variations of size-frequency distributions could be as important as intra-site variations (Fig. 2). While the 4 samples from Genesis formed one group and had the lowest distance value with respect to one another, the 2 samples from Elsa were strongly separated. One sample (Elsa 1379) was linked to the Genesis samples while the other (Elsa 1359) was joined to the Grandbonum sample. However, such a difference was mainly due to the relative importance of small individuals among the two samples from Elsa rather than differences in size of medium and large individuals.

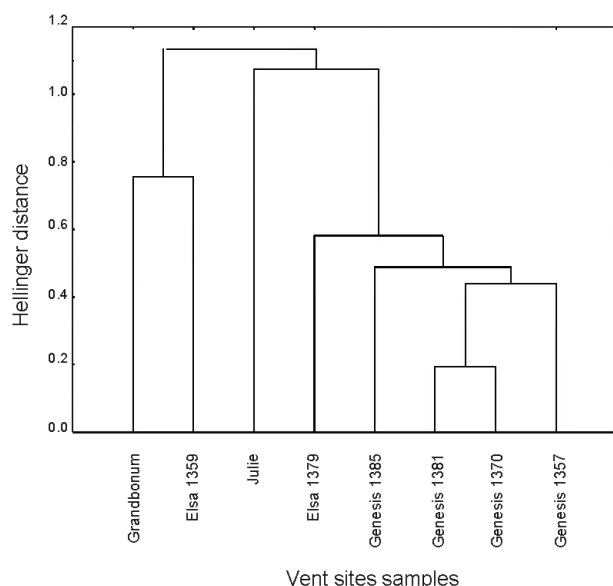


Figure 2: Cluster analysis of *Lepetodrilus elevatus* size-frequency distributions from samples collected in April-May 1999 on different vent sites at 13°N/EPR. Where several samples were collected at the same vent site, the dive number is also given.

Discussion

Modal decomposition of the size-frequency histograms of each sample showed that each distribution can be decomposed in 2 to 6 Gaussian components assumed to represent successive distinct cohorts. If, in most samples, modes were well separated and evenly spaced, overlapping in smallest size-classes could partly explain the variation in the number of Gaussian components. Thus, for a similar

size range of between 2 and 6 mm, 2 to 3 modal classes were identified from the Genesis samples while only one modal class was calculated from the Elsa samples. Different hypotheses may be proposed to explain such differences in the number of size groups between samples: (i) a bias in the sampling, (ii) a micro-spatial scale heterogeneity in the distribution of limpets according to their size and (iii) an insufficient number of individuals measured to perform the modal decomposition.

Whatever the demographic nature of each mode, the polymodal size-distributions clearly indicated that recruitment of *L. elevatus* is discontinuous, as reported for most hydrothermal vent species studied to date. These include polychaetes (e.g. Zal et al., 1995), bivalves (Comtet & Desbruyères, 1998) and vestimentiferans (Thiébaud et al., 2002). This result is also consistent with previous observations by Mullineaux et al. (1998) where colonization of experimental basalt plates by *L. elevatus* resulted from discrete settlement events rather than continuous recruitment.

Although size-frequency histograms displayed the same general pattern with the dominance of one or two massive modal classes of medium and large-size individuals, large variations in the average size of these classes occurred among samples, from about 6 mm at Julie to about 9.5 mm at Grandbonum. Three hypotheses can be formulated to explain such variations: (i) variation in the timing of recruitment, (ii) variations in the mean growth rates and (iii) differential mortality.

Mullineaux et al. (1995) suggested that larvae of vent gastropods are entrained into neutrally-buoyant hydrothermal plumes, whereas Kim & Mullineaux (1998) showed that near bottom currents could transport a particle up to 2 km through the axial graben during a single tidal excursion. In addition, experiments of colonization on artificial settlement panels demonstrated that the recruitment of *L. elevatus* was spatially coherent at a scale of at least 1 km (Mullineaux et al., 1998). Therefore, peaks in the abundance of *L. elevatus* in medium and large size classes observed in our samples could be related to a major episodic larval supply at the scale of the 13°N EPR vent field.

Variability of population structures among samples is more likely a result of variations in growth and mortality rates, possible related to inter-site differences in the physical and chemical environment and/or biotic interactions after settlement. From the analysis of fluorescent age pigments, Mullineaux et al. (1998) suggested that metabolism of *L. elevatus*, and consequently growth, may be affected by temperature. In contrast with other marine benthic habitats, there is presently little information available on the role of biotic interactions on the population dynamics of hydrothermal vent species. Branch (1975), for example, highlighted the crucial role of intraspecific density-dependent competition on the growth and mortality rates of the coastal limpet, *Patella cochlear*. During field collections, the percent cover of *L. elevatus* on the *Riftia pachyptila* tubes was observed to vary substantially. Together with abiotic factors, growth and mortality differences among samples could be partly explained by

such density variation and related competition. Finally, spatial variability of predation pressure by zoarcid fishes could directly influence the population structure of *L. elevatus* by reducing the abundance of limpets and indirectly by reducing intraspecific competition (Micheli et al., 2002).

To conclude, the present data suggest: a discontinuous recruitment of *L. elevatus* with major episodic larval supply; a spatial coherence of larval supply at the scale of a vent field; inter-site variations of individual growth related to abiotic and biotic factors.

Acknowledgements

The authors gratefully acknowledge the captain and crew of the N/O *L'Atalante* and the pilots and team of the submersible *Nautile*. We thank F. Lallier, the chief scientist of the HOPE'99 cruise, who allowed us to conduct this work, and T. Jolly for English proof reading.

References

- Branch G.M. 1975.** Intraspecific competition in *Patella cochlear* Born. *Journal of Animal Ecology*, **44**: 263-281.
- Comtet T. & Desbruyères D. 1998.** Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez Gwen Hydrothermal vent fields (37°17' N and 37°50' N on the Mid-Atlantic Ridge). *Marine Ecology Progress Series*, **163**: 165-177.
- Craddock C., Lutz R.A. & Vrijenhoek R.C. 1997.** Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. *Journal of Experimental Marine Biology and Ecology*, **210**: 37-51.
- Gros P. & Cochard J.-C. 1978.** Biologie de *Nyctiphanes couchii* (Crustacea, Euphausiacea) dans le secteur nord du golfe de Gascogne. *Annales de l'Institut Océanographique*, **54**: 25-46.
- Jollivet D., Empis A., Baker M.C., Hourdez S., Comtet T., Jouin-Toulmond C., Desbruyères D. & Tyler P. 2000.** Reproductive biology, sexual dimorphism, and population structure of the deep-sea hydrothermal vent scale-worm *Branchipolynoe seepensis* (Polychaeta : Polynoidae). *Journal of the Marine Biological Association of the United Kingdom*, **80**: 55-68.
- Kim S.L. & Mullineaux L.S. 1998.** Distribution and near-bottom transport of larvae and other plankton at hydrothermal vents. *Deep-Sea Research II*, **45**: 423-440.
- Legendre P. & Legendre L. 1998.** *Numerical Ecology*, 2nd English Edition. Elsevier: Amsterdam. 853 pp.
- Lutz R.A., Bouchet P., Jablonski D., Turner R.D. & Waren A. 1986.** Larval ecology of molluscs at deep-sea hydrothermal vents. *American Malacological Bulletin*, **4**: 49-54.
- MacLean J.H. 1988.** New archaeogastropod limpets from hydrothermal vents ; superfamily Lepetodrilacea. Systematic descriptions. *Philosophical Transactions of the Royal Society of London*, **319B**: 1-32.
- Micheli F., Peterson C.H., Johnson G.A., Mullineaux L.S., Mills S.W., Sancho G., Fisher C.R. & Lenihan H.S. 2002.** Predation structures communities at deep-sea hydrothermal vents. *Ecological Monographs*, **72**: 365-382.
- Mullineaux L.S., Wiebe P.H. & Baker E.T. 1995.** Larvae of benthic invertebrates in hydrothermal vent plumes over Juan de Fuca Ridge. *Marine Biology*, **122**: 585-596.
- Mullineaux L.S., Mills S.W. & Goldman E. 1998.** Recruitment variation during a pilot colonization study of hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research II*, **45**: 441-464.
- Thiébaud E., Huther X., Shillito B., Jollivet D. & Gaill F. 2002.** Spatial and temporal variations of recruitment in the hydrothermal vent tube worm *Riftia pachyptila* (Vestimentifera) on the East Pacific Rise (9°50'N and 13°N). *Marine Ecology Progress Series*, **234**: 147-157.
- Tunnicliffe V. 1991.** The biology of hydrothermal vents: ecology and evolution. *Oceanography and Marine Biology an Annual Review*, **29**: 319-407.
- Tyler P.A. & Young C.M. 1999.** Reproduction and dispersal at vents and cold seeps. *Journal of the Marine Biological Association of the United Kingdom*, **79**: 193-208.
- Zal F., Jollivet D., Chevvaldonné P. & Desbruyères D. 1995.** Reproductive biology and population structure of the deep-sea hydrothermal vent worm *Paralvinella grasslei* (Polychaeta : Alvinellidae) at 13°N on the East Pacific Rise. *Marine Biology*, **122**: 637-648.