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)

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ABSTRACT: Population structure and recruitment pattern of undescribed mytilid bivalves that dominate the animal communities associated with vents of the Lucky Strike and Menez Gwen hydrothermal vent fields (37° 17' N and 37° 50' N on the Mid-Atlantic Ridge) were studied from size-frequency analyses. Intra-site comparisons reveal that length-frequency distributions differ significantly from one location to the other. This spatial segregation of the sizes could be due to spatio-temporal variability in environmental conditions and to intraspecific competition processes, especially adult-larval interactions (competition for space and food resources, intraspecific larviphagy) that could prevent larvae from settling on surfaces covered by adults. A modal decomposition analysis was conducted after pooling samples collected from different locations at the same site. Polymodal structure of length-frequency distributions indicates that recruitment is likely discontinuous in time. The presence of postlarvae in each population of the Lucky Strike vent field suggests that a recruitment event took place just before sampling in June 1994, and that mytilid recruitment is synchronized between sites, which is confirmed by the comparison of modal values. Length-frequency distribution of the Menez Gwen mytilid population displays similar modal values, especially for the smallest mode. This suggests a synchronization of the recruitment between the 2 vent fields, which are separated by a distance of 60 km. No seasonal pattern in recruitment could be identified although newly recruited individuals were observed in June 1993 on Lucky Strike sites.

KEY WORDS: Hydrothermal vents · Mytilidae · Recruitment · Population structure · Size frequency · Spatial segregation · Intraspecific competition · Mid-Atlantic Ridge

INTRODUCTION

The deep-sea hydrothermal ecosystem is characterized by great spatial and temporal instability due to the combination of non-periodic changes related to tectonic events and convection of the heated fluids through the seafloor (Watremez & Kervevan 1990) and periodic events, some of which correspond to tidal signals (Little et al. 1988, Chevaldonné et al. 1991, Johnson et al. 1994). On fast spreading ridges, such as the East Pacific Rise (EPR) at 13° N, vent sites appear to have a short lifetime (generally no longer than ca 100 yr) and the locus of hydrothermal activity shifts along the ridge (Lalou et al. 1985, 1993a). On slow spreading ridges, such as the Mid-Atlantic Ridge (MAR), the hydrothermal activity is spatially more focused and stable over the long term, even if the lifetime of an individual vent site is similar to that on the fast spreading ridges (Fouquet et al. 1993, Lalou et al. 1993a, b, Y. Fouquet, J. L. Charlou, J. P. Donval, J. Radford-Knoëry, H. Ondréas et al. unpubl.). Variability in the hydrothermal discharge causes changes in the animal communities associated with vents (Hessler et al. 1985, 1988, Fustec et al. 1987, Jollivet 1993). As a consequence, the vent fauna must adapt to unstable environmental conditions and nutrient supply by rapidly

colonizing new vents. One might therefore expect vent organisms to display an r-type ecological strategy and large dispersal capabilities (Desbruyères & Laubier 1983).

The population dynamics of hydrothermal-vent-associated species are poorly known because of the lack of long-term data and the difficulty in gathering the information needed in such studies (i.e. population structure, growth rate, reproductive biology, recruitment, and larval dispersal). A few studies of population structure by means of size-frequency analysis have been conducted on vestimentiferan worms (Siferd 1984, Tunnicliffe 1991, Jollivet 1993), alvinellid polychaetes (McHugh 1989, Jollivet 1993, Zal et al. 1995), serpulid polychaetes and bythograeid crabs (Jollivet 1993), from samples collected at 13°N on the EPR and on the Juan de Fuca-Explorer ridge system, which are, respectively, fast and medium spreading ridges (Hékinian et al. 1983, Canadian American Seamount Expedition 1985, Tunnicliffe et al. 1986). These studies give some indication of the dynamics of these species, allowing a better understanding of the processes controlling the evolution and maintenance of the populations. Discontinuous recruitment has been shown to occur most frequently in the hydrothermal invertebrates studied to date, but a continuous pattern has also been documented in some cases. Jollivet (1993) and Zal et al. (1995) hypothesized that recruitment in *Alvinella pompejana*, *Alvinella caudata* and *Paralvinella grasslei* (3 alvinellid polychaetes) might occur at least once a year. Moreover, the occurrence of more than one breeding period over a year seems to be confirmed by theoretical calculations for these alvinellid species (Jollivet et al. in press).

Undescribed bivalves belonging to the family Mytilidae dominate the animal communities associated with 2 newly discovered hydrothermal vent fields on the Mid-Atlantic Ridge, Lucky Strike (37° 17′ N) and Menez Gwen (37° 50′ N) (Langmuir et al. 1993, Desbruyères et al. 1994, Fouquet et al. 1995, Van Dover et al. 1996). Morphological and anatomical studies indicated that mytilids from both vent fields belong to a single new species of the genus *Bathymodiolus* (R. von Cosel, T. Comtet & E. Krylova unpubl.), distinct from *Bathymodiolus puteoserpentis* Cosel, Métivier & Hashimoto, 1994, found at Snake Pit (23° N on the MAR), from *Bathymodiolus* sp. found at the Logatchev vent field (14° 45′ N on the MAR), from the mytilids of the Broken Spur vent field (29° N on the MAR), from *Bathymodiolus thermophilus* Kenk & Wilson, 1985, found from 13° N to 22° S on the EPR and on the Galapagos Rift, and from 7 other mytilid species inhabiting hydrothermal vents and cold seeps (Craddock et al. 1995). Preliminary results of DNA sequencing for mytilids from Lucky Strike and Menez Gwen confirm

that they belong to the same species and differ from *B. thermophilus* from 13° N on the EPR (T. Comtet & D. Jollivet unpubl. data).

The population structure of mytilid bivalves from hydrothermal vents has never been studied in detail, although length-frequency histograms have been published by Rhoads et al. (1982), Smith (1985) and Hessler et al. (1988) for *Bathymodiolus thermophilus* from the Galapagos Rift vents without any interpretation in terms of population dynamics. Preliminary results on population structure of the mytilid bivalves of Lucky Strike have also been published by Comtet (1994) and Van Dover et al. (1996), from 4 samples collected in June 1993 from 3 sites at Lucky Strike, and suggested a discontinuous recruitment. Their studies asked 3 main questions which the present study will attempt to answer: (1) Is discontinuity in recruitment a general feature of the mytilids from Lucky Strike, i.e. can it be confirmed on the other sites of this vent field? (2) Considering such a discontinuity, is recruitment periodic, and if it is, what is its periodicity? (3) Is recruitment synchronized among the different sites at Lucky Strike and between Lucky Strike and the newly discovered Menez Gwen vent field? We present here the results of the analysis of size-frequency distributions in 6 mytilid bivalve populations sampled in June 1994 during the DIVA 2 cruise at Lucky Strike and Menez Gwen.

MATERIALS AND METHODS

Study area and sampling. Accurate reference to spatial scales is very important in patchy habitats such as vents. In an attempt to standardize the terms used relative to the spatial scales, we will use the definitions given by Chevaldonné et al. (1997): 'vent' describes a single localized emission of hydrothermal fluid, 'vent site' or 'site' refers to a spatially continuous venting area made of several emissions only a few metres apart, 'vent field' or 'field' refers to a cluster of vent sites located a few 100s of metres apart, linked by subterranean ducts and which undergo the same temporal variations. Vent fields can be grouped within larger spatial units termed 'venting sectors' or 'venting areas' which correspond to ridge segments.

The Lucky Strike hydrothermal vent field is located at 37° 17.5′ N, 32° 16′ W on the MAR, in the Azores triple junction area (Fig. 1A) at a depth of ca 1700 m. The active venting area consists of a depression located between 3 volcanic cones (Fig. 1B). The central part of this depression is a lava lake surrounded by several active vent sites (Y. Fouquet et al. unpubl.). The Lucky Strike fauna is dominated by dense mytilid beds that cover surfaces of active sulfide edifices and occur in
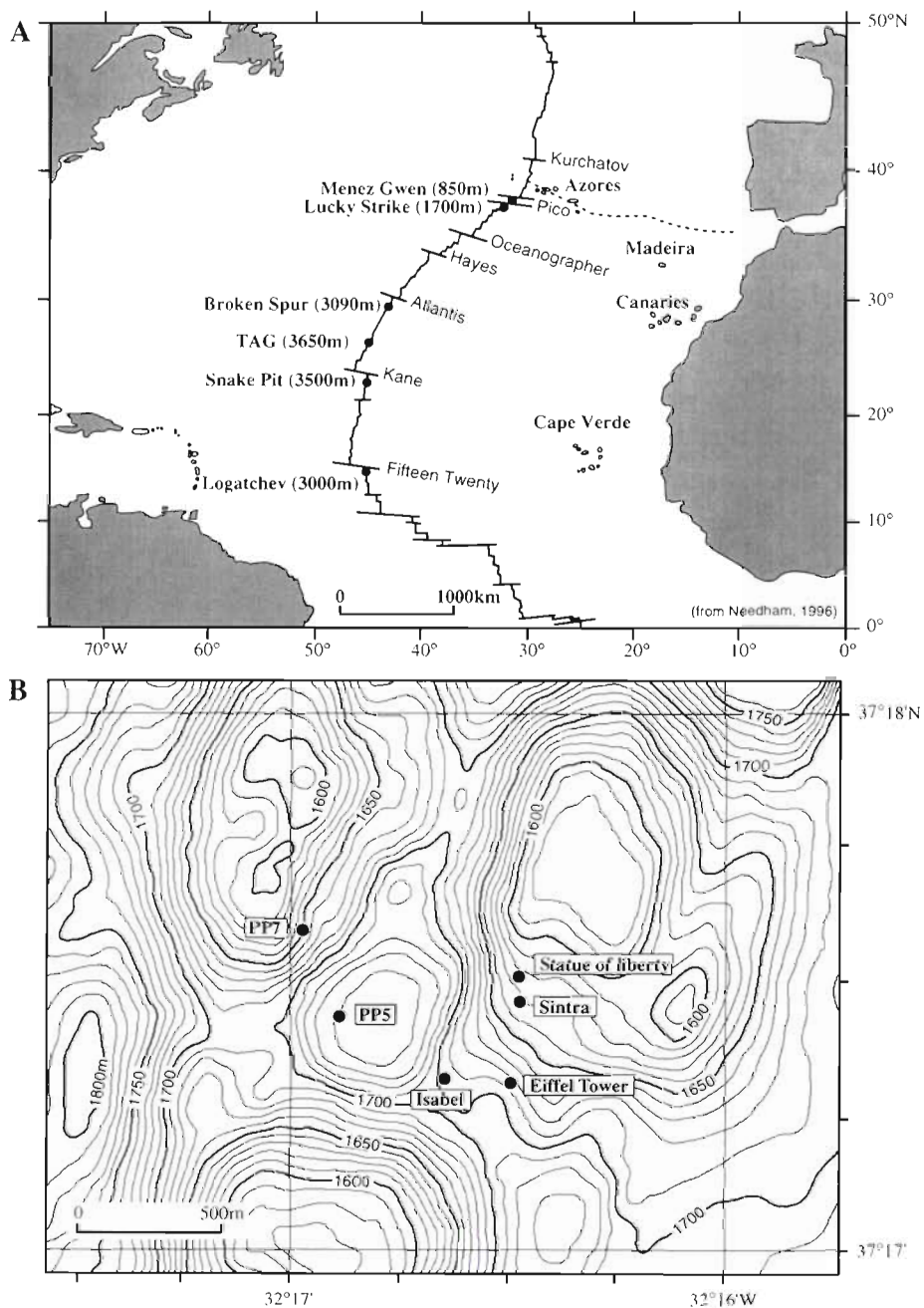
Fig. 1. (A) Locations of the Lucky Strike and Menez Gwen hydrothermal vent fields on the Mid-Atlantic Ridge (MAR). (B) The Lucky Strike hydrothermal vent field, showing locations of the sampling sites. Statue of Liberty was not sampled during the DIVA 2 cruise. Isobaths every 10 m

cracks in the seafloor (Van Dover et al. 1996). The Menez Gwen hydrothermal vent field is located at 37° 50' N, 31° 31' W on the MAR (Fig. 1A), 60 km north of Lucky Strike, at ca 850 m depth near the top of a young volcano. The venting site looks very young (10 to 100 yr) but is already very active (Y. Fouquet et al. unpubl.). Scarce clumps of mytilid bivalves dominate the fauna of Menez Gwen (Desbruyères et al. 1994).

Mytilid bivalves were collected during the first leg of the DIVA 2 cruise (D. Desbruyères, chief scientist) in June 1994, using the arm of the French submersible 'Nautile', from 5 sites of the Lucky Strike vent field, PP5 (Pico), PP7 (Bairro Alto), Sintra, Isabel and Eiffel Tower (Fig. 1B), and 1 site at the Menez Gwen vent field (see Table 1). Several samples of mytilids were collected from different locations at a single site, in

order to avoid a bias that could result from heterogeneity in size distribution, as observed by Comtet (1994), Desbruyères et al. (1994) and Van Dover et al. (1996). Sampling areas were thus selected *in situ* according to the dominant size of individuals, empirically defined as large or small, and samples of mytilids were collected from both types of locations in order to take all size classes into account. Sampling was done according to 2 criteria: (1) one single sample (composed of several batches collected from a single location) was collected on each dive, (2) mytilids were collected with the sulfide block they occupied to avoid size selection during sampling. After arrival onboard, mytilids and sulfide blocks were fixed with 3% neutral formalin in seawater, and preserved in 70% ethanol. In the laboratory, mytilids were sorted from sulfide blocks. Given the large size of the sample collected during Dive 10 (n = 10 019 individuals), it was not possible to measure all individuals and stratified subsampling was performed according to Frontier (1983): mytilids were sorted through a series of sieves of decreasing mesh size (3.15 mm, 2 mm, 1 mm, 500 μm, 250 μm, 160 μm); in each size fraction, a proportion of individuals of about 12.5% was randomly sampled; the actual proportion of each fraction was then calculated and used to extrapolate the results to the total number of individuals. To validate this procedure, the size-frequency distribution of the 3.15 mm fraction subsample was compared to that of the rest of this fraction, by means of a Kolmogorov-Smirnov 2-sample test (Scherrer 1984).

Mytilid length (the greatest antero-posterior dimension) was measured with calipers to the nearest 0.01 mm for individuals more than 5 mm long (Fig. 2). Individuals between 1 and 5 mm long were measured under a dissecting microscope (Leica Wild M10) to the nearest 0.01 mm. The smallest individuals (less than 1 mm long) were measured to the nearest 0.01 mm using the Mocha 1.2 image analysis software (Jandel Scientific). Fig. 2 shows the dimension measured as length for the smallest individuals. This dimension was chosen to be consistent with the dimension measured for adults. On a subsample of 93 postlarval individuals from Dive 10, the length of the prodissoconch II was measured to estimate size at settlement (Fig. 2).

Data analysis. Length-frequency histograms were generated with a size-class interval of 3 mm chosen according to 2 criteria: (1) the main classes (i.e. classes with highest frequencies) should have at least 30 individuals and (2) the number of adjacent empty classes
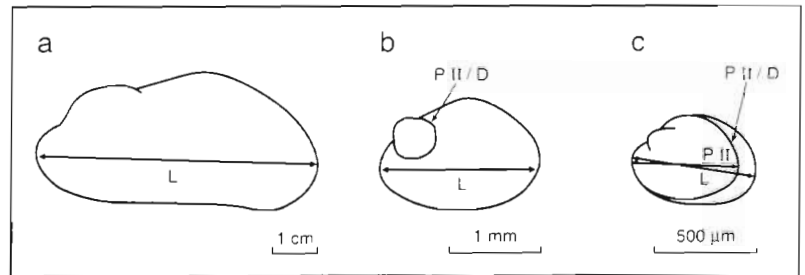

Fig. 2. Length (L) measurements on mytilid bivalves of different sizes. (a) Adult; (b) juvenile; (c) postlarva. From the Dive 10 sample, 93 postlarval individuals were measured for prodissoconch II (PII) length. PII/D: prodissoconch II/dissoconch boundary in order to estimate size at settlement

must be minimized (Bhattacharya 1967). Length-frequency histograms were then smoothed using a weighted moving average at the third order to rule out spurious peaks (Frontier & Pichod-Viale 1991, Jollivet 1993, Zal et al. 1995).

Modal decomposition of length-frequency distributions was done using the MIX 2.3 program package (MacDonald & Green 1986), assuming that mytilid sizes follow a Gaussian distribution within a single cohort. This iterative method, described by MacDonald & Pitcher (1979), provides the best mathematical fit between a theoretical mixture of normal distributions and the observed one, following the maximum likelihood criteria.

RESULTS

Validation of Dive 10 subsampling procedure

To validate the subsampling procedure, the size-frequency distribution of the 3.15 mm fraction subsample was compared to that of the rest of the 3.15 mm fraction by means of the non-parametric Kolmogorov-Smirnov 2-sample test. The result (D_{obs} = 0.0926, p = 0.1237) shows that the frequency distributions in the subsample and in the rest do not differ significantly. The subsampling method therefore did not generate any statistical bias.

Population structure

Length-frequency histograms were generated from measurements of a total of 8600 mytilids. Mytilid lengths ranged from 0.5 mm, for newly settled individuals attached to sulfide blocks, to 113 mm for the largest adults (Table 1).

Length-frequency distributions of each sample display a polymodal structure (Fig. 3) and are character-

ized by a large number of very small individuals (<1 cm), except that for Dive 13 from Menez Gwen (Fig. 3).

Fig. 4 shows length-frequency distributions for each sampling site after pooling the samples collected on that site. All these distributions show a clear polymodal structure, characterized by a great positive skewness, resulting from the high number of small individuals that dominate the populations of each site except Menez Gwen.

Lucky Strike field

Intra-site comparisons. Three of the Lucky Strike vent field sites (Isabel, Eiffel Tower and PP7) were sampled more than once. For Isabel, the size-frequency distributions of Samples 1 and 3 (i.e. the samples taken during Dives 1 and 3, respectively) were significantly different (Kolmogorov-Smirnov test, p < 0.0001). Sample 3 was only composed of small mytilids (<30 mm), whereas a greater size range was observed in Sample 1, even though it had a smaller sample size (Table 1, Fig. 3). The 2 samples (Dives 6 and 7) collected at PP7 showed a similar size range (Table 1), but their size-frequency distributions were significantly different (Kolmogorov-Smirnov test, p < 0.0001), Sample 7 being composed of a greater proportion of small individuals (<30 mm) (Fig. 3). For Eiffel Tower, Sample 10 was clearly different from Samples 4 and 8, being exclusively composed of small mytilids (Fig. 3). Comparison between Samples 4 and 8 also indicated a significant difference in their length-frequency distributions (Kolmogorov-Smirnov test, p < 0.0001). Sample 8 showed the largest size-range, with a great proportion of large individuals, whereas

Sample 4 was dominated by individuals of small and medium sizes (Fig. 3). At a finer spatial scale, the length-frequency distributions of 2 mytilid batches collected a few cm apart on the sulfide block during Dive 2 were clearly different (Fig. 5).

Inter-site comparisons. Length-frequency histograms for each site at the Lucky Strike vent field are given in Fig. 4a–e. These distributions have similar structures, with a great positive skewness due to the abundance of small individuals.

Results of the modal decomposition are given in Table 2. For each distribution, more than 1 well-fitted solution, with 5 to 7 Gaussian components, can be proposed. The main differences between the modal decompositions proposed for a given site consist of the separation of 1 mode into 2, with the other components showing slightly shifted modal values, and are indicated in Fig. 6 by circled areas. For PP7 and Eiffel Tower, the solutions with 6 and 7 modes, respectively, give a better p-value for the χ^2 goodness-of-fit test. The modal decomposition of the size distribution for Isabel gives 3 solutions with p-values equal to 1, making discrimination between these solutions difficult. Histograms of the 2 single-sample sites PP5 and Sintra can be decomposed into 6 and 5 components, respectively. For PP5, a solution with 5 modes (PP5 a) is proposed, but in this case the χ^2 test may be invalid because of 3 expected frequencies lower than 1.

Menez Gwen field

Three samples were collected from the same site of the Menez Gwen vent field. Length-frequency distributions of each sample are given in Fig. 3j–l. Kolmogorov-Smirnov 2-sample tests showed that each size

Table 1. Characteristics of each mytilid bivalve sample collected in June 1994 from the Lucky Strike and Menez Gwen hydrothermal vent fields on the Mid-Atlantic Ridge (MAR). DIX and PP11 are 2 markers placed on a single site at Menez Gwen

| | Dive no. | Date | Site | Depth (m) | Sample size | Length (mm) | | |
						Range	Mean	SD
Lucky Strike	01	Jun 3	Isabel	1685	277	0.60–112.56	29.55	29.77
	02	Jun 4	Sintra	1622	558	0.46–83.60	14.84	20.11
	03	Jun 5	Isabel	1685	974	1.16–26.54	5.52	3.65
	04	Jun 6	Eiffel Tower	1685	618	1.03–84.12	22.46	19.40
	05	Jun 7	PP5	1725	245	0.50–102.86	20.16	27.04
	06	Jun 8	PP7	1629	274	0.52–99.81	22.10	28.52
	07	Jun 9	PP7	1629	871	0.51–101.66	11.90	17.94
	08	Jun 10	Eiffel Tower	1685	321	0.81–112.99	49.93	31.41
	10	Jun 12	Eiffel Tower	1685	10019	0.48–53.73	5.63	5.67
Menez Gwen	11	Jun 13	DIX	866	185	0.58–74.54	39.56	22.40
	12	Jun 14	PP11	866	144	2.75–92.78	57.39	25.87
	13	Jun 15	PP11	866	29	62.68–111.56	92.66	11.97
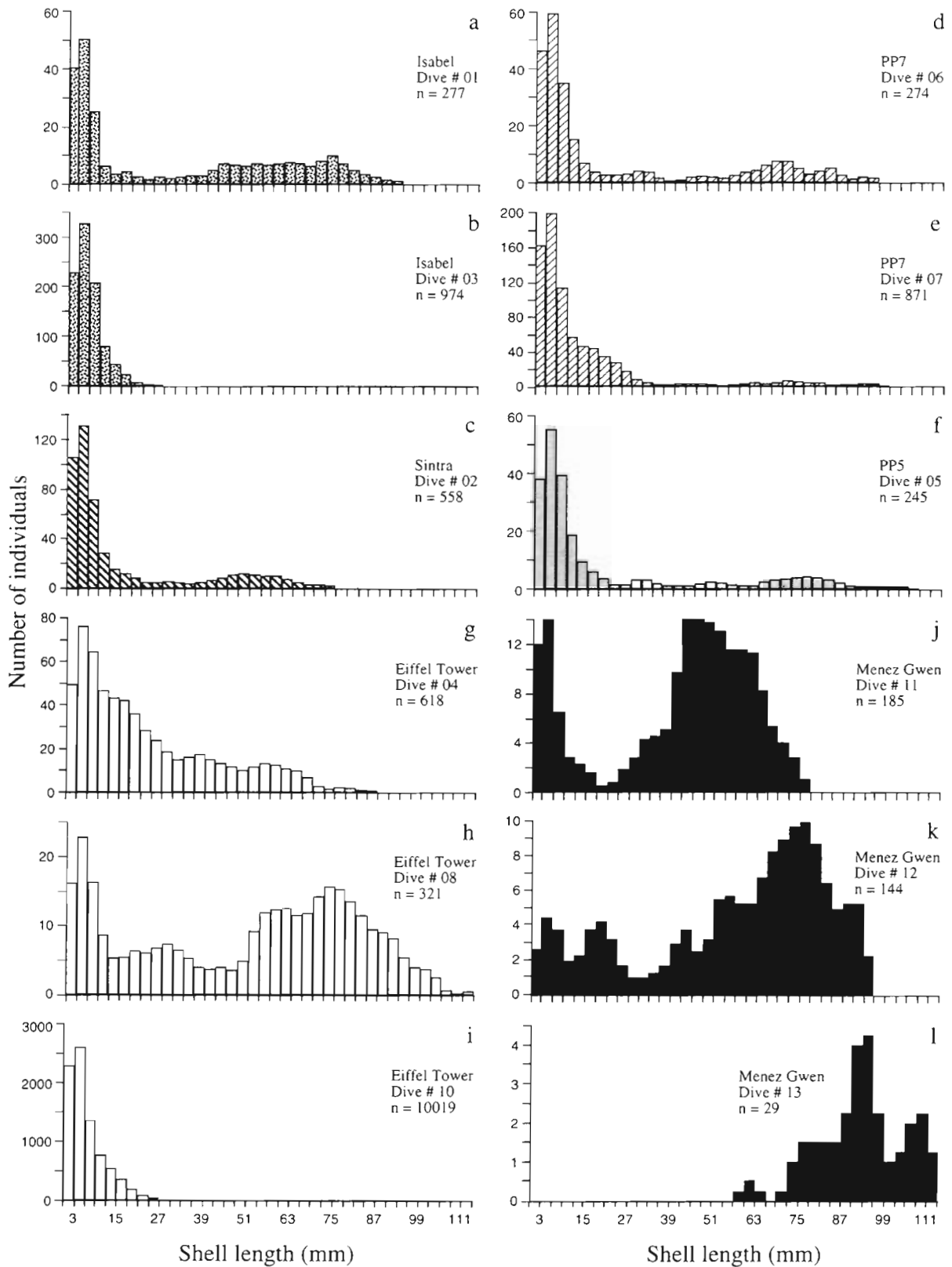
Fig. 3. Shell length frequency histograms of 12 mytilid samples from different dives on the Lucky Strike and Menez Gwen hydrothermal vent fields (MAR). n = sample size
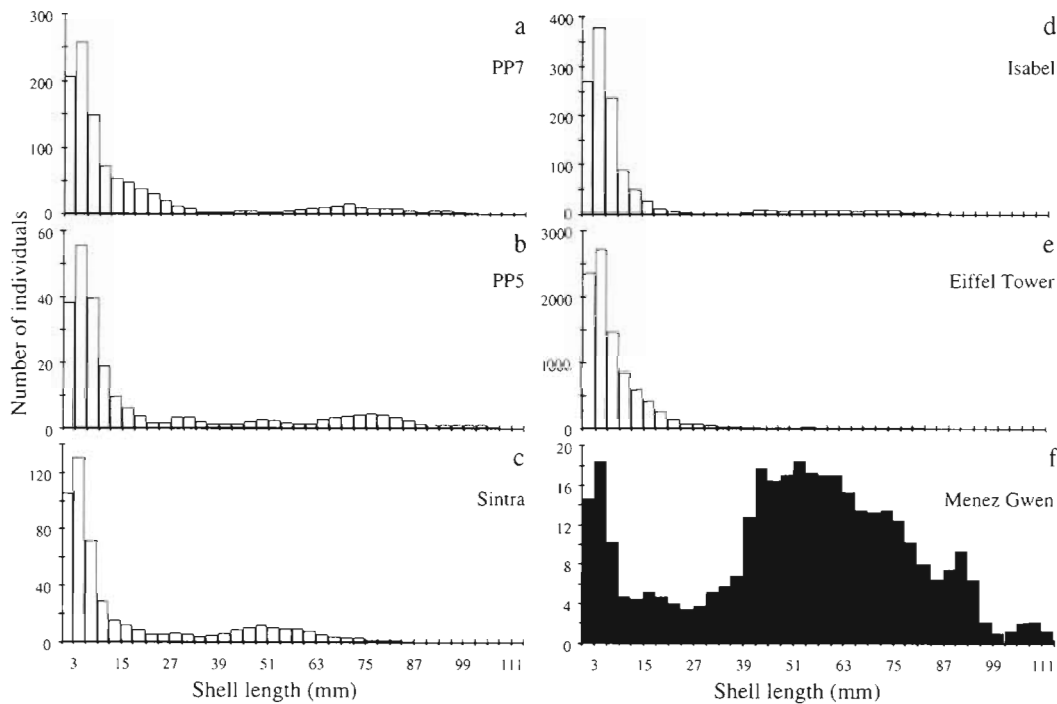
Fig. 4. Shell length frequency histograms of 6 mytilid populations from sampling sites at the Lucky Strike and Menez Gwen hydrothermal vent fields (MAR) obtained by pooling the data from all samples collected from the given site

distribution differed significantly from the 2 others ($p < 0.0001$ for each of the 3 pairwise comparisons). Sample 13 showed a small size range and was exclusively composed of individuals larger than 60 mm (Table 1). Samples 11 and 12 had a greater size range. Sample 11 was dominated by individuals of medium sizes, whereas Sample 12 was dominated by larger individuals.

Fig. 4f shows the length-frequency histogram of the mytilid population at Menez Gwen, after pooling of the 3 samples. The population structure at Menez Gwen differs from that at Lucky Strike, in particular by the dominance of individuals of shell length ranging from 40 to 80 mm. Individuals of small sizes were also present, but in lower proportion. The size distribution at Menez Gwen can be decomposed into 6 or 7 modes (Table 3, Fig. 6), both solutions giving a χ^2 test p-value equal to 1.

Size at settlement

Size at settlement was estimated by measuring the length of the prodissoconch II (i.e. the larval shell). The mean length of the prodissoconch II, obtained from a subsample of 93 postlarval individuals from Lucky Strike collected during Dive 10 at Eiffel Tower, was 527 µm (SD 20 µm, range 472 to 604 µm).
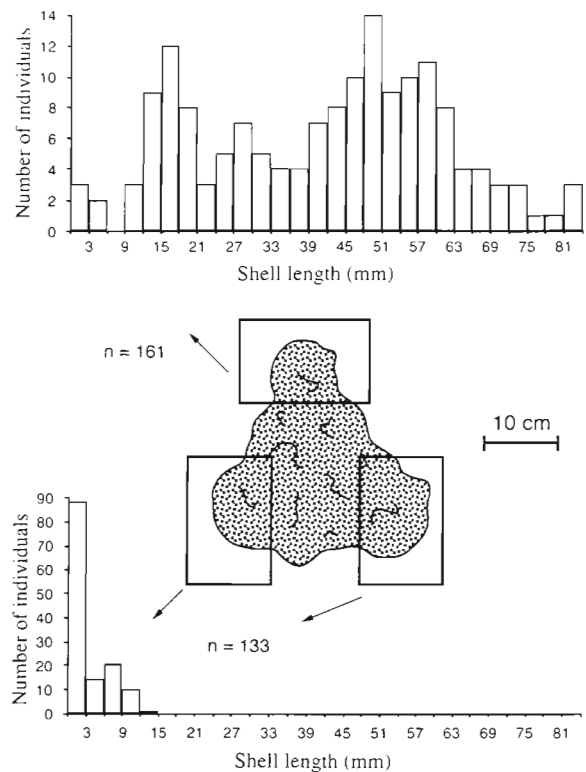

Fig. 5. Shell length frequency histograms for 2 mytilid batches collected on a sulfide block during Dive 2 at Sintra (Lucky Strike hydrothermal vent field). (n = batch size)

Table 2. Modal decomposition of shell length distributions in 5 mytilid bivalve populations from the Lucky Strike hydrothermal vent field, using MIX 2.3. The best solutions (goodness-of-fit χ^2 test) obtained after runs with various numbers of modes are presented. More than 1 solution is proposed for each population except Sintra

| Site	Component						
	1	2	3	4	5	6	7
PP7 a							
$\chi^2 = 7.33$, p = 0.9992, df = 23							
Proportion	0.58	0.28	0.04	0.08	0.02		
Mode (mm)	4.26	15.45	43.38	70.42	90.18		
SD (mm)	2.90	7.17	11.73	8.17	5.82		
PP7 b							
$\chi^2 = 5.20$, p = 0.9998, df = 21							
Proportion	0.59	0.21	0.07	0.03	0.08	0.02	
Mode (mm)	4.18	13.74	24.22	44.38	70.07	90.36	
SD (mm)	2.83	5.05	4.80	8.11	8.43	5.74	
Eiffel Tower a							
$\chi^2 = 9.81$, p = 0.9971, df = 25							
Proportion	0.37	0.23	0.13	0.11	0.12	0.04	
Mode (mm)	4.33	13.88	32.01	57.19	74.72	91.63	
SD (mm)	2.95	6.06	9.15	6.80	8.45	8.45	
Eiffel Tower b							
$\chi^2 = 7.27$, p = 0.9992, df = 23							
Proportion	0.39	0.18	0.08	0.08	0.11	0.11	0.04
Mode (mm)	4.35	13.56	24.13	36.74	57.15	74.77	91.42
SD (mm)	2.96	4.52	4.86	6.39	6.77	8.17	8.45
Isabel a							
$\chi^2 = 3.19$, p = 1.0000, df = 21							
Proportion	0.75	0.14	0.02	0.04	0.05		
Mode (mm)	4.43	11.88	23.67	49.36	72.64		
SD (mm)	2.76	4.13	6.93	8.92	9.18		
Isabel b							
$\chi^2 = 2.51$, p = 1.0000, df = 19							
Proportion	0.71	0.18	0.02	0.03	0.03	0.04	
Mode (mm)	4.34	10.62	24.24	45.07	58.26	74.18	
SD (mm)	2.68	4.69	6.94	6.29	7.19	8.56	
Isabel c							
$\chi^2 = 1.57$, p = 1.0000, df = 17							
Proportion	0.74	0.15	0.01	0.03	0.03	0.03	0.01
Mode (mm)	4.42	11.79	26.92	44.49	58.49	73.61	86.38
SD (mm)	2.76	4.45	5.42	5.36	5.99	5.22	5.14
PP5 a							
$\chi^2 = 3.74$, p = 1.0000, df = 24							
χ^2 test may be invalid with 3 expected frequencies lower than 1							
Proportion	0.60	0.14	0.06	0.04	0.16		
Mode (mm)	4.86	13.03	30.90	49.46	75.61		
SD (mm)	3.04	4.55	5.57	3.97	12.34		
PP5 b							
$\chi^2 = 2.15$, p = 1.0000, df = 22							
Proportion	0.57	0.17	0.06	0.06	0.11	0.03	
Mode (mm)	4.77	12.17	30.30	51.72	74.53	94.43	
SD (mm)	2.96	4.93	5.09	7.94	6.78	7.98	
Sintra							
$\chi^2 = 1.61$, p = 1.0000, df = 17							
Proportion	0.61	0.13	0.05	0.14	0.06		
Mode (mm)	4.12	12.08	27.57	49.81	64.89		
SD (mm)	2.78	4.93	6.00	8.18	10.97		
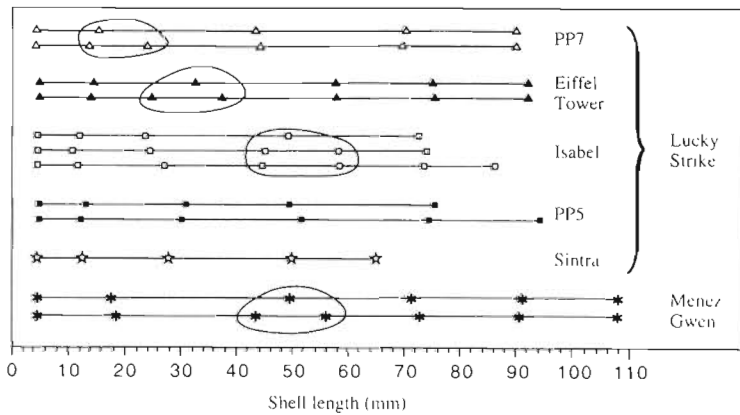
Fig. 6. Summary of the modal decomposition showing the position of each modal value along the shell length axis (see Tables 2 & 3 for detailed results). The main differences observed between alternative solutions obtained for a given site have been circled

DISCUSSION

Intra-site spatial variability of size structure

On the Lucky Strike vent field, 3 sites were sampled more than once during the series of dives. The size-frequency distributions in samples collected from different locations at the same site differ in the relative proportions of size classes, although each sample contains small individuals. This is particularly clear considering the different size structures of the 3 samples collected from 3 distinct locations at Eiffel Tower (Fig. 3g–i). The same phenomenon occurs at Menez Gwen (Fig. 3j–l). These results indicate a spatial segregation of sizes and confirm the preliminary studies of Comtet (1994) and Van Dover et al. (1996) which showed that size distributions of 2 mytilid samples

('Alvin' Dives 2604 and 2605, MAR 93 cruise) collected at Statue of Liberty (Lucky Strike, Fig. 1B) seemed to be complementary. The generalization of this phenomenon to other sites of the Lucky Strike and Menez Gwen vent fields shows the importance of the spatial scale in the definition and study of populations of vent mytilids. Populations need to be defined at the scale of a whole vent site in order to take all the size classes into account. Spatial segregation of the sizes also occurs at a finer scale, e.g. on a single sulfide block a few tens of centimetres in size (Fig. 5).

Both in situ and video observations strengthen these findings. Moreover, video observations and time-series temperature measurements revealed a distribution of the sizes (through an empirical distinction between 'large' and 'small') related to the position of the individuals relative to the fluid sources, the largest individuals living in the warmest areas, with a higher sulfide concentration and lower pH than areas covered by small mytilids (T. Comtet unpubl. data, P. M. Sarradin, J. C. Caprais, R. Riso, A. Aminot, R. Kerouel & A. M. Alayse unpubl.). Considering the broad size range observed in our samples (Table 1), it is more likely that the spatial segregation of sizes reflects the spatio-temporal variability in recruitment rather than spatially different growth rates that could occur with respect to the position of the individuals relative to the vents, as reported by Smith (1985) and Fisher et al. (1988) for Bathymodiolus thermophilus from the Galapagos Rift. The spatio-temporal variability of the recruitment could be explained by the spatio-temporal variability in environmental conditions and intraspecific competition, especially through adult-larval interactions.

Table 3. Modal decomposition of shell length distribution in a mytilid bivalve population from the Menez Gwen hydrothermal vent field, using MIX 2.3. Two solutions are presented

Site	Component						
	1	2	3	4	5	6	7
Menez Gwen a							
$\chi^2 = 3.17$, p = 1.0000, df = 25							
Proportion	0.12	0.08	0.42	0.27	0.09	0.02	
Mode (mm)	4.15	17.49	49.43	71.59	91.00	107.95	
SD (mm)	2.75	7.05	9.99	8.81	4.24	3.48	
Menez Gwen b							
$\chi^2 = 3.32$, p = 1.0000, df = 23							
Proportion	0.12	0.09	0.20	0.24	0.23	0.10	0.02
Mode (mm)	4.16	18.20	43.40	56.07	72.62	90.45	108.17
SD (mm)	2.77	7.56	7.19	7.18	7.28	4.78	3.27

Variability of the hydrothermal activity

The hydrothermal activity is characterized by a great spatial and temporal variability. Despite the difficulty in distinguishing spatial and temporal effects, the spatial variability of the hydrothermal discharge is known to influence the spatial structure and distribution of the megafauna associated with vents. The steep physico-chemical gradients create various micro-environments in which the different species live with respect to their ecological affinities (Desbruyères et al. 1982, Fustec et al. 1987, Fisher et al. 1988, Hessler et al. 1988, Jollivet 1993). At the Lucky Strike sites, the spatial variability, mainly produced by different types of fluid emissions, i.e. low-temperature diffusing fluids, high-temperature fluids expulsed through black smoker chimneys or trapped by flanges, provides micro-habitats that are more or less suitable for the settlement of young mytilids. Spatial heterogeneity of bottom currents and substratum characteristics (e.g. presence or absence of irregularities or crevices) could also play a role since hydrothermal vent mytilids have planktonic larvae (Lutz et al. 1980). In addition, the temporal variability of the hydrothermal discharge (e.g. fluctuations of intensity, displacement of the activity) probably affects settlement at a given location by changing the suitability of the micro-habitats between successive recruitment events. At Menez Gwen, the spatial segregation of the sizes was more accentuated, with Sample 13 containing no small individuals. However, the small size of this sample necessitates some caution in making interpretations. In this case, spatial heterogeneity in the nature of the substratum could play an important role, since the major part of the site is covered by soft substratum made of barite (Y. Fouquet et al. unpubl.) that is less suitable for settlement than hard structures.

Intraspecific interactions

Johnson et al. (1994) showed that dense mytilid clumps laterally disperse the vent fluids, and suggested that this process could interfere with the settlement of other hydrothermal vent organisms. Such a process could also influence the settlement of the offspring of adults in the clumps, by driving settling individuals to the periphery of the bed. At Lucky Strike, one might suppose that such interactions could occur, since mytilids reach high densities (up to 10 000 ind. m^{-2}; A. Colaço pers. comm.).

Lucky Strike mytilids might compete for both space and nutrient resources. Since hydrothermal mytilid larvae live in the plankton, intraspecific competition for food is probably weak between adults and larvae. This process, if it exists, is therefore more likely to occur at the time of settlement and between adults and postlarvae, and could affect the survival of the postlarvae. Mytilids of Lucky Strike and Menez Gwen feed mainly on both methanotrophic and sulfide-oxidizing endosymbiotic intracellular bacteria which are located in their gills (Fiala-Médioni et al. 1996). Therefore, the reduction by adults of the sulfide concentration in the venting fluid as it passes through their aggregations (Johnson et al. 1994) could prevent larvae from settling in adult clumps, or reduce the survival of newly recruited individuals.

Mytilids associated with hydrothermal vents can feed on particulate material (Le Pennec et al. 1990, Page et al. 1991), in which could be included their own larvae. This has been observed in the mytilids from the Logatchev vent field (14° 45' N/MAR), for which juvenile specimens have been found in the stomachs of adults (R. von Cosel et al. unpubl.). Such an intraspecific larviphagy (cannibalism) is known to significantly influence the population dynamics of shallow-water and freshwater filter-feeding bivalves and is considered a regulating mechanism of the population size, providing a negative relationship between recruitment success and adult densities (Timko 1979, André & Rosenberg 1991, Bachelet et al. 1992, André et al. 1993). For the Lucky Strike mytilids, this process, if it exists, does not totally prevent larvae from settling in adult beds, since juveniles have been observed on the shells of living adults (Van Dover et al. 1996) and since very small individuals were obtained in every sample (Fig. 3). This could be related to the fact that reduction of larval settlement at the scale of a single adult may be small or moderate, i.e. larvae can settle in the vicinity of adults by escaping the inhalant current, but may be significant at the scale of a population (Ertman & Jumars 1988, André et al. 1993).

Recruitment pattern of the Lucky Strike and Menez Gwen mytilids

Due to the spatial heterogeneity of the size structure within a single site, study of recruitment pattern was conducted after pooling the samples collected from different locations of the same site. Modal decomposition of the length-frequency histograms of each site (Fig. 4, Tables 2 & 3) shows that each distribution can be considered as a mixture of 5 to 7 Gaussian components assumed to represent successive cohorts. It is necessary to be cautious when using the term cohort, which should be associated with a birth date, since to date no method of age determination exists for hydrothermal vent mytilids. More than one solution is proposed for each distribution, both in terms of number and location of the modes, due to the limits of the method we used.

MacDonald (1987) and Le Guen & Morizur (1989) noted that the choice between the different decompositions obtained through the MIX method (MacDonald & Pitcher 1979) is difficult without prior knowledge about the biology of the species. However, Gage (1995) indicated that this type of method, based on non-linear optimization procedures, offers a more powerful and less subjective approach than the graphical ones (Harding 1949, Cassie 1954, Bhattacharya 1967) when overlapping of modes is low. In our study, we graphically rejected the solutions in which overlapping between successive modes was too great.

Polymodality of size distributions indicates that mytilid recruitment is discontinuous in time, as has been hypothesized for the majority of hydrothermal vent species studied to date (Table 4). Furthermore, the size distributions of the 5 Lucky Strike populations (Fig. 4a–e) show similar structures characterized by a peak of small individuals with a modal value of ca 4.5 mm (range 4.18 to 4.86 mm) and a high proportion (Table 2), above 50 % for PP7, Isabel, PP5 and Sintra, and near 40 % for Eiffel Tower. Such an occurrence of postlarval and juvenile stages at each Lucky Strike site suggests that a massive recruitment event took place just before sampling in June 1994 and that this event was synchronized between sites (inter-site distances range from 200 to 1000 m). The position of the next modes depends on the individual growth rates. The lack of growth data for Lucky Strike mytilids makes any inference on the recruitment synchrony for the modes other than the first one tentative,

and makes the use of statistical methods to test it invalid. Even if successive recruitment events are synchronized, the position of corresponding modes along the length axis could be statistically different due to growth variability between vent sites. Therefore, a statistical difference between mode values will not necessarily imply a lack of synchrony. However, some modal values are consistently encountered in the distributions (Fig. 6, Table 2): modes near 13 mm (range 10.62 to 15.45 mm), 72 mm (range 70.07 to 75.61 mm) and 90 mm (range 86.38 to 94.43 mm) are present in every sample except Sintra. The middle of the distributions is more difficult to decompose, as illustrated by the 3 circled areas represented in Fig. 6 for Lucky Strike. If we consider only the sites sampled several times (PP7, Eiffel Tower and Isabel), 3 other modes seem to be present at ca 25, 45 and 57 mm (Table 2), but not at every site. Recruitment thus may not occur (at least with the same intensity) at all sites of the Lucky Strike vent field even if it is synchronized over the whole field (as is hypothesized in regard to the first mode).

The pronounced positive skewness observed in each distribution might imply either a high mortality in the early post-settlement stages, if we assume that each recruitment event is of the same amplitude, or a high variability in the number of recruits. Mortality could be explained by the intraspecific competition discussed above and predation by fishes, the bythograeid crab *Segonzacia mesatlantica* and the undescribed conid gastropod *Phymorhynchus* sp.

Table 4. List of hydrothermal-vent-associated species for which recruitment pattern has been inferred from size-structure analysis. JdF: Juan de Fuca; Ax: Axial Seamount; EPR: East Pacific Rise (13°N); Gal: Galapagos Rift; LS-MG: Lucky Strike-Menez Gwen

Species	Localization	Recruitment pattern	Source
Vestimentiferan worms			
Ridgeia piscesae	Taylor vent (JdF, Ax)	Possibly continuous?	Siferd (1984), Tunnicliffe (1991)
	Shepherd vent (JdF, Ax)	Discontinuous	Siferd (1984)
Tevnia jerichonana	EPR	Discontinuous	Jollivet (1993)
Oasisia spp.	EPR	Discontinuous	Jollivet (1993)
Riftia pachyptila	EPR	Discontinuous	Jollivet (1993)
Alvinellid polychaete worms			
Paralvinella pandorae pandorae	Explorer (JdF)	Continuous or semi-continuous	McHugh (1989)
Paralvinella palmiformis	Explorer (JdF)	Discontinuous (synchronized oogenesis)	McHugh (1989)
Paralvinella pandorae irlandei	EPR	Discontinuous	Jollivet (1993)
Paralvinella grasslei	EPR	Discontinuous (synchronized)	Jollivet (1993), Zal et al. (1995)
Alvinella pompejana	EPR	Discontinuous	Jollivet (1993)
Alvinella caudata	EPR	Discontinuous	Jollivet (1993)
Serpulid polychaete worms			
Protis hydrothermica	EPR	Discontinuous	Jollivet (1993)
Mytilid bivalves			
Undescribed species	LS-MG	Discontinuous (synchronized)	Comtet (1994), Van Dover et al. (1996), present study

Size distribution of the Menez Gwen population (Fig. 4f) shows a different structure characterized by the dominance of individuals of shell length ranging between 40 and 80 mm. However, modal decomposition reveals that modal values are close to those obtained for the Lucky Strike populations, especially the mode at 4.16 mm (Table 3), indicating a recruitment event just before sampling in June 1994. The small size of the recruitment peak could indicate a small number of recruits produced during the last event. We cannot exclude a sampling bias, since the spatial distribution of the Menez Gwen mytilids is more scarce than at Lucky Strike, thus requiring a more extensive sampling. Despite its small size, the recruitment peak is clearly distinct and suggests that recruitment is synchronized between Menez Gwen and Lucky Strike (60 km apart).

It is noteworthy that newly recruited mytilids were observed at Statue of Liberty (Lucky Strike) in June 1993 (Comtet 1994, Van Dover et al. 1996), i.e. 1 yr before sampling for this study. However, the lack of data from other times of the year does not allow us to draw any conclusion about the potential seasonality of the recruitment.

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