



Biology of the Lucky Strike hydrothermal field

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Abstract—Newly discovered hydrothermal vent communities at Lucky Strike on the Mid-Atlantic Ridge (37°18'N, 32°16'W) are comprised of an invertebrate fauna sufficiently different from known vent faunas of TAG and Snake Pit to consider Lucky Strike part of a new biogeographic province. The dominant component of the fauna is a new species of mussel, and the most unusual feature of the fauna is an echinoid echinoderm, *Echinus* sp. An abundance of small mussels (<5 mm) indicates a recent recruitment event at Lucky Strike, and modal analysis of length–frequency data indicate a discontinuous recruitment process in space and time. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

The Lucky Strike hydrothermal area (Fig. 1) was first discovered during the FAZAR Expedition (C. Langmuir, Chief Scientist; Fall 1992) by the collection of massive sulfides and attached vent animals during a routine rock dredge up the slope of what is now known as the Lucky Strike Seamount in the middle of the rift valley at 37°18'N (FAZAR Cruise Report, 1992). In addition, water column prospecting for hydrothermal plumes using hydrocasts, CTD and manganese sensors detected significant anomalies in the Lucky Strike area (FAZAR Cruise Report, 1992).

An *Alvin* dive series (Langmuir *et al.*, in press) in late spring 1993 located the hydrothermal field and carried out preliminary studies on the geological setting, the geochemistry of the hydrothermal fluids, and the nature of the hydrothermal vent community. Lucky Strike (~1650 m) is the third high-temperature field to be documented on the Mid-Atlantic Ridge. Two previously known sites, TAG at 26°N and Snake Pit at 23°N (both ~3600 m), were discovered in 1985. More recent exploration has led to discovery and preliminary characterization of three additional sites—Broken Spur (3300 m) at 29°N (Murton *et al.*, 1995), the 14°45'N vent site (3100 m; Batuyev *et al.*, 1994; Sudarikov and Galkin, 1995) and Menez Gwen at 37°51'N (~850 m; Fouquet *et al.*, 1994, 1995;

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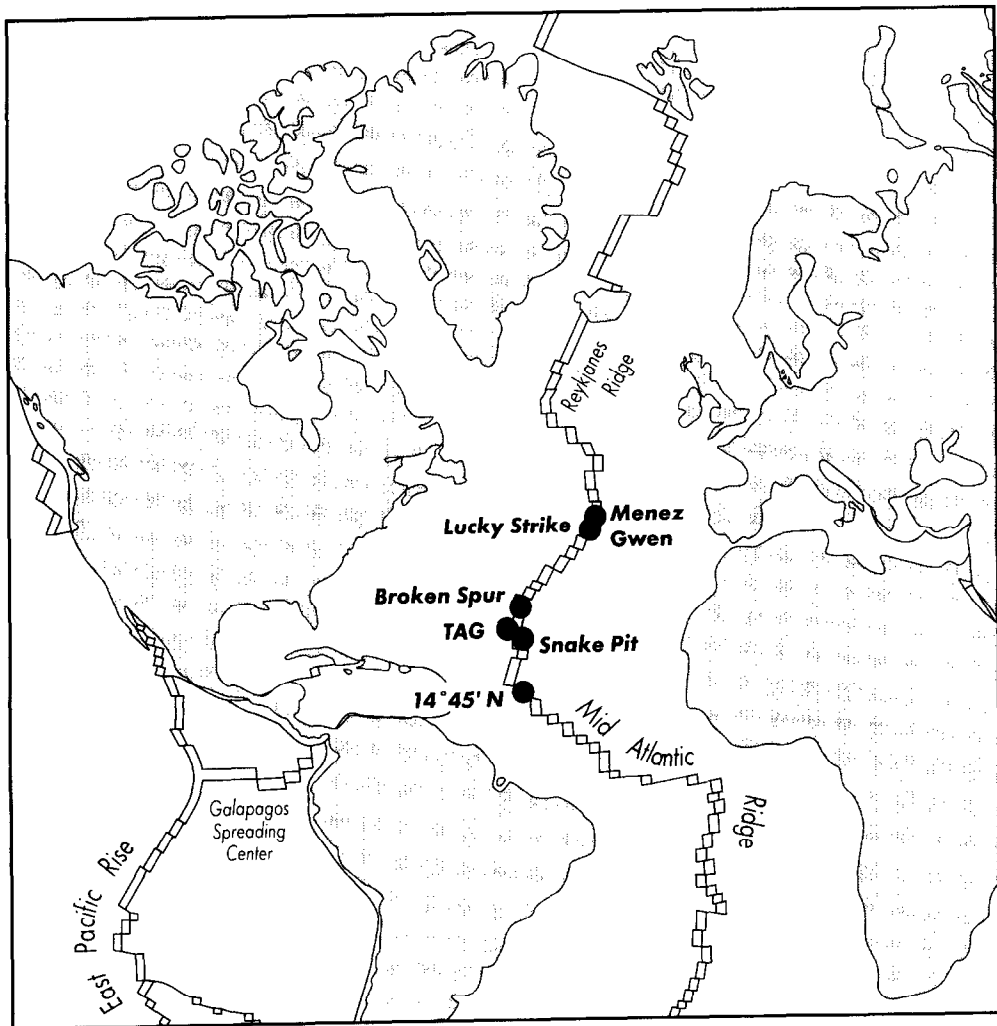


Fig. 1. Location of Lucky Strike on the Mid-Atlantic Ridge. Other deep-sea sites where vent communities have been well-documented are Broken Spur, TAG and Snake Pit. The 14°45'N site is a newly discovered site about which little is known at present.

Desbruyères *et al.*, 1994b). The Rainbow site at 36°N (2200 m) is known so far only from its plume characteristics (German *et al.*, 1996).

Lucky Strike is a relatively shallow (~ 1650 m) hydrothermal field centered at 37°18.5'N, 32°16.5'W, and consists of a series of at least six sulfide structures (Fig. 2) of various morphologies following a N-S line in a depression between three cones that form the summit of the seamount (Langmuir *et al.*, 1993). In addition to sulfide structures, the Lucky Strike hydrothermal area includes extensive aprons of an unusual substrate consisting of variably silicified volcanic and hydrothermal debris that forms plate-like sheets (Humphris *et al.*, 1993). High temperature fluid chemistry is distinctive relative to other Mid-Atlantic Ridge fluids analyzed (Langmuir *et al.*, in press), with low chlorinity ($\sim 20\%$ below seawater

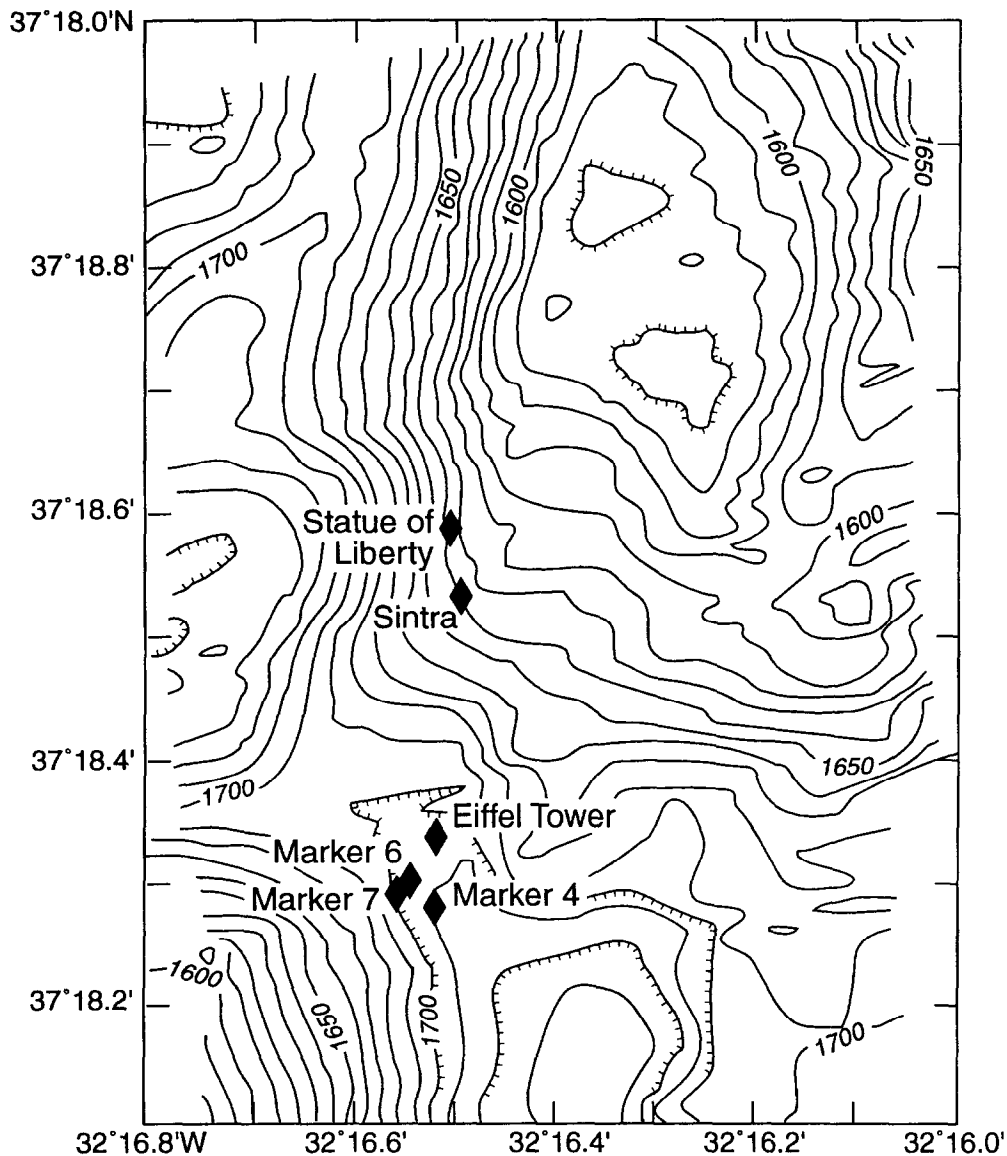


Fig. 2. Locations of six hydrothermally active sulfide structures explored during the 1993 *Alvin* dive series at Lucky Strike. Statue of Liberty, Sintra and Eiffel Tower supported the largest mussel beds.

values), high gas volumes (430–680 ml NTP/kg), CH_4 and N_2 enrichments (up to 0.89 mmol/kg) and low concentrations of sulfide (<3.3 mM). Fluid compositions and morphological and mineralogical attributes of some of the sulfide structures suggest that Lucky Strike may have been recently reactivated (Humphris *et al.*, 1993; Colodner *et al.*, 1993). Details of the geological setting and geochemistry of the vent fluids can be found in Langmuir *et al.*, in press.

A biological survey program was included in the *Alvin* dive series to Lucky Strike that took place in May/June 1993. The objectives of the program were to provide a synoptic characterization of the Lucky Strike fauna and to identify novel features of the biology that might guide subsequent field observations and experiments. The survey included *in situ* observations of animal distributions, sampling of biota, and exploration of multiple vent sites and the surrounding seafloor habitat. A preliminary faunal list has been compiled and is presented here, together with a discussion of how this fauna relates to the Atlantic and global chemosynthetic faunas. The Lucky Strike fauna is dominated by dense mussel beds that cover surfaces of hydrothermally active sulfides and occur in cracks in the seafloor where warm water emanates. At some locations, large numbers of small mussels (< 5 mm in length) were observed attached to larger mussels. Length–frequency distributions within mussel samples collected from three different sulfide structures are examined. A small number of stable isotope analyses were performed as a preliminary assay for unusual trophic processes.

FAUNAL COMPOSITION (WITH ECOLOGICAL NOTES) (TABLE 1)

Cnidaria

Hydrozoa. *Candelabrum phrygium* (Fabricius 1780) was observed on active sulfide mounds, sometimes on mussel shells (Segonzac and Vervoort, 1995).

Anthozoa. The non-vent seafloor environment of Lucky Strike Seamount is covered by large patches of black, manganese encrusted skeletons of a branching coral, *Lophelia* sp. (J. Wilson, pers. comm., 1994). The predominantly dead coral was particularly abundant on pillow ridges at the summit of the seamount. Dead coral was regularly recovered in the 1992 and 1993 rock dredge programs in the area. The cause and timing of the mortality are unknown.

Mollusca

Mytilidae. Allozyme analysis indicates that the Lucky Strike mussel is a species distinct from that found at Snake Pit (Craddock *et al.*, 1995) but its alliance to the Broken Spur mussel remains to be determined. Variations observed in mussel morphology suggest that at least one additional bathymodiolid mussel may occur at Lucky Strike.

Mussels on Lucky Strike sulfide structures occur in densities that make them visually reminiscent of a mussel-dominated shallow-water intertidal zone (Fig. 3). Mussels also colonize leaky cracks in sheets of the apron of silicified volcanic and hydrothermal debris, but the proportion of mussels in cracks is small, estimated at less than 5% of the total mussel population at the Eiffel Tower and Statue of Liberty sites. Mussels were less abundant at the southern sites (markers 4, 6 and 7) than at northern sites.

Point measurements of temperature within mussel beds on the upper surface of a flange ranged from close to ambient (4.7°C) to a maximum of 13.7°C. Pooled water beneath the flanges reached as high as 190°C and the maximum smoker temperature was 333°C.

Limpets and other gastropods

Washings from mussel collections included a number of small gastropods which were sent to Anders Warén (Swedish Museum of Natural History) for preliminary identification. Of

Table 1. Invertebrate and fish taxa from the Lucky Strike hydrothermal area

Taxon	Previous records
Phylum Cnidaria	
Class Hydrozoa	
<i>Candelabrum phrygium</i>	Non-vent deep sea
Class Anthozoa	
<i>Lophelia</i> sp. (not observed at vents)	Non-vent deep sea
Phylum Annelida	
Class Polychaeta	
Order Phyllodocida	
Family Polynoidae	
<i>Branchipolynoe seepensis</i>	Snake Pit, Gulf of Mexico Seeps
unidentified	?
Order Orbiniida	
Family Glyceridae	
unidentified	?
Order Terebellida	
Family Ampharetidae	
unidentified	?
Phylum Mollusca	
Class Gastropoda	
Neritacea	
Family indeterminate	?
Skeneidae	
<i>Protolira valvatoides</i>	Snake Pit
<i>Protolira</i> sp.	?
? <i>Leptogyra</i>	?
Rissoidae	
new species	New
Lepetodrilidae	
<i>Lepetodrilus</i> sp.	?
Peltospiridae	
<i>Peltospira</i> sp.	?
Turridae	
<i>Phymorhynchus</i> sp.	Snake Pit?
Class Bivalvia	
Order Filibranchia	
Family Mytilidae	
Bathymodiolid new species	New
Phylum Arthropoda	
Class Arachnida	
Order Acarina	
<i>Halacarellus alvinus</i> (probably not restricted to vent site)	New
<i>Copidognathus alvinus</i> (probably not restricted to vent site)	New
Subphylum Crustacea	
Subclass Malacostraca	
Order Amphipoda	
Family Eusiridae	
<i>Luckia striki</i>	New
<i>Bouvierella curtirama</i>	New
Family Amphilochidae	
<i>Gitanopsis alvina</i>	New

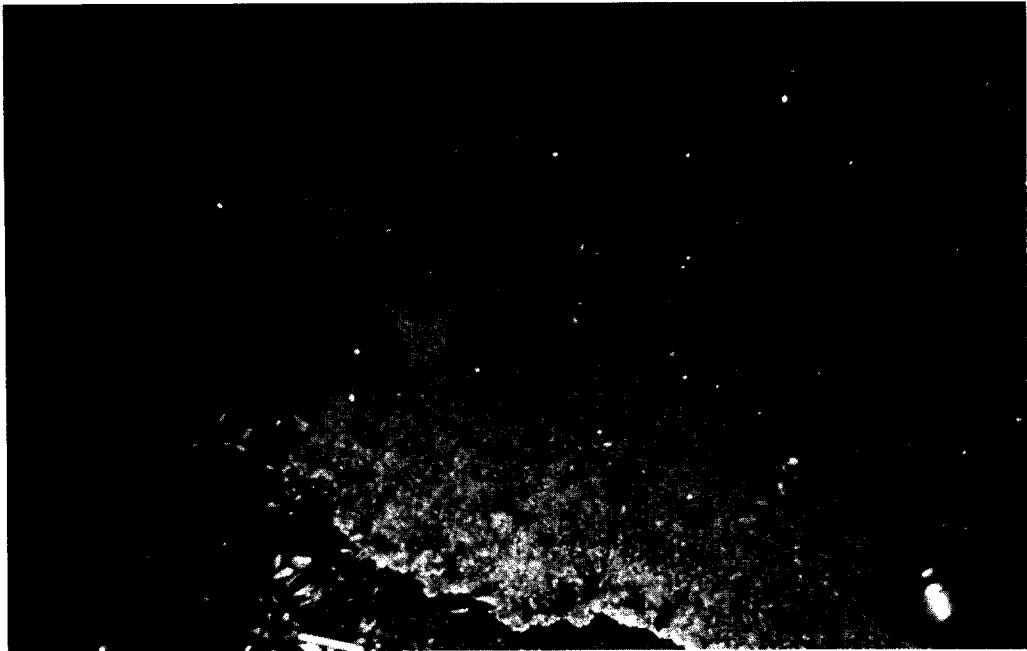
Table 1. (Continued.)

Order Decapoda	
Infraorder Caridea	
Family Bresiliidae	
<i>Chorocaris fortunata</i>	New
<i>Chorocaris chacei</i>	Snake Pit, TAG, Broken Spur (?)
<i>Rimicaris</i> sp. (? <i>exoculata</i>)	? Snake Pit, TAG, Broken Spur
Infraorder Brachyura	
Family Bythograeidae	
<i>Segonzacia mesatlantica</i>	Snake Pit, TAG, Broken Spur
Phylum Echinodermata	
Class Echinoidea	
Family Echinidae	
<i>Echinus</i> sp.	New(?)
Phylum Chordata	
Subphylum Vertebrata	
Class Pisces	
Family Morididae	
unidentified	Non-vent deep sea
Family Chimaeridae	
<i>Hydrolagus pallidus</i>	Non-vent deep sea
Family Bythitidae	
<i>Cataetyx laticeps</i>	Non-vent deep sea

at least seven gastropod species collected from Lucky Strike, only one species has so far been identified as a previously described taxon, the skeneid *Protolira valvatoidea*, known from the Snake Pit site (Warén and Bouchet, 1993). A few specimens of a second *Protolira* species, one specimen of an undetermined genus of skeneid gastropod, and one specimen tentatively assigned to the genus *Leptogyra* in the Skeneidae were also collected. *Protolira valvatoidea* and an unidentified neritacean limpet (~5–7 mm length) were the most abundant gastropod species in the Lucky Strike samples. Two gastropod families not previously known from hydrothermal vents are represented in the Lucky Strike material, including the neritacean limpet (family indeterminate) referred to above, and at least 20 specimens of an undescribed species in the family Rissoiidae. Two additional limpet families (Lepetodrilidae and Peltospiridae) are represented at Lucky Strike (*Lepetodrilus* sp. and *Peltospira* sp.). *Peltospira* sp. was fairly abundant in the Lucky Strike material collected. Most of the limpets shells were fouled by small (0.75 mm) irregularly ovoid/pill-box-shaped egg capsules, some filled with five to 20 shelled embryos. One specimen of a turrid gastropod, *Phymorhynchus* sp., was collected at Lucky Strike. Representatives of this genus are known from several vent sites, including TAG on the Mid-Atlantic Ridge (*Phymorhynchus moskalevi*, Sysoev and Kantor, 1995).

Polychaeta

Polynoidae Nearly 95% of the mussels examined contained the blood-red commensal polynoid polychaete *Branchipolynoe seepensis*, making this polychaete an “invisible” but dominant component of the Lucky Strike fauna. A free-living, white to cream-



(a)

(b)



Fig. 3. (a) Mussel-covered sulfide flanges at the Statue of Liberty site. Note two urchins perched at the top of an inactive chimney. (b) New mussel recruits on a larger mussel cohort.

colored polynoid polychaete was observed crawling over surfaces of mussels but was not collected.

Other Polychaeta

A small ampharetid polychaete occurs frequently on the hinge line of the mussels, on sulfides and on plate-like substrate of silicified hydrothermal and volcanic debris. This polychaete appears to be a new species (D. Desbruyères, personal observation) related to the tribe Samythinini but distinct from the genus *Amphisamytha* which occurs at hydrothermal vents (Zottoli, 1983). A single glycerid polychaete of uncertain taxonomic affinity was recovered from among a clump of mussels. Sorting of the bulk mussel material collected during the dive series is still underway and is likely to contribute additional polychaete and other small invertebrate taxa to the Lucky Strike species list.

Arthropoda

Arachnida

Halacarina. Two new species of halacarid mites—*Halacarellus alvinus* and *Copidognathus alvinus*—were sorted from megafaunal washings and have been described by Bartsch (1994). According to Bartsch, *H. alvinus* closely resembles *H. caecoides*, a species found below 2600 m in the Norwegian basin. Neither of the mite species is thought to be restricted to hydrothermal vents.

Crustacea

Bresiliidae. A new species of bresiliid shrimp, *Chorocaris fortunata* (Martin and Christiansen, 1995) is found at Lucky Strike in moderate numbers among mussels and in areas of shimmering water otherwise barren of macroinvertebrates. The shrimp reach maximum densities of about 5 per 10 cm² in localized patches. The maximum temperature in which they could be found was not documented. Like other members of the genus *Chorocaris*, this shrimp has a modified, reflective photoreceptive organ that extends back into the cephalothorax, beneath the transparent carapace. Compared to other bresiliid shrimp species of Atlantic and Pacific hydrothermal vents, this new species is small (~10 mm carapace length, gravid females). At the time of sampling, the population included a large number of egg-bearing females. A second, larger species of bresiliid shrimp, *Chorocaris chacei*, known from TAG and Snake Pit (Williams and Rona, 1986) is reported from this site (J. Martin, personal communication, 1994), as is *Rimicaris* sp. (Desbruyères *et al.*, 1994b).

Bythograeidae. Crabs were observed only rarely among mussel beds at Lucky Strike. One specimen was collected and has been identified as *Segonzacia mesatlantica* (Guinot, pers. comm. via D. Desbruyères), a species known elsewhere on the Mid-Atlantic Ridge (TAG, Snake Pit, Broken Spur). On a subsequent dive series to Lucky Strike, bythograeid crabs were observed to be abundant within mussel clumps and on sulfides (Desbruyères *et al.*, 1994b).

Amphipoda. Small white amphipods were fairly abundant in some samples from Lucky Strike sites. On videotapes, amphipods can be seen both on mussel beds and moving about

over patches of sulfides barren of mussels and are considered to be benthic in habit. The amphipods belong to two families and include one new genus (*Luckia*) and three new species (*Luckia striki*, *Bouvierella curtirama*—fam. Eusiridae; *Gitanopsis alvina*—fam. Amphilochidae) (Bellan-Santini and Thurston, 1995).

Echinodermata

Echinoidea. The most unusual element of the Lucky Strike faunal community is tentatively identified as a new species of sea urchin in the genus *Echinus* (Sibuet, personal communication, 1994). The urchin is white to light-pink in color, with long spines and a total diameter (test plus spines) of 12 cm. It was observed in low densities (1–15 per site) at the edge of the mussel beds but not in the surrounding non-vent environment. Urchins were only very rarely observed at Lucky Strike vents during the 1994 *Nautilé* dive series (Desbruyères *et al.*, 1994b). No other echinoderms were observed at Lucky Strike. Sea urchins occurred at water temperatures of just a few 10ths of a degree warmer than ambient.

Other invertebrates

Other invertebrate taxa sorted from Lucky Strike hydrothermal material include nematodes, nemerteans, tanaids and asellote isopods.

Fish

Saldanha (1994) reports on the fish biota observed at Lucky Strike. Chimaerids were the most abundant fishes. *Hydrolagus pallidus* was observed numerous times hovering near vents, in cold water. Several individuals of the bythitid fish, *Cataetix laticeps* were also observed. One bythitid specimen was collected from among mussels beneath a sulfide flange, in warm water (5.7–13°C). Gut contents of this fish indicate it had fed on bresiliid shrimp and mollusks (Saldanha, 1994). Morid fish were also noted at the vents, but their specific identification from video images is difficult. Several sharks, possibly *Deania calceus*, were noted near the sulfide structures. A characteristic hydrothermal vent fish fauna was not observed.

MUSSEL POPULATION STRUCTURE

Sulfide samples covered with mussels were collected from Statue of Liberty (dive 2604, $n = 186$; dive 2605, $n = 1156$) (collected on two different dives), Sintra (dive 2606, $n = 263$) and Eiffel Tower (dive 2608, $n = 52$) (Table 2). This sampling method is relatively unbiased with respect to mussel size on a particular surface of hydrothermally active sulfide, given the attachment of mussels to surfaces by byssus threads and the observation of coherence of the mussel clump during sampling. Bias is introduced in choosing which particular piece of sulfide and mussel clump is to be sampled. Mussel length (the greatest antero-posterior dimension) was measured with calipers to the nearest 0.1 mm. Smallest individuals were measured with a dissecting microscope to the nearest 0.01 mm.

Length–frequency histograms were generated with the size-class interval chosen according to two criteria: (i) no fewer than 30 individuals must make up the main classes

Table 2. Location of mussel samples collected in the Lucky Strike hydrothermal area

Vent site	Latitude	Longitude	Depth (m)	Dive	Sample size
Statue of Liberty	37°17.590'N	32°16.497'W	1635	2604	186
Statue of Liberty	37°17.588'N	32°16.499'W	1635	2605	1156
Sintra	37°17.538'N	32°16.490'W	1625	2606	263
Eiffel Tower	37°17.338'N	32°16.508'W	1694	2608	52

and (ii) the number of adjacent empty classes must be minimized (Bhattacharya, 1967). The same size-class interval was used for all four samples to permit comparison of the length–frequency distributions by means of a χ^2 -test (Sokal and Rohlf, 1980).

For modal analysis, a different size-class interval was used for each sample to optimize modal decomposition. We assumed that each modal component has a normal distribution. We used a combination of Bhattacharya (1967) and an iterative method using the MIX program (MacDonald and Pitcher, 1979). The latter method provides the best mathematical fit between a theoretical mixture of normal distributions and the observed one, by the maximum likelihood criteria.

Comparison of frequency distributions (Fig. 4) using χ^2 (Table 3) demonstrates that the length–frequency distributions of each sample are significantly different. Sample 2608 from Eiffel Tower was not included in this comparison because of its small n . However, this sample was dominated by the larger size classes (Fig. 4) and thus seems to be very different from the others.

Results of the modal decomposition are shown in Fig. 5, with parameters estimated by MIX for each mode provided in Table 4. All samples showed a plurimodal length–frequency distribution. The number of modes (3–6) and their characteristics are different from one sample to another. Sample 2604 from Statue of Liberty is dominated by small individuals (< 5 mm) from the last recruitment. Samples 2605 (Statue of Liberty) and 2606 (Sintra) are dominated by mussels of medium size (between 10 and 30 mm). Sample 2608 (Eiffel Tower) consists of essentially large mussels (> 50 mm), a size class not represented in the other samples.

STABLE ISOTOPE COMPOSITIONS

A small number of invertebrate samples were analyzed for stable isotope compositions as a preliminary screen for any unusual trophic conditions at Lucky Strike. Sample preservation and analysis followed methods described in Van Dover and Fry (1994), Minagawa *et al.* (1984) and Yanagisawa and Sakai (1983). Results are summarized in Table 5 and are discussed below.

DISCUSSION

A total of 25 invertebrate taxa are listed from the Lucky Strike hydrothermal area (Table 1). Four of these species (*Branchiopolynoe seepensis*, *Protolira valvatooides*, *Chorocaris chacei* and *Segonzacia mesatlantica*) are shared with other hydrothermal systems on the Mid-Atlantic Ridge. Two additional taxa (*Phymorhynchus* sp. and *Rimicaris* sp.) may also be

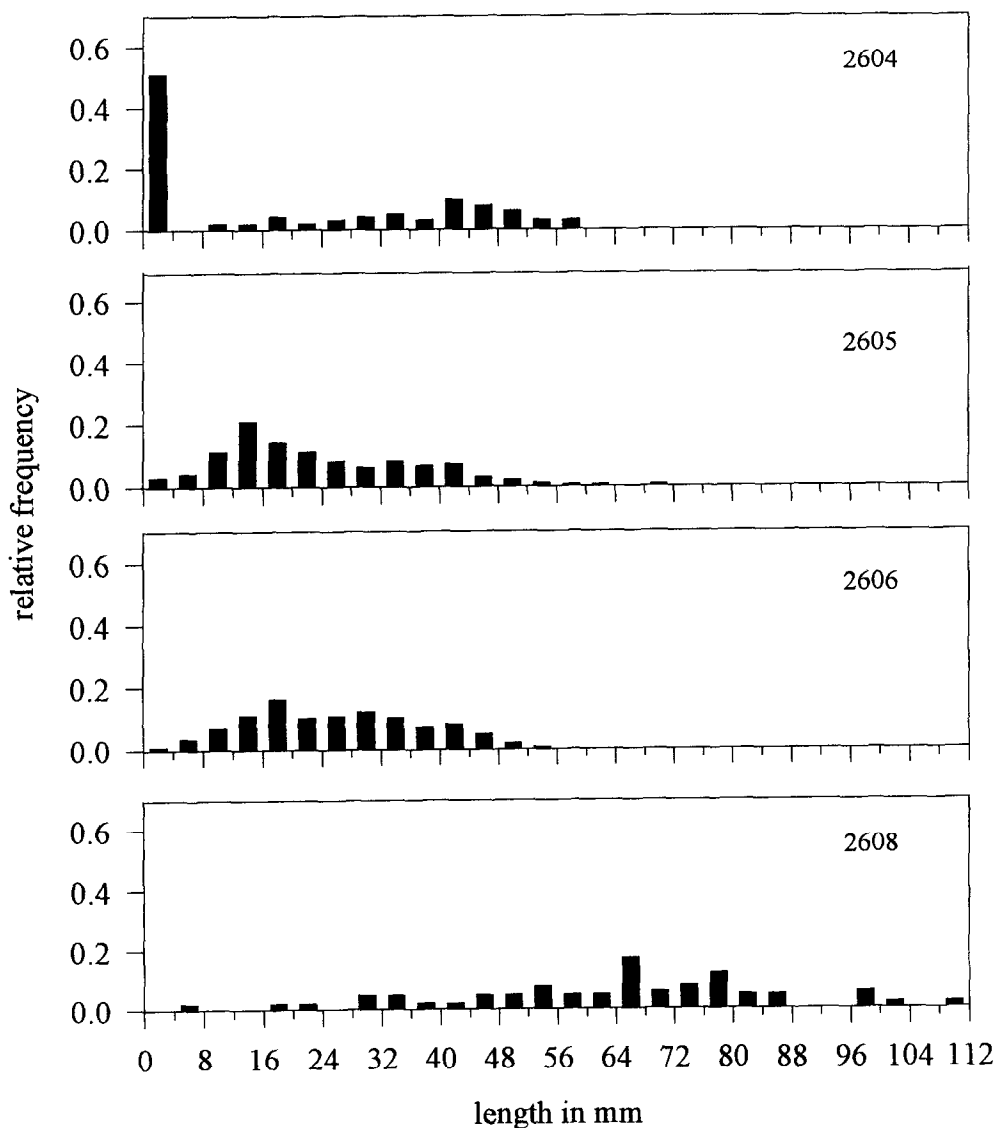


Fig. 4. Length-frequency histograms of four samples of mussels collected at three different sites of the Lucky Strike area. Class interval is 4 mm.

Table 3. χ^2 comparison of length-frequency distributions of mussels from Lucky Strike

Sample	χ^2_{obs}	df	p	Decision
2604, 2605, 2606	630.13	26	<0.005	Rejected
2605, 2606	41.55	13	<0.005	Rejected

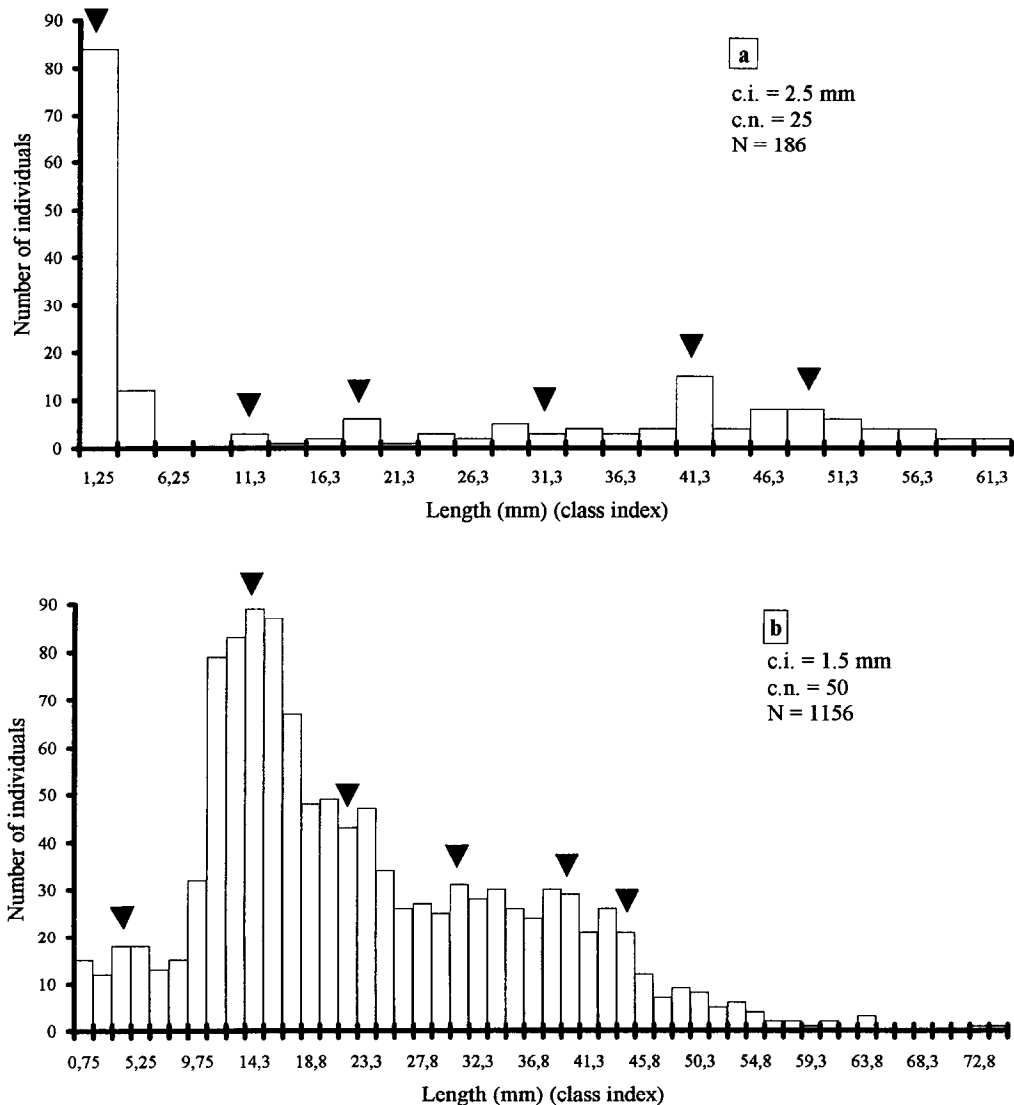


Fig. 5. Length–frequency histograms of four samples of mussels collected at three different sites of the Lucky Strike area: (a) Sample 2604; (b) Sample 2605; (c) Sample 2606; (d) Sample 2608. Arrows indicate position of each mode as determined by the MIX program; c.i.: class interval; c.n.: class number; N : sample size.

known from other vent sites, but specific identifications remain to be determined. Seven taxa are identified as previously undescribed new species closely associated with hydrothermal activity. These seven new species include taxa that are conspicuous components of the Lucky Strike community (e.g. the bathymodiolid mussel and a bresiliid shrimp). Nine taxa belong to genera known from other vents, but species determinations have not yet been made. Absent from Lucky Strike are several taxa typical of eastern Pacific vents or western

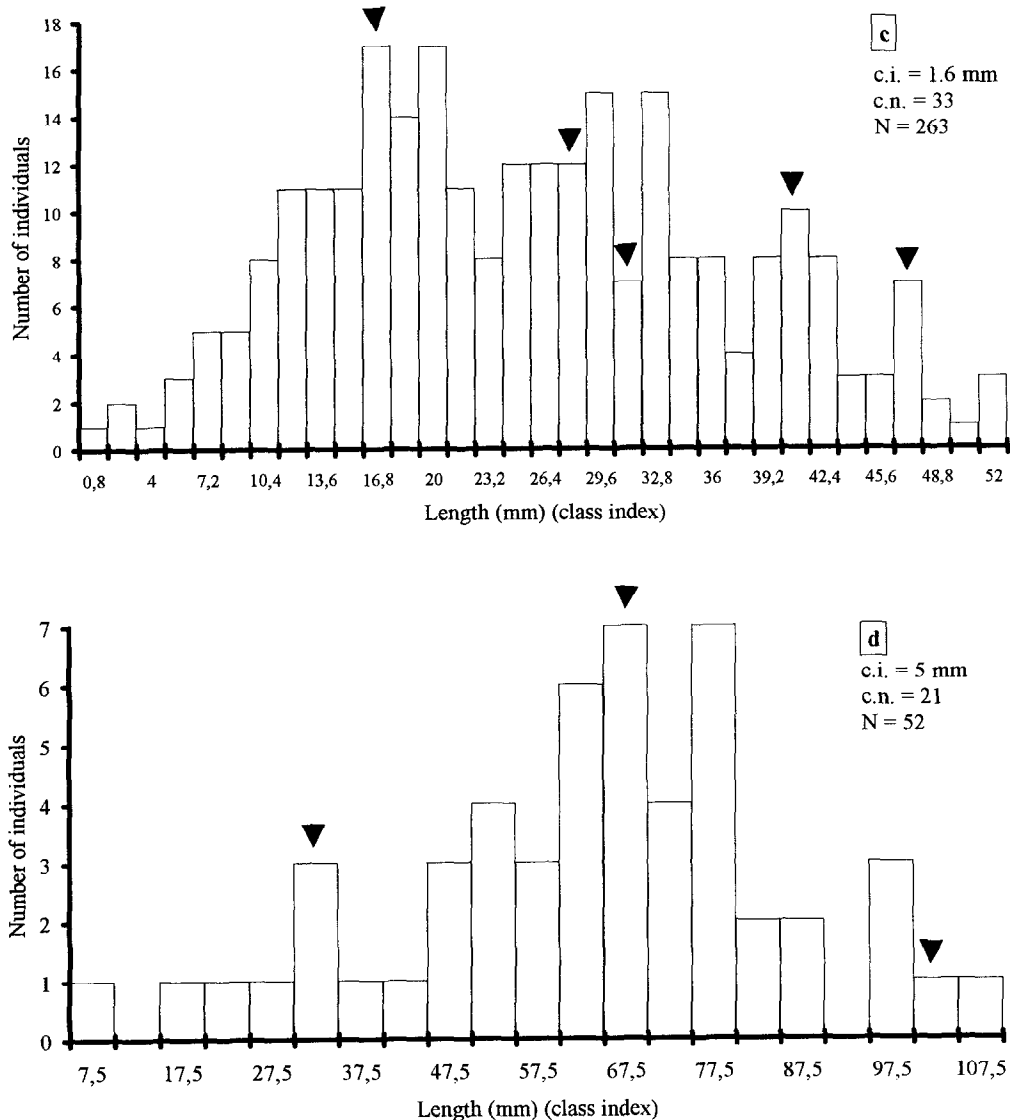


Fig. 5. (Continued.)

Pacific back-arc hydrothermal systems (tubeworms, vesicomid clams, alvinellid and serpulid polychaetes, alviniconchid gastropods).

At the species level, Lucky Strike may prove to have a fairly novel gastropod fauna relative to Snake Pit, with only one species definitely shared (*Protolira valvatoides*, fam. Skeneidae) and one species possibly shared (*Phymorhynchus* sp., fam. Turridae). Compared to the published Snake Pit gastropod fauna (Segonzac, 1992), the gastropod fauna differs at the familial level in the presence of Lepetodrilidae, Peltospiridae, Neritidae, and Rissoidae and in the absence of Clypoelectidae and Scissurellidae at Lucky Strike.

Table 4. Modal decomposition of length–frequency histograms of Lucky Strike mussel populations using the MIX program. Mode (mm), standard deviation (s.d.; mm), proportion and size of each component are given for each sample. The mean (μ ; mm) and standard deviation σ (mm) of lengths in each sample are also given

Component	1	2	3	4	5	6
Sample 2604 $\mu = 19.7 \sigma = 20.6$						
Mode	1.5	12.1	18.2	31.7	41.3	49.4
s.d.	0.8	0.6	0.9	6.7	0.5	6.5
Proportion	0.52	0.02	0.04	0.14	0.06	0.23
Size	97	4	7	26	11	43
Sample 2605 $\mu = 22.9 \sigma = 12.7$						
Mode	3.8	13.8	21.8	31.3	39.9	43.8
s.d.	2.5	2.8	3.4	3.2	3.8	9.7
Proportion	0.07	0.39	0.22	0.11	0.12	0.10
Size	81	451	254	127	139	116
Sample 2606 $\mu = 25.6 \sigma = 11.5$						
Mode	17.2	28.1	31.4	40.9	47.5	
s.d.	6.5	7.2	4.0	1.5	3.1	
Proportion	0.54	0.06	0.24	0.09	0.07	
Size	142	16	63	24	18	
Sample 2608 $\mu = 63.4 \sigma = 21.7$						
Mode	34.4	68.2	100.7			
s.d.	15.7	11.2	4.1			
Proportion	0.22	0.69	0.09			
Size	11	36	24			

One of the most interesting biogeographic distributions of polychaetes occurring at Lucky Strike is that of the commensal polynoid polychaete, *Branchipolynoe seepensis*. This species was first described from a mussel species found at seep sites of the Florida Escarpment, Gulf of Mexico (Pettibone, 1986) and has since been recorded as a commensal in the Snake Pit mussel (Segonzac, 1992). Lack of host specificity in this commensal polychaete species, its occurrence at both seep and vent chemosynthetic habitats and its

Table 5. Stable isotope data (‰) for dominant invertebrates at Lucky Strike [$\bar{x} \pm \text{s.d. (n)}$]

Species	Tissue	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
<i>Chorocaris chacei</i>	Abdomen	−17.9	+1.4	—
<i>Chorocaris</i> n. sp.	Abdomen	−16.2	+3.0	—
<i>Bathymodiolus</i> n. sp.	Muscle	−24.1 ± 1.1 (3)	−6.9 ± 0.2 (3)	3.7 ± 0.5 (3)
Limpet	Entire soft tissue	−14.5 ± 1.5 (3)	+4.1 ± 0.6 (3)	—

broad geographic distribution give it an enigmatic biogeographic significance and point to the need for more detailed genetic characterization of its populations.

Lucky Strike crustaceans include a mixture of shared and novel species. The most abundant bresiliid shrimp species, *Chorocaris fortunata*, is not known from TAG or Snake Pit where bresiliid shrimp are especially abundant. *Chorocaris chacei* occurs at all four of the known Mid-Atlantic Ridge vent fields, as does the genus *Rimicaris* (and possibly the species *R. exoculata*). The copepod *Stygiopontius pectinatus* that lives in the branchial chamber of *Chorocaris vandoverae* (Mariana vents, western Pacific) and *Rimicaris exoculata* (TAG, Snake Pit), was not observed in *Chorocaris fortunata*. The amphipod fauna associated with Lucky Strike mussels is totally novel at the species level and includes a new genus.

We consider the Lucky Strike fauna sufficiently unique to be a fifth biogeographic hydrothermal province, together with eastern Pacific (East Pacific Rise and Galapagos Spreading Center), northeastern Pacific (Gorda, Juan de Fuca, Explorer Ridges), western Pacific (Back-Arc) and Mid-Atlantic Ridge (TAG and Snake Pit). This differentiation raises the issue of isolating mechanisms. One possibility is that some hydrothermal species may be relatively stenobathic. The more than 1300 m depth differential between Lucky Strike (~1700 m) and the other known Mid-Atlantic Ridge sites (> 3000 m) may preclude the occurrence of certain species at one site or another. Support for or against this hypothesis might develop from future discovery and characterization of hydrothermal sites along depth gradients north and south of Lucky Strike. Additional evidence could be derived from measurement of physiological barotolerances of individual species. Other isolating barriers or filters are plausible, such as the Oceanographer Transform Fault (120 km offset and 4 km relief) which separates Lucky Strike from Broken Spur to the south. Careful taxonomic assessment of alliances between Lucky Strike and Broken Spur faunas should prove valuable in evaluating the potential isolating role of this transform offset. Exploration of hydrothermal systems at intermediate depths on the Famous and Amar segments (between Broken Spur and Lucky Strike) may reveal a continuum in faunal composition and population interactions and comprise part of a gradual transition from Snake-Pit and TAG faunas to the fauna found at Lucky Strike rather than strict isolation due to a putative geographic barrier. A difficult biological/chemical interaction to assess is the influence of the somewhat unusual chemistry of Lucky Strike high temperature fluids—especially the low sulfide/high methane concentrations reported (Colodner *et al.*, 1993)—on the faunal composition. Phase separation may have significant implications for vent ecology. Phase-separated fluids may be depleted in metals and sulfide, making them less toxic to non-vent deep-sea fauna and permitting them to penetrate further into a vent field than usual. By monitoring changes in the chemistry of low-temperature fluids and the biota over time, correlations between chemistry and biota, if they exist, might be discerned. The a priori expectation is that the chemistry is not sufficiently anomalous to account for the particular community structure observed during the 1993 dive series.

The Lucky Strike hydrothermal community is interesting as much because of faunal types that are absent as by the fauna that is present. In particular, there is no well-developed peripheral fauna as is found at other deep-water Mid-Atlantic Ridge vent sites. There are no anemone beds nor chaetopterid polychaetes as at TAG and Snake-Pit, and large gastropods (*Phymorhynchus* sp.) and galatheid crabs (*Munidopsis* sp.) are rare. The boundary of the Lucky Strike vent community is abrupt and coincides with the outer

limit of distribution of the mussel. Even the urchin, which occupies the least hydrothermally-influenced waters, appears to be more closely associated with the edge of the mussel beds than with a surrounding peripheral environment. The only biological clue of proximity to an active hydrothermal area is scattered shell chaff from mussel beds upslope.

Another important aspect of the Lucky Strike fauna, one which holds for other deep-water hydrothermal vents on the Mid-Atlantic Ridge, is the monotony of species dominance at all sites within a vent field. At Lucky Strike, mussels are ubiquitously dominant at each of six sulfide structures explored; at Snake Pit, the shrimp *Rimicaris exoculata* dominates the active mounds found there. In contrast, on the East Pacific Rise, one vent site may be dominated by tubeworms, an adjacent one by mussels, and yet another by clams. We have yet to understand how much of the contrast in regional diversity between East Pacific Rise and Mid-Atlantic Ridge vents is controlled by cycles of hydrothermal activity and the dynamics of community development.

The Lucky Strike hydrothermal community, dominated exclusively by dense beds of mussels, is visually distinct from most other known vent communities. Distribution of mussels on vertical surfaces of sulfide chimneys and upper surfaces of sulfide flanges has been observed at vents in the North Fiji Basin (Desbruyères *et al.*, 1994a), but dominance of sulfide habitats is not typical for mussel populations at vents on the East Pacific Rise and elsewhere on the Mid-Atlantic Ridge. In these areas, mussels in general are restricted to diffuse flows emanating from cracks in basalt (e.g. 9°N, East Pacific Rise) or lower regions of sulfide mounds (Broken Spur and Snake Pit, Mid-Atlantic Ridge).

Data on mussel size–frequency distributions show that these distributions are plurimodal, indicating a discontinuous recruitment in space and time and implicating a synchronizing factor. Rhoads *et al.* (1982) and Hessler *et al.* (1988) report size–frequency data (class interval = 1 cm) for Rose Garden (Galapagos Spreading Center) hydrothermal mussels (*Bathymodiolus thermophilus*). No modal decomposition was performed, but the distributions appear to be unimodal or bimodal.

Mussel size–frequency histograms differ from theoretical representations of size–frequency data, which usually show a logarithmic decrease due to mortality in higher size classes. This difference could be explained by the variability of both recruitment and mortality due to the temporal variability of the hydrothermal biotope. In samples collected from dives 2605, 2606 and 2608, the histograms are dominated by intermediate sizes. Lack of new recruits in these samples may be due to sampling bias related to the nature of submersible manipulations. However, using the same collection method, the sample from dive 2604 is dominated by very small individuals arising from the most recent recruitment event. This suggests a spatio-temporal variability in recruitment within the vent field. At the Statue of Liberty site, the length–frequency distributions of two samples (dives 2604 and 2605) seem to be complementary: sample 2604 is dominated by small individuals whereas sample 2605 is dominated by the intermediate sizes. Such a spatial segregation of “cohorts” was actually observed *in situ* at the Eiffel Tower site. Intraspecific competition for substrate and food resources, or competition by larviphagy, might account for this segregation (Berthou and Glémarec, 1988; Diop and Glémarec, 1990). These hypotheses seem likely given the high mussel densities observed (up to 600 ind/m², estimated biomass = 3.5 kg/m²). MacDonald *et al.* (1990) report similar spatial variability in the recruitment of Louisiana cold-seep mytilids, but explained it by the spatial variability of the biotope.

The size–frequency data obtained raise the issue of the definition of a population in a hydrothermal context: the possible spatial segregation of cohorts on a site makes it necessary to consider the mussel population of the entire system in order to take all of the age classes into account. The plurimodal nature of the Lucky Strike mussel population may prove useful in studies of population genetics within a vent site through cohort-by-cohort comparisons.

Carbon stable isotope values for the Lucky Strike mussel ($\delta^{13}\text{C} = -24.1\text{‰}$; Table 5) are anomalous relative to values reported for all other hydrothermal vent mytilids (average value $\sim -35\text{‰}$; Fisher, 1990), including mussels from Snake Pit ($\delta^{13}\text{C} = -32.7$ to -35.6‰ ; Cavanaugh *et al.*, 1992). Preliminary microscopy of the endosymbionts in mussel gill tissues indicates that, as in the mussel from Snake Pit (Cavanaugh *et al.*, 1992), the Lucky Strike mussel hosts both sulfide-oxidizing and methylotrophic bacteria (Fiala-Médioni, unpublished data). The Lucky Strike mussel carbon isotope value is difficult to interpret and may reflect some mixture of organic material synthesized by the dual nutritional pathways of its endosymbionts and intake of suspended particulates. Knowledge of the carbon isotope composition of source methane would be useful in evaluating the organic carbon isotope composition of the mussel, but such data are not available. The sulfur isotope composition of non-gill tissue in the Lucky Strike mussel ($\delta^{34}\text{S} = +3.7\text{‰}$; Table 2) is similar to that of other invertebrates that derive their organic sulfur from hydrothermal sulfides rather than seawater sulfate (e.g. Fry *et al.*, 1983) and indicates that sulfide oxidation is important in the biochemistry of this bivalve. As in all other host–endosymbiont relationships at vents, the nitrogen isotope composition of the Lucky Strike mussel ($\delta^{15}\text{N} = -6.9\text{‰}$; Table 2) is enriched in ^{14}N relative to non-vent invertebrates, indicating that the inorganic nitrogen source is autochthonous and that the vent mussel is near the base of the food web (Van Dover *et al.*, 1988; Fisher *et al.*, 1994).

Carbon stable isotope composition of bresiliid shrimp ($\delta^{13}\text{C} = -16.2$, -17.9‰) from Lucky Strike fall within the range of values ($\delta^{13}\text{C} = -10$ to -18‰) observed for *Rimicaris exoculata* from TAG and Snake Pit on the Mid-Atlantic Ridge (Van Dover *et al.*, 1988; Van Dover, unpublished data), but nitrogen values ($\delta^{15}\text{N} = +1.4$, $+3.0\text{‰}$) are several per mil more negative. As in *Rimicaris exoculata*, mouthparts of *Chorocaris fortunata* are covered by epibiotic microorganisms which may play an important role in the nutrition of the shrimp. Stable carbon and nitrogen isotope compositions of Lucky Strike limpet (*Protolira valvatoidea*) tissues ($\delta^{13}\text{C} = -14.5\text{‰}$; $\delta^{15}\text{N} = +4.1\text{‰}$; Table 5) are comparable to those of the shrimp muscle and suggest that these invertebrates may consume similar food resources within the Lucky Strike habitat, i.e. microorganisms growing on sulfide and other surfaces.

Subsequent exploration of the Lucky Strike Hydrothermal Field scheduled by U.S. scientists using *ARGO II* in 1996 will provide critical data on the regional hydrothermal setting and diversity of biological communities in the area. Proximity of Lucky Strike to staging areas in the Azores and international interests in time-series observations of hydrothermal communities suggest that Lucky Strike may become a principal area of ridge-crest hydrothermal research.

The Lucky Strike urchin has recently been identified as *Echinus alexandri* (P. Tyler, pers. commun., 1996). The ampharetid polychaete is described as a new species in Desbruyères (in press), *Proceedings of the Biological Society of Washington*.

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