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Deep-sea hydrothermal communities in Southwestern Pacific back-arc basins (the North Fiji and Lau Basins): Composition, microdistribution and food web

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ABSTRACT

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During the year 1989, two diving cruises of the French deep-sea submersible *Nautile* were devoted to the study of hydrothermal vent biology in spreading centers of two Southwestern Pacific back-arc basins (Lau Basin and North Fiji Basin). In both cases, two major active sites were visited: White Lady and Mussel Valley in the North Fiji Basin and Hine Hina and Vaï Lili in Lau Basin. The faunal associations clustered around active vents are dominated by two species of snails *Ifremeria nautilei* and *Alviniconcha hessleri* and one or two species of mytilids belonging to *Bathymodiolus*. These species are associated with chemoautolithotrophic bacteria in intracellular symbiosis as detected by the activity of the Calvin-Benson cycle diagnostic enzyme RuBPcase. Pedunculate and sessile barnacles dominated the outer rim of the site and are analogs of the fiter-feeding serpulids living in the EPR sites. The hot extremes of the sites are poorly or not colonized by alvinellids or other taxa. In the Lau Basin, "cold seep" sites are found at the periphery of active hot or warm ventsand are dominated by vestimentiferans and pogonophorans. No major differences were seen between associations of the two back-arc basins at the generic level with the exeption of the abundance of synaptid holothurians associated with *Bathymodiolus* in side the "Mussel Valley" site.

Introduction

The exploration cruises conducted along mid-oceanic ridges since 1976 have shown that occurrence of vent communities is not exeptional and not controlled by ridge spreading rate (for a review, see Tunnicliffe, 1991 and Laubier, 1989). Such communities have been described along the East Pacific Rise (EPR) and the Galapagos Spreading Center (GSC), as well as along the Juan de Fuca/Explorer/Gorda Ridges and on the Mid-Atlantic Ridge. In these locations, the biomass encountered is considerably greater (Fustec et al., 1988, for 13°N/EPR) than for non-vent deep-sea communities. The food web relies on the production of organic matter via free or symbiotic bacterial chemoautolithotrophy (for review see Jannasch, 1989). The populations are distributed throughout the zone where hydrothermal fluid and sea-water mix. In the close vicinity of the superheated fluids, on chimney walls, populations are dominated by bacterial mat grazers and suspension

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feeders, while in the warm part of the temperature gradient, populations are dominated in biomass by invertebrates containing endosymbiotic chemoautotrophic bacteria (see Fisher, 1990). The faunal composition of these communities is rather surprising: Tunnicliffe (1991) reported 94% of the species are endemic. Though very rich, these populations are spatially confined to the few hundred square meters surrounding vents. They are separated from each other by barren areas, populated only by typical deep-sea assemblages dominated by filter feeders like sponges and actinians. Multi-year surveys conducted on the Galapagos vents, at 13°N/EPR and on the cleft segment (Juan de Fuca Ridge), have shown that the environment is highly unstable over a time scale of a few decades.

In the Southwestern Pacific, back-arc basins offer the conditions necessary to the development of intense hydrothermal exchanges similar to oceanic ridges: (1) a heat source located close to the interface that activates convective exchanges, (2) the presence of lines of weakness (faults and clefts) allowing lava injection and hydrothermal convection. The western rim of the Pacific Ocean (Fig. 1) consists of a complex network of back-arc basins: the Okinawa Trough, Mariana, Manus, Woodlark, Coriolis, North Fiji, Lau and Havre. These basins are relatively recent and remain active only during a rather short time (Hessler and Lonsdale, 1991); they constitute biogeographic entities, relatively isolated from each other. Exploration of active vents in these spreading centers is currently underway and is the topic of several international programs. Active hydrothermalism first discovered in the Manus Basin (Both et al. 1986), with the use of a "deep-tow" from the surface. Additional data were then collected in 1987 in the Mariana Basin with the submersible *Alvin* (Hessler and Lonsdale, 1991). These data revealed the existence of communities of organisms, taxonomically close to those of mid-oceanic ridges, but differing in terms of dominance (gastropods, barnacles and actinians instead of bivalves, vestimentiferans and polychaetes). More recently (1988 and 1989), submersible dives with the Japanese *Shinkai* 2000 in the Okinawa Basin led to the description of different populations in several active hydrothermal zones (Ohta, 1990).

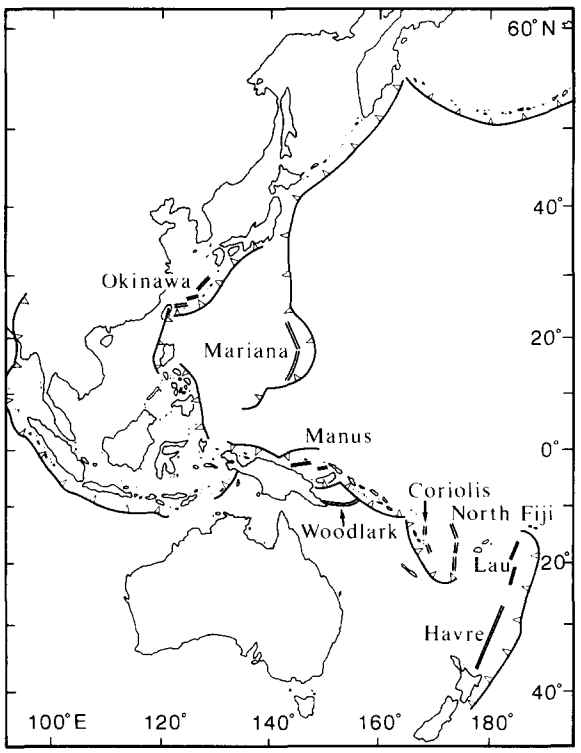


Fig. 1. Map of the main Western Pacific back-arc basins.

The Lau Basin is currently under study within the framework of a Franco-German cooperation program combining surveys from surface equipment (R/V *Jean Charcot* and *Nadir*, and R/V *Sonne*) and the *Nautile* manned submersible (The Nautilau Group, 1990). In addition, a study of the North Fiji Basin was conducted under a Franco-Japanese cooperation program, involving the R/V *Kaiyo* (Jollivet et al., 1989), *Nadir* (Auzende et al., 1989) and *Yokosuka* as well as the submersibles *Nautile* and *Shinkai* 6500.

The purpose of this paper is to present our findings on the composition and distribution of the communities, and on the food web of the hydrothermalism-related fauna found in the Lau and North Fiji back-arc basins, during the BIOLAU and STARMER II cruises (spring and summer 1989).

The North Fiji and the Lau basins (Fig. 2) are located at the boundary between the Pacific and Indo-Australian plates. They are bordered on the north by the Vitiaz fossil subduction zone. The North Fiji Basin is limited in the south by the

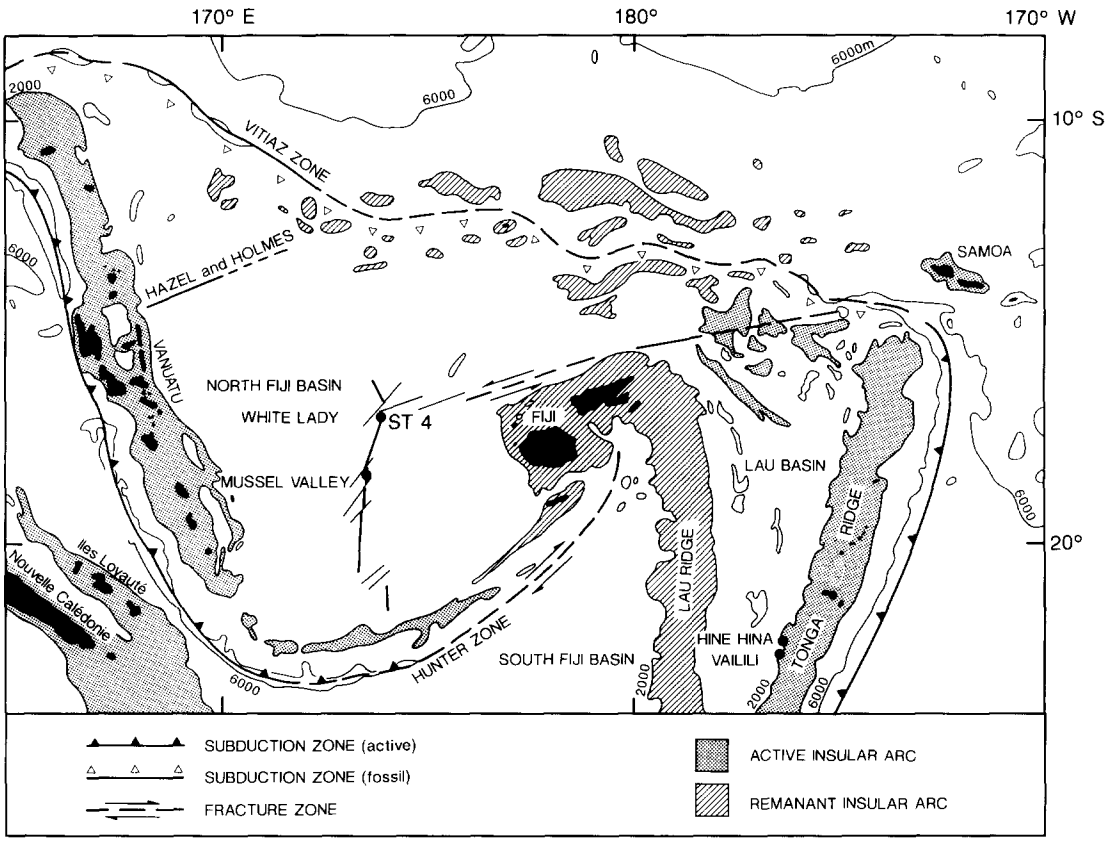


Fig. 2. Map of the North Fiji and Lau Basins in the Southwestern Pacific.

Matthew–Hunter Fracture Zone. An active ridge separates the North Fiji Basin into two almost equal sections. Between 22°S and 18°10′S, this ridge is oriented N–S; it has been dated to 3 Ma. Its morphology is typical of a ridge with a high spreading rate, such as the East Pacific Rise. Between 18°10′S and 16°40′S, the accretion zone is oriented N15° and consists of a double ridge framing an axial valley with a depth of 100 to 200 m. It is younger than 1 Ma. A triple junction area is located at 16°40′S. The other two branches of this triple junction consist of an accretion axis oriented N160° and the Fiji Fracture Zone oriented N60° (Auzende et al., 1988). The spreading rates are 7 cm/yr at 22°S and 5 cm/yr at 17°S. The spreading zone has an average depth of 2000 m above the triple junction area, and 2700 m further south.

The Lau Basin is bordered to the west by the fossil Lau Ridge and to the east by the Tofua Volcanic Arc. The Valu Fa Ridge, spreading center of the southern section of the Lau Basin, is located in the immediate vicinity of the Tofua Volcanic Arc, i.e. 40 km only in the most southern area where we focused our work. The ridge morphology is complex, with numerous segments, secondary ridges and volcanoes located between the ridge and the arc (The Nautilau Group, 1990). According to Auzende et al. (1988), the Lau Basin opening may be younger than 3 Ma. Its average spreading rate is 7.4 cm/yr. These authors propose the following hypothesis on the evolution of these two back-arc basins: the beginning of the Lau Basin opening could be contemporary (3–0.7 Ma) with the formation of the triple ridge system in the northern part of the North Fiji Basin, following a rotation of the Hebrides block and collisions with the Loyalty Islands. Thus, the isolation of

the North Fiji Basin and of the Lau Basin spreading centers occurred very recently.

Methods

The BIOLAU cruise took place from May 12 to 27, 1989, (Anne-Marie Alayse-Danet chief scientist) followed the Franco-German NAUTILAU geological survey. The French submersible was launched from the *Nadir* mother vessel. Twelve dives were conducted over two areas: six on "Hine Hina" and six on "Vaï Lili".

The Franco-Japanese STARMER II cruise took place from June 30 to July 19, 1989, (Daniel Desbruyères and Suguru Ohta co-chief scientists). It was a follow-up of the STARMER I cruise devoted to geosciences. Two active hydrothermal zones were visited during twelve dives, nine of which focused on "White Lady" and three on "Mussel Valley".

Observations were recorded either directly through the viewports by the scientist in the submersible, or a posteriori aboard the mother ship during the display of the video recorded by two cameras fitted on the *Nautile* (3CCD Sony and Hytec) on standard VHS and BVU tape. 122 hours of video tape were recorded during these two biological cruises. Animals were sampled with use of mechanical arms, a revolving "slurp gun" for small-size fauna, baited traps for larger carnivorous and scavenging fauna and a hydraulic force cup. During the dives, the samples were placed directly into a "coffin" with thick walls to minimize the temperature variations during the ascent. Temperature data were recorded with a temperature probe with range 0°–400°C (approximately 1% precision for temperatures over 200°C and 10% for temperatures below 50°C). Additional temperature measurements were taken with THYDRO a multi-probe temperature recorder (Chevaldonné et al., 1991).

To detect symbiosis between chemoautotrophic bacteria and consumers RuBPcase activity measurements were performed in tissue homogenates according to the method described by Felbeck (1981). Ribulose biphosphate carboxylase is a diagnostic enzyme of the Calvin-Benson cycle in which CO_2 is fixed into organic molecules.

Results

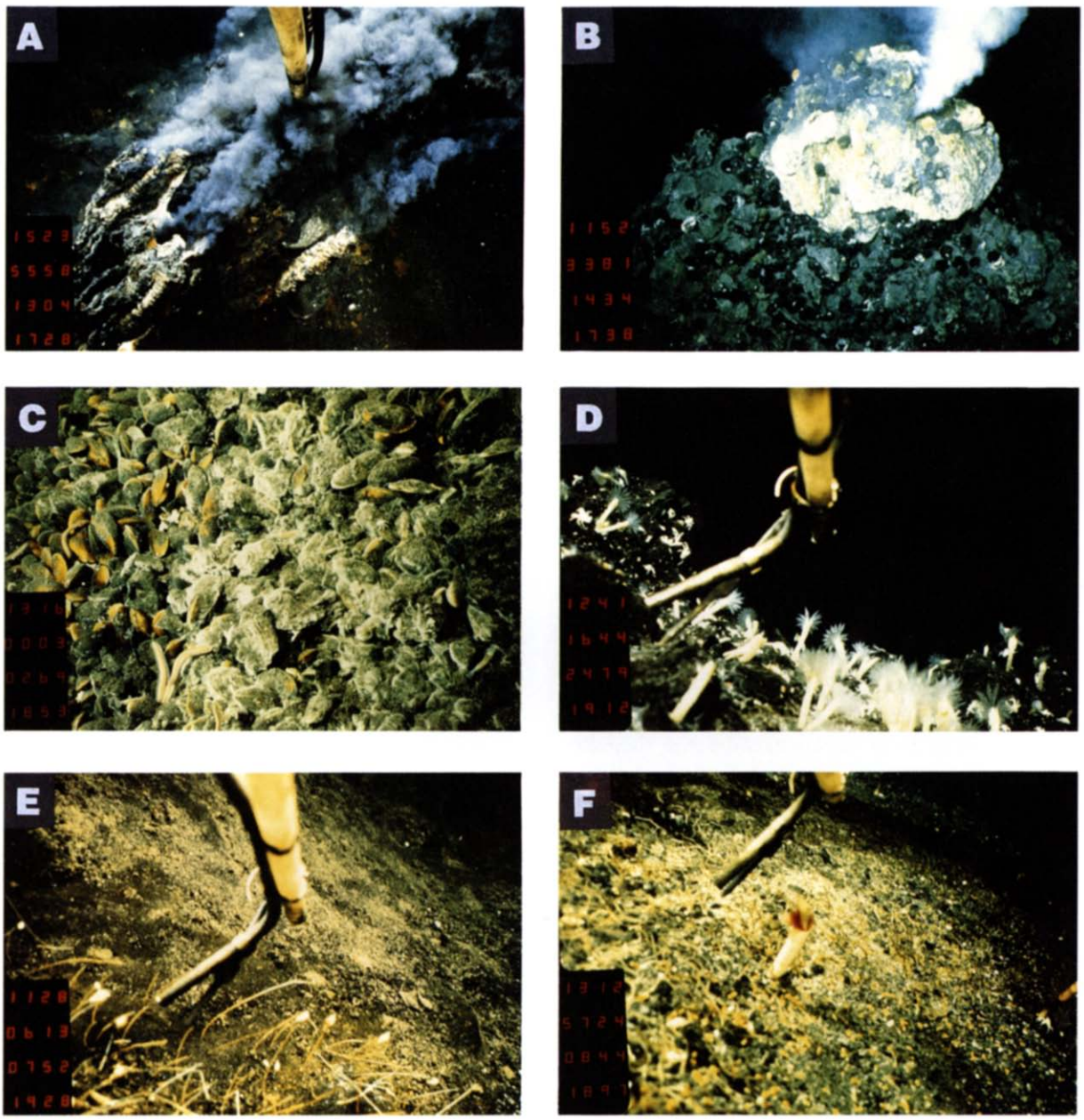
Location and physical settings of the studied vent fields

Lau Basin: Vaï Lili site (F: 22°13′S and G: 176°37′W; $Z = 1764$–1707 m). This site is one of the most active observed to date. The active area is approximately 400 m long and 100 m wide, with a great number of active smokers of two types: white smokers with an open pipe whose temperatures range from 240° to 309°C, and black smokers with temperatures ranging from 330° to 400°C (Plate I A and B). The presence of vesicular lava and brecciated rocks at the base of polymetallic sulfides facilitates the circulation of sea-water and hydrothermal fluid. Temperatures recorded to 33°C and mineral deposits spread beyond the high temperature area. All the fluids sampled have an end member *p*H value of 2, representing the lowest value ever determined in hydrothermal sites. The fluid salinity and the metallic ions content (As and Pb in particular) are much higher than in the fluids collected along the East Pacific Rise (Fouquet et al., 1991).

Lau Basin: Hine Hina site (F: 22°32′S and G: 176°43′W; $Z = 1832$–1887 m). The fluid temperature in this hydrothermal field is generally low and under 20°C. The fluid is released through a dome of highly vesiculated and brecciated andesite. The near-surface rocks are impregnated with sulfides. The site itself is formed by a massive deposit oriented NE–SW, with a 4–5 m overhang above a basin lined with small-size blocks separated by small faults and crevices. South of this site, lies an extensive field of brecciated rocks containing oxide deposits and bacterial mats. No thermal anomaly could be detected in that area (Momoko site).

North Fiji Basin: White Lady site (F: 16°59′S and G: 173°55′E; $Z = 2000$ m). This active site is one of the components of a complex hydrothermal field, approximately 300 m in its largest dimension and oriented WSW–ENE. It comprises both warm fluid vents (31°C) and active chimneys with high temperatures (91°C and 296°C as maximum measured in two different chimneys). Tepid fluid vents (< 10°C) were observed along the graben axis and on the eastern scarp. Beds of partially dissolved

PLATE I



(A and B) Black and white smokers on which walls *Ifremeria nautilei* are dwelling (Lau Basin, Vaï Lili site). (C) Mussel beds (*Bathymodiolus* sp.) covered by bacterial mats. Bresiliid shrimps, galatheids and anguilliform fishes (*Thermobiotes mytilogeiton*) are present in the Hine Hina site (Lau Basin). (D) Stalked barnacles (*Neolepadidae* gen. n., sp. n.). (E) Pogonophorans (*Siphonobranchia columna*) in the Momoko site (Lau Basin). (F) Vestimentifera (*Lamellibrachia columna*) buried within brecciated lava in a "cold seeps" area located southward of Hine Hina (Lau Basin).

and fenestrated dead shells were found all around the active sites. The fluids emitted in this zone are always translucent, even at high temperature. A 5–7 m-thick oxide deposit lies on the bottom of the axial valley and the active site is located at the center of this deposit. It consists of a chimney formed by several diffusers and smokers oriented along the NNE–SSW axis. The upper structure is composed of whitish anhydrite, with a 2.5 m × 1 m base and a maximum height of 3 m (see also Auzende et al., 1989). Numerous vents are arranged at the base of the complex structure. The maximum temperature of the emitted fluid is 285°C. It remained stable over month. During a recent Japanese submersible cruise, a slight decrease in the maximum temperature was recorded (Auzende et al., 1992). The fluid analysis displays a low chlorinity and a relatively high pH (pH = 4.5). H_2S concentration in the pure fluid is close to 2 nmol/l. Fe and Mn concentrations (10–15 µmol/kg) are one hundred-fold lower than in the fluids found in other known hydrothermal systems. A possible explanation proposed this phenomenon is the existence of a phase separation in sub-surface.

North Fiji Basin: Mussel Valley site (F: 18°49′S and G: 173°29′E; Z = 2700 m). At this site, the volcanic dome is flat and the graben not as distinct. During the *Kaiyo* 87 cruise Nojiri et al. (1989) identified a very large-size hydrothermal plume with an intensity comparable to the "megaplume" described at Juan de Fuca. The active site is framed by a group of collapsed lava lakes with a great number of pillars. In the vicinity of these lakes, the rocks are covered with a thin film of sediment which accumulates in cracks. The site shows no oxide or sulfide accumulation, but fresh formations of basaltic glass were observed and collected in this area. The limpid fluid is expelled through a series of low temperature vents (maximum 8.5°C).

Hydrothermal vent assemblages

Lau Basin, Vaï Lili site

A warm fluid (< 35°C) is emitted from the dips located at the the chimney bases. There, the fauna is abundant and dominated by the gastropods *Alviniconcha hessleri* and *Ifremeria nautilei*, two species belonging to the family Provannidae (Caenogastropoda), recently erected by Warén and Ponder (1991). The chimney walls are bare, except in rare cases where some *Ifremeria nautilei* and a few sessile cirripeds (*Eochionelasmus ohtai*) were observed on flanges or at the base of the smokers, in areas where temperature does not exceed 6°C. Morphologically, the specimens composing the population of the both gastropod species are identical to those found in the North Fiji Basin (Warén and Bouchet, 1993); however, a preliminary study on enzyme affinities between *Alviniconcha hessleri* populations of the two basins, reveals a highly significant genetic differentiation. The calculated genetic distance is significantly higher than the mean theoretical distance between two morphologically differentiated species (Denis et al., 1993). This is not the case for the *Ifremeria nautilei* population whose zymograms are closer to those of the North Fiji populations. *Alviniconcha hessleri* clumps are located in the central portion of the emission zone (15°–33.5°C), while *Ifremeria nautilei* population congregates in the areas where the fluid temperature ranges between 6° and 21°C. Numerous smaller-sized gastropods belonging to three species are present as well and their description will be shortly published by Warén and Bouchet (Skeneidae n.g., n. sp., *Leptogyra* n. sp., Provannidae n. g., n. sp.). Extensive populations of mytilids belonging to the genus *Bathymodiolus* (n. sp 1., fide Von Cosel and Métivier) are present throughout a wide range of thermal conditions (2°–19°C). They predominate wherever walls and faults are found. The commensal *Branchipolynoe pettibonae* polynoid worm is present within this population. Along the outside rim of the site where temperatures range from 2° to 5°C, populations of cirripeds are present, belonging to a sessile species of the genus *Eochionelasmus*, along with numerous specimens belonging to a new genus of scalpellid related to *Neolepas*.

Relatively dense populations of several shrimp species are observed on the mytilids and gastropods, among which the *Bresiliidae Chorocaris* sp. and *Alvinocaris* sp. as well as numerous specimens of *Lebbeus*. The anguilliform fish *Thermobiotes mytilogeiton*, belonging to the family Synaphobranchidae is present in the surroundings

of mussel beds and among the gastropods. The carnivorous specimens caught in the baited traps belong to two Bythograeidae species, *Austinograea alaysae* and *Austinograea* aff. *williamsi*. The galatheid crustaceans are represented by the species *Munida magniantennula*.

Lau Basin, Hine Hina site

In the dip located in the center of the site, the fauna is dominated by mytilids (*Bathymodiolus* sp.) arranged along faults, or aggregates in the areas of brecciated rocks (Plate IC). The mean temperatures recorded over 22 hours at two spots of the mytilid beds (on the surface and inside a clump of *Bathymodiolus* n. sp. 1) were 7.7°C and 12.7°C, respectively, whereas the range was 5.3°–12.2° and 3.7°–17°C (Chevaldonné et al., 1991). These populations are covered with thick grayish bacterial mats. A population of stalked cirripeds covers the surrounding basaltic rocks in a zone where the temperature ranges from 2.5° to 4.5°C. These specimens belong to a new type of Scalpellidae. Around the mussel populations, a small population of vestimentiferan worms belonging to *Alaysia spiralis* is present with a spiral tube less than 20 cm long, and with a Lamellibrachiidae, *Lamellibrachia columna* (Plate IF). A large multispecific population of shrimps Bresiliidae (*Alvinocaris* sp.) and Hippolytidae (*Lebbeus* sp.) lives on the rock surfaces and in the mussel beds. Previously mentioned *Austinograea* species are present as well. In this site three species of galatheids were caught *Munida magniantennulata* as in Vaï Lili site and two new one *Munidopsis lauensis* and *Munidopsis starmer* (Baba and De Saint-Laurent, 1992). The fish Synaphobranchidae *Thermobiotes mytilogeiton* lives in the mussel beds where it appears to burrow.

Lau Basin, South Hine Hina and Momoko sites

Extensive fields of brecciated rocks and minerals were observed frequently covered with oxides and bacterial mats south of Hine Hina. They are present even where no thermal anomaly could be detected. The perviate pogonophorans *Siphonobrachia laui* (Plate IE) and vestimentiferan worms *Lamellibrachia columna* live in these sites. One species of bivalve, *Acharax alinae*, lives at the base of the vestimentiferan tubes, buried within the rabbles of brecciated lava. Mussels and stalked cirripeds were also observed in these "cold" sites (Plate ID) as well as two species of bonnelis *Alomasoma chaetiferum* and a new one for science *Hamingia* n. sp. (Bisewar, in press).

North Fiji Basin, "White Lady" site

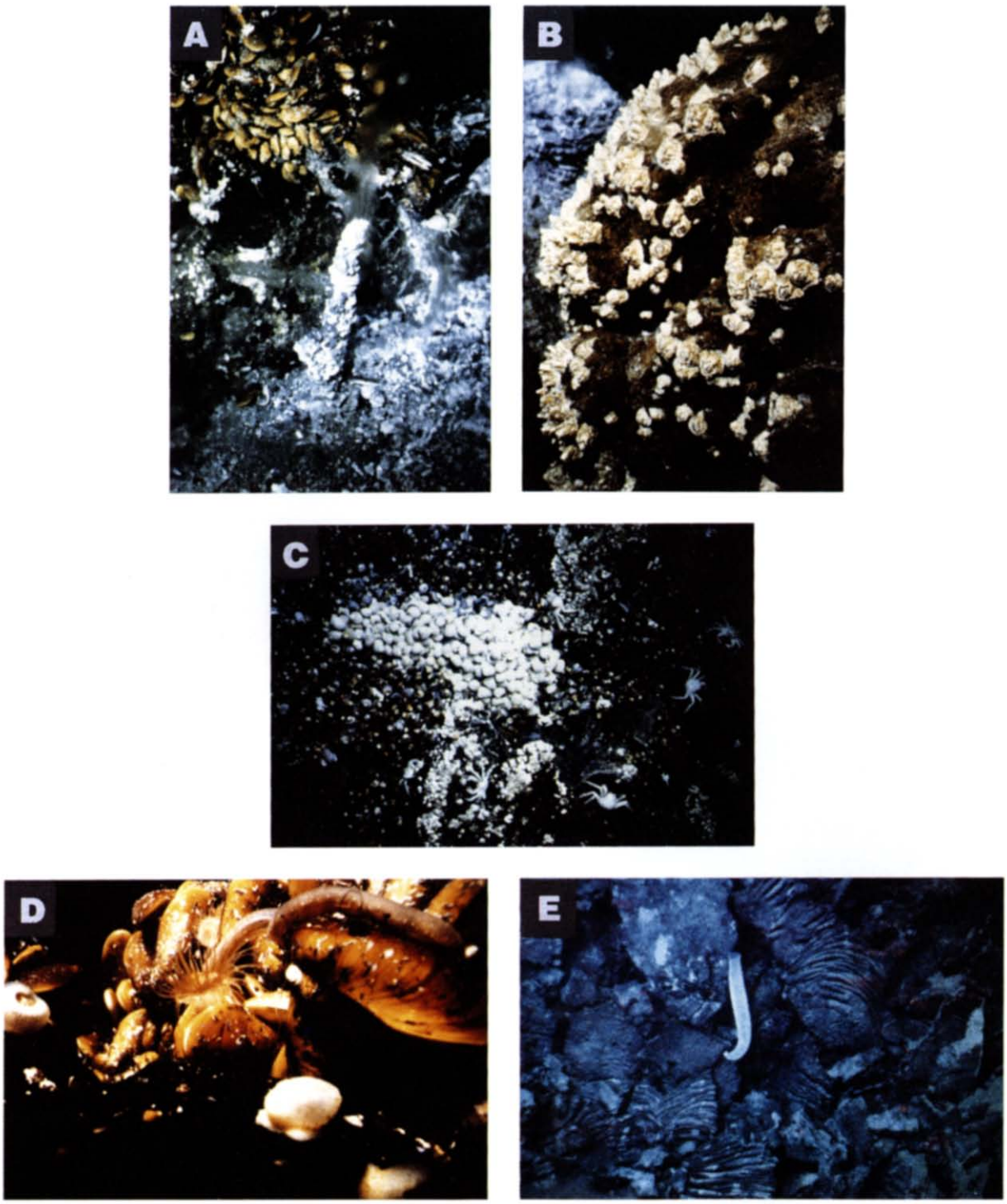
The associations are dominated, in terms of biomass, by gastropod and bivalve molluscs.

– In areas where the fluid is warm, i.e. where the mean temperature recorded over 22 hours (Chevaldonné et al., 1991) is 7°C (range 6.92°–13.33°C), two species of large gastropods (Plate IIC) are present: *Ifremeria nautilei* and *Alviniconcha hessleri*. Maximum shell heights are 95 and 85 mm, respectively. They are roughly arranged in the form of concentric bands, with the *A. hessleri* population in the middle and the *I. nautilei* population around. While the average temperatures are similar for both populations, the range is much more greater for *I. nautilei* than for the other species (2.72°–17.00°C against 5.26°–12.18°C). These populations comprise a few tens of individuals and spread over 0.25–0.5 m^2 around warm vents.

– At the chimney base and on the walls, extensive bispecific populations of large mytilids (Plate IIA) congregate in areas where the mean temperature recorded over 22 hours is 17°C (range 8.51°–21.36°C). These mytilids belong to the genus *Bathymodiolus* (*Bathymodiolus* n. sp. 1 and 2, fide Von Cosel and Métivier), very frequently they harbor the polynoid symbiont *Branchypolynoe pettibonae*. In most cases, the mytilids may be found along the vertical walls to which they attach with their powerful byssus threads, or between the ledges of a fault. Unidentified limpets are present in large numbers on the mytilid shells.

– In areas bathed with the hot fluid, small populations of alvinellid polychaetes were sampled along the anhydrite smoker walls. These annelids belong to two new species assigned to the genus *Paralvinella* (Desbruyères and Laubier, 1993). The populations, were neither large nor dense. Behavior of individuals of both species appeared to be very similar to what we previously observed on the EPR sites for the genus *Paralvinella*: the

PLATE II



(A) Mussel bed thriving on a smoker wall in the "White Lady" site (North Fiji Basin). (B) *Eochionelasmus ohtai*, a sessile barnacles developped along the crest of the basaltic blocks. (C) Clumps of *Alviniconcha hessleri* surrounded by a rim of *Ifremeria nautilei* in the "White Lady", North Fiji Basin. (D) *Chiridota* n. sp. a synaptid holothurian on *Bathymodiolus* clumps in the "Mussel Valley" site in the North Fiji Basin. (E) Euplectellid sponge at the boundary of active vent area in North Fiji Basin.

gills extend out of the mucous tube and are held within the shimmering fluid. Temperature could not be measured with accuracy at that level due to the complex chimney architecture. In the immediate vicinity, polynoids were observed, which belong to the subfamily Branchinotogluminae. A number of bresiliid shrimps, belonging to the genera *Alvinocaris* and *Chorocaris* are present in a patchy distribution. They, likely, feed from the smoker walls bacteria. In the outer part of the site, among the mollusc populations, numerous galatheids (*Munidopsis lauensis* and *starmer*, Baba and De Saint Laurent, 1992) and chirostylids (*Uroptychus bivacus* and *thermalis*, Baba and De Saint Laurent, 1992) are observed. At the end, a Lithodidae of the genus *Paralomis* is very abundant.

– In the outer portion of the site, and particularly along the crest of sulfide and basaltic blocks, as well as over the shells of some mytilids at the periphery of the mussel bed, dense population of the sessile cirriped (Plate IIB) *Eochionelasmus ohtai* occur with sparse individuals of a stalked cirriped belonging to the genus *Neolepas*. Discrete temperature measurements with the submersible probe, reveal that the hydrothermal fluid input remains significant; temperatures range from 2.5° to 4°C, while ambient water is approximately 1.7°C. Large numbers of small anemones are also present. Their taxonomic affinity has not yet been determined clearly. Contrary to what was observed on the active sites of the East Pacific Rise, the "non-vent" fauna is found virtually in contact with the peripheral thermal anomalies. Two species in particular are very frequent: an euplectellid sponge (Plate IIE) within which lives a stenopodid shrimp belonging to the genus *Spongicola*, and a brisingid asteroid. This penetration of non-vent taxa concentrated around the vents, may be due to the limited particle content of the fluid, and thereby to a lower toxicity. No temperature anomaly could be detected in this zone.

– On this site, the only carnivorous specimen collected in the baited traps is a bythograeid whose systematic position still remains unclear. It could be a form related to *Austinograea williamsi* which was described in active vents of the Mariana back-arc Basin (Guinot, 1989). No fish was observed or collected from this site.

North Fiji Basin, "Mussel Valley" site

The fauna is dominated by the two bivalve species belonging to the genus *Bathymodiolus* described above. One of these species, slender and light brown, is the same new species described in the Lau Basin. According to Moraga et al. (in press), the very small genetic distance found between these populations and those of the Lau Basin suggesting that the gene flow is maintened between the two basins. Conversely the distances are bigger between both of these populations and those of *Bathymodiolus thermophilus* found at 13°N/EPR. This only genetic data do not allow us to come to the conclusion on the reproductive isolation of these populations. These mytilids form widespread mussel beds around the vents and in the faults. Despite considerable sampling, no commensal worm (*Branchipolynoe* sp.) could be found in the sampled mussels. Along the periphery of this population are relatively dense populations of a synaptid holothurian (Plate IID), a new species belonging to the genus *Chiridota*. It should be noted that it is the first observation of echinoderms in the hydrothermal environment. A synallactid holothurian was also collected. This species is very akin or identical to the Atlantic deep-sea species, *Synallactes longipapillata*. One gastropod, *Lepetodrilus elevatus*, was present in large quantities in our samples. Inside the warm vents themselves, a small vestimentiferan worm, most likely new to science (currently under study by S. Ohta), forms small populations. The two dominant gastropods found at the "White Lady" site are absent. Predators are represented by a species of Bythograeidae *Austinograea* aff. *williamsi* and by a fish related to the Bythitidae which could not be caught. Other than vent-specific medium-size "eelpouts" (probably consisting of zoarcids, synaphobranchids and/or slender brotulids), larger fishes such as brotulids, macrourids, chimaeras and sometimes cephalopods (*Vampyroteuthis* sp.) visited the vent communities. Usually they were concentrated at the peripheral zone of the vent fields. They are probably taking an active part to the outflow of organic matter from the vent communi-

ties. Mat grazers are represented by galatheids belonging a species of the genus *Munidopsis*. At the rim of the site and along the faults, large numbers of undetermined actinians were observed (Plate IID).

Food web

In the four surveyed sites, the biomass of the communities was dominated by bivalves (*Bathymodiolus* spp.) and gastropods (*Ifremeria nautilei* and *Alviniconcha hessleri*). The Lau Basin bivalves appear to have a trophic position similar to the mytilids of the East Pacific Rise.; i.e. presence of endocellular bacteria (Fiala-Médioni et al., in prep.; Otha and Kim, 1992) and RuBPcase activity (Table 1) in their gills. Whereas endocellular bacteria are present in the gills (A. Fiala-Médioni, pers. commun.) no RuBPcase enzymatic activity was detected in the mytilids from the North Fiji Basin. In *Ifremeria nautilei*, the gills and circulatory apparatus are hypertrophied, while the stomach volume is reduced to 1/10 of the volume found in other Provannidae (Bouchet and Warén, 1991). RuBPcase activity was positive suggesting the occurrence of a symbiosis with chemoautotrophic bacteria (Table 1). In this species, Bouchet and Warén (pers. commun.) observed several commensals living in the pallial cavity (one Polynoidae) and in the umbilicus (*Amphisamytha galapagensis*). In *Alviniconcha hessleri*, our findings (Table 1) are in agreement with the previous results demonstrating the existence of a symbiosis with chemoautotrophic bacteria (Stein et al., 1988; Endow and Ohta, 1989). As for *Ifremeria nautilei*, the gills are hypertrophied and the digestive tract appears to be reduced although functional. Warén and Bouchet (1993) describe the stomach content of this species as consisting primarily of mucus with a whitish, granular essence, occasionally containing mineral particles, sponge spicules and fragments of crustacean tests. This would therefore suggest that, in addition to the symbiosis, these gastropods have a mixotroph diet and that the contribution from grazing or deposit feeding could be significant. Thus, the three dominant taxa (by weight) all have mixotrophic diets. Mixotrophy constitutes a response to the instability in fluid

TABLE 1

RuBPcase activity as displayed by tissues of different taxa inhabiting deep-sea hydrothermal vents

Species	Locality	*n*	RuBPcase activity (U/g tissue)
Bivalves			
Calyptogena magnifica (1988)	Galapagos	22	0.088 ± 0.016—Fisher et al.
Bathymodiolus thermophilus	Galapagos	20	0.003 ± 0.003—idem
Bathymodiolus spp.	Lau Basin, Hine Hina	3	0.01—Fiala-Medioni et al. (in prep.)
Bathymodiolus sp.	Lau Basin, Vailili	1	0.017 ± 0.006—idem
Bathymodiolus sp.	Fiji Basin, White Lady	3	not detected—this study
Undescribed mussel	Louisianna slope	3	0.018 ± 0.008—Fisher et al. (1987)
Gastropods			
Alviniconcha hessleri	Mariana basin	5	0.2 ± 0.02—Stein et al. (1988)
Alviniconcha hessleri	Lau Basin, Vailili	4	0.081 ± 0.036—this study
Alviniconcha hessleri	Fiji Basin, White Lady	3	0.155 ± 0.140—idem
Ifremeria nautilei	Lau Basin, Vailili	3	0.023 ± 0.030—idem
Ifremeria nautilei	Fiji Basin, White Lady	3	0.072 ± 0.072—idem
Vestimentiferans			
Riftia pachyptila	Galapagos	3	1.01 ± 0.1—Fisher et al. (1988)
Escarpia laminata (1989)	Florida Escarpment	4	0.1 ± 0.026—Cary et al.
Lamellibrachia columna study	Lau Basin, Hine Hina	2	0.007 and 0.016—this study
Lamellibrachia columna	Lau Basin, Momoko	2	0.166 and 0.236—idem

emission. The RuBPcase enzyme is present as well in *Lamellibrachia columna*, the vestimentiferan worm of the Lau Basin. Its activity is variable (Table 1) and is highest in specimens collected from the cold area of the Momoko Field.

The outer rim of the sites is inhabited by filter feeders and mat grazers. Stalked and operculate cirripeds occupy areas, such as block and basalt crests. Discrete temperature measurements show the existence of a non-negligible hydrothermal input ($2.5°C < T < 4°C$) among these populations. Large numbers of small actinians can also cover the walls of faults where temperature anomalies were detected. Bacterial mat grazers are mainly represented by Bresiliidae (*Alvinocaris* spp.) and Hippolytidae (*Lebbeus* sp.). Galatheids (*Munidopsis* sp.) and lithodids (*Paralomis* sp.) are found in abundance.

Scavengers organisms are represented by crabs (*Austinograea alaysae* and *Austinograea* aff. *williamsi*). In the Lau Basin, the Synaphobranchidae *Thermobiotes mytilogeiton* is abundant in the mussel beds. In the North Fiji Basin, no fish could be observed on the "White Lady" sites, while a number of anguilliform specimens were observed in the "Mussel Valley". Scavenging organisms are represented by a gastropod Trochidae (aff. *Phymorhynchus*).

Discussion

We now have a clearer insight into the composition and structure of the vent communities associated with active hydrothermalism in the back-arc basins of the western Pacific (Table 2). Since the initial observations made by Both et al. (1986) in the Manus Basin, a great number of surface and diving cruises have been devoted to their study: the Mariana Basin was explored by the submersible *Alvin* in 1987 (Hessler et al., 1988; Hessler and Lonsdale, 1991) and the submersible *Shinkai* 6500 in 1992; the Okinawa Basin was the subject of an intensive multi-annual study program by Japanese teams with the submersible *Shinkai* 2000 (Ohta, 1990); several active areas in the Manus Basin were visited by a Japanese team using a "deep-tow" (S. Ohta, unpubl. data) and by German teams working from the surface aboard the *Sonne* (Tufar, 1990), as well as by a Soviet team using the submersibles MIR (Galkin, 1991). A number of additional studies on the Lau Basin have been carried out by the German and Soviet teams. Although exploration efforts have been considerable, the results derived from all these surveys remain difficult to synthesize due to the heterogeneity of the methods used and to the different stages of completion of the sample analyses.

The faunal composition of these vent communities is highly heterogeneous, with a first order influence from the edaphic factors: *Calyptogena* were dominant in the sediment-covered fields of the Iheya Ridge, Minami-Ensei Knoll and in the "Desmos Cauldron" (also in the sediment), on a ridge in the eastern part of the Manus Basin (S. Ohta, unpubl. data). However, these species are not present whenever the basaltic rocks are bare. The contrary was observed in the East Pacific Rise communities where *Calyptogena magnifica* is present. In the basaltic environment of the Mariana, Lau, Manus and North Fiji Basins, populations of *Alviniconcha hessleri* are extremely abundant, forming clumps around low temperature vents. While the morphology of the individuals looks alike with the exception of few external variations (Warén and Bouchet, 1993), allozyme study distinguishes that the allopatric populations of the Lau and North Fiji Basins differ in terms of enzymatic equipment (Denis et al., 1993). *Ifremeria nautilei*, which is present both in the Lau and North Fiji Basins, was also sampled in the Manus Basin (where it was described as *Olgaconcha tufari*); but it is not present in the Okinawa and Mariana Basins. Pogonophorans and vestimentiferans never constitute biomasses comparable to those observed on the East Pacific Rise (Fustec et al., 1988). Nevertheless, they are present in the basins of Lau (Momoko Field), Okinawa (Iheya Ridge), Manus (Vienna Woods) and in the North Fiji Basin (Mussel Valley). Although their taxonomic study has not yet been completed in most cases, their taxonomic status appears to be highly diversified. Long-term study conducted on the East Pacific Rise sites (D. Desbruyères, unpubl. data) reveals that the presence and the growth of vestimentiferan populations are strongly influenced by temporal variability. Several mytilid species assigned to the

TABLE 2

Species list for hydrothermal vents in the Lau (LB) and North Fiji Basin (NFB)

Phylum	Class	Family	Genus	Species	Authors	Date	Location
Vestimentifera	Basibranchia	Alaysiidae*	*Alaysia**	*spiralis**	Southward	1991	LB
		Lamellibrachiidae	*Lamellibrachia*	*columna**	Southward	1991	LB
Pogonophora	Perviata	Lamellisabellidae	*Siphonobrachia*	*lauensis**	Southward	1991	LB
Annelida	Polychaeta	Polynoidae	*Branchipolynoe*	*pettibonae*	Miura	1991	LB and NFB
		Ampharetidae	*Amphisamytha*	*galapagensis*	Zottoli	1993	LB and NFB
		Alvinellidae	*Paralvinella*	*unidentata* A*	Desbruyères and Laubier	1993	NFB
				fijiensis B*	Desbruyères and Laubier	1993	NFB
Echiuria		Bonelliidae	*Alomasoma*	*chaetiferum*	Zenkevitch	1958	LB
			Hamigia	n. sp.*	Biseswar	in prep.	LB
Mollusca	Gastropoda	Peltospiridae	*Pachydermia*	sp. n.*	Warén and Bouchet	in prep.	LB and NFB
			Peltospirid gen. n.*	sp. n.*	Warén and Bouchet	in prep.	LB
		Skeneidae	*Skeneid* (?) gen. n.	sp. n.	Warén and Bouchet	in prep.	L.B.
		Lepetodrilidae	*Lepetodrilus*	*elevatus*	McLean	1988	LB
		Trochidae	*Vetulonia*	sp. n.*	Warén and Bouchet	in prep.	NFB
		Scissurellidae	*Anatoma*	sp.	Warén and Bouchet	in prep.	LB
		Provannidae	*Alviniconcha*	*hessleri*	Okutani and Ohta	1988	LB and NFB
			*Ifremeria**	*nautilei**	Bouchet and Warén	1991	LB and NFB
			Provanna	sp. n.*	Warén and Bouchet	in prep.	LB and NFB
				*segonzaci**	Warén and Ponder	1991	LB and NFB
			Provannid gen. n.*	sp. n. 1*	Warén and Bouchet	in prep.	LB and NFB
				sp. n. 2*	Warén and Bouchet	in prep.	LB and NFB
				sp. n. 3*	Warén and Bouchet	in prep.	LB and NFB
		Buccinidae	*Buccinid* gen.	sp.	Warén and Bouchet	in prep.	LB and NFB
	Bivalvia	Mytilidae	*Bathymodiolus*	sp. n. 1*	Von Cosel and Métivier	in prep.	NFB
				sp. n. 2*	Von Cosel and Métivier	in prep.	LB and NFB
		Solemyidae	*Acharax*	*alinae**	Métivier and Von Cosel	1993	LB
Arthropoda	Acari	Halacaridae	*Copidognatus*	*papillatus*	Bartsh	1991	LB and NFB
	Crustacea (Cirripedia)	Scalpellidae	Aff. *Neolepas* n. gen.*	n. sp.	fide Newman	pers. commun.	LB
		Scalpellidae	*Neolepas*	n. sp.	fide Newman	pers. commun.	NFB
		Brachylepadomorph fam.	n. gen.*	n. sp.*	fide Newman	pers. commun.	LB

		Neoverrucidae	*Neoverrucine* gen. n.*	n. sp.*	fide Newman	pers. commun.	LB
		Pachylasmatidae	*Eochionelasmus**	*ohtai**	Yamaguchi and Newman	1990	NFB
				n. sp.*	fide Newman	pers. commun.	LB
	Crustacea (Ostracoda)	Cytheruridae	*Eucytherurine* gen. n.*	sp. n.*	Van Harten	1992	LB
	Crustacea (Copepoda)	Dirivultidae	*Chasmatopontius*	*thescalus*	Humes	1990	LB
			Stygiopontus	*brevispina**	Humes	1991	LB
				*lauensis**	Humes	1991	LB
	Crustacea (Tanaidacea)	Leptognathiidae	*Leptognathia*	*ventralis*	Hansen	1913	NFB
				sp. 1	fide Gutu	pers. commun.	NFB
				sp. 2	fide Gutu	pers. commun.	LB
				sp. 3	fide Gutu	pers. commun.	LB
			Typhlotanais	sp. 1	fide Gutu	pers. commun.	NFB
				sp. 2	fide Gutu	pers. commun.	NFB
	Crustacea (Decapoda)	Bresiliidae	*Alvinocaris*	sp.	fide Saint Laurent	pers. commun.	LB and NFB
			Chorocaris	sp.	fide Saint Laurent	pers. commun.	LB and NFB
		Hyppolytidae	*Lebbeus*	sp.	fide Saint Laurent	pers. commun.	LB
		Bythograeidae	*Austinograea*	*alaysae**	Guinot	1989	LB
				aff. *williamsi**	Guinot	1989	LB and NFB
		Chirostylidae	*Uroptychus*	*bivacus**	Baba and Saint Laurent	1992	NFB
				*thermalis**	Baba and Saint Laurent	1992	NFB
		Galatheidae	*Munidopsis*	*lauensis**	Baba and Saint Laurent	1992	NFB and LB
				*starmer**	Baba and Saint Laurent	1992	NFB
			Munida	*magniantennulata*	Baba and Saint Laurent	1992	LB
		Lithodidae	*Paralomis*	sp.	fide Saint Laurent	pers. commun.	LB and NFB
Echinodermata	Holothuria	Synaptidae	*Chiridota*	n. sp.	fide Ohta	pers. commun.	NFB
Chordata	Vertebrata (Pisces)	Synaphobranchidae	*Thermobiotes**	*mytilogeneiton**	Geisdoerfer	1991	LB

genus *Bathymodiolus*, are present in all back-arc basins. Similarly to what has been observed on the EPR, they form extensive mussel beds characterized by a small-size and highly diversified fauna. The mytilids along with their commensal Branchipolynoid are elements found throughout the deep-sea chemosynthetically-sustained communities in inter-tropical regions. They seem to disappear from areas located further north (e.g. 21°N/EPR, complex of Juan de Fuca/Explorer ridges), due most likely to limitations imposed by biogeographic factors linked to the planktotrophic mode of dispersal (Lutz, 1988). The successful colonization of these areas by mytilids is probably related both to their ability for colonizing steep surfaces with their byssus threads, and to their mixotrophic diet which enables them to withstand the unstable emission conditions (Ohta and Kim, 1992).

Along the walls of active smokers, several species of *Paralvinella* are present in the back-arc basins of Mariana (Desbruyères and Laubier, 1989), Okinawa (*Paralvinella hessleri*, fide Miura and Ohta, 1991), Manus (Alvinellidae n. d., fide Tufar, 1990) and in the North Fiji Basin. However, none of the populations studied appears to colonize the hot areas of the habitat or to constitute, as is the case for certain eastern species (*Alvinella* spp. and the *Paralvinella sulfincola*), any real biogenic structures on the smokers. The walls of the Lau Basin smokers are virtually abiotic, which seems to be an exception in the field of hydrothermalism. The geochemistry of fluids with high arsenic and lead contents, two metals regarded as toxic, along with a lower porosity of hydrothermal chimneys with a high barite content (less soluble than anhydrite) could provide an explanation to this lack of colonization. The primitive balanomorph *Eochionelasmus ohtai* was dominant in abundance in the North Fiji Basin compared to the brachylepadomorph in the Lau Basin and the primitive verrucomorph *Neoverruca brachylepadoformis* in the Mariana back-arc Basin. Another primitive verrucomorph was dominant in the Izena Ridge of the mid-Okinawa Trough and on the Kaikata Seamount. *Neolepas*-type scalpellids were minor constituents in the North Fiji Basin and in the Mariana Basin, while two species of them were the most dominant group on the Iheya Ridge. So far, every hydrothermal vent in the western Pacific has been found to have endemic primitive cirripeds, the trophic analogues of the eastern Pacific serpulids. Similar to the Eastern Pacific, the food web is based on symbioses between primary and secondary producers. The fauna in the North Fiji Basin and in the Lau Basin is very similar under equivalent edaphic conditions, which may be explained by the recent geological history of both basins. Our observations corroborate those made by Hessler and Lonsdale (1991): the faunas found in the back-arc basins of the Western Pacific differ only slightly from that of the Eastern Pacific, at both genus and family levels. This close affinity implies the existence of extensive migration pathways between the back-arc basins and the mid-oceanic ridges.

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