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The French contribution to hydrothermal vent and cold-seep biology and ecology

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Introduction

The first involvement of French biologists in hydrothermal vent biology followed the 1973-1974 French-American cruise FAMOUS on the Mid-Atlantic Ridge, and the American discovery in 1978 of a new and abundant deep-sea life around warm vents near the Galapagos Islands. This involvement was closely linked with the 1978 CYAMEX exploration of the East Pacific Rise (EPR) at 21°N when a French-American team of geologists and geophysicists, using the submersible *Cyana*, found large fossil polymetallic chimneys. In 1979, active black and white smokers were discovered a few kilometres away by the French-American-Mexican RISE expedition, using the submersible *Alvin*. The “Pompeii worm” collected by *Alvin* during this cruise was described one year later as a new genus and species of Ampharetidae, *Alvinella pompejana* Desbruyères & Laubier, 1980. Over the next twelve years, this collaboration continued and to-day the new family Alvinellidae comprises a dozen of species and sub-species, two genera and three sub-genera. An important review dealing with all aspects of the biology of these amazing worms has been recently published (Desbruyères et al., 1998).

The first steps

Hydrothermal vents. Following the results of the *Jean Charcot* cruise HYDROFAST in 1980, the French group on deep-sea biology and ecology[1] decided to plan a first cruise to hydrothermal vents on the EPR, near 13°N. This cruise called BIOCYATHERM took place in spring 1982, using *Cyana*. Three active vents were discovered, including a large chimney 15 metres high. Beginning in 1980, the French biologists had begun to develop different sampling devices and instruments to be used by *Cyana*. These developments were very useful during the second cruise on 13°N, BIOCYARISE, in March 1984. A short movie entitled *“Oases under the sea”* was produced by F. Dupeyron.

In April 1982, a NATO Advanced Research Institute on hydrothermal processes at seafloor spreading centres was organized by P. Rona at Cambridge. As a member of the organizing committee, I became co-editor of the Proceedings and presented a paper with D. Desbruyères on primary consumers.

Collaboration with American scientists was developed during BIOCYATHERM and BIOCYARISE cruises, and some French scientists attended the first symposium on hydrothermal vents organized in Philadelphia, in December 1983.

[1] This group was created in January 1977, as a “Recherche coopérative sur programme” (RCP #462) with the following title : Recherches écologiques et biologiques sur les communautés benthiques profondes”. It comprised scientists from CNEXO, CNRS, MNHN and from several French universities laborarories.

In December 1985, the French group organized in Paris the second symposium on biology and ecology of hydrothermal vents. North American scientists contributed to six papers on a total of 25 (Laubier, 1988).

The third oceanographic cruise HYDRONAUT to the 13°N hydrothermal vent field was organized by the French group in 1987, with the new manned submersible *Nautile*. During that cruise, a new bottom temperature recorder fitted with four different probes was deployed, providing the first results on short-time temperature variability.

Cold-seeps. During summer 1985, the Japanese-French cruise KAIKO explored the subduction trenches off Japan with the submersible *Nautile*, discovering rich cold-seeps communities of bivalves down to a depth of 6000 metres, associated with a slight increase of temperature and high concentrations of methane. Video pictures and biological samples collected during the KAIKO cruise were studied by Japanese and French scientists (Ohta & Laubier, 1987). Over the next several years, biologists and geochemists disputed the nature of the substrate used by chemolithotrophic bacteria. Biologists recorded bacteria identical to those of hydrothermal vent bivalves and found sulphur crystals in the mantle, while geochemists measured high concentrations of methane in bottom-water, but no sulphide. Both observations were accurate: sulphide is produced within the sediment by sulphate reduction coupled to methane oxidation (Sibuet & Olu, 1998).

Microbiology. Numerous studies had suggested that a microbial chemosynthesis was the main source of energy **:** H_2S oxidation to elemental sulphur and sulphates released energy to efficiently reduce CO_2 to organic carbon, a chemical process replacing photosynthesis. At the same period, Woese (1987) introduced the new kingdom of Archaebacteria (later named Archaea) and proposed a new tree of life with three kingdoms, Eucaryotes, Procaryotes and Archaea. The poorly known Archaea gathered micro-organisms living in extreme conditions of temperature or salinity. The exploration of thermophilic micro-organisms became an active field of research. This interest in thermophiles and hyperthermophiles was also related to the question of the origin of life as well as to their biotechnological potential.

A review paper on both hydrothermal vent and cold-seep communities was delivered during the Joint Oceanographic Assembly (Intergovernmental Oceanographic Commission and Scientific Committee for Oceanographic Research) held in Mexico in 1988 (Laubier, 1989).

Scientific organization

First period 1984-1992. The preliminary scientific results of the BIOCYATHERM cruise plus the research activities conducted by the French group led to a proposal to CNRS to create a "Groupe de recherches coordonnées" (GRECO) in fall 1983. Its activities were divided among four themes, one of them devoted to the study of animal communities associated with hydrothermal processes, chemolithotrophy and primary consumers, biology and physiology.

Following a positive scientific evaluation, the GRECO ECOPROPHYCE (for "*Ecosystèmes profonds et processus physico-chimiques associés*") was created for a four year period, bringing together a total of 29 scientists plus 12 associate scientists, belonging to CNEXO, CNRS, MNHN and four universities. A first four year report was submitted in February 1988 (Ecoprophyce, 1988). The Group was renewed for a second period (1988-1991), following a positive review by its scientific committee in September 1988, and a CNRS evaluation. The scientific themes were reduced to three, with an emphasis on the structure and function of chemosynthetically based ecosystems.

A second four year report was submitted in July 1992 (Ecoprophyce, 1992). Despite positive reviews by the GRECO scientific council and the CNRS committees, the CNRS directorates decided not to renew the Group, considering that its scientific success made it able to go ahead without any specific support. Consequently, the group was dissolved at the end of 1992.

Second period 1993-2001. In 1992, IFREMER decided to create joint research units called "Unités de recherche marine" (URM), between CNRS, university laboratories and its own research teams. One of them, URM n°7 was created in April 1993 under the title: "*Ecologie et écophysiologie des organismes hydrothermaux thermophiles*". URM n°7 comprised part of the *Deep-Sea Environment* department of IFREMER (headed by D. Desbruyères), together with the *Ecophysiology* (headed first by A. Toulmond, then by F. Lallier) and *Biopolymers from extreme environments* (headed by F. Gaill) research teams of the Roscoff Laboratory (CNRS and Pierre & Marie Curie University).

After a positive evaluation in April 1997 by the relevant scientific commission of IFREMER, URM 7 was renewed for a second four year period.

The new program was focused on hydrothermal vent biology and microbiology. This had several important advantages, as far as technological developments, organization of research cruises and participation in European calls for proposals are concerned. The final report for the period 1993-2001 (URM n°7, 2001) has been recently submitted.

French national framework. As early as 1983, four institutions (CNEXO, CNRS, BRGM and ORSTOM) set up a joint research programme on hydrothermal processes and biological communities. The *Programme national d'étude de l'hydrothermalisme océanique* (PNEHO) organized a symposium in November 1988. A session was devoted to hydrothermal vent biology. Nevertheless, the level of funding was limited.

Following the creation of the international programme InterRidge in 1993, the French organization decided to set up a new programme, *Dorsales*, under the umbrella of InterRidge. *Dorsales* comprises two panels, one for geosciences and one for life sciences, managed by a steering committee and a multidisciplinary scientific committee.

Major scientific results

Technical developments. From the very beginning, the importance of new equipment to be deployed from scientific submersibles was recognized. The last ten years have been very productive, with an increasing importance of on board experiments and in situ chemical environmental measurements. Recently, two new equipment systems have been developed, the *Ipocamp* and the *Piccel*, both closed systems (20 l and 100 ml) which can maintain temperature and pressure up to the equivalent depth of 3200 metres, with open sea water circulation up to 20 litres per hour for the former. Different chemicals (hydrogen sulphide, oxygen, carbon dioxide) can be added to the inflowing current.

Another important equipment has been the *Alchimist*, which can be fitted on both the *Nautile* and the ROV *Victor*. This automatic chemical analysis system is based on flow injection analysis and colorimetric detection. It can measure 24 times per hour the concentrations of two chemicals, such as nitrate + nitrite, total sulphide, Fe II and Fe II + Fe III. A temperature measurement is made at the end of the sampling nozzle. An in situ pH probe allows distinguishing different microbiotopes.

Hydrothermal vent and cold-seep sites
Several new sites have been discovered by the French group. Following the East Pacific Rise (from 11 to 13°N) and KAIKO's cold-seeps areas, the exploration in 1989 of the north Fiji basin with a Japanese group and of the Lau basin (cruises STARMER with the *Nautile*) provided the southernmost hydrothermal sites of the western Pacific. Then, new hydrothermal sites were discovered on the Mid-Atlantic Ridge, near the Azores triple junction. More cold-seeps areas were discovered by French expeditions on the Peruvian margin, the Barbados accretionary prism and, more recently, on the active margins of Angola and Gaboon.

Taxonomical results
Hydrothermal vent communities provided an unexpected high number of new taxa, often at a high taxonomic level. In 1985, a first review of animal new species from hydrothermal vents and cold seeps added up to 58 species. In 1990, another paper gave the figure of 223 new species on a total of 236 species from hydrothermal vent communities. I reported 300 animal species at least from hydrothermal vents and cold seeps communities (Laubier, 1993). The *Handbook on deep-sea hydrothermal vent fauna* listed 473 animal species (Desbruyères & Segonzac, 1997). At present, there are probably more than 600 animal species described. The French group has contributed to approximately one fourth of this total. They described, alone or in co-operation with other taxonomists, the deepest *Calyptogena* from the Kurile trench, a new cladorhizid sponge hosting methane-oxidizing bacteria from the Barbados mud volcanoes (Vacelet et al., 1995, Vacelet & Boury-Esnault, 2002) and a new species of *Bathymodiolus* hosting two metabolically distinct symbionts, methanotrophic and thiotrophic bacteria, an obvious advantage to the host mussel allowing its adaptation to spatial and temporal changes in the environmental conditions.

Ecology and population genetics
Quantitative estimates were derived from biomasses of different parts of an hydrothermal field. Time series observations on the EPR at 13°N site enabled the first descriptions of the biological consequences of time variability in physico-chemical parameters. Colonization processes were analysed, showing the role of bythograeid crabs in carrying propagules from different species. The gene flow of some species such as *Alvinella pompejana* has been studied from 7°N to 14°N on the EPR. It has been shown that changes of the hydrothermal activity led to the genetic homogeneity of populations.

Another area of research is that of the biological production of the hydrothermal vent community, whose biomass is comparable to that of highly productive ecosystems such as the coral reefs. For the tube worm *Riftia pachyptila* Jones, 1981, the production of tubes of a population of 700 ind m^{-2} represents over 400 gC m^{-2} yr^{-1}. Population dynamic of bivalves has also been studied.

Ecophysiology
Structural and functional properties of collagens and of intra- and extracellular oxygen-binding proteins (haemoglobins and haemocyanins) of various polychaetes, vestimentiferan and crustaceans have been demonstrated by French physiologists. In addition, Zal et al. (1998) identified the sulphide-binding site of the extracellular haemoglobins of *Riftia pachyptila*. More than 90 papers have been published on these topics during the 1993-2001 period (see URM n° 7 report for a complete bibliography).

Chemoautotrophic symbioses
The first French contribution to sulphur-oxidizing symbioses has been published by Bosch & Grassé (1984a, b), who studied the ultrastructure of the trophosome of *Riftia pachyptila*. Since then, most studies of chemoautotrophic symbioses by French scientists have focused on bivalve molluscs and a review of autotrophic

processes in invertebrate nutrition and bacterial symbiosis in bivalve was published jointly (Fiala-Medioni & Felbeck, 1990).

The application of molecular biology techniques to hydrothermal invertebrates during the last ten years led to the discovery of new evolutionary trends: some results are presented in this volume, such as the co-evolution between *Bathymodiolus* and the commensal polynoid *Branchipolynoe* or the genetic evidence that *Oasisia* and *Ridgeia* are congeneric sibling species instead of belonging to two different families as proposed by Jones. Cryptic species have also been found in other groups of invertebrates.

Microbiology

In the mid-1980's, IFREMER decided to create a research team in Brest to isolate microbial strains collected at different hydrothermal vent sites and look at their biotechnological potential. Microbial culture collections were built up and studied and many new strains of Bacteria and Archaea were described, the majority during the 1990's.

Thermostable enzymes are produced commercially by genetic engineering, cloning and expression of encoding genes. Consequently, whole genome sequencing brings new ways to harvest useful genes. *Methanocaldococcus jannashii* Jones, 1984, was the first Archaea to be fully sequenced. Perhaps more biotechnological research should be directed at exploiting these sequenced genomes. Whole sequences of *Pyrococcus horikoshii* Gonzalez et al., 1998 and *Pyrococcus abyssi* Erauso et al., 1993 are now available in Japan and France, respectively.

In addition to the IFREMER microbiological work, the group led by D. Prieur at Roscoff and Brest has been active in hydrothermal vent microbiology research since 1984. From 1988 to 1992, they led the CNRS Research Group Bactocéan and, more recently, the group led two cruises devoted to microbiology, MICROSMOKE and AMISTAD. Several species of Bacteria and Archaea and a new genus have been described, including *Pyrococcus abyssi*, whose genome has been completely sequenced by the French Génoscope. Baro-thermophilic bacteria belonging to the Thermococcales have been studied in view of their resistance to ionizing radiation. The group has also investigated the role of extrachromosomic organites, such as plasmids and viruses, within these Bacteria.

International co-operation

From the beginning of the hydrothermal vent research, French scientists had closely co-operated with US biologists from the Woods Hole Oceanographic Institution, the Rutgers University, the Scripps Institution of Oceanography, and taxonomists from the Smithsonian Institution. French scientists have regularly been invited on US cruises, and vice versa. This active co-operation has resulted in a large number of joint scientific papers.

A further step was accomplished through relations between the French group and Canadian scientists of the University of Victoria working with the submersible *Pisces* during mid-80's. This co-operation slightly decreased with the decision of the Canadian government to cancel *Pisces* scientific programme. Recently, a new impetus has been provided with the development of the Canadian ROV *Ropos*.

Following the KAIKO cruise, IFREMER and the Science and Technology Agency of Japan decided to establish a co-operative project for the study of hydrothermal vents in the western Pacific (STARMER project). The North-Fiji basin was chosen, and a first cruise with the *Nautile* took place in mid-1989. Two years later, in summer 1991, the YOKOSUKA-STARMER cruise returned to the North-Fiji basin sites using the new manned Japanese submersible *Shinkai 6500*.

Following discussions during the 1988 Joint oceanographic assembly, IFREMER and the autonomous University of Mexico (UNAM) decided to co-operate for the study of vent biology and microbiology in the Guaymas basin. The cruise GUAYNAUT took place in fall 1991, with two ships, the French *Nadir* with the *Nautile* and its small ROV *Robin*, and *El Puma* from UNAM.

The next important development in international co-operation related to hydrothermal vent research occurred within Europe. While hydrothermal vent research during the period 1982-1992 was mainly devoted to the Pacific Ocean, the international community has moved to the Atlantic over the last ten years, beginning with the joint French-US co-operation (FARA). URM N° 7 organized the first biological cruise DIVA 2 on the Lucky Strike site (1700 metres depth, 37°17'N, 32°16'W), in summer 1994.

Since 1993, an important change in scale of multilateral co-operation was induced by the European project MARFLUX/ATJ mainly in the field of geosciences, coordinated by H. Bougault, then followed by the European project AMORES coordinated by D. Desbruyères, shared between Belgian, French, Irish, Portugese and British teams. AMORES was developed from 1996 to 1998. A third European project in the same area, called VENTOX, is now going on under the coordination of D. Dixon. The Atlantic sites discovered near the Azores occur over a large range of depths, from 800 metres (*Menez Gwen*) to 2300 metres (*Lucky Strike* and *Rainbow*), allowing an analysis of the response of hydrothermal communities to depth.

During that period, a co-operation programme with US scientists for the study of the EPR hydrothermal field at 13°N set up two cruises in 1996 (HOT) and in 1999 (HOPE). During the latter cruise, in situ chemical analyses were conducted using *Alchimist*, and pressure experiments were carried out on board, using *Ipocamp*.

French cruises on hydrothermal vent and cold seeps

All cruises organized by French biologists alone or together with foreign partners are listed chronologically, together with a few individual participations to other cruises, whose names appear in italics (see Appendix).
Two major points arise very clearly from this list of cruises:
1. an increasing number of cruises with time; field work is absolutely necessary to improve tools and specific instruments, and to confirm or modify earlier hypotheses and results.
2. the importance of international relationships and exchange of scientists for the study of hydrothermal vent and cold-seep ecosystems. The strength of the US-French co-operation link is especially impressive.

Science and education

During the URM period, the increasing scientific results on hydrothermal vents and cold-seeps communities led the French community to prepare a proposal for a European course in marine sciences. This project was granted by the European Union, and a three-week course entitled *Deep benthic communities based on chemosynthesis* was organized by Laubier and Pavillon in September 1997 (Institut Océanographique Paris).

Publications

It is difficult to develop an accurate idea of the scientific production of GRECO and URM during the last twenty years. Using three different reports cited herein, and reducing the investigation to those papers published in "international journals" (i.e. excluding papers published in national journals, communications to congresses as well as articles written for general public information), I found the following results for five time intervals:

1980-1983	1984-1987	1988-1991	1993-1997	1997-2001
8	56	60	73	78

Although the first three columns are four year intervals and the two last five year intervals, the general trend is clear. After a slow start, the first cruise performed in 1982 provided new observations and biological samples. A second area of interest arose with the discovery of cold-seep communities of the Japanese trenches. Even considering the fact that the URM focused its activity on hydrothermal ecology and biology, the increase in scientific productivity is impressive.

Since the very beginning, the French research community was also active in scientific education and public outreach. Several publications appeared in journals such as *La Recherche, Pour la science* and *Biofutur* in France. The first book on hydrothermal vents biology for the general public was published in France (Laubier, 1986). This book was then translated in Russian and published in 1989 by the Meteo Izdat. Several videos have also been produced by the French group, including series for teachers in earth sciences and biology, as for the general public.

Conclusion

At the time of the discovery of animal life associated with hydrothermal vents, French biologists had previous experience in deep-sea research, including the use of manned submersibles. Their country had a long tradition in deep-sea submersibles, going back to the bathyscaphs. The French group reacted rather quickly to the 1977-79 discoveries, developing close co-operation with the US scientists via a bottom-up process. At the national level, a more official collaborative framework was soon established between different institutions and laboratories. The collaborative focusing on hydrothermal vent communities was high.

Appendix

1. BIOCYATHERM, March 1982, East Pacific Rise (EPR), 12°53"N. 5 dives of *Cyana*.
2. BIOCYARISE, March 1984, EPR, 11°-13° N. 15 dives of *Cyana*.
3. HYDRONAUT, October 20-December 7 1987, EPR, 11°-13° N. 30 dives of *Nautile*.
4. BIOLAU, May 12-27 1989, Lau basin. 8 dives of *Nautile*.
5. STARMER 2, June 30-July 19 1989, north Fiji basin. 14 dives of *Nautile*.
6. *KAIKO-NANKAI*, July 29-August 29 1989, Japan subduction trenches.
7. *MMVT 90*, May 23-June 15, 1990, EPR, 21°N, 13°N, 11°N and Guaymas basin.
8. *NAUTIPER*, March 7-April 22, 1991, Peru subduction trench. 36 dives of *Nautile*.
9. YOKOSUKA-STARMER, August-September 1991, north Fiji basin. Several dives of *Shinkai 6500*.
10. HERO'91, September 30-November 4 1991, EPR, 9°50 and 13°N. 27 dives of *Nautile*.
11. GUAYNAUT, November 8-December 7, 1991, Guaymas basin. 18 dives of *Nautile*.
12. *LUCKY STRIKE*, May 1993, Azora triple junction (ATJ). Several *Alvin* dives.
13. MAR KANE 93, June 1993, mid-Atlantic Ridge, Kane fracture zone. Several *Alvin* dives.
14. DIVA 2, June 1994, ATJ. Several dives of *Nautile*.
15. *EPR 94*, EPR, 9°N. Several dives of *Alvin*.
16. *HERO 94*, November 1994, EPR, 9°N. Several dives of *Alvin*.

17. *LARVE 1* and *LARVE 2*, EPR, 9°N. Several dives of *Alvin*.
18. HOT 96, February 1996, EPR 9°N and 13°N. Several dives of *Nautile*.
19. MARVEL, August 13-September 13 1997, ATJ. Several dives of *Nautile*.
20. *EPR 97*, December 1997, EPR 9°N.
21. *EPR May 98*, May 10-June 1, 1998. Several dives of *Alvin*.
22. PICO, June 25-July 11, 1998, ATJ. Several dives of *Nautile*.
23. *EPR 98*, March-April 1998, several dives of *Alvin*.
24. *EPR 98*, December 15-28 1998. Several dives of *Alvin*.
25. HOPE 99, April 9-May 22 1999, EPR, 13°N and 9°N. Several dives of *Nautile*.
26. *DISPO 99*, December 1999, EPR 9°N. Several dives of *Alvin*.
27. *EPR 2000*, May 2-28, 2000, EPR 9°N. Several dives of *Alvin*.
28. BIOZAIRE 1, January 2001, Angola and Gaboon active margins.
29. ATOS, June 20-July 20, 2001, ATJ. Several *Alvin* dives.
30. PHARE, April 30-June 3, EPR, 13°N. 250 hours of ROV *Victor*.

[2] In ordinary case, cruises that have been organized by the French group; in italics, other cruises to which a few French scientists have participated.

References

Autem M., Salvidio S., Pasteur N., Desbruyères D. & Laubier L. 1985. Mise en évidence de l'isolement génétique des deux formes sympatriques d'*Alvinella pompejana* (Polychaeta : Ampharetidae), annélides inféodées aux sites hydrothermaux actifs de la dorsale du Pacifique oriental. *Comptes Rendus de l'Académie des Sciences*, *Paris* **301** (sér. III): 131-135.

Bosch C. & Grassé P.-P. 1984. Cycle partiel des bactéries chimioautotrophes symbiotiques et leurs rapports avec les bactériocytes chez *Riftia pachyptila* Jones (Pogonophore Vestimentifère). I. Le trophosome et les bactériocytes. II. L'évolution des bactéries symbiotiques et les bactériocytes. *Comptes Rendus de l'Académie des Sciences*, **299** (sér. III), n° 9: 371-376 and n° 10: 413-419.

Chevaldonné P., Fisher C., Childress J., Desbruyères D., Jollivet D., Zal F & A. Toulmond A. 2000. Thermotolerance and the "Pompeii worms". *Marine Ecology Progress Series*, **208**: 293-295.

Desbruyères D. & Laubier L. 1980. *Alvinella pompejana* gen. sp. n., Ampharetidae aberrant des sources hydrothermales de la ride Est Pacifique. *Oceanologica Acta*, **3**: 267-274.

Desbruyères D. & Segonzac M. 1997. Handbook of Deep-Sea Hydrothermal Vent Fauna. IFREMER ed., 279 pp., ISBN 2-905434-78-3.

Desbruyères D., Chevaldonné P., Alayse A.-M., Jollivet D., Lallier F.H., Jouin-Toulmond C., Zal F., Sarradin P.-M., Cosson R., Caprais J.-C., Arndt C., O'Brien J., Guezennec J., Hourdez S., Riso R., Gaill F., Laubier L. & Toulmond A. 1998. Biology and ecology of the "Pompeii worm" (*Alvinella pompejana* Desbruyères and Laubier), a normal dweller of an extreme deep-sea environment: A synthesis of current knowledge and recent developments. *Deep-Sea Research* part II, **45** (1998): 383-422.

Fiala-Médioni A. & Felbeck H. 1990. Autotrophic processes in invertebrate nutrition: bacterial symbiosis in bivalve molluscs. In: *Comparative Physiology* (R.K.H. Kinne, E. Kinne-Safran, K.W. Beyenbach eds), pp. 49-69. Karger publ.

Laubier L. 1986. Des oasis au fond des mers. Science et Découvertes, n° 3, Le Rocher édit., 1986, pp. 1-155.

Laubier L. 1989. Deep-sea ecosystems based on chemosynthetic processes: recent results on hydrothermal and cold-seep biological assemblages. *In: Oceanography 1988*, (A. Ayala-Castañares, W. Wooster, A. Yáñez-Arancibia eds), pp. 129-148. UNAM Press, Mexico.

Laubier L. (ed) 1988. Biology and ecology of hydrothermal vents. *Oceanologica Acta*, spec. vol. **n° 8**, pp. 1-233.

Ohta S. & Laubier L. 1987. Deep biological communities in the subduction zone of Japan from bottom photographs taken during 'Nautile' dives in the Kaiko project. *Earth and Planetary Science Letters*, **83**: 329-342.

URM n° 7 2001. Ecologie et ecophysiologie des organismes hydrothermaux thermophiles. Rapport final (1993-2001). Rapport interne, juillet 2001, pp. 1-77.

Sibuet M. & Olu K. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Research* pt. II, **45** (1998): 517-567.

Vacelet J., Fiala-Médioni A., Fisher C.R. & Boury-Esnault N. 1995. New symbiosis between methane oxidising bacteria and a deep sea carnivorous cladorhizid sponge. *Nature*, **377**: 296.

Vacelet J. & Boury-Esnault N. 2002. A new species of carnivorous deep-sea sponge (Demospngiae: Cladorhizidae) associated with methanotrophic bacteria. *Cahiers de Biologie Marine*, **43**: 141-148.

Woese C. R. 1987. Bacterial Evolution. *Microbiological Reviews*, **51**: 221-271.

Zal F., Leize E., Lallier F.H., Toulmond A., Van Dorselaar A. & Childress J.J. 1998. S-sulfhemoglobin and disulfide exchange: the mechanisms of sulfide binding by *Riftia pachyptila* hemoglobins. *Proceedings of the National Academy of Sciences*, **95**: 8997-9002.