ISSN 0717-652X

BIOGEOGRAPHY OF DEEP-WATER CHEMOSYNTHETIC ECOSYSTEMS (CHESS): EXPLORING THE SOUTHERN OCEANS

BIOGEOGRAFIA DE ECOSISTEMAS QUIMIOSINTETICOS PROFUNDOS (CHESS): EXPLORANDO EL HEMISFERIO SUR

Eva Ramírez Llodra*, Paul A. Tyler & Christopher R. German

Southampton Oceanography Centre, European Way, SO14 3ZH Southampton, UK *ezr@soc.soton.ac.uk

ABSTRACT

The vast majority of the mid-ocean ridge system and of the continental margins around the globe have not yet been explored. A relatively small number of vent and seep sites have been analysed and are the focus of long-term research programmes. However, the exploration of new areas will certainly provide the discovery of new vent and seep sites. Furthermore, the study of these key locations will lead to the description of new species and improve our understanding of the abundance, diversity, and distribution of species from chemosynthetically-driven systems around the world's oceans. It is the aim of ChEss to develop an exploration field phase to discover new deep-water hydrothermal vents and cold seeps at key locations, to describe their fauna, and to study the processes driving these ecosystems. The main objective is to obtain a thorough understanding of the biogeography of chemosynthetic ecosystems at a global scale. This goal can only be reached through international cooperation, which will be coordinated by the ChEss scientific steering committee. The southern oceans are the less studied regions for deep-water chemosynthetic sites. Mainly, the Indian Ocean Ridges, the southern Mid-Atlantic Ridge, the East Scotia Ridge, and the Chile Rise for vents; and the continental margins of Brazil, Peru, Chile and Africa for seeps, are crucial for the biogeographic puzzle of chemosynthetic systems.

KEYWORDS: Biogeography, hydrothermal vents, cold seeps, southern oceans.

RESUMEN

La mayor parte del sistema de dorsales oceánicas y los márgenes continentales de nuestro planeta todavía no han sido explorados. Un número limitado de fuentes hidrotermales y frías han sido estudiadas y son el objeto de programas de investigación a largo término. Sin embargo, la exploración de nuevas áreas quimiosintéticas llevará sin lugar a dudas a descubrir nuevas fuentes hidrotermales y coladuras frías. Además, el estudio de estas localidades llevará a descripciones de nuevas especies, así como a un mayor y más completo conocimiento sobre la abundancia, la diversidad y la distribución de especies de sistemas quimiosintéticos, alrededor de los oceános del mundo. Uno de los componentes principales de ChEss es un programa de campo a largo término para el descubrimiento y la exploración de nuevas fuentes hidrotermales y surgencias frías en áreas claves, así como la descripción de su fauna y el estudio de los procesos que dirigen a dichas comunidades. El objetivo principal es obtener un conocimiento sólido sobre la biogeografía de ecosistemas quimiosintéticos de profundidad a escala global. Este objetivo sólo se puede alcanzar a través de cooperación internacional, la cual será coordinada por el comité científico internacional de ChEss. En cuanto a sistemas quimiosintéticos de profundidad se refiere, los océanos del hemisferio sur engloban las regiones menos exploradas del planeta. Las dorsales del Océano Indico, el sur de la dorsal Atlántica, la dorsal ártica de Scotia y la dorsal de Chile para fuentes hidrotermales, así como los márgenes continentales de Brasil, Perú, Chile y Africa para surgencias frías, son esenciales para resolver el puzle biogeográfico de sistemas quimiosintéticos.

PALABRAS CLAVES: Biogeografía, fuentes hidrotermales, coladuras frías, océano Austral.

INTRODUCTION

ChEss (Biogeography of Chemosynthetic Ecosystems) is one of the nine field projects within the Census of Marine Life (CoML) programme. The CoML initiative is a ten year long international programme aiming at assessing and understanding the diversity, abundance, and distribution of species in the oceans at a global scale. To reach this ambitious goal, pilot projects are being developed from coastal waters to the abyss.

The main aim of ChEss is to determine the biogeography of deep-water hydrothermal vent and cold seep species at a global scale, and to understand the forces driving these ecosystems.

This paper does not intend to be an exhaustive review of hydrothermal vent and cold seep biogeography. It only provides the basic background information for the setting of the ChEss programme and the development of the project at a global scale, emphasising the exploration of the southern oceans.

THE CHESS PROGRAMME

To determine the biogeography of deep-water chemosynthetic ecosystems at a global scale and to understand the processes shaping vent and seep communities, ChEss will follow two approaches:

1. Creation of a web-based relational database (ChEssBase) for vent and seep species.

2. Development of a long-term field phase for the discovery and exploration of new vent and seep sites and the description of their fauna.

DATABASE

ChEssBase will be a geo- and bio-referenced database available in the ChEss web page and integrated with OBIS (Ocean Biological Information System). At the biological level, the database will contain taxonomical, biological, ecological, and distributional information, including photography galleries, video, references, links to specific data (quantitative data, cruises), and scientific contacts in a userfriendly interface. At the geographical level, the database will include information on the location of vent and seep sites, general characteristics of the sites, faunal community descriptions, and references. The database will be built as a centralised source of information for vent and seep species and expects to receive input from most large programmes working on chemosynthetically-driven ecosystems.

FIELD PROGRAMME

Mid-ocean ridges form a relatively continuous system extending along ~65000 km (Figure 1). Cold seeps are found globally along continental margins. Only a limited number of sections of the mid-ocean ridges and of the continental margins have been studied to date (Figure 1). The area covered by potential vents and seeps is too large to be completely explored and sampled. Therefore, ChEss proposes to develop a field programme for the discovery of new vents and seeps at key locations that will provide valuable information on the biogeography of chemosynthetic ecosystems on a global scale. A small number of key areas have been selected based upon our present knowledge on the geological, physical, and chemical aspects of deep-water ecosystems and the known distribution and ecology of vent and seep species. The preliminary main target areas for vents are in the southern hemisphere (Indian Ridge, South Mid-Atlantic Ridge, Scotia Arc, Chile Rise) and in remote high latitudes (Arctic under the ice cap) (Figure 2). The main key locations for seeps are off Brazil, off NW Africa, East coast of USA, and NE Atlantic (Figure 2).

The field programme will advance in parallel with the refinement and development of new technologies for deep-sea exploration (AUTOSUB, TOBI, ROVs, and new sensors). The programme will also encourage the use of new analytic techniques such as molecular biology and biochemistry to complement traditional methods for taxonomical, ecological, and reproductive studies.

In any study of biogeography, a sound knowledge of the taxonomical status of the species is essential. Traditional taxonomy is based on morphological methods. In recent years, however, molecular methods are rapidly developing and are one of the most innovative aspects of deep-sea research. The molecular approach offers the possibility, not only to identify cryptic species, but also to measure gene flow and to analyse the phylogeography, evolution, and possible origin of the present genetic types. Used in parallel with traditional morphological taxonomy, molecular biology will significantly increase our understanding of the biogeography of chemosynthetic fauna.

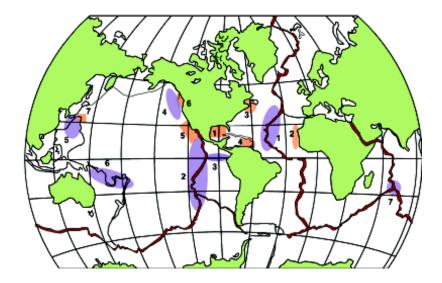


FIGURE 1. The mid-ocean ridge system with well known deep-water hydrothermal vent (ellipses) and cold seep (oblongs) regions. Vents: 1, Mid-Atlantic Ridge; 2, East Pacific Rise; 3, Galapagos Rift; 4, NE Pacific; 5 and 6, W Pacific back-arc spreading centres; 7, Central Indian Ridge. Cold seeps: 1, Gulf of Mexico; 2, NW Africa; 3, Laurentian Fan; 4, Barbados accretionary prism; 5, Monterey Bay; 6, Oregon subduction zone; 7, Sagami bay.

FIGURA 1. El sistema de cadenas del medio océano con regiones bien conocidas de fuentes hidrotermales de aguas profundas (elipses) y filtraciones frías (rectángulos). Brechas: 1, Cordillera mesoatlántica; 2, Cordillera del Pacífico oriental; 3, Cordillera de los Galápagos; 4, el Pacífico Noreste; 5 y 6, centros del arco trasero del Pacífico Oeste; 7, Cordillera Central Indica. Coladuras frías: 1, el Golfo de México; 2, el noroeste de Africa; 3, Abanico Laurenciano; 4, el prisma de acreción de Barbados; 5, la bahía de Monterrey; 6, la zona de subducción de Oregón; 7 la bahía de Sagami.

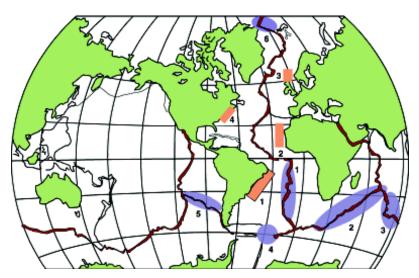


FIGURE 2. Key locations for discovery and exploration under the ChEss field phase. Vents (ellipses): 1, South Mid-Atlantic Ridge; 2, SW Indian Ridge; 3, SE Indian Ridge; 4, Scotia Arc; 5, Chile rise; 6, Arctic under the ice cap. Cold seeps (oblongs): 1, continental margin off Brazil; 2, off NW Africa; 3, N of Scotland; 4, East coast of USA.

FIGURA 2. Ubicaciones claves para el descubrimiento y exploración en la fase en terreno del ChEss. Fuentes hidrotermales (elipses): 1, Cordillera mesoatlántica del Sur; 2, Cordillera Indica Suroccidental; 3, Cordillera Indica Suroriental; 4, Arco de Escocia; 5, Cordillera de Chile; 6, el Artico bajo la capa de hielo. Coladuras frías (rectángulos): 1, el margen continental frente a Brasil; 2, frente al noroeste de Africa; 3, al norte de Escocia; 4, la costa este de los Estados Unidos.

A main factor determining the distribution of species is their reproductive patterns and larval characteristics. This is of special interest in a discrete environment such as hydrothermal vents and cold seeps. However, only a few species described from these environments have had their reproductive cycles studied in detail (Tyler & Young 1999). The dispersal potential of larvae plays a major role in ecosystem and biogeographical studies. Much evidence to date would suggest that the larval life of most invertebrates found at hydrothermal vents would be long enough for settlement sympatrically, but would not be long enough for advection to the next vent site along the ridge or an adjacent cold seep (Chevaldonné et al. 1997, Marsh et al. 2001). Recent evidence suggests that the larvae of at least one species may arrest larval development until a vent site is found (Pradillon et al. 2001). By contrast, much of the molecular evidence suggests that gene flow is relatively high (Vrijenhoek 1997, Tyler and Young 1999). The study of the life-history strategies of vent and seep species (gametogenesis, age at first maturity, egg size, fecundity, larval development) together with geo-physical factors (deep-water currents, barriers), is crucial to understand the distribution, dispersal, and colonisation potential of these species.

FAUNAL DISTRIBUTION OF KNOWN VENT AND SEEP SPECIES HYDROTHERMAL VENTS

Hydrothermal vents were first discovered in 1997, during an expedition to the Galapagos Rift in the Eastern Pacific (Corliss et al. 1979). With this, came the remarkable discovery that hydrothermal vents were surrounded by a high-biomass community of invertebrates previously unknown to science. Within months, it became apparent that the ecosystem associated to hydrothermal vents was sustained by chemical primary production (chemosynthesis) rather than by vertical flux of photosynthesised organic matter (Cavanaugh et al. 1981). The chemical energy is in the form of dissolved reduced gases (especially H_2S , H_2 , and CH_4) present in the hydrothermal fluids. Free living bacteria as well as ecto- and endo-symbionts with resident invertebrates are responsible for primary production. Hydrothermal vents were the first ecosystem where chemosynthetic primary production had been observed on such a large scale and sustaining such high biomass.

Since the first dives on the Galapagos Rift, many other vent sites have been discovered and explored. Research on hydrothermal vents has focused on certain areas of the mid-ocean ridges and, to date, 5 biogeographical provinces have been described: Mid-Atlantic Ridge, East Pacific Rise, NE Pacific, NW Pacific, and Central Indian Ridge (for reviews see Tunnicliffe, 1991; Tunnicliffe *et al.* 1998, Van Dover 1995, Van Dover *et al.* 2001, 2002) (Figure 1). However, more provinces are likely to be recognised as exploration extends south of 30° S and on high northern latitudes.

The fauna at the Galapagos Rift vents is mainly dominated by tubeworms (*Riftia pachyptila*), clams (*Calyptogena magnifica*), mussels (*Bathymodiolus thermophilus*), gastropods, and polychaetes. The faunal invertebrate and fish communities at the East Pacific Rise (EPR, from 26° S EPR to Guaymas) share species with the Galapagos Rift. The EPR vents also have alvinellid polychaetes which are not found at the Galapagos Rift vents because of an absence of habitat (Desbruyères & Laubier 1982). However, the EPR and Galapagos Rift form a single biogeographical province.

The NE Pacific system (Gorda, Juan de Fuca, and Explorer) is the remnant of a larger system that has been destroyed by the southwestward migration of the North American Plate (Tunnicliffe 1991, Tunnicliffe *et al.* 1998). The faunal composition of NE Pacific vent communities is related to the EPR at higher taxonomical levels, with vestimentiferan tubeworms, alvinellid polychaetes, crabs, and anemones being the dominant fauna. There are, however, differences at the generic and species level between the two areas, and *Calyptogena* spp and *Bathymodiolus* spp are absent in the NE Pacific (Tunnicliffe *et al.* 1986, Tunnicliffe *et al.* 1991).

The NW Pacific vents are found along back-arc spreading centres (Lau Basin, Manu Basin, Marianas Trough, Fiji Basin, and Okinawa Trough). These vents have an heterogeneous faunal composition, mainly dominated by mussels and gastropods, clams, barnacles and, at some sites, vestimentiferans and anemones.

Hydrothermal vents on the Mid-Atlantic Ridge (MAR) were first discovered in the mid-1980s at TAG (Rona *et al.* 1986). Since then, exploration on central MAR (from 37° N to 14° N) has resulted in

the discovery and description of a number of vent sites (Menez Gwen, Lucky Strike, Rainbow, Broken Spur, TAG, Snake Pit, and Logatchev). The MAR fauna is very distinct from the Pacific fauna, being mainly dominated by dense aggregations of motile caridean shrimp (Rimicaris exoculata) and bathymodiolid mussels. The associated fauna is composed by other caridean shrimp, limpets, anemones, scale worms, bythograeid, and galatheid crabs and zoarcid fish (for a review, see Van Dover 1995). The last vent biogeographical region to have been recognised is composed by the invertebrate communities found at the Kairei and Edmond sites in the Central Indian Ridge (CIR). The CIR faunal communities have a high similarity to that of the EPR, but one of the dominant species is the shrimp Rimicaris sp. related to the Atlantic species (Van Dover et al. 2001).

In recent years, explorations of high latitudes have led to the detection of hydrothermal plume signals along the Scotia Ridge (Antarctic) and the Knipovitch and Gakkel Ridges (Arctic) (German *et al.* 2000, Edmonds *et al.* 2001, Connelly & German 2002).

COLD SEEPS

The interest in large chemosynthetic ecosystems was strengthened by the discovery of chemosynthetically supported fauna in the cold seeps at the base of the western Florida Escarpment in 1983 (Paull et al. 1984). Cold seeps occur in both active and passive continental margins. In passive margins, seepage of fluids occurs through salt tectonic fracturation, from brine sulfide-rich seeps, from petroleum and gas seeps, or from sediment accumulation from slides. On active margins, fluids are expelled from accretionary prisms by sediment compaction, at erosive margins at distensive active margins and at subduction zones (Olu et al. 1996, Sibuet & Olu 1998). Cold seep communities have also been described from sites of organic enrichment such as whale falls (Bennett et al. 1994). Cold seeps support high biomass and have a low biological diversity. Faunal communities at cold seeps are mainly composed by large vesicomyid clams, mytilid mussels, and vestimentiferan tubeworms. At high taxonomical levels, this faunal composition is similar to that of Pacific vents, but there are significant differences in species composition, diversity, and abundances (Olu *et al.* 1996; Sibuet & Olu 1998; Kojima 2002). The biogeography of cold seep ecosystems is less well-known than that of vents, mainly because there are less long-term focused studies of cold seep sites.

EXPLORING FOR VENTS AND SEEPS, WITH FOCUS IN THE SOUTHERN OCEANS

To help organise the ChEss field programme and narrow the field for exploration, a number of sitespecific hypotheses/questions will be addressed. In relation to hydrothermal vents in the southern oceans, it is noticeable that no systematic investigations have been carried out on most of the continuous ridge system from the equatorial MAR, along the southwest Indian Ridge, to the southeast Indian Ridge and the southern Pacific Ridge to the southernmost EPR and the Pacific-Antarctic Ridge (see Fig. 1 and below). The ridge system of high northern latitudes (>70° N) is also unexplored. In relation to cold seeps, increasing interest is building for exploration and analyses along the Peruvian and Chilean continental slopes on the west and off the Brazilian coast on the east (see below). This is, in many cases, linked to potential exploitation of gas and oil resources. Other key locations for seep exploration include the continental margin off NW Africa, the East coast of USA and the NE Atlantic (see Fig. 1 and below).

1. Indian Ridge: do vent species along the South East Indian Ridge (SEIR) show increasing influence of Pacific faunas while species along the South West Indian Ridge (SWIR) show greater influences from the Atlantic?

In April 2001, a multidisciplinary cruise on board R/V Knorr was conducted to analyse geological, geochemical and ecological aspects of hydrothermal systems in the Indian Ocean (Van Dover *et al.* 2001). The study focused on the Kairei and Edmond vent fields, in the southern portion of the Central Indian Ridge. The Kairei vent field is located at 25°19'S - 70°02'E between 2415 and 2460 m depth and was discovered in August 2000 by Japanese scientists (Hashimoto *et al.* 2001). The Edmond vent field is located at 23° 52'S – 69° 35'E between 3290

and 3320 m depth and was discovered during the above R/V Knorr cruise.

The fauna of both vent fields is similar. There is a strong relationship to Western Pacific vent fauna (one third of the species belong to genera until now only described from the Pacific) with the notable exception of a dominant shrimp species (*Rimicaris* aff. exoculata) that belongs to a genus only known from Atlantic vents. There are dense aggregations of the caridean shrimp Rimicaris aff. exoculata on the high temperature black smokers, and populations of the anemone Marianactis sp. dominating the peripheral ambient temperature (1°-2° C) areas. At the foot of the shrimp aggregations and in the transition zone between the shrimps and anemones, there are populations of mussels, gastropods, barchyuran crabs, other caridean shrimp, nemerteans, tur-bellarian flatworms, polychaetes, and barnacles. The absence of common Pacific fauna, such as alvinellid polychaetes and vestimentiferans, and the absence of amphipods commonly found at both Pacific and Atlantic vents are significant (for a review of the fauna, see Van Dover et al. 2001).

The Central Indian Ridge has been defined as the newest biogeographical province for deep-sea hydrothermal vent communities (see Fig. 2) with affinities to both the Pacific and Atlantic vent faunas (Van Dover et al. 2001, 2002). The faunal observations at the Kairei and Edmond vent fields, together with molecular analyses on some of the species suggest that the Indian Ridge serves as a conduit for dispersal between ocean basins. If vent sites along the Indian Ridge system work as stepping stones for the dispersal of invertebrate vent fauna, we would expect to find increasing similarities with Atlantic vents on the SWIR and increasing Pacific similarities on the SEIR. To solve these questions, further exploration, mapping, and biological analyses of the Indian Ridge system as well as of the southern MAR system and the SW Pacific system are needed.

2. Southern Mid-Atlantic Ridge: do the Romanche and Chain fracture zone create a barrier for the dispersal of vent organisms between north and south MAR?

A James Clark Ross cruise in September-October 2001 to the southern Mid-Atlantic Ridge (2°S -

14°S) provided evidence for hydrothermal activity on the Southern Mid-Atlantic Ridge (SMAR) (German *et al.*, in press). The authors propose the segment south of the Ascension Fracture Zone as the best area, to date, to locate individual hydrothermal vents in the SMAR. Preliminary studies of plume signals and seafloor geology will be undertaken under the core science programme of the Challenger Division for Seafloor Processes (Southampton Oceanography Centre) funded by the Natural Research Council of the UK.

Exploration of the SMAR ridge and their associated fauna will determine if the southern MAR vents exhibit a distinct fauna from those north of the equator caused by barrier isolation from the Romanche and Chain fracture zones. Furthermore, the description of chemosynthetic communities from the southern portion of the MAR will provide critical data to understand the distribution and dispersal of vent organisms across ocean basins towards the Indian Ridge and the Scotia Arc.

3. East Scotia Ridge: what are the relative relationships of the East Scotia Ridge (ESR) faunal communities with Pacific and Atlantic fauna?

German et al. (2000) described for the first time, the presence of hydrothermal activity along the ESR. The ESR is an isolated back-arc spreading centre located at 55° - 60° S in the southern Atlantic Ocean. The exploration of the ESP to locate individual vent sites and describe their faunal communities would play a crucial role in our understanding of the biogeography of vent species. The ESR is equidistant to the known vent sites on both the MAR and the EPR. If larval vent species disperse through the water column by water currents (Mullineaux et al. 1996), the ESR fauna might have a strong influence of south EPR species, with colonisation occurring through the Drake Passage by the Antarctic Circumpolar Current (Meredith et al. 2001). If, however, the ESR is influenced by its tectonic attachment to the Atlantic, its faunal composition would be increasingly related to the southern MAR, which in turn should show influences of the northern MAR or the SWIR. A final possibility would be that the faunal communities of the ESR have evolved independently from both the Pacific and Atlantic and have become a unique biogeographical province (German et al. 2000).

4. Chile Ridge: is the Chile Ridge a faunal end?

Little is known about hydrothermal activity on the Chile Ridge. Marienfeld & Marchig (1992) report a preliminary investigation of a segment of the Chile ridge where it was demonstrated that hydrothermal input in the sediment was taking place. The study was undertaken because of the interest of Chilean marine geologists in an area of the spreading centre, which partly reaches into their territorial waters, and recommendations of further investigations were made in order to locate massive sulfides and hydrothermal ecosystems. To date, however, no more information is available. Biogeographically, it would be of major interest to locate individual vents along the ridge and to analyse their faunal composition. This would reveal if the Chile rise has strong influences from the EPR and then becomes a vent-faunal end, or if otherwise there is a faunal continuity with the ESR (see Fig. 2).

5. South American cold seeps

PERU: The northern Peruvian margin is an extensional active margin with a steep slope, massive subsidence, and lack of well-developed accretionary prism (Duperret et al. 1995). In 1991, a cruise to the Paita area (5° - 6° S) discovered and analysed cold seep communities in this location (Olu et al. 1996). The Paita seep communities were dominated by vesicomyid bivalves containing sulfur-oxidizing symbiotic bacteria and were found along scarps on tectonic features where fluid seepage occur. The existence of an extended field (1000 m²) with high density populations of clams suggested the occurrence of a high and continuous fluid expulsion over that area. The fauna associated to the clam beds included pennatulids, actininians, amphipods, holothurians, serpulid polychaetes, galatheid crabs, shrimps, octopuses, and macrourid and zoarcid fishes (Olu et al. 1996). The description of the Paita area was the first study of the spatial distribution of chemosynthetic communities on an erosive margin along a 40 km transect. Future exploration of other areas on the Peruvian margin would provide important information for a global picture of the occurrence of seepage and distribution of biological communities on the Pacific side of South America.

CHILE: A three year study is being conducted to

analyse and evaluate the presence of gas hydrates and their future exploitation along the Chilean margin $(31^{\circ} - 34^{\circ} \text{ S} \text{ and } 36^{\circ} - 39^{\circ} \text{ S})$ (E. Morales pers. com.).

BRAZIL: The closest evidence of the existence of chemosynthetic ecosystems on the Brazilian continental margin is the description of a new species of Vesicomyidae (*Calyptogena birmani*) off the coast of Paraná (Domaneschi & Lopes 1990). To date, no individual cold seeps have been located, but there is growing interest from Brazilian scientists to develop research programmes to map and study cold seeps and the associated biological communities (P. Sumida, pers. com.).

6. Northern high latitudes

Recently, research in high northern latitudes (Arctic basin) has demonstrated the presence of hydrothermal venting in ultraslow spreading ridges. Evidence of venting has been found on the ultraslow spreading Gakkel Ridge (Edmonds *et al.* 2001, Edwards *et al.* 2001, Michael *et al.* 2001) and Knipovich Ridge (Connelly and German 2002). Hydrothermal activity is also known form the slow spreading Kolbeinsey and Mohns ridges north of Iceland (Stoffers *et al.* 1997).

Faunal communities at vents along the Kolbeinsey, Mohns, Knipovich, and Gakkel Ridges may be quite distinct from those along the MAR because the Iceland mantle hotspot has precluded pathways for deep-water communication between these basins since the opening of the North Atlantic Ocean (ca. 60 Ma). The remote location of these ridges and the ice cover in the Artic basin make exploration difficult. However, further research and the development of oceanographic instruments such as the autonomous underwater vehicle AUTOSUB 2 (Southampton Oceanography Centre) would be crucial to locate individual vent sites and describe their fauna along high latitude ridges.

7. NW Africa cold seeps

Recently discovered seep fauna off NW Africa may be directly related to the Gulf of Mexico fauna, via strong advection of southward-flowing Atlantic deep waters that cross from west to east at equatorial latitudes (Van Dover *et al.* 2002, M. Sibuet, pers. com.).

CONCLUSIONS

The potential location of hydrothermal vents and cold seeps at a global scale extends over a vast area which cannot be realistically explored in its totality. Accordingly, ChEss proposes to explore and study selected key locations which would provide valuable information to understand the biogeography of chemosynthetically-driven ecosystems.

For hydrothermal vents, the best known areas are along the central MAR, the EPR, NE Pacific, western Pacific, and central Indian Ocean Ridge. The description of vent sites and their associated fauna from the southern MAR, SWIR and SEIR, Chile Ridge, Scotia Arc, and Arctic Ridges would provide critical data to understand the dispersal and colonisation of vent species along mid-ocean ridges. This would allow the construction of a relatively comprehensive picture of the world's vent biogeographical regions.

The biogeography of cold seeps is less well understood than that of vents. However, interest in cold seeps is increasing, often in relation with potential exploitation of natural resources such as gas hydrates and oil. Geological and ecological surveys of the continental margins will provide useful data to understand the extension of seep communities along continental margins and the biogeographical relationships among them.

ChEss will develop a dynamic relational database to include information on all vent and seep species, both archived and newly collected. In parallel, the programme will develop a long term international field phase for the exploration and discovery of new vent and seep sites and the description of their associated fauna. The final goal will be to construct a global map for the biogeography of chemosynthetic ecosystems.

REFERENCES

- BENNETT, B.A., C.R. SMITH, B. GLASER & H.L. MAYBAUM. 1994. Faunal community structure of a chemotrophic assemblage on whale bones in the deep northeast Pacific Ocean. Marine Ecology Progress Series 108: 205-223.
- CAVANAUGH, C.M., S.L. GARDINER, M.L. JONES, H.W. JANNASCH & J.B. WATERBURY. 1981. Prokaryotic cells in hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. Science 213: 340-342.

- CHEVALDONNÉ, P., D. JOLLIVET, A. VANGRIESHEIM & D. DESBRUYERES. 1997. Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 1. Influence of vent site distribution, bottom currents, and biological patterns. Limnology and Oceanography, 421: 67-80.
- CONNELLY, D.P. & C.R. GERMAN. 2002. Total Dissolvable Manganese Anomalies Over the Knipovich Ridge: Evidence for Hydrothermal Activity. EOS Transactions American Geophysical Union 83: OS205-206.
- CORLISS, J.B., J. DYMOND, L.I. GORDON, J.M. EDMOND, R.P. VON HERZEN, R.D. BALLARD, K. GREEN, D. WILLIAMS, A. BAINBRIDGE, K. CRANE & T.H. AN-DEL. 1979. Submarine thermal springs on the Galapagos Rift. Science 203: 1073-1083.
- DESBRUYÈRES, D. & L. LAUBIER. 1982. Paralvinella grasslei, new genus, new species of Alvinellidae Polychaeta: Ampharetidae from the Galapagos Rift geothermal vents. Proceedings of the Biological Society of Washington 95: 484-494.
- DOMANESCHI, O. & S.G.B.C. LOPES. 1990. Calyptogena (Calyptogena) birmani, a new species of Vesicomyidae (Mollusca- Bivalvia) from Brazil. Malacologia 31: 363-370.
- DUPERRET, A., J. BOURGOIS, Y. LAGABRIELLE & E. SUESS. 1995. Slope instabilities at an active continental margin: large-scale polyphase submarine slides along the northern Peruvian, between 5S and 6S latitude. Marine Geology 122: 303-328.
- EDMONDS, H.N., P.J. MICHAEL, E.T. BAKER, D.W. GRAHAM, M. VOCK, J. SNOW, R. MUHE, D.P. CONNELLY & C.R. GERMAN. 2001. Hot springs in a cold ocean: evidence for abundant hydrothermal venting on the ultra-slow spreading Gakkel Ridge. EOS Transactions, American Geophysical Union 82: F647.
- EDWARDS, M.H., G.J. KURRAS, M. TOLSTOY, D.R. BOHNENSTIEHL, B.J. COAKLEY & J.R. COCHRAN. 2001. Evidence for recent volcanic activity on the ultraslow-spreading Gakkel ridge. Nature 409: 807-812.
- GERMAN, C.R., R.A. LIVERMORE, E.T. BAKER, N.I. BRUGUIER, D.P. CONNELLY, A.P. CUNNINGHAM, P. MORRIS, I.P. ROUSE, P.J. STATHAM & P.A. TYLER. 2000. Hydrothermal plumes above the East Scotia Ridge: an isolated high-latitude back-arc spreading centre. Earth and Planetary Science Letters 184: 241-250.
- HASHIMOTO, J. & OTHERS. 2001. Hydrothermal vents and associated biological communities in the Indian Ocean. InterRidge News 10: 21-22.
- KoJIMA, S. 2002. Deep-sea chemoautosynthesis-based communities in the Northwestern Pacific. Journal of Oceanography 58: 343-363.
- MARIENFELD, P. & V. MARCHIG, 1992. Indications of hydrothermal activity at the Chile Ridge spreading centre. Marine Geology 105: 241-252.
- MARSH, A.G., L.S. MULLINEAUX, C.M. YOUNG & D.T. MANAHAN, 2001. Larval dispersal potential of the

tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411: 77-80.

- MEREDITH, M.P., A.C.N. GARABATO, D.P. STEVENS, K.J. HEYWOOD & R.J. SANDERS. 2001. Deep and bottom waters in the eastern Scotia Sea: rapid changes in properties and circulation. Journal of Physical Oceanography 31: 2157-2168.
- MICHAEL, P., J. THIEDE, C. LANGMUIR, W. JOKAT, H. DICK, J. SNOW, D. GRAHAM, E. WEIGELT, S. GOLDSTEIN, R. MUHE, H. EDMONTS, O. RITZMANN, G. KURRAS, A. BUECHL, L. KUHNZ, S. GAUGER, K. LEHNERT, M. SCHMIDT-AURSCH, J. STANDISH, T. SCHMIDT, J. BRODA, B. SCHRAMM, J. HATZKY, G. STOFFER & (PARTIAL LIST, AMORE SHIPBOARD SCIENTIFIC PARTIES OF USCGC HEALY AND RV POLARSTERN.). 2001. Results of the Arctic Mid-Ocean Ridge Expedition - AMORE 2001 - Seafloor spreading at the top of the world. InterRidge News 10: 57-60.
- MULLINEAUX, L.S., S.L. KIM, A. POOLEY & R.A. LUTZ. 1996. Identification of archaeogastropod larvae from a hydrothermal vent community. Marine Biology. 124: 551-560.
- OLU, K., A. DUPERRET, M. SIBUET, J.P. FOUCHER & A. FIALA-MEDIONI. 1996. Structure and distribution of cold seep communities along the Peruvian active margin: Relationship to geological and fluid patterns. Marine Ecology Progress Series 132: 109-125.
- PAULL, C.K., B. HECKER, R. COMMEAU, R.P. FREEMAN-LYNDE, C. NEUMANN, W.P. CORSO, S. GOLUBIC, J.E. HOOK, E. SIKES & J. CURRAY. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. Science 226: 965-967.
- PRADILLON, F., B. SHILLITO, C.M. YOUNG. & F. GAILL. 2001. Developmental arrest in vent worm embryos. Nature 413: 698-699.
- RONA, P.A., G. KLINKHAMMER, T.A. NELSON, J.H. TREFRY. & H. ELDERFIELD. 1986. Black smokers, massive sulphides and vent biota at the Mid-Atlantic Ridge. Nature 321: 33.
- SIBUET, M. & K. OLU. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep

communities at active and passive margins. Deep-Sea Research II, 45: 517-567.

- STOFFERS, P., R. BOTZ, D. GARBE-SCHONBERG, M. HANNINGTON, B. HAUZEL, P.M. HERZIG, K. ISSMANN, R. HUBER, J.K. KRISTJANSSON, S.K. PETURSDOTTIR, J. SCHAEUR, M. SCHMIDTT & M. ZIMMERER. 1997. Cruise Report Poseidon 229a "Kolbeinsey Ridge". Kiel, Geologisch - Palaontologisches Institut.
- TUNNICLIFFE, V. 1991. The biology of hydrothermal vents: Ecology and Evolution. Oceanography and Marine Biology: An Annual Review 29: 319-407.
- TUNNICLIFFE, V., M. BOTROS, M.E. DE BURGH, A. DINET, H.P. JOHNSON, S.K. JUNIPER & R.E. MCDUFF. 1986. Hydrothermal vents of Explorer Ridge, Northeast Pacific. Deep-Sea Research A 33: 401-412.
- TUNNICLIFFE, V., A.G. MCARTHUR & D. MCHUGH. 1998. A Biogeographical Perspective of the Deep-Sea Hydrothermal Vent Fauna. Advances in Marine Biology 34: 353-442.
- TYLER, P.A., & C.M. YOUNG. 1999. Reproduction and dispersal at vents and cold seeps. Journal of the Marine Biological Association of the United Kingdom 79: 193-208.
- VAN DOVER, C.L. 1995. Ecology of Mid-Atlantic hydrothermal vents. *In:* L.M. Parson, C.L. Walker and D. Dixon (eds.), Hydrothermal vents and processes. Geological Society of London, London, pp. 257-294.
- VAN DOVER, C.L., S.E. HUMPHRIS, D. FORNARI, C.M. CAVANAUGH, R. COLLIER, S.K. GOFFREDI, J. HASHIMOTO, M.D. LILLEY, A.L. REYSENBACH, T.M. SHANK, K.L. VON DAMM, A. BANTA, R.M. GALLANT, R.C. VRIJENHOEK & *et al.* 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents. Science 294: 818-823.
- VAN DOVER, C.L., C.R. GERMAN, K.G. SPEER, L.M. PARSON & R.C. VRIJENHOEK. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. Science 295: 1253-1257.
- VRIJENHOEK, R.C. 1997. Gene flow and genetic diversity in naturally fragmented metapopulations of deepsea hydrothermal vent animals. Journal of Heredity 88: 285-293.

Fecha de recepción: 06/05/03 Fecha de aceptación: 12/09/03